Mathematical Modelling of Plant-Pathogen-Herbivore Interaction Incorporating Allee Effect and Harvesting

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Authors' contributions

This work was carried out in collaboration among all authors. Author IKB designed the study, performed the statistical analysis, wrote the protocol and wrote the first draft of the manuscript. Authors SBA and AOW managed the analyses of the study. All authors read and approved the final manuscript.

Original Research Article

Abstract

Plant-pathogen-herbivore model describe interaction between plants, pathogens and herbivores. Plants are invaded by pathogens and herbivores while the herbivores are harvested by natural enemies such as predators and human. On the other hand, the abundance of food does not guarantee exponential growth of species who reproduce sexually and plants governed by carrying capacity. Therefore, the Allee effect may be crucial for sustaining such species. In this paper, a model of plant-pathogen-herbivore interactions that takes Allee effect and harvesting into account was developed and analyzed. The stability analysis showed that the ratio intrinsic growth rate to the environmental carrying capacity of susceptible plants must be greater than certain threshold value to raise sufficient plant biomass to sustain other species. Numerical simulations shows that all species coexist when intrinsic growth rate of plants is greater than the harvesting rate and when conversion rate of what is eaten by herbivores to newborn ones is greater than that of their natural enemies. It also shows that in the absence of susceptible plants, herbivores migrates in search of food, while others deteriorate and dies out. Furthermore, regardless of the availability of susceptible plants, the herbivores population crashes to extinction if the herbivore population is less than the lower limit required to keep the herbivores existing in the ecosystem.

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In the interest of conservation of all species and the environment, policy developers will greatly benefit from understanding the solutions to address clearing land for human settlement, human activities and herbivore or their natural enemies hunting. In addition, monitor species closely, especially those that reproduce sexually by establishing and maintaining the least number required to keep the species existing.

Keywords: Ecology; Allee effect; harvesting; extinction.

2010 Mathematics Subject Classification: 53C25; 83C05; 57N16.

1 Introduction

All types of organisms coexist in different habitats. Given that all species feed on their varied food sources to provide them with energy for life, growth, and development, their sources of food link them together within these ecosystems. For instance, plants produce their own food from water and sunlight, whereas animals feed on other species in order to survive. Therefore, the law of nature for all living things in every ecosystem is based on the struggle for food, with the weak being eliminated from the ecosystem while the strong species survive [1, 2, 3]. Interactions between species have an impact on an ecosystem biomass, productivity, and population size of each species [4]. As a result, the existence of all species is necessary for an ecosystem to be in balance. According to [1, 5], the entire ecosystem equilibrium will change if one type is abundant or scarce.

The biological process of herbivory involves a species (herbivore) feeding on plants or their byproducts. The plant-herbivore interaction is one of the fundamental interactions between species in an ecosystem that shapes the natural habitats found in all ecosystems [6, 7, 8]. The presence of herbivores hinders the growth, development, and reproduction of plants. The plant-herbivore model assumed that plants are only invaded by herbivores with analogy of classical predator prey interaction. However, this may not be the case in real life situation since plants are also affected by other environmental perturbations. For instance, human activities where plants are cleared for settlement and human activities. Furthermore, the model did not incorporate other species and phenomenon including plant pathogens, species harvesting, Allee effect and natural enemies of herbivores whose behaviors govern the ecosystem were assumed [9, 6, 10, 11]. Pathogens also invades plants, according to [12]. This pathogens causes modifications that modify plant-insects interactions, plant fitness and growth. In turn, this modification has an impact on the kind and number of pollinators that the plants can attract, which may lower plant reproduction. On the other hand, pathogens may have an impact on plant-herbivore interactions by modifying plant qualities that serve as cues for herbivores.

Allee effect and harvesting of species have been incorporated in the interaction of the plant-herbivore models [1, 2, 11]. However, the models did not incorporate plant pathogen and natural enemies of herbivores. In addition [1, 11] did not incorporate harvesting of species. On other hand, the plant-pathogen-herbivore models, for instance [13, 14] did not incorporate the Allee effect and harvesting of species. Yet, the unpredicted collapse of many harvested species is just one illustration of the need to bring Allee effect to the forefront of conservation and management strategies of the ecosystem. The Allee effect phenomena is a fundamental ecological mechanism that establishes lower limits on a species' density below which population crash to extinction [15, 16]. There are a variety of mechanism that create Allee effect, including mating systems, predation, environmental modification, the smallest group size essential to successfully rear offspring, produce seeds, increase genetic inbreeding among others [17, 11].

On the other hand, harvesting involves elimination of the species from the ecosystem [3]. For instances, through forest fire, prolonged drought, deforestation where plants are cleared for farming, settlement and charcoal burning. In addition herbivores can be harvested through predators who prey on herbivores, diseases which may lead to death, migration and natural calamities like fire and drought or through human activities such as hunting of herbivores and natural enemies of herbivores. Therefore, it is very important to find out how harvesting of species and Allee effect may affect the interaction of species who are governed by the environmental carrying capacity such as plants and those that are assumed to reproduce sexually where the abundance of food does not guarantee exponentially growth of the species.

In this paper, plant-pathogen-herbivore model incorporating Allee effect and harvesting where plants serve as food for pathogen and herbivores. In this study, other plants are harvested where plants are cleared for human activities which when may affect the plant population densities. On the other hand, herbivores are harvested through hunting by their natural enemies or migration from one habitat to another. The objective of this paper is to formulate and analyze a mathematical model of plant-pathogen-herbivore interaction incorporating Allee effect and harvesting. In the second section, we describe Plant-Pathogen-Herbivore model incorporating Allee effect and harvesting along with posistivity and boundedness of the solution of the model. In the third section, the stability properties of various equilibrium points of the model was analyzed. The fourth section deals with numerical simulations of the model to verify the theoretical results obtained graphically and this paper ends with conclusion presented in the last section.

2   The Model

In this study, different types of population densities at time t are considered. The plant population is divided into susceptible plant population denoted by $S(t)$ that comprises of the plant population that are at risk of being invaded by pathogens. The infected plant is denoted by $I(t)$ it comprises of the plant population that are already invaded by the pathogens. On the other hand, $H(t)$ and $Y(t)$ are the herbivore population and their natural enemies population respectively. The model is governed by the following system of ordinary differential equations:

$$
\begin{aligned}
\frac{dS}{dt} &= S[r(1 - \frac{S}{k}) - \frac{\eta I}{1 + aS} - p_1 H - \epsilon] \\
\frac{dI}{dt} &= I[\frac{\eta S}{1 + aS} - \sigma - \epsilon] \\
\frac{dH}{dt} &= H[c_1 p_1 S(\frac{H}{\theta + H}) - \mu - p_2 Y] \\
\frac{dY}{dt} &= Y[c_2 p_2 H - d]
\end{aligned}
$$

(2.1)

With initial conditions given by $S(0) \geq 0$, $I(0) \geq 0$, $H(0) \geq 0$ and $Y(0) \geq 0$

Where, r is the intrinsic growth rate of susceptible plants, k is the environmental carrying capacity, η is the pathogen transmission rate and a is the preventive measures taken by susceptible plants to protect themselves from invasion. The term p_1 and p_2 are the consumption rate of susceptible plant-herbivore and predation rate herbivore-natural enemies respectively. Furthermore, c_1 and c_2 are corresponding conversation rates of what is eaten to newborns by herbivores and natural enemies of herbivores respectively. The parameter, μ is the removal rate of herbivores in the habitat. The mortality rate of the natural enemies of herbivores is denoted by d and σ is the mortality rate of the infected plants due to pathogens attack. The parameter ϵ is the harvesting rate of susceptible and infected plant population while θ is the Allee threshold.

The assumption of this model are as follows:

(i) Herbivores feed on the susceptible plants thus the infected plants survive until killed by pathogens or harvested due to less attack by herbivores.

(ii) Infected plants are less attractive to pollinators than healthy plants thus no reproduction of infected plants.

(iii) Susceptible plant population grows bounded by the carrying capacity of the environment in absence of herbivores, pathogens and harvest.

(iv) The species interaction and consumption are assumed to be of the same type in any ecosystem. The only difference could be due to different kingdom or families which is typical for ecological systems.

The equation $\frac{dS}{dt}$ describes how susceptible plant populations are attacked by pathogens, herbivores, and harvesting of in the system of equation (2.1). The carrying capacity of the ecosystem controls the expansion of the susceptible plant populations in the absence of pathogens, herbivores, and harvesting. Infected plant populations interact according to the equation $\frac{dI}{dt}$, where some plants die from pathogen invasion at a rate denoted by σ while others can be harvested at a rate denoted by ϵ. The rate of herbivore reproduction is expressed in the first term of the equation $\frac{dH}{dt}$. This demonstrates that an individual herbivore will reproduce more if it eats more, and will be wiped out in the absence of susceptible plants, i.e. $c_1 p_1(0)(\frac{H}{\theta+H}) = 0$.

Due to the fact that $c_1 p_1 S(\frac{H}{\theta+H})$ goes to zero when susceptible plant population density disappears. The coexistence of the herbivore population is very crucial and is protected by $(\frac{H}{\theta+H})$ because it is believed that herbivores reproduce sexually, each individual herbivore strives to locate mates or avoids inbreeding. Allee Constant takes care of this to ensure that the number of herbivores doesn't go to extinction.

2.1   Invariant region

It is crucial to demonstrate positivity and boundedness of the solutions of the system of equation (2.1) since the variables indicate biological population densities. Positivity denotes population survival, and boundedness denotes a growth limitation brought on by natural resource constraints. For the model to be mathematically and biologically well posed, the state variables $S(t)$, $I(t)$, $H(t)$ and $Y(t)$ at all time must be non-negative. This implies that the positive quadrant $\mathbb{R}_4^+ = [(S, I, H, Y) \in \mathbb{R}_4 : S \geq 0, I \geq 0, H \geq 0, Y \geq 0]$ is positively invariant. This will be done by showing positivity and boundedness of the formulated model. This is shown by the lemma as follows:

Lemma 2.1. (Positivity) All solutions $[S(t), I(t), H(t), Y(t)]$ of the system of equation (2.1) starting in $(S_0, I_0, H_0, Y_0) \in \mathbb{R}_4^+$ remain positive for all $t > 0$.

Proof. The positivity of $S(t), I(t), H(t), Y(t)$ can be verified by the equations:

$$\frac{dS}{dt} = S[r(1 - \frac{S(t)}{k}) - \frac{\eta I}{1+aS(t)} - p_1 H(t) - \epsilon]$$

Let $v = t$ then $dv = dt$. Substituting in equation above and integrating both sides, we have

$$\frac{dS}{dv} = S[r(1 - \frac{S(v)}{k}) - \frac{\eta I}{1+aS(v)} - p_1 H(v) - \epsilon]$$

$$\frac{dS}{S} = [r(1 - \frac{S(v)}{k}) - \frac{\eta I}{1+aS(v)} - p_1 H(v) - \epsilon]dv$$

$lnS = \int_0^t [r(1 - \frac{S(v)}{k}) - \frac{\eta I}{1 + aS(v)} - p_1 H(v) - \epsilon]dv + S_0$

Introducing exponential, we have

$S(t) = S_0 exp \int_0^t [r(1 - \frac{S(v)}{k}) - \frac{\eta I}{1 + aS(v)} - p_1 H(v) - \epsilon]dv$

Applying, the same on entire system of equation (2.1), we have

$I(t) = I_0 exp \int_0^t [\frac{\eta S(v)}{1 + aS(v)} - \sigma - \epsilon]dv$

$H(t) = H_0 exp \int_0^t [c_1 p_1 S(v)(\frac{H}{\theta + H}) - \mu - p_2 Y(v)]dv$

$Y(t) = Y_0 exp \int_0^t [c_2 p_2 H(v) - d]dv$

with $S_0, I_0, H_0, Y_0 > 0$. If $S(0) = S_0 \geq 0$ then $S(t) > 0$ for all $t > 0$. The same argument is valid for $I(t)$, $H(t)$ and $Y(t)$. Hence $int(\mathbb{R}_4^+)$ is positively invariant set. $\square$

Lemma 2.2. (Boundedness) All solutions of system of equation (2.1) will lie in the region $A = [(S, I, H, Y) \in \mathbb{R}_4^+ : 0 \leq S + I + H + Y \leq \frac{B}{\gamma}]$ for all positive initial values $(S(0), I(0), H(0), Y(0)) \in \mathbb{R}_4^+$ where $\gamma = \min(r, \sigma, \epsilon, \mu, d)$ and $B = rk + c_1 c_2$.

Proof. Let us consider the function $Z(t) = S + I + H + Y$

Taking the derivative along a solution of system of equation (2.1)

$\frac{dZ(t)}{dt} = S[r(1 - \frac{S}{k}) - \epsilon] - I(\sigma + \epsilon) - \mu H - dY$

For each $\gamma > 0$, the following inequality is satisfied:

$\frac{dZ}{dt} + \gamma Z \leq B + (\gamma - r)S + (\gamma - \epsilon)S + (\gamma - \sigma)I + (\gamma - \epsilon)I + (\gamma - \mu)H + (\gamma - d)Y$

Now choose γ such that $0 < \gamma = \min(r, \epsilon, \sigma, \mu, d)$ the the above equation can be written as

$\frac{dZ}{dt} + \gamma Z \leq B$

By comparison theorem [18], we obtain

$0 \leq Z(S(t), I(t), H(t), Y(t)) \leq \frac{B}{\gamma} + Z(S(0), I(0), H(0), Y(0))/e^{\gamma t}$

Taking limit when $t \to \infty$, we have

$0 \leq Z(t) \leq \frac{B}{\gamma}.$

Hence the system of equation (2.1) is bounded. $\square$

Clearly, the total population is bounded. Therefore, each sub-population S, I, H, Y is bounded for all future times. Thus the system of equation (2.1) is biologically and mathematically well posed.

3 Model Analysis

3.1 Equilibrium points

In order to find the equilibrium points or steady states of the model system, we set the right hand side of the system of equations (2.1) equal to zero. The following equilibrium points are clearly present in the system of equation (2.1):

$E_0 = (0,0,0,0)$, $E_1 = (\frac{k(r-\epsilon)}{r}, 0, 0, 0)$, $E_2 = (0, 0, \frac{d}{c_2 p_2}, \frac{-\mu}{p_2})$, $E_3 = (S_3, I_3, 0, 0)$, $E_4 = (S_4, 0, H_4, Y_4)$, and the last equilibrium point of the system is $E_5 = (S_5, I_5, H_5, Y_5)$. Where:

$S_3 = \frac{-\epsilon-\sigma}{-\eta+a\epsilon+a\sigma}$

$I_3 = \frac{r-\epsilon-\frac{ra(-\epsilon-\sigma)^2}{k(-\eta+a\epsilon+a\sigma)^2}-\frac{r(-\epsilon-\sigma)}{k(-\eta+a\epsilon+a\sigma)}+\frac{ra(\epsilon-\sigma)}{(-\eta+a\epsilon+a\sigma)}-\frac{dp_1}{c_2 p_2}-\frac{da(-\epsilon-\sigma)p_1}{(-\eta+a\epsilon+a\sigma)c_2 p_2}}{\eta}$

$S_4 = \frac{-dkp_1+krc_1 p_2-k\epsilon c_2 p_2}{rc_2 p_2}$

$H_4 = \frac{d}{c_2 p_2}$

$Y_4 = \frac{-d^2 kc_1 p_1^2-dr\mu c_2 p_2+dkrc_1 c_2 p_1 p_2-dk\epsilon_1 c_2 p_1 p_2-r\theta\mu c_2^2 p_2^2}{rc_2 p_2^2(d+\theta c_2 p_2)}$

$S_5 = \frac{-\epsilon-\sigma}{-\eta+a\epsilon+a\sigma}$

$I_5 = \frac{r-\epsilon-\frac{ra(-\epsilon-\sigma)^2}{k(-\eta+a\epsilon+a\sigma)^2}-\frac{r(-\epsilon-\sigma)}{k(-\eta+a\epsilon+a\sigma)}+\frac{ra(\epsilon-\sigma)}{(-\eta+a\epsilon+a\sigma)}-\frac{dp_1}{c_2 p_2}-\frac{da(-\epsilon-\sigma)p_1}{(-\eta+a\epsilon+a\sigma)c_2 p_2}}{\eta}$

$H_5 = \frac{d}{c_2 p_2}$

$Y_5 = -\mu + \frac{(-\epsilon-\sigma)c_1 p_1}{-\eta+a\epsilon+a\sigma} - \frac{\theta(-\epsilon-\sigma)c_1 p_1}{-\eta+a\epsilon+a\sigma(\theta+\frac{d}{c_2 p_2})}$

3.2 Local stability

Stability analysis examines the solutions of differential equation formulated and trajectories of dynamical systems under small perturbations of initial conditions. In this study, local stability analysis of the system of equation (2.1) is performed. This involves examining the jacobian matrix of the model around the equilibrium points where the characteristic roots(eigenvalues) from characteristic equations are obtained. Using this eigenvalues, the behavior of the solutions of the model can be analyzed.

To examine the local stability of the equilibrium points E_0, E_1, E_2,E_3, E_4 and E_5, we have to find the eigenvalues of the jacobian matrix of the system of equation (2.1) around the equilibrium points. The jacobian matrix of system of equation (2.1) at any given point $J(S,I,H,Y)$ is given by:

$$J(S,I,H,Y) = \begin{bmatrix} b_{11} & \frac{\eta S}{(1+aS)} & -p_1 S & 0 \\ \frac{\eta I}{(1+aS)^2} & \frac{\eta S}{1+aS}-\sigma-\epsilon & 0 & 0 \\ Hc_1 p_1(\frac{H}{(\theta+H)}) & 0 & c_1 p_1 S(\frac{H(2\theta+H)}{(\theta+H)^2})-\mu-p_2 Y & -p_2 H \\ 0 & 0 & c_2 p_2 Y & c_2 p_2 H - d \end{bmatrix} \quad (3.1)$$

Where, $b_{11} = r[1-\frac{2S}{k}]-\frac{\eta I}{(1+aS)^2}-p_1 H-\epsilon$

The stability of the equilibrium points are determined by the nature of the eigenvalues of the jacobian matrix evaluated at the corresponding equilibrium points. Evaluating the Jacobian matrix at the population free equilibrium point $E_0 = (0,0,0,0)$ takes the form;

$$J(E_0) = \begin{bmatrix} r - \epsilon & 0 & 0 & 0 \\ 0 & -\sigma - \epsilon & 0 & 0 \\ 0 & 0 & -\mu & 0 \\ 0 & 0 & 0 & -d \end{bmatrix} \tag{3.2}$$

Where the eigenvalues of $J(E_0)$ are give by $\lambda_1 = -\mu$, $\lambda_2 = r - \epsilon$, $\lambda_3 = -\sigma - \epsilon$ and $\lambda_4 = -d$ which are real. Clearly, $E_0 = (0,0,0,0)$ is unstable for $r > \epsilon$ and stable if $r < \epsilon$. Therefore, regardless of the values of other parameters, the ecological species do not exist at the population-free equilibrium point. This could happen as a result from the occurrence of prolonged droughts or forest fires. These occurrences could result in the extinction of all species in the habitat. However, at long run, when $r < \epsilon$ the plant population may grow and the system becomes stable.

At equilibrium point $E_1 = (\frac{k(r-\epsilon)}{r}, 0, 0, 0)$, the Jacobrium matrix takes the form:

$$J(E_1) = \begin{bmatrix} -r + \epsilon & 0 & -p_1 \frac{k(r-\epsilon)}{k} & 0 \\ 0 & -\sigma - \epsilon & 0 & 0 \\ 0 & 0 & -\mu & 0 \\ 0 & 0 & 0 & -d \end{bmatrix} \tag{3.3}$$

The eigenvalues of $J(E_1)$ are given by $\lambda_1 = -\mu$, $\lambda_2 = -r + \epsilon$, $\lambda_3 = -\sigma - \epsilon$, $\lambda_4 = -d$ which are real. Therefore E_1 is locally asymptotically stable for $r > \epsilon$ otherwise unstable if $r < \epsilon$. This demonstrates that the population of susceptible plants can grow logistically up to the environment's carrying capacity in the absence of pathogens, herbivores, and a high rate of harvesting. This is a biological observation because, given a certain piece of ground with sufficient soil resources, no pathogens or herbivores, and a low harvest rate, plant populations can expand to the maximum extent that the land would support. The absence of herbivores in a limited ecosystem also ensures the extinction of herbivores' natural enemies. The system is stable when intrinsic growth rate of susceptible plant is greater than their harvesting rate $(r > \epsilon)$ otherwise, the system is unstable when intrinsic growth rate is less than the harvesting rate $(r < \epsilon)$.

The Jacobian matrix evaluated at $E_2 = (0, 0, \frac{d}{c_2 p_2}, \frac{-\mu}{p_2})$ takes the form:

$$J(E_2) = \begin{bmatrix} r - \epsilon - p_1 H_2 & 0 & 0 & 0 \\ 0 & -\sigma - \epsilon & 0 & 0 \\ H_2 c_1 p_1 (\frac{H_2}{\theta + H_2}) & 0 & -\mu & \frac{-d}{c_2} \\ 0 & 0 & -\mu c_2 & 0 \end{bmatrix} \tag{3.4}$$

Where the eigenvalues of $J(E_2)$ are given by $\lambda_1 = r - \epsilon - p_1 \frac{d}{c_2 p_2}$, $\lambda_2 = -\sigma - \epsilon$, $\lambda_3 = \frac{1}{2}(-\mu - \sqrt{\mu(4d + \mu)})$ and $\lambda_4 = \frac{1}{2}(-\mu + \sqrt{\mu(4d + \mu)})$ which are real. The equilibrium point E_2 is a saddle point which is unstable for $r > \epsilon + p_1 \frac{d}{c_2 p_2}$ otherwise stable for $r < \epsilon + p_1 \frac{d}{c_2 p_2}$. Since no species exists in isolation and herbivore survival is fully dependent on the availability of food, in this case plants. Therefore, it is more likely that the population of herbivores will starve to death if they have little or no food available. Therefore, in the absence of populations of susceptible plants, the herbivore populations lacks a source of food and eventually become extinct. Furthermore, since the population of herbivores is declining as a result of a lack of food, the natural enemies of herbivores gradually die out or move to another area thus the system is unstable.

This situation is evident over the world, especially in arid and semi-arid regions and during extended droughts when plant populations decline owing to a lack of water or soil nutrients. For instance, Osborne [19] stated that during the drought of 1993 in Kenya, fewer herbivores were present in several ecosystems. According to reports, 70 percent of them perished from famine as a result of a lack of a source of food. This highlights the necessity of caring for the plant population, which serves

as food to herbivores, pathogens and a water catchment region. Evidently, lack of populations of plant species causes herbivores to die out, which causes the natural enemies of herbivores in the constrained habitat to become extinct.

Theorem 3.1. *If $\frac{r}{k} > r - \frac{\eta I_3}{(1+aS_3)^2} - \epsilon$ and $\frac{\eta S_3}{1+aS_3} < \sigma + \epsilon$ then E_3 is locally asymptotically stable.*

Proof. The jacobian matrix evaluated at $E_3 = (S_3, I_3, 0, 0)$ takes the form:

$$J(E_3) = \begin{bmatrix} r(1 - \frac{2S_3}{k}) - \frac{\eta I_3}{(1+aS_3)^2} - \epsilon & \frac{\eta S_3}{1+aS_3} & -p_1 S_3 & 0 \\ \frac{\eta I_3}{(1+aS_3)^2} & \frac{\eta S_3}{1+aS_3} - \sigma - \epsilon & 0 & 0 \\ 0 & 0 & -\mu & 0 \\ 0 & 0 & 0 & -d \end{bmatrix} \quad (3.5)$$

Clearly, the first two eigenvalues of $J(E_3)$ are given by $\lambda_1 = -d$ and $\lambda_2 = -\mu$. The other eigenvalues are given by the following characteristic equation;

$\lambda^2 - (A - E)\lambda + BC$ where $\lambda_3 = \frac{1}{2}(A - E - \sqrt{A^2 - 2AE + E^2 + 4BC})$, $\lambda_4 = \frac{1}{2}(A - E + \sqrt{A^2 - 2AE + E^2 + 4BC})$
Where $A = r(1 - \frac{2S_3}{k}) - \frac{\eta I_3}{(1+aS_3)^2} - \epsilon$, $B = \frac{\eta S_3}{1+\alpha S_3}$, $C = \frac{\eta I_3}{(1+aS_3)^2}$, $E = \frac{\eta S_3}{1+aS_3} - \sigma - \epsilon$ ☐

According to the theorem, the other two eigenvalues from the equation $\lambda^2 - (A - E)\lambda + BC$ are real and have a negative sign. As a result, we draw the conclusion that, subject to a few constraints, the equilibrium state E_3 is locally asymptotically stable. Evidently, the susceptible plant populations grows logistically to a specific threshold value needed to maintain the population when the rate of pathogen transmission and harvesting of the susceptible population is less than the intrinsic growth rate of the susceptible plant population. This holds in the absence of herbivores, who depend on populations of susceptible plants to survive, and when there is less harvesting of plant population.

Theorem 3.2. *The equilibrium point $E_4 = (S_4, 0, H_4, Y_4)$ is locally asymptotically stable if $\frac{r}{k} > r - \epsilon - p_1 H_5$ and $\frac{\eta S}{1+aS} < \sigma + \epsilon$*

Proof. The Jacobian matrix evaluated at E_4 takes the form:

$$\begin{bmatrix} r(1 - \frac{2S_4}{k}) - \epsilon - p_1 H_2 & -\frac{\eta S_4}{1+aS_4} & -p_1 S_4 & 0 \\ 0 & -\sigma - \epsilon + \frac{\eta S_4}{1+aS_4} & 0 & 0 \\ H_4 c_1 p_1(\frac{H_4}{\theta + H_4}) & 0 & -\mu - p_2 Y + c_1 p_1 S_4(\frac{H_4(2\theta + H_4)}{(\theta + H_4)^2}) & 0 \\ 0 & 0 & c_2 p_2 Y_4 & -d + c_2 p_2 H_4 \end{bmatrix} \quad (3.6)$$

Clearly, the first two eigenvalues at $J(E_4)$ are given by $-d + c_2 p_2 H_4 < 0$ and $-\epsilon - \sigma + \frac{\eta S_4}{1+aS_4} < 0$. The other two eigenvalues are given by the following equation.

$\lambda^2 - (A + F)\lambda - Ep_1 S_4 = 0$ where, $\lambda_3 = \frac{1}{2}(A + F - \sqrt{A^2 - 2AF + F^2 - 4Ep_1 S_4})$ and $\lambda_4 = \frac{1}{2}(A + F + \sqrt{A^2 - 2AF + F^2 - 4Ep_1 S_4})$

where $A = r(1 - \frac{2S_4}{k}) - \epsilon - p_1 H_2$, $F = -\mu - p_2 Y + c_1 p_1 S_4(\frac{H_4(2\theta + H_4)}{(\theta + H_4)^2})$ and $E = H_4 c_1 p_1(\frac{H_4}{\theta + H_4})$ ☐

The theorem implies that all the four eigenvalues at $J(E_4)$ are real and have negative signs. Therefore, we conclude that E_4 is locally asymptotically stable when $\frac{r}{k} > r - \epsilon - p_1 H_5$ and $\frac{\eta S}{1+aS} < \sigma + \epsilon$. The absence of infected plant population implies absence of pathogen in the system. Therefore, the plant population, herbivore population and natural enemies of herbivore population can coexist.

For the coexistence of the three species, the initial susceptible plant population must be greater than the minimum required to sustain the herbivore population. Similar to this, the initial population of

herbivores should be greater than the required number to maintain the population and provide food for natural enemies. For herbivores to ensure food availability, the average density of susceptible plant populations growth must be able to sustain each population

Theorem 3.3. *If $\frac{r}{k} > r - \frac{\eta I_5}{(1+aS_5)^2} - \epsilon$, then E_5 is locally asymptotically stable*

Proof. At positive interior equilibrium point of system of equation (2.1) about $E_5 = (S_5, I_5, H_5, Y_5)$ where

E_5 is feasible if

$r - \epsilon - \frac{ra(-\epsilon-\sigma)^2}{k(-\eta+a\epsilon+a\sigma)^2} - \frac{r(-\epsilon-\sigma)}{k(-\eta+a\epsilon+a\sigma)} + \frac{ra(\epsilon-\sigma)}{(-\eta+a\epsilon+a\sigma)} - \frac{dp_1}{c_2 p_2} - \frac{da(-\epsilon-\sigma)p_1}{(-\eta+a\epsilon+a\sigma)c_2 p_2} > 0$

and

$\frac{d\mu}{dc_1 p_1 + \mu a} < \frac{\sigma+\epsilon}{\eta} < \frac{1}{a}$

The Jacobian matrix evaluated at $J(E_5)$ reduces to

$$\begin{bmatrix} b_{12} & -\frac{\eta S_5}{1+aS_5} & -p_1 S_5 & 0 \\ \frac{\eta I_5}{(1+aS_5)^2} & -\sigma - \epsilon + \frac{\eta S_5}{1+aS_5} & 0 & 0 \\ H_5 c_1 p_1 (\frac{H_5}{\theta+H_5}) & 0 & -\mu - p_2 Y + c_1 p_1 S_5 (\frac{H_5(2\theta+H_5)}{(\theta+H_5)^2}) & 0 \\ 0 & 0 & c_2 p_2 Y_5 & -d + c_2 p_2 H_5 \end{bmatrix} \quad (3.7)$$

$b_{12} = r - \frac{2rS_5}{k} - \frac{\eta I_5}{(1+aS_5)^2} - \epsilon - p_1 H_5$

Choosing a positive definite function about E_5 given as

$W(t) = r_1(S - S_5)S(t) + r_2(I - I_5)I(t) + r_3(H - H_5)H(t) + r_4(Y - Y_5)Y(t)$ where r_1, r_2, r_3 and r_4 are positive constants chosen to be: $r_1 = 1, r_2 = 1 + aS_5$, $r_3 = \frac{1}{c_1}$, and $r_4 = \frac{1}{c_1 c_2}$

Differentiate W with respect to t along the solution of system of equation (3.1) we get

$\frac{dW}{dt} = r_1(S - S_5)\frac{dS(t)}{dt} + r_2(I - I_5)\frac{dI(t)}{dt} + r_3(H - H_5)\frac{dH(t)}{dt} + r_4(Y - Y_5)\frac{dY(t)}{dt}$

$\frac{dW}{dt} = r_1(S-S_5)[S(r(1-\frac{S}{k}) - \frac{\eta I}{1+aS} - p_1 H - \epsilon)] + r_2(I-I_5)[I(\frac{\eta S}{1+aS} - \sigma - \epsilon)] + r_3(H-H_5)[H(c_1 p_1 S(\frac{H}{\theta+H}) - \mu - p_2 Y)] + r_4(Y - Y_5)[Y(c_2 p_2 H - d)]$

Expanding $\frac{dW}{dt}$ about E_5, we obtain

$\frac{dW}{dt} = r_1(S - S_5)^2[r - \frac{2rS_5}{k} - \frac{\eta I_5}{(1+aS_5)^2} - \epsilon] - r_1 p_1(S - S_5)(H - H_5) + r_2[\frac{\eta}{(1+aS_5)^2}(I - I_5)(S - S_5)] - r_2(\sigma - \epsilon)(I - I_5) + r_3 c_1 p_1(\frac{H_5(2\theta+H_5)}{(\theta+H_5)^2})(H - H_5)(S - S_5) - r_3 p_2(H - H_5)(Y - Y_5) - r_3\mu(H - H_5) + r_4 c_2 p_2(H - H_5)(Y - Y_5) - r_4 d(Y - Y_5)$+Higher Order Terms

Such that the cross product $(S - S_5)(H - H_5)$, $(H - H_5)(Y - Y_5)$ and $(I - I_5)(S - S_5)$ equals to zero and we obtain

$\frac{dW}{dt} = r_1(S - S_5)^2[r - \frac{r}{k} - \frac{\eta I_5}{(1+aS_5)^2} - \epsilon] - r_2(\sigma + \epsilon)(I - I_5) - r_3\mu(H - H_5) - r_4 d(Y - Y_5)$

Hence if $\frac{r}{k} > r - \frac{\eta I_5}{(1+aS_5)^2} - \epsilon$ then $\frac{dW}{dt}$ is negative definite everywhere so that the value of W is decreasing along the solutions and W is a lyapunov function about E_5. The solution implies that on any level, they curve into the region bounded. Thus, E_5 is locally asymptotically stable. $\square$

The existence of locally stable positive interior equilibrium ensures the coexistence of susceptible plant population, infected plant population, herbivore population and natural enemies of herbivores

in the system. Therefore, the susceptible plant population grows to the carrying capacity when the intrinsic growth rate of plants r is greater that the rate of pathogen attack η and harvesting rate ϵ. Furthermore, herbivore population increases as result of availability of food. Similarly, natural enemies of herbivores increases. To maintain stability of the system, activities on the system that increase mortality rate of species should be controlled.

From biological point of view, the existence of E_5 demand

(i) The ratio of the intrinsic growth rate to carrying capacity for susceptible plant population must be greater than some threshold value to raise the plant biomass for herbivores and pathogens to feed on and become established.

(ii) The conversion rate of plant biomass eaten by herbivore to give rise to newborn must be greater than their harvest rate and predation rate of natural enemies to sustain the natural enemies population to guarantee the non-extinction of any species.

This ensures the long term survival and persistence of all population density, that is, none of the species goes to extinction.

4 Numerical Simulation of the Model

In this study, numerical simulations are performed by the use of MATLAB software using secondary data obtained from [2, 14]. These simulations are performed to analyze the effect of harvesting of species and Allee effect on the ecosystem where time is in years. This will help to verify theoretical results obtained graphically. The results obtained will give more insights and prediction of long term behaviour of the solutions.

4.1 Description of parameters

**Table 4.1. Description of the model parameters**

Parameter	Description	Units
r	Intrinsic growth rate of susceptible plants	Per year
k	Environmental carrying capacity	Assumed
η	Pathogen transmission rate	Per infected plant
a	Measure of inhibition effects taken by susceptible plants to protect themselves	per susceptible plants
p_1	Predation rate of plant-herbivore	per herbivore
p_2	Predation rate of herbivore-natural enemies	per natural enemy
c_1	Conversation rate of what is eaten to newborns by herbivores	per herbivore
c_2	Conversation rate of what is eaten to newborns by natural enemies of herbivore	per natural enemy of herbivores
ϵ	Harvest rate of plants	per total plant population
σ	Mortality rate of infected plants due to pathogens attack	per total infected plant population
θ	Allee constant	least herbivore number per total herbivore population
μ	removal rate of herbivores in the confined habitat	per total herbivore population
d	mortality rate of the natural enemies of herbivores	per total natural enemy population

4.2 Simulation for susceptible and infected plants interactions

To illustrate theorem 1, we simulate the susceptible and infected plant population over time using the values adopted from [14] where $r = 4.5$, $k = 5000$, $\sigma = 1.5$ and $a = 2$. The numerical simulation of susceptible and infected plants gives Fig. 1 and Fig. 2 shown below:
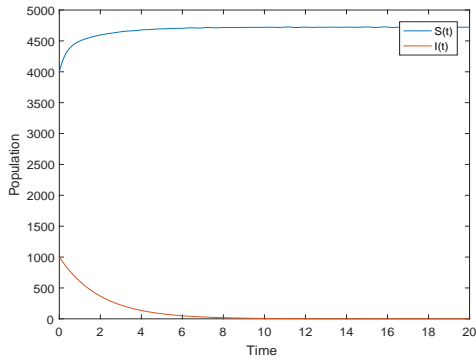

Fig. 1. $\eta = 2.5$, $\epsilon = 0.25$
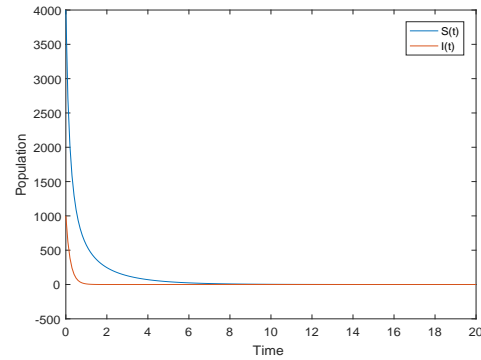

Fig. 2. $\eta > 3$, $\epsilon = 5$

From Fig. 1 when the intrinsic growth rate of susceptible plant density is greater than the transmission rate of pathogen or the susceptible plants are resistant to pathogens, the infected plants density reduces and goes to extinction. Furthermore, susceptible plant density grows to the environmental carrying capacity when transmission rate of pathogen is $\eta = 2.5$ and harvesting rate of plant population is $\epsilon = 0.25$. On the other hand when $\eta = 3.4$ and $\epsilon = 5$, the susceptible plant density and infected plant density becomes extinct over a time as seen in Fig. 2. Under certain restriction, the susceptible plants density and infected plant density coexists since pathogens may survive based on the prevailing climatic conditions and some pathogens must be at a critical life stage for them to cause infections.

4.3 Simulation of susceptible plants, herbivores and their natural enemies interaction
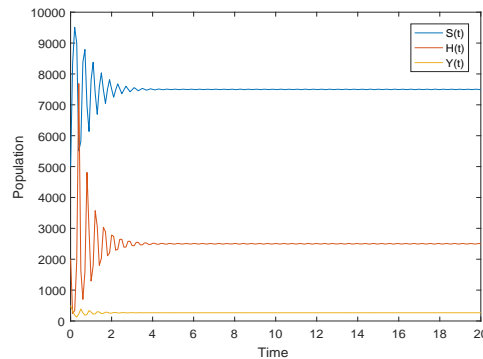
In the absence of pathogens, we have susceptible plants, herbivores and their natural enemies. Performing numerical simulation for this population dynamics using data adopted from [2, 14] where, $r = 20$, $k = 10000$, $c_1 = 1.22$, $\theta = 0.4$, $p_2, c_2 = 0.2$, $d = 0.2$ where we get the graphs in Fig. 3, Fig. 4 and Fig. 5.
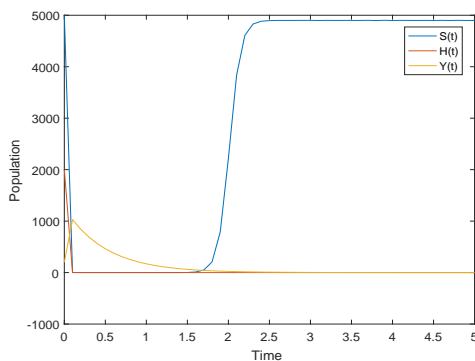
Fig. 3. $p_1 = 4$, $\mu = 0.2$ $\epsilon = 0.1$
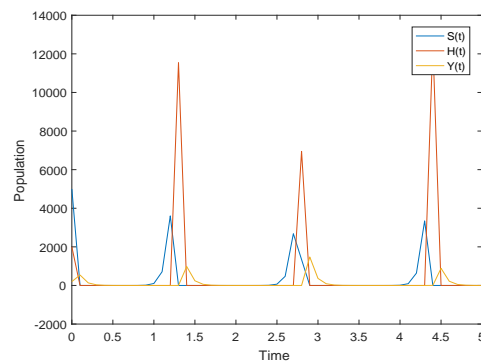
Fig. 4. $p_1 = 0.4, \mu = -0.14, \epsilon = 0.001$

**Fig. 5.**$p_1 = 0.002, d = 0.6, \mu = -0.14 p_2 = 0.12$

From Fig. 3, the susceptible plant population decreases drastically when the predation rate of herbivore and harvesting rate is high. This leads to increase of natural enemies of herbivores population due to availability of food(herbivores). When susceptible plant population becomes extremely small, the herbivores decrease and goes to zero implying the herbivores dies out or some migrate away as they look for food hence extinction of herbivore at that confined habitat. Similarly, the natural enemies of herbivores also die out or migrate to different habitat looking for food due to decrease of herbivore. In long run, the susceptible plant population regenerates, grows and eventually reaches the carrying capacity of the environment. This attract the herbivores who in turn attract their natural enemies back in the same habitat and the cycle occurs again as seen in Fig. 4.

Fig. 4 shows that the three populations depend on each other. The susceptible plant population is negatively affected by harvesting activities where they are harvested at the rate ϵ and herbivores feed on them at the rate p_1. On the other hand natural enemies of herbivores depend on the availability of food (herbivores) for survival. High herbivore population negatively affects the susceptible plant population and positively affects the natural enemies of herbivore population. With the reduction of susceptible plant density, the herbivore population also reduces due to limited sources of food. Likewise, the density of the natural enemies of herbivores declines. This implies that a decrease in one species may lead to a decrease of another species and also an increase in one species density imply an increase in other species densities. The cycle occurs again and again over time.
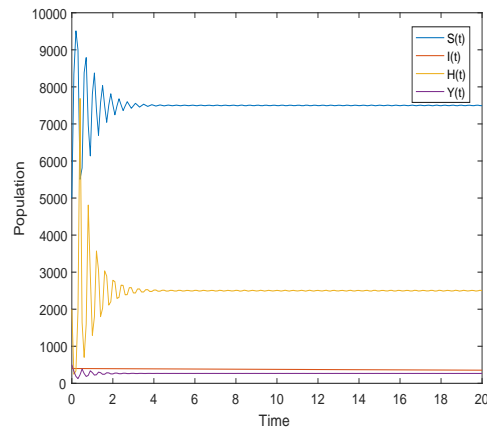
From the Fig. 5, the susceptible plants, herbivores and their natural enemies population coexists without attaining the specific equilibrium at first. However in the long run, the system becomes stable and the species coexists. The coexistence of the three species demands that the initial susceptible plant population must be above the minimum required with less harvesting to sustain herbivore population. On the other hand, the average density of newborn herbivores from herbivore mother must be greater than that of natural enemies of herbivores to secure food. The system becomes stable where the susceptible plant density is higher followed by herbivores then their natural enemies.

4.4 Simulation of susceptible plants, infected plants, herbivores and their natural enemies

For theorem 3, where we have the susceptible plants, infected plants, herbivores and their natural enemies populations with the following parameter values:$r = 4.8$, $k = 10000$, $p_1 = 0.002$, $c_1 = 1.22, \theta = 0.4, \mu = -14$, $p_2 = 0.12, c_2 = 0.02, \epsilon = 0.001, a = 10$, $\sigma = 0.025$ we obtain graphs in Fig. 6 and Fig. 7.
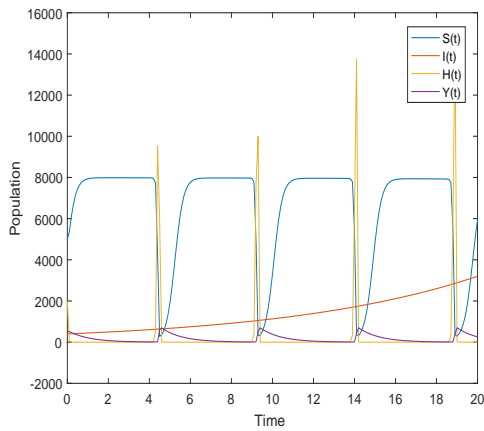
Fig. 6. $r = 4.8, d = 1, \eta = 1.3$

Fig. 7. $\eta = 0.2, d = 6$

From Fig. 6, the susceptible plants, herbivores and their natural enemies depend on each other. Presence of pathogens, herbivores and harvesting activities negatively affects the susceptible plant population where pathogens reduces the susceptible plant density at the rate σ. When pathogens, herbivore and harvesting of plant decrease in the habitat, the susceptible plant population grows bounded by the environmental carrying capacity. In the long run, this attract herbivores who may migrate to such habitat due to availability of food. This justify why μ is negative, which shows that herbivores migrate to the habitat where there is food. This in turn attract their natural enemies in the same habitat. When herbivore density, pathogens and harvest of plants density is high, the natural enemies of herbivore increases while on other hand the susceptible plant populations decreases. Decrease of susceptible plant population result into decrease of herbivores which in turn leads to decrease of natural enemies of herbivore population. When susceptible plants reduces to certain threshold, they regenerate again and the cycle occurs again.

Moreover, the susceptible plants, infected plants, herbivores and their natural enemies population coexists without attaining a specific equilibrium point at first. However, in the long run, when consumption rate of herbivores, predation rate of natural enemies of herbivores and harvesting of susceptible plants is lower while the intrinsic growth rate of susceptible plants is higher, the system becomes stable and coexists as seen in Fig. 7. Infected plants may increase or decrease depending on prevailing climatic condition in a certain habitat and measures taken by the susceptible plants to protect themselves from pathogen attack. Moreover, host plants may be resistance to pathogens or other pathogens must be at a critical stage in order to cause infections while others have evolved and therefore they can live for a prolonged periods such as brown spot. On the other hand, some susceptible plants releases VOC and HIVP to protect themselves.

Most species are prone to extinction especially herbivore population which is assumed to reproduce sexually. Allee effect plays an important role for coexistence. In absence of Allee effect, say $\theta = 0$ or below the lowest threshold value, regardless of the other parameters, say $r = 4.8$, $k = 10000, p_1 = 4, c_1 = 2$, $\mu = 0.3, p_2 = 0.2$, $c_2 = 0.25$, $d = 2$, $\epsilon = 0.1, \eta = 2$, $a = 1$, $\sigma = 1.6$ the simulation of susceptible plants, infected plants, herbivores and their natural enemies over time is as shown in Fig. 8.

From Fig. 8, when the susceptible plant population declines, herbivores start to decrease and goes to zero when the herbivore density is less than the least number of herbivores required to keep the population existing in the system. The herbivore population becomes extinct regardless of

availability of susceptible plants to feed on. That is when $\theta = 0$, there will be no least number of herbivores. This leads to decrease of their natural enemies of herbivores to extinction in the same habitat. For some time, susceptible population regenerates and grows to the carrying capacity since there is less enemies pressure.

Therefore for coexistence of all the species in the habitat, there is need to control harvesting rate of plant population where plants are cut down, destroyed by fire and other human activities. This can be achieved by setting harvest rate at $\epsilon = 0.001$ to secure availability of food for herbivores and pathogens. On the other hand, there is need to set lower bound on herbivore population that can result in critical population thresholds below which population go to extinction and also $c_1 > 1$ since the herbivores are assumed to reproduce sexually.
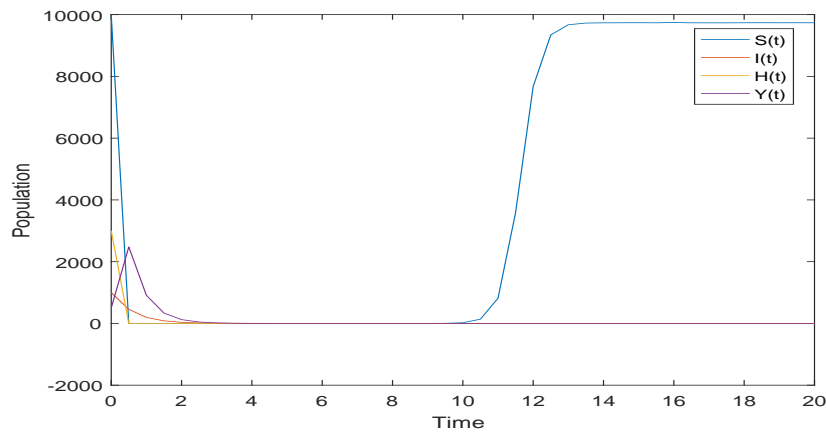

Fig. 8. In the absence of Allee effect

5 Conclusion

A mathematical model of plant-pathogen-herbivore interaction incorporating Allee effect and harvest was formulated. Plant population was divided into susceptible and infected plant densities with logistic growth rate for the susceptible plant population. In this model, infected plants are plants invaded by pathogens and remains in the system until they are harvested through human activities or killed by pathogen. It is assumed that herbivores do not feed on infected plants. For herbivore conversation rate for new ones, a linear multiple of the functional response and Allee effect were taken into consideration. Herbivore population is more prone to Allee effects than plants. With the fact that no species is isolated and live forever in the ecosystem, constant removal rate of natural enemies of herbivore and constant removal of herbivore from the habitat was taken into account. The herbivores can be removed through natural death, killed by human or predators or migrate from the habitat. The effects of human interference in terms of the harvest rate ϵ on susceptible plants and infected plants was also considered.

The stability analysis shows that the ratio intrinsic growth rate to the environmental carrying capacity of susceptible plants must be greater than certain threshold value to raise sufficient plant biomass to sustain other species. It also shows that the intrinsic growth rate of plants must be greater than the harvesting rate of plant population for plants to get established. Given this circumstance, all species coexists. Numerical simulations shows that all species coexist when intrinsic growth rate of plants is greater than the harvesting rate and when conversion rate of what is eaten by herbivores to newborn ones is greater than that of their natural enemies. It also shows that

in the absence of susceptible plants, herbivores migrates in search of food, while others deteriorate and dies out. Furthermore, regardless of the availability of susceptible plants, the herbivores population crashes to extinction if the herbivore population is less than the lower limit required to keep the herbivores existing in the ecosystem. In the interest of conservation of all species and the environment, policy developers will greatly benefit from understanding the solutions to address human activities for example, clearing land for farming, settlement, infrastructure construction, burning charcoal, and herbivore or their natural enemies hunting. In addition, monitor species closely, especially those that reproduce sexually by establishing and maintaining the least number required to keep the species existing.

Acknowledgement

Competing Interests

Authors have declared that no competing interest exist

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