



On the dynamics of a generalized predator–prey system with Z-type control



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ABSTRACT

We apply the Z-control approach to a generalized predator–prey system and consider the specific case of indirect control of the prey population. We derive the associated Z-controlled model and investigate its properties from the point of view of the dynamical systems theory. The key role of the design parameter λ for the successful application of the method is stressed and related to specific dynamical properties of the Z-controlled model. Critical values of the design parameter are also found, delimiting the λ -range for the effectiveness of the Z-method. Analytical results are then numerically validated by the means of two ecological models: the classical Lotka–Volterra model and a model related to a case study of the wolf–wild boar dynamics in the Alta Murgia National Park. Investigations on these models also highlight how the Z-control method acts in respect to different dynamical regimes of the uncontrolled model.

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1. Introduction

In population dynamics, a large variety of mathematical models [23,32] have been developed to capture – at least qualitatively – the essential features of many complex phenomena involved in community ecology. Population dynamics models can play a role in the ecosystem services management perspective [15,25]. The most popular current definition of ecosystem services (ES) is the functions and products of ecosystems that benefit humans, or yield welfare to society [1,27]. An ecological system can provide different ecosystem services spanning from regulatory or provisional to cultural ones, as defined e.g., by the Common International Classification of Ecosystem Services (CICES) [19]. In many protected areas, according to their regulation framework, the exploitation of such services produces a disturbance factor which demands for counteractions in order to guarantee the equilibria of the areas relevant ecological systems. A clear example is the introduction of alien species, or a massive introduction of particular species, even if autochthon, for leisure hunting/fishing purposes. These activities, having a heavy impact on most fragile ecosystems, have been permitted in the past, or even currently, in some protected areas. The challenge the managing authority of the protected areas has to face, is how to make the fruition of the natural capital

sustainable, by balancing the immediate benefits it can provide with the conservation targets to make the natural capital still available for future generations. That requires a number of actions to be put in place to obtain, preserve and enforce equilibrium states for ecosystems. The dynamics of a given predator–prey pair influences and is influenced by the ecosystem it is embedded in. Since it constitutes a segment of a food chain, the system equilibria and their stability is often relevant for the preservation of the whole chain, especially if one of the species in the pair is a keystone species, i.e. a species whose extinction may generate a heavy and unpredictable effect on the environment. The main goal of the population dynamics modeling is to describe the changes in populations size and composition and, at the same time, to study those biological or environmental factors that can influence these changes. Such factors are birth and death rates, immigration, emigration and, since ecological communities are often made up by a large number of species, interspecific interactions such as competition and predation.

Since most of the interactions among species generally involve nonlinear effects of the density of one species on the per capita growth rate of other species [2], a large class of models in population dynamics can be described as nonlinear dynamical systems. As a consequence, dynamical systems theory [17,36] has been extensively used to investigate such systems and has become an important tool for addressing many fundamental questions in population dynamics, [21,30,39].

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One of the main advantages of gaining insight into the dynamics of a certain dynamical system, is the possibility to provide qualitative indications on the mechanisms that are responsible of specific system behaviors, hence suggesting possible management strategies to avoid undesirable situations. Typical examples in the ecological context are the capability to prevent species from extinction or to avoid periodic or chaotic regimes since dramatic oscillations can drive the ecological system towards extinction.

On this line many studies have been concerned with the problem to induce, by the means of ‘controls’, suitable changes into the dynamics of Lotka–Volterra type models [29,41], which are still the most commonly used theoretical framework for modeling multispecies interactions. For example, in [33] and [16] a speed gradient method of adaptive control of oscillations was used to control the populations of a multispecies Lotka–Volterra system; in [14] a general approach for the control of uncertain nonlinear dynamical systems – known as induced internal feedback – was applied to a class of Lotka–Volterra systems; in [31], the classical Lotka–Volterra model was used as benchmark to compare different approaches for the control of nonlinear dynamical systems as the static sliding-mode approach that was applied for nonlinear plant control [22] or the method based on the notions of system immersion and manifold invariance that was presented in [3] to design asymptotically stabilizing and adaptive control procedures for nonlinear systems. Meza et al. [31] also proposed a control method for Lotka–Volterra systems based on the application of the control Lyapunov functions [35], of the backstepping idea [34] and on the concept of real and virtual equilibria [10]. In [12] an impulsive control law was also derived for multiple Lotka–Volterra systems.

Within the framework of the control procedures, a neural dynamic approach – the Z-type dynamic method [42] – has been proposed to solve dynamic problems [18,28,44]. The Z-type dynamic method is an error-based dynamic approach in which the key element is the design formula which ensures that each element of the error function converges to zero exponentially. Since the Z-type control laws have exponential convergence performances, the convergence time can be estimated and populations will converge to the desired state in a fast or predefined rate. This feature enables the Z-type dynamic method to be particularly efficient for specific time limited applications.

In [43], the Z-type dynamic method has been applied to the classical Lotka–Volterra predator–prey model to prevent species from extinction and to promote ecological coexistence. Two different situations have been considered: (i) the case of direct control for both the species, namely when exogenous measures are applied to both predator and prey for the simultaneous control of their dynamics; (ii) the case of indirect control of predator (or prey) population, namely when the control measure is only applied to one species but it is the other species that needs to be controlled. In [43], the theoretical analysis of the convergence performance of the Z-type controller groups has been performed for both the direct and indirect control problems and then confirmed by numerical simulations.

In this paper, we apply the Z-type control to a generalized Lotka–Volterra model expressed as

$$\begin{aligned}\dot{n} &= n[H(n) - \beta p] \\ \dot{p} &= pF(n)\end{aligned}\quad (1)$$

where $n = n(t)$ and $p = p(t)$ denote the populations of prey and predator species; the coupling parameter $\beta > 0$ represents the predation coefficient; $H(n)$ is a positive function of n at least in an interval. The Z-type control laws have the effect to change the dynamics of the *uncontrolled* model (1) – that may admit the predator–prey extinction equilibrium $P_0 = (0, 0)$, the predator’s extinction equilibria $P_i = (n_i, 0)$, and the coexistence equilibrium $P = (n^*, p^*)$ – as to make the prey and predator populations con-

verge exponentially to a desired state $P^* = (n_d, p_d)$. Our aim is to investigate the dynamical properties of the resulting Z-controlled predator–prey system and to show that the success as well as the failure of the Z-type approach can be related to specific dynamical properties (i.e. existence, uniqueness and stability of the coexistence equilibrium; positiveness of solutions, etc) of the underlying Z-controlled model.

In the following, we show that a population model with a Z-control can have two positive effects on the dynamics, which turn out to be interesting in the perspective of ecosystem services management. The first one is the stability: for some population models, the introduction of a control can lead to the same equilibria of the original uncontrolled model, but with additional stability properties. A further advantage is the capability to generate new, stable equilibria, by construction. That might be interesting by an ecological point of view in the case the new equilibria turn out to be more robust with respect to external, uncontrolled, disturbance factors.

The paper is organized as follows. In Section 2, we briefly recall the theoretical framework of the Z-control approach and derive the generalized predator–prey model (1) in the specific case of indirect control of the prey population. In Section 3, the resulting Z-controlled model is analyzed in terms of its equilibria, stability properties and positiveness of solutions. In Section 4, the effectiveness of the method is then explicitly tested on two specific predator–prey systems: the (more theoretical) classical Lotka–Volterra model and the (more realistic) aggregated model of the wolf–wild boar dynamics. In both these cases, we provide constraints on the design parameter λ ensuring the Z-control to be successfully applied. In Section 5, concluding remarks close the paper.

2. Methods

2.1. The basic idea of the Z-type control approach

In this section, we briefly recall the basic idea of the Z-type control method which will be the guide for the following Sections. We refer to [42–44] for a detailed description of the approach. Given a certain dynamical system, the goal of the Z-control problem is to design an analytical expression for the system input, say $u(t)$, so that the actual system output $n(t)$ is forced to achieve a desired output $n_d(t)$. More precisely the Z-control is successful if the error between the actual output of the system and its desired state approaches zero, namely if

$$e(t) = n(t) - n_d(t) \rightarrow 0.$$

This goal is certainly achieved by forcing the error function $e(t)$ to converge to zero exponentially which is obtained by requiring that the error function verifies the differential equation

$$\dot{e}(t) = -\lambda e(t). \quad (2)$$

Eq. (2) is also named *design formula* and the strictly positive parameter λ is the *design parameter* which indicates the convergence rate. The control procedure by the Z-type dynamic method is hence based on the following two steps: (i) define the error function(s); (ii) use the design formula whenever necessary to obtain an explicit expression for the input $u(t)$. These two steps will be concretely applied in the next section for the indirect control of the prey population of model (1).

2.2. The Z-controlled model

By pursuing an indirect control on the prey population, model (1) becomes:

$$\begin{aligned}\dot{n} &= n[H(n) - \beta p] \\ \dot{p} &= p[F(n) - u_{pred}]\end{aligned}\quad (3)$$

where $u_{pred} = u_{pred}(t)$ denotes the indirect control variable for the prey population, acting on the predator dynamics, that can be both a positive and a negative quantity, [43]. Following the key steps indicated in Section 2.1, we apply the indirect Z-type control procedure. Let $n_d = n_d(t)$ the desired state for the prey population and define the first error function as $v_1 = n - n_d$. Suppose that v_1 decays exponentially in time, namely

$$\dot{v}_1 + \lambda v_1 = 0 \quad (4)$$

with $\lambda > 0$. Again, let $v_2 = \dot{v}_1 + \lambda v_1$ and suppose that v_2 behaves in time as v_1 , i.e. $\dot{v}_2 = -\lambda v_2$. Therefore we have

$$\dot{v}_2 + \lambda v_2 = 0.$$

From the definition of v_2 and from (4) it follows that

$$\ddot{v}_1 + 2\lambda \dot{v}_1 + \lambda^2 v_1 = 0. \quad (5)$$

Let us rewrite the above formula in terms of prey and predator populations. Firstly,

$$J(n, p) = \begin{pmatrix} H(n) - \beta p + n \frac{\partial H}{\partial n} & -\beta n \\ \frac{1}{\beta} [2(H(n) - \beta p + \lambda) \frac{\partial H}{\partial n} + \frac{\partial}{\partial n} \dot{H}(n)] + \frac{\lambda^2 n_d}{\beta n^2} & -2(H(n) - \beta p + \lambda) + \frac{1}{\beta} \frac{\partial}{\partial p} \dot{H}(n) \end{pmatrix}.$$

$$\dot{v}_1 = n[H(n) - \beta p] - \dot{n}_d; \quad (6)$$

then,

$$\dot{v}_1 = n[H(n) - \beta p]^2 + n\dot{H}(n) - \beta n p F(n) + \beta n p u_{pred} - \ddot{n}_d. \quad (7)$$

Plugging (6) and (7) in (5), and solving for u_{pred} we get

$$u_{pred} = F(n) - \frac{f(t; n, p)}{p(t)} \quad (8)$$

where

$$f(t; n, p) = \frac{n[(H(n) - \beta p + \lambda)^2 + \dot{H}(n)] - (\ddot{n}_d + 2\lambda \dot{n}_d + \lambda^2 n_d)}{\beta n}. \quad (9)$$

From

$$\dot{H}(n) = \frac{\partial H}{\partial n} \dot{n} = n \frac{\partial H}{\partial n} (H(n) - \beta p), \quad (10)$$

it follows that (9) can be written as

$$f(t; n, p) = \frac{n \left[(H(n) - \beta p)^2 + \left(2\lambda + n \frac{\partial H}{\partial n} \right) (H(n) - \beta p) + \lambda^2 \right] - (\ddot{n}_d + 2\lambda \dot{n}_d + \lambda^2 n_d)}{\beta n}. \quad (11)$$

The expression of u_{pred} in (8) allows to rewrite the modified system (3) as

$$\begin{aligned}\dot{n} &= n[H(n) - \beta p] \\ \dot{p} &= f(t; n, p)\end{aligned}\quad (12)$$

In the following we refer to model (12) as to the Z-controlled system and specifically focus on the case $n_d(t) = n_d$, with n_d strictly positive constant.

3. Results

3.1. Equilibria and local stability properties

We search for the equilibria of the Z-controlled model (12) and, by using linear stability analysis, we establish the related stability

properties. The following result explains – in terms of the dynamical properties of the Z-controlled model (12) – why the Z-control method ensures the system to achieve exponentially the desired state (n_d, p_d) .

Theorem 3.1. *The controlled equilibrium $P^* = (n_d, \frac{H(n_d)}{\beta})$, is the unique equilibrium of (12) and is locally asymptotically stable, i.e. it is a stable node.*

Proof. We start by observing that since $n_d(t) = n_d = \text{constant}$, in (11) $f(t; n, p)$ does not explicitly depend on time. Hence, the equilibria of model (12) are the solutions of the system:

$$\begin{aligned}n^*[H(n^*) - \beta p^*] &= 0 \\ f(n^*, p^*) &= 0\end{aligned}\quad (13)$$

where $f(n^*, p^*)$ is given by (11). Straightforward calculations allow hence to conclude that the couple $(n_d, \frac{H(n_d)}{\beta})$, is the unique solution of system (13). As far as the stability properties are concerned, we observe that the Jacobian matrix of the Z-controlled system (12), in correspondence of the generic constant desired prey state $n_d(t) = n_d > 0$, is given by:

By using (10), let us evaluate

$$\begin{aligned}\frac{\partial}{\partial n} \dot{H}(n) &= \frac{\partial^2 H}{\partial n^2} n(H(n) - \beta p) + \frac{\partial H}{\partial n} \left(H(n) - \beta p + n \frac{\partial H}{\partial n} \right) \\ \frac{\partial}{\partial p} \dot{H}(n) &= -\beta n \frac{\partial H}{\partial n}.\end{aligned}$$

The Jacobian matrix, evaluated at $P^* = (n_d, \frac{H(n_d)}{\beta})$, is given by

$$J(P^*) = \begin{pmatrix} n_d \frac{\partial H}{\partial n}(n_d) & -\beta n_d \\ \frac{1}{\beta} \left[2\lambda \frac{\partial H}{\partial n}(n_d) + \left(\frac{\partial H}{\partial n}(n_d) \right)^2 n_d \right] + \frac{\lambda^2}{\beta n_d} & -2\lambda - n_d \frac{\partial H}{\partial n}(n_d) \end{pmatrix}$$

It turns out that $\text{tr}(J(P^*)) = -2\lambda < 0$ and $\det(J(P^*)) = \lambda^2 > 0$. As a consequence, the characteristic equation $(\mu + \lambda)^2 = 0$ provides the two eigenvalues $\mu_{1/2} = -\lambda$ so that the controlled equilibrium $P^* = (n_d, \frac{H(n_d)}{\beta})$ is locally asymptotically stable and, more precisely, it is a stable node. $\square$

3.2. Positiveness of solutions

First observe that solving (5) with initial conditions in the interior of the first quadrant, i.e. $n_0 = n(0) > 0$ and $p_0 = p(0) > 0$, we obtain the exact solution for the prey dynamics:

$$n(t) = n_d(t) + c_1 e^{-\lambda t} - (c_2 - \lambda c_1) t e^{-\lambda t}, \quad (14)$$

where

$$c_1 = n_0 - n_d, \quad c_2 = n_0 (\beta p_0 - H_0), \quad (15)$$

and $H_0 = H(n_0)$. The following theorems provide conditions in order $n(t)$ to be positive for all $t \geq 0$.

Theorem 3.2. *Suppose $n_d(t) = n_d > 0$ for all $t \geq 0$. If $\beta p_0 - H_0 \leq 0$ or $\lambda \geq \beta p_0 - H_0 > 0$, then $n(t) > 0$ for all $t \geq 0$.*

Proof. By exploiting (14), we search for conditions which verify the following inequality:

$$n_d e^{\lambda t} \geq (c_2 - \lambda c_1) t - c_1. \quad (16)$$

Denote with $y(t) = n_d e^{\lambda t}$ and $z(t) = (c_2 - \lambda c_1) t - c_1$. Notice that $y(0) = n_d > n_d - n_0 = z(0)$; consequently, if the slope of $z(t)$ is lower than the value of the derivative $\dot{y}(0) = \lambda n_d$, i.e.

$$c_2 - \lambda c_1 - \lambda n_d = c_2 - \lambda n_0 \leq 0, \quad (17)$$

then inequality (16) holds true for $t \geq 0$ and $n(t)$ is strictly positive for all $t \geq 0$. By (15), it is easy to see that if $\beta p_0 - H_0 \leq 0$, then $c_2 \leq 0$ and the inequality (17) is verified for all values of $\lambda > 0$. On the contrary, if $\beta p_0 - H_0 > 0$, then the inequality (17) is verified provided that $\lambda \geq \frac{c_2}{n_0} = \beta p_0 - H_0$. $\square$

Theorem 3.3. Suppose $n_d(t) = n_d > 0$ for all $t \geq 0$ and $\beta p_0 - H_0 > 0$. If $0 < \lambda_T \leq \lambda < \beta p_0 - H_0$, where λ_T solves the non linear equation

$$\log\left(\frac{c_2 - \lambda_T c_1}{\lambda_T n_d}\right) - \frac{c_2}{c_2 - \lambda_T c_1} = 0,$$

then $n(t) \geq 0$ for all $t \geq 0$.

Proof. It is easy to see that, for values of $\lambda < \beta p_0 - H_0$, the inequality $\frac{c_2 - \lambda c_1}{\lambda n_d} > 1$ is verified and, consequently, there exists and it is positive the time

$$T = \frac{1}{\lambda} \log\left(\frac{c_2 - \lambda c_1}{\lambda n_d}\right)$$

where $\dot{y}(T) = \dot{z}(T)$. In order to keep, for all $t > 0$, the exponential function $y(t)$ above the straight line $z(t)$, the value of λ can be decreased until the value λ_T which corresponds to the case when $z(t)$ overlaps the tangent line to $y(t)$ at T where $y(T) = z(T)$. In this case, the value of λ_T solves the nonlinear equation

$$\log\left(\frac{c_2 - \lambda_T c_1}{\lambda_T n_d}\right) = \frac{c_2}{c_2 - \lambda_T c_1}$$

and the result follows. $\square$

In real applications, prey density values are often required to be bounded between a lower and upper bound. The following results provide conditions which guarantee $n(t) \in [A, K] \subset R_+$ for all t .

Theorem 3.4. Suppose $n_0, n_d \in [A, K] \subset R_+$ and

$$\begin{aligned} \lambda &> \frac{n_0(\beta p_0 - H_0)}{n_0 - A}, \quad \text{if } \beta p_0 - H_0 > 0 \\ \lambda &> -\frac{n_0(\beta p_0 - H_0)}{K - n_0}, \quad \text{if } \beta p_0 - H_0 < 0. \end{aligned} \quad (18)$$

then $n(t) \in [A, K]$ for all $t \geq 0$.

Proof. Set $y_A(t) = (n_d - A) e^{\lambda t}$, $y_K(t) = (n_d - K) e^{\lambda t}$, and $z(t) = -c_1 + (c_2 - \lambda c_1)t$. For assuring $n(t) \in (A, K)$, the following condition should be verified for all $t \geq 0$:

$$y_K(t) < z(t) < y_A(t). \quad (19)$$

We follow a similar reasoning to the one adopted for proving the prey positiveness in Theorem 3.2. Notice that $y_K(0) = n_d - K < n_d - n_0 = z(0) < n_d - A = y_A(0)$; consequently, if the slope of $z(t)$ is bounded between the values of the derivatives $\dot{y}_K(0) = \lambda(n_d - K)$, and $\dot{y}_A(0) = \lambda(n_d - A)$ i.e. if conditions

$$c_2 - \lambda(c_1 + n_d - A) = c_2 - \lambda(n_0 - A) < 0, \quad (20)$$

and

$$\lambda(c_1 + n_d - K) - c_2 = -c_2 - \lambda(K - n_0) < 0, \quad (21)$$

are both verified, then (19) is satisfied. We observe that condition (20) holds true if $c_2 < 0$ while it leads to the bound $\lambda > \frac{c_2}{n_0 - A}$ when $c_2 > 0$. Similarly, condition (21) is always verified when $c_2 > 0$ whereas it leads to the bound $\lambda > \frac{-c_2}{K - n_0}$ when $c_2 < 0$. Hence, bounds (18) can be set for λ accordingly to the sign of c_2 . $\square$

Theorem 3.5. Suppose $n_0, n_d \in [A, K] \subset R_+$ and

$$\begin{aligned} \lambda_{T_A} &\leq \lambda < \frac{n_0(\beta p_0 - H_0)}{n_0 - A}, \quad \text{if } \beta p_0 - H_0 > 0 \\ \lambda_{T_K} &\leq \lambda < -\frac{n_0(\beta p_0 - H_0)}{K - n_0}, \quad \text{if } \beta p_0 - H_0 < 0. \end{aligned} \quad (22)$$

where λ_{T_A} and λ_{T_K} solve the non linear equations

$$\log\left(\frac{c_2 - \lambda_{T_A} c_1}{\lambda_{T_A}(n_d - A)}\right) - \frac{c_2}{c_2 - \lambda_{T_A} c_1} = 0 \quad (23)$$

$$\log\left(\frac{c_2 - \lambda_{T_K} c_1}{\lambda_{T_K}(n_d - K)}\right) - \frac{c_2}{c_2 - \lambda_{T_K} c_1} = 0, \quad (24)$$

with $T_A, T_K \geq 0$ satisfying

$$(n_d - A) e^{\lambda_{T_A} T_A} = -c_1 + (c_2 - \lambda_{T_A} c_1) T_A,$$

$$(n_d - K) e^{\lambda_{T_K} T_K} = -c_1 + (c_2 - \lambda_{T_K} c_1) T_K,$$

then $n(t) \in [A, K]$ for all $t \geq 0$.

Proof. In case $\beta p_0 - H_0 > 0$, for values of $\lambda > \frac{n_0(\beta p_0 - H_0)}{n_0 - A}$ there exists and is positive the time T_A where $\dot{y}_A(T_A) = \dot{z}(T_A)$ i.e.

$$T_A = \frac{1}{\lambda} \log\left(\frac{c_2 - \lambda c_1}{\lambda(n_d - A)}\right);$$

similarly, in case when $\beta p_0 - H_0 < 0$ and $\lambda < -\frac{n_0(\beta p_0 - H_0)}{K - n_0}$ there exists and is positive the time T_K where $\dot{y}_K(T_K) = \dot{z}(T_K)$, i.e.

$$T_K = \frac{1}{\lambda} \log\left(\frac{c_2 - \lambda c_1}{\lambda(n_d - K)}\right).$$

In order to keep for all $t > 0$, the exponential functions $y_A(t)$ and $y_K(t)$ above and below, respectively, the straight line $z(t)$, the value of λ can be decreased until $z(t)$ overlaps the tangent lines at T_K and T_A , respectively, to $y_K(t)$ and $y_A(t)$. It follows that $y_A(T_A) = z(T_A)$, $y_K(T_K) = z(T_K)$ i.e.

$$\log\left(\frac{c_2 - \lambda_{T_A} c_1}{\lambda_{T_A}(n_d - A)}\right) = \frac{c_2}{c_2 - \lambda_{T_A} c_1}$$

and

$$\log\left(\frac{c_2 - \lambda_{T_K} c_1}{\lambda_{T_K}(n_d - K)}\right) = \frac{c_2}{c_2 - \lambda_{T_K} c_1},$$

should be verified and the result follows. $\square$

However in the ecological context, taking initial conditions in the interior of the first quadrant or in a subset of the first quadrant, both prey and predator densities are required to be positive $\forall t > 0$. The following results give sufficient conditions to this aim. In the following we have set

$$\lambda_{\min} = \frac{c_2}{c_1} = \frac{n_0(\beta p_0 - H_0)}{n_0 - n_d}. \quad (25)$$

Theorem 3.6. Suppose $n_0, p_0 \geq 0$ and $H(n) \geq 0$ whenever $n > 0$ and let:

- (i) $n_0 > n_d > 0$,
- (ii) $\beta p_0 - H_0 > 0$,
- (iii) $\lambda \geq \lambda_{\min}$.

Then $n(t) > 0$ and $p(t) \geq 0$ for all $t \geq 0$.

Proof. We start by observing that, because of (i) and (ii), condition (iii) implies that $\lambda > \beta p_0 - H_0$. In fact

$$\lambda \geq \frac{n_0(\beta p_0 - H_0)}{n_0 - n_d} > \beta p_0 - H_0.$$

Therefore it follows from Theorem 3.2 that $n(t) > 0$ for all $t > 0$. The predator dynamics $p(t)$ can be evaluated by the prey evolution equation in (1), i.e. $p = \frac{1}{\beta} \left(H(n) - \frac{\dot{n}}{n} \right)$. By using (14), we have

$$\frac{\dot{n}}{n} = \frac{\lambda t(c_2 - \lambda c_1) - c_2}{n_d e^{\lambda t} + c_1 - (c_2 - \lambda c_1)t},$$

so that $p(t)$ can be equivalently described by:

$$p = \frac{1}{\beta} [H(n) + g(t)], \quad (26)$$

with

$$g(t) = \frac{c_2 + \lambda t(\lambda c_1 - c_2)}{n_d e^{\lambda t} + c_1 - (c_2 - \lambda c_1)t}. \quad (27)$$

As far as the positiveness of $p(t)$ is concerned, we observe that $p(t)$ in (26) turns out to be the sum of two positive quantities. In fact since $n(t) > 0$ – recalling (16) – we have that the denominator in (27) is positive. Recalling (15), it also results that (i) implies $c_1 > 0$ and (ii) implies $c_2 > 0$. Moreover by (15) and (i)–(iii) it follows

$$\lambda c_1 - c_2 = \lambda(n_0 - n_d) - n_0(\beta p_0 - H_0) \geq 0,$$

so that also the numerator in (27) is positive for all $t \geq 0$. $\square$

Theorem 3.7. Suppose $H(n) \geq 0$ whenever $n > 0$ and let:

- (i) $0 < n_0 < n_d$,
- (ii) $\beta p_0 - H_0 < 0$,
- (iii) $\lambda \geq \lambda_{\min}$.

Then $n(t) > 0$ and $p(t) > 0$ for all values of λ such that $g(t) \geq -H(n(t))$ holds true for all $t > 0$.

Proof. From (ii) and Theorem 3.2 it follows that $n(t) > 0$ for all $t > 0$ and $H(n) \geq 0$. Moreover, conditions (ii) and (iii) imply that $c_2 < 0$ and $\lambda c_1 - c_2 < 0$. Consequently, the function $g(t)$ in (27) is negative for all $t \geq 0$. From (26), we have that $p(t) > 0$ for values of $\lambda > \lambda_{\min}$ such that $g(t) \geq -H(n(t))$ for all $t > 0$ and the result follows. $\square$

Theorem 3.8. Suppose $H(n) \geq 0$ whenever $n \in [A, K] \subset \mathbb{R}_+$ and let:

- (i) $K > n_0 > n_d > A$,
- (ii) $\beta p_0 - H_0 > 0$,
- (iii) $\lambda \geq \lambda_{\min}$.

Then $n(t) \in [A, K]$ and $p(t) \geq 0$ for all $t \geq 0$.

Proof. It is enough to observe that conditions (i)–(iii) imply that the relation in (18) which corresponds to $\beta p_0 - H_0 > 0$, is verified. Indeed,

$$\lambda \geq \frac{n_0(\beta p_0 - H_0)}{n_0 - n_d} \geq \frac{n_0(\beta p_0 - H_0)}{n_0 - A}$$

and from (ii) and by Theorem (3.4) it follows that $n(t) \in [A, K]$. Consequently, $H(n)$ is positive and the positivity of $p(t)$ follows as in proof of Theorem 3.6. $\square$

Theorem 3.9. Suppose $H(n) \geq 0$ whenever $n \in [A, K] \subset \mathbb{R}_+$ and let:

- (i) $A < n_0 < n_d < K$,
- (ii) $\beta p_0 - H_0 < 0$,
- (iii) $\lambda \geq \lambda_{\min}$.

Then $n(t) \in [A, K]$ and $p(t) > 0$ for all values of λ such that $g(t) \geq -H(n(t))$ holds true for all $t > 0$.

Proof. It is enough to observe that conditions (i)–(iii) imply that the relation in (18) which corresponds to $\beta p_0 - H_0 < 0$, is verified. Indeed,

$$\lambda \geq \frac{n_0(\beta p_0 - H_0)}{n_0 - n_d} \geq \frac{n_0(\beta p_0 - H_0)}{n_0 - K},$$

By Theorem (3.4), it follows that $n(t) \in [A, K]$ and, consequently, $H(n)$ is positive. Then the result of positivity of $p(t)$ is obtained by following the same reasoning used in Proof of Theorem (3.7). $\square$

We observe that Theorems 3.7 and 3.9 provide a range of the parameter λ , i.e. $\lambda \in [\lambda_{\min}, \lambda_{\max}]$, ensuring the positiveness of $n(t)$ and $p(t)$ for all $t > 0$. More precisely $\lambda_{\min}$ is given by (25) whereas $\lambda_{\max}$ is the maximum value of λ such that $g(t) \geq -H(n(t))$ for all $t \geq 0$. Further details on this critical value $\lambda_{\max}$ are given in the following remark:

Remark 3.1. Let us assume the hypotheses of Theorems 3.7 and 3.9 to hold. Since $g(0) + H_0 = \beta p_0 > 0$, the threshold value $\lambda_{\max}$ solves

$$|g(t_{\lambda_{\max}}) + H(n(t_{\lambda_{\max}}))| = \min_{\lambda} |g(t_{\lambda}) + H(n(t_{\lambda}))| \quad (28)$$

at the time $t_{\lambda} > 0$ implicitly defined through $\dot{g}(t_{\lambda}) + \dot{H}(n(t_{\lambda})) = 0$, under the hypothesis that $g(t) > -H(n(t))$ for all $t > t_{\lambda}$.

In Section 4.1 and in Section 4.2, we will detect numerically the critical value $\lambda_{\max}$ with reference to two examples of ecological interest: the classical Lotka–Volterra model [41] and the aggregated model for the wolf–wild boar dynamics [24].

4. Ecological applications

4.1. Z-control of the classical Lotka–Volterra model

The case of indirect Z-control of the prey population for the classical Lotka–Volterra predator prey model [41]

$$\begin{aligned} \dot{n} &= n(\alpha - \beta p) \\ \dot{p} &= p(\gamma n - \delta), \end{aligned} \quad (29)$$

was recently considered in [43]. In this section we revisit their results within the dynamical system framework we developed in the previous Sections. Let us preliminary observe that, in the absence of control, system (29) admits the extinction equilibrium $P_0 = (0, 0)$ which is a saddle and the coexistence equilibrium $P_e = (\delta/\gamma, \alpha/\beta)$ that is a center and hence Lyapunov stable but not asymptotically stable. The orbits of model (29) in the positive quadrant correspond to the level set of the function

$$V(n, p) = \gamma n - \delta \log n + \beta p - \alpha \log p \quad (30)$$

and are a family of closed curves surrounding the coexistence equilibrium P_e , Fig. 1. The aim of the indirect Z-control on the prey population is to apply a control measure on the predators so that the prey population is forced to achieve the desired level n_d . As discussed in Section 2.2, the related Z-controlled system takes the form of model (12) with $H(n) = \alpha$ and

$$f(n, p) = \frac{1}{\beta} (\alpha - \beta p + \lambda)^2 - \frac{\lambda^2 n_d}{\beta n}$$

since $n_d = \text{constant}$. Moreover, the control measure exerted on the predator population is given by

$$u_{\text{pred}} = \gamma n(t) - \delta - \frac{f(n, p)}{p(t)}. \quad (31)$$

As in [43] we set the model parameters as $\alpha = \delta = 0.6$, $\beta = \gamma = 0.01$, we choose the constant desired state $n_d = 100$ and

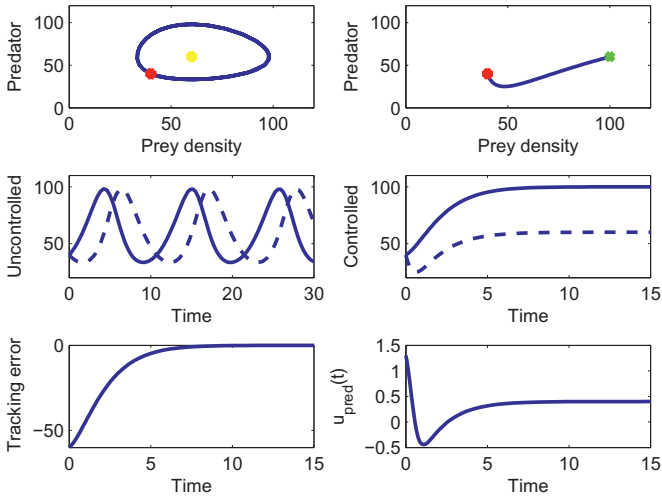


Fig. 1. The Lotka–Volterra model. First row: Phase-plane curves of predator versus prey for both the uncontrolled (i.e. $u_{pred} = 0$, left) and the Z-controlled model (right) with $\lambda = 0.8$. For both the models the initial conditions and the system parameters are $n(0) = p(0) = 40$, $\alpha = \delta = 0.6$, $\beta = \gamma = 0.01$. The system trajectory for the uncontrolled model is a closed orbit around the neutrally stable equilibrium $P_e = (60, 60)$, while the Z-control forces the system dynamics towards the asymptotically stable equilibrium $P^* = (100, 60)$. In the phase-plane, the initial point $P_0 = (n(0), p(0))$ is plotted as a red full circle; the uncontrolled equilibrium P_e is plotted as a yellow full circle; the Z-controlled equilibrium P^* is plotted as a green full circle. Second Row: Time dependent behavior of the prey and predator populations. Third row: Temporal evolution for both the tracking error v_1 and the control measure u_{pred} exerted on the predator population. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

consider as initial state $n(0) = p(0) = 40$. With this choice for the parameters, the coexistence equilibrium of the uncontrolled system (29) is the neutrally stable equilibrium $P_e = (60, 60)$ and, according to Theorem 3.1, the Z-controlled system admits the coexistence equilibrium $P^* = (n_d, \frac{H(n_d)}{\beta}) = (100, 60)$ as the unique attractor for the system dynamics. Therefore the effect of the Z-control is to *destroy* the undamped oscillations around the neutrally stable equilibrium P_e and to drive the system towards the desired state P^* .

In Fig. 1 we numerically validate the above analytical finding by showing the dynamics of the Z-controlled Lotka–Volterra system when the design parameter λ is chosen $\lambda = 0.8$.

In Section 3.2, we found that – in order the Z-control to ensure the positiveness of the involved populations – the choice of the design parameter λ needs to be carefully calibrated. Numerical experiments also confirm this peculiar role of the design parameter λ on the dynamics of the Z-controlled model. In fact, by decreasing the value of λ the convergence towards the desired equilibrium P^* is reached very slowly whereas by increasing the value of λ , the stronger and stronger indirect prey control may induce predator extinction.

We will use the analytical results derived in Section 3.2 to gain insight on the possible values of the parameter λ ensuring a successful ecological application of the Z-control approach.

The Z-controlled Lotka–Volterra system is in the condition of Theorem 3.7. In fact, the function $H(n) = H_0 = \alpha = 0.6$ is always strictly positive and it results $c_1 = n_0 - n_d = -60 < 0$, $\beta p_0 - H_0 = -0.2 < 0$ and $\lambda = 0.8$ verifies the inequality $\lambda \geq \lambda_{min} = 0.1333$. The function $g(t)$ defined in (27) is negative for all $t \geq 0$ as shown in Fig. 2 (left). Provided that its minimum value is greater than $-H(n) = -0.6$, the predator function in (26) stays positive for all $t \geq 0$, Fig. 2 (right). As also shown in the same Figure, for $\lambda > \lambda_{max} \approx 1.4049$, it results $\min_{t \geq 0} g(t) < -0.6$ (Fig. 2, right) so that negative values for the predator dynamics $p(t)$ are obtained (Fig. 2, left).

We conclude by observing that, for each set of initial conditions (n_0, p_0) , one can detect a λ -range $[\lambda_{min}, \lambda_{max}]$ ensuring the Z-control approach to be ecologically meaningful. For the classical Lotka–Volterra predator–prey model, in respect to the initial conditions $P_0 = (n_0, p_0) = (40, 40)$, the parameter λ has to be chosen such that $\lambda < 1.4049$.

Fig. 3 shows the basin of attraction of the Z-controlled equilibrium P^* for increasing values of the parameter $\lambda := 0.2; 0.8; 1.4$. We recall that the basin of attraction of a given attractor (i.e. a stable equilibrium, a stable limit cycle) is the set of initial conditions which leads to the long-time behavior that approaches that attractor [17]. In Fig. 3 the set of initial conditions asymptotically leading to the Z-controlled equilibrium P^* are inside the green and the yellow regions. However, only the green region (dark grey in the printed version) is meaningful from the ecological point of view since the related trajectories preserve the positivity of both predator and prey populations for all $t > 0$. For this reason we will call the green region *ecological basin of attraction* of P^* . As expected by the theoretical analysis above, in the three cases in Fig. 3, the initial point $P_0 = (40, 40)$ is inside the ecological basin of attraction of P^* . However, it is possible to observe that, with

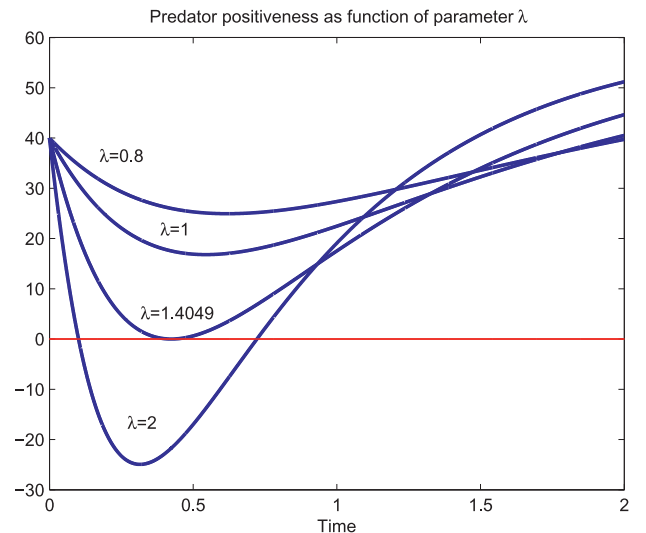
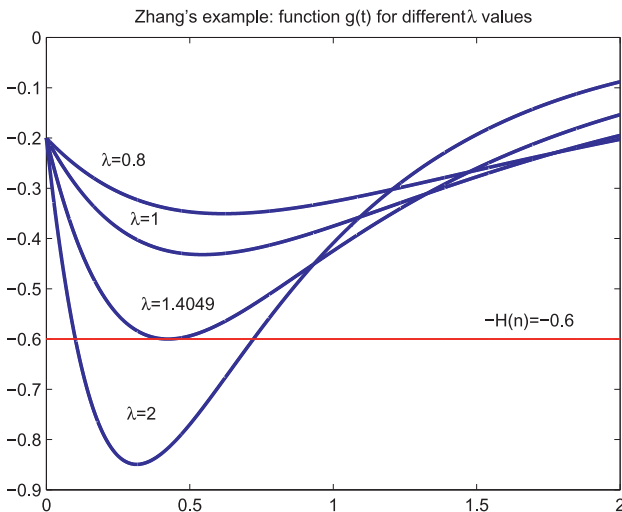


Fig. 2. The Z-controlled Lotka–Volterra predator prey model. On the left: Plot of the function $g(t)$ and $-H(n) = -H_0$ versus time for different choices of the parameter λ . We recall that $n(t)$ is given by (14) and $n_d = 100$. On the right: The related predator solution $p(t)$.

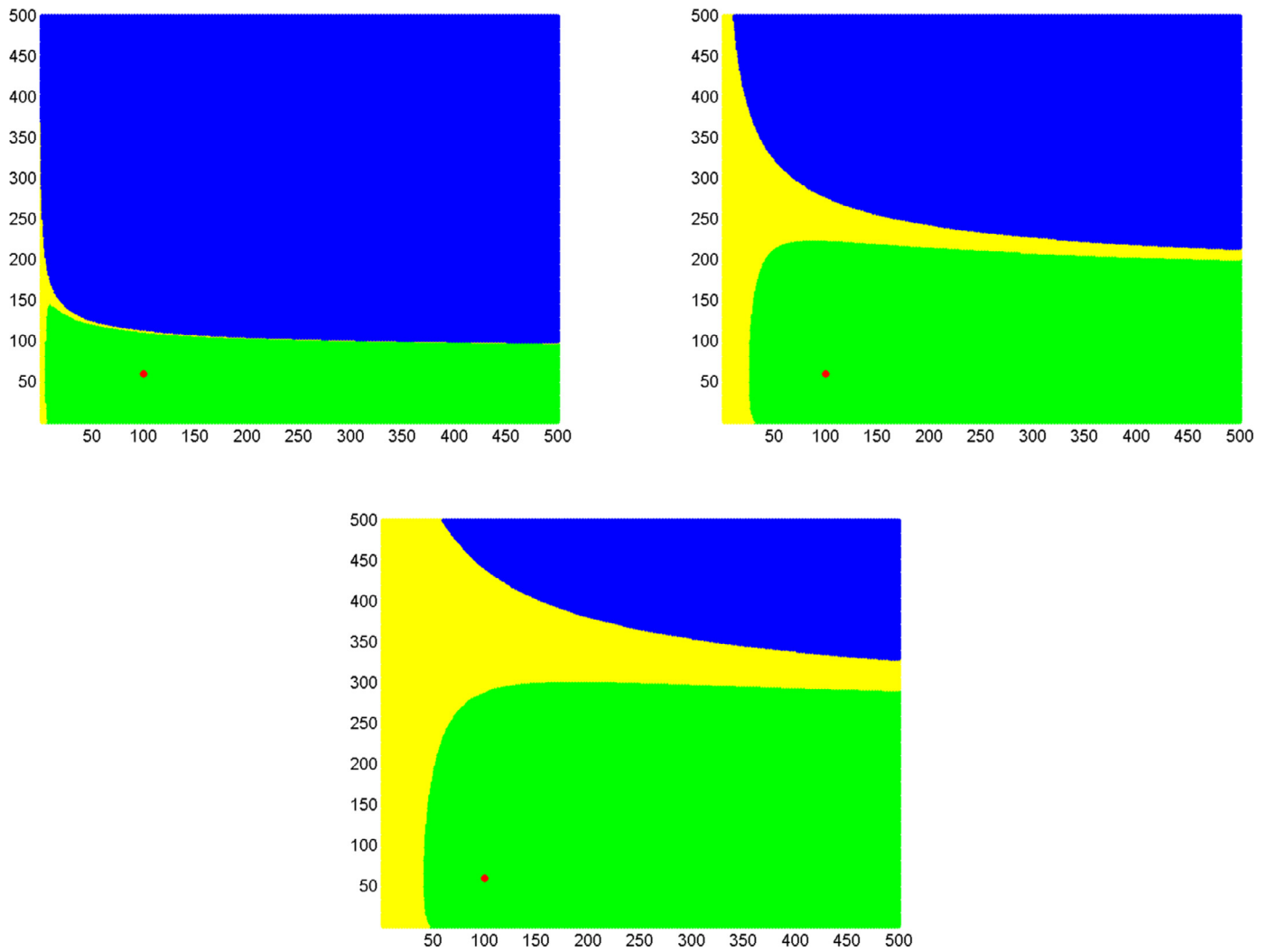


Fig. 3. The Z-controlled Lotka–Volterra predator prey model: basin of attraction of the Z-controlled equilibrium P^* , for different values of the parameter λ . The green region (dark grey in the printed version) represents the *ecological basin of attraction* of the Z-controlled equilibrium P^* , i.e. the set of initial conditions leading to the Z-controlled equilibrium with trajectories that preserve the positivity of both predator and prey populations. The yellow region (light grey in the printed version) represents the set of initial conditions for which the Z-control approach still works but it is not ecologically meaningful because, although the related trajectories asymptotically tends towards P^* , the predator positivity is lost in the transient dynamics. The blue region (black in the printed version) represents the set of initial conditions for which the Z-control approach fails. This occurs because, for this set of initial conditions, the positivity of the prey is not guaranteed for all $t > 0$; hence a t^* exists such that $n(t^*) = 0$ and (11) and has a singularity. From an ecological point of view, a t^* such that $n(t^*) = 0$ would imply prey and hence predator extinction. The different panels are distinguished by the different numerical values assigned to parameter λ : first row (left), $\lambda = 0.2$; first row (right), $\lambda = 0.8$; second row, $\lambda = 1.4$. In each panel, the stable equilibrium P^* is marked through a red filled circle. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

increasing the value of λ , the ecological basin of attraction of the Z-controlled equilibrium P^* enlarges thus suggesting a situation of higher ecological resilience [40]: in fact, a stochastic event could eventually move the controlled system towards extinction less likely for higher values of λ than for lower ones.

4.2. Z-control of the wolf-wild boar dynamics

In [24], we used a modeling approach to gain qualitative insights for the management of the wild boar and wolf population dynamics in the Italian Alta Murgia National Park. We introduced a two-patch predator–prey model where both migration processes between patches and prey control policies were taken into account and, by applying the aggregation method [4–7], we derived a reduced model that was able to mimic the dynamics of the full model with respect to equilibria and stability properties. In this section we want to apply the indirect Z-control of the prey to the

aggregated model of the wolf-wild boar dynamics:

$$\begin{cases} \frac{dn}{dt} = n \left[r \left(1 - \frac{n}{k} \right) \left(\frac{n}{a} - 1 \right) - a_1 dp - qE \right], \\ \frac{dp}{dt} = p [-\mu + ea_1 dn - qEd], \end{cases} \quad (32)$$

where $n(t)$ and $p(t)$ are the total prey (wild-boar) and predator (wolf) densities respectively. The choice of controlling the prey population through a modified mortality of the predator is of interest in cases where the local protection status (e.g., a national park as in the case of Alta Murgia) prevents massive hunting on the prey (the wild boar), while targeted removal (and possibly transplant) and/or introduction of predators from other parks can be effectively managed by the park personnel.

In [24], we performed theoretical investigations on the dynamical behavior of model (32). All the parameters involved are strictly positive. More precisely, the parameters d and E were considered as bifurcation parameters and the others were fixed as in [24].

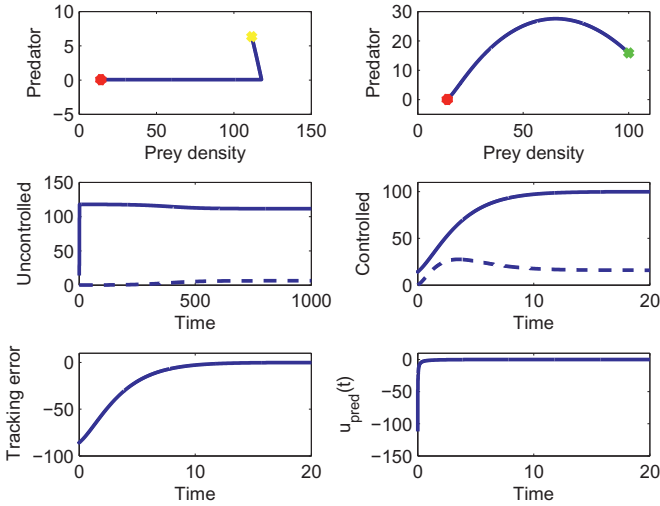


Fig. 4. The aggregated model of the wolf-wild boar dynamics [24]; Scenario I. First row: Phase-plane curves of predator versus prey for the aggregated model without control (left) and with control (right). The design parameter of the Z-controlled model is $\lambda = 0.5$. For both the models the initial conditions are $n(0) = 14$, $p(0) = 0.0563$. The parameters E and d are chosen as $E = 0.16$, $d = 0.6446$. The other system parameters are chosen as $a_1 = 0.1108$, $r = 0.0484$, $e = 0.0280$, $\mu = 0.12$, $k = 120$, $\alpha = 0.6182$, $q = 1$. The uncontrolled system dynamics asymptotically reach the stable equilibrium $P_e = (111.545, 6.325)$ while the Z-control forces the system dynamics towards the desired equilibrium $P^* = (100, 15.9124)$. In the phase-plane, the initial point $P_0 = (n(0), p(0))$ is plotted as a red full circle; the uncontrolled equilibrium P_e is plotted as a yellow full circle; the Z-controlled equilibrium P^* is plotted as a green full circle. Second row: Time-dependent behavior of the prey and predator populations of the aggregated model. Third row: Temporal evolution for the tracking error v_1 and for the control measure u_{pred} exerted on the predator population. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

According to the specific choice for the bifurcation parameters, three kinds of equilibria were found: the predator-prey extinction equilibrium $P_0 = (0, 0)$; the predator's extinction equilibria $P_1 = (n_1, 0)$ and $P_2 = (n_2, 0)$; the coexistence equilibrium $P_e = (n_e, p_e)$. We showed that the predator-prey extinction equilibrium P_0 is stable for every parameter values whereas the predator's extinction equilibria P_i and the coexistence equilibrium P_e can be stable or unstable according to the specific choice of the

parameter values. A remarkable feature related to the coexistence equilibrium P_e is that – when the bifurcation parameter E reaches a threshold value – it can lose its stability by the means of a supercritical Hopf bifurcation so that coexistence can also occur by the means of self-sustained oscillations [23,24].

By applying the indirect Z-control of the prey population to the aggregated model (32), we get the Z-controlled model (12) with $H(n) = r(1 - \frac{n}{k})(\frac{n}{a} - 1) - qE$ and,

$$f(t; n, p) = \frac{\sum_{k=0}^5 C_k(p) n^k}{k^2 a^2 a_1 d n}, \quad (33)$$

with the coefficients $C_k(p)$ given by:

$$\begin{aligned} C_5 &= 3r^2; \\ C_4 &= -5r^2(a+k); \\ C_3 &= r[2r(a^2+k^2) + 2ak(\lambda+4r) - ak(4a_1dp + 3Eq)]; \\ C_2 &= akr(3a_1dp + 2Eq - 2\lambda - 3r)(a+k); \\ C_1 &= k^2a^2[(\lambda+r-a_1dp)(\lambda+r-a_1dp-Eq) - Eq\lambda]; \\ C_0 &= -k^2a^2(\lambda^2n_d + 2\lambda\dot{n}_d + \ddot{n}_d). \end{aligned}$$

However, since $n_d = \text{constant}$, (33) reduces to

$$f(n, p) = \frac{n \left[\left(r \left(1 - \frac{n}{k} \right) \left(\frac{n}{a} - 1 \right) - qE - a_1dp + \lambda \right)^2 + \dot{H}(n) \right] - \lambda^2 n_d}{a_1 d n},$$

with

$$\dot{H}(n) = \frac{nr}{ka} (k+a-2n) \left[r \left(1 - \frac{n}{k} \right) \left(\frac{n}{a} - 1 \right) - qE - a_1dp \right].$$

Moreover,

$$u_{pred} = -\mu + e a_1 d n - qEd - \frac{f(n, p)}{p(t)}. \quad (34)$$

In the following, we apply the Z-control approach to modify two different dynamical scenarios of the uncontrolled model (32): (i) coexistence through a stable equilibrium P_e ; (ii) coexistence through self-sustained oscillations surrounding the unstable equilibrium P_e .

4.2.1. Scenario I: Coexistence via the stable equilibrium P_e

As a first step, we fix the E and d parameter values so that, in the uncontrolled model (32), populations coexistence is reached

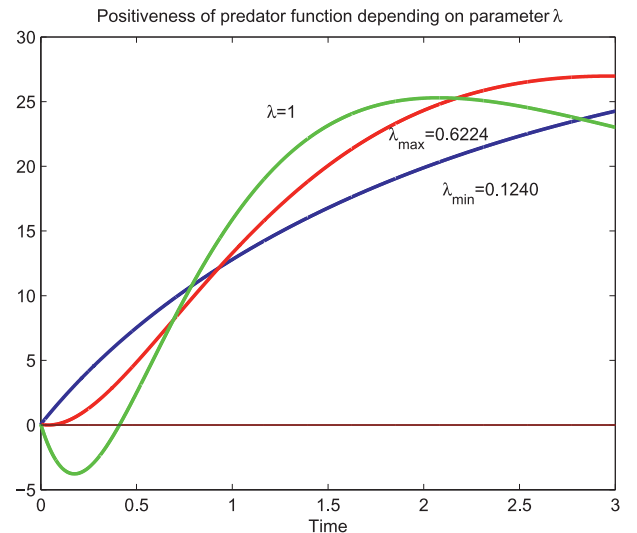
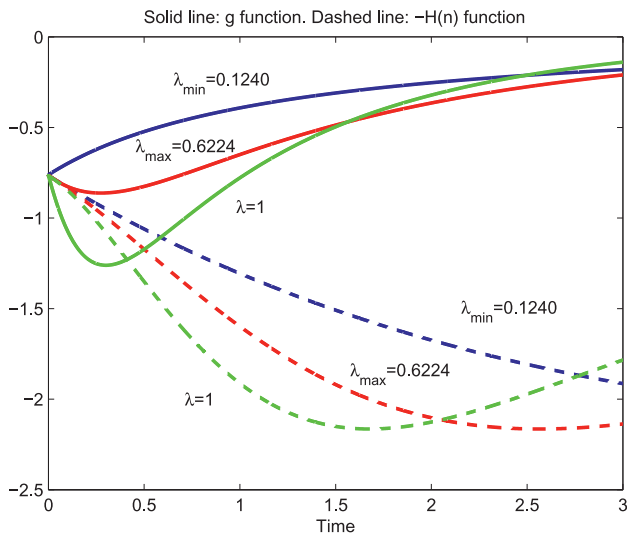


Fig. 5. The Z-controlled aggregated model of the wolf-wild boar dynamics: Scenario I. On the left: plot of the functions g and $-H(n)$ versus time for different values of the parameter λ . On the right: the related predator solutions $p(t)$.

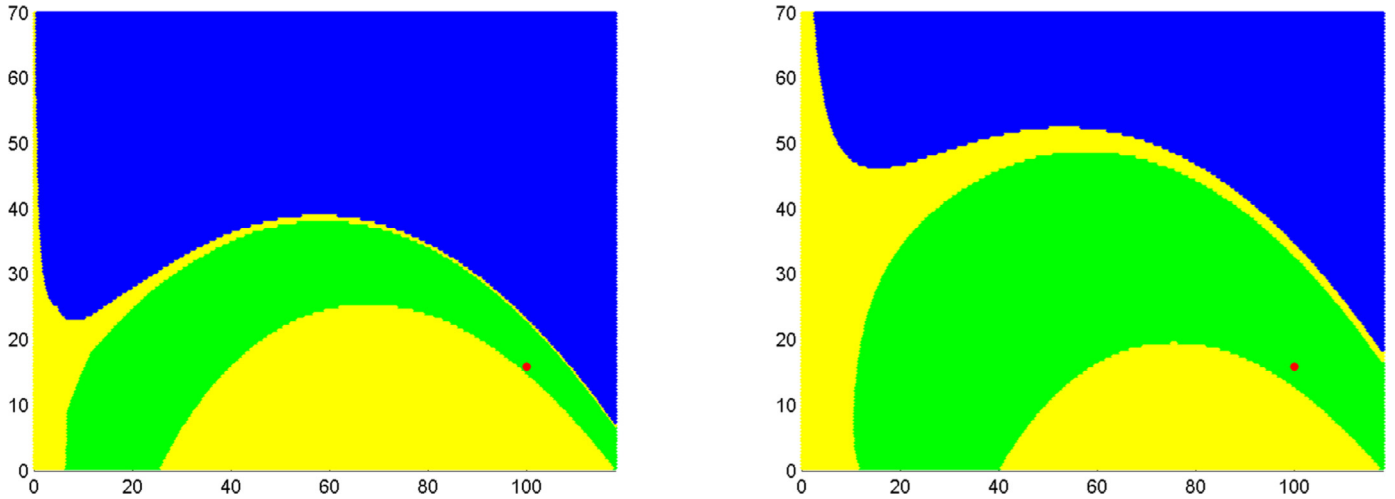


Fig. 6. The Z-controlled aggregated model of the wolf-wild boar dynamics: Scenario I. Basin of attraction of the Z-controlled equilibrium P^* , for different values of the parameter λ . The green region (dark grey in the printed version) represents the ecological basin of attraction of the Z-controlled equilibrium P^* . The yellow region (light grey in the printed version) represent the theoretical but not ecologically feasible basin of attraction of the Z-controlled equilibrium P^* . The blue region (black in the printed version) represents the set of initial conditions for which the Z-control approach fails. The different panels are distinguished by the different numerical values assigned to parameter λ : left, $\lambda = 0.2$; right, $\lambda = 0.5$. In each panel, the stable equilibrium P^* is marked through a red filled circle. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

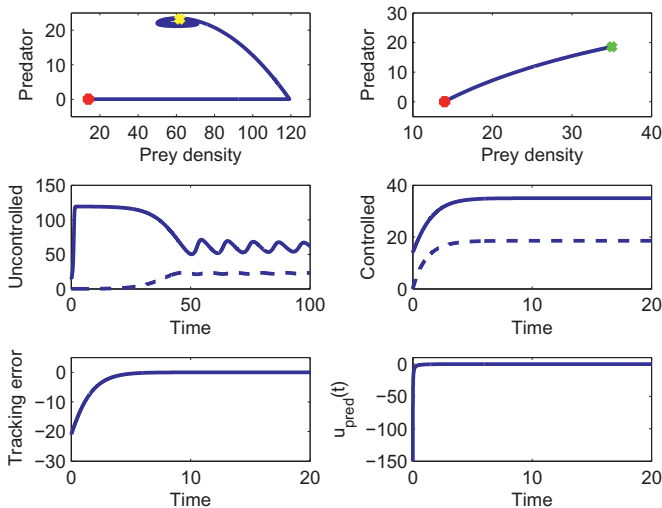


Fig. 7. The aggregated model of the wolf-wild boar dynamics [24]: Scenario II. First row: Phase-plane curves of predator versus prey for the aggregated model without control (left) and with control (right). The design parameter of the Z-controlled model is $\lambda = 1$ and the initial conditions are $n(0) = 14$, $p(0) = 0.0563$. The parameters E and d are chosen as $E = 0.0537$, $d = 0.9$. The other system parameters are chosen as $a_1 = 0.1108$, $r = 0.0484$, $e = 0.0280$, $\mu = 0.12$, $k = 120$, $a = 0.6182$, $q = 1$. The uncontrolled system dynamics asymptotically reach a stable limit cycle surrounding the unstable equilibrium $P_e = (60.268, 22.766)$ while the Z-control forces system dynamics towards the desired equilibrium $P^* = (35, 18.577)$. In the phase-plane, the initial point $P_0 = (n(0), p(0))$ is plotted as a red full circle; the uncontrolled equilibrium P_e is plotted as a yellow full circle; the Z-controlled equilibrium P^* is plotted as a green full circle. Second row: Time-dependent behavior of the prey and predator population for the aggregated model. Third row: Temporal evolution for both the tracking error v_1 and the control measure u_{pred} exerted on the predator population. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

by the mean of a stable equilibrium. We hence choose $E = 0.16$, $d = 0.6446$ and set the other model parameters as $a_1 = 0.1108$, $r = 0.0484$, $e = 0.0280$, $\mu = 0.12$, $k = 120$, $a = 0.6182$, $q = 1$. Basing on field-data, the chosen initial conditions are: $n(0) = 14$, $p(0) = 0.0563$, [24]. As a consequence, for the uncontrolled model (32), system dynamics tends towards a stable coexistence equilibrium $P_e = (111.545, 6.325)$, Fig. 4.

When applying the indirect Z-control on the prey population – according to Theorem 3.1 – the resulting Z-controlled system admits the coexistence equilibrium $P^* = (n_d, \frac{H(n_d)}{\beta})$. Hence by selecting $n_d = 100$, we have $P^* = (100, 15.9124)$ as the unique attractor for the system dynamics, Fig. 4.

Numerical experiments on the role of the parameter λ have suggested that two thresholds for λ can be found, λ_{min} and λ_{max} such that for $\lambda > \lambda_{max}$ and $\lambda < \lambda_{min}$ negative values of predator population $p(t)$ can be obtained. These results can be further explained by the means of the analytical results of Section 3.2.

In fact observe that we are in the condition of Theorem 3.9 since, in the aggregated model of the wolf-wild boar dynamics, $H(n) = r(1 - \frac{n}{k})(\frac{n}{a} - 1) - qE$ is positive whenever n is bounded between $A = 2.709$ and $K = 117.9$. Moreover, since $c_1 = n_0 - n_d = -86 < 0$, and $\beta p_0 - H_0 = -0.7615 < 0$ it follows that for values of $\lambda \geq \lambda_{min} = 0.1240$, the function g assumes negative values but, until $g(t) \geq -H(n(t))$ for $n(t)$, the predator function $p(t)$ is positive for all $t \geq 0$ as shown in Fig. 5 (left). Fig. 5 (right) also shows that for $\lambda > \lambda_{max} \approx 0.6224$ negative values of predator function $p(t)$ are obtained.

Hence, for the chosen parameter values and in respect to the initial conditions $P_0 = (n_0, p_0) = (14, 0.0563)$, the parameter λ has to be chosen such that $0.1240 \leq \lambda \leq 0.6224$ in order the Z-control approach to be ecologically meaningful for the aggregated model of the wolf-wild boar dynamics.

Fig. 6 shows the basin of attraction of the Z-controlled equilibrium P^* for increasing values of the parameter $\lambda := 0.2; 0.5$. In both these cases, as expected, the initial point $P_0 = (14, 0.0563)$ is inside the ecological basin of attraction of P^* that – similarly to the case of the Lotka–Volterra system – considerably enlarges for increasing values of λ .

4.2.2. Scenario II: Coexistence via self-sustained oscillations

In this section, we fix the E and d parameter values so that, in the uncontrolled model (32), populations coexistence is reached by the mean of self-sustained oscillations. We hence choose $E = 0.0537$, $d = 0.9$ and set the other model parameters as $a_1 = 0.1108$, $r = 0.0484$, $e = 0.0280$, $\mu = 0.12$, $k = 120$, $a = 0.6182$, $q = 1$. As in the previous example, the chosen initial conditions are: $n(0) = 14$, $p(0) = 0.0563$. As a consequence, for the uncontrolled

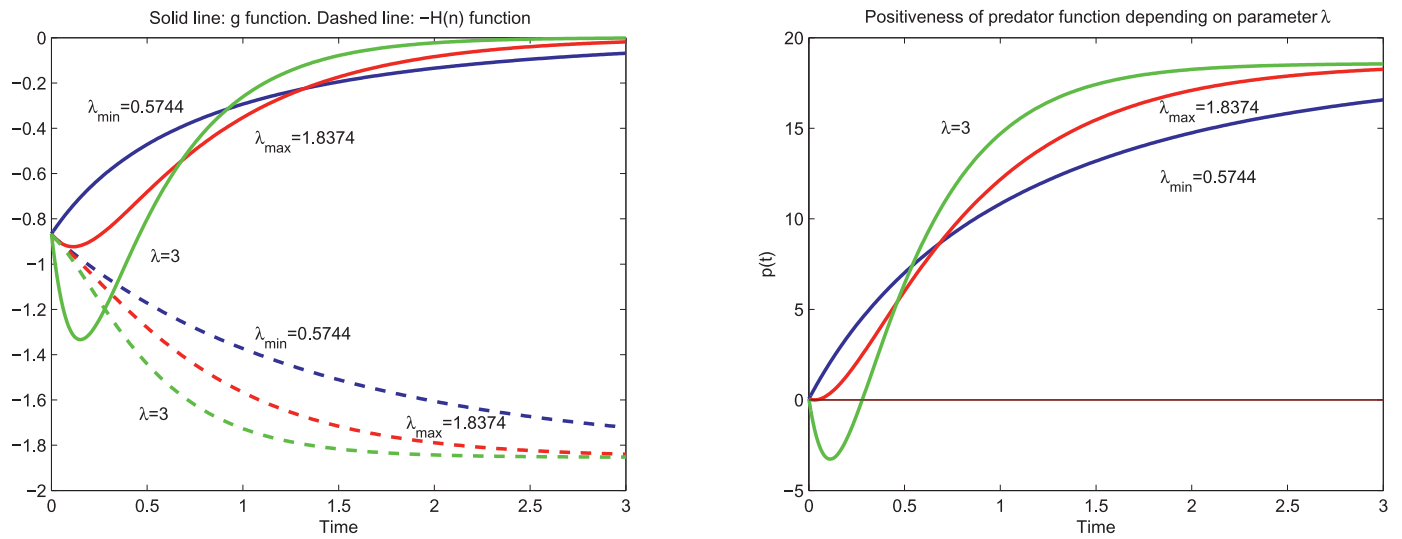


Fig. 8. The Z-controlled aggregated model of the wolf-wild boar dynamics: Scenario II. On the left: plot of the functions g and $-H(n)$ versus time for different values of the parameter λ . On the right: the related predator solutions $p(t)$.

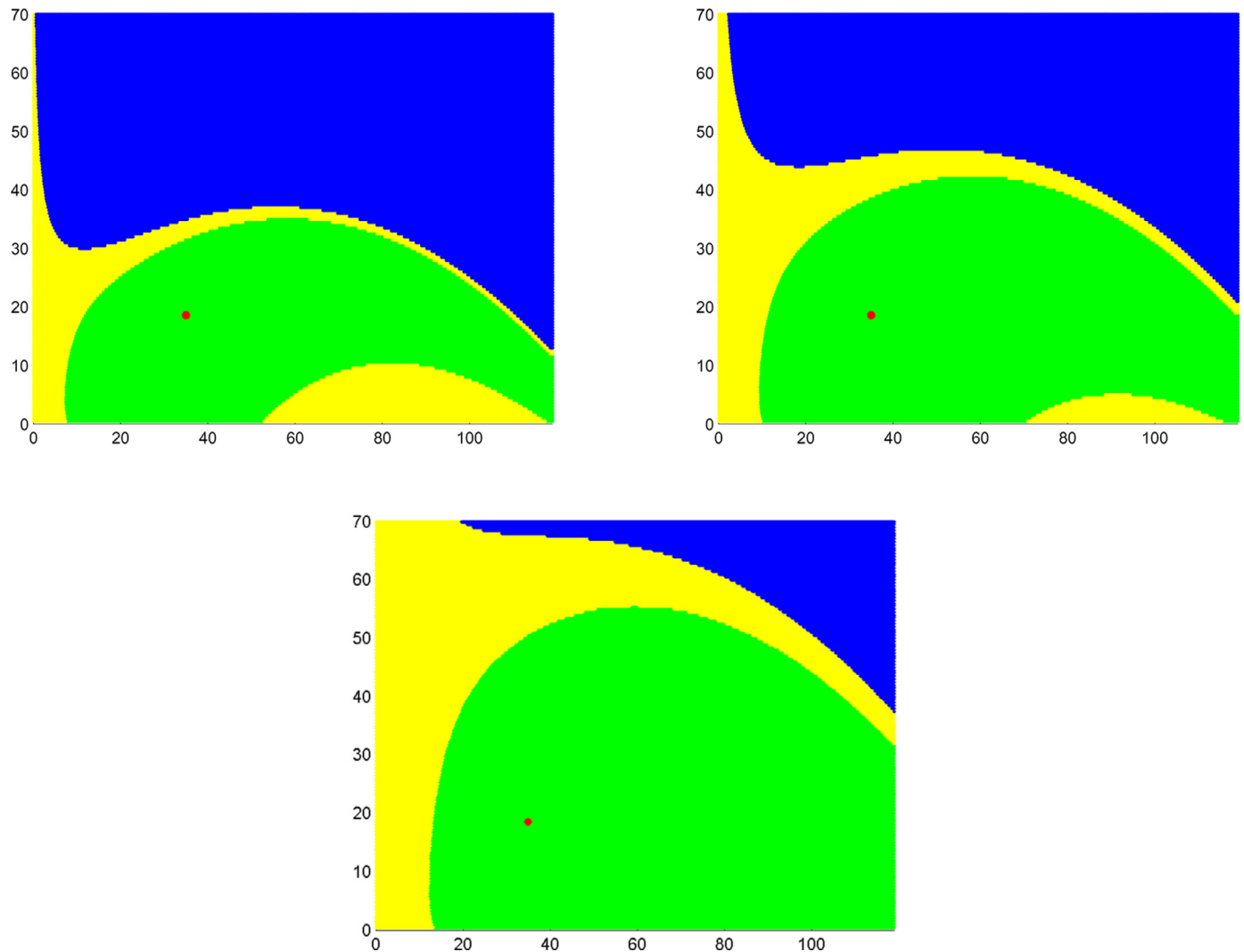


Fig. 9. The Z-controlled aggregated model of the wolf-wild boar dynamics: Scenario II. Basin of attraction of the Z-controlled equilibrium P^* , for different values of the parameter λ . The green region (dark grey in the printed version) represents the ecological basin of attraction of the Z-controlled equilibrium P^* . The yellow region (light grey in the printed version) represents the portion not ecologically meaningful of the theoretical basin of attraction of P^* . The blue region (black in the printed version) represents the set of initial conditions for which the Z-control approach fails. The different panels are distinguished by the different numerical values assigned to parameter λ : first row (left), $\lambda = 0.6$; first row (right), $\lambda = 1$; second row: $\lambda = 1.8$. In each panel, the stable equilibrium P^* is marked through a red filled circle. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Table 1
Approximation accuracy of $\lambda_{\max}$.

Case	$\lambda_{\max}$	$t_{\lambda_{\max}}$	$ \dot{g}(t_{\lambda_{\max}}) + \dot{H}(n(t_{\lambda_{\max}})) $	$ g(t_{\lambda_{\max}}) + H(n(t_{\lambda_{\max}})) $
Lotka-Volterra	1.4049	0.4241	0	2.585 10^{-6}
WW: Scenario I	0.6224	0.0394	1.2212 10^{-15}	5.686 10^{-7}
WW: Scenario II	1.8374	0.0290	0	5.894 10^{-7}

model (32), system dynamics tends towards a stable limit cycle surrounding the unstable equilibrium $P_e = (60.268, 22.766)$, Fig. 7.

As in the previous scenario, we are again in the condition of Theorem 3.9 since, in the aggregated model of the wolf-wild boar dynamics, $H(n) = r(1 - \frac{n}{k})(\frac{n}{a} - 1) - qE$ is positive whenever n is bounded between $A = 1.3116$ and $K = 119.3065$. We choose $n_d = 35$ so that $P^* = (n_d, \frac{H(n_d)}{\beta}) = (35, 18.577)$. The value $c_1 = n_0 - n_d = -21 < 0$, and, from $\beta = 0.0998$ and $H_0 = -0.0537$, it results $\beta p_0 - H_0 = -0.7615 < 0$; consequently, for values of $\lambda \geq \lambda_{\min} = 0.5774$, the function g assumes negative values but, until $g(t) \geq -H(n(t))$, the predator function $p(t)$ is positive for all $t \geq 0$ as shown in Fig. 8 (left). Fig. 8 (right) also shows that for $\lambda > \lambda_{\max} \approx 1.8374$ negative values of predator function $p(t)$ are obtained.

Hence, for the parameter values chosen in this section and in respect to the initial conditions $P_0 = (n_0, p_0) = (14, 0.0563)$, the parameter λ has to be chosen such that $0.5774 \leq \lambda \leq 1.8374$ for the effectiveness of the Z-control approach.

Fig. 9 depicts the basin of attraction of the Z-controlled equilibrium P^* for increasing values of the parameter $\lambda := 0.6; 1; 1.8$. Confirming the theoretical results, in all the three cases the initial point $P_0 = (14, 0.0563)$ is inside the ecological basin of attraction of P^* and, increasing values of λ , the ecological basin of attraction of the Z-controlled equilibrium P^* considerably enlarges.

4.3. Numerical details

The main numerical integration scheme used to validate our theoretical findings is the Dormand–Prince method [13], implemented in the MATLAB's ode45 code. It is an explicit, variable stepsize method of the Runge–Kutta family, here applied with absolute and relative tolerance set at 10^{-13} and 10^{-15} , respectively. The low dimension of the test dynamics, both in terms of number of variables and length of temporal horizons, allowed us to set tolerances close to machine precision, so achieving very accurate approximations. As an example, for the uncontrolled Lotka–Volterra dynamics discussed in Subsection 4.1, the error $|V(n, p) - V(n_0, p_0)|$ in preserving the level set (30) throughout the evolution stays below 10^{-13} , as plotted in Fig. 10. For the controlled Lotka–Volterra dynamics, we monitored the accuracy by comparing the approximated solutions provided by the Matlab code with the theoretical solutions given in (14) and (26–27), see Fig. 11: the error is of order 10^{-10} . Similar results were observed for the wolf-wild boar controlled dynamics we considered in Subsection 4.2 (results not showed).

For detecting the threshold values $\lambda_{\max}$ defined in (28) we rely on the MATLAB solver fzero for finding a zero of a single-variable nonlinear function, here applied with default tolerances. We searched for $\lambda_{\max}$ by spanning a meshgrid of values $\lambda_k = k \delta_\lambda$ with stepsize $\delta_\lambda = 10^{-5}$. For each λ_k , by means of the solver, we found $t_{\lambda_k} > 0$ such that $\dot{g}(t_{\lambda_k}) + \dot{H}(n(t_{\lambda_k})) = 0$, starting from $t_0 = 0$. Finally, we selected $\lambda_{\max}$ as the value λ_k which minimized the quantity $|g(t_{\lambda_k}) + H(n(t_{\lambda_k}))|$. In Table 1 we summarize the detected values for the test examples in the previous sections together with the values of the functions to be minimized.

The basins of attraction were computed by taking a large discrete set of initial conditions on a uniformly distributed mesh with spatial stepsizes δ_n and δ_p in a rectangular domain $(0, N]$

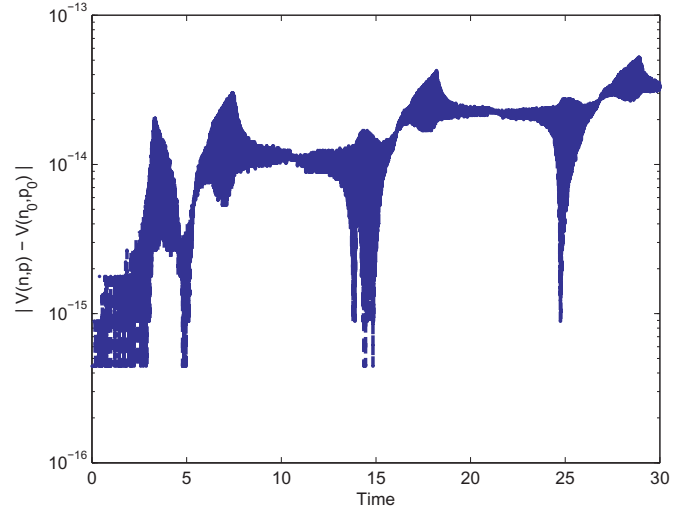


Fig. 10. Error in the preservation of the invariant $V(n, p)$ for the uncontrolled Lotka–Volterra model. Initial conditions and the system parameters are $n(0) = p(0) = 40$, $\alpha = \delta = 0.6$, $\beta = \gamma = 0.01$. The system trajectory for the uncontrolled model is a closed orbit around the neutrally stable equilibrium $P_e = (60, 60)$.

$\times (0, P]$ in the strictly positive octant $\mathbb{R}_+^2$. In details, to reproduce the basins in Fig. 3, we chose $N = P = 500$ and we used a spatial mesh with stepsizes $\delta_n = \delta_p = 1$; for generating Figs. 6 and 9 we used $N = 118$, $P = 70$ and $\delta_n = 0.1$, $\delta_p = 0.5$. Again, the low dimensionality of the problem and the simple qualitative dynamic of the systems (an unique stable equilibrium) allows this ‘direct’ approach; for richer dynamics the numerical detection of basins of attraction would require more reliable and sophisticated techniques as described in [9].

In our examples, for a fixed value of the parameter λ , we discriminate initial values that lead the solution of the controlled system to the (unique) theoretical equilibrium P^* , from starting values that lead to the blowing up of the solution. Once the time integration interval $[0, T]$ has been set, the Matlab routine ode45 stops the integration and provides a warning if the solution blows up before the final time T is reached; we verified this occurrence for initial prey values $n(t_0) = n_0$ that force the solution in (14) towards negative values; in this case since $n_0 > 0$, by continuity there exists a $t^* < T$ such that $n(t^*) = 0$. Consequently, the function $f(t, n, p)$ in (11) has a singularity at t^* and the solution of the dynamical system (12) blows up: in Figs. 3, 6 and 9 we plot the corresponding areas with blue points (black in the printed version).

When the initial conditions allow for the convergence of the solution, the integration is continued until the distance between the approximated values $(n(T), p(T))$ and the theoretical equilibrium P^* goes down to a tolerance value of 10^{-5} . Those initial points assure strictly positive values for the prey for the whole integration interval; however, for the predators the convergence does not prevent the densities to take negative values during the evolution of the dynamics. In our figures, initial conditions that lead the system to the equilibrium P^* for which there exists at least a negative component of the approximated predator vector ($p_j(\approx p(t_j)) < 0$) were plotted in yellows (light grey in the printed

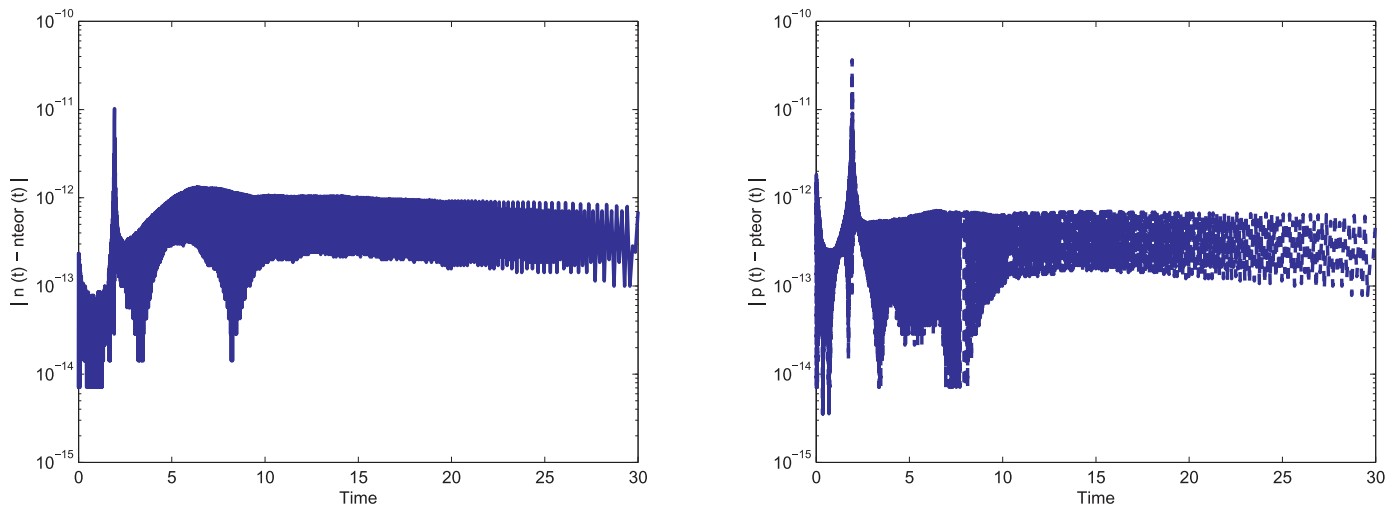


Fig. 11. Error in the approximation of the controlled Lotka-Volterra model. Initial conditions and the system parameters are $n(0) = p(0) = 40$, $\alpha = \delta = 0.6$, $\beta = \gamma = 0.01$. Z-control forces the system dynamics towards the asymptotically stable equilibrium $P^* = (100, 60)$.

version). On the contrary, points that provide all positive approximations of predator values ($p_j \geq 0$ for all j) were plotted in green (dark grey in the printed version).

5. Concluding remarks

In this paper, we have applied the Z-control approach to a generalized predator-prey system in the specific case of indirect control of the prey population. This method was originally developed within the engineering context and has been recently extended to the ecological framework with reference to one of the most popular models in population dynamics, the classical Lotka-Volterra system. More precisely, in [43], the effectiveness of the Z-control method to the Lotka-Volterra predator-prey system has been shown through a theoretical analysis of the convergence of the method and then substantiated by numerical simulations carried out for suitable choices of the design parameter λ . In this regard, it is also qualitatively stressed that the value of the design parameter cannot be too large and that a critical value of λ exists above which the control law is not effective.

The goal of this paper has been to show that, in the ecological context, the success as well as the possible failure of the Z-control method can be strictly related to specific dynamical properties of the resulting Z-controlled model.

As far as the success is concerned, we have shown that the capability of the Z-control approach to change the dynamics of the uncontrolled system – that is driven towards the controlled equilibrium P^* – is completely based on the fact that, by construction, P^* turns out to be the unique attractor for the Z-controlled model. Nevertheless, to avoid the failure of the Z-method within the ecological framework, the value of the design parameter λ needs to be carefully calibrated. We have shown that this last feature is essentially linked to the loss of positiveness for the solutions of the Z-controlled model and we have analytically derived quantitative constraints on the value of the design parameter λ . More precisely, for each given set of initial conditions (n_0, p_0) , two thresholds values $\lambda_{\min} = \lambda_{\min}(n_0, p_0)$ and $\lambda_{\max} = \lambda_{\max}(n_0, p_0)$ have been found such that choosing $\lambda \in [\lambda_{\min}, \lambda_{\max}]$ ensures the success of the Z-control approach. This analytical result turns out to be perfectly consistent with the ecological evidence that the control intensity which an ecological system can tolerate is obviously limited. In fact, the value of the design parameter λ represents the strength of the control exerted on the system and the two critical thresholds $\lambda_{\min}$ and $\lambda_{\max}$ respectively indicate the

minimum and maximum control intensity the system can sustain in order to successfully obtain the desired species coexistence.

Concerning the numerical approximation, in this paper we rely on the Matlab code ode45 for the solution of differential systems, with absolute and relative tolerance close to machine precision. This choice allows to reach high accuracy in order to minimize the effect of the numerical algorithm on the obtained results. Indeed, we stress that a bad choice of the numerical algorithm (or not enough request of accuracy to general purpose solvers) for the approximation of the system dynamics may induce in the long run numerical behaviors that do not correspond to any theoretical scenario. In this regard, we briefly remark that Lotka-Volterra model is a Poisson system that requires, for its numerical approximation, Poisson integrators [20], [8] (e.g., Symplectic Euler method and composition of symplectic Euler steps) in order to show a good long-time approximation. Poisson integrators that, starting from positive values, also preserve positive solutions regardless the value of the timestep and that is featured by an explicit functional form, are analyzed in [11] in the more general context of population dynamics.

To show the range of applicability of the Z-control approach we have considered two different ecological models. The first one is the classical Lotka-Volterra model for which we have revisited, within a dynamical system perspective, the results presented in [43]. Such results have also been enriched by quantitative indications about the range of the parameter λ ensuring the success of the Z-control method. The second example is a more realistic ecological model related to a case study of the wolf-wild boar dynamics in the Alta Murgia National Park in Italy, [24]. In a protected area, the choice of controlling the predator density through transplant/introduction by the park management is more feasible than massive removal/hunting of the prey. Also in this case, the Z-control turns out to be successful provided that the design parameter λ is chosen in a suitable range that we were able to estimate quantitatively.

The study of this latter ecological model has also clarified how the Z-control method can act in respect to different dynamical regimes of the uncontrolled system. In fact, in Section 4.2, two different dynamical behaviors have been considered for the uncontrolled model of the wolf-wild boar dynamics: (i) coexistence through an asymptotically stable equilibrium and (ii) coexistence through predator-prey self-sustained oscillations around an unstable equilibrium. For the same set of initial conditions $P_0 = (n_0, p_0) = (14, 0.0563)$, we have shown that λ has to be chosen

such that $0.5774 < \lambda < 1.8374$ to change the self-sustained oscillations into the desired controlled equilibrium P^* whereas λ needs to be such that $0.1240 < \lambda < 0.6224$ to change the uncontrolled stable equilibrium P_e into the desired controlled equilibrium P^* . This seems to suggest that it is relatively easier for the Z-method to turn oscillations of the uncontrolled model into the desired controlled equilibrium rather than to change the uncontrolled equilibrium P_e into the desired controlled equilibrium P^* . In fact, in this latter case, a very small range of λ allow the method to be successful whereas dynamical regimes as oscillations – allowing a larger range of λ – seem to oppose less resistance to the efficacy of the Z-method. This result may hence enable a preventive analysis of the Z-method feasibility in respect to different ecological models.

Moreover, investigations on the basin of attraction of the controlled equilibrium P^* in the two different ecological models have allowed: (i) to identify the ecological basin of attraction of P^* , i.e. the portion of the theoretical basin of attraction of P^* corresponding to initial conditions such that the related trajectories keep positive for all time; (ii) to better highlight the role of the parameter λ ; in fact higher values of λ have the effect of enlarging the ecological basin of attraction of the Z-controlled equilibrium leading to situations of higher ecological resilience [40].

We stress that the Z-control laws – that we have applied in this paper to two-species predator–prey models – can be easily generalized to the case of multispecies systems. This point is particularly crucial in order the Z-control to be potentially applied in ecosystem services management since in many contexts it could be enough difficult – if not impossible – to isolate just two species. This is the reason why in mathematical ecology the generalization of Lotka–Volterra type models to the case of N species has been widely studied [26,32,37,38] and a number of methods have been developed for solving non-traditional control problems of nonlinear networks models [12,33].

As a further remark on the potential applications of the Z-control in the management of protected areas, we consider the fish–zooplankton dynamics in alpine lakes, which will be object of further studies. This is typical cases where a control can be more easily applied on the predator than on the prey. As an example, we report the case of the Gran Paradiso National Park (GPNP) and a conservation issue the managing authority of the park have to face. In some GPNP lakes, the introduction of an allochthonous fish species, the brook trout (*Salvelinus fontinalis*) for leisure fishing purposes, performed in years when such fishing activities were permitted, is currently harming the lake ecosystem, by dramatically reducing the zooplankton populations, which include the rare species *Daphnia middendorffiana*, as well as the invertebrate and *Rana temporaria* populations, thus reducing biodiversity. To restore some of the original lake ecosystems present before the introduction of the brook trout, the ongoing European Life+ BIOAQUAE project has allowed to attempt the eradication of this fish from three test lakes. In GPNP, the eradication of the brook trout has profound ecological motivations. According to the International Union for the Conservation of Nature (IUCN) view, the introduction of non-indigenous species is the second greatest cause of the drastic loss of biodiversity that is affecting our planet, since the fast proliferation of alien species alters the delicate balance of the colonized ecosystems. Being fishery currently banned in the area, and for the above reason, in GPNP lakes there is no need for a controlled coexistence of allochthonous fishes and zooplankton. However, in some protected areas, where similar conditions apply and conservation issues are less severe, the managing authorities might be dealing with a trade-off between biodiversity preservation and the maintenance of provisional/cultural ecosystem services. For those cases, a solution may come from a control action on the predators, which might be implemented through a well designed deployment of traps.

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