## Stabilizing Populations with Adaptive Limiters: Prospects and Fallacies\*

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Abstract. Adaptive limiter control has been proposed as a method for stabilizing fluctuations in unstable population dynamics. This method invokes a dynamic thresholding and restocks the population if it falls below a certain proportion of its previous size. The reference state for the adaptive threshold can be the previous population size after (ALC) or before (ALCb) intervention. The former has been tested experimentally and analyzed theoretically, whereas the latter has been proposed for biological populations but not yet studied. Here, we investigate the consequences of choosing a different basis for adaptive limiter control. We thoroughly explain the mechanisms that allow ALCb to reduce the magnitude of population fluctuations under certain conditions. However, we also find that ALCb may be counterproductive in other situations, actually increasing fluctuations and extinction risk. We show that this effect is further promoted by an alternative attractor with undesirable properties. The bistability is triggered by basing the adaptive threshold on a different reference population size. The results in this paper highlight the importance of making correct references to system states in the past and the dramatic consequences this can have in chaos control schemes. In the ecological application, a desirable support intervention might backfire into unintended extinction.

Key words. chaos control, population oscillations, stabilization, alternative attractor

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1. Introduction. Several methods have been proposed for stabilizing the dynamics of biological populations via seasonal interventions, e.g., [10, 11, 20, 24, 26, 31, 35, 37, 43, 46]. These methods have the common feature of perturbing state variables rather than system parameters and, similarly to other strategies of controlling chaos, e.g., [1, 6, 7, 12, 42], aim at creating a stable population size, which should ideally be a global attractor.

Limiter control methods are a particular type of these techniques characterized by establishing a threshold that the population size is not allowed to surpass [15, 30, 31, 44, 47, 48, 49]. Depending on whether the population sizes must be above or below such a threshold, the control method stipulates an augmentation (restocking) or reduction (harvesting) procedure, respectively. Limiter control is easy and fast to implement, as it does not require detailed

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information about the system or a potentially tedious computation of the control signal. The method has therefore been suggested for high-speed electronic implementation [16, 38, 39] but also for regulating cardiac rhythms [25], arithmetic computations [45], and commodity markets [14, 27], for instance.

Recently, Sah, Salve, and Dey [41] proposed a stocking limiter method for controlling biological populations and metapopulations without creating a stable population size. It is called adaptive limiter control (ALC), since the limiter is defined as a fraction of the previous population size  $x_{t-1}$  (after intervention) and therefore is variable.

While there is increasing experimental evidence for chaotic dynamics in biological populations [18, 3, 4], none of the established control strategies has been tested empirically yet. The only exception is the work by Desharnais et al. [21]. Guided by mathematical modelling, they augmented, at certain times, a population of the flour beetle *Tribolium castaneum* by a constant number of adult individuals to reduce population fluctuations. The significance of the work by Sah, Salve, and Dey is that they not only proposed, but also provided experimental evidence for, the ALC method. Using laboratory populations and metapopulations of the fruit fly *Drosophila melanogaster*, they showed that increasing the control intensity of ALC enhances population stability, measured in terms of reduced fluctuations.

Hence, ALC is a somewhat unusual method because experimental results were available before any rigorous mathematical analysis. The first theoretical support for the experimentally observed reduction of fluctuations is given in [23]. Essentially, the authors prove that increasing the control parameter globally shrinks the range of possible population sizes around the positive equilibrium of the uncontrolled system, even when this positive equilibrium can never be stabilized by ALC. However, this result is for a model that describes the experiments performed in [41], but it does not match the model put forward by [41]. The latter suggested the following second-order piecewise-smooth difference equation:

(1.1) 
$$x_{t+1} = \begin{cases} f(x_t), & x_t \ge c \cdot x_{t-1}, \\ f(c \cdot x_{t-1}), & x_t < c \cdot x_{t-1}, \end{cases}$$

where 0 < c < 1 is a control parameter measuring the intensity of the ALC, f describes the population production, and  $x_t$  denotes the population size at generation t. In formulation (1.1), the adaptive limiter is determined by the population size in the previous generation before intervention. We shall refer to the method described by this adaptive limiter as ALCb. In the experiments (and the model in [23]), however, the adaptive limiter is determined by the previous population size after intervention. We shall refer to this method simply as ALC, to be consistent with previous papers [23, 41]. The only difference between ALC and ALCb is a slight delay in selecting the threshold value.

In this paper, we analyze the ALCb model given by (1.1). It does not require any additional measurements in comparison to the alternative ALC method. It is a biologically meaningful strategy and deserves to be studied in its own right. Our main aim is to investigate whether, and if so to what extent, the change in the timing of the adaptive limiter affects the performance of the control.

We rigorously show that ALCb shares several properties with ALC. In particular, we prove that, under certain conditions, large control parameters cause the population to have

lower variation in size over time. We also perform a range of numerical simulations that cast shadows on the stabilizing property of ALCb. We identify many situations in which ALCb is not only ineffective but actually worsens population stability. The main pitfall is that ALCb can provoke bistability and that, as a consequence, its stabilizing effect depends on the initial population size. For a substantial range of parameter values and initial conditions, our numerical simulations suggest that ALCb enhances fluctuations and is thus actually detrimental for population stability.

To lend robustness to our results, we consider a suite of numerical simulations that extends the models to more realistic forms from an ecological perspective. More specifically, we take into account environmental and demographic noise as well as lattice effects.

## 2. Modelling ALCb.

**2.1. Underlying population dynamics.** Before introducing the control method, we briefly describe the underlying population dynamics. Let  $x_t$  be the population size at time step t. Then, in the absence of control, the population follows the discrete-time dynamical system given by

(2.1) 
$$x_{t+1} = f(x_t), \quad x_0 \in [0, \infty), \ t \in \mathbb{N}.$$

The function f describes the population production and satisfies the following conditions:

- (C1)  $f: [0, L] \to [0, L]$  ( $L = \infty$  is allowed) is continuously differentiable and satisfies f(0) = 0 and f(x) > 0 for all  $x \in (0, L)$ .
- (C2) f has exactly two nonnegative 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 < K such that f'(x) > 0 for all  $x \in (0, d)$ , f'(x) < 0 for all x > d, and  $f'(0^+), f'(L^-) \in \mathbb{R}$ .

From a biological point of view, the above conditions mean that the population dynamics are overcompensatory. The population has two fixed points, namely the extinction state x=0 and a positive equilibrium x=K, henceforth referred to as the carrying capacity. There is no demographic Allee effect [19]. A well-known example of a map satisfying conditions (C1)–(C3) is the Ricker map,  $f(x) = x \exp(r(1-x/K))$ , with growth parameter r>0, carrying capacity K>0, and  $L=\infty$ . This map is commonly used in applied population biology and was proposed as a model of fisheries in 1954 [40].

**2.2. Effect of the control.** ALCb does not allow the population size to fall below a fixed proportion of the previous population size, where this previous population size is selected as the population size before any intervention due to the control. Mathematically, this leads us to consider the following system:

(2.2) 
$$b_{t+1} = f(a_t) \quad \text{and} \quad a_{t+1} = \begin{cases} b_{t+1}, & b_{t+1} \ge c \cdot b_t, \\ c \cdot b_t, & b_{t+1} < c \cdot b_t, \end{cases}$$

where  $b_t$  is the population size before intervention,  $a_t$  is the population size after intervention, and 0 < c < 1 is a control parameter measuring the intensity of ALCb.

The second equation in system (2.2) implies that

$$a_{t} = \begin{cases} b_{t}, & b_{t} \ge c \cdot b_{t-1}, \\ c \cdot b_{t-1}, & b_{t} < c \cdot b_{t-1}. \end{cases}$$

Substituting this expression for  $a_t$  in the first equation of system (2.2), we obtain that the dynamics of the population sizes are completely determined by the dynamical system given by

(2.3) 
$$b_{t+1} = \begin{cases} f(b_t), & b_t \ge c \cdot b_{t-1}, \\ f(c \cdot b_{t-1}), & b_t < c \cdot b_{t-1}. \end{cases}$$

As announced in the introduction, (2.3), defining the dynamics of ALCb, is exactly (1.1).

ALCb transforms the one-dimensional dynamical system (2.1) into a piecewise smooth dynamical system of second order [5]. Second-order systems require an initial condition of two population sizes. In principle, any pair  $(b_0, b_1) \in (0, L) \times (0, L)$  can be an initial condition for the controlled equation (2.3). However, from now on we consider only initial conditions  $(b_0, f(b_0))$ , determined by any given single initial population size  $b_0 \in (0, L)$ . Biologically, this restriction arises naturally before we start applying the control. In the appendix (see Lemma A.1), we prove that there is no loss of generality in our results for making such an assumption.

**3. Similarities with ALC.** An essential element employed in [23] to characterize the stabilizing properties of ALC is the *activation threshold*,  $A_T$ . It will also play a crucial role in the analysis of ALCb. This threshold is geometrically defined as the first component of the intersection point of the graph of f and the straight line  $y = c \cdot x$ . It exists under very general conditions, as established in the following lemma.

Lemma 3.1. Assume that (C1)–(C3) hold.

- (i) If  $L = +\infty$  or f(L) = 0, then  $c \cdot x f(x) = 0$  has a unique positive solution  $A_T$  for any  $c \in (0,1)$ .
- (ii) If  $L < \infty$  and f(L) > 0, then  $c \cdot x f(x) = 0$  has a unique positive solution  $A_T$  if and only if  $c \in (f(L)/b, 1)$ .
- (iii) In both previous cases,  $c \cdot A_T < K < A_T$  holds.

The proofs of this and all other results in this section can be found in the appendix.

The name activation threshold is due to the following property of ALC: Only if the population size after control,  $a_t$ , exceeds  $A_T$  in some generation t, will ALC be triggered in the next generation t+1. Our first result shows that a very similar property holds for ALCb.

Proposition 3.2. Assume that (C1)–(C3) hold and  $c \in (0,1)$  is such that  $A_T$  exists. Then ALCb adds individuals in generation t with  $t \ge 1$  if and only if  $b_{t-1} > A_T$ .

Our next result states that if the initial condition is chosen appropriately and the activation threshold  $A_T$  satisfies certain conditions, then ALCb confines the population sizes within a certain region around the carrying capacity, i.e., the positive equilibrium of f.

Theorem 3.3. Assume that (C1)–(C3) hold. Additionally, suppose that for a fixed  $c \in (0, 1)$  the activation threshold  $A_T$  exists and satisfies the inequalities

(3.1) 
$$d \le c \cdot A_T \quad and \quad f(c \cdot A_T) \le \frac{A_T}{c},$$

where d is the population size generating the maximum offspring; cf. (C3).

Then, applying ALCb with intensity c confines the population sizes before intervention to the following interval around K:

(3.2) 
$$I_b := [f^2(c \cdot A_T), f(c \cdot A_T)],$$

provided that the initial population size  $b_0$  belongs to the interval

$$[c \cdot A_T, f(c \cdot A_T)] \subset I_b.$$

A direct consequence of Theorem 3.3 is that ALCb can reduce the fluctuation magnitude. The interval  $I_b$  corresponds to a trapping region of possible population sizes before intervention and thus confines the oscillation amplitudes. This trapping region is defined by means of  $A_T$ ; that is, it is completely determined by the map f and the control parameter c. The diameter of this trapping region is  $f^2(c \cdot A_T) - f(c \cdot A_T)$ . Notably, as the control parameter c tends to 1, the activation threshold  $A_T$  tends to the carrying capacity K (see Lemma 3.1(iii)). Therefore the diameter of the trapping region tends to 0 as c tends to 1. In consequence, as long as conditions (3.1) and (3.3) hold, increasing the control parameter c shrinks the trapping region  $I_b$ .

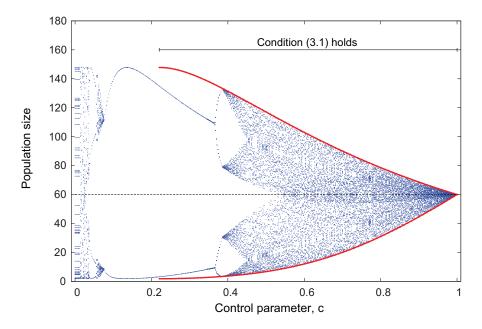
Theorem 3.3 is not a global result. It determines the dynamics only for initial conditions that satisfy (3.3). As this range is included in the trapping region, increasing the control parameter also reduces the range of suitable initial conditions. Theorem 3.3 does not characterize the asymptotic behavior for other initial conditions; while initial conditions may be attracted by the same trapping region, we will later see examples of an alternative attractor inducing bistability.

Figure 1 illustrates the stabilizing effect of ALCb for appropriately chosen initial conditions. The size of the attractor monotonically shrinks to zero as the control approaches its maximum possible value c=1, provided the control satisfies parameter conditions (3.1). The trapping region follows the attractor closely for large control intensities. Furthermore, the chaotic behavior of the uncontrolled population disappears for small to intermediate values of c, but resurfaces again for intermediate to large values of c. Even though long-term predictions of the population size are generally impossible in the presence of deterministic chaos, the range of possible population sizes can be significantly reduced by ALCb.

In consequence, increasing c confines the population size around the carrying capacity—even though this carrying capacity can never be an asymptotically stable fixed point, as the following result states.

Proposition 3.4. Assume that (C1)–(C2) hold and that the fixed point K is unstable for the uncontrolled system (2.1). Then, independent of the ALCb intensity,  $c \in (0,1)$ , the controlled system (2.3) has no asymptotically stable equilibria.

Theorem 3.3 imposes two conditions on the model parameters in form of the inequalities (3.1). The first inequality in (3.1) was also employed in the study of ALC and essentially establishes a lower bound for the control intensity; i.e., it always holds if c is large enough. The second inequality in (3.1) is more difficult to interpret. Nevertheless, for the Ricker map we have observed that a large growth parameter reduces the interval of control parameters satisfying the condition. That is, highly unstable population dynamics tend to be more difficult to



**Figure 1.** Bifurcation diagram illustrating the reduction of population fluctuation as the intensity of ALCb increases. The initial population size is chosen from the interval (3.3) of initial conditions established in Theorem 3.3. The bold red curves enveloping the chaotic attractor mark the limits of the trapping region  $I_b$ , given in (3.2). The black horizontal dashed line marks the carrying capacity K. Note that the trapping interval cannot be improved over a wide range of control parameter. The diagram is based on the Ricker map  $f(x) = x \exp(r(1-x/K))$  with r = 3 and K = 60, showing the last 100 of a total of 1,000 generations.

stabilize. The second inequality was also used in the theoretical study of ALC, but not when dealing with the reduction of the oscillation range. Instead, it was necessary to guarantee that ALC does not modify the population in two consecutive generations. For ALCb such a property holds without having to impose an extra condition.

Proposition 3.5. Assume that (C1)–(C3) hold. Then ALCb never acts in two consecutive generations.

So far we have found that the dynamics imposed by ALC and ALCb are very similar. Although neither of them can stabilize an unstable equilibrium, both are able to confine the population sizes in the same trapping region with interventions every other time step. Moreover, both have the same activation threshold that needs to be surpassed to trigger the control. Nevertheless, the time at which the population size is evaluated to determine the adaptive threshold affects the behavior of the control strategy. The next section describes a fundamental difference between ALC and ALCb.

**4. Differences from ALC.** In this section, we show that, in contrast to ALC, the ability of ALCb to reduce fluctuations is not global.

Figure 2(a) shows that the stabilizing property established in Theorem 3.3 is not global; that is, it does not hold for all initial conditions. We consider the same map as in Figure 1, where the conditions imposed by Theorem 3.3 reduce the range of population fluctuations as the control parameter increases. Now, however, we consider initial population sizes

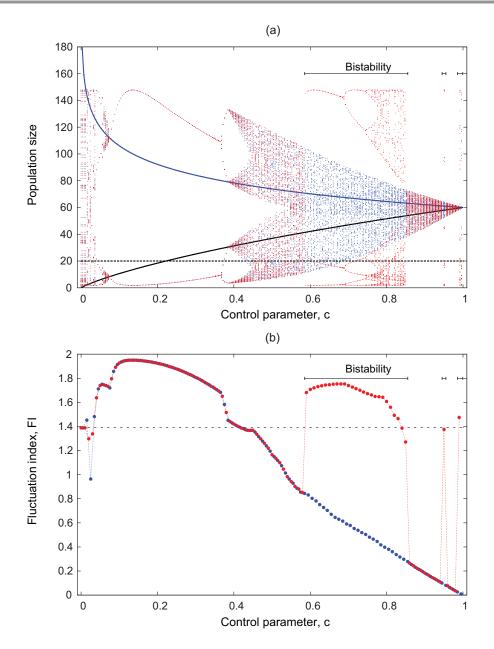


Figure 2. (a) Bifurcation diagram with the blue points generated as in Figure 1, i.e., for an initial condition satisfying Theorem 3.3, whereas the red points are generated from the initial population size  $b_0 = 20$ . This population size is outside the interval (3.3) guaranteeing a reduced fluctuation magnitude for  $c \geq 0.22$ , where the initial population size (dashed black line) falls below the lower bound of (3.3), which is given by  $c \cdot A_T$  (bold black curve). Note the existence of two different attractors over a large range of control intensities. For example, when  $0.59 \leq c \leq 0.87$ , whether or not ALCb is able to reduce the fluctuations depends on the initial population size. There are also sporadic alternative attractors for larger control parameters. The blue bold curve marks the value of  $A_T$ . (b) Fluctuation index (see (4.1)): in red for the initial population size  $b_0 = 20$  and in blue for an initial population within the interval (3.3). The horizontal line marks the fluctuation index (FI) of the uncontrolled population. Both plots use the Ricker map  $f(x) = x \exp(r(1 - x/K))$  with growth parameter r = 3 and carrying capacity K = 60.

outside the interval (3.3) specified in the theorem. Numerical simulations suggest the existence of at least one alternative attractor, which appears rather spontaneously in a period-3 saddle-node bifurcation ( $c \approx 0.59$ ) and disappears in an attractor boundary crisis ( $c \approx 0.87$ ). The alternative attractor coexists with the previously observed attractor. This causes bistability over a wide range of control intensities. Which one of the coexisting attractors is approached depends on the initial condition. Consequently, the population is no longer guaranteed to be inside the trapping region specified in Theorem 3.3, but may instead be driven towards an alternative attractor.

Importantly, the alternative attractor does not reduce the range of population fluctuations. We illustrate this by considering the fluctuation index (FI). This index is a dimensionless measure of the average one-step variation of the population size scaled by the average population size in a certain period. Mathematically, the FI is given by

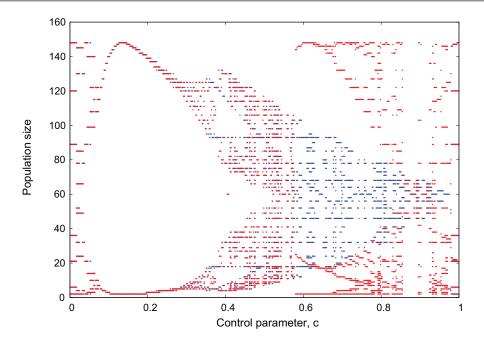
(4.1) 
$$FI = \frac{1}{T \, \overline{b}} \sum_{t=0}^{T-1} |b_{t+1} - b_t|,$$

where  $\overline{b}$  is the mean population size over a period of T generations. The FI was introduced in [22] and employed by Sah, Salve, and Dey [41] to study the stability properties of ALC.

In Figure 2(b), we plot how the FI varies with respect to the control parameter c. For very small control intensities, when the dynamics are still chaotic (cf. the bifurcation diagram in Figure 2(a)), there seems to be no clear trend in the FI. For not so small control parameters, but  $c \leq 0.4$ , the FI of the controlled system is considerably greater than the FI of the uncontrolled system. This is due to a period-2 cycle with an extreme fluctuation range. Here, the increased FI is independent of the initial population size. However, further increasing the control intensity has different consequences depending on the initial population size. If the initial population size is inside the interval (3.3), then the FI decreases as c increases. But if the initial population size is outside the interval (3.3), then the FI can abruptly jump to large values whenever there is an alternative attractor. This is related to the bistability, as different initial conditions approach different attractors. These fluctuations are again greater in magnitude than those of the uncontrolled system. In the case considered in Figure 2, ALCb increases rather than decreases fluctuations for more than 60% of the possible values for c, if the initial condition is  $b_0 = 20$ .

The dynamics of the controlled system (2.3) can be very rich. In Figure 2(a), we have plotted the value of  $A_T$  as a function of the control parameter using a blue continuous curve. The graph and the expression for the size of the population in generation two given in Lemma A.2 indicate that the stable period-2 cycle appears at  $c \approx 0.08$  in a border collision bifurcation. At  $c \approx 0.36$ , there is a period-doubling bifurcation creating a period-4 cycle, which disappears in a border collision bifurcation at  $c \approx 0.39$ . The alternative attractor appears in a period-3 saddle-node bifurcation and disappears in an attractor boundary crisis.

5. Incorporating biological realities. We have found that ALCb can increase or decrease the population fluctuations in the simple deterministic models considered so far. In this section, we address the question of whether this behavior may be due to the intrinsic simplifications of these models and may not be observable in the laboratory. With this aim, we



**Figure 3.** Bifurcation diagram of the integerized population model subject to ALCb in order to account for the lattice effect. Blue and red points are iterates of the initial conditions  $b_0 = 59$  and  $b_0 = 20$ , i.e., inside and outside the interval (3.3), respectively. The shape of the blue attractor as c varies suggests that Theorem 3.3 is not affected by considering the model on a lattice. The alternative attractors in red demonstrate that bistability is robust against the lattice effect. Dynamics are based on the discrete-state model (5.1) using the Ricker map  $f(x) = x \exp(3(1 - x/60))$ .

extend the models to be biologically more realistic. More specifically, we account for the integerization of the population size as well as for stochasticity. We are particularly interested in how these factors affect the occurrence of bistability, since this is one of the drivers increasing the fluctuation range.

**5.1. Lattice model.** The models we have considered until now assume a continuum of system states. But individuals come in discrete numbers, and it is therefore more realistic to consider a discrete-state dynamical system. Interestingly, the dynamics of a continuous-state model and its associated discrete-state version can be quite different [28]. Hence, discrete-state models can show properties which are not observable in similar continuous-state models. These properties are called lattice effects. We remark that lattice effects have been found experimentally, for example in laboratory populations of the flour beetle *Tribolium* [28].

For the discrete-state version of ALCb, we need to integerize not only the underlying population dynamics, but also the perturbation related to the control. The lattice model then reads

(5.1) 
$$b_{t+1} = \begin{cases} \inf[f(b_t)], & b_t \ge \inf[c \cdot b_{t-1}], \\ \inf[f(\inf[c \cdot b_{t-1}])], & b_t < \inf[c \cdot b_{t-1}]. \end{cases}$$

Figure 3 shows the resulting bifurcation diagram when varying the control parameter. The diagram features small horizontal lines, because the control perturbations are no longer continuous with c, but become effectively integerized with the rounded number of added individuals.

Despite the discrete nature of the dynamics, we can again observe alternative attractors and thus regimes of bistability. Actually, bistability occurs over a wider range of parameters than in the continuous-state model; compare Figure 3 with its continuous analogue in Figure 2. For appropriately chosen initial conditions, Theorem 3.3 still appears to hold.

In summary, the emergence of bistability is robust against the integerization of population size. Actually, the lattice effect seems to promote the occurrence of alternative attractors, which suggests enhanced fluctuations over a wider range of control parameters.

**5.2. Stochastic models.** In [41] it is argued that noise does not affect the ability of ALC to reduce fluctuations and, as a consequence, that ALC is a robust method for enhancing population stability. Here, we obtain a different conclusion for ALCb.

We incorporate noise using a different approach than that of [41]. Instead of adding a uniformly distributed noise term  $\epsilon$  ( $-0.2 < \epsilon < 0.2$ ) to the intrinsic growth parameter r or to the control parameter c every generation, we consider two models specifically designed to capture the main sources of stochasticity in biological populations: environmental and demographic noise [9]. The former arises from variation in extrinsic factors such as the environment over time (e.g., weather conditions) and affects all (or at least many) individuals in the population in the same way. The latter is due to intrinsic variability between individuals, e.g., in birth, death, and migration. For environmental noise we select the model

$$(5.2) b_{t+1} = f(b_t) \exp\left(s \cdot \epsilon_t - \frac{s^2}{2}\right).$$

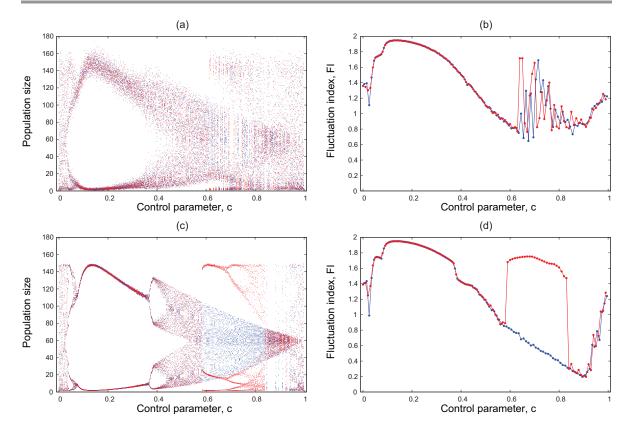
For demographic noise we select the model

$$(5.3) b_{t+1} = f(b_t) \exp\left(\sqrt{\frac{s^2}{f(b_t)}} \cdot \epsilon_t - \frac{s^2}{2f(b_t)}\right).$$

In both cases,  $\epsilon_t$  is a normally distributed variable with expectation 0 and variance 1. The parameter s measures the intensity of the noise, and we have fixed it to a value of s = 0.05, which can be considered as small compared to the estimates in [9].

Figure 4 shows that stochasticity clearly affects the ability of ALCb to reduce fluctuations. This effect appears strongest for environmental stochasticity. The bifurcation diagram (Figure 4(a)) illustrates how the noise smears over the asymptotic population sizes. As a consequence, in the presence of bistability, the basins of the different attractors are no longer strictly separated as in the deterministic system. The FI for initial conditions in the interval (3.3) goes up, whereas the FI for initial conditions outside (3.3) goes down (Figure 4(b)). The noise tends to blur the boundaries between the alternative deterministic attractors.

Demographic stochasticity mainly affects smaller population sizes; hence the bifurcation diagram looks less noisy (Figure 4(c)). For the chosen level of noise intensity s, the deterministic domains of attraction appear to remain intact between  $0.6 \lesssim c \lesssim 0.8$ . However, for larger control parameters, the population again switches back and forth between the sporadic alternative attractors. In particular, note that the FI increases towards c = 1, whereas in the deterministic system the FI decreases towards c = 1 (compare Figure 4(b), (d) with Figure 2(b)).



**Figure 4.** Behavior of ALCb when applied to stochastic models capturing environmental (top row) and demographic (bottom row) noise. The left column shows asymptotic bifurcation diagrams, and the right column the fluctuation index as a function of the control parameter. Calculations are based on (5.2) and (5.3) with noise intensity s = 0.05 and the Ricker map  $f(x) = x \exp(3(1 - x/60))$ . Blue and red points respectively arise from initial population sizes inside and outside interval (3.3) of Theorem 3.3.

## 6. Discussion.

**6.1. The curse of bistability.** One of the major differences between ALC and ALCb is that the latter can induce bistability. This implies coexisting alternative attractors. In such a case, the population dynamics depend critically on the initial condition, with the population approaching either (i) the "well-behaved" attractor, which reduces in magnitude with increasing control parameter, or (ii) the new alternative attractor. The latter tends to have properties that are extremely undesirable from a control point of view. The population sizes oscillate over a large range with extreme amplitudes (Figure 2(a)), thus enhancing the fluctuation index (Figure 2(b)).

Moreover, these extreme fluctuations reach low population floors, which significantly increase the risk of extinction. We have demonstrated this effect in simulations calculating the extinction risk in the next 50 generations, based on stochastic extinction if the population falls below a certain minimum viable population size and including both the lattice effect and environmental or demographic noise (results not shown here).

These undesirable effects can arise because the stabilizing properties of ALCb are only

"local" rather than "global" as for ALC; i.e., they apply only to certain rather than all possible initial conditions. Note that Theorem 3.3 identifies a range of initial conditions that are guaranteed to approach the "well-behaved" attractor. This interval shrinks for increasing c; see (3.3). Consequently, at a larger control intensity, the set of initial conditions which could potentially approach an alternative attractor is also larger.

Having an analytical expression for the trapping region (3.2), this information could be exploited by steering the system to this range of initial conditions. For example, one could use a dedicated targeting algorithm [7, 33]. However, this appears a bit intricate for a biological population and one might use a different control strategy from the start.

It is worth noting that ALCb, similarly to ALC, can destabilize the population for small values of the control parameter, i.e., when parameter condition (3.1) of Theorem 3.3 is violated. In the case of Figure 2(b), ALCb increases the fluctuation index—as a proxy for fluctuation magnitude or instability—for almost 40% of the possible control intensities in comparison to the uncontrolled system. However, accounting for bistability, this number increases to approximately 65%. Additionally, biologically realistic factors like stochasticity and the lattice effect tend to increase the proportion of counterproductive control parameters even further.

Hence, while small control intensities may increase fluctuations anyway, the presence of bistability destabilizes the population for large control intensities as well. A controller is therefore between a rock and a hard place.

**6.2.** The importance of timing. Control strategies often aim at reducing the fluctuations of a system. ALC has been shown experimentally [41] and theoretically [23] to possess this capability. The strategy of ALCb is very similar to ALC in design, but it chooses its adaptive limiter value based on a population size at a different point in time, namely the population size of the previous time step *before* intervention (rather than *after* intervention as for ALC).

This seemingly small modification causes a large effect in the control efficacy and resulting population dynamics. The regimes of bistability with their adverse consequences are the most obvious case in point, and we have shown that they are robust against lattice effects and noise. That is, they also occur in biologically more realistic models.

These results highlight the importance of "timing" the choice of the adaptive limiter. Similar effects have been observed in threshold harvesting models [17, 24], where the threshold can be chosen based on the population stock measured at different points in time. Small differences in this timing can also lead to completely different dynamics [24]. Even a simple constant effort harvest strategy can depend critically on the timing of its implementation, as the perturbation in population size is nonlinearly reinforced due to the density-dependent reproductive effects [13]. More generally, the order of events in discrete-time models is important [2, 8, 29, 32, 36]. If, as for ALCb, the dynamical system is of second order rather than first order, this opens the possibility for even more different dynamical effects.

**6.3.** Some useful characteristics. Apart from the various pitfalls identified in this paper, our analytical results also reveal some properties that are useful for the practical implementation of ALCb. First of all, there is an activation threshold, which the population size has to surpass to activate the control in the next generation (Proposition 3.2). This property can be used to plan ahead in intervention programs. Furthermore, we show that control actions never occur in two consecutive generations (Proposition 3.5), thus informing intervention pro-

grams about the maximum frequency of perturbations required. We also find that a control intervention actually ensures that the offspring in the next generation is greater in number than its parent generation (Lemma A.2). These are all very useful properties. Our analytical results therefore provide a deep theoretical understanding of ALCb.

7. Conclusion. ALCb is capable of reducing, in certain situations, the range of population fluctuations. However, contrary to what happens for ALC, there is a major caveat, namely that ALCb can be counterproductive in many other situations—especially (and unexpectedly) for larger values of the control parameter. In some sense, implementing any of these control methods resembles rubbing the magic lantern, wishing for a good genie that stabilizes the population. But in the case of ALCb the genie might be particularly evil and make things worse. Perfidiously, the more stubbornly we rub the magic lantern and wish for the good to happen (by increasing the ALCb intensity), the more prevailing may become the influence of an alternative attractor with undesirable properties (enhanced fluctuations and, as a result, increased extinction risk). The results presented in this paper send a mixed message. On the one hand, they provide estimates of parameters and initial conditions where ALCb is effective and similar in behavior to ALC. On the other hand, they warn against employing ALCb. Hence, before you rub the magic lantern, think carefully about what you wish for.

**Appendix A. Proofs of the analytical results.** We recall, e.g., [34]: that if I is an interval of real numbers and  $F: I \times I \to I$  is a continuous map, then the difference equation

(A.1) 
$$b_{t+1} = F(b_t, b_{t-1}), \quad t = 1, 2, \dots,$$

has a unique solution  $\{b_t\}_{t=0}^{\infty}$  for each given initial conditions  $b_0, b_1 \in I$ . We also recall that a point  $b \in I$  is an equilibrium of (A.1) if b = f(b, b), that is, if  $b_t = b$  is a solution of (A.1).

Our first result establishes that for the purpose of our investigation, i.e., the study of the asymptotic behavior, it is no restriction to assume that the initial condition of (2.3) belongs to the graph of f:

$$\{(b_0, f(b_0)) : b_0 \in (0, L)\}$$
.

Lemma A.1. Assume that (C1)–(C2) hold. Then for any initial conditions  $b_0, b_1 \in (0, L)$  there exists  $\tau \geq 1$  such that

$$b_{\tau} = f(b_{\tau-1}).$$

*Proof.* Let  $\{b_t\}_{t=0}^{\infty}$  be the solution of the controlled system (2.3) with initial conditions  $b_0, b_1 \in (0, L)$  and suppose that  $\tau$  does not exist. Then we have that

(A.2) 
$$0 < b_t < c \cdot b_{t-1}$$
 for  $t \ge 2$ 

and, as a consequence,

$$0 < b_t < c^{t-1} \cdot b_1$$
 for  $t \ge 2$ .

The last inequality above and condition (C2) guarantee that there exists a natural number n such that

$$(A.3) b_t < K for t \ge n,$$

where K is the positive fixed point of f.

Since by condition (C2) we have f(x) > x for 0 < x < K, inequalities (A.2) and (A.3) drive us to the following contradiction:

$$c^2 \cdot b_n > c \cdot b_{n+1} > b_{n+2} = f(c \cdot b_n) > c \cdot b_n.$$

Next, we prove Lemma 3.1.

Proof of Lemma 3.1. For claims (i) and (ii) see Lemmas 1 and 2 in [23]. There, it is also proved that in such cases  $K < A_T$  holds. Using the monotonicity of f, assumed in condition (C3), and the previous inequality, we get  $c \cdot A_T = f(A_T) < f(K) = K$ . Thus,  $c \cdot A_T < K < A_T$  holds.

Propositions 3.2 and 3.5 are direct consequences of the following result.

Lemma A.2. Assume that (C1)-(C3) hold and  $c \in (0,1)$  is such that  $A_T$  exists. Then the population size in generation two of a solution of the controlled system (2.3) is

$$b_2 = \begin{cases} f^2(b_0), & b_0 \le A_T, \\ f(c \cdot b_0), & b_0 > A_T, \end{cases}$$

where  $b_0$  is the initial population size.

Moreover, if the initial population size is greater than the activation threshold, i.e.,  $b_0 > A_T$ , then  $b_2 > b_1$ , and, as a consequence, no individuals are added in generation three.

*Proof.* We begin with the first affirmation. We know that the population size  $b_2$  in generation two depends on the sign of

$$b_1 - c \cdot b_0 = f(b_0) - c \cdot b_0.$$

Conditions (C1)–(C3) guarantee that

$$b_1 - c \cdot b_0 = f(b_0) - c \cdot b_0 > 0 \quad \Leftrightarrow \quad b_0 < A_T$$

and

$$b_1 - c \cdot b_0 = f(b_0) - c \cdot b_0 < 0 \quad \Leftrightarrow \quad b_0 > A_T.$$

Therefore, substituting in (2.3), we get

$$b_2 = \begin{cases} f^2(b_0), & b_0 \le A_T, \\ f(c \cdot b_0), & b_0 > A_T, \end{cases}$$

and the first affirmation is proved.

We note that the map giving the size in generation two is continuous but not differentiable at  $A_T$  (see Figure 5).

Now we deal with the second affirmation. First, note that the population size after intervention,  $c \cdot b_0$ , belongs to the interval  $[c \cdot A_T, b_0]$ . Clearly, if  $c \cdot A_T \geq d$ , we are done because f would be decreasing in the interval  $[c \cdot A_T, b_0]$  by condition (C3) and consequently

$$f(c \cdot b_0) \geq f(b_0)$$
.

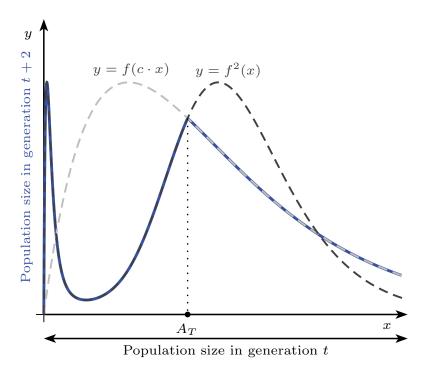


Figure 5. The bold blue curve gives the size of the population in two generations' time when applying ALCb. If  $b_t > A_T$ , then the control changes the population size after two generations compared to the size  $f^2$  of the uncontrolled system (dark grey dashed line). Instead, it coincides with  $f(c \cdot x)$  (light grey dashed line). If  $b_t \leq A_T$ , there is no change due to ALCb, and the expected offspring after two generations coincides with  $f^2$ . In this figure we have used the Ricker map  $f(x) = x \exp(2.7(1-x))$ .

Let us assume that  $c \cdot A_T < d$ . On the one hand, by Lemma 3.1, we know that  $c \cdot A_T < K$ . And by condition (C2), we have that

$$(A.4) f(c \cdot A_T) > c \cdot A_T.$$

On the other hand, we have

$$(A.5) f(A_T) \ge f(b_0)$$

because f is decreasing in the interval  $[A_T, b_0] \subset [d, b_0]$ . Therefore, recalling that the activation threshold satisfies  $f(A_T) = c \cdot A_T$  and using inequalities (A.4) and (A.5), we have

$$f(c \cdot A_T) > c \cdot A_T = f(A_T) \ge f(b_0).$$

Additionally, conditions (C1)–(C3) imply that f attains its minimum value on any compact interval contained in (0, L) in the extremes of such compact interval. In particular, we have

$$\min_{\{y \in [c \cdot A_T, b_0]\}} f(y) = \min\{f(c \cdot A_T), f(b_0)\}.$$

Thus

$$f(c \cdot b_0) \ge \min_{\{y \in [c \cdot A_T, b_0]\}} f(y) = \min\{f(c \cdot A_T), f(b_0)\} = f(b_0),$$

as we wanted to prove.

Next, we show that ALCb is able to confine the population in a trapping region defined by the value of the control parameter and the map f.

*Proof of Theorem* 3.3. We are going to show that the population size before intervention is confined to the interval

$$I_b = [f^2(c \cdot A_T), f(c \cdot A_T)],$$

provided that the initial population size belongs to the interval  $[c \cdot A_T, f(c \cdot A_T)] \subset I$ .

First, note that the intervals are well defined because, in the conditions of the theorem, f is decreasing in the interval  $[c \cdot A_T, L)$ . Therefore, using the definition of  $A_T$  and the monotonicity of f, we have

$$f(c \cdot A_T) \ge f(A_T) = c \cdot A_T$$

and

$$f^2(c \cdot A_T) \le f(c \cdot A_T).$$

Since K = f(K) and  $K < A_T$ , an argument similar to the previous one shows that K belongs to  $[c \cdot A_T, f(c \cdot A_T)] \subset I_b$ , as affirmed in the result.

We recall that, by assumption, the iterate following the initial population size  $b_0 \in [c \cdot A_T, f(c \cdot A_T)]$  is  $b_1 = f(b_0)$ . Next, we consider two cases depending on the relative position of the initial population size  $b_0$  with respect to the activation threshold.

(I) We assume that  $b_0 \in [c \cdot A_T, A_T]$ . Since  $b_0 \leq A_T$ , we have that the iterate following  $b_0$  and  $b_1 = f(b_0)$  in the solution of (2.3) is  $b_2 = f^2(b_0)$ .

Using the definition of  $A_T$  and the monotonicity of f, we have that

$$f(c \cdot A_T) \ge b_1 = f(b_0) \ge f(A_T) = c \cdot A_T$$

and

$$f^2(c \cdot A_T) \le b_2 = f^2(b_0) \le f(c \cdot A_T).$$

Therefore, the iterate  $b_2$  belongs to  $I_b$ . On the other hand, since the iterate  $b_1 \in [c \cdot A_T, f(c \cdot A_T)]$  and  $b_2 = f(b_1)$ , the study of the iterate  $b_3$  is either reduced to the situation we have just considered or to the following case.

(II) We assume that  $b_0 \in (A_T, f(c \cdot A_T)]$ . Clearly, the monotonicity of f guarantees that  $b_1 \in I$ . Since  $b_0 > A_T$ , we know that the iterate following  $b_0$  and  $b_1 = f(b_0)$  in the solution of (2.3) is  $b_2 = f(c \cdot b_0)$ .

Using the second inequality in condition (3.1), we have

$$c \cdot A_T < c \cdot b_0 < c \cdot f(c \cdot A_T) < A_T$$

and by the monotonicity of f

$$f(c \cdot A_T) \ge b_2 = f(c \cdot b_0) \ge f(A_T) = c \cdot A_T.$$

Therefore, we have obtained that

$$b_2 \in [c \cdot A_T, f(c \cdot A_T)] \subset I_b$$
.

By Proposition 3.5 the next iterate is  $b_3 = f^2(c \cdot b_0) \in I_b$ . Thus, since the iterate  $b_2 \in [c \cdot A_T, f(c \cdot A_T)]$  and  $b_3 = f(b_2)$ , the study of the iterate  $b_4$  is reduced to the situation we have just considered or to the previous one.

Finally, we prove that ALCb cannot create an asymptotically stable equilibrium.

*Proof of Proposition* 3.4. First, let us determine the equilibria of the controlled system (2.3). We rewrite system (2.3) in one line by using the maximum function

(A.6) 
$$b_{t+1} = f(\max\{b_t, c \cdot b_{t-1}\}), \quad c \in (0, 1).$$

Clearly,  $b \in [0, L]$  is an equilibrium of (A.6) if and only if it satisfies

$$b = f(\max\{b, c \cdot b\}) = f(b).$$

Thus, the controlled system and the uncontrolled system have the same equilibria, which are 0 and K by condition (C2).

Next, we must show that no equilibrium is asymptotically stable. The trivial equilibrium is not asymptotically stable, by a reasoning similar to that in the proof of Lemma A.1. Now, let us consider the positive equilibrium K. Clearly, it is possible to find a small enough neighborhood  $\mathcal{N}$  of K such that

$$\max\{y, c \cdot x\} = y$$

for  $(x,y) \in \mathcal{N} \times \mathcal{N}$ . Therefore, the second-order equation (A.6) is given by the uncontrolled system

$$x_{t+1} = f(x_t)$$

in  $\mathcal{N} \times \mathcal{N}$ . Since we are assuming that K is unstable for the uncontrolled system, we obtain that K is unstable for the controlled system (2.3).

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