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Adaptive limiter control of unimodal population maps

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HIGHLIGHTS

- We give theoretical support to recent experimental findings.
- Adaptive limiter control can be a global method to stabilize population oscillations.
- Our analytical results provide guidance how to choose the control intensity.
- The initial transients can be important and inflate the control effort.
- We present new properties with important practical implications.

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ABSTRACT

We analyse the adaptive limiter control (ALC) method, which was recently proposed for stabilizing population oscillations and experimentally tested in laboratory populations and metapopulations of *Drosophila melanogaster*. We thoroughly explain the mechanisms that allow ALC to reduce the magnitude of population fluctuations under certain conditions. In general, ALC is a control strategy with a number of useful properties (e.g. being globally asymptotically stable), but there may be some caveats. The control can be ineffective or even counterproductive at small intensities, and the interventions can be extremely costly at very large intensities. Based on our analytical results, we describe recipes how to choose the control intensity, depending on the range of population sizes we wish to target. In our analysis, we highlight the possible importance of initial transients and classify them into different categories.

1. Introduction

Stability of biological populations has attracted a lot of attention because it determines, amongst others, extinction probability (Thomas et al., 1980; Berryman and Millstein, 1989; Allen et al., 1993), effective population sizes and genetic diversity (Mueller and Joshi, 2000) as well as population fitness (Charlesworth, 1994). A large range of fluctuation in the population size over time tends to invoke a low stability of the population. Several authors have therefore proposed control strategies to stabilize a population (e.g. McCallum, 1992; Solé et al., 1999; Stone and Hart, 1999; Hilker and Westerhoff, 2006, 2007a; Liz, 2010; Carmona and Franco, 2011; Dattani et al., 2011; Franco and Perán, 2013). These control strategies typically aim at creating stable population sizes by removing (harvesting/thinning) or adding (stocking) individuals following certain rules. Although the mechanisms of these strategies are theoretically well understood, experimental demonstration of reduced population fluctuations remains rare (Desharnais et al., 2001; Becks et al., 2005; Dey and Joshi, 2007, 2013) and there is, in general, a lack of empirical evidence for the stabilizing properties of control methods.

Recently, Sah et al. (2013) have proposed adaptive limiter control (ALC) as a novel method for controlling population oscillations. The idea behind ALC is to restock the population if there is too large a crash in the population size. More specifically, individuals are added if the population size falls below a certain fraction of its value in the previous generation. ALC is related to the family of limiter control methods (see the next section for a more detailed description of the method). Sah et al. (2013) have tested ALC in experiments with laboratory populations and metapopulations of the fruit fly *Drosophila melanogaster*. Their results suggest that increased ALC intensity enhances population stability, measured in terms of reduced fluctuations and extinction frequencies.

ALC is in some sense ‘atypical’ when compared to other control methods, because it is one of the few methods that have been

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studied empirically. Sah et al. (2013) corroborate their experimental results also by some numerical simulations of a mathematical model. However, it is inherent to the method of numerical simulations that they only apply to particular situations, specified for example by the values of model parameters and initial conditions. It is not clear whether results observed for some simulations will hold for other simulations. For instance, we support the observation of Sah et al. (2013) that in some situations ALC is not only ineffective, but actually worsens population stability. Hence, the question arises whether or not, and under which circumstances, ALC is a good strategy to stabilize biological populations.

In this paper, we present mathematically rigorous results on ALC. They provide a theoretical basis for the stabilizing properties observed in the experiments and simulations by Sah et al. (2013). Currently, there is a lack in the theoretical understanding of ALC, as there are no results available that explain the mechanisms and effects of ALC. Our analytical results thus contribute to filling this gap.

In the next section, we begin with introducing ALC in a simple deterministic setting. We then present a number of analytical results. The main one confirms the observation of Sah et al. (2013) that greater ALC intensities invoke the population to have lower variation in size over time, measured in terms of the fluctuation range. In addition, we present a number of novel results. We work out a number of useful properties that can be relevant for the implementation and applicability of ALC. This includes the frequency and the cost of interventions; a description of initial transients; how to plan ahead; and how to choose the ALC intensity in order to attain a certain desired reduction in the fluctuation magnitude. Moreover, we show that the stabilizing effect of ALC is global, i.e. independent of the initial population size, for a wide range of population models.

2. Adaptive limiter control

2.1. Underlying population dynamics

Before introducing the ALC method and some of its effects, we describe the underlying population dynamics in the absence of control. We assume that the uncontrolled population follows the discrete-time dynamical system given by

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

where x_t denotes the population size at time step t. Function f describes the population production, sometimes also called the stock–recruitment curve, and is assumed to satisfy the following conditions:

(C1) $f : [0, b] \to [0, b)$ ($b = \infty$ is allowed) is continuously differentiable and such that $f(0) = 0$ and $f(x) > 0$ for all $x \in (0, b)$.

(C2) f has 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 $d < K$ in such a way that $f'(x) > 0$ for all $x \in (0, d)$, $f'(x) < 0$ for all $x > d$, and $f'(0^+), f'(b^-) \in \mathbb{R}$.

These conditions are standard assumptions in the study of discrete-time population dynamics (e.g. May, 1976; Singer, 1978; Cull, 1981; Schreiber, 2001; Liz, 2007; Carmona and Franco, 2011). Essentially, they describe a hump-shaped population production (peaking at $x = d$). From a biological point of view, the population dynamics are overcompensatory, caused e.g. by scramble competition (Britton, 2003). The population has two fixed points, namely the extinction state $x = 0$ and a positive equilibrium $x = K$. There is no demographic Allee effect. Examples include the Ricker (1954), Hassell (1975) and generalized Beverton–Holt (Bellows, 1981) maps, in their overcompensatory regimes where applicable.

2.2. Modelling ALC

If the population size x_t at time step t drops below a certain threshold, then there is an intervention augmenting the population back to this threshold. In this, ALC is similar to limiter control methods (Corron et al., 2000; Hilker and Westerhoff, 2005, 2006). Since the threshold is a fraction of the previous population size and as such variable, the limiter is considered 'adaptive'. In Fig. 1 we illustrate how ALC modifies the dynamics of the population. In particular, we can observe a reduction in the fluctuation range.

When applying ALC, we have two different population sizes at time step t, namely the population size before and after the action of ALC. In discrete-time models, the order of events is important (Åström et al., 1996; Bodine et al., 2012; Lutscher and Petrovskii, 2008). Let us denote by b_t (respectively a_t) the population size before (respectively after) the action of ALC in time step t. We note that $b_t \leq a_t$, because ALC never removes individuals.

If ALC augments the population size, this induces an 'intra-generation' variation. We illustrate this in Fig. 1 with dashed red lines. In this example, we can observe that the sizes of b_t and a_t are different when ALC is applied.

A direct consequence of having two population sizes at time step t is that we must choose one of them to define the adaptive threshold in the next time step $t+1$. In their experiments and

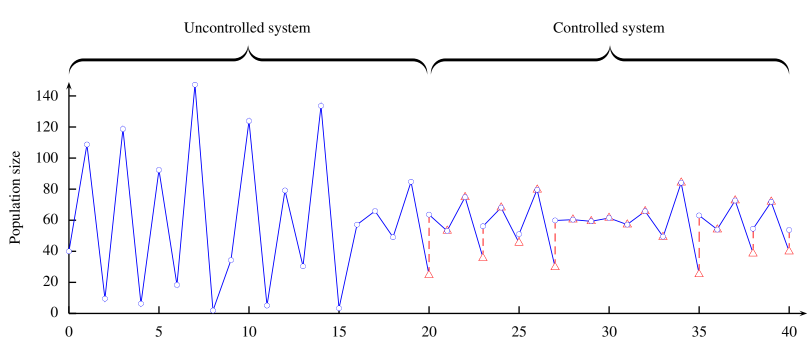

Fig. 1. During the first 20 generations, the population is uncontrolled and follows Eq. (1). In the next 20 generations, the population is controlled by ALC, following system (2). Blue circles and red triangles indicate the population size after and before ALC, respectively. Therefore, a blue circle inside a red triangle corresponds to a generation where ALC did not modify the population. Dashed lines connecting blue circles with red triangles indicate ALC interventions (thus inducing intra-generation variation). Note the clear reduction of the fluctuation range in the controlled population compared to the uncontrolled population. Population dynamics follow the Ricker map $f(x) = x\exp(r(1-x/K))$ with growth parameter $r = 3$ and carrying capacity $K = 60$. ALC is applied with intensity $c = 0.75$. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

numeric simulations, Sah et al. (2013) select a_t rather than b_t. With this choice, the populations dynamics are captured by the following system of difference equations:

$$b_{t+1} = f(a_t) \quad \text{and} \quad a_{t+1} = \begin{cases} b_{t+1}, & b_{t+1} \geq c \cdot a_t, \\ c \cdot a_t, & b_{t+1} < c \cdot a_t, \end{cases} \tag{2}$$

where $0 < c < 1$ is a control parameter measuring the ALC intensity.

Substituting the value for b_{t+1} in the first equation of system (2) into the second one, we obtain that the population dynamics are determined by the piecewise smooth dynamical system given by the first-order difference equation

$$a_{t+1} = \begin{cases} f(a_t), & f(a_t) \geq c \cdot a_t, \\ c \cdot a_t, & f(a_t) < c \cdot a_t, \end{cases} \tag{3}$$

which can be written in one line by using the maximum function

$$a_{t+1} = \max\{f(a_t), c \cdot a_t\}. \tag{4}$$

In the following sections, we will assume (unless stated otherwise) that the population is censused after ALC, i.e. $x_t := a_t$. We then get the equation

$$x_{t+1} = \max\{f(x_t), c \cdot x_t\}. \tag{5}$$

Note that neither system (2) nor Eq. (5) can be transformed into the following equation proposed by Sah et al. (2013):

$$x_{t+1} = \begin{cases} f(x_t), & x_t \geq c \cdot x_{t-1}, \\ f(c \cdot x_{t-1}), & x_t < c \cdot x_{t-1}, \end{cases} \tag{6}$$

which is the same as

$$x_{t+1} = f(\max\{x_t, c \cdot x_{t-1}\}).$$

This equation assumes population census *before* ALC, i.e. $x_t := b_t$, and can be obtained from

$$b_{t+1} = f(a_t) \quad \text{and} \quad a_{t+1} = \begin{cases} b_{t+1}, & b_{t+1} \geq c \cdot b_t, \\ c \cdot b_t, & b_{t+1} < c \cdot b_t. \end{cases} \tag{7}$$

Even though Sah et al. (2013) wrote down Eq. (6), they have used Eq. (5) for their numerical simulations and their laboratory experiments (personal communication with the authors). In this paper, we will exclusively consider Eq. (5) and refer to it as ALC.

We will consider Eq. (6) in a separate paper, showing that it has more complex dynamics with possibly adverse consequences. Note that Eq. (6) is of second order, whereas Eq. (5) is of first order. Another difference is that the thresholding in Eq. (6) is based on population sizes before control (see Eq. (7)), whereas the thresholding in Eq. (5) is based on population sizes after control (see Eq. (3)). We propose to distinguish between the two strategies by denoting them as ALCb and ALCa, respectively. Since we only consider ALCa in this paper, we refer to it as ALC in short.

The thresholding in ALCb is determined by b_{t-1}. This extra time lag is the reason why ALCb is second order, and also why ALCb and ALCa are not topologically conjugated. They therefore have qualitatively different dynamics, even though there are only two processes of reproduction and control (Hilker and Liz, 2013). A similar effect occurs in the threshold harvesting strategies proposed by Costa and Faria (2011) and Franco and Perán (2013), as the respective thresholds are defined at different points of time.

2.3. Activation threshold

Before focusing on the stability properties, we highlight an interesting feature of ALC. It concerns the intervention patterns of ALC and, despite its potential practical implications, has not been previously reported.

To begin with, recall that ALC only modifies the population in certain generations, namely if the population has dropped below a fraction of its size in the preceding generation. In principle, this

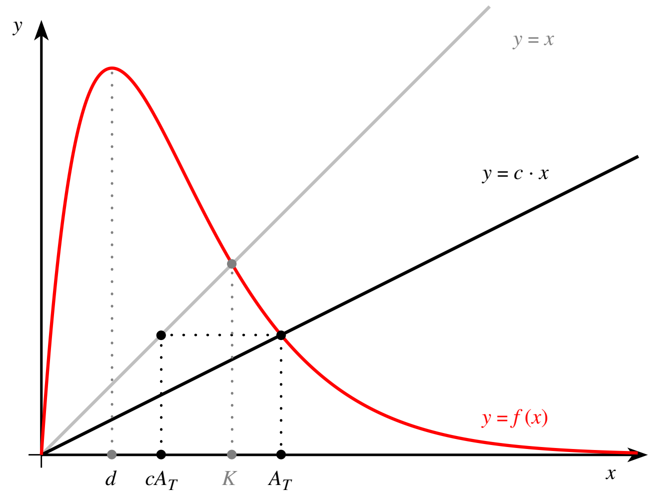

Fig. 2. ALC is implemented whenever the straight line $y = c \cdot x$ (shown in bold black line) is above the graph of the population production f (shown in red curve). The activation threshold A_T is defined by their intersection. Note how for each value of the control parameter $c \in (0, 1)$ the carrying capacity K of f is enveloped by $c \cdot A_T$ and A_T. As c increases (i.e. the bold black line approaches the thin grey line), the difference $A_T - c \cdot A_T$ shrinks to zero. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

would imply that the controller has to wait until measuring the population size in generation t before deciding whether or not control action is necessary. However, Fig. 1 seems to indicate that ALC only acts if the previous population size is large enough (notice that interventions indicated by the red dashed lines are always preceded by large population sizes). This suggests the existence of a 'hidden' threshold level, i.e. ALC is activated in generation t only if the population size in the previous generation $t-1$ exceeds this threshold level.

This threshold level does indeed exist (rigorously shown in Appendix A, see Lemmas 1 and 2). Henceforth, we will refer to it as the *activation threshold* and denote it with A_T. We also prove the following: Only if a_t, the population size after ALC, exceeds the activation threshold A_T in some generation t, this will trigger the control in the next generation $t+1$ (see Corollary 2 in Appendix A). This knowledge can be proved to be very useful in practical situations, as the controller will know in advance that an intervention is necessary in the next generation. In some sense, surpassing the activation threshold is a kind of 'early-warning signal' for impending control action.

Geometrically, the activation threshold can be found as the first component of the intersection point of the graph of f and the straight line $y = c \cdot x$ (see Fig. 2). It is related to the carrying capacity K of the uncontrolled map by the inequality

$$c \cdot A_T \leq K \leq A_T.$$

In particular, the activation threshold is greater than the carrying capacity. This implies that ALC will never act in (under-)compensatory population dynamics when starting from small initial conditions, as the approach to the carrying capacity is monotonically increasing.

Fig. 3 illustrates the practical importance of the activation threshold. As before, red triangles mark the generations in which ALC perturbs the population. We observe that this happens if and only if the preceding population size is greater than the activation threshold (marked by blue filled circles).

3. Reduction of the fluctuation range

First of all, we point out that ALC is not able to stabilise oscillations towards an equilibrium point (see Proposition 2 in

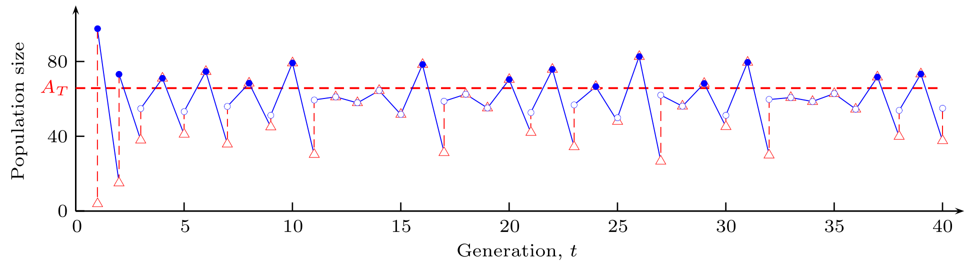

Fig. 3. Time series of a controlled population. Red triangles and blue circles indicate the population size before and after ALC, respectively. The horizontal red dashed line gives the activation threshold A_T, and filled blue circles indicate population sizes after ALC greater than the activation threshold. These instances are always followed by vertical red dashed lines in the next generation, where ALC is implemented. Moreover, note that, after an initial transient, there is always at least one generation in between two control interventions. Parameter values as in Fig. 1 with $c=0.75$ and $A_T \approx 65.8$. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

Appendix A). But if the control parameter satisfies a certain condition, then ALC confines the population sizes within a region around the carrying capacity. This 'trapping region' can be defined by means of A_T, that is, it is completely determined by the map f and the control parameter c.

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

$$d \le c \cdot A_T, \tag{8}$$

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

Then, applying ALC with intensity c confines the population sizes a_t and b_t into the following intervals around the carrying capacity K:

$$I_a := [c \cdot A_T, f(c \cdot A_T)] \quad \text{and} \quad I_b := f(I_a), \tag{9}$$

for any $x_0 \in (0, b)$.

The proof of Theorem 1 is in Appendix A. Theorem 1 can be used to rigorously prove that ALC is able to reduce the fluctuation magnitude, as observed by Sah et al. (2013). The intervals I_a and I_b correspond to a trapping region of possible population sizes and thus confine the oscillation amplitudes. Hence, the smaller the trapping regions the smaller the fluctuation range. Note that as the control parameter c tends to 1, the activation threshold A_T tends to the carrying capacity K. In consequence, as long as Condition (8) holds, increasing ALC intensity c shrinks the trapping region. Moreover, the result establishes that such behaviour is global, i.e. independent of the initial population size.

Fig. 4a shows bifurcation diagrams of the population size with varying ALC intensity. The blue and red attractors correspond to the population sizes after and before ALC, respectively. Note that the population sizes after ALC intervention are generally greater than the ones before intervention, because ALC augments the population. In the absence of control ($c=0$), the oscillations are chaotic and extend over a wide range of values with extreme amplitudes. With increasingly larger ALC intensity, however, the range over which the population sizes fluctuate begins to shrink. In particular, the size of both the blue and red attractors (i.e. the fluctuation ranges) shrinks to zero as the control tends to its maximum possible value $c=1$. Hence, increasing c confines the population size around the carrying capacity even though this carrying capacity can never be an asymptotically stable fixed point.

The fluctuation ranges are well approximated by the trapping regions I_a and I_b given in Theorem 1. In fact, these intervals are sharp, that is, they cannot be improved. To illustrate this, Fig. 4a shows their upper and lower limits as black curves. Observe how these limits cannot be improved for $c \gtrsim 0.4$, because it is impossible to find smaller intervals which enclose the asymptotic population sizes.

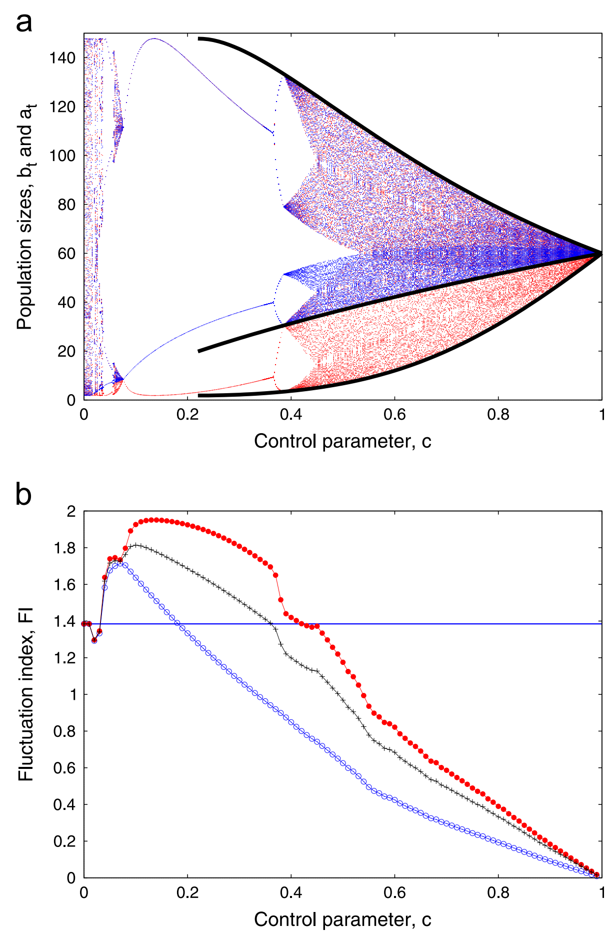

Fig. 4. (a) Bifurcation diagram illustrating the reduction of population fluctuation as the ALC intensity increases. Red dots represent population sizes before ALC, b_t, and blue dots population sizes after ALC, a_t. The bold black curves enveloping the attractors mark the limits of the intervals defining the trapping regions given in Eq. (9). Note that the trapping regions cannot be improved over a wide range of control parameters. (b) Fluctuation indices (FIs) considering only inter-generation variations (red line with filled circles for b_t and blue line with empty circles for a_t) and considering the intra-generation changes in the population (black line with crosses). The horizontal line marks the FI of the uncontrolled population. The diagrams are based on the Ricker map $f(x) = x\exp(r(1-x/K))$ with $r=3$ and $K=60$, removing initial transients. The initial population size is chosen as a pseudo-random number in $[0, f(d)]$. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

Note that chaos is suppressed and replaced by periodic dynamics for small to intermediate ALC intensities, but reappears for larger ALC intensities. This has already been observed by Sah et al. (2013). The blue attractor in Fig. 4a corresponds to the bifurcation diagram in Sah et al. (2013, their Fig. 2a). We also show the population sizes before ALC interventions (red attractor in Fig. 4a), in order to complete the picture.

Theorem 1 imposes a condition on the model parameters in the form of Inequality (8). It is easy to verify this condition numerically or graphically. For example, in the case of Fig. 4a, Theorem 1 holds for $c \gtrsim 0.22$. In fact, we can use Condition (8) to obtain a lower bound for the ALC intensity. The condition holds if and only if

$$c > \frac{d}{\max f^{-1}(d)}. \quad (10)$$

This lower bound depends purely on the shape of the production map f. The kind of species that are most likely to satisfy this condition are those that (i) reach their maximum offspring at a small population size d, i.e. with a large reproduction potential and (ii) have only a slight reduction in their offspring after surpassing the carrying capacity, i.e. scramble competition is mild. This would suggest species with unstable, but not strongly chaotic population dynamics.

So far, we have considered the fluctuation range as a measure of constancy stability (in the sense of population size staying essentially unchanged). We remark that this measure is close to what is captured by the coefficient of variation, i.e. the variation of the time series data (e.g. Mueller and Joshi, 2000; Prasad et al., 2003). However, there are many different measures to quantify this stability concept (Grimm and Wissel, 1997). In the remainder of this section, we will consider another measure, namely the fluctuation index (FI). We will see that the stabilizing properties may differ depending on the choice of measure.

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 in Dey and Joshi (2006) and employed by Sah et al. (2013) to study the stability properties of ALC. Mathematically, the FI is given by

$$FI = \frac{1}{T\overline{x}} \sum_{t=0}^{T-1} |x_{t+1} - x_t|,$$

where $\overline{x}$ is the mean population size over a period of T time steps.

When measuring population sizes before and after ALC intervention, there are three natural choices for the FI. Obviously, we can consider FIs based on population sizes only (i) after and (ii) before ALC. They represent inter-generation variation in population sizes. Moreover, we can additionally consider intra-generation variation. For this, (iii), we calculate the FI as the one-step change in population size including intra-generation variation, that is,

$$\frac{2}{T(\overline{a}+\overline{b})} \sum_{t=0}^{T-1} (|a_{t+1} - b_{t+1}| + |b_{t+1} - a_t|).$$

The results are shown in Fig. 4b.

The value of all three FIs is the same when the ALC intensity is zero, i.e. for the uncontrolled system, or very small. But otherwise the FIs take different values from each other. We observe that the FIs considering inter-generation variations envelope the FI considering the intra-generation variations. Moreover, for a given ALC intensity, the FI of a_t is always smaller than the others. It is also the first to drop below the value of the uncontrolled system (at $c \approx 0.19$). The other FIs require significantly larger control parameters ($c \approx 0.37$ and $c \approx 0.43$) to drop below the baseline set by the uncontrolled system.

Crucially, the FI can be larger than in the uncontrolled system. This has been touched upon only briefly by Sah et al. (2013), but it is worth noting that it can happen for a considerable range of ALC intensities. In the case of Fig. 4b, ALC increases the FI for almost 20% of possible parameter values, when considering a_t, and for around 40% of possible parameter values when considering b_t or incorporating the intra-generation variation. We remark that these percentages will vary when considering other population maps and parameter values. However, it is clear that ALC does not always enhance population stability (when measured in terms of the FI), but may actually make things worse.

4. How to choose the ALC intensity

We have already seen that Theorem 1 gives us a lower bound of the control parameter, see Condition (10). In practical situations, however, one often wants to know how to choose the control intensity, in order to achieve a certain outcome, e.g. a desired reduction of the fluctuation range or preventing outbreaks or very small population sizes. In fact, targeting can be a main issue when controlling a population (Hilker and Westerhoff, 2007b; Dattani et al., 2011). In this section we show how Theorem 1 can be used to actually calculate the ALC intensity required to establish a lower or upper bound for the population size, or to reduce the oscillation range to a desired value.

Firstly, we consider the case that we want to avoid population sizes dropping below a certain value L. For instance, this can be important for the persistence of endangered species. Notice that we are looking for $c \in (0,1)$ such that Condition 8 holds and $\min I_b = f^2(c \cdot A_T) = L$ because in such a case Theorem 1 guarantees the desired behaviour. We denote, as usual, $f^2 := f \circ f$, $f^3 := f \circ f^2$ and so on. Since by definition $c \cdot A_T = f(A_T)$, we have that $f^2(c \cdot A_T) = f^3(A_T)$, $c = f(A_T)/A_T$, and Condition 8 can be rewritten as $A_T \in (K, \max f^{-1}(d)]$.

Therefore, if we want to know the ALC intensity required to avoid population sizes dropping below L, we have to solve the equation $f^3(x) = L$ in the interval $(K, \max f^{-1}(d)]$. This equation can have at most one solution in such an interval, since by conditions (C1)–(C3) the restriction of f^3 to the interval $(K, \max f^{-1}(d))$ is increasing. If the solution exists and we denote it by $\hat{x}$, then the ALC intensities

$$c \geq \frac{f(\hat{x})}{\hat{x}}$$

do not allow the population size to go below L. We point out that, by the way we constructed $\hat{x}$, the above condition ensures that Theorem 1 holds.

Secondly, consider the case that we want to prevent population outbreaks, e.g. if the species is a pest. Suppose that we want to calculate the ALC intensity required to maintain the population size below a prefixed amount U. We look for c such that Condition 8 holds and $\max I_a = f(c \cdot A_T) = U$, because in such a case Theorem 1 guarantees the desired behaviour. As in the former case, equality $c \cdot A_T = f(A_T)$ allows us to reduce the problem of finding such c to that of solving the equation $f^2(x) = U$ in the interval $(K, \max f^{-1}(d)]$. This equation can have at most one solution in such interval, because f^2 is decreasing in this interval. If the solution exists and we denote it by $\hat{x}$, then the ALC intensities $c \geq f(\hat{x})/\hat{x}$ maintain the population size below the upper bound U.

Finally, consider the case that we want to guarantee that the population sizes are in a range of diameter D. Then, similar to the cases above, we have to solve the equation

$$f^2(x) - f^3(x) = D \quad (11)$$

in the interval $(K, \max f^{-1}(d)]$. This equation can have at most one solution in such interval because of the above monotonicity properties of f^2 and f^3. If the solution exists and we denote it by $\hat{x}$, then the ALC intensities $c \geq f(\hat{x})/\hat{x}$ are able to confine the population fluctuations within an interval of diameter D or smaller.

4.1. Examples

We illustrate the above results in the following three examples, where we consider the Ricker map $f(x) = x\exp(r(1-x/K))$ with $r=3$ and $K=60$. We recall that in this case $d = K/r = 20$.

1. Suppose that we want the population size to be greater than $L=25$. Solving $f^3(x) = 25$ in the interval $[60, \max f^{-1}(20)) \approx [60, 90.1048)$, we obtain that $\hat{x} \approx 65.7942$. Therefore, the ALC intensity we are looking for is $c = 30/\hat{x} \approx 0.7485$ or greater. Fig. 5a shows that such an ALC intensity indeed has the desired effect. The control begins to act in generation 20. Note that, after a short transient of two time steps, the population size never drops below $L=25$.
2. Suppose that we want the population size not to surpass the upper limit $U=75$. In order to figure out the adequate ALC intensity, following the indications above, we need to solve the equation $f^2(x) = U$ in the interval $[60, 90.1048)$. Its solution is $\hat{x} \approx 63.6182$. Therefore, the ALC intensity we are looking for is $c = 30/\hat{x} \approx 0.8345$ or greater. In Fig. 5b we apply ALC with $c=0.8345$, beginning after 20 generations. Then, the population sizes do not exceed the upper bound $U=75$. As in the previous example, the last affirmation is true after a short transient of two generations, in which the population still exceeds the prefixed upper bound. In the next section we will discuss the behaviour of these initial transients in more detail.
3. Suppose that our objective is to guarantee that the population oscillates around the carrying capacity with a variation ofless than $D=75$. Solving Eq. (11) in the interval $[60, 90.1048)$, we obtain that $\hat{x} \approx 67.8083$. Therefore, the ALC intensity we are looking for is $c = f(\hat{x})/\hat{x} \approx 0.6768$ or greater. Fig. 5c illustrates that the ALC intensity $c=0.6768$ yields the desired dynamics.

5. Costs of applying ALC

In this section we investigate the initial transients and the frequency of interventions. Both issues have not been considered before and are closely related to the cost of applying ALC. Therefore, they are very interesting from the practical point of view. We also consider the effort, i.e. the number of individuals that have to be added when augmenting the population.

5.1. Initial transients

In the previous section we have proven that ALC asymptotically (i.e. in the long run) confines the population size to a trapping region. However, the asymptotic state (or dynamics) can be

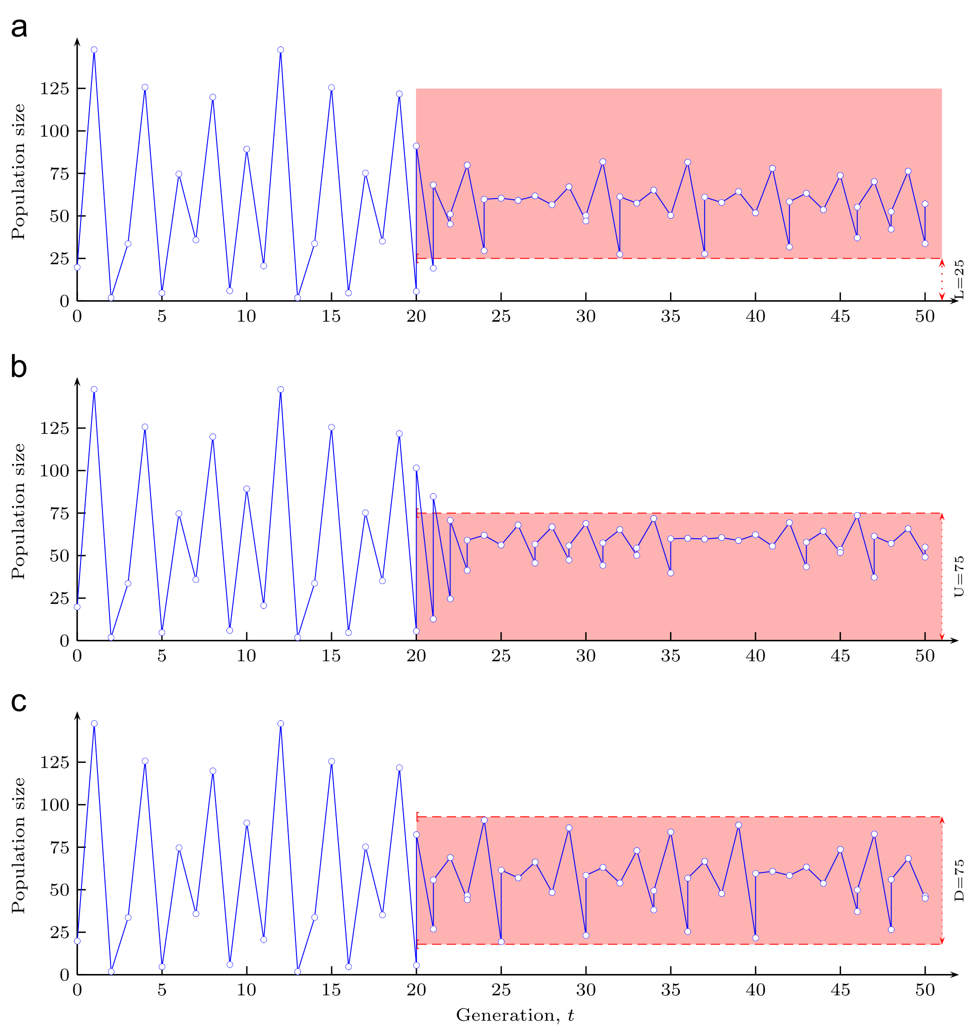

Fig. 5. Illustration of how to choose the ALC intensity to achieve different objectives. The shadowed areas correspond to the target of the control: (a) minimum population size of $L=25$; (b) maximum population size of $U=75$; (c) maximum oscillation range of diameter $D=75$. The first 20 generations are without control. Note how the population size enters, after some initial transients in cases (a) and (b), into the target region. In all cases f is the Ricker map with $r=3$ and $K=60$. The ALC intensities are calculated in the examples of the main text.

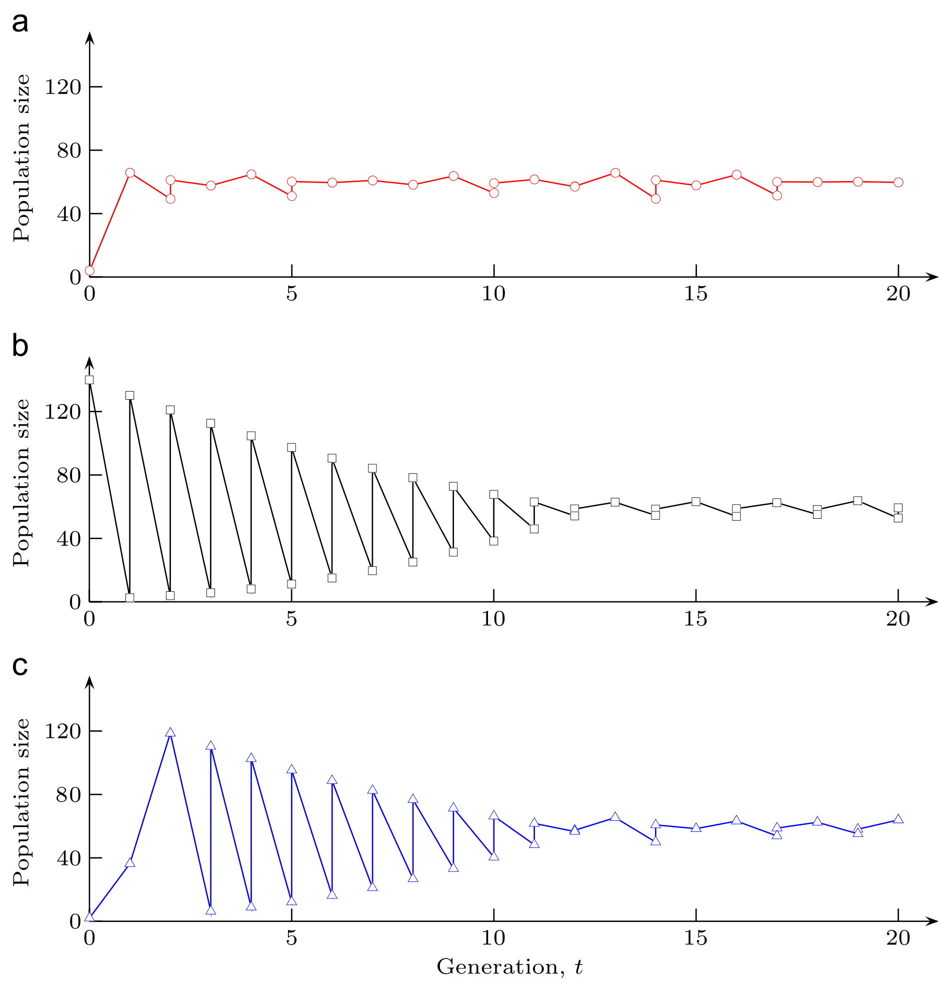

Fig. 6. Three different types of initial transients that ALC can produce. Red circles, black squares and blue triangles respectively correspond to initial transients of type (a), (b) and (c) in Corollary 3. Initial conditions are chosen as 4, 140 and 2; control intensity is set to $c=0.93$; and $f(x)=x\,\exp(r(1-x/K))$ with $r=3$ and $K=60$. Interventions by ALC to augment the population are indicated by strictly vertical lines joining two population sizes, which correspond to the population sizes before and after ALC. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

preceded by an initial transient where the population is outside the trapping region (see Fig. 5). These initial transients are, of course, finite. That is, they comprise a limited number of time steps, and for that reason they are frequently neglected when considering the properties of control strategies. Yet, considering these initial transients is critical for understanding and predicting the consequences of control strategies (Ezard et al., 2010; Frank et al., 2011; Hastings, 2004). Firstly, despite being finite, the initial transients can last over tens or hundreds or generations, which renders them highly relevant from a practical point of view. Secondly, nature is full of perturbations, environmental fluctuations and stochastic effects. Hence, transients appear continuously. In fact, one could argue that the asymptotic dynamics might never be reached, and many of the observations might be influenced by transients. Here, we describe the possible initial transients for ALC, how they affect the performance of ALC and how long they might last.

There can be three different types of initial transients when implementing ALC (see Corollary 3 in Appendix A for mathematical details). They are illustrated in Fig. 6.

(a) In the first type of initial transients, the population size increases monotonically until reaching the trapping region (red circles in Fig. 6). No control intervention is necessary, hence ALC is actually never applied during this initial transient. This corresponds to type (a) in Corollary 3.
(b) In the second type of initial transients, ALC always acts in consecutive interventions before the population size reaches the trapping region (black squares in Fig. 6). Hence, ALC is applied every generation and the population alternates between peaks and troughs in a damped oscillation due to the effect of the control. This initial transient corresponds to type (b) in Corollary 3.
(c) The third type of initial transients is a mixture of (a) and (b). Initially, the population size increases as in type (a), but then ALC acts every generation as in type (b) until the population size reaches the trapping region. See the blue triangles in Fig. 6. In some sense, this initial transient has two 'sub-transients'. It corresponds to type (c) in Corollary 3).

We have detected that there exists an upper bound for the number of interventions during the initial transients (see Corollary 3 in Appendix A). This gives us an estimate of how long the initial transient might possibly last. We also find that the upper bound depends on the ALC intensity: the higher the ALC intensity the greater the upper bound for the interventions. Moreover, the maximum population sizes decrease in time during the initial transient with consecutive ALC interventions (i.e. in type (b) and after the first sub-transient in type (c)). Therefore, applying ALC with very high control intensities makes it more likely that there are relatively long initial transients.

5.2. Effort

We have seen that the initial transients can be substantial in terms of both length and number of interventions. This raises the

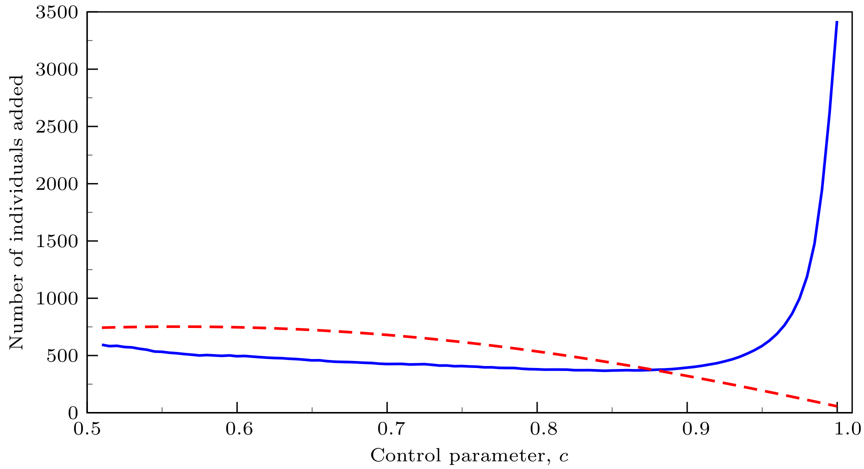

Fig. 7. Expected value of the effort of applying ALC (blue line) and LC (red dashed line) over the first 50 generations. Observe that, for ALC, the effort increases when c is greater than approximately 0.85 and blows up near the maximum ALC intensity $c=1$. Also observe that for high ALC intensities (greater than approximately 0.87) the effort is smaller for LC than for ALC. In all cases f is the Ricker map with $K=60$ and $r=3$. Initial population sizes are uniformly distributed in the interval $[0, f(d)]$. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

question how the initial transients can affect the effort of applying ALC, measured as the total number of individuals added during a certain number of generations. We notice that such an effort was already calculated for ALC in Sah et al. (2013, their Fig. 3c) and for a pure limiter control (LC) strategy in Hilker and Westerhoff (2005), but both papers considered the asymptotic effort with transient cut off.

Here, we consider the (transient) effort by taking into account initial transients. We numerically approximate the expected value of the effort over a time period of 50 generations, as a function of the ALC intensity (blue line in Fig. 7). Moreover, for the sake of comparison, we also approximate such an effort for the limiter control strategy, in which the limiter is not adaptive but constant (see red dashed line in Fig. 7). For this, we have fixed the limiter as $c \cdot A_T$, since this value asymptotically yields the same reduction of the fluctuation range for both control strategies. Therefore, the population controlled by LC follows the equation $x_{t+1} = \max\{f(x_t), c \cdot A_T\}$.

While the effort of applying ALC tends to decrease for intermediate values of the control parameter, it increases sharply for larger ALC intensities and blows up near the maximum ALC intensity. This is backed by our previous finding that the maximum length of the transients with possibly costly interventions increases with c. Hence, the controller may be in a dilemma. On the one hand, large control parameters reduce the fluctuation range significantly. On the other hand, they are also likely to create costly initial transients.

The (transient) effort curve in Fig. 7 is very different from the asymptotic effort calculated by Sah et al. (2013). They found that the asymptotic effort decreases to 0 when the ALC intensity approaches its maximum value. Hence, finite-time considerations may change the conclusions from effort analyses drastically. It seems important not to neglect the impact of initial transients.

Interestingly, the effort of the pure LC strategy is greater than the effort of ALC for intermediate to large values of the control parameter. But for very large control intensities, LC is less costly, even when achieving a similar reduction of the fluctuation range. Therefore, the initial transients may be less costly when a fixed limiter is employed instead of an adaptive limiter. This suggests that in some cases using a mixed strategy could be a more effective way of applying limiter control with high control intensities (e.g. if we need to achieve a big reduction in the fluctuation range). First, a pure limiter control can be applied for avoiding the costly initial transients, and afterwards we switch to adaptive limiter control.

5.3. Asymptotic frequency of interventions

Let us consider a scenario in which having access to individuals is not difficult, but implementing the intervention is very costly logistically, for example because the habitat of the population is remote and difficult to reach. Clearly, in such a scenario it would be desirable to maintain the number of interventions as low as possible to reduce the cost of the control. The previous section informed us about the frequency of interventions during initial transients. Here, we complete such information with a result about the asymptotic frequency of interventions inside the trapping region.

Proposition 1. *Assume that conditions of Theorem 1 hold and that, in addition, the following inequality holds*

$$c \cdot f(c \cdot A_T) < A_T. \tag{12}$$

Then ALC never acts consecutively if the population size is inside the trapping region (9).

The proof of Proposition 1 is in Appendix A. Proposition 1 guarantees that, after augmenting the population in one generation, the next generation will not be affected by the control if Condition (12) holds. Hence, there is at least one generation without intervention before the next intervention takes place. In particular, over a period of N generations, there are at most $\lfloor N/2 \rfloor$ interventions, inside the trapping region.

Condition (12) depends on the control intensity and the parametrization of the production function f. Fig. 8a shows the number of consecutive ALC interventions as a function of the control intensity and the growth parameter of the Ricker map. The simulations confirm that no consecutive interventions are required if Condition (12) holds. Moreover, this condition is sharp for small to intermediate control intensities.

Fig. 8b shows the total number of interventions (which can include consecutive interventions). It appears that it is generally somewhat advantageous to be in the parameter region enclosed by Conditions (12) and (8) of Theorem 1, the latter of which gives a lower bound for the ALC intensity to reduce the fluctuation range. For example, consider a fixed $r=3$ and vary c between 0.4 and 0.6 (following the upper horizontal white line). Then the number of interventions changes in a smooth way. But if we fix $r=3.5$ and vary c in the same interval (following the upper horizontal white line), the number of intervention changes abruptly and increases drastically. This happens when crossing the curve representing Condition (12).

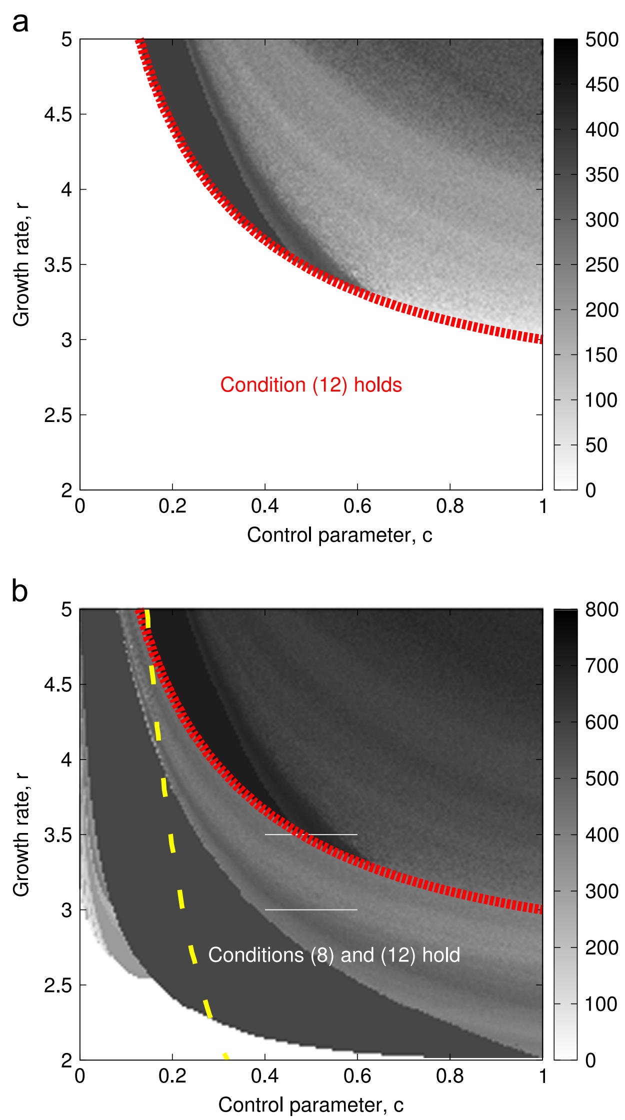

Fig. 8. Contour plots of (a) the number of consecutive interventions and (b) the total number of interventions as functions of the growth parameter and the ALC intensity using a grey scale. White means zero interventions and black corresponds to the maximum value found in each case, so intervention frequencies are higher in darker than in lighter areas. The curves enclose the region where Condition (12) in Proposition 1 (short red dashes) and Condition (8) of Theorem 1 (long yellow dashes) hold. In both cases $f(x) = x\exp(3(1-x/60))$, the initial condition was chosen as a pseudo-random number in the interval $[0, f(d)]$, and we considered a total of 1000 time steps with transients excluded. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)

6. Discussion

Adaptive limiter control is one of the few chaos control methods in population biology that have been tested experimentally (Sah et al., 2013). In this paper, we provide a rigorous theoretical foundation for the stabilizing effect of ALC. Moreover, we provide a range of analytical insights that have very practical relevance: how to choose the control intensity in order to achieve different types of desired outcomes; how to plan ahead and expect the next intervention; and the efficiency of control in terms of effort and intervention frequency.

Sah et al. (2013) pointed out that one of the main characteristics of ALC is that for enhancing constancy stability no information about parameters like the growth rate or carrying capacity are needed, as long as the control intensity is not too small. In practice, however, it is difficult to judge what this means exactly and how the control intensity has to be chosen. In this paper, we have quantified this critical control intensity by finding an analytical expression of its lower bound (see Condition (10)). This expression clearly reveals that the effectiveness of ALC does depend on the model parameterization. However, we remark that the corresponding maps can often be easily estimated from time series data (e.g. Rinaldi et al., 2001). Since the activation threshold is also a function of model parameters, it can be approximated in a similar way.

In this paper, we have considered deterministic models of population dynamics, but real populations are of course exposed to various sources of stochasticity. Clearly, in stochastic systems exceeding the activation threshold does not necessarily imply an ALC intervention in the next generation. Similarly, staying below the activation threshold does not imply a guarantee that there will be no need for an ALC intervention in the next generation. However, the activation threshold still remains useful as a signpost for potential future control actions, even if it has to be understood probabilistically.

The presence of noise can be critically important if there is bistability in the dynamics. This is caused by the ALCb strategy, where demographic and environmental stochasticity can induce a switching between alternative attractors. One of the attractors corresponds to the stabilized regime, whereas the other one can considerably increase instability and extinction risk.

6.1. *When ALC is effective*

The concept of constancy stability describes that the population size remains essentially unchanged (Grimm and Wissel, 1997). As a measure of such stability we have considered the fluctuation range, that is the extent between minimum and maximum of population sizes that oscillate over time. The smaller the fluctuation range the more stable we consider the population to be. Theorem 1 guarantees that, for sufficiently large control intensities, the fluctuation range decreases if the control intensity is increased. Therefore, it provides a rigorous analytical basis for the stabilizing effect of ALC and thus offers a theoretical explanation for the reduction in fluctuation range observed in Sah et al. (2013).

There are two caveats, however. Firstly, there is a lower bound on the control intensity. That is, Theorem 1 only holds (and ALC is therefore guaranteed to be effective) for sufficiently large control parameters. If this lower bound is surpassed, the more effective the ALC is the larger the control intensity.

The second caveat concerns a different measure of stability. If we consider the fluctuation index rather than the fluctuation range, then ALC may actually further destabilize the population as observed by Sah et al. (2013). That is, ALC may not only be ineffective, but actually counter-productive. Again, this happens for smaller values of the control parameter (see Fig. 4b).

6.2. *Cost of control*

The above considerations suggest to choose a sufficiently large control intensity. The drawback, however, is that the costs associated with such control intensities may be considerable. The effort during the initial transients is very sensitive to the control intensity and tends to explode for very large control parameters (see Fig. 7). Also, the asymptotic number of consecutive interventions rises sharply once an upper bound of the control parameter is exceeded (see Fig. 8a).

Our analytical results also reveal some properties that appear useful from a practical point of view. First of all, there is an activation threshold, which the population size has to surpass to activate the control in the next generation (Corollary 2). This property can be used to plan ahead in intervention programs.

Furthermore, we have shown that, under easy-to-check conditions, control interventions never occur in two consecutive generations inside the trapping region (Proposition 1), thus informing intervention programs about the maximum frequency of perturbations required. These are all very interesting properties, none of which was known before, however.

6.3. Transient effects

Transient effects are often neglected in modelling, but they may be actually as important as or even more relevant than the asymptotic dynamics, because the latter may never be reached in reality (Hastings, 2004). In this paper, we have identified three different types of initial transients when applying ALC. They may not only last over a long period of time, but they can also come with a significant number of interventions and require a large effort.

6.4. Determining the control intensity

Theorem 1 informs us how to choose the control intensity. If we want to reduce the population fluctuations to a certain magnitude, it gives us the critical value of the ALC intensity to achieve this desired outcome. This is an advantageous property of a control strategy, and is shared, for instance, by the strategies of constant feedback (Gueron, 1998; Wieland, 2002), proportional feedback (Liz, 2010) and target-oriented control (Franco and Liz, 2013).

In general, chaos control methods aim to stabilize chaotic oscillations, no matter if its in form of a stable equilibrium point or a stable periodic attractor (Schuster and Wiley, 1999). However, it is often implicitly understood that the aim is a stable equilibrium point or cycle (Silvert, 1978; Liz, 2010; Braverman and Liz, 2012). This cannot be achieved by ALC, because it is not able to create an asymptotically stable population (Proposition 2).

In many situations the main aim of control is not stabilization, but to steer the population size to a certain desirable range (Hilker and Westerhoff, 2007b; Dattani et al., 2011) or to prevent the population from reaching an undesirable range (Hilker and Westerhoff, 2007a). There is actually a type of strategy called chaos anti-control, because it avoids undesirable outcomes while maintaining chaos, which may have some beneficial aspects in itself (Yang et al., 1995).

Similar outcomes can be accomplished by ALC. This has been alluded to by Sah et al. (2013, Section 2) in a verbal description, but it remained unclear whether and how this could be achieved in practice. In particular, it was an open question how to choose the control parameter if the aim is to steer the population to a certain part of the attractor. In this paper, we provide not only a rigorous analysis of the dynamics, but also explain in detail how ALC can be used for different aims. In fact, we describe a recipe how to choose the control intensity if we want to avoid small population sizes (close to extinction); prevent large population sizes (corresponding to outbreaks); or restrict the population sizes in a range of certain diameter (see the examples in Fig. 5).

Note that ALC prescribes a perturbation to the population when a crash has already happened. This is a different approach to the strategy in Hilker and Westerhoff (2007a), which uses available time series data to prevent a crash happening in the first place.

The recipes for choosing appropriate control intensities complement the (i) lower and (ii) upper bounds, which arise from ALC being (i) effective (see Theorem 1) and (ii) not too costly in the long-term (see Proposition 1) and in the short-term (see Fig. 7).

6.5. Global behaviour

We have shown that the trapping region imposed by ALC is globally asymptotically stable. That is, all (rather than just a few or nearby) initial conditions will end up in the trapping region. This is a useful property for a control strategy and is shared by, for instance, proportional feedback (Liz, 2010) and prediction-based control (Liz and Franco , 2010). However, there are also strategies that are only locally stable (e.g. constant feedback control; Gueron, 1998), or that can be either locally or globally stable depending on parameter values (e.g. targetoriented control; Dattani et al., 2011; Franco and Liz, 2013).

6.6. Conclusion

We have provided a mathematically rigorous basis for the stabilizing effect of ALC. This control method comes with a number of useful properties, such as inducing global stability or having the capability to steer the system to (or away from) certain (un-)desirable states. In fact, we have shown how to calculate the control intensity required for such behaviour. On the downside, there are a few caveats. For small values of the control parameter, ALC may not be effective (or even counter-productive if we consider a different stability measure). And for very large values of the control parameter, ALC can be costly in terms of interventions and effort. Hence, intermediate control intensities appear to be generally a ‘safe’ choice. However, there may different priorities depending on the context and specific aims of the control. Our analytical results provide some guidance how to choose to the control intensity depending on different situations. Note that we also take into account transient effects and classify three different types of initial transients.

Acknowledgements

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Appendix A. Proofs of the analytical results

Here we prove the results stated along the paper. To make this appendix self-contained, we recall that we are considering the following conditions:

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

Additionally, we recall that Eq. (1) controlled by ALC follows a dynamical system determined by the system of difference equations

$$\begin{cases} b_{t+1}=f(a_t), \\ a_{t+1}=\max\{f(a_t),c\cdot a_t\}, \end{cases} \tag{A.1}$$

where $c\in(0,1)$ is the ALC intensity.

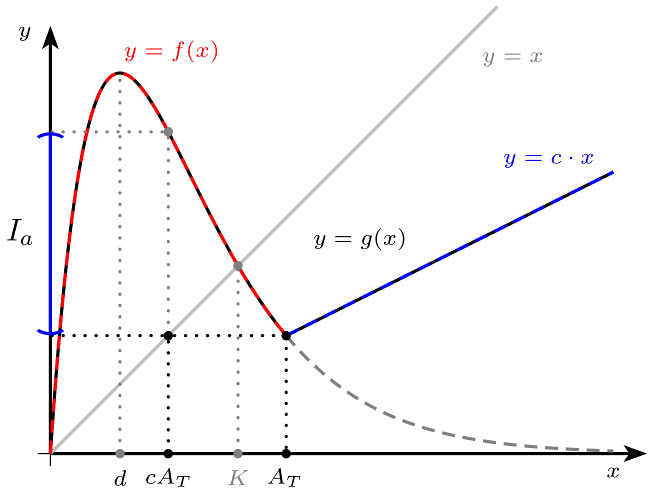

Fig. A1. Graph of the map g defining the dynamics of the population sizes after ALC. For population sizes lower than or equal to A_T, it coincides with the graph of the uncontrolled map f; and for population sizes greater than A_T, it coincides with the straight line $c \cdot x$.

Our first result shows that ALC cannot create an asymptotically stable equilibrium.

Proposition 2. *Assume that* (*C1*) *and* (*C2*) *hold and that the fixed point K is unstable for the uncontrolled system* (1). *Then, independent of the magnitude of ALC,* $c \in (0,1)$, *the controlled system* (A.1) *has no asymptotically stable equilibria.*

Proof. Clearly, $(x,y) \in [0,b] \times [0,b]$ is an equilibrium of system (A.1) if and only if it satisfies

$$\begin{cases} x = f(y), \\ y = \max\{f(y), c \cdot y\}. \end{cases}$$

By Condition (C2), the controlled system has at most two equilibria, $(0,0)$ and (K,K).

Next, we must show that no equilibrium is asymptotically stable. The trivial equilibrium is not asymptotically stable. Let (x,y) be in the neighbourhood $[0,K) \times [0,K)$ of $(0,0)$. Since by Condition (C2) we have $f(y) > y$ for $0 < y < K$, the second equation of system (A.1) is given by the equation

$$a_{t+1} = f(a_t) \tag{A.2}$$

in $[0,K) \times [0,K)$. And conditions (C1) and (C2) imply that the trivial equilibrium is unstable for Eq. (A.2).

Now, let us consider the nontrivial equilibrium (K,K). By the continuity of f, it is possible to find a small enough neighbourhood, $\mathcal{N}$, of K such that

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

for $(x,y) \in \mathcal{N} \times \mathcal{N}$. Therefore, the second equation of system (A.1) is given by Eq. (A.2) in $\mathcal{N} \times \mathcal{N}$. Since we are assuming that K is unstable for such an equation, we obtain that (K,K) is unstable for the controlled system (A.1). □

A consequence of the following results is that the graph of the map defining the dynamics of the population under ALC has to be similar to the one plotted in Fig. A1. In this figure, we have included elements that could help the reader to visually understand the previous and the following proofs.

We define the activation threshold A_T as the positive solution of the equation

$$c \cdot x - f(x) = 0. \tag{A.3}$$

The following results show that A_T is well defined under general conditions.

Lemma 1. *Assume that* (*C1*)–(*C3*) *hold. If* $b = +\infty$ *or* $f(b) = 0$, *then Eq.* (A.3) *has a unique positive solution for any* $c \in (0,1)$.

Proof. Firstly, we note that Eq. (A.3) has no solutions in the interval $(0,K)$ by Condition (C2). Next, we have that

$$c \cdot K - f(K) = c \cdot K - K = (c-1) \cdot K < 0.$$

Additionally, the assumption that $b = +\infty$ or $f(b) = 0$ and Condition (C3) imply

$$\lim_{x \to b} c \cdot x - f(x) > 0.$$

Therefore, the existence of A_T follows by Bolzano's Theorem and its uniqueness is a consequence of Condition (C3). □

Lemma 2. *Assume that* (*C1*)–(*C3*) *hold. If* $b < \infty$ *and* $f(b) > 0$, *then Eq.* (A.3) *has a unique positive solution if and only if* $c \in (f(b)/b, 1)$.

Moreover, applying ALC with an intensity smaller than $f(b)/b$ *does not modify the uncontrolled system* (1).

Proof. The proof of the first affirmation is similar to the proof of the previous result, so we omit it.

The second affirmation follows by noting that, if $0 < c < f(b)/b$, the graph of f is above the straight line $y = c \cdot x$, which delimits the region where ALC does not modify the population. □

Using the activation threshold we can write the map defining the dynamics of ALC in the following way.

Corollary 1. *Assume that* (*C1*)–(*C3*) *hold and* $c \in (0,1)$ *is such that* A_T *exists. Then the map describing the dynamics of* a_t,

$$g(x) = \max\{f(x), c \cdot x\},$$

can be rewritten as

$$g(x) = \begin{cases} f(x), & x \le A_T, \\ c \cdot x, & x > A_T. \end{cases} \tag{A.4}$$

The graph of the map g appears in Fig. A1.

A direct consequence of the previous corollary is the following result, which establishes that for the maps satisfying (C1)–(C3) the activation threshold has the role described by its name.

Corollary 2. *Assume that* (*C1*)–(*C3*) *hold and* $c \in (0,1)$ *is such that* A_T *exists. Then ALC acts in generation t if and only if* $a_{t-1} > A_T$.

We are in the position to prove our main analytical results, Theorem 1 and Proposition 1. We restate then here for completeness.

Theorem 2. *Assume that* (*C1*)–(*C3*) *hold. Additionally, suppose that for a fixed* $c \in (0,1)$ *the activation threshold* A_T *exists and satisfies the inequality*

$$d \le c \cdot A_T,$$

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

Then, applying ALC with intensity c confines the population sizes a_t *and* b_t *into the following intervals around the carrying capacity K*:

$$I_a := [c \cdot A_T, f(c \cdot A_T)] \quad \text{and} \quad I_b := f(I_a),$$

for any $x_0 \in (0,b)$.

Proof. Firstly, note that the interval

$$I_a = [c \cdot A_T, f(c \cdot A_T)]$$

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

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

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

Next, note that it is enough to show that the population size after ALC, a_t, is confined to the interval I_a, because $b_t = f(a_t)$ and $I_b = f(I_a)$. We consider several cases depending on the relative position of a_0, the initial population size after ALC, with respect to the activation threshold.

1. Firstly, we assume that $a_0 \in [c \cdot A_T, A_T]$. Using the definition of A_T and the monotonicity of f on $[c \cdot A_T, A_T] \subset [d, b]$, we have that

   $$f(c \cdot A_T) \geq a_1 = f(a_0) = \max\{f(a_0), c \cdot a_0\} \geq f(A_T) = c \cdot A_T.$$

   Therefore, the iterate a_1 belongs to I_a.
2. Next, we assume that $a_0 \in (A_T, b)$. We are going to show that there exists a natural number n such that $a_n \in [c \cdot A_T, A_T]$, and thus $a_{n+1} \in I_a$ by the previous case.
   Suppose that $a_t \notin [c \cdot A_T, A_T]$ for all t. We have that $c \cdot A_T \leq a_1 = c \cdot a_0$, which together with $a_1 \notin [c \cdot A_T, A_T]$ implies that $a_1 \in (A_T, b)$. The same argument shows that if $a_k \in (A_T, b)$, then $a_{k+1} \in (A_T, b)$. By induction, we have that

   $$a_t \in (A_T, b) \tag{A.5}$$

   for all t. Moreover, we obtain that $a_t = c^t \cdot a_0$, which implies

   $$a_t \to 0 \tag{A.6}$$

   as t tends to infinity. Since (A.5) and (A.6) are contradictory, we obtain, as we desire, that there exists n such that $a_n \in [c \cdot A_T, A_T]$. And thus by the first case, $a_{n+1} \in I_a$.
3. Next, we assume that $a_0 \in [d, c \cdot A_T)$. Then, by the monotonicity of f, we have $c \cdot A_T \leq K \leq f(c \cdot A_T) \leq a_1 = f(a_0) < b$. And this case can be reduced to one of the previous two cases.
4. Finally, we assume that $a_0 \in (0, d)$. We are going to show that there exists a natural number n such that $a_n \in [d, b)$, and therefore this case can be reduced to one of the previous three cases.
   Suppose that $a_t \in (0, d)$ for all t. Using Condition (C2) and reasoning by induction, one has that the sequence a_t is increasing and bounded. Therefore, it is convergent to $l \in (0, d]$. On the other hand, the continuity of f, and the fact that in this case $a_{t+1} = f(a_t) = \max\{f(a_t), c \cdot a_t\}$, implies $f(l) = l$, which contradicts that the only fixed points of f are 0 and $K > d$. Therefore, our supposition is false and there exists an n such that $a_n \in [d, b)$.

Therefore, we have that for any positive initial condition the solution enters the trapping region $I_a = [c \cdot A_T, f(c \cdot A_T)]$ in a finite number of time steps. Finally, we show that I_a is invariant under ALC, and thus the solution remains in I_a once it enters this interval. If $f(c \cdot A_T) \leq A_T$ and $a_t \in I_a$, then $a_{t+1} \subset I_a$ by the previous case 1; for the same reason, if $f(c \cdot A_T) > A_T$ and $a_t \in I_a$ with $a_t \leq A_T$, then $a_{t+1} \subset I_a$; and if $f(c \cdot A_T) > A_T$ and $a_t \in I_a$ with $a_t > A_T$, then, by Corollary 1, we have $a_{t+1} = c \cdot a_t \in I_a$. □

Proposition 3. *Assume that conditions of Theorem 2 hold and that, in addition, the following inequality holds*

$$c \cdot f(c \cdot A_T) < A_T. \tag{A.7}$$

Then ALC never acts consecutively if the population size is inside the trapping region (9).

Proof. First, we point out that by Corollary 2 the necessary condition for ALC to act consecutively in generations $t+1$ and $t+2$ is that

$$a_t > A_T \quad \text{and} \quad a_{t+1} > A_T.$$

Now suppose that $a_t > A_T$. We are going to prove that under Condition (A.7) inequality $a_{t+1} \leq A_T$ always holds.

By Corollary 1 we have that $a_{t+1} = c \cdot a_t$ and since $a_t \in I_a = [c \cdot A_T, f(c \cdot A_T)]$, we obtain that

$$a_{t+1} \leq c \cdot f(c \cdot A_T).$$

And Condition (A.7) imposes that a_{t+1} cannot be greater than A_T. □

The following result about the possible initial transients of ALC is a direct consequence of the proof of Theorem 2 and the definition of ALC.

Corollary 3. *Assume that (C1)–(C3) hold and $c \in (0, 1)$ is such that A_T exists. If the positive initial population size is outside the trapping region defined in Theorem 1, then only one of the following initial transients before reaching the trapping region is possible*:

(a) *There is no control until reaching the trapping region. The population sizes b_t and a_t coincide and increase during this transient.*
(b) *ALC acts consecutively until reaching the trapping region. The population size b_t increases and the population size a_t decreases. Moreover, the length of this initial transient is at most N with N being the smallest natural number satisfying* $A_T \leq c^N \cdot f(d)$.
(c) *There is a mixture of (a) and (b) with two sub-transients. First, as in (a), there is a certain number of time steps without having to apply ALC, in which the population increases but does not enter the trapping region. This sub-transient finishes when a_t surpasses the activation threshold A_T. After that, and as in (b), ALC acts consecutively until reaching the trapping region. The maximum length of the second sub-transient is the same as in case (b).*

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