



# Pervasive Threats and Optimal Control of *Lantana Camara* Invasion in an Ecosystem

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## Abstract

*Lantana camara* is a highly invasive plant species that poses serious ecological threats to native vegetation and herbivores in savanna ecosystems. This study develops and analyzes a mathematical model to understand the competitive dynamics between *L. camara*, native vegetation, and herbivores. The model incorporates interspecific competition, herbivory, and logistic growth, and it is extended to include three targeted control strategies: mechanical uprooting, biological control via insect introduction, and enhancement of competitive native species. Analytical results reveal conditions for species extinction and persistence, while sensitivity analysis identifies key parameters influencing the herbivore survival threshold. An optimal control problem is formulated and solved using Pontryagin's Maximum Principle and numerical simulations. Results indicate that individual controls can reduce *L. camara* impact, but an integrated approach yields the most ecologically beneficial outcomes, supporting native vegetation recovery and herbivore persistence. These findings offer a quantitative basis for designing effective, multi-pronged strategies to manage invasive species in complex ecosystems.

**Keywords** *Lantana camara* · Optimal control · Uprooting · Insect species · Competitive plants

## 1 Introduction

*Lantana camara* (*L. camara*), commonly known as tickberry or *lantana*, is a thicket-forming shrub that is very adaptive and can inhabit a variety of ecosystems [1]. Several species of *L. camara* are widely distributed in the tropics, subtropics, and warm temperate areas of the world and are naturalized in about 60 countries [2]. Since its introduction in around 1858 in Cape Town from South and Central America [1], *L. camara* has invaded over 2 million hectares of land and is widely distributed in the provinces of KwaZulu-Natal,

Limpopo, Eastern Cape, Mpumalanga, and Gauteng [3]. It is rated as one of the worst 100 weeds in the world [4] and considered a weed of national concern in South Africa due to its invasiveness and negative impacts on agriculture and the environment [5]. With its ability to form dense and impenetrable thickets, *L. camara* can easily outcompete the native vegetation species. The effects of *L. camara* on the ecosystem include changes in fire regimes [6], hydrology [7] and soil properties [8, 9]. It can also reduce the composition [10] and diversity of the native vegetation species [5] and their consumers (herbivores). *L. camara* fruits, leaves, and stems have toxic compounds that, if consumed, can cause photosensitization, damage to organs, and even death in animals [11].

Despite the significant negative impacts of *L. camara* on ecosystems in different areas of the world, no standard control measures are in place for its effective management [3]. This could be due to factors such as widespread invasions with high density, huge associated costs, and poor accessibility of the invaded areas [2]. Among the methods for the management of *L. camara* spread, chemical control is believed to be the most effective [3]. However, chemicals are very expensive and not suitable for use in areas where herbivores exist, like nature reserves and game parks, due

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to their hazardous effects. The non-chemical measures that may be suitable for use in areas where herbivores live include: biological control where insect species are released into the invaded areas [3, 12]; mechanical control where small stands are uprooted by hand equipment or dense thickets cleared by a tractor [2]; and growing plant species such as *Helicteres isora*, *Petalidium barlerioides*, and *Olex scandens* that can outcompete *L. camara* [13]. These methods require continuous follow-up and high effort, which may be constrained by inadequate funding. There is a need to determine the cost-effectiveness of these control measures, which is important in designing sustainable management programs. Forming this as a mathematical control problem, we determine how the spread of *L. camara* can be managed cost-effectively using uprooting, insect species, or competitive plant species.

Mathematical models and optimisation are popular tools for assisting management in designing sustainable control programs and have been used to study the control of invasive plant species. Odom et al. [14] used a deterministic dynamic programming optimisation model to study the optimal management strategies for scotch broom in an Australian national park. Using a similar modelling approach as in [14, 15] explored the management strategies for Californian thistle in New Zealand. They showed that a combination of a biological control agent (an insect species that reduces the growth rate) with one or more control options is the optimal strategy. Chalak and Pannell [16] used a stochastic dynamic optimisation model to identify optimal strategies for an agricultural weed in Australia. They showed that the application of a biological control agent (*Phragmidium violaceum*) has little benefit and is not worth introducing. Whittle et al. [17] used a discrete model to determine whether it is best to control an invasive plant by controlling the epicentre of the weed, outlier populations, or a combination of these. Kern et al. [18] developed an ordinary differential equation model to analyze the impact of flooding as a control variable in growth terms for competition between cottonwood (native) and salt cedar (invasive). In this study, optimal control strategies for *L. camara* using an ordinary differential equation model are studied.

Following the consumer-resource model formulation approach used in the study by [19], an ordinary differential equation model for *L. camara*, native vegetation, and herbivore interactions is developed. It is known that a disturbed system can easily be invaded by alien species [20], we determine whether a high population density of herbivores (grazers and browsers) in an area such as a nature reserve or national park can aid the invasion of *L. camara*. In addition, the impacts of *L. camara* on the density of the native vegetation species and their consumers are established. The optimal control of *L. camara* spread is studied by analyzing the model for the effects of three control measures: uprooting, use of an

insect species, and artificial introduction of a competitive plant species using Pontryagin's Maximum Principle [21].

## 2 Methods

### 2.1 Model Formulation

An ordinary differential equation model for two vegetation species (native and alien) and an herbivore species (consumers of the native vegetation) in an ecosystem is formulated. In the model, let  $X(t)$  and  $Y(t)$  be the population densities for the alien species (*Lantana camara*) and the native vegetation species, respectively, and  $M(t)$  be the population density of herbivores that consume the native vegetation, all at time  $t$ .

The invasive species  $X$ , in the absence of  $Y$ , grows logistically with an intrinsic growth rate  $r_x$  and carrying capacity  $K_x$ , so its growth is governed by

$$\frac{dX}{dt} = r_x X \left( 1 - \frac{X}{K_x} \right).$$

Similarly, the native vegetation species  $Y$ , in the absence of  $X$  and  $M$ , grows logistically with intrinsic rate  $r_y$  and carrying capacity  $K_y$ :

$$\frac{dY}{dt} = r_y Y \left( 1 - \frac{Y}{K_y} \right).$$

These carrying capacities,  $K_x$  and  $K_y$ , represent the maximum biomass densities the environment can support for *L. camara* and native vegetation, respectively.

To account for interspecific competition, we modify the logistic terms to include the effects of competition for shared resources such as space, nutrients, and light. This yields:

$$\frac{dX}{dt} = r_x X \left( 1 - \frac{X + a_y Y}{K_x} \right), \quad \frac{dY}{dt} = r_y Y \left( 1 - \frac{Y + a_x X}{K_y} \right),$$

where  $a_y$  is the competition coefficient representing the impact of native vegetation on *L. camara*, and  $a_x$  is the competition coefficient representing the impact of *L. camara* on native vegetation. These terms reflect that the presence of one vegetation type can reduce the growth potential of the other due to limited resources [22].

The herbivores  $M(t)$  represented in this model are generalist grazers and browsers such as *impala*, *bushbuck*, and other ungulates commonly found in savanna and woodland ecosystems where *L. camara* has invaded. These animals primarily consume native vegetation, and their population dynamics are therefore tightly coupled to the availability of edible plant biomass.

As considered in the study by Turchin [23], herbivore-vegetation interactions are modeled using the hyperbolic functional response

$$\frac{bY}{\alpha + Y},$$

where  $b$  is the maximum vegetation removal rate by herbivores, and  $\alpha$  is the half-saturation constant (the vegetation density at which the removal rate is half of the maximum). In the absence of native vegetation, the herbivore population declines at a natural mortality rate  $\mu$ .

Combining all components, the full model becomes:

$$\begin{aligned} \frac{dX}{dt} &= r_x X \left( 1 - \frac{X + a_y Y}{K_x} \right), \\ \frac{dY}{dt} &= r_y Y \left( 1 - \frac{Y + a_x X}{K_y} \right) - \frac{bYM}{\alpha + Y}, \\ \frac{dM}{dt} &= \frac{bcMY}{\alpha + Y} - \mu M, \end{aligned} \quad (2.1)$$

with initial conditions  $X(0) \geq 0$ ,  $Y(0) \geq 0$ , and  $M(0) \geq 0$ .

The meanings and possible values of the parameters in system (2.1) are given in Table 1.

## 2.2 Parameter Sources and Assumptions

Table 1 lists the parameter values used in the model. Some of these values, such as the intrinsic growth rates and carrying capacities, were obtained directly from ecological studies on *L. camara* and native vegetation species. For example, Duffy et al. [24] simulated vegetation dynamics under herbivory in savannah ecosystems, which closely match the setting of our model, and provided baseline values for  $r_y$  and  $K_y$ . Osunkoya et al. [25] reported experimental data on the growth characteristics of *L. camara*, informing our choice for  $r_x$  and supporting the assumed range for  $K_x$ .

The herbivore consumption rate  $b$  was set to 0.006/day to reflect moderate grazing pressure from generalist herbivores such as impala and bushbuck, which typically consume 1.5–2.5% of their body mass per day in dry matter [26, 27]. Translating this to a per-area vegetation removal rate under realistic foraging conditions gives a value within the range 0.005–0.01/day. The chosen value ensures that herbivore persistence is ecologically viable (i.e.,  $bc > \mu$ ) without leading to excessive depletion of native vegetation, thereby maintaining long-term coexistence.

The half-saturation constant  $\alpha$  and conversion efficiency  $c$  were taken from Collins et al. [19], who studied herbivore feeding rates and biomass conversion in African savannah

**Table 1** Parameters values of the model (2.1)

| Parameter | Description                                                   | Unit             | Value  | Reference    |
|-----------|---------------------------------------------------------------|------------------|--------|--------------|
| $r_x$     | Intrinsic growth rate of <i>L. camara</i>                     | /day             | 0.01   | [25]         |
| $r_y$     | Intrinsic growth rate of the native vegetation                | /day             | 0.014  | [24]         |
| $K_x$     | Carrying capacity of <i>L. camara</i>                         | g/m <sup>2</sup> | 200    | Assumed      |
| $K_y$     | Carrying capacity of the native vegetation                    | g/m <sup>2</sup> | 235    | [24]         |
| $a_y$     | Effect of native vegetation on <i>L. camara</i>               | Dimensionless    | 0.1    | Assumed [22] |
| $a_x$     | Effect of <i>L. camara</i> on native vegetation               | Dimensionless    | 0.5    | Assumed [22] |
| $b$       | Removal rate of vegetation by herbivores                      | /day             | 0.025  | [26, 27]     |
| $\alpha$  | Half saturation constant of herbivores                        | g/m <sup>2</sup> | 50     | [19]         |
| $c$       | Conversion rate of vegetation biomass into that of herbivores | Dimensionless    | 0.8    | [19]         |
| $\mu$     | Natural mortality rate of herbivores                          | /day             | 0.0007 | [28]         |

contexts. Although their study did not focus specifically on *L. camara*, the vegetation types and herbivore species considered are ecologically similar to those in our model.

The natural mortality rate of herbivores  $\mu$  was set to 0.0007/day, based on typical adult survival rates of ungulates in African ecosystems, which range between 70 and 80% per year [28]. This corresponds to an average annual mortality rate of 20–30%, yielding a realistic daily rate of approximately 0.0007/day.

The completion parameters ( $\alpha_x$  and  $\alpha_y$ ) are not directly reported in the literature although they are estimated in [22]. Using these estimates, values were assumed within biologically plausible ranges based on competitive interactions. These assumptions ensure mathematical tractability and ecological realism.

### 2.3 Existence of the Equilibrium Points

The model (2.1) has the following equilibrium points:

- $E_1 = (0, 0, 0)$ : extinction of all species;
- $E_2 = (K_x, 0, 0)$ : only *L. camara* survives at its carrying capacity;
- $E_3 = (0, K_y, 0)$ : only the native vegetation survives at its carrying capacity;
- $E_4 = (X_4, Y_4, 0)$ : coexistence of *L. camara* and native vegetation without herbivores, where

$$X_4 = \frac{K_x - \alpha_y K_y}{1 - \alpha_y \alpha_x}, \quad Y_4 = \frac{K_y - \alpha_x K_x}{1 - \alpha_y \alpha_x}.$$

- $E_5 = (0, Y_5, M_5)$ : coexistence of native vegetation and herbivores only, where

$$Y_5 = \frac{\mu \alpha}{bc - \mu}, \quad M_5 = \frac{r_y c (K_y - Y_5) Y_5}{\mu K_y}.$$

- $E_6 = (X_6, Y_5, M_6)$ : coexistence of all three species, with

$$X_6 = (1 - \alpha_y \alpha_x) X_4 + \alpha_y (K_y - Y_5),$$

$$M_6 = \frac{r_y \alpha c (1 - \alpha_y \alpha_x) (Y_4 - Y_5)}{K_y (bc - \mu)}.$$

To ensure biological feasibility, certain conditions must be satisfied:

- For  $E_4$  to exist, we require  $0 < \alpha_y \alpha_x < 1$ . This ensures that both  $X_4$  and  $Y_4$  are positive. In other words, if inter-specific competition is not too strong which ensures both vegetation types to maintain positive densities.
- For  $E_5$ , the consumption-conversion threshold condition must be satisfied:

$$bc > \mu.$$

This guarantees a positive herbivore growth rate (when herbivore consumption and conversion rates are high enough to offset natural mortality). In addition,  $Y_5 = \frac{\mu \alpha}{bc - \mu}$  must satisfy  $Y_5 < K_y$  to be biologically meaningful.

- For  $E_6$ , in addition to the above conditions, we require  $Y_4 > Y_5$  so that the presence of *L. camara* does not suppress native vegetation below the level required to sustain the herbivores.

These conditions offer insights into ecological balances. For example, if herbivores overgraze or *L. camara* becomes too dominant, coexistence may break down, leading to species exclusion.

### 2.4 Stability of the Equilibrium Points

To assess the local stability of the equilibrium points, we compute the Jacobian matrix (A.1) of the system (2.1), as presented in Appendix A, evaluated at the equilibrium points given above.

An equilibrium point is locally asymptotically stable if all the eigenvalues of the Jacobian evaluated at that point have negative real parts. The stability of each equilibrium is analyzed below:

#### 2.4.1 Trivial Equilibrium $E_1 = (0, 0, 0)$

The eigenvalues are:

$$\lambda_1 = r_x, \quad \lambda_2 = r_y, \quad \lambda_3 = -\mu.$$

Since both *L. camara* and native vegetation have positive intrinsic growth rates ( $r_x, r_y > 0$ ),  $E_1$  is always unstable.

#### 2.4.2 Invasive-only Equilibrium $E_2 = (K_x, 0, 0)$

The eigenvalues are:

$$\lambda_1 = -r_x, \quad \lambda_2 = \frac{r_y (1 - \alpha_y \alpha_x) Y_4}{K_y}, \quad \lambda_3 = -\mu.$$

Here,  $Y_4 > 0$  if  $0 < \alpha_y \alpha_x < 1$ . Thus,  $\lambda_2 > 0$  and  $E_2$  is unstable (when native vegetation can grow in the presence of *L. camara*). This happens if competition is not too strong.

#### 2.4.3 Native-only Equilibrium $E_3 = (0, K_y, 0)$

The eigenvalues are:

$$\lambda_1 = \frac{r_x (1 - \alpha_y \alpha_x) X_4}{K_x}, \quad \lambda_2 = -r_y, \quad \lambda_3 = \frac{(bc - \mu) (K_y - Y_5)}{\alpha + K_y}.$$

This equilibrium is unstable when both  $X_4 > 0$  and  $Y_5 < K_y$ , i.e., when both *L. camara* and herbivores can establish. Specifically, when  $E_5$  exists (i.e.,  $bc > \mu$  and  $Y_5 < K_y$ ), the third eigenvalue is positive and hence  $E_3$  becomes unstable. Herbivores can thrive, and *L. camara* still has competitive room.

#### 2.4.4 Vegetation-only Coexistence Equilibrium

$$E_4 = (X_4, Y_4, 0)$$

$C_0$ , the consumption number, is a threshold value that determines the conditions under which the herbivores will survive or not in the system [19]. If  $C_0 < 1$ , the herbivores go extinct, and if  $C_0 > 1$ , they survive. This quantity is calculated for the model (2.1) in Appendix A.

The first two eigenvalues,  $\lambda_{1,2}$ , which have real parts less than unity, are provided in Appendix A. The third eigenvalue is given by  $\lambda_3 = \mu(C_0 - 1)$ , where  $C_0$  is the consumption number (Appendix A). Thus,

- If  $C_0 < 1$ , then  $\lambda_3 < 0$  and  $E_4$  is stable (herbivores go extinct).
- If  $C_0 > 1$ , then  $\lambda_3 > 0$  and  $E_4$  becomes unstable (herbivores can invade).

#### 2.4.5 Vegetation-herbivore Coexistence Equilibrium

$$E_5 = (0, Y_5, M_5)$$

The first eigenvalue is given by

$$\lambda_1 = \frac{r_x a_y}{K_x} \left( \frac{K_x}{a_y} - Y_5 \right).$$

The remaining eigenvalues,  $\lambda_{2,3}$ , which have negative real parts, are defined in Appendix A.

- $E_5$  is locally stable if  $Y_5 > \frac{K_x}{a_y}$  (so  $\lambda_1 < 0$ ). In other words, if the equilibrium vegetation density  $Y_5$  is sufficiently high to resist invasion by the alien species.
- If  $Y_5 < \frac{K_x}{a_y}$ , then  $\lambda_1 > 0$  and  $E_5$  becomes unstable due to potential *L. camara* invasion.

#### 2.4.6 Full Coexistence Equilibrium $E_6 = (X_6, Y_5, M_6)$

Analytical expressions for the eigenvalues at  $E_6$  are intractable, but numerical simulations in Sect. 4 suggest it is stable, representing a balanced, biodiverse ecosystem. The condition  $Y_4 > Y_5$  must hold for feasibility and to ensure that the vegetation level in the absence of herbivores is higher than what herbivores require to persist. In the next section, model (2.1) is transformed into an optimal control problem.

### 3 Optimal Control

In this section, optimal control analysis is performed to establish the best strategies for managing the pervasive effects of *L. camara* on native vegetation and herbivore species. Control functions  $\phi_1(t)$  and  $\phi_2(t)$  are introduced into model (2.1). The parameter  $a_y$ , which was considered a constant in the preceding analysis, now changes into a time-dependent variable  $a_y(t)$  to act as a control measure. The function  $\phi_1(t) \in [0, 1]$  is aimed at directly reducing the density of *L. camara*. This can be done by uprooting the plants [3]. The function  $\phi_2(t) \in [0, 1]$  is aimed at reducing the growth rate parameter  $r_x$  of *L. camara*. This can be achieved by using biological control agents such as a flower-feeding moth, a seed-feeding fly, a leaf-mining beetle, and a sap-sucking bug [29]. The control function  $a_y(t) \in [0, 1]$  is aimed at increasing the competition of native vegetation species against *L. camara*. This can be attained through the sowing of plant species such as *Helicteres isora*, *Petalidium barlerioides*, and *Olex scandens* that can outcompete *L. camara* [13]. The modified model becomes

$$\begin{aligned} \frac{dX}{dt} &= (1 - \phi_2(t))r_x X \left( 1 - \frac{X + a_y(t)Y}{K_x} \right) - \phi_1(t)X, \\ \frac{dY}{dt} &= r_y Y \left( 1 - \frac{Y + a_x X}{K_y} \right) - \frac{bYM}{\alpha + Y}, \\ \frac{dM}{dt} &= \frac{bcMY}{\alpha + Y} - \mu M. \end{aligned} \quad (3.1)$$

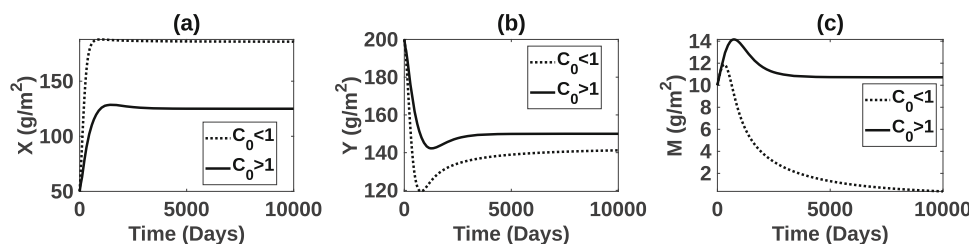
The objective is to minimize the density of *L. camara* and the cost of implementing the controls over a fixed time horizon  $[0, t_f]$ . This leads to the objective functional:

$$\begin{aligned} J(\phi_1, \phi_2, a_y) &= \int_0^{t_f} \left[ W_1 X(t) + \frac{1}{2} W_2 \phi_1^2(t) + \frac{1}{2} W_3 \phi_2^2(t) \right. \\ &\quad \left. + \frac{1}{2} W_4 a_y^2(t) \right] dt. \end{aligned} \quad (3.2)$$

where  $t_f$  is the total time of the control program,  $W_1 > 0$ ,  $W_2 > 0$ ,  $W_3 > 0$  and  $W_4 > 0$  are weights. We consider the control set:

$$\begin{aligned} \Phi &= \left\{ (\phi_1, \phi_2, a_y) : [0, t_f] \rightarrow [0, 1]^3 \right. \\ &\quad \left. \mid \text{each control is piecewise continuous} \right\}. \end{aligned}$$

Note that the upper bound of 1 for each control does not imply complete and instantaneous removal or suppression in a single time step. Rather, it represents the maximum feasible level of control effort or intensity achievable within a given



**Fig. 1** The dynamics of the model (2.1) at the equilibrium point  $E_4$  illustrating the extinction of the herbivore population (c) and the coexistence of *L. camara* and the native vegetation (a) and (b) if

$\mathcal{C}_0 = 0.99 < 1$ . It also illustrates a switch from  $E_4$  to  $E_6$  (coexistence of all species) if  $\mathcal{C}_0 = 1.04 > 1$ . The parameter values used are as given in Table 1 with the value of  $\alpha_y$  as stated in the text

time frame. For instance,  $\phi_1 = 1$  corresponds to the maximum feasible mechanical uprooting effort, not total removal of all Lantana in that time step. This formulation maintains biological realism while allowing mathematical tractability.

Using Pontryagin's Maximum Principle [21], we derive the optimality system consisting of the state equations (3.1), the adjoint (co-state) equations (B.1), and the control characterizations (B.2). Full derivations are presented in Appendix B. While we do not provide a formal proof of existence for the optimal control, the simulations in Sect. 4.3 yield admissible, bounded, piecewise continuous controls and biologically meaningful state trajectories. The consistent convergence of these simulations and the improved objective functional values strongly support the practical existence and feasibility of an optimal control strategy for managing *L. camara*. The simulations in Sect. 4.3 are obtained using Runge–Kutta methods. The forward-backward sweep method [30] is used to numerically solve the optimality system by iteratively integrating the state system forward in time and the adjoint system backward in time until convergence.

and  $E_5$ , the native vegetation competition parameter  $\alpha_y$  is set at different values. For  $E_4$ , setting  $\alpha_y = 0.5$  leads to  $\mathcal{C}_0 = 1.04 > 1$ , and  $\alpha_y = 0.1$  results in  $\mathcal{C}_0 = 0.99 < 1$ . For  $E_5$ , setting  $\alpha_y = 0.7$  results in the real parts of the eigenvalues of Eq. A.3 being negative ( $\text{Re}(\lambda_1) < 0$ ,  $\text{Re}(\lambda_2) < 0$ , and  $\text{Re}(\lambda_3) < 0$ ), and setting  $\alpha_y = 0.5$  leads to  $\lambda_1 > 0$ . The dynamics of the model (2.1) at  $E_4$  and  $E_5$  based on these conditions are depicted in Figs. 1 and 2, respectively.

From Fig. 1, when the consumption threshold  $\mathcal{C}_0 < 1$ , the trajectories of the model (2.1) approach a stable equilibrium  $E_4 = (X_4, Y_4, M_4) \approx (186, 142, 0)$  with the dominance of *L. camara* and extinction of the herbivore population. When  $\mathcal{C}_0 > 1$ , the model solutions approach a stable coexistence equilibrium  $E_6 = (X_6, Y_6, M_6) \approx (125, 150, 11)$ .

From Fig. 2a–c, when  $\alpha_y = 0.7$ , the native vegetation and herbivores coexist while *L. camara* goes extinct (the model trajectories approach  $E_5 \approx (0, 70, 41)$ ). On the other hand, when  $\alpha_y = 0.5$ , all the species coexist ( $E_5$  switches to  $E_6 \approx (25, 70, 35)$ ). The density of herbivores is higher at  $E_5$  than at  $E_6$ .

## 4 Numerical Results

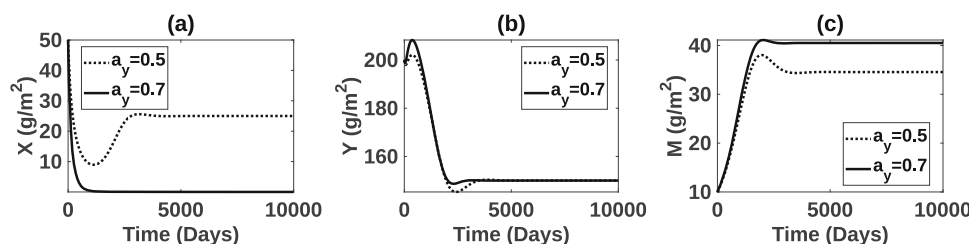
### 4.1 Model Dynamics

The analytical results presented in Sect. 2.4 are verified numerically using the parameter values given in Table 1. To obtain the stability conditions for the equilibrium points  $E_4$

### 4.2 Sensitivity Analysis

To determine the influence of each parameter on the threshold consumption number  $\mathcal{C}_0$ , the normalized forward sensitivity index is used, as introduced by Chitnis et al. [31]. This index is defined as

$$\gamma_{\tau}^{\nu} = \frac{\partial \nu}{\partial \tau} \times \frac{\tau}{\nu}. \quad (4.1)$$



**Fig. 2** The dynamics of the model (2.1) at  $E_5$  illustrating the extinction of *L. camara* (a) and the coexistence of the native vegetation and herbivores (b) and (c) for  $\alpha_y = 0.7$ . It also illustrates a switch from

$E_5$  to  $E_6$  with stable dynamics if  $\alpha_y = 0.5$ . The parameter values used are as given in Table 1 with the value of  $\alpha_y$  as stated in the text

**Table 2** Sensitivity index of  $\mathcal{C}_0$ . The parameter values used are as given in Table 1

| Parameter  | Sensitivity index |
|------------|-------------------|
| $\mu$      | -1.0000           |
| $\alpha$   | -0.2603           |
| $b$        | 1.0000            |
| $c$        | 1.0000            |
| $K_y$      | 0.4531            |
| $K_x$      | -0.1928           |
| $\alpha_x$ | -0.1791           |
| $\alpha_y$ | 0.0137            |

This formulation quantifies the relative change in an outcome variable  $v$  (here,  $\mathcal{C}_0$ ) in response to a relative change in the parameter  $\tau$ . A positive index ( $\Upsilon_\tau^v > 0$ ) indicates that an increase in  $\tau$  leads to an increase in  $v$ , while a negative index means that increasing  $\tau$  decreases  $v$ . This method is standard

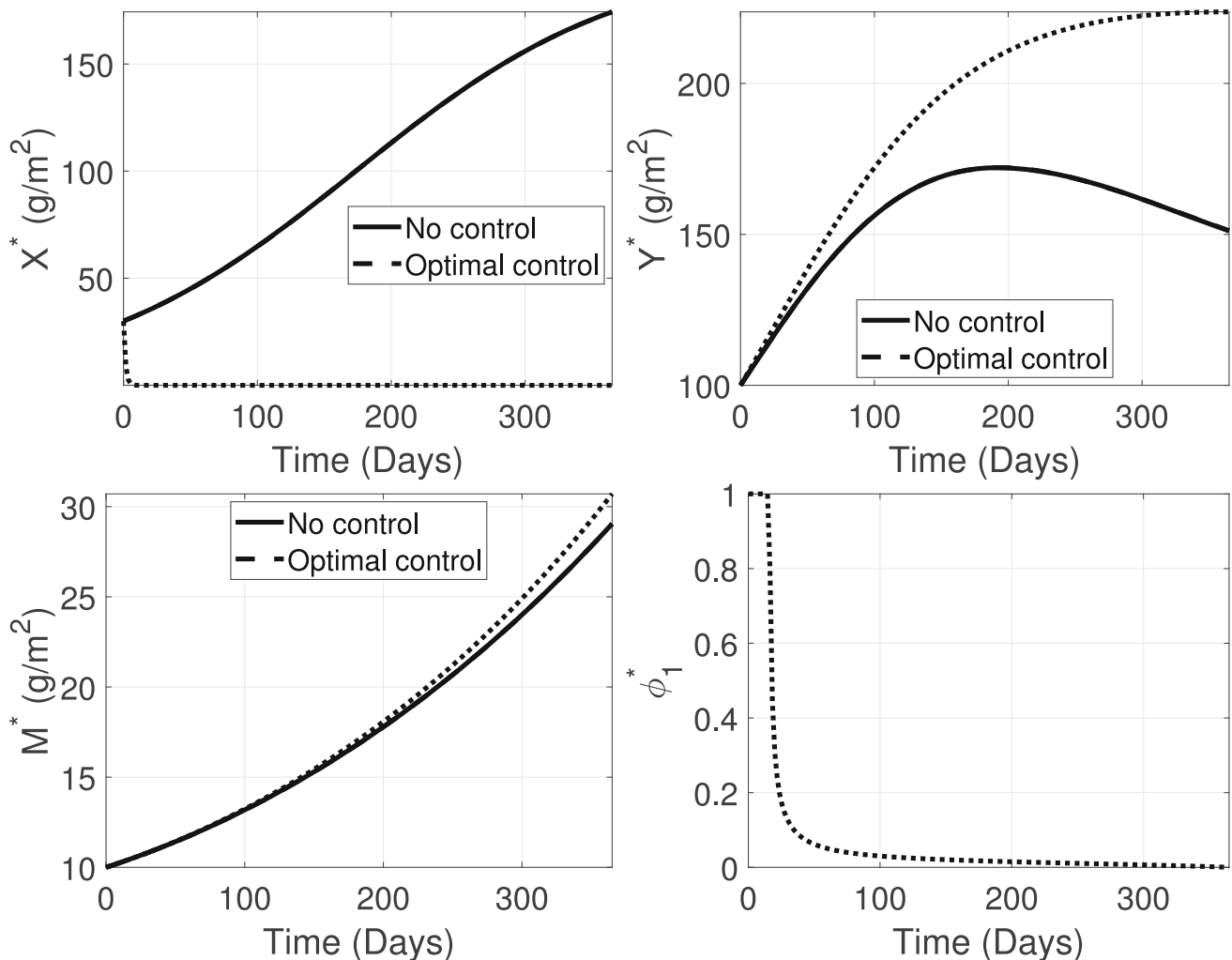
in mathematical biology and invasion modeling, allowing for comparison across parameters with different scales and units.

Using (4.1), the sensitivity indices of  $\mu$ ,  $b$ , and  $c$  are given by  $\Upsilon_\mu^{\mathcal{C}_0} = -1$ ,  $\Upsilon_b^{\mathcal{C}_0} = 1$ , and  $\Upsilon_c^{\mathcal{C}_0} = 1$ , respectively. The sensitivity indices of the remaining parameters are calculated from Eq. 4.1 using the parameter values in Table 1 and recorded in Table 2.

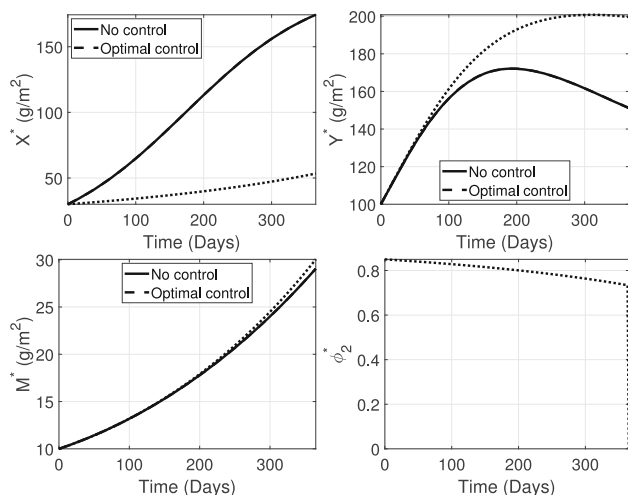
From Table 2, the parameters with the highest influence on the magnitude of  $\mathcal{C}_0$  are  $\mu$ ,  $b$ ,  $c$ , and  $K_y$ . The *L. camara* parameters  $\alpha_x$  and  $K_x$  have negative indices.

### 4.3 Optimal Control

The parameter conditions that can result in the worst-case scenario (where *L. camara* may lead to the extinction of herbivores) are considered. In other words, the conditions that lead to  $E_4$  (when  $\mathcal{C}_0 < 1$ ) as described in Fig. 1. The weights  $W_1, W_2, W_3$ , and  $W_4$  in the objective functional represent



**Fig. 3** Effects of a mechanical (uprooting) control strategy. The parameter values used are in Table 1. The initial conditions and weighting factors are as stated in the text



**Fig. 4** Effects of using an insect species strategy. The initial conditions and weighting factors are as stated in the text

the relative importance of minimizing the invasive *L. camara* density and the cost of implementing different control strategies. A high value is assigned to  $W_1 = 1000$  to reflect the significant ecological and long-term economic damage caused by the persistence of *L. camara*, including its adverse effects on biodiversity, native vegetation, and herbivore populations. The weight  $W_2 = 1$  is used to normalize the cost of direct manual removal (e.g., uprooting), which is labor-intensive and costly. Biological control, though slower and requiring ecological planning, is assumed to be less resource-

intensive; hence,  $W_3 = 0.5$ . On the other hand, promoting competition through native vegetation restoration is logistically demanding and may require extensive intervention, so a higher weight of  $W_4 = 2$  is assigned. Simulations are initialized with  $X(0) = 20$ ,  $Y(0) = 100$ , and  $M(0) = 10$ . The following control strategies are analyzed:

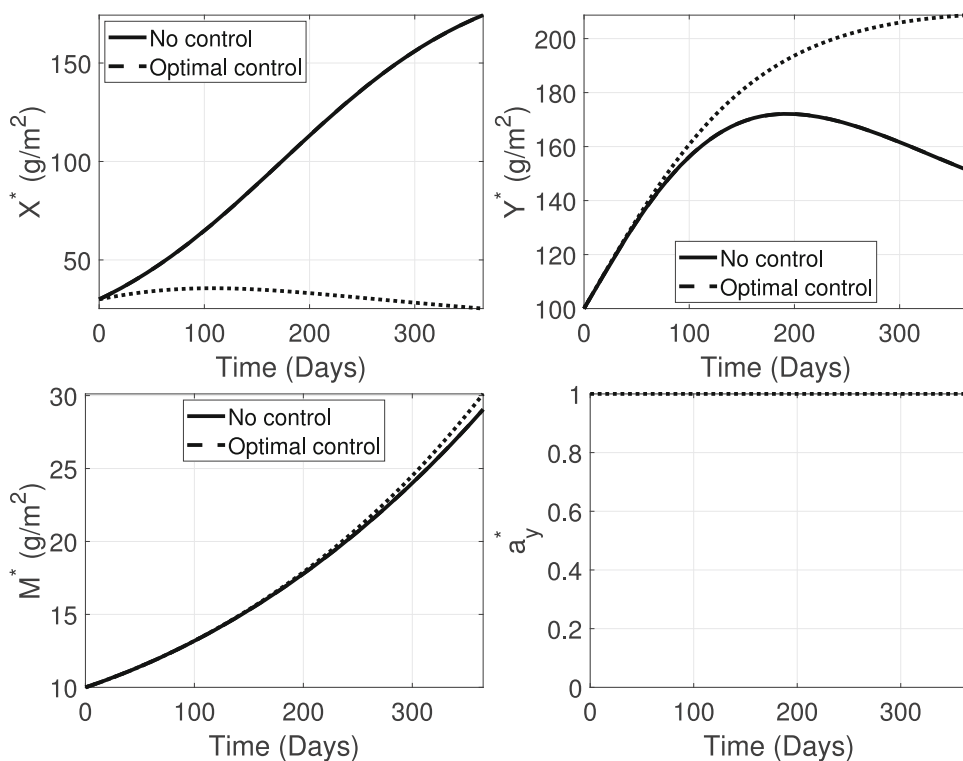
- (i) **Mechanical control strategy:**  $\phi_1 > 0$ ,  $\phi_2 = 0$ , and  $\alpha_y = 0$ .
- (ii) **Biological control strategy (insect species):**  $\phi_1 = 0$ ,  $\phi_2 > 0$ , and  $\alpha_y = 0$ .
- (iii) **Competitive vegetation strategy:**  $\phi_1 = 0$ ,  $\phi_2 = 0$ , and  $\alpha_y > 0$ .
- (iv) **Integrated control strategy:**  $\phi_1 > 0$ ,  $\phi_2 > 0$ , and  $\alpha_y > 0$ .

#### 4.3.1 Effects of Mechanical Control Strategy

Figure 3 presents the simulation outcomes under the application of mechanical control alone, represented by the control variable  $\phi_1$  (with  $\phi_2 = \alpha_y = 0$ ). The results indicate a marked decline in the population of *L. camara* due to sustained uprooting efforts. This suppression is most pronounced during the initial phase of the intervention, after which the invasive population remains consistently low.

The removal of *L. camara* enables the native vegetation to recover, showing a noticeable increase in biomass compared to the no-control scenario. Correspondingly, herbivore

**Fig. 5** Effects of using a competitive plant species strategy. The parameter values used are in Table 1. The initial conditions and weighting factors are as stated in the text



density improves over time, reflecting enhanced availability of native forage. The optimal control profile for  $\phi_1$  is high at the beginning and gradually drops, indicating that intense early effort is most effective for controlling the invasion while minimizing sustained resource input.

#### 4.3.2 Effects of Using an Insect Species

Figure 4 presents the system dynamics under the application of biological control using an insect species, modeled by the control variable  $\phi_2$ , with  $\phi_1 = \alpha_y = 0$ . The results show a notable reduction in the biomass of *L. camara* over time due to the suppressive effect of the insects on its intrinsic growth rate. As the invasive species declines, native vegetation begins to recover steadily. This resurgence leads to improved forage availability for herbivores, reflected in a gradual increase in their population. The control profile for  $\phi_2$  remains active for most of the simulation period, with a slightly decreasing intensity toward the end, indicating the need for sustained but reducing insect deployment.

#### 4.3.3 Effects of Using a Competitive Plant Species

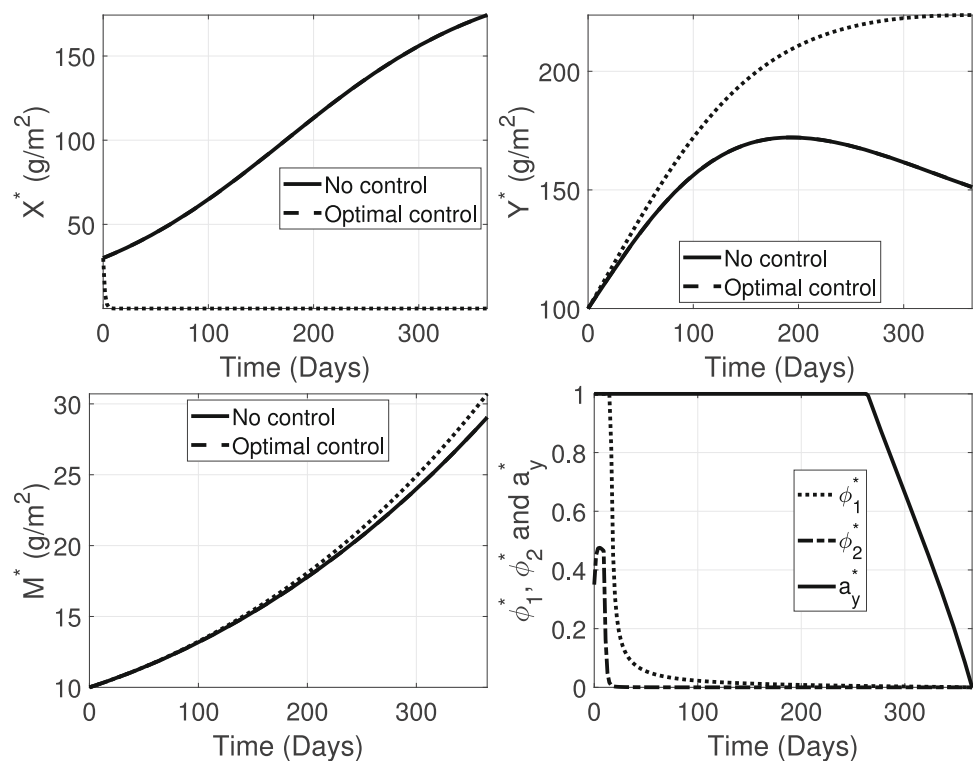
Figure 5 illustrates the impact of introducing competitive native plant species, modeled through the control variable  $\alpha_y$ , with  $\phi_1 = \phi_2 = 0$ . The simulation shows a grad-

ual reduction in the density of *L. camara* over time, as the increased competition for shared environmental resources limits its growth. The native vegetation biomass increases steadily, particularly during the mid-to-late stages of the control period. This recovery supports a parallel rise in herbivore population due to the improved forage availability. The control profile for  $\alpha_y$  remains relatively active throughout the simulation period, indicating that sustained competition is necessary to maintain ecological pressure on the invasive species.

#### 4.3.4 Effects of an Integrated Approach

Figure 6 presents the system's dynamics under a combined control strategy, where uprooting ( $\phi_1$ ), insect deployment ( $\phi_2$ ), and competitive planting ( $\alpha_y$ ) are applied simultaneously. The results demonstrate a strong suppression of *L. camara*, similar in trend to the uprooting-only scenario (Fig. 3), with a steep decline in its population early in the control period. The optimal control profiles reveal varying intensities over time: uprooting starts strong but decreases gradually, insect control is sustained at moderate levels, and competition remains active throughout. This demonstrates that timing and coordination among controls are critical for maximizing ecological restoration.

**Fig. 6** Effects of using all the three control strategies simultaneously. The parameter values used are in Table 1. The initial conditions and weighting factors are as stated in the text



### 4.3.5 Cost Comparison of the Control Strategies

To demonstrate the cost-effectiveness of candidate optimal controls, we compute and compare the values of the objective functional under six scenarios given in Table 3.

Table 3 presents the computed values of the objective functional under various control strategies. The simulated optimal control strategy, which dynamically adjusts the control functions over time, yields the lowest objective value ( $J = 4506$ ), indicating the most effective balance between suppressing *L. camara* and minimizing control costs. In comparison, the maximum constant control strategy ( $\phi_1 = \phi_2 = \alpha_y = 1$ ) significantly reduces the objective value relative to the no-control scenario, but remains over six times less efficient than the optimal control. Among the single-control strategies, uprooting alone ( $\phi_1 \neq 0$ ) is markedly more cost-effective ( $J = 4838$ ) than either biological control ( $\phi_2 \neq 0$ ) or competitive planting ( $\alpha_y \neq 0$ ), which both result in objective values exceeding 32 million.

## 5 Discussion

A deterministic model (2.1) for two vegetation species (native and alien) and a herbivore species (consumers of the native vegetation) is presented and used to determine the pervasive effects of *L. camara* in an ecosystem. The equilibrium points of the model and consumption threshold ( $\mathcal{C}_0$ ) are obtained and analyzed. Using optimal control theory, the model is also used to analyze the effects of four control strategies: mechanical uprooting, the introduction of competitive native plant species, the use of insect species that reduce the growth rate of *L. camara*, and an integrated strategy that combines all three approaches.

As expected, if the consumption threshold is less than unity, the herbivores go extinct, and they persist if it is greater than unity (Fig. 1). Sensitivity analysis of  $\mathcal{C}_0$  with respect to model parameters reveals that the carrying capacity ( $K_x$ ) and the competition rate ( $\alpha_x$ ) parameters of *L. camara* have negative sensitivity indices (Table 2). This indicates that an increase in these parameters will decrease the magnitude of  $\mathcal{C}_0$ , which can result in the extinction of the herbivores.

This finding aligns with observations by [32], which demonstrate that areas dominated by *L. camara* are associated with reduced mammal abundance and diversity.

From Fig. 2, when the consumption number  $\mathcal{C}_0$  is less than the threshold  $\frac{K_y}{\alpha}$ , which represents the ratio of the native vegetation's carrying capacity to the herbivore's half-saturation constant, and the competition rate of native vegetation ( $\alpha_y$ ) is large, *L. camara* fails to invade the ecosystem. However, if  $\mathcal{C}_0 > \frac{K_y}{\alpha}$ , this indicates that herbivore pressure on native vegetation is excessive. In such a case, herbivores consume vegetation at a rate that depletes it below its regenerative capacity, a classic feature of *overgrazing or browsing*. This weakens native vegetation's competitive ability, thus creating ecological space that can be exploited by invasive species like *L. camara*. This finding aligns with the study by [20], which emphasize that disturbed systems are more susceptible to invasion. Thus, to avoid *L. camara* invasion, overgrazing needs to be avoided, and this can be done by reducing the population of herbivores (as indicated by the negative sensitivity index of the removal rate ( $\mu$ ) in Table 2) through authorized hunting and/or translocation.

The simulation results of mechanical control through uprooting (Fig. 3) reveal that early and targeted intervention can effectively suppress *L. camara* populations. This strategy reduces competitive stress on native plants, thereby promoting their regrowth. As native vegetation recovers, herbivores benefit indirectly, demonstrating the cascading ecological value of vegetation management. Interestingly, the optimal control effort is concentrated in the early stages, suggesting that short-term intensive action may be more cost-effective than prolonged moderate intervention. This aligns with ecological management practices where early eradication of invasive species often leads to better long-term outcomes [33]. However, while mechanical control alone improves ecosystem structure, integrating it with other strategies, such as biological or competitive planting, may offer greater resilience against reinvasion and environmental variability.

The results in Fig. 4 indicate that insect-based biological control is an ecologically viable approach to managing *L. camara*. By directly reducing the growth capacity of the invasive species, the insects help suppress its dominance,

**Table 3** Comparison of objective functional values under different control strategies

| Control strategy                                                 | Objective value J |
|------------------------------------------------------------------|-------------------|
| No control ( $\phi_1 = \phi_2 = \alpha_y = 0$ )                  | 37,612,840        |
| Maximum control ( $\phi_1 = \phi_2 = \alpha_y = 1$ )             | 30,638            |
| Optimal integrated approach ( $\phi_1^*, \phi_2^*, \alpha_y^*$ ) | 4506              |
| Optimal uprooting ( $\phi_1^*$ )                                 | 4838              |
| Optimal insect species ( $\phi_2^*$ )                            | 32,765,489        |
| Optimal competitive plant species ( $\alpha_y^*$ )               | 37,569,583        |

thereby facilitating the recovery of native vegetation. This strategy is advantageous because it requires minimal habitat disruption and, once established, can provide long-term suppression with moderate maintenance [34]. The associated improvement in herbivore population underscores the broader ecological benefits of this method. The sustained activity of the control profile for this strategy suggests that long-term success may depend on continued ecological monitoring and reinforcement of the insect population to maintain effective suppression levels.

Enhancing ecological competition via the introduction of vigorous native plants (Fig. 5) provides a sustainable, indirect mechanism to limit *L. camara* spread. Unlike direct removal or suppression, this approach works indirectly by improving the resource competitiveness of native vegetation. The consistent activity of this strategy throughout the simulation period suggests that the continued presence of strong native competitors is required to suppress *L. camara* effectively. This finding aligns with ecological restoration principles that promote plant community resilience as a barrier to invasion [35]. By restoring native biodiversity and structural complexity, the ecosystem becomes less susceptible to reinvasion and more capable of sustaining herbivore populations in the long term.

The integrated control strategy combining mechanical removal, biological agents, and competitive planting (Fig. 6) demonstrates synergistic benefits beyond what any single method achieves. While mechanical uprooting alone produces comparable short-term reductions in *L. camara* biomass, the combined approach enhances native species recovery and stabilizes herbivore populations more robustly. This synergy likely arises because each control targets different ecological processes: mechanical control reduces existing biomass, biological control inhibits regrowth, and competitive planting limits reinvasion. Consequently, the integrated method offers superior long-term ecosystem restoration and reduced control burden, making it a more robust and practically desirable solution.

The cost comparison (Table 3) clearly demonstrates that an integrated, time-dependent control strategy is essential for the effective and economical management of *L. camara* infestations. The substantially lower objective function value

achieved under the simulated optimal control emphasizes the importance of dynamically adjusting control intensity rather than applying static or maximum-effort strategies. Interestingly, uprooting alone produced results comparable to the integrated approach, suggesting that mechanical removal may serve as a practical and efficient stand-alone intervention when resource constraints limit broader implementation. In contrast, relying solely on insect-based biological control or competitive planting yielded outcomes nearly indistinguishable from inaction, implying these methods are costly in isolation and should be used only as complementary tactics.

Overall, if left uncontrolled, *L. camara* can drive herbivore extinction by altering ecosystem dynamics, with its establishment often facilitated by overgrazing of native vegetation. Effective management requires a multifaceted strategy integrating mechanical uprooting, biological control, and competitive native planting. Early and intensive uprooting significantly reduces invasive biomass and fosters native vegetation recovery, while combining it with ecological interventions enhances long-term ecosystem stability and herbivore persistence. The model highlights that dynamic, optimal control efforts outperform static interventions by balancing ecological benefits and implementation costs. Importantly, biological and competitive methods are insufficient when applied alone but serve as valuable complements within an integrated management framework. These findings support adaptive, cost-effective strategies that prioritize early intervention and sustained ecological restoration to mitigate *L. camara*'s pervasive threats. Future research could extend the model spatially to examine how dispersal agents such as birds and rodents influence *L. camara*'s spread.

## Appendix. Mathematical Details

In this section, the mathematical details referenced in the text are presented.

### A: Jacobian Matrix and Stability Conditions

The Jacobian matrix of system (2.1) at any point  $E_j = (X_j, Y_j, M_j)$ ,  $j = 1, 2, \dots, 6$  is:

$$J(E_j) = \begin{bmatrix} r_x \left( 1 - \frac{2X_j + a_y Y_j}{K_x} \right) & -\frac{r_x X_j a_y}{K_x} & 0 \\ -\frac{r_y Y_j a_x}{K_y} & r_y \left( 1 - \frac{2Y_j + a_x X_j}{K_y} \right) - \frac{b M_j \alpha}{(\alpha + Y_j)^2} & -\frac{b Y_j}{\alpha + Y_j} \\ 0 & \frac{b c M_j \alpha}{(\alpha + Y_j)^2} & \frac{b c Y_j}{\alpha + Y_j} - \mu \end{bmatrix}. \quad (\text{A.1})$$

The following are the eigenvalues of Eq. A.1 for each equilibrium point.

- For  $E_1$ , the eigenvalues are:  $\lambda_1 = r_x$ ,  $\lambda_2 = r_y$  and  $\lambda_3 = -\mu$ .
- For  $E_2$ , the eigenvalues are:  $\lambda_1 = -r_x$ ,  $\lambda_2 = \frac{r_y(1 - a_y a_x)Y_4}{K_y}$  and  $\lambda_3 = -\mu$ .
- For  $E_3$ , the eigenvalues are:  $\lambda_1 = \frac{r_x(1 - a_y a_x)X_4}{K_x}$ ,  $\lambda_2 = -r_y$  and  $\lambda_3 = \frac{(bc - \mu)(K_y - Y_5)}{\alpha + K_y}$ .
- For  $E_4$  the eigenvalues are:

$$\begin{aligned}\lambda_1 &= \frac{-1}{2} \left( \frac{r_x X_4}{K_x} + \frac{r_y Y_4}{K_y} \right) \\ &\quad + \frac{1}{2} \sqrt{\left( \frac{r_x X_4}{K_x} - \frac{r_y Y_4}{K_y} \right)^2 + \frac{4a_y a_x r_x r_y X_4 Y_4}{K_x K_y}}, \\ \lambda_2 &= \frac{-1}{2} \left( \frac{r_x X_4}{K_x} + \frac{r_y Y_4}{K_y} \right) \\ &\quad - \frac{1}{2} \sqrt{\left( \frac{r_x X_4}{K_x} - \frac{r_y Y_4}{K_y} \right)^2 + \frac{4a_y a_x r_x r_y X_4 Y_4}{K_x K_y}}, \\ \lambda_3 &= \mu(\mathcal{C}_0 - 1),\end{aligned}$$

where

$$\mathcal{C}_0 = \frac{bc(K_y - a_x K_x)}{[(1 - a_x a_y)\alpha + K_y - a_x K_x]\mu}. \quad (\text{A.2})$$

The real parts of  $\lambda_1$  and  $\lambda_2$  are negative. The eigenvalue  $\lambda_3 < 0$  if  $\mathcal{C}_0 < 1$ . The quantity  $\mathcal{C}_0$  is the consumption number. It is a threshold value that determines the conditions under which the herbivores will survive or not in the system (2.1) [19]. This quantity has the same interpretation as the basic reproduction number ( $R_0$ ) for disease systems. For the model (2.1), if  $\mathcal{C}_0 < 1$ , the herbivores go extinct, and if  $\mathcal{C}_0 > 1$ , they survive.

- For  $E_5$  the eigenvalues are:

$$\begin{aligned}\lambda_1 &= \frac{r_x a_y}{K_x} \left( \frac{K_x}{a_y} - Y_5 \right), \\ \lambda_2 &= \frac{1}{2K_y bc} \left( A(\mathcal{C}_1 - \frac{K_y}{\alpha}) \right. \\ &\quad \left. + \sqrt{\left[ A(\mathcal{C}_1 - \frac{K_y}{\alpha}) \right]^2 - 4\mu^2 r_y K_y bc(\alpha + K_y)(\mathcal{C}_1 - 1)} \right), \\ \lambda_3 &= \frac{1}{2K_y bc} \left( A(\mathcal{C}_1 - \frac{K_y}{\alpha}) \right. \\ &\quad \left. - \sqrt{\left[ A(\mathcal{C}_1 - \frac{K_y}{\alpha}) \right]^2 - 4\mu^2 r_y K_y bc(\alpha + K_y)(\mathcal{C}_1 - 1)} \right),\end{aligned}$$

where  $\mathcal{C}_1 = \frac{K_y bc}{\mu(\alpha + K_y)}$  and  $A = \frac{\mu^2 \alpha r_y (\alpha + K_y)}{K_y (bc - \mu)}$ .  $\mathcal{C}_1 = \mathcal{C}_0$  if  $a_x = a_y = 0$ . Thus,  $\mathcal{C}_1$  is the consumption threshold in the absence of competition between native vegetation species and *L. camara*. The eigenvalues  $\lambda_2$  and  $\lambda_3$  for  $E_5$  have negative real parts if  $\mathcal{C}_1 < \frac{K_y}{\alpha}$ . On the other hand, the eigenvalue  $\lambda_1 < 0$  if  $Y_5 > \frac{K_x}{a_y}$ .

- For  $E_6$ , analytical results of the equilibrium point cannot easily be obtained; numerical results are given in Sect. 4.

## B: Hamiltonian and Optimality Conditions

The Hamiltonian associated with the optimal control problem is:

$$\begin{aligned}\mathcal{H} &= W_1 X + \frac{1}{2} W_2 \phi_1^2 + \frac{1}{2} W_3 \phi_2^2 + \frac{1}{2} W_4 a_y^2 \\ &\quad + \lambda_1 \left[ r_x X \left( 1 - \frac{X + a_y Y}{K_x} \right) (1 - \phi_2) - \phi_1 X \right] \\ &\quad + \lambda_2 \left[ r_y Y \left( 1 - \frac{Y + a_x X}{K_y} \right) - \frac{bYM}{\alpha + Y} \right] \\ &\quad + \lambda_3 \left[ \frac{bcMY}{\alpha + Y} - \mu M \right].\end{aligned}$$

The adjoint equations are obtained as:

$$\frac{d\lambda_1}{dt} = -\frac{\partial \mathcal{H}}{\partial X}, \quad \frac{d\lambda_2}{dt} = -\frac{\partial \mathcal{H}}{\partial Y}, \quad \frac{d\lambda_3}{dt} = -\frac{\partial \mathcal{H}}{\partial M},$$

with transversality conditions  $\lambda_i(t_f) = 0$  for  $i = 1, 2, 3$ .

The adjoint variables  $\lambda_1(t)$ ,  $\lambda_2(t)$ , and  $\lambda_3(t)$  corresponding to the state variables  $X(t)$ ,  $Y(t)$ , and  $M(t)$  satisfy the following differential equations:

$$\begin{aligned}\theta'_1 &= -W_1 - \theta_1 \left\{ (1 - \phi_2) r_x \left( 1 - \frac{2X^* + a_y Y^*}{K_x} \right) - \phi_1 \right\} \\ &\quad + \theta_2 \frac{a_x r_y Y}{K_y}, \\ \theta'_2 &= \theta_1 \frac{a_y (1 - \phi_2) r_x X}{K_x} - \theta_2 r_y \left( 1 - \frac{2Y^* + a_x X^*}{K_y} \right) \\ &\quad + \frac{bM^* \alpha}{(\alpha + Y^*)^2} (\theta_2 - c\theta_3), \\ \theta'_3 &= \frac{bY^*}{\alpha + Y^*} (\theta_2 - c\theta_3) + \theta_3 \mu,\end{aligned} \quad (\text{B.1})$$

with terminal (transversality) conditions:

$$\lambda_1(t_f) = \lambda_2(t_f) = \lambda_3(t_f) = 0.$$

The optimal controls are obtained by minimizing the Hamiltonian with respect to each control variable. It is important to note that the condition  $\frac{\partial \mathcal{H}}{\partial u} = 0$  (for a control  $u$ ) is only valid when the optimal control lies in the interior of the admissible control set  $[0, 1]$ . To handle potential boundary values, we use the standard projection (min–max) formulation, which ensures the controls remain within admissible bounds.

The optimal controls are characterized by minimizing the Hamiltonian with respect to each control variable, leading to:

$$\begin{aligned}\phi_1^* &= \max\left\{0, \min\left(1, \frac{\theta_1 X^*}{W_2}\right)\right\}, \\ \phi_2^* &= \max\left\{0, \min\left(1, \frac{\theta_1 r_x X^*}{W_3} \left(1 - \frac{X^* + a_y Y^*}{K_x}\right)\right)\right\}, \quad (\text{B.2}) \\ a_y^* &= \max\left\{0, \min\left(1, \frac{\theta_1 r_x (1 - \phi_2) X^* Y^*}{W_4 K_x}\right)\right\}.\end{aligned}$$

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**Data Availability** No datasets were generated or analyzed during the current study.

## Declarations

**Competing Interests** The authors declare no competing interests.

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