Structured Population Dynamics and Calculus: An Introduction to Integral Modeling

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Will an exotic species thrive in a new territory? What are the best management options to eradicate a population (pest species) or to facilitate population recovery (endangered species)? Population modeling is one method of integrating mathematics and biology in order to help answer these questions. Most commonly, researchers use population projection matrices to model a stage structured population. In general, a large number of life history stages increases model accuracy, but at the cost of increasing parameter uncertainty, since each non-zero matrix entry needs to be estimated from data. This tradeoff can often be avoided by using integral projection models which utilize continuous life history functions and describe a continuous range of stages. In this article we illuminate the differences and similarities between matrix population models and integral population models for single-species stage structured populations. We illustrate the use of integral models with an application to Platte thistle, a species in decline in its native environment.

1 Stage Structured Population Models

In a stage structured population model, the individuals are partitioned into demographically different stage classes. For example, it is natural to divide an insect population into egg, larva, pupa and adult stages. For mammals, age classes are often used to partition the
population. For many plants, the stages can be better described as a continuous function of stem diameter, or any other indicator of size. In this case one can either maintain the continuous stage structure, or partition the continuous range of stages into a finite number of stages. To do such a discretization effectively, one must ensure that each stage consists of individuals with comparable growth, survival and fecundity (number of offspring per capita), because the accuracy of the approximation largely depends on the similarity of individuals within each stage class. The choice of the stage variable and the breakdown into the stages is very dependent on the type of population and requires biological intuition. For instance, fecundity in animals is often influenced by age, while in plants, size is usually a better measure.

Another basic modeling decision is how time will be treated. Field data is often collected at regular time intervals, for instance on a yearly or seasonal basis, so it is often easier and more practical to model time discretely. There is actually a great deal of controversy about the relative merits of discrete-time versus continuous-time modeling (see, for example, [6]). In this article we will follow in the tradition of most of the literature on single-species structured populations, and consider time to be a discrete variable.

A Population Projection Matrix (PPM) model is typically used when both time and stage structure are discrete, and an integro-difference model, known in this context as an Integral Projection Model (IPM), is used when time is discrete but the stage structure is continuous. (The continuous-time analogues are ordinary differential equations and integro-differential or partial differential equations). PPM’s are ubiquitous in ecology, but for many purposes the IPM might be easier and/or more accurate to use. In Table 2 at the end of this paper we summarize the similarities between the PPMs and IPMs.

2 Matrix Models

Matrix models were introduced in the mid 1940s, but did not become the dominant paradigm in ecological population modeling until the 1970s. The modern theory is described in great detail in Caswell [3], which also contains a good short history of the subject. We summarize some of this history here. The basic theory of predicting population growth by analyzing life history parameters such as survival and fecundity can be traced back to Cannan [2] in 1895. Matrix models in particular were developed independently by Bernardelli [1], Lewis [15], and Leslie [14]. The greatest contributions to the fledgling theory were made by P.H. Leslie, a physiologist and self-taught mathematician. While working at the Bureau of Animal Population at Oxford between 1935 and 1968, Leslie sought a way of synthesizing mortality and fertility data into a single model. In searching for a viable method, he experimented
with the idea of modeling a population using matrices. We briefly describe his basic models in the next section. Leslie then used these models for population description, analysis and prediction.

Although he was highly regarded and well-connected in the ecology community, Leslie’s work in matrix modeling initially received little attention. One of the few, and most important, contemporaries who did use the matrix model was Leonard Lefkovitch. In [13] he also implemented a matrix model, but introduced the concept of dividing individuals into classes based on developmental stage rather than age. This was a great boon to plant ecologists who began defining stage classes by size rather than age - a change which usually resulted in better predictions.

As Caswell [3] points out, it took some 25 years for the ecology community to adopt matrix projection models after Leslie’s influential work. There were two major reasons for this delay. The ecology community at that time thought of matrix algebra as an advanced and esoteric subject in mathematics. More importantly, there was a more accessible method, also contributed by Leslie, called life table analysis. Before the widespread use of computers, there was no information that a matrix model could provide that a life table could not. This would change as more sophisticated matrix algebra and computation methods emerged to convince ecologists the worth of matrix models. For instance, using elementary linear algebra, one can predict asymptotic growth rates and stable age distributions from spectral properties. As one example, the use of eigenvectors facilitated the development of sensitivity and elasticity analyses, allowing a population manager to determine how small changes in life history parameters effect the asymptotic population growth rate. This is an especially important question for ecological models, which typically have high uncertainty. Sensitivity and elasticity analyses are sometimes used to make recommendations on what stage class conservation managers should focus on to increase the population growth rate of an endangered species.

2.1 Transition matrices

To set up a matrix model we start with a population divided into \( m \) stage classes. Let \( t \in \mathbb{N} \) be time, measured discretely, and let \( \mathbf{n}(t) \) be the population column vector

\[
\mathbf{n}(t) = [n(1,t), n(2,t), \ldots, n(m,t)]^T,
\]

where each entry \( n(i,t) \) is the number of individuals belonging to class \( i \). A discrete-time matrix model takes the form

\[
\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t),
\]
where \( A = (a_{i,j}) \) is the \( m \times m \) PPM containing the life-history parameters. It is also called a transition matrix, since it dictates the demographic changes occurring over one time step. We can write (1) as

\[
n(i, t + 1) = \sum_{j=1}^{m} a_{ij} n(j, t).
\]

(2)

The entries \( a_{i,j} \) determine how the number of stage \( j \) individuals at time \( t \) effect the number of stage \( i \) individuals at time \( t + 1 \). This is the form we will generalize when we discuss integral equations.

In their simplest form, the entries of \( A \) are survivorship probabilities and fecundities. For example, a Leslie matrix is of the form

\[
A = \begin{bmatrix}
  f_1 & f_2 & \cdots & f_m \\
  s_1 & 0 & \cdots & 0 \\
  0 & s_2 & \cdots & 0 \\
  \vdots & 0 & \ddots & 0 \\
  0 & \cdots & \cdots & s_m
\end{bmatrix},
\]

where \( s_i \) is the probability that an individual survives from age class \( i \) to age class \( i + 1 \), and \( f_i \) is the fecundity, which is the per capita average number of offspring reaching stage 1 born from mothers of the age class \( i \). The transition matrix has this particular structure when age is the stage class variable and individuals either move into the next class or die. In general, entries for the life-history parameters can be in any entry of the \( m \times m \) matrix.

For any matrix \( A \), it follows from (1) that

\[
n(t) = A^t n(0).
\]

(3)

The long-term behavior of \( n(t) \) is determined by the eigenvalues and eigenvectors of \( A \). We say that \( A \) is non-negative (denoted \( A > 0 \)) if all of its entries are positive and that \( A \) is primitive if \( A^k > 0 \) for some \( k \in \mathbb{N} \). This second condition is equivalent to every stage class having a descendent in every other stage class at some time step in the future. PPMs are generally positive and primitive, thus the following Perron-Frobenius Theorem (see for instance [19]) is extremely useful:

**Theorem 2.1.** Let \( A \) be a square, non-negative, primitive matrix. Then \( A \) has an eigenvalue, \( \tilde{\lambda} \), which satisfies:

1. \( \tilde{\lambda} \) is real and \( \tilde{\lambda} > 0 \),

2. \( \tilde{\lambda} \) has right and left eigenvectors whose components are strictly positive,
3. \( \tilde{\lambda} > |\lambda| \) for any eigenvalue \(|\lambda| \neq \tilde{\lambda} \),

4. \( \lambda \) has algebraic and geometric multiplicity 1.

Assume that \( A \) is primitive. Letting \( \|n\| \) denote the \( \ell_1 \) norm, i.e.

\[
\|n\| = |n_1| + |n_2| + \ldots |n_m|, \tag{4}
\]

and letting the dominant (i.e. greatest magnitude) eigenvalue of \( A \) be given by \( \lambda \), and its associated eigenvector by \( v \), then

\[
\lim_{t \to \infty} \frac{\|n(t+1)\|}{\|n(t)\|} = \lambda, \quad \lim_{t \to \infty} \frac{n(t)}{\|n(t)\|} = v. \tag{5}
\]

Thus \( \lambda \) is the asymptotic growth rate, and \( v \) is the stable age structure of the population.

### 2.2 Problems with stage discretization

To use a population projection matrix model, the population needs to be decomposed into a finite number of discrete stage classes that are not necessarily reflective of the true population structure. Easterling [7] and Easterling et al. [8] showed that erroneous predictions of the asymptotic growth rate occur if the stage classes are chosen in a way which is not biologically realistic. Fortunately it is often possible to decompose a particular population in a biologically sensible fashion. Vandermeer [20] and Moloney [16] crafted algorithms to minimize errors associated with choosing class boundaries. While such algorithms help to derive more reasonable matrices they cannot altogether eliminate the sampling and distribution errors associated with discretization [3].

With or without a sensible decomposition of the population into stages, there is also the problem that in a matrix model individuals of a given stage class are treated as though they are identical through every time step. That is, two individuals starting in the same class will always have the same probability of transitioning into a different stage class at every time step in the future, which is not necessarily the case for real populations. There is also a crucial tradeoff between biological realism and parameter uncertainty when choosing the number of stage classes. A model will lose realism as the number of stage classes diminishes because increasingly dissimilar individuals are grouped together. Alternatively, if too many stage classes are used, the model becomes overburdened with new parameters and there is increased parameter uncertainty because fewer and fewer data points are used to estimate life-history parameters. Furthermore, sensitivity and elasticity analyses both have been shown to be affected by changes in stage class division [8].
3 Integral Projection Models

An alternate approach to discretizing continuous variables like size is to use integral projection models. A class of IPMs is introduced in Easterling [7], Easterling et al [8] and Ellner and Rees [9]. These models retain much of the analytical machinery which makes the matrix model appealing, while allowing for a continuous range of stages. In [7, 8] it is shown how to construct such an integral projection model, using continuous stage classes and discrete time, and provided sensitivity and elasticity formulas comparable to those of matrix models. In [9] an IPM analogue of the Perron-Frobenius Theorem is given. In particular, there are readily checked conditions under which such a model has an asymptotic growth rate which is the dominant eigenvalue of an operator whose associated eigenvector is the asymptotic stable population distribution.

Just as ecologists were slow to adopt matrix models, integral models are not yet widely used. Stage structured IPMs of the type considered in this paper appeared in the scientific literature around ten years ago, and can be found in [4, 5, 7, 8, 9, 10, 17, 18]. There is a large literature on integral models for spatial spread of a population, see for instance Kot, et al. [11, 12]. In this case the kernel for the integral operator can be very different than for the integral projection models discussed in this paper. For instance, the kernel describing spatial spread will typically have a support which is not finite, and might not even be square integrable; this makes the spectral analysis, and hence the asymptotic analysis, much more difficult. The integral operators discussed in this paper are compact operators, which have many properties that are similar to those for matrices.

3.1 Continuous stage structure and integral operators

Let \( n(x, t) \) be the population distribution as a function of the stage \( x \) at time \( t \). For example, \( x \in [m_s, M_s] \) could be the size of the individual, where \( m_s \) is the minimum size, and \( M_s \) is the maximum size. The analogue of the matrix entries \((a_{i,j})\) (for \( i, j \in \{0, 1, \ldots, m\} \)) is a projection kernel \( k(y, x) \) (for \( y, x \in [m_s, M_s] \)), and the role of the matrix multiplication operation is analogous to an integral operator. The analogue of (2) is

\[
n(y, t + 1) = \int_{m_s}^{M_s} k(y, x) n(x, t) dx.
\]

In particular, the kernel determines how the distribution of stage \( x \) individuals at time \( t \) moves to the distribution of stage \( y \) individuals at time \( t + 1 \), in much the same way that in (2) the \((i, j)\)th entry of a projection matrix determines how an individual in stage \( j \) at time \( t \) moves to state \( i \) at time \( t + 1 \). The kernel is determined by statistically derived functions for
survival, growth and fecundity. An advantage of the integral approach is that data over the entire distribution can be used to estimate the parameters of the functions, thus minimizing the parameter uncertainty. In contrast, in matrix models transitions between life history stages are estimated for subsets of data.

The stage variable \( x \) does not have to be a scalar, but the range of stage variables should be a compact metric space. For example, for a plant, a stage could contain information on both size and quality. In cases like this where \( x \) is not a scalar, the Riemann integration over a subset of \( \mathbb{R} \) will be replaced by more general integration over a product space; see Ellner and Rees [9] for such an example.

Integral equations such as (6) can be analyzed in much the same way as matrix-based models of the form (1). Consider the \( L^1 \)-norm

\[
\| f \| := \int_{m_s}^{M_s} |f(x)| dx,
\]

which is analogous to (4). The space

\[
L^1(m_s, M_s) = \{ f : (m_s, M_s) \to \mathbb{R} \mid \| f \| < \infty \}
\]

is well-known to be a compact metric space. For every \( t > 0 \), the population distribution \( n(t, \cdot) \) is in \( L^1(m_s, M_s) \), and the total population is \( \| n(t) \| \). Hence \( L^1(m_s, M_s) \) plays the same role in an IPM that \( \mathbb{R}^m \) (with norm (4)) plays in a PPM.

For a population distribution \( n(x, t) \), it is sometimes useful to distinguish between the function \( n(x, t) \) of two variables and the \( L^1(m_s, M_s) \)-valued function of a single variable \( n(t) = n(\cdot, t) \); we refer to \( n(t) \) as a “vector” in \( L^1(m_s, M_s) \). Define the operator \( A : L^1(m_s, M_s) \to L^1(m_s, M_s) \) by

\[
(Av)(\cdot) := \int_{m_s}^{M_s} k(\cdot, x)v(x) dx.
\]

It is not hard to show that \( A \) is bounded on \( L^1(\Omega) \). Then (6) is equivalent to

\[
n(t + 1) = An(t),
\]

which is analogous to (1).

Ellner and Rees [9] show that for a large class of kernels \( k \), the integral operator \( A \) satisfies the conclusions of the Perron-Frobenius Theorem, so for these operators there is a dominant real eigenvalue \( \lambda \) which is the asymptotic growth rate, and an associated eigenvector \( v \).
which is the stable stage distribution. In the operator case the eigenvectors are functions in $L^1(m_s, M_s)$, rather than vectors in $\mathbb{R}^m$. In this case the first equation in (5) holds, and the second equation holds if the convergence is interpreted as $L^1(m_s, M_s)$ convergence.

3.2 The kernel

To construct the kernel, we construct a growth and survival function $p(y, x)$ and a fecundity function $f(y, x)$, and let

$$k(y, x) = p(y, x) + f(y, x).$$

Here $p(y, x)$ is the probability that an individual of size $x$ will survive and grow to be an individual of size $y$ in one time step. The function $f(y, x)$ is the number of offspring of size $y$ that an individual of size $x$ will produce in one time step. Typically $p(y, x)$ can be written as $s_1(x)g(y, x)$, where $s_1(x)$ is the probability of survival for a size $x$ individual to the next time step and the growth function $g(y, x)$ is the probability that an individual of size $x$ will be of size $y$ at the next time step. The growth function can describe both the probability of growing to a larger size and the probability of shrinking to a smaller size. The fecundity function $f(y, x)$ is typically written as $f_1(x)f_2(y, x)$, where $f_1(x)$ is the average number of offspring of parents of size $x$, and $f_2(y, x)$ is the probability that the offspring of a size $x$ parent are size $y$ at the next time step. We should point out that the fecundity function allows for the possibility of a seedling or newborn moving, in one time step, to a large size, but in practice the probability of this happening will virtually be zero.

The function $s_1(x)$, $g(y, x)$, $f_1(x)$, and $f_2(y, x)$ are estimated using from the data using standard statistical methods. For instance, logistic regression analysis can be used to describe survival as a function of size. For more details on the appropriate statistical models for integral projection models see Easterling et al. [8], Ellner and Rees [9], and Rose et al. [18].

3.2.1 Estimating the kernel for Platte thistle

We now show how a specific model is constructed, using a version of the model for Platte thistle ($Cirsium canescens$) found in Rose et al. [18], modified to ignore effects of herbaceous predators. Platte thistle is an indigenous perennial plant in the midgrass sand prairies of central North America. It is strictly monocarpic, meaning that plants die after reproducing, so the flowering probability will need to be incorporated into the kernel. It is in decline in its native environment, possibly due to a biocontrol agent introduced to manage a different invasive thistle. In this model, we use the root crown diameter $x$ as the continuous class variable. The survival probability $s(x)$ and flowering probability $f_p(x)$ respectively, are given
in Table 1. Since the Platte thistle is monocarpic, we have to include the probability of not flowering, which is $1 - f_p(x)$, so $s_1(x) = s(x)(1 - f_p(x))$. Also given in Table 1 is the average growth $\mu(x)$ and the variance of growth $\sigma(x)$ (which in this case is constant). The growth function $g(y, x)$ is a normal distribution in the variable $y$, with mean $\mu(x)$ and variance $\sigma(x)$.

We now turn our attention to the fecundity term of the kernel, $f(y, x)$. To best illustrate the basic concepts, we simplify the model by ignoring the effects of herbivores on fecundity, and the possible slight effect of maternal size on offspring size. In order to reproduce, a plant must survive, and it must also flower. Each plant will produce seeds, and these seeds must germinate for an offspring to be included in the next population count. The number of seeds $S(x)$ produced by each plant is an exponential function of size $x$. The average germination probability $P_e$, also known as the recruitment probability, is constant - later we will consider the case where this is not constant. Finally, we also need a distribution of the offspring sizes $J(y)$; we assume here that this is a normal distribution with constant mean $\mu_f$ and variance $\sigma_f$. Therefore,

$$f(y, x) = P_e s(x) f_p(x) S(x) J(y),$$

$$k(y, x) = p(y, x) + f(y, x) = s(x)(1 - f_p(x))g(y, x) + P_e s(x) f_p(x) S(x) J(y)$$

and

$$n(t + 1) = An(t) = \int_{m_x}^{M_x} k(\cdot, x)n(x, t) \, dx.$$  

A graph of the kernel is shown in Figure 1, and the component functions are summarized in Table 1.

![Platte Thistle Kernel](image)

Figure 1: The kernel for the Platte thistle integral projection model.
Demography

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<tr>
<th>Equation</th>
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<tbody>
<tr>
<td>Survival: ( s(x) = \frac{e^{-0.62+0.85x}}{(1+e^{-0.62+0.85x})} )</td>
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<tr>
<td>Flowering Probability: ( f_p(x) = \frac{e^{-10.22+4.25x}}{(1+e^{-10.22+4.25x})} )</td>
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<tr>
<td>Growth Distribution: ( g(x,y) = \text{Normal Distribution} ) with ( \sigma^2 = 0.19 ) and ( \mu(x) = 0.83 + 0.69x )</td>
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<td>Individual Seed Set: ( S(x) = e^{0.37+2.02x} )</td>
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<tr>
<td>Juvenile Size Distribution: ( J(y) = \text{Normal Distribution} ) with ( \sigma_f^2 = 0.17 ) and ( \mu_f = 0.75 )</td>
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<tr>
<td>Germination Probability: ( P_e = 0.067 ) density independent or ( P_e = S_T(t)^{-0.33} ) density dependent where ( S_T(t) ) is the total seed set</td>
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<th>Equation</th>
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<tr>
<td>( (\text{An})(y,t) = \int_{m_s}^{M_s} k(y,x)n(x,t)dx \approx \frac{M_s - m_s}{N} \sum_{j=1}^{N} k(y,x_j)n(x_j,t). )</td>
<td>11</td>
</tr>
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Let

\[ a_{i,j} = \frac{M_s - m_s}{N} k(x_i,x_j) \text{ for } i,j = 1,2,\ldots N, \quad A_N = (a_{i,j}) \]

Table 1: Life History Functions for Platte Thistle [18].

3.3 Numerical solution of the integro-difference equation

Analytic evaluation of the integral operator is difficult if not impossible to perform. Thus, we will use numerical integration to obtain an estimate of the population. A conceptually easy and relatively accurate method is the midpoint rule. Let \( N \) be the number of equally sized intervals, and let \( x_j \) be the midpoints of the intervals. Then

\[ (\text{An})(y,t) = \int_{m_s}^{M_s} k(y,x)n(x,t)dx \approx \frac{M_s - m_s}{N} \sum_{j=1}^{N} k(y,x_j)n(x_j,t). \] (11)
and
\[ n_N(t) = [n(x_1, t), n(x_2), \ldots, n(x_N, t)]^T. \]

Then \( n_N(t) \) is a discrete approximation of \( n(x, t) \), \( A_N \) is a discrete approximation of the integral operator \( A \), and
\[
A_N n_N = \frac{M_s - m_s}{N} \sum_{j=1}^{N} k(x_i, x_j) n(x_j, t).
\]

Since \( k(x, y) \) is continuous, the Riemann sum uniformly approximates the integral as \( N \to \infty \). Hence the integrodifference equation \( n(t+1) = A n(t) \) can be approximated at the midpoints \( x_j \) by \( n_N(t+1) = A_N n_N(t) \).

This matrix model can be analyzed much like a traditional matrix model. Since the dominant eigenvalue of \( A_N \) converges to the dominant eigenvalue of \( A \) as \( N \to \infty \) (Ellner and Rees [9], Easterling [7]), the long term growth rate is easily estimated. Figure 2 shows this convergence of \( \lambda_N \) to \( \lambda = 1.325 \) as \( N \) increases. The leading eigenvalue of \( A_5 \) is 1.332, so we see that fairly small dimensional approximations of \( A \) lead to very good approximations of the long-term growth of the system.

We should emphasize the difference between a PPM and the matrix model obtained from the IPM. In the former every nonzero entry is estimated directly; a large matrix of this type is not intended to approximate the IPM. In the latter, the life history functions are estimated, giving rise to a kernel, and this kernel is used to obtain a matrix which does approximate the IPM for large \( N \).

We now turn to the stable size distribution, that is, the limiting distribution given by the second equation in (5). This can be found by approximating the leading eigenvector of \( A \), and normalizing it so that it has \( L^1(m_s, M_s) \) norm of 1. This eigenvector, which is shown in Figure 3, is uniformly approximated by the normalized leading eigenvector of \( A_N \) for large \( N \) (see Ellner and Rees [9]).

### 3.4 Density dependence

In the Platte thistle model above, we made the simplifying assumption that the average germination probability, \( P_e \), is constant, and obtained a density independent model. By “density independence” we mean that \( n(t+1) \) is a linear function of \( n(t) \), or equivalently, the operator \( A \) does not depend upon \( n(t) \). The growth rate of 1.332 we obtain from this model is unrealistically large, so we consider a more realistic model where \( P_e \) is dependent upon \( S_T(t) \), the total number of seeds produced. Since the number of seeds produced depends
on $n(x, t)$, the resulting system will be density dependent. Rose et al. [18] found that the germination probability of seeds can be modeled by $P_e(t) = (S_T(t))^{-0.33}$. This new germination probability substantially changes the qualitative and quantitative nature of the model. For instance, instead of the model having an asymptotic growth rate determined by the leading eigenvalue and a stable age structure determined by the eigenvector associated with the leading eigenvalue, solutions of this model have a limiting population and age structure which is independent of the initial population vector (provided the initial vector is nonzero).

If $P_e$ is replaced by $(S_T(t))^{-0.33}$, (9) and (10) becomes the nonlinear system

$$n(y, t + 1) = \int_{M_s}^M p(y, x)n(x, t) dx + J(y)(S_T(t))^{-0.33} \int_{M_s}^M s(x)f_p(x)S(x)n(x, t) dx. \quad (12)$$

We need to obtain a formula for $S_T(t)$ in terms of $n(t)$. For a Platte thistle to produce seeds, it must survive through a time step and flower. It will then produce seeds as a function of root crown diameter $x$. Thus, each plant of root crown diameter size $x$ will produce $s(x)f_p(x)S(x)$ seeds on average, so the number of seeds produced by all plants of size $x$ at
time \( t \) is \( s(x)f_p(x)S(x)n(x,t) \). Hence the total number of seeds at time \( t \) is

\[
S_T(t) = \int_{m_s}^{M_s} s(x)f_p(x)S(x)n(x,t)dx.
\] (13)

Therefore, (12) becomes

\[
n(y,t+1) = \int_{m_s}^{M_s} p(y,x)n(x,t)\,dx + J(y)(S_T(t))^67.
\] (14)

It is possible to prove that the solutions \( n(\cdot, t) \) of (14) converges in \( L_1(m_s, M_s) \) as \( t \to \infty \), and that the limit is independent of the initial population vector (provided that the initial population vector is nonzero). We denote the limit by \( w(\cdot) \), and the normalized limit (the second equation in (5)) by \( v(\cdot) \). This latter vector is the stable age distribution for this system, and is shown in Figure 3. It follows from the Dominated Convergence Theorem that the total population \( N(t) = \|n(\cdot, t)\| \) converges to \( \|w\| \) as \( t \to \infty \), and that the limiting total population is independent of the initial population vector. This is illustrated in Figure 4, where the total population as a function of time is shown for five different initial conditions.
Figure 4: Circles indicate every stage of the population contains 1000 individuals; triangles indicate the population consists of 10,000 individuals of sizes 0 to 1.1 mm only; X’s indicate the population consists of 1000 individuals of sizes 54.45-55 mm only; plusses indicate a population of 500,000 individuals of sizes 0-.55 mm; and diamonds indicate a population of 10,000 consisting only of sizes 54.45-55 mm.

To clarify the limiting behavior of the solutions to this nonlinear system, let $P_0 = \lim_{t \to \infty} (S_T(t))^{-33}$ and take the limit as $t \to \infty$, in equation (12) to see that $w(\cdot)$ satisfies

$$w(y) = \int_{m_s}^{M_s} p(y, x)w(x) \, dx + P_0 J(y) \int_{m_s}^{M_s} s(x) f_p(x) S(x) w(x) \, dx.$$  \hfill (15)

Define $A_0$ and $A_1$ by

$$(A_0 \varphi)(y) = \int_{m_s}^{M_s} p(y, x) \varphi(x) \, dx \quad \text{for } \varphi \in L^1(m_s, M_s),$$

$$(A_1 \varphi)(y) = \int_{m_s}^{M_s} p(y, x) \varphi(x) \, dx + P_0 J(y) \int_{m_s}^{M_s} s(x) f_p(x) S(x) \varphi(x) \, dx \quad \text{for } \varphi \in L^1(m_s, M_s).$$

It follows from (15) that $A_1$ has an eigenvalue of 1 and associated eigenvector $w = w(\cdot)$. Rather than taking a limit in order to get $P_0$, which can be time-consuming and inaccurate,
it can be shown that (letting \( I \) denote the identity operator)

\[
P_0 = \left( \int_{m_S}^{M_S} s(x)f_p(x)S(x)[(I - A_0)^{-1}J](x) \, dx \right).
\]

To evaluate this, the operator \( A_0 \) and hence \((I - A_0)^{-1}\) and \((I - A_0)^{-1}J\), can be approximated as in section 3.3. Once we have \( P_0 \), the limiting population distribution \( v(\cdot) \) is the normalized eigenvector of \( A_1 \).

### 4 Further Reading

For further information on using matrices in the biological sciences, Caswell [3] gives a thorough treatment of the subject. For more information concerning integro-difference equations Eastering et al. [8] is a good introduction with the theoretical footings of the method contained in the appendices of Ellner and Rees [9].
<table>
<thead>
<tr>
<th>Population Projection Matrix</th>
<th>Integral Projection Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>vector entry</td>
<td>number of individuals in stage class i at time t</td>
</tr>
<tr>
<td>state vector</td>
<td>$n(t) = [n(1,t), \ldots, n(m,t)]^T \in \mathbb{R}^m$</td>
</tr>
<tr>
<td>probability</td>
<td>$p_{ij}$</td>
</tr>
<tr>
<td>function</td>
<td>$f_{ij}$</td>
</tr>
<tr>
<td>matrix entry</td>
<td>$k_{ij} = p_{ij} + f_{ij}$</td>
</tr>
<tr>
<td>matrix</td>
<td>$A = [k_{ij}]$</td>
</tr>
<tr>
<td>discrete stage variables</td>
<td>$j \sim t$ and $i \sim t+1$</td>
</tr>
<tr>
<td>difference equation</td>
<td>$n(j,t+1) = \sum_{i=1}^{m} k_{ij} n(i,t)$</td>
</tr>
<tr>
<td>vector form</td>
<td>$\vec{n}(t+1) = A \vec{n}(t)$</td>
</tr>
</tbody>
</table>

Table 2: Comparison of Matrix and Integral Models
Acknowledgements

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References


