Extinction Equilibria of Stage Structured Populations

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July 30, 2010

Abstract

Invasive species have disrupted ecosystems worldwide threatening native populations that are often ill equipped to out compete them. The interaction between invasive and native populations can be complicated by varying intensities of competition at different life stages. In this study, we analyzed competition of two stage-structured populations. The model takes the form of two Lefkovitch matrix models interacting through density dependent terms. The stability of equilibrium densities was investigated under varying competition strength and intrinsic growth rates of the two populations. We show that it is possible for both partial extinction equilibria (persistence of only one population) and the total extinction equilibrium (extinction of both populations) to be simultaneously stable under some parameters.

1 Introduction

Developed by Lefkovitch in the mid-1960s, Lefkovitch matrix modeling improved on existing population modeling techniques by allowing populations to exhibit staged life cycles with varying vital rates for juveniles and adults. The Lefkovitch model, a stage model, is often used as an alternative to the Leslie matrix model which divides populations by age. Stage divisions allow individuals to stay in the same stage for multiple time steps allows researchers to base parameter values like survivorship on size, which is often more realistic. The division into life stages also allows competition between some age groups while the populations diverge in resource use in other stages. However, the Leslie model has difficulties when applied to species with continuous reproduction. The Leslie matrix model assumes that all reproduction takes place at the beginning of the time interval making this a good fit for fish with a short spawning season but not for species with a year round reproductive season[**?**].

Throughout nature, species have developed different strategies for survival and competition. Varying maturation rates, p, and adult survival, s_2, divides populations into differing life history strategies:

(i) Precocious (p large): individuals mature quickly and reproduce soon;

(ii) Delayed (p small): long juvenile period, reproduce late in life;

(iii) Iteroparous (s_2 large): remain adults for many generations, reproduce multiple times; and

(iv) Semelparous (s_2 small): adults live for a short time and reproduce only once [?].

Each life history parameter (i.e. survival s, maturation p, or fecundity F) can be density dependent, meaning it is a function of $n_1(t)$ and/or $n_2(t)$. Neubert and Caswell [?] analyzed density dependence in precocious semelparious, delayed semelparious, precocious iteroparous, and delayed iteroparous populations, mainly focusing on stability given different density dependent parameters.

Matrix modeling can be used to determine the impact of some environmental factor on a population. Perry [?] used Leslie matrices to model environmentally sensitive populations with and without the environmental effects of a power plant. Leslie matrices to modeling the effects of elevation on mosquitos and the effects of turtle excluder devices on loggerhead sea turtles [?] [?]. Research on characteristics of invasive species has been pursued, particularly pertaining to bird and plant species [?]. Past studies have found that the number of invasive individuals released and the number of release attempts contribute to invasive success [?].

The aim of this paper is to find the stability of equilibrium points. If these points are stable, then the introduction of a small number of the second population will temporarily move the population away from equilibrium, but the invasive population will die out and the original equilibrium will be maintained. If the equilibrium is not stable, an invasive species introduced in small numbers will be able to take hold and grow changing the equilibrium to a state where both populations are positive or the invasive population completely outcompetes the native population.

2 General Stage-Structured Single Species Model

In a basic Lefkovitch model, the population is divided into two stages. Let $n_1(t)$ be the number of juveniles (non-reproducing) and $n_2(t)$ be the number of adults (reproducing). Usually, only the females are counted in the population. Because the model inherently includes pulse reproduction, a time step should be chosen such that the population will reproduce once in each interval. Each stage has a rate of survival, s_1 and s_2 respectively, between 0 and 1. Of the juvenile survivors, some proportion p mature to adulthood, while $(p-1)$ remain in the juvenile stage in a single time step. Let F represent the fertility rate [?]. Often, only the females of a population are modeled, so F is the number of young per female, not per pair. The life cycle is illustrated in Figure 1.

The population at the next time step is calculated using a Leslie matrix A. The main diagonal of A contains the rates at which each stage persists into
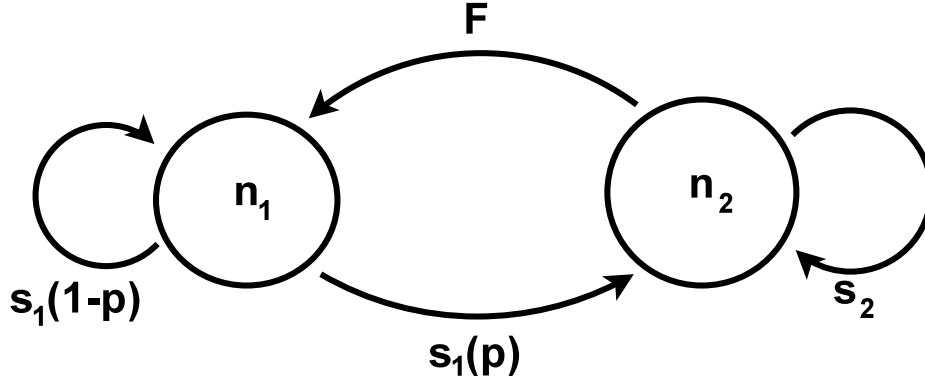
Figure 1: Staged Population Life Cycle

the next generation. The subdiagonal is the maturation rate to the next stage and the top row is the fertility rate at each stage [**?**]. For the two stage model described above, the Leslie matrix will be :

$$A = \left[\begin{array}{cc} s_1(1-p) & F \\ s_1(p) & s_2 \end{array} \right]$$

Multiplication by a population vector, $\tilde{n}(t) = \left[\begin{array}{c} n_1(t) \\ n_2(t) \end{array} \right]$, yields the population vector of the next generation:

$$A \left[\begin{array}{c} n_1(t) \\ n_2(t) \end{array} \right] = \left[\begin{array}{c} n_1(t+1) \\ n_2(t+1) \end{array} \right]$$

At equilibrium, $\left[\begin{array}{cc} s_1(1-p) & F \\ s_1(p) & s_2 \end{array} \right] \left[\begin{array}{c} n_1^* \\ n_2^* \end{array} \right] = \left[\begin{array}{c} n_1^* \\ n_2^* \end{array} \right]$. The equilibrium population vector reflects the proportional division of the population stages.

3 Two Species Competition: density dependent fertility

Density dependent fertility is incorporated into the model to limit the population size and express competition without predation between the native and invading populations. We used the Beverton-Holt density dependence function[**?**, eqn 16.12]. The fertility term is expressed:

$$F(t) = \alpha/(1 + \beta(n_2(t)))$$

where α is the maximum fertility rate of the population that is reached when $n_2(t)$ is very small. As $n_2(t)$ grows, the fertility rate declines to avoid overpopulation. β determines the strength of density dependence.

Table 1: Two Species Model

	Species 1	Species 2
juvenile population	$n_1(t)$	$m_1(t)$
adult population	$n_2(t)$	$m_2(t)$
juvenile survival	s_1	r_1
adult survival	s_2	r_2
maturity rate	p	q
fertility	F_1	F_2

This model allows competition between two populations where A is the two species Leslie matrix. Both populations are dynamic with density dependent fertility. Matrix A is defined by:

$$A = \begin{bmatrix} s_1(1-p) & F_1 & 0 & 0 \\ s_1(p) & s_2 & 0 & 0 \\ 0 & 0 & r_1(1-q) & F_2 \\ 0 & 0 & r_1(q) & r_2 \end{bmatrix}$$

and the equilibrium population vector is:

$$\tilde{n}^* = \begin{bmatrix} n_1^* \\ n_2^* \\ m_1^* \\ m_2^* \end{bmatrix}$$

The model may make use of only two β values; β_1 represented the density dependence of fertility on the adult population of the first population and β_2 was the density dependence of fertility on the adult population of the second population. Both populations have the same intensity of dependence on n_1 and n_2. The two populations may share a similar, but not identical, niche. The model is now generalized to include four β parameters. The fecundity functions become:

$$F_1 = \alpha_1/(1 + \beta_1(n_2) + \beta_2(m_2))$$

$$F_2 = \alpha_2/(1 + \beta_3(n_2) + \beta_4(m_2))$$

To find stability, we start with the following system of equations developed by expanding $A\tilde{n}(t) = \tilde{n}(t+1)$:

$$n_1(t+1) = s_1(1-p)n_1(t) + \alpha_1/(1 + \beta_1(n_2(t)) + \beta_2(m_2(t)))(n_2(t))$$

$$n_2(t+1) = s_1(p)n_1(t) + s_2 n_2(t)$$

$$m_1(t+1) = r_1(1-q)m_1(t) + \alpha_2/(1 + \beta_3(n_2(t)) + \beta_4(m_2(t)))(m_2(t))$$

$$m_2(t+1) = r_1(q)m_1(t) + r_2 m_2(t))$$

Calculate the Jacobian, J, which is the matrix of partial derivatives.

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$$J = \begin{bmatrix} \frac{\partial n_1(t+1)}{\partial n_1(t)} & \frac{\partial n_1(t+1)}{\partial n_2(t)} & \frac{\partial n_1(t+1)}{\partial m_1(t)} & \frac{\partial n_1(t+1)}{\partial m_2(t)} \\ \frac{\partial n_2(t+1)}{\partial n_1} & \frac{\partial n_2(t+1)}{\partial n_2} & \cdots & \cdots \\ \frac{\partial n_3(t+1)}{\partial n_1} & \cdots & \cdots & \cdots \\ \frac{\partial n_4(t+1)}{\partial n_1} & \cdots & \cdots & \cdots \end{bmatrix}$$

In the general case, J simplifies to the following matrix:

$$J = \begin{bmatrix} s_1(1-p) & \frac{(1+\beta_1 n_2+\beta_2 m_2)\alpha_1-\alpha_1\beta_1 n_2}{(1+\beta_1 n_2+\beta_2 m_2)^2} & 0 & \frac{-\alpha_1\beta_2 n_2}{(1+\beta_1 n_2+\beta_2 m_2)^2} \\ s_1 p & s_2 & 0 & 0 \\ 0 & \frac{-\alpha_2\beta_3 m_2}{(1+\beta_3 n_2+\beta_4 m_2)^2} & r_1(1-q) & \frac{(1+\beta_3 n_2+\beta_4 m_2)\alpha_2-\alpha_2\beta_4 m_2}{(1+\beta_3 n_2+\beta_4 m_2)^2} \\ 0 & 0 & r_1 q & r_2 \end{bmatrix}$$

We evaluate J at the equilibrium that we wish to analyze. In order to find the stability of the equilibrium, we need only look at the stability of J. If the largest complex modulus of the eigenvalues of J, $\lambda_{max} = main(real(eig(J)))$, is less than 1 then the equilibrium is stable, whereas is $\lambda_{max} > 1$ then the equilibrium is unstable. If $\lambda_{max} = 1$ let $\tilde{\epsilon}$ be a small perterbation of the population vector away from equilibrium. This equates to a small number of individuals of population two being introduced.$\tilde{\epsilon}_{j+1} = J\tilde{\epsilon}_j$ Working from this equation we see that $\tilde{\epsilon}_n = J^n\tilde{\epsilon}_0$. Iterate J to see if it will become the zero matrix to determine stability.

4   Total Extinction Equilibrium

At total extinction $n_1 = n_2 = m_1 = m_2 = 0$, J is a block diagonal matrix with eigenvalues equal to the eigenvalues of the two-by-two blocks corresponding to the two populations:

$$J = \begin{bmatrix} s_1(1-p) & \alpha_1 & 0 & 0 \\ s_1 p & s_2 & 0 & 0 \\ 0 & 0 & r_1(1-q) & \alpha_2 \\ 0 & 0 & r_1 q & r_2 \end{bmatrix}$$

Using the parameters given in Table 1 for the four cases, the eigenvalue, and thus the stability, is seen to be dependent on the intrinsic growth rate, α. The eigenvalue of the upper left block is:

$$\lambda = \frac{s_2 + s_1(1-p) \pm \sqrt{(s_2 + s_1(1-p))^2 - 4s_1(s_2(1-p) - \alpha_1 p)}}{2}$$

For the four life history strategies, Table 2 shows the upper limit on α, U_{α_i}, that will result in a stable total extinction equilibrium, $\lambda < 1$.

$$U_{\alpha_i} = \frac{(2 - s_1(1-p) - s_2)^2 - (s_1(1-p) + s_2)^2 + 4s_1(1-p)s_2}{4s_1 p}$$

Figure 2 shows the contour lines of the λ_{max} at total extinction in the two species model. Population 1 and population 2 use the parameters of case 1

Table 2: Upper limit of α for stability

Case	s_1	s_2	p	U_α
1	0.9	0.1	0.1	1.900000000
2	0.9	0.1	0.9	1.011111111
3	0.9	0.9	0.1	0.211111111
4	0.9	0.9	0.9	0.112345679

and case 2 respectively. Notice that the contour line for $\lambda_{max} = 1$ falls where the intrinsic growth rate of population 1 is 1.9 and the intrinsic growth rate of population 2 is 1.011111.
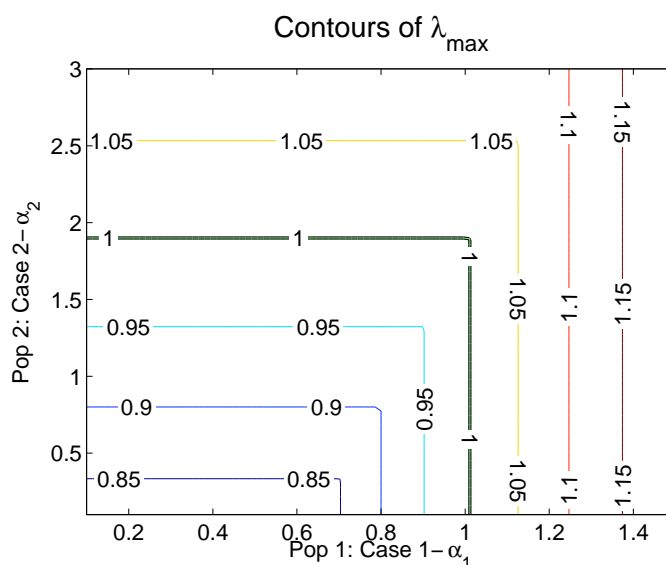

Figure 2: Contours of $\lambda_{max}(\alpha_{1,2}$

5   Partial Extinction Equilibrium

In each scenario, we test the stability of the equilibrium at partial extinction where one population is at the positive equilibrium found without competition and the other population is at the local extinction equilibrium. If the equilibrium is stable then population two is not capable of surviving if introduced in small numbers. If this equilibrium is unstable, population two has the potential to be an invasive species. At partial extinctions, the Jacobian does not reduce to a

block diagonal matrix.

$$J = \begin{bmatrix} s_1(1-p) & \frac{(1+\beta_2 m_2)\alpha_1}{(1+\beta_2 m_2)^2} & 0 & 0 \\ s_1 p & s_2 & 0 & 0 \\ 0 & \frac{-\alpha_2 m_2 \beta_3}{(1+\beta_2 m_2)^2} & r_1(1-q) & \frac{(1+\beta_4 m_2)\alpha_2 - \alpha_2 m_2 \beta_4}{(1+\beta_4 m_2)^2} \\ 0 & 0 & r_1 q & r_2 \end{bmatrix}$$

Keeping the general form and solving for the eigenvalues we find that the eigenvalues λ are:

$$\lambda = \frac{((s_1(1-p)+s_2) \pm \sqrt{(s_1(1-p)+s_2)^2 - 4((s_1(1-p)s_2) - \alpha_1(s_1 p)/(1+\beta_2 m_2))}}{2}$$

$$\lambda = \frac{((r_1(1-q)+r_2) \pm \sqrt{(r_1(1-q)+r_2)^2 - 4((r_1(1-q)r_2) - \alpha_2(r_1 q)/(1+\beta_4 m_2)^2)}}{2}$$

Solving these equations reveals the criteria for partial extinction stability, namely $\alpha_1 < U_{\alpha_1}(1+\beta_2 m_2)$ and $\alpha_2 < U_{\alpha_2}(1+\beta_4 m_2)^2$

Since both β values and the non-extinction population will be nonzero, we see that the criteria for partial extinction stability is weaker than total extinction stability. As a result, if the total extinction is stable, the partial extinctions will be stable as well. Three stable equilibrium cannot be obtained using the more traditional non-staged population models. In future research, we hope to examine the possibility of simultaneous stability in partial extinctions and coexistence.