

Population viability analysis for herbaceous vegetation: A stochastic model and projections by simulation

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Population viability analysis (PVA) is one of the major areas of research in ecological studies. Rapidity of changes occurring to biodiversity has increased the importance of PVA. Demographic and environmental stochastic events are continuously influencing population viability. Anthropogenic activities are altering these dimensions of operation, and are pressurizing the viability of population. Under these changing scenarios, it is imperative to find out how a population is driven towards extinction, and at what stage(s) human intervention is necessary to alter the course of direction. Keeping this in mind, the present study has been made to propose a suitable model and to study its behaviour through simulation experiments for PVA. The model is developed keeping herbaceous plants with three distinct phases in life cycle as a background. Different shocks occurring at the three phases separately and the fourth one occurring at any of the phases are considered in this study to take care of environmental stochasticity. Probabilities of occurrence of shocks and their levels of likely impact on population are considered. In all the simulations, population showed a 'perfect' oscillation. The long-term simulations revealed that the population oscillated between sizeable numbers. The model can be used to check the population viability exposed to environmental shocks with different probabilities. It can be used to find out critical levels of population for its continuity of existence. The model is good for populations with minimal dispersal abilities. The model can be used to predict the continuity of heterogeneous herbaceous populations where the species are functioning largely as facilitators.

POPULATION viability analysis (PVA) is one of the major areas of research in ecological studies. PVA is becoming a valid and sufficiently accurate tool for categorizing and managing endangered species^{1,2}. The importance of PVA is increasing as the pressures from anthropogenic activities are driving the extinction rates of populations to newer scales of magnitude³⁻⁶. It is becoming increasingly difficult to say whether an organism is driven towards extinction due to natural processes or due to anthropogenic pressures. It is time to accept the fact that populations are continuously exposed to a myriad of shocks coming out of human endeavours. Some of the factors influencing the

distribution and diversity of vegetation are habitat fragmentation, degradation and destruction, creation of new pests, pollutants, over-exploitation and simplification of the ecosystems^{5,7}. Habitat destruction is one of the causes of extinction⁸. Availability of a suitable habitat to evaluate specificities of natural evolution processes has become impossible because of the non-availability of pristine habitats untouched by anthropogenic activities^{9,10}. Intervention by humans, the very agents of the current environmental crises, is required for any possible short-term recovery of biota. Hence we must apply feasible recovery strategies to various aspects of the biota that are not filtered out during the transformation⁷. This helps in the maintenance and possibly an improvement of the existing biodiversity in the long run.

The biodiversity crisis is not a mass-extinction event. Our inability to make clear predictions (beyond sweeping generalizations) about the future of life on earth has serious consequences to both biodiversity and the well-being of humanity. Actions taken over the next few decades will determine how impoverished the biosphere will be when many species will suffer reduced evolvability and require interventionist genetic and ecological management⁵. Better understanding of local population demography of rare species is a critical step towards the incorporation of demographic features into management decisions and practices¹¹. Incorporating variations in demographic parameters into projection matrices may be critical to developing realistic models of populations and species viability. In his Mac Arthur award-winning lecture, Levin¹² said that the key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns. The understanding of pattern, along with its causes and consequences, is central to understanding evolutionary processes such as speciation, as well as ecological processes such as succession, community development, and the spread and persistence of species. Planning and decision-making can be improved by access to reliable forecasts of ecosystem state, ecosystem services and natural capital¹³. Availability of new datasets, together with progress in computation and statistics, will increase our ability to forecast ecosystem change. Population biologists are attempting to assess population viability and formulating strategies for recovery of many other populations that have been reduced to low abundance through human activities^{14,15}. Because the pattern of random influences of environment is poorly known, there is a need for better understanding of how variability at different points in a life history affects extinction risk^{11,16}. Keeping these aspects specifically in mind, the present study has been made so as to propose a suitable model for the size of the population at any time and to study its movement through simulation experiments for PVA.

The model is developed keeping herbaceous plants growing in tropical environs as a background. These plants complete their life cycle within a year's time. The popu-

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lation comes into existence again the next year, and the cycle goes on. The plants have three dominant phases in their life cycle – establishment, growth and reproduction (seed-set). The model has been developed for herbaceous vegetation which reproduces exclusively by seed-set. Each of these phases has an impact on demographic stochasticity of the population. Similarly, environmental stochasticity also has an impact selectively at the three specific phases, and on the life cycle as a whole. Factors such as grazing, flooding, fire and pollution, have an influence on the growth and establishment of vegetation¹⁷⁻²⁰.

Among the three phases, the growth phase was considered as the critical one influencing demographic stochasticity. Plants spend maximum duration in this phase. This increases the probability of exposure to shocks thereby allowing for greater damages. The other two phases last for shorter durations than the growth phase, thereby minimizing the impact of shocks. We assume that a plant and its yield are likely to be affected by three types of shocks denoted S_1 , S_2 , and S_3 . The occurrence of a shock may affect the life cycle of a plant depending on its timing. More specifically, we assume that S_1 , S_2 and S_3 will have an impact only if they occur respectively, in phases one (P_1), two (P_2), and three (P_3) of the life cycle of the plant. A catastrophic event (E) may occur at any stage with different levels of impact. We assume that each of the three shocks may occur atmost once in a life cycle, i.e. a year. We assign chances a , b and c of occurrence of shocks S_1 , S_2 , and S_3 in phases P_1 , P_2 and P_3 respectively, for any of the three shocks to have a significant impact. It is also assumed that if S_1 occurs in P_2 or P_3 , it will have negligible impact. Similar will be the case with the other shocks. The event E is likely to occur in phase P_1 , P_2 and P_3 , with probabilities d_1 , d_2 , and d_3 respectively. It can be noted that $d_1 + d_2 + d_3$ may be less than one, implying that E may not occur in a life cycle with probability $d = 1 - (d_1 + d_2 + d_3)$. We assume that the probability of damage to the plant and/or its produce due to occurrence of S_1 in P_1 is $1 - p$, of S_2 in P_2 is $1 - q$, and of S_3 in P_3 is $1 - r$, while the same due to the occurrence of event E in P_k is $(1 - s_k)$, $k = 1, 2, 3$.

The probability of survival of a plant in a given phase includes the chance of not being affected at all and also of recovering from the effect due to a shock in the same phase. Thus the parameters p , q , r and s_i denote the probabilities of non-damage and/or recovery in the same phase after being damaged. We assume that phase 3 is of short duration, where each plant would produce an average number, M , of seeds which are subjected to the vagaries of nature, but are otherwise good enough to germinate in the following year. However, all the produced seeds may not germinate because of inherent variations in soil and its capacity to support the germination of all the seeds. This phenomenon may result in the germination of varying percentage of seeds. We assume that the higher the

number of seeds available for germination, the smaller will be the number that actually germinates in the following year. It is because all the seeds cannot germinate due to resource limitation and also due to competition. Thus the percentage of seeds that germinate is denoted by $t(N)$ 100%, where $t(N)$ takes different values for values of N in different intervals; for example,

$$t(N) = \begin{cases} t_1 & \text{if } 0 < N < N_1 \\ t_2 & \text{if } N_1 \leq N < N_2, \\ t_3 & \text{if } N \geq N_2 \end{cases}$$

with $0 < t_3 < t_2 < t_1 \leq 1$, where N is the number of seeds present in the plot before the onset of a new life cycle. It is imperative that produced seeds lie on the ground and no significant immigration or emigration takes place.

Working with this model, we simulate the size of the population for 100 years and study the nature of movement of the population sizes with respect to stability. In the simulation study we assume suitable values for the parameters of the model.

Studies on herbaceous vegetation growing in different microclimatic regions provided useful information (unpublished data). Probability values used in the simulation are taken from these studies. These values are given in Table 1.

The population was allowed to have a 100 m² area for growth and dispersion²¹. Species population size and seeds per plant varied from few dozens to few hundreds. Based on the observed densities, an upper limit of 150 individuals per m² was kept for density-dependent regulation. An average output value of hundred seeds per plant was considered.

At this stage we mention that the theoretical model developed here has the well-known Markov property.

The assumption that due to occurrence of the shock S_1 in P_1 , a plant has a chance α of survival cannot be interpreted, as αN plants survive if N plants are exposed to the shock. For example, suppose there are three plants, each of which has 50% chance of survival after a shock. Then there is a chance of (1/8) that all the plants survive and (1/8) that none of the plants survive because each plant's survival or otherwise is independent of the others. In general, there is always a small probability of all surviv-

Table 1. Probability values used in the simulation

Probability of occurrence of shocks/catastrophic event	Probability of non-damages
$a = 0.1$	$p = 0.4$
$b = 0.25$	$q = 0.2$
$c = 0.15$	$r = 0.6$
$d_1 = 0.3$	$s_1 = 0.3$
$d_2 = 0.2$	$s_2 = 0.2$
$d_3 = 0.4$	$s_3 = 0.6$

ing or none surviving. Instead the number of plants that survive the shock is a random variable which is binomial with parameters N and p , and is denoted by poN . If N was a random variable, as it will be, then the conditional distribution of poN , given $N = n$ is binomial (n, p) . This operation 'o' was introduced by Steutel and Van Harn²² while defining discrete self-decomposable distributions. Important properties of this operator are given in the Appendix. The average number of seeds produced (M) by a plant is multiplicative. Further, the factor $t(N)$ is multiplicative. The resultant $(Nt(N))$ may turn out to be a fraction. We shall, however, take the integral part only, ignoring the fractional part.

The number of sub-models, which result in this setting, is discussed now. Let X_n denote the number of plants in the plot soon after the first showers in the n th year. Then the stochastic process $\{X_n\}$ is a Markov chain and the conditional distribution of X_n given $X_{n-1} = N$ takes as many as 32 (4×2^3) forms depending on the occurrence or nonoccurrence of the four causes (three shocks and a catastrophic event) and the corresponding damages to each of the N plants and the seeds produced. For example, if all the causes occur in the initial phase P_1 of the life cycle of a plant, then this conditional random variable will have the same distribution as

$$[\{(ps_1)oN\}M] \cdot t\{(ps_1)oN\}M],$$

where p and s_1 are non-damage probabilities due to shock S_1 and catastrophic event E respectively.

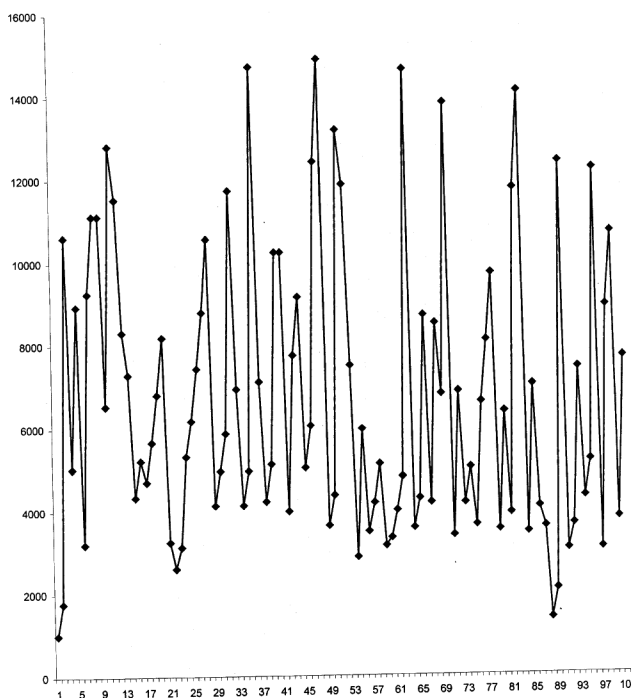


Figure 1. Simulation for 100 years.

The complete listing of all the 32 sub-models is given in the Appendix. We recall that the behavior of X_n given X_{n-1} does not depend on the values in the previous generations, viz. $n - 2, n - 3, \dots, 2, 1$, so that $\{X_n\}$ is a Markov chain.

Using the model, simulations were run for 100 years taking 1000 plants (10 plants per m^2) as the initial size. The runs were repeated 50 times using random numbers. It can be repeated many more times and with any initial size. In all these simulations, the plant population showed a 'perfect' oscillation (Figure 1). On a few occasions the size of the population came close to the initial number taken. Similarly, it crossed the 14,000 mark (140 plants per m^2) a few times, indicating density-dependent regulation. For a large number of years the population oscillated between 2000 and 8000 individuals. This indicates that with the set of assumptions made for demographic and environmental stochastic events, a plant population of size 1000 individuals (10 per m^2) can continue to exist for a long time. The conceptual basis for population regulation has bounded fluctuations in abundance, in contrast to the unbounded fluctuations of random walk populations²³. Regulation arises as a result of a potentially stabilizing, density-dependent process, even when brought about by non-equilibrium mechanisms. The model of Grenfell *et al.*²⁴ showed a noisy exponential increase in population size, when numbers were low following a crash. At higher densities, the population either remained constant or fell or showed an increase depending on environmental conditions. The pattern seen in this study mimics these concepts. Another important feature of the model is that by changing the probabilities of the four causes and corresponding damage levels, a different set of simulations can be made. At this stage we conclude that the experimental values of the parameters given are quite reasonable and close to the ones seen around herbaceous vegetation.

The impact of both environmental and demographic stochastic events are clearly seen. Removal of environmental processes allowed the population to touch the upper limit (150 per m^2) within three years and the population stayed there all through the run time (Figure 2a). Similarly, if all the four environmental causes are allowed to occur continuously, the size of population came down to zero (Figure 2b). It can be deduced that the assumed probabilities of occurrence of environmental shocks and their impact levels are sufficient enough to bring down the population of herbaceous plants exposed to a myriad of environmental shocks. We can say that size dependency is a critical factor in its continuity. Human interventions are pushing habitats towards homogenization, altering the composition of herbaceous vegetation.

Lowering the initial population size (< 1 plant per m^2) and performing the simulation runs led to the extinction of populations after a few years for a few runs. This indicates that the model can be used for predicting the critical

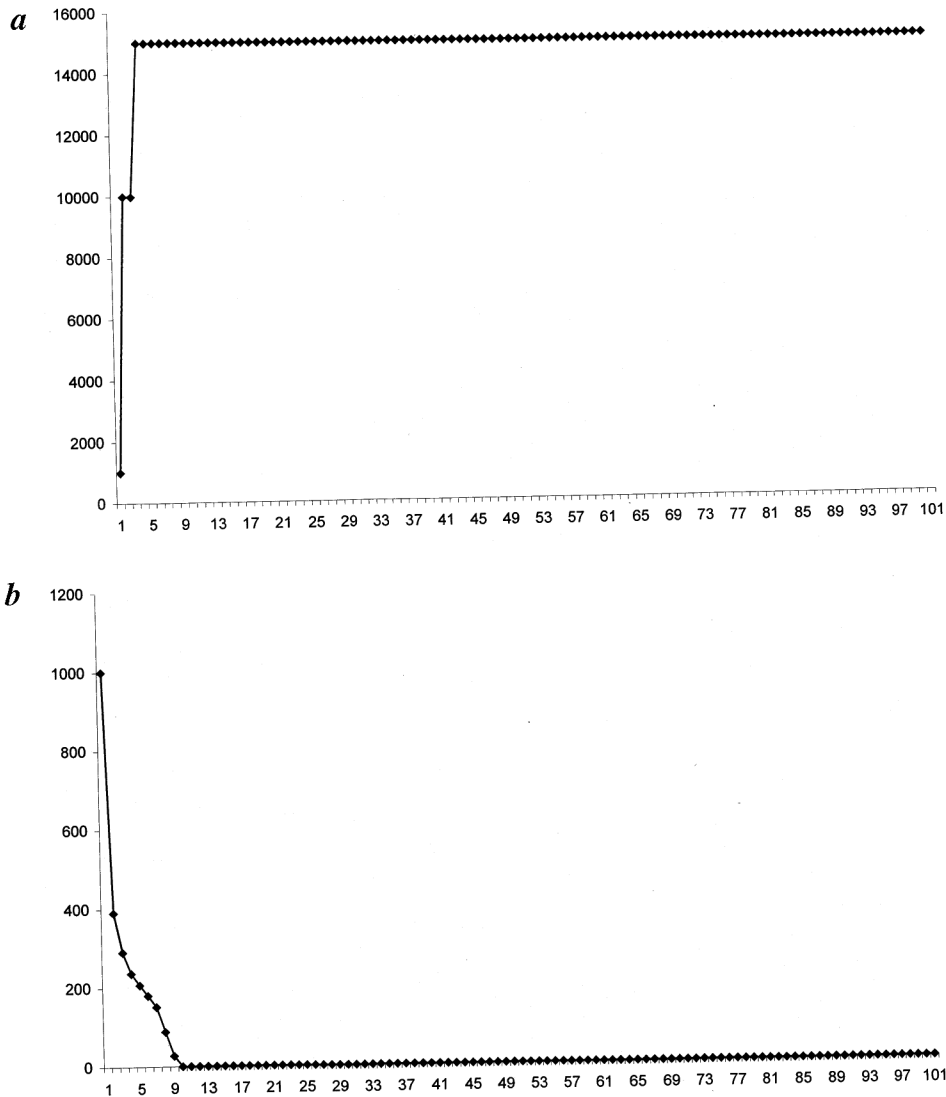


Figure 2. Simulation run for 100 years (a) without environmental events and (b) with all environmental and demographic events.

size of the population for its continuity under changing environs. The model is useful for single-species population. It can also be used for communities where facilitation is largely seen. It can be used to test the likely continuity of composition of heterogeneous herbaceous vegetation, where all species function as facilitators. The ever-increasing anthropogenic activities and corresponding pressures are pushing the natural heterogeneous environs towards artificial homogenous ones. As herbaceous vegetation has populations with minimal dispersal abilities, local extinctions are likely to reach the zenith for regional extinctions²⁵. Hence, it is important to focus on the recovery plans for smaller populations narrowly adapted to specific habitats¹⁹. Future works is planned to look into the more intriguing competition – facilitation trade-off and continuity of population.

Appendix

If X takes the values $0, 1, 2, \dots$ with the probability generating function (pgf) $P_X(s)$, $|s| \leq 1$, then $Y = a \circ X$ for $0 < a < 1$ has the pgf $P_Y(s) = P_X(1 - a + as)$. The following result is easily obtained.

Result 1. If $Z = b \circ Y$, $0 < b < 1$, then
 $P_Z(s) = P_X(1 - ab + abs)$
 so that $b \circ (a \circ X) = (ab) \circ (X)$.

Let X_n be the population size of the n th generation, i.e. the number of seeds that germinate at the onset of the monsoon during the n th year. Then X_{n+1} given $X_n = N$ is given by

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$$X_{n+1} = [\{a_k o \{(b_k o N)Z\}\}t] \text{ with probability } P_k, k = 1, 2, \dots, 32,$$

where Z denotes the average number of seeds produced by a plant and t is the proportion of seeds that germinate out of the total produce of seeds.

$$a_{3n+i} = \begin{cases} r & \text{for } i = 1, 2, n = 0, 2, 3, 6; i = 1, n = 8, 9, 10, i = 0, n = 9 \\ rs_3 & \text{for } i = 3, n = 0, 2, 3, 6 \\ 1 & \text{for } i = 1, 2, n = 1, 4, 5, 7; i = 2, n = 8, 9, 10, i = 0, n = 10 \\ s_3 & \text{for } i = 3, n = 1, 4, 5, 7 \end{cases}$$

$$b_{3n+i} = \begin{cases} pqs_i & \text{for } i = 1, 2, n = 0, 1 \\ pq & \text{for } i = 1, 2, n = 8; i = 3, n = 0, 1 \\ ps_i & \text{for } i = 1, 2, n = 2, 4 \\ p & \text{for } i = 0, 2, n = 9; i = 3, n = 2, 4 \\ ps_i & \text{for } i = 1, 2, n = 3, 5 \\ q & \text{for } i = 1, n = 9; i = 3, n = 3, 5, 9 \\ s_i & \text{for } i = 1, 2, n = 6, 7 \\ 1 & \text{for } i = 3, n = 6, 7; i = 1, 2, n = 10 \end{cases}$$

$$P_{3n+i} = \begin{cases} abcd_i, & n = 0, i = 1, 2, 3 \\ ab(1-c)d_i, & n = 1, i = 1, 2, 3 \\ a(1-b)cd_i, & n = 2, i = 1, 2, 3 \\ (1-a)bcd_i, & n = 3, i = 1, 2, 3 \\ a(1-b)(1-c)d_i, & n = 4, i = 1, 2, 3 \\ (1-a)b(1-c)d_i, & n = 5, i = 1, 2, 3 \\ (1-a)(1-b)cd_i, & n = 6, i = 1, 2, 3 \\ (1-a)(1-b)(1-c)d_i, & n = 7, i = 1, 2, 3 \\ abcd, & n = 8, i = 1 \\ ab(1-c)d, & n = 8, i = 2 \\ a(1-b)cd, & n = 8, i = 3 \\ (1-a)bcd, & n = 8, i = 4 \\ a(1-b)(1-c)d, & n = 8, i = 5 \\ (1-a)b(1-c)d, & n = 8, i = 6 \\ (1-a)(1-b)cd, & n = 8, i = 7 \\ (1-a)(1-b)(1-c)d, & n = 8, i = 8, d = 1 - d_1 - d_2 - d_3 \end{cases}$$

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