Original Research Article

Mathematical Modeling of Plants,herbivore and natural enemies of herbivores interaction with harvesting

Abstract

Plant-herbivore-natural enemies of herbivores interaction is one of the basic interactions that drives of the ecosystem yields. In this interaction, plants are the primary food source for herbivores while natural enemies of herbivores depends on herbivores for food and on plants for shelter. Harvesting of every species which is common in many habitat may affect the population densities of the species and even the entire ecosystem. Therefore, conservation and maintenance of the harvested species is critical for ecosystem balance. In this paper, a model of plant-herbivore-natural enemies interactions with the constant effort harvesting of every species was developed and analyzed. The positive invariant set, the conditions of existence and locally asymptotically, stability of the equilibria were determined using the stability theory of ordinary differential equations. The results shows that the species being harvested would become extinct if harvesting effort exceeded a threshold value for the given population. While maintaining the coexistence of populations in the ecosystem requires sensible harvesting practices. Therefore, it is fair to choose a reasonable harvesting effort to allow all species to coexist in order to govern the species' dynamic behavior. The insights of the solutions of this study are of great essence to ecologists and policy developers in environmental conservation. The authorities to pay attention to the minimum number required based on the area coverage in deciding when to harvest and also be cautious to the amount and effort of harvesting in view of conserving the species and the environment.

Keywords: Ecology; Harvesting; Extinction;

1 Introduction

Ecology is the study of how different species including humans relate to their surroundings (13; 5). The diverse behaviors displayed by these species in the ecosystem has sparked great interest in the formulation of dynamical models to illustrate the interaction of the species and their environment (6). The concept of ecosystem was introduced by Jones *et al.* (11) who defined ecosystem engineers as species that generate, significantly modify, maintain, or destroy the resources (other than themselves) that are available to other organisms by generating physical change in living and non-living elements.

The biomass, productivity, and population size of each species within an ecosystem are all affected by interactions between species. Since no species can survive on its own and all species depend on one another for survival(5). For instance, the ecosystem is affected by the consumption of plants by herbivores and herbivores by predators. Similarly, plants, herbivores and natural enemies are harvested from ecosystems by other factors including human activities. As a result, for an ecosystem to function properly, all species must exist. The equilibrium of the entire ecosystem will shift if one type is abundant or scarce, according to (1; 3).

The biological process of herbivory involves a species (herbivore) feeding on plants or their byproducts. This is one of the fundamental interactions between species in an ecosystem that shapes the natural habitats found in all ecosystems (9; 12). All food chain start with energy source that is the sun. These energy is then captured by plants. Thus the living part of the food chain always starts with plant life. Herbivores cannot make their own food so they must eat plants while natural enemies of herbivores such predators consumers the herbivores (8; 10). Therefore, plant herbivore and natural enemies of herbivores interactions may have an impact on ecosystem characteristics such as primary productivity and diversity of food webs among others (8).

Most species including plants, herbivores and natural enemies of herbivores have been harvested and mined from the ecosystem. Harvesting involves elimination of the species from the ecosystem (13; 5). For instance, through forest fire, deforestation where plants are cleared for farming, settlement and charcoal burning. On the other hand, herbivores and natural enemies of herbivores can be harvested through migration and natural calamities like fire and drought or through human activities on the system such as hunting and poaching.

Harvesting of species have been incorporated in the interaction of the plant-herbivore models for instance, in(2). However, the models did not incorporate the natural enemies of herbivores such as carnivores. In addition (1; 6; 14) did not incorporate harvesting of species. On the other hand (4), formulated a tritrophic interaction model with volatile compounds in plants this incorporated plants, herbivores and natural enemies of herbivores. However, the model assumed harvesting of species that is common in the ecosystem which is resulting in the unpredicted collapse of many harvested species.

In this paper, plant-herbivore-natural enemies of herbivores model with harvesting of every species is taken into account. In this study, plants serve as food for herbivores and other plants are harvested. On the other hand, herbivores serve as food to natural enemies while others are harvested through different ways such natural calamities and human activities. In addition, natural enemies of herbivores are also harvested though human activities and natural calamities. The objective of this paper is to develop and analyze a mathematical model of plant-herbivore-natural enemies of herbivore interaction with harvesting of every species.

This paper is structured as follows. In Section two, we present the model. Positivity and boundedness of solutions of system are given in Section three. Dynamical behavior of the system and impact of harvesting is investigated in Section four. In Section five, we discuss 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 Mathematical Model

In this study, different types of population densities with constant effort harvesting at time t are considered. The plant population denoted by $S(t)$, the herbivore population is denoted by $H(t)$ and $Y(t)$ natural enemies of herbivores population. The model is governed by the following system of ordinary differential equations:

$$\begin{aligned}\frac{dS}{dt} &= S[r(1-\frac{S}{K}) - \frac{bH}{1+aS} - q_1E_1] \\ \frac{dH}{dt} &= H[\frac{mbS}{1+aS} - c - \frac{\beta Y}{1+\mu H} - q_2E_2] \\ \frac{dY}{dt} &= Y[\epsilon S + \frac{p\beta H}{1+\mu H} - d - q_3E_3] \end{aligned} \quad (2.1)$$

With initial conditions given by $S(0) > 0$, $H(0) > 0$ and $Y(0) > 0$

Where, r is the intrinsic growth rate of plants population, K is the environmental carrying capacity, b is the plant-herbivores consumption rate and a is the preventive measures taken by plants to protect themselves from invasion. The term, m and p are corresponding conversion rates of what is eaten to newborns by herbivores and natural enemies of herbivores respectively. The parameters c and d are the removal rate of herbivores and natural enemies of herbivore in the habitat respectively. The term ϵ is the enhanced attraction rate of natural enemies of herbivores towards plant population and μ is the preventive measures taken by herbivores to protect themselves from natural enemies.

$E_1 > 0$, $E_2 > 0$, $E_3 > 0$ express the harvesting capabilities of plants, herbivores and natural enemies of herbivores respectively. The terms q_1E_1S, q_2E_2H and q_3E_3Y represents the harvest of respective species where q_1, q_2 and q_3 represents catch efforts coefficient of plants, herbivores and the natural enemies herbivores respectively.

The assumption of this model are as follows:

(i) Herbivores feed on the plants and natural enemies feed on the herbivores only.

(ii) Plant population grows bounded by the carrying capacity of the environment in absence of herbivores and harvesting.

(iii) 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 first equation in (1) represents plant population which grows logistically in the absence of herbivores and harvesting which eventually reaches the carrying capacity of the environment. Herbivores consumes plants at the rate $\frac{bHS}{1+aS}$. The second equation in (1) represents the average herbivore reproduction rate at the rate $\frac{mbSH}{1+aS}$. This reflect the fact that herbivores reproduce more when food is available and in the absence of plants, the herbivores goes to extinction. The third equation in (1) represents the average number of natural enemies of herbivores in the habitat. The natural are attracted to plant population and they depend on herbivores as food. In addition, removal rates among herbivores and natural enemies of herbivores may be caused by various events such as scarcity of food, nutrients, water, grass or forest fire, migration etc.

3 Model Analysis

3.1 Invariant Region

It is crucial to demonstrate positivity and boundedness of the solutions of the system of equation (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 is shown by the lemma as follows: (Positivity) All solutions $[S(t), H(t), Y(t)]$ of the system of equation (1) starting in $(S_0, H_0, Y_0) \in \mathbb{R}_3^+$ remain positive for all $t > 0$.

Proof. The positivity of $S(t), H(t), Y(t)$ can be verified as shown:
Let $u = t$ then $du = dt$. Substituting in each equation of system of equation (1) and integrating both sides and introducing exponential in each case we obtain
$S(t) = S_0 exp \int_0^t [r(1 - \frac{S(v)}{K}) - \frac{bH}{1+aS(v)} - q_1E_1]dv$
$H(t) = H_0 exp \int_0^t [\frac{mbS}{1+aS} - c - \frac{\beta Y}{1+\mu H} - q_2E_2]dv$
$Y(t) = Y_0 exp \int_0^t [\epsilon S + \frac{p\beta H}{1+\mu H} - d - q_3E_3]dv$
Since $S(0) = S_0 > 0$, $H(0) = H_0 > 0$ and $Y(0) = Y_0 > 0$ for all $t > 0$ then $S_0, H_0, Y_0 > 0$. Hence $int(\mathbb{R}_3^+)$ is positively invariant set. ☐

(Boundedness) All solutions of system of equation (1) lie in the region $= [(S, H, Y)|S \leq K_*, \eta S + H + \frac{1}{q}Y \leq (\eta r + \frac{\epsilon}{q} - q_1E_1 + 1)\frac{K_*}{\omega}]$ where $\omega = \min{(\frac{1}{\eta}, n, \sigma)}$ and $K_* = Max(S_0, K)$

Proof. Let $S(t)$, $H(t)$, $Y(t)$ be any solution of system of equation 1 with positive initial condition (S_0, H_0, Y_0). Since $\frac{dS}{dt} = rS(1 - \frac{S}{K})$ is given as $S(t) = \frac{KS_0}{S_0+(K-S_0)\exp^{-rt}}$, by a standard comparison theorem (7) we have
$Lim_{t\longrightarrow\infty} S \leq K_*$
Let $N(t) = \eta S + H + \frac{1}{q}Y$
$= \eta(rS(1 - \frac{S}{K}) - \frac{bSH}{1+aS} - q_1E_1S) + H(\frac{mbS}{1+aS} - c - \frac{\beta Y}{1+\mu H} - q_2E_2) + \frac{1}{q}(\epsilon SY + \frac{p\beta HY}{1+\mu H} - d - q_3E_3Y)$
$\leq \eta(rS(1 - \frac{S}{K}) - q_1E_1S) - H(c + q_2E_2) + \frac{1}{q}(\epsilon SY - d - q_3E_3Y$
$\leq (\eta r - q_1E_1 + \frac{\epsilon}{q})S - nH - \sigma Y$
$\leq (\eta r - q_1E_1 + \frac{\epsilon}{q} + 1)S - S - nH - \sigma Y$
$\leq (\eta r - q_1E_1 + \frac{\epsilon}{q} + 1)K_* - \omega N$
Then $N(t) \leq (\eta r + \frac{\epsilon}{q} - q_1E_1 + 1)\frac{K_*}{\omega}$
Therefore, $0 \leq N(t) \leq (\eta r + \frac{\epsilon}{q} - q_1E_1 + 1)\frac{K_*}{\omega}$ for t sufficiently large so all solution of system of equation(1) are bounded and enter the region ☐

3.2 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 (1) equal to zero(5). The following equilibrium points are clearly present in the system of equation (1):
$E_a = (0, 0, 0)$, $E_b = (\frac{k(r-q_1E_1)}{r}, 0, 0)$, $E_* = (S_*, H_*, Y_*)$ Where
$S_* = \frac{1}{\epsilon}(d + q_3E_3 - \frac{p\beta H_*}{1+\mu H_*})$
$H_* = (r - \frac{rS_*}{K} - q_1E_1)\frac{1+aS_*}{b}$
$Y_* = \frac{mbS_*}{1+\mu S_*} - c - q_2E_2)\frac{1+\mu H_*}{\beta}$

3.3 Local Stability

To examine the local stability of the equilibrium points E_a, E_b,and E_*, the eigenvalues of the jacobian matrix of the system of equation (1) around the equilibrium points is determined. The jacobian matrix of the system of equation (1) at any given point $J(S, H, Y)$ is given by:

$$J(E) = \begin{bmatrix} b_{11} & -\frac{bS}{(1+aS)} & 0 \\ \frac{mbH}{(1+aS)^2} & \frac{mbS}{1+aS} - c - \frac{\beta Y}{(1+\mu H)^2} - q_2E_2 & -\frac{\beta H}{1+\mu H} \\ \epsilon Y & \frac{p\beta Y}{(1+\mu H)^2} - \epsilon YS & \epsilon S + \frac{p\beta H}{1+\mu H} - d - q_3E_3 \end{bmatrix} \quad (3.1)$$

Where, b_{11}=$r(1 - \frac{2S}{K}) - \frac{bH}{(1+aS)^2} - q_1E_1$
Evaluating the Jacobian matrix (2)at the population free equilibrium point $E_0 = (0, 0, 0)$ takes the

form;

$$J(E_a) = \begin{bmatrix} r - q_1E_1 & 0 & 0 \\ 0 & -c - q_2E_2 & 0 \\ 0 & 0 & -d - q_3E_3 \end{bmatrix} \tag{3.2}$$

Where the eigenvalues of $J(E_0)$ are give by $\lambda_1 = r - q_1E_1$,$\lambda_2 = -(c + q_2E_2)$, and $\lambda_3 = -(d + q_3E_3)$ which are real. Clearly, $E_0 = (0, 0, 0)$ is stable for $r < q_1E_1$ and unstable for $r > q_1E_1$.

At equilibrium point $E_b = (\frac{k(r-q_1E_1)}{r}, 0, 0)$, the Jacobian matrix (2)takes the form:

$$J(E_b) = \begin{bmatrix} -r + q_1E_1 & \frac{\frac{-bK(r-q_1E_1)}{r}}{r+aK(\frac{r-q_1E_1}{r}} & 0 \\ 0 & \frac{\frac{mbK(r-q_1E_1)}{r}}{r+aK(\frac{r-q_1E_1}{r}} - c - q_2E_2 & 0 \\ 0 & 0 & \frac{\epsilon r - \epsilon q_1E_1 - d - q_3E_3}{r} \end{bmatrix} \tag{3.3}$$

The eigenvalues of $J(E_b)$ are given by $\lambda_1 = -r + q_1E_1$, $\lambda_2 = \frac{\frac{-bK(r-q_1E_1)}{r}}{r+aK(\frac{r-q_1E_1}{r}} - c - q_2E_2$, $\lambda_3 = \frac{\epsilon r - \epsilon q_1E_1 - d - q_3E_3}{r}$ which are real. Therefore E_b is locally asymptotically stable when $r > q_1E_1$, $\epsilon r - \epsilon q_1E_1 - d - q_3E_3 < 0$ and $\frac{mbK(r-q_1E_1)}{r} < 0$ otherwise unstable. This shows that the population of susceptible plants can grow logistically up to the environmental carrying capacity in the absence of herbivores and when intrinsic growth rate of plants is greater than the constant effort harvesting rate.

The Jacobian matrix evaluated at the equilibrium point E_* is given by

$$\begin{bmatrix} B_{11} & B_{12} & 0 \\ B_{21} & B_{22} & B_{23} \\ B_{31} & B_{32} & B_{33} \end{bmatrix} \tag{3.4}$$

Where $B_{11} = r(1 - \frac{2S_*}{K}) - \frac{bH_*}{(1+aS_*)^2} - q_1E_1$
$B_{12} = -\frac{bS_*}{(1+aS*)}$
$B_{21} = \frac{mbH_*}{(1+aS_*)^2}$
$B_{22} = \frac{mbS_*}{1+aS_*} - c - \frac{\beta Y_*}{(1+\mu H_*)^2} - q_2E_2$
$B_{23} = -\frac{\beta H_*}{1+\mu H_*}$
$B_{31} = \epsilon Y_*$
$B_{32} = \frac{p\beta Y_*}{(1+\mu H*)^2} - \epsilon Y_*S_*$
$B_{33} = \epsilon S_* + \frac{p\beta H_*}{1+\mu H_*} - d - q_3E_3$
The characteristic equation at E_* is
$\lambda^3 + b_1\lambda^2 + b_2\lambda + b_3 = 0$ where
$b_1 = -B_{11} - B_{22} - B_{33}$
$b_2 = B_{11}B_{22} + B_{11}B_{33} + B_{22}B_{33} - B_{12}B_{21} - B_{23}B_{32}$
$b_3 = -B_{11}B_{22}B_{33} - B_{12}B_{23}B_{31} + B_{12}B_{21}B_{33} + B_{11}B_{23}B_{32}$
$b_1b_2 - b_3 = (-B_{11} - B_{22} - B_{33})(B_{11}B_{22} + B_{11}B_{33} + B_{22}B_{33} - B_{12}B_{21} - B_{23}B_{32}) + B_{11}B_{22}B_{33} + B_{12}B_{23}B_{31} - B_{12}B_{21}B_{33} - B_{11}B_{23}B_{32}$
$= -B_{11}B_{22}B_{33} + B_{11}B_{23}B_{32} - B_{11}(B_{11}B_{22} + B_{11}B_{33} - B_{12}B_{21}) - B_{22}(B_{11}B_{22} + B_{11}B_{33} + B_{22}B_{33} - B_{12}B_{21} - B_{23}B_{32}) + B_{11}B_{22}B_{33} + B_{12}B_{23}B_{31} - B_{12}B_{21}B_{33} - B_{11}B_{23}B_{32}$
Now using the Routh-Hurwitz criteria, the coexistence equilibrium point will be stable if the equation $\lambda^3 + b_1\lambda^2 + b_2\lambda + b_3 = 0$ will satisfy the conditions $b_1 > 0$,$b_2 > 0$, $b_3 > 0$, $b_1b_2 > b_3$and have negative real parts. Therefore, the interior equilibrium point E_* exists and it is locally asymptotically stable. This ensures the coexistence of plant population, herbivore population and natural enemies of herbivores in the system.

4 The Effect of Harvesting Species

The aspects discussed here include;E_1 which denote harvesting of plants, E_2 denote harvesting of herbivores and E_3 which denote harvesting of natural enemies of herbivores.

4.1 Harvesting of plant population

The increase in the harvesting effort E_1, decrease the quantity of plant population and not the quantity of herbivores and natural enemies of herbivores. For instance, from stability analysis, at population free equilibrium E_a, plant population will not be established when $E > \frac{r}{q_1}$. In the long run, extinction of plant population will affect herbivore population which in turn affects the natural enemies leading to the collapse of the ecosystem. For plant population to be established at E_b then $E_1 < \frac{r}{q_1}$, this will enable plants to support other species including herbivores and natural enemies of herbivores. For coexistence of all species the harvesting effort should be strategically controlled such that
$r - \frac{r}{K} - q_1E_1 > 0$ that is $E_1 > \frac{rK-r}{Kq_1}$
Therefore, optimal level of harvesting effort will be $\frac{rK-r}{Kq_1} < E_1 < \frac{r}{q_1}$

4.2 Harvesting Herbivores

Increase of harvesting effort E_2 may decreases the quantity of herbivores and natural enemies of herbivores not change the quantity of the plant due lack of food for natural enemies of herbivore to feeds on. In the long run, overharvesting of herbivores results to extinction of the herbivores and the natural enemies of herbivores. Therefore, for herbivores to be established and sustain the natural enemies, the harvesting effort should be strategically controlled, that is,
$\frac{mbS_*}{1+aS_*} - c - q_2E_2 > 0$ implying
$E_2 < \frac{mbS_* - c(1+q_1)}{q_2(1+aS_*}$

4.3 Harvesting Natural enemies of herbivores

Increasing the harvesting effort E_3 can result in decrease of the quantity of natural enemies of herbivores and increase in the quantity of herbivores. Increase of herbivore quantity will also affect the plant population that acts as food to herbivores. This results in decrease of plant population due to increased consumption by herbivores. This cycle continues over and over and some species may end up being wiped out. Therefore there is need to control harvesting of each species for coexistence of all species, that is, For natural enemies harvesting effort should be controlled such that
$d + q_3E_3 - \frac{p\beta H_*}{1+\mu H_*} > 0$
$E_3 < \frac{p\beta H_* - d(1+\mu H_*)}{1+\mu H_* q_3}$

5 Numerical Simulation of the Model

In this study, numerical simulations are performed by the use of MATLAB software using secondary data obtained from (5; 4). These simulations are performed to analyze the effect of harvesting of species effect on the ecosystem where time is in years. where,$r = 20$, $k = 1000$,$a = 0.5$ $m = 0.45$, $b = 0.4$, $c = 011$,$p = 0.2$, $d = 0.02$,$\beta = 0.03$, $\mu = 0.1$,$\epsilon = 0.3$. By assuming some parameters from perspective of practical problem and changing different parametric values of q_1, q_2, q_3, E_1, E_2,E_3 we obtain the graphs in figure 1, figure 2 and figure 3

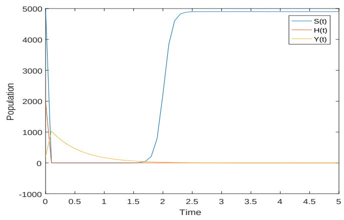

Figure 1

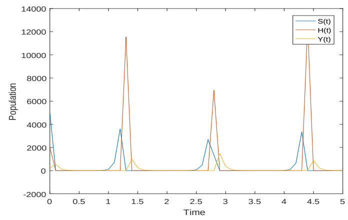

Figure 2

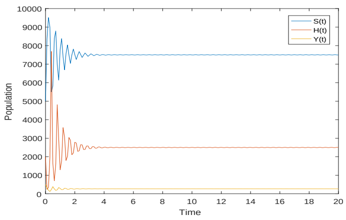

Figure 3

Fig.1.-3. Numerical Simulation of the Model

Along with q_1E_1 increasing, and decreasing q_2E_2 and q_3E_3 the plants and herbivoress begins to tend to 0 as shown in $figure 1$. This leads to increase of natural enemies of herbivores population at first due to availability of food(herbivores). When 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 $figure$2. The cycle occurs again and again over time.

Along varying the values of q_1E_1, q_2E_2 and q_3E_3 the 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 as shown in $figure 3$. The coexistence of the three species demands strategically harvesting of species to avoid overharvesting or exploitation of species. Therefore, we can chose different harvesting of each species to control their existence.

6 Conclusion

A mathematical model of plant-herbivore-natural enemies of herbivores interaction with constant effort harvesting of every species was formulated. Plant population was assumed to observe logistic growth rate, initially it seems to grow exponentially but eventually it grows only up to the carrying capacity of the environment. This is biologically observable because the plant population in a certain land with enough water resource and nutrients in the soil and without herbivore interference can grow only as much as the land can hold. On the other hand, feed on plants while natural enemies of herbivore feeds on herbivores.

Multiple equilibrium points were obtained that is E_a, E_b, and E_*,. Local stability conditions for equilibrium points were obtained in terms of system parameters where E_a , E_b, E_* are locally asymptotically stable under certain conditions. The equilibrium point E_* guarantees coexistence plants, herbivores and their natural enemies. The stability analysis showed that harvesting effort must be less than certain threshold value for all species to be established and sustain each other. 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.

Numerical analysis of the model was performed and showed that all the species depend on each other and coexist as seen in figure 1, figure 2 and figure 3. The population densities increases when there is sufficient resources whereas limited resources lead to extinction of the species in certain habitat. Excessive harvesting is a danger to vegetation, herbivores and natural enemies of herbivores.

These results have implications for the management of game parks where the park area is confined but the herbivore population and their natural enemies are allowed to increase and culling takes place at irregular intervals. The herbivore population could affect the quality of the park. For examples in support of this model revelations. First, the elephant population will increase rapidly in the parks, due to availability of water supplementation and better vegetation which have provided a conducive environment for the elephant population.

However, the increase in the population has fluctuated depending on food availability and drought for instances, recently, due to prolonged drought in Kenya, many herbivore have died in many parks, including Nairobi National Park. On the other hand, the antelope number has been reduced due to frequent droughts, increased predation by lions and loss of habitat due to human invasion. The provision of artificial water-points within the antelope range also resulted in extensive habitat degradation and competition with other herbivores. This affects their natural enemies including lions and other predators. Therefore, policy makers and authorities to pay attention to the minimum number required based on the area coverage in deciding when to harvest and also be cautious to the amount of harvesting. The authorities in the game park should also be cautious on when to allow or ban hunting depending on this threshold.

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