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Extensions of Lefkovitch matrix for modeling invasive *Cestrum aurantiacum* population *Dynamics*

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Abstract

Modeling of invasive species using stage based matrix methods can be exploited to understand population dynamics of plants using stage based Leftkovitch matrix models. This study reviewed and extended the stage based matrix incorporating invasion variables of invasive *Cestrum aurantiacum* across different forest types, ecological zones and altitudes. The estimation of eigenvalues of the extended stage based Lefkovitch matrix and its corresponding right and left eigenvectors representing stage structure and reproductive value respectively were determined. The results shows the growth rates for Kiptogot λ =4.84 and Kimothon λ =3.21, Suam λ=2.89, Kitale λ =3.91 and Saboti λ=3.58. The stable stage distribution of individuals species in each of the three life stages for Kimothon forest block is 84.6% for seedling, 12.9% sapling and 2.5% mature trees while Kiptogot was 88.9% seedling, 9.7% sapling, 1.3% mature trees. Suam block was 82.8% for seedling, 16% sapling, 1.2% mature trees. This study provides various extensions of stage based matrix for estimation and projection of the invasive tree population and information for managing invasive trees species within the forests ecosystems.

Keywords: *Lefkovitch matrix, growth rate, Stable stage distribution, extension of stage based matrix.*

1 Introduction

Matrix population modeling provides insight into the dynamics of a population by establishing relationships among the population parameters of interests (Berg and Greilhuber (1993)). The first matrix models were developed by Bernardelli (1941), Lewis (1942) and Leslie (1945) based on age-dependent while the matrix model that classifies the population based on the stage of life was later developed by Lefkovitch (1965) and Bruce (2002). The age-classified version referred to as a Leslie matrix developed by Leslie (1945) is given by the equation below:

$$N_{t+1}=LN_t \qquad (1)$$

Where N is the population vector and L is the population projection matrix. These equations can be conveniently be written in matrix form as:

$$\begin{pmatrix} N_1 \\ N_2 \\ . \\ N_w \end{pmatrix}(t+1) = \begin{pmatrix} P_{11} & F_{12} & . & F_{1w} \\ \vdots & P_{22} & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots \\ . & . & . & P_{ww} \end{pmatrix} . \begin{pmatrix} N_1 \\ N_2 \\ . \\ N_w \end{pmatrix}(t) \qquad (2)$$

The Lefkovitch (1965) equations of stage based matrix can also be conveniently written in matrix form as:

$$\begin{pmatrix} N_1 \\ N_2 \\ \cdot \\ N_w \end{pmatrix}(t+1) = \begin{pmatrix} P_{11} & F_{12} & \cdot & F_{1w} \\ G_{21} & P_{22} & \vdots & \vdots \\ \cdot & \cdot & \vdots & \vdots \\ \cdot & \cdot & G_{w,w-1} & P_{ww} \end{pmatrix} \cdot \begin{pmatrix} N_1 \\ N_2 \\ \cdot \\ N_w \end{pmatrix}(t) \quad (3)$$

The Lefkovitch (1965) stage based matrix entries consists of the rate of reproduction ($F_{ij} \geq 0$, where i, j = 1, 2, 3, 4..., w), survival and growth rate in each stage, where G_{ij} as the probability of surviving and growing into next stage (i = 1, 2, 3, 4..., w − 1) and P_{ii} the probability of survival and remaining in the same stage (i = 1, 2, 3, 4...,w).
Doubleday (1975) extended Lefkovitch stage based matrix model by incorporating harvesting rates, where harvests are eliminating a group of individuals from the population as indicated by Edgar (2011). The extended matrix (H) model containing the transitions rates of the population that is harvested given by h_i, $0 \leq h_i \leq 1$, i =1, 2, 3... w taking the form of the equation 4 below

$$H=\begin{bmatrix} h_1 & \cdots & \cdot \\ \vdots & \ddots & \vdots \\ \cdot & \cdots & h_w \end{bmatrix} \quad (4)$$

Huifeng et.al. (2015) used fire stage transition matrix to model the dynamics of China’s forests. They assumed that between two sequential inventories, for forest at one stage class, one part would remain in its stage class, another part would transfer to the next stage class, and the rest would die or be harvested. They developed a stage-classified matrix model to predict biomass Carbon stocks of China’s forests from 2005 to 2015 as indicated in the Figure 1 below.

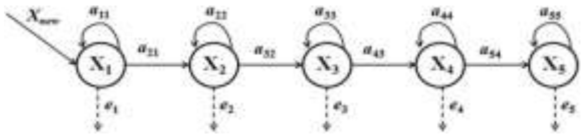

Figure 1. Stage based matrix model for carbon stock of China

Where X_{new}, X_1, X_2, X_3, X_4 and X_5 represent the forest area of newly planted, young-aged, mid-aged, premature, mature and over mature forests in inventory, respectively and a_{21}, a_{32}, a_{43} and a_{54} represent the transition probability from stages to the class between two sequential inventory periods, respectively. a_{11}, a_{22}, a_{33}, a_{44} and a_{55} represent the probability for remaining within itself between two sequential inventory periods, respectively, e_1,e_2, e_3, e_4 and e_5 represent the probability of die or being harvested, respectively.

Pyy et. al.(2017) developed non-stationary models for aged *Pinus sylvestris* in Finland, assuming that the explicit matrix equation for the size class distribution at time t^{k+1} is given as $y^{k+1} = U(y^k)y^k - h^k$, where $U(y^k)$ is the forest growth matrix, which has the following equation structure at time event t^k

$$U(y^k) = \begin{bmatrix} a_1^k & 0 & 0 & 0 \\ b_2^k & a_2^k & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & a_{N-1}^k & a_N^k \end{bmatrix} \quad (5)$$

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2 Material and methods

The experimental design with 1km transects and plots sampled randomly 300m apart depending within 5 different forest blocks namely Kiptogot, Kimothon, Suam, Saboti and Kitale of Mt Elgon ecosystem. A total of 175 plots were sampled within the forest block as follows: Suam -24 plots, Kitale-30 plots, Kiptogot- 48, Kimothon-42 and Saboti-33 plots. These plots were measure for mature tree 10 × 10m, 5 × 5m for sapling and 1 × 1m for seedling. The data was collected within a three year span period twice during December 2017 and December 2019 rainy seasons. The construction of population projection matrix model process involved four procedures according to Morris and Doak (2003) involving detailed demographic study, measuring survival over the census period, estimating vital rates and lastly building projection matrix. The extension of projection matrix was also developed considering the factors such gazing effect, ecological zones, and altitudinal range. The following are maps showing the ranges of the ecological and altitudinal within the sampled forest blocks (Figure 2).

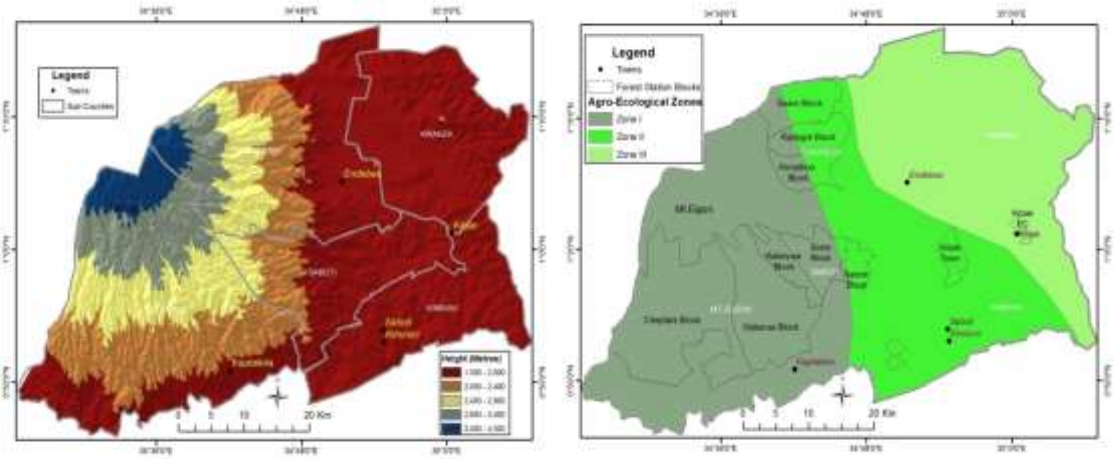

Figure 2. The ecological and altitudinal ranges of the sampled forest blocks of Mt Elgon ecosystem

Table 1. Mean invasive species per forest block and plot sampled in 2017 and 2019

Forest Block	**2017-census period**			**2019 census period**		
Plots sampled	**Stage 1**	**Stage 2**	**Stage 3**	**Stage 1**	**Stage 2**	**Stage 3**
Kiptogot 1	108	32	17	64	15	13
Kiptogot 2	88	25	12	50	20	9
Kiptogot 3	116	23	13	48	19	7
Kiptogot 4	40	26	22	12	15	10
Kiptogot 5	92	31	34	43	17	7
Kiptogot 6	40	11	16	29	10	7
Kiptogot 7	112	50	30	50	28	7
Kimothon 1	108	18	38	72	7	22
Kimothon 2	54	76	37	36	13	10
Kimothon 3	26	19	38	20	17	3
Kimothon 4	104	7	13	3	6	4
Kimothon 5	176	24	19	27	19	7
Kimothon 6	22	12	8	20	8	7

Kimothon 7	52	15	40	36	14	13
Saboti 1	53	25	27	25	10	20
Saboti 2	92	7	132	88	15	35
Saboti 3	73	31	63	44	25	15
Saboti 4	58	37	85	28	23	41
Saboti 5	105	42	9	11	3	8
Suam 1	25	10	20	4	2	9
Suam 2	88	15	35	1	2	5
Suam 3	73	25	63	25	10	20
Suam 4	88	23	85	58	15	35
Suam 5	73	25	63	11	3	8
Suam 6	105	42	85	58	23	9
Kitale 1	245	58	8	200	30	4
Kitale 2	150	60	29	100	34	14
Kitale 3	60	24	15	54	18	13
Kitale 4	7	3	5	5	2	4
Kitale 5	55	22	13	45	12	11
Kitale 6	35	17	24	30	16	22
Kitale 7	73	29	20	73	20	18
Kitale 8	83	33	27	73	23	19
Kitale 9	80	32	23	76	28	21
Kitale 10	113	35	27	89	23	21

3 Extended stage based model

3.1 Stage based matrix model for invasive *Cestrum aurantiacum*

The construction of population projection matrix model categorized development stages of the invasive *Cestrum aurantiacum* species into three finite stages comprising of seedling, sapling and mature trees. We considered factors affecting the survival, transition state and reproduction at each stage of growth. The growth per stage of development of an invasive tree was determined by the height of the individual tree distributed within the time interval [t, t+1], within different forest blocks. Grazing (***g***) factors were also considered to affects all the stages of growth of the invasive species and distributed within the time interval [t,t+1]. The ecological zones also affected all the stages of growth of the invasive species; denoted by ***e*** distributed as $e^t = e^t{}_1, e^t{}_2,\ldots\ldots, e^t{}_{w.}$ Vegetation per forest block also affected the stages of growth of the invasive species; denoted by ***v*** with a distribution given as $v^t = v^t{}_1 , v^t{}_2,\ldots\ldots, v^t{}_z$. The forest tree height (H) is considered to be linearly dependent on altitude (temperature T and precipitation), grazing factors (ratio of palatable species) and vegetation (forest cover and soil depth).

$$H^t{}_i = \psi_i + \psi_{1i}g + \psi_{2i}A + \psi_{3i}V + \psi_{4i}P + e \qquad (6)$$

Also we denoted $\boldsymbol{m^t_i}$ as the probability that a tree from height ***i*** dies between the interval [t, t + 1] and $\boldsymbol{P^t_{ii}}$ given as:

$$P_{ii}{}^{t} = 1 - G_{ij}{}^{t} - m_i{}^{t} \qquad (7)$$

3.2 Extension of stage based matrix models.

The following are the extensions considered for modeling the growth development of invasive tree modeled by Lefkovitch stage based matrix models. These extensions are based on the grazing, deforestation, dispersion by animals, ecological zone and altitudinal factors.

(i) The stage based matrix model can be extended and expressed due to grazing effects having positive or negative effects on the stage based matrix model

$$X(t+1)=\begin{pmatrix} P_{11} & \cdot & \cdot & F_{n-1,1} & F_{n,n} \\ G_{12} & P_{22} & \cdot & \cdot & \cdot \\ .. \cdot & G_{23} & P_{33} & \cdot & \cdot \; . \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & G_{n-1,n} & P_{nn} \end{pmatrix} X(t) \pm \begin{pmatrix} g_{11} & \cdot & \cdot & \cdot & \cdot \\ g_{12} & g_{22} & \cdot & \cdot & \cdot \\ . \; . & g_{23} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & g_{n-1,n-1} & \cdot \\ \cdot & \cdot & \cdot & g_{n-1,n} & g_{nn} \end{pmatrix} \qquad (8)$$

Where **g** is the grazing effects on the transition matrix per stage of growth of invasive species within the ecosystem at time (t) of the population projection matrix. The distribution of grazing effects takes the form of discrete Poisson probability distribution with the counts of no of livestock dungs cited per the sampled plots within the sampled forest blocks within a time interval [t, t+1] taking the form of a Poisson distribution give by:

$f(x) = e^{-\lambda} \lambda^x / x!$, Where x is the number of dung per plot in a given interval and λ being the mean number of dungs within the time interval [t, t+1].

(ii) Deforestation of invasive tree species can be treated as loss due to harvest of trees as either an absolute loss due to tree harvesting or clarence of land aiding the growth and colonization by invasive species hence affecting survival of invasive trees per stage.

$$X(t+1)=\begin{pmatrix} P_{11} & \cdot & \cdot & F_{n-1,1} & F_{n,n} \\ G_{12} & P_{22} & \cdot & \cdot & \cdot \\ .. \cdot & G_{23} & P_{33} & \cdot & \cdot \; . \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & G_{n-1,n} & P_{nn} \end{pmatrix} X(t) \pm \begin{pmatrix} h_{11} & \cdot & \cdot & \cdot & \cdot \\ h_{12} & h_{22} & \cdot & \cdot & \cdot \\ . \; . & h_{23} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & h_{n.1,n-1} & \cdot \\ \cdot & \cdot & \cdot & h_{n-1,n} & h_{nn} \end{pmatrix} \qquad (9)$$

Where **h** is the harvesting effect on the transition matrix per stage of growth of invasive species within the ecosystem at time (t) of the population projection matrix.

(iii) The effects due to ecological zones factors on the survival probabilities of the trees per stages of growth of the invasive tree population are simulated using the matrix model below.

$$X(t+1)=\begin{pmatrix} P_{11} & \cdot & \cdot & F_{n-1,1} & F_{n,n} \\ G_{12} & P_{22} & \cdot & \cdot & \cdot \\ .. \cdot & G_{23} & P_{33} & \cdot & \cdot \; . \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & G_{n-1,n} & P_{nn} \end{pmatrix} X(t) \pm \begin{pmatrix} e_{11} & \cdot & \cdot & \cdot & \cdot \\ e_{12} & e_{22} & \cdot & \cdot & \cdot \\ . \; . & e_{23.} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & e_{n.1,n-1} & \cdot \\ \cdot & \cdot & \cdot & e_{.n-1,n} & e_{nn} \end{pmatrix} \qquad (10)$$

The ecological effect is denoted by **e**, affecting the transition probabilities of matrix per stages of growth of invasive species within the forest ecosystem at time (t) of the population projection matrix.

(iv) The effects of altitudinal ranges factors can also alter survival per stage as simulated in the stage based matrix model given below.

$$Xf(t+1)=\begin{pmatrix} P_{11} & \cdot & \cdot & F_{n-1,1} & F_{n,n} \\ G_{12} & P_{22} & \cdot & \cdot & \cdot \\ ..\cdot & G_{23} & P_{33} & \cdot & \cdot\ . \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & G_{n-1,n} & P_{nn} \end{pmatrix} X(t) \pm \begin{pmatrix} a_{11} & \cdot & \cdot & \cdot & \cdot \\ a_{12} & a_{22} & \cdot & \cdot & \cdot \\ \cdot\ \cdot & a_{23} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & a_{n.1,n-1} & \cdot \\ \cdot & \cdot & \cdot & a_{n-1,n} & a_{nn} \end{pmatrix} \quad (11)$$

Where **a** is the altitudinal effects on the transition matrix per stage of growth of invasive species within the ecosystem at time (t) of the population projection matrix.

3.3 Population parameters estimation

The following are stage based population matrix developed and constructed using the extended stage based population transition matrix per forest blocks sampled. The estimated vital rates (P_{ii}, G_{ij}, F_{ij}) with a constant effects of grazing, deforestation, ecological and altitudinal effects of 20% reduction of survival rates to the next stage of growth of the invasive tree species per stage in the form of population projection matrix.

$$Kiptogot = \begin{pmatrix} 0.519 & 0 & 292 \\ 0.481 & 0.491 & 0 \\ 0 & 0.571 & 0.629 \end{pmatrix}; Kimothon = \begin{pmatrix} 0.015 & 0 & 38 \\ 0.984 & 0.314 & 0 \\ 0 & 0.686 & 0.439 \end{pmatrix};$$

$$Saboti = \begin{pmatrix} 0.538 & 0 & 126 \\ 0.430 & 0.407 & 0 \\ 0 & 0.593 & 0.254 \end{pmatrix}; Suam = \begin{pmatrix} 0.622 & 0 & 166 \\ 0.378 & 0.835 & 0 \\ 0 & 0.165 & 0.628 \end{pmatrix};$$

$$Kitale = \begin{pmatrix} 0.603 & 0 & 231 \\ 0.397 & 0.587 & 0 \\ 0 & 0.413 & 0.461 \end{pmatrix}$$

The stage based projection matrix of the invasive species was used to calculate the asymptotic growth rate (Figure 3) of the population (dominant eigenvalue), the dominant eigenvectors, the stable stage distribution, and the reproductive values (right and left eigenvectors, respectively). The asymptotic population growth rate were estimated from the mean transition matrix indicated a stable growth rate showing (Table 2) increasing the population of invasive species with Kiptogot $\lambda = 4.84$, Kitale $\lambda = 3.91$, Saboti $\lambda = 3.58$, Kimothon $\lambda = 3.31$ and Suam $\lambda = 2.89$.

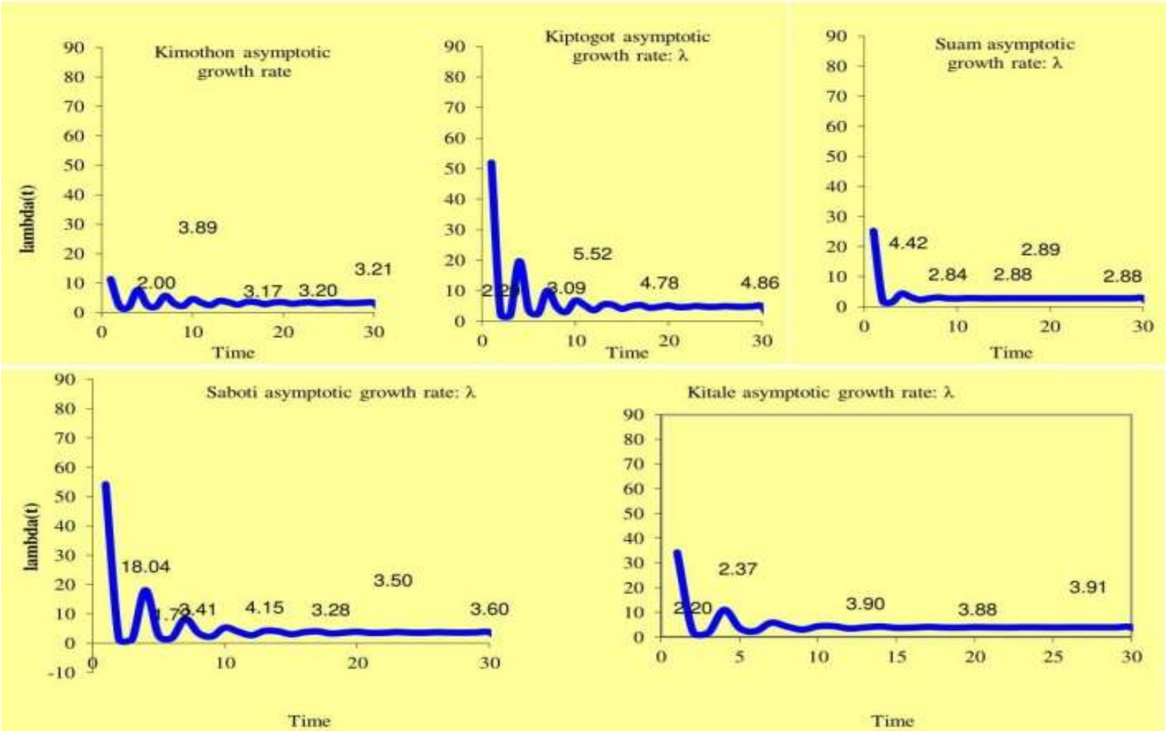

Figure 3. Stable population growth rate per forest block

Table 2. Reproductive values and Stable stage distribution per forest block

Variable	**Forest Blocks**					
	Stage	Kimothon	Saboti	Kiptogot	Suam	Kitale
Left eigenvector	1	1.00	1.00	1.00	1.00	1.00
	2	3.25	7.08	8.98	5.70	8.33
	3	13.71	37.87	69.36	70.82	66.99
Right eigenvector	1	0.85	0.86	0.89	0.83	0.88
	2	0.13	0.12	0.09	0.16	0.11
	3	0.02	0.02	0.02	0.01	0.01
Growth	λ	3.21	3.58	4.84	2.89	3.91

The population structure will converge to a unique stable distribution given by the vector ***w*** whose entries sum to one after 10 years of growth as the population gets close to the stable stage distribution (Figure 3). The results indicates the proportion of individuals species in each of the three life stages at stable stage distribution (SDD) for Kimothon forest block was 84.6% seedling, 12.9% sapling, 2.5% mature trees while Kiptogot block was 88.9% seedling, 9.7% sapling, 1.3% mature trees. Suam block was 82.8% seedling, 16.0% sapling, 1.2% mature trees. These stable stage distributions provide insights of management of the invasive tree species using their population structures per stage under different set of environmental conditions within ecological zones and altitudinal range.

4 Conclusion

The main aim of this research was to obtain an extension stage based matrix, for the purpose of analyzing population dynamics of invasive Cestrum Aurantiacum. The study gives clearly the extensions and growth pattern using the λ which will assist in management of invasion. This would assist in social and economic policy making and choice of the desired management strategies per stage of growth of invasive trees.

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