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Sensitivity analyses of population projection matrix of *Cestrum aurantiacum*

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Abstract

The Lefkovich stage specific matrix population models are divided into discrete stage classes defined by a growth variable such as size, height and diameter at breast height for trees. In matrix model, the deterministic matrix projection models are used to estimate growth rate, stable size distribution, reproductive values, and sensitivities of the growth rate to changes in vital rates. This study sampled five forest blocks (Kiptogot, Kimothon, Suam, Saboti and Kitale within Mt. Elgon forest ecosystem) and used stage base matrix models to estimate asymptotic growth rate, sensitivity and elasticity values of invasive tree population within the forest ecosystem. The result concludes that the dominant eigenvalue is more sensitive to transition probabilities from stage 2 (sapling) to stage 3 (Mature trees) stages of *Cestrum aurantiacum* than to transition probability of stage 1 (seedling) to stage 2 (sapling) and lower in fertility of the stage 3 (Mature trees). The results further shows that the growth parameters in the forest blocks shows that Kiptogot block had the largest elasticity values than the other blocks, indicating that the invasive tree growth survival probabilities had greatest impact on population growth.

Keywords: Population structure, elasticity, matrix population models, population growth rate, sensitivity analysis, size-specific sensitivity and elasticity, structured population model

1. Introduction

The sensitivity analysis of λ is the effect of a small change in any matrix element (a_{ij}) in the projection matrix. The sensitivity denoted by $s_{ij}(\lambda)$ to a_{ij} is the effect of element in the i^{th} row and j^{th} column of that matrix, given mathematically by (Donovan and Welden (2002))^[8] as:

$$s_{ij} = \frac{\delta \lambda}{a_{ij}}$$

If $L_{ij} > 0$ is the projection matrix which is non-negative with a dominant eigenvalue λ , left eigenvectors v and right eigenvector u , then $Lu = \lambda u$. The sensitivity equation with minimal change on the projection matrix $(L + \delta L)$ is as a result in perturbations of λ and of u , which satisfy the expression as outlined by Doak *et al* (1994)^[7] below:

$$(L + \delta L)(u + \delta u) = (\lambda + \delta \lambda)(u + \delta u)$$

Expanding the products, and setting second order terms to zero, then we have:

$$L(\delta u) + (\delta L)u = \lambda(\delta u) + u(\delta \lambda)$$

When we multiply on the left by v^T we obtain

$$(\delta)v^T u = v^T (\delta L) u$$

If the perturbation only affects one entry in the population projection matrix, for example a_{ij} , of L , then we have:

$$\delta\lambda = \frac{v_i \delta a_{ij} u_j}{v^T u}$$

Dividing both sides by δa_{ij} and taking the limit as $\delta a_{ij} \rightarrow 0$ gives the relationship:

$$\frac{(\delta\lambda)}{(\delta a_{ij})} = \frac{(v_i u_j)}{(v^T u)}$$

The elasticity of the projection matrix is denoted e_{ij} and is defined from the projection matrix L_{ij} as given by Caswell (2001) [2]:

$$e_{ij} = \frac{a_{ij}}{\lambda} s_{ij}$$

Elasticity analysis estimates the effect of proportional change in the vital rates on λ . The elasticity of a matrix element, e_{ij} , is the product of the sensitivity of a matrix element s_{ij} and the matrix element itself a_{ij} , divided by λ .

Caswell (2011) [3] denotes elasticity analysis as a similar measure on a logarithmic scale used to estimate the proportional change in λ which results from a proportional change in element a_{ij} . In this paper we shall apply sensitivity analysis of the deterministic matrix models to make decisions about which vital rates to focus on in management and conservation efforts of invasive species. Hence through sensitivity analyses of the matrix models, we provide some insight into how best to manage an invasive tree population.

2. Literature Review

Crouse *et al.* (1987) [10] and Doak *et al.* (1994) [7] used sensitivity and elasticity analyses to rank alternative population management strategies. Silvertown *et al.* (1992) [22] applied sensitivity analysis to group species with similar life history strategies. Grant (1996) and Caswell (2001) [2] used sensitivity to estimate the selection pressures acting on different demographic rates.

The Leslie (1945) [16] and Usher (1969) [23] applied sensitivity analysis of the deterministic matrix models to make decisions about which vital rates to focus on in management and conservation efforts. This study also applied sensitivity analysis of deterministic matrix models to make decisions about which stage of growth of invasive trees to focus on in management and control of the invasion within forest ecosystems to manage their population.

Crooks and Soule (1999) [5] used matrix models to investigate how variation in the survival and fecundity of cheetahs (*Acinonyx jubatus*) in the Serengeti National Park in Tanzania might influence the persistence of the population. Their results suggested that juvenile survival had a relatively small impact on population growth rate compared to adult survival. They concluded that conservation efforts outside the park, targeted at reducing poaching of adult cheetahs, might be the

most effective way of ensuring the persistence of the population within the Park.

Cortes (2002) [6] used elasticity values from a wide range of shark species to show that populations of large, slow-growing, long-lived species were most vulnerable to changes in the survival of the juveniles (as opposed to the adults). Such a result suggests that management arrangements that protect juveniles (e.g. nursery area closures) would provide greater benefit to the population than those that protect adults as cited by Caswell (2001) [2].

The sensitivity analysis was also used by Morr, Shertzer and Rice (2011) [14] to determine that lionfish population growth (λ) sensitivity to parameters of projection matrix. The result indicates that the growth rate is very sensitive to lower-level mortality parameters of larval, juvenile, and adult mortality. However, the larvae have venomous spines, probably making them less appealing prey than many of the native reef fish.

Edgar (2011) [11] indicated that the results of the analysis of sensitivity and elasticity indicate that an increase or decrease in either fertility or survival rates has an effect on the growth of a population, depending on the value of the dominant eigenvalue. The sensitivity of the growth rate factor to fertilities is found to be a decreasing function of age, for exponentially increasing populations.

Haimei, Yanhong and Fujiwara (2013) [12] used sensitivity analysis to estimate the stages (s) with the most effect on population growth and effective conservation strategy of the rare endangered plant *Davidi involucrata*. They analyzed the dynamics and the contributions of life-history components on population dynamics based on Lefkovitch matrix model. Our study will estimate λ sensitivity and elasticity analysis of invasive tree (*Cestrum aurantiacum*) populations from differing forest blocks characterized ecologically.

3. Methodology

The sensitivity analysis was begun by construction of the projection of stage based matrix model for a stable stage distribution. The forest blocks were considered from Mt Elgon ecosystem were Kimothon, Kiptogot, Suam, Saboti and Kitale considered as affected by invasive trees (Mullah, 2011) [20]. The projection of the population system per block we developed and stable stage distribution and reproductive rate determined. We calculated the asymptotic finite rate of increase (dominant eigenvalue), stable stage distribution and reproductive values in each stage. The stable stage distribution is given by the right eigenvector u ; and the reproductive values for the different stage classes, are given by the left eigenvector v . The reproductive value is the "worth" of individuals of different stage of growth in terms of future offspring they are destined to contribute to the next generation. Caswell (2001) [2] noted that the amount of reproduction per stage is the probability of surviving to realize it, and the time required for the offspring produced to enter into the reproductive value of a given stage of growth. The reproductive values are low at birth stages and increase towards the first stage of reproduction but decreases toward post-reproductive (Donovan and Welden, 2002) [8]. We then calculated sensitivity and elasticity of matrix elements using standard definitions based on the characteristic equation of the matrix (Caswell 2001) [2], and then we later visualized the relationship between these estimates of elasticity per forest blocks and stage of growth by linear regression.

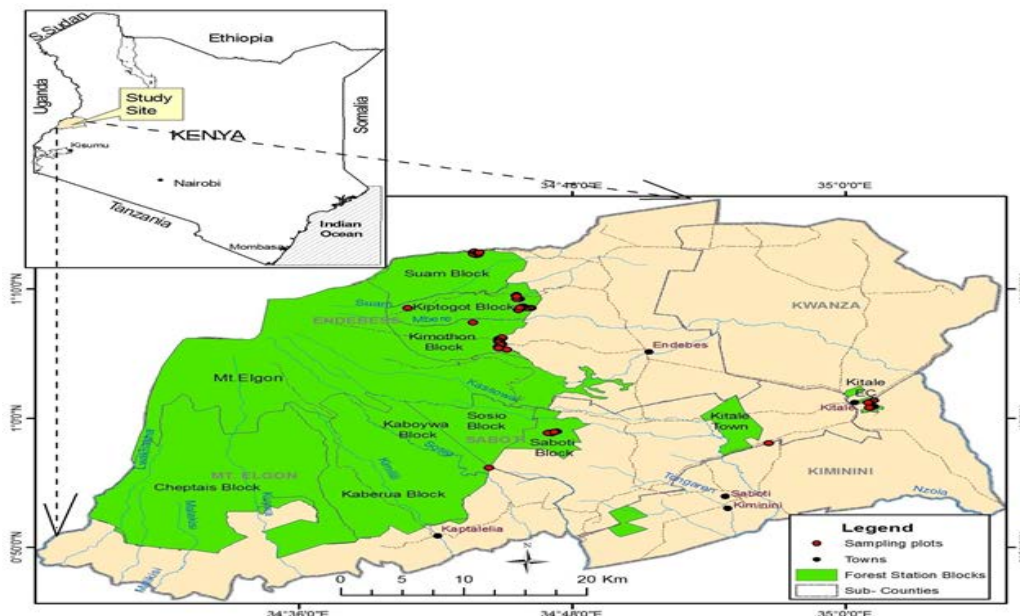


Fig 1: Study area Map, showing the forest block sampled.

4. Results and Discussion

4.1 Projection matrix

The following is the projection matrix per forest block sampled and the corresponding eigenvalues is given in the Table 1 below.

Table 1: The population Projection matrix and dominant eigenvalue per forest block

Matrix	Matrix=L _{Kiptogot}			Matrix=L _{Kimothon}			Matrix=L _{Suam}			Matrix=L _{Saboti}			Matrix=L _{Kitale}		
	Stage 1	Stage 2	Stage 3	Stage 1	Stage 2	Stage 3	Stage 1	Stage 2	Stage 3	Stage 1	Stage 2	Stage 3	Stage 1	Stage 2	Stage 3
Stage 1	0.52	0	292	0.02	0	38	0.62	0	166	0.53	0	126	0.6	0	237
Stage 2	0.42	0.49	0	0.98	0.31	0	0.38	0.84	0	0.43	0.41	0	0.4	0.59	0
Stage 3	0	0.57	0.63	0	0.69	0.44	0	0.17	0.68	0	0.59		0	0.41	0.46

4.2 Sensitivity analysis

The sensitivity analysis for each vital rates were calculated using the R software from population projection matrix computed to help us determine the contributions of each transition (F_{ij} , G_{ij} and P_{ii}) to λ . Considering the various forest block sampled and their population projection matrix, we found that the most sensitive stages vital rates were for Kitale $G_{12}=2.819$, Suam $G_{23}=4.38$, Kiptogot $G_{12}=2.988$, Kimothon $G_{12}= 2.303$ and Saboti $G_{12}=2.462$. Hence the sensitivity analysis is interpreted in light of the capacity for vital rates to change λ , thus for management of the invasive species it's key to manage these vital rates to stop the spread on increase invasion. Then if we change G_{12} , by a small amount in the

Kitale population projection matrix and hold the remaining matrix entries constant, the corresponding λ will change with a factor of 2.819. From the above results, we conclude that the dominant eigenvalue is more sensitive to transition probabilities of stage 2 (Sapling) to stage 3 (Mature stages) of *cestrum aurantiacum* than to transition probability of stage 1 (seedling) to stage 2 (sapling) and lower in fertility of the stage 3 (Mature trees). This shows the importance of sapling survivorship in determining future invasive tree population (Mullah *et al.* (2014)) [4]. Hence the sensitivity analysis is interpreted in light of the capacity for vital rates to change λ , thus for management of the invasive species it's key to manage these vital rates stop the spread on increase invasion.

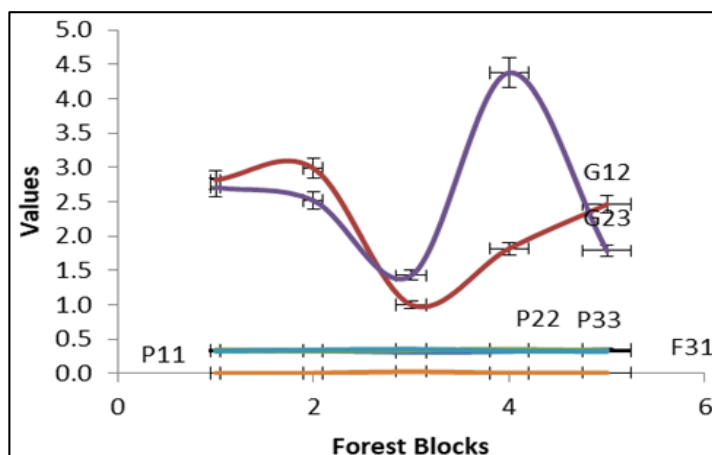


Fig 2: Sensitivity per stages of growth, to changes to survival, growth and production rates per stage of growth within forest ecosystems: 1- Kitale, 2- Kimothon, 3- Kiptogot, 4- Suam and 5 Saboti.

4.3 Elasticity of vital rates

The parameters of population projection matrix are measured on different scales, thus it is helpful to calculate proportional effects of proportional perturbations called elasticity. The elasticity is sensitivities, weighted by transition probabilities. Elasticity are usually shown as point values for each vital rate, relating to proportional changes (rather than actual values) of λ and vital rate. Elasticity is the standard way to recalibrate sensitivity analysis to account for differences in the scale of measurement of different vital rates. Equal elasticity means that the same proportional change in two different vital rates would result in the same effect (the same proportional change) in λ . These elasticity proportion indicates the relative contribution of each matrix elements to λ per stage within each forest block sampled. Elasticity analyses revealed the differences in life stages between the forest block and ecological zones that most influence population structure (λ).

$$Kiptogot = \begin{pmatrix} 0.036 & 0.000 & 0.297 \\ 0.297 & 0.029 & 0.000 \\ 0.000 & 0.297 & 0.044 \end{pmatrix}$$

$$Kimothon = \begin{pmatrix} 0.043 & 0.000 & 0.291 \\ 0.291 & 0.060 & 0.000 \\ 0.000 & 0.291 & 0.025 \end{pmatrix}$$

$$Saboti = \begin{pmatrix} 0.052 & 0.000 & 0.296 \\ 0.296 & 0.038 & 0.000 \\ 0.000 & 0.296 & 0.0323 \end{pmatrix}$$

The elasticity for are Kitale ($P_{11}=0.052$, means that a 1% increase in seedling survival will cause 0.052% increase in λ , Suam ($P_{11}= 0.069$, means that a 1% increase in seedling survival will cause 0.069% increase in λ), Kiptogot ($P_{11}= 0.036$, means that a 1% increase in seedling survival will cause 0.036% increase in λ), Kimothon ($P_{11}=0.043$, means that a 1% increase in seedling survival will cause 0.043% increase in λ) and lastly for Suam ($P_{11}= 0.052$, means that a 1% increase in seedling survival will cause 0.052% increase in λ). A regression analysis estimated the elasticity and stages of growth showing a negatively relation for Kitale ($R^2=0.6879$), Saboti ($R^2= 0.9494$) and Kimothon ($R^2 = 0.2644$) since as we move to stage 3 the elasticity decreases while positively in Suam ($R^2 = 0.0653$) and Kiptogot ($R^2 = 0.284$) since as the invasive plant grow to stage 3 the elasticity of the stages also grow.

$$Kitale = \begin{pmatrix} 0.050 & 0.000 & 0.286 \\ 0.286 & 0.051 & 0.000 \\ 0.000 & 0.286 & 0.038 \end{pmatrix}$$

$$Suam = \begin{pmatrix} 0.069 & 0.000 & 0.251 \\ 0.251 & 0.102 & 0.000 \\ 0.000 & 0.251 & 0.078 \end{pmatrix}$$

Table 2: Estimated sensitivities for vital rates of invasive *Cestrum aurantiacum* per Forest block

Forest Block	λ	Sensitivity analysis of vital rates per stage of growth within forest blocks					Reproduction rate of mature tree
		Survival seedling stage	Survival sapling stage	Survival mature tree stage	Survival seedling and moving to sapling stage	Survival sapling and moving to mature trees stage	
Kitale	3.91	0.339	0.337	0.325	2.819	2.710	0.005
Suam	2.89	0.319	0.353	0.325	1.820	4.380	0.005
Kiptogot	4.84	0.333	0.326	0.341	2.988	2.517	0.005
Kimothon	3.21	0.334	0.350	0.316	2.303	1.597	0.010
Saboti	3.58	0.348	0.334	0.318	2.462	1.786	0.008

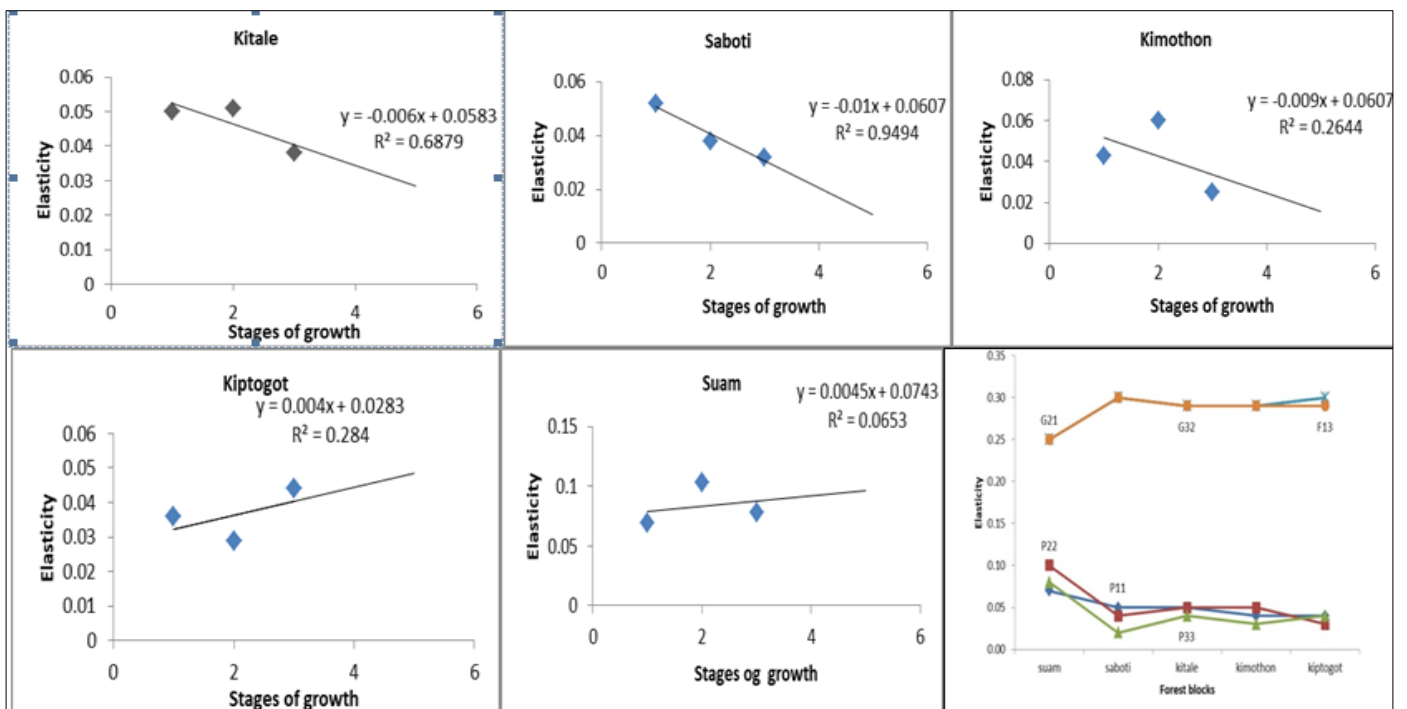


Fig 2: Elasticity per forest blocks zones and changes of λ through survival rate per stages (stage 1-Seedling, stage 2-Sapling and stage 3-Mature trees).

5. Conclusion

The results obtained in this paper comprise a fairly complete perturbation analysis of deterministic population matrix linear demographic models. The management of invasive species needs to consider growth stages which are more sensitivity in controlling the invasive species. Much consideration in the control of invasive species of trees within the forest should consider for Kitale stage 2 (0.051), Saboti stage 1 (0.052), Kiptogot stage 3 (0.044), Kimothon stage 2 (0.06) and Suam stage 2 (0.103). Thus we would recommend for management efforts that aim to decreasing saplings and mature trees fecundity values (i.e., more sapling and mature trees in the forest ecosystem will increase the population of invasive trees).

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