ARTICLES

Structured Population Dynamics: 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 helps answer these questions by integrating mathematics and biology.

Often, a single species cannot be properly modeled as one population, but instead is best treated as a *structured* population, where the individuals in the population are partitioned into classes, or *stages*. As an example of a stage structured population, it is natural to partition an insect population into egg, larva, pupa, and adult stages. The choice of the stages and the breakdown of the population into stages depend heavily on the type of population, and are informed by biological intuition. For instance, fecundity (number of offspring per capita) in animals often varies with age, while in plants, fecundity typically depends on size. This implies that for mammals, the stages might be best determined by age, so that age is a good *stage variable* for mammals, while size might be a good stage variable for plants. Furthermore, for many animals there are natural classes of ages—the egg/larva/pupa/adult partition of an insect population—while for many plants, the stages can be better described as a continuous function of stem diameter, or another indicator of size. When the stages are discrete, a matrix model is used, and when the stages are continuous, an integral model is used. Both integral and matrix models are commonly used in population viability analysis and are both important tools in guiding population management [**4, 19**]. These models are used to predict long-term and transient behavior of a population, and they inform wildlife managers about which populations are in danger of going extinct or of growing unacceptably large.

Another basic modeling choice is whether time is modeled as a discrete variable or a continuous variable. Field data is often collected at regular time intervals, for

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instance on a yearly or seasonal basis, so it is often easier and more practical to model time discretely. There is some controversy about the relative merits of discrete-time versus continuous-time modeling [**7**]. Nonetheless, in most of the ecological literature on single-species structured populations, time is modeled as a discrete variable, so in this article we also model time as a discrete variable.

For a population that is partitioned into finitely many stages and modeled at discrete times, the evolution of the population can often be described using a Population Projection Matrix (PPM). The entries in a PPM are determined by the life history parameters of the population, and the properties of the matrix—for instance, its spectrum—determine the behavior of the solutions of the model. In the next section we describe PPMs in detail.

When stages are described by a continuous variable, one can either maintain the continuous stage structure, or partition the continuous range of stages into a finite number of stages. The latter is called a discretization of the population. To do it effectively one must ensure that each stage consists of individuals with comparable growth, survival, and fecundity, because the accuracy of the approximation depends on the similarity of individuals within each stage class. In general, a large number of life history stages increases model accuracy, but at the cost of increasing parameter uncertainty, since each nonzero matrix entry needs to be estimated from data, and the more stages there are, the less data is available per stage. This tradeoff can often be avoided by maintaining the continuous structure, and using an Integral Projection Model (IPM) that uses continuous life history functions that are functions of a continuous range of stages. We discuss IPMs in detail below.

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, following Rose et al. [**22**], showing how the model is determined by basic life history functions. PPMs are ubiquitous in ecology, but for many purposes an IPM might be easier and/or more accurate to use. In TABLE 1 we summarize the similarities between PPMs and IPMs. In order to compare the predictions for PPMs and IPMs, enough data must be available to find the parameters in both models. This is done for models for the plant monkshood in Easterling et al. [**9**]. We should mention that if time is treated as a continuous variable, the analogue of a PPM model is an ordinary differential equation, and the analogue of a IPM is an integro-differential equation.

AuQ: Relocated and renumbered table

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 [**4**], which also contains a good short history of population projection matrices in its Section 2.6. We summarize some of this history here. The basic theory of describing, predicting, and analyzing population growth by analyzing life history parameters such as survival and fecundity can be traced back to Cannan [**3**] in 1895. Matrix models in particular were developed independently by Bernardelli [**2**], Lewis [**16**], and Leslie [**15**]. The latter is most relevant to the modern theory. P. H. Leslie was a physiologist and self-taught mathematician, who, while working at the Bureau of Animal Population at Oxford between 1935 and 1968, synthesized mortality and fertility data into single models using matrices. We briefly describe his basic models, which are still used 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

TABLE 1: Comparison of matrix and integral models

Population Projection Matrix			**Integral Projection Model**		
vector entry	$n(i,t)$	number of individuals in stage class i at time t	continuous function	$\int_{y_0}^{y_1} n(y,t)\,dy$	number of individuals expected between sizes y_0 and y_1
state vector	$\mathbf{n}(t) = [n(1,t), \cdots, n(m,t)]^T \in \mathbb{R}^m$	stage distribution of population at time t	continuous state function	$n(\cdot,t) \in \mathbb{L}^1(m_s, M_s)$	stage distribution of population at time t
probability	p_{ij}	probability of an individual transitioning from class j to i	probability density function	$\int_{y_0}^{y_1} p(y,x)\,dy$	probability an individual of size x will grow and survive to a size between y_0 and y_1
scalar	f_{ij}	number of newborns size i from parents size j	function	$\int_{y_0}^{y_1} f(y,x)\,dy$	number of newborns between sizes y_0 and y_1 from parents of size x
matrix entry	$k_{ij} = p_{ij} + f_{ij}$	the ijth entry of the transition matrix	function	$k(y,x) = p(y,x) + f(y,x)$	kernel
matrix	$A = [k_{ij}]$		integral operator	$(Av)(y) = \int_{m_s}^{M_s} k(y,x)v(x)\,dx$	
discrete stage variables	$j \sim t$ and $i \sim t+1$	matrix indices associated with time t and time $t+1$	continuous stage variables	$x \sim t$ and $y \sim t+1$	variables associated with time t and time $t+1$
difference equation	$n(j,t+1) = \sum_{i=1}^{m} k_{ji} n(i,t)$		integral equation	$n(y,t+1) = \int_{m_s}^{M_s} k(y,x)n(x,t)\,dx$	
vector form	$\mathbf{n(t+1) = An(t)}$	matrix multiplication	operator form	$\mathbf{n}(t+1) = A\mathbf{n}(t)$	integration

contemporaries who did use the matrix model was Leonard Lefkovitch. He also implemented a matrix model [**14**], but with an innovation: The populations were partitioned into classes based on developmental stage rather than age. This made the method more applicable to plant ecologists, who began defining stage classes by size rather than age—a change that usually resulted in better predictions.

As Caswell points out [**4**], 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 mathematical subject. More importantly, there was a more accessible method, also contributed by Leslie, called life table analysis [**4**, Section 2.3].

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 of the worth of matrix models. For instance, using elementary linear algebra, one can predict asymptotic population growth rates and stable stage distributions from the spectral properties of the matrix. Also, the use of eigenvectors facilitated the development of *sensitivity and elasticity analyses*, giving an easy way 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 are typically very uncertain. Sensitivity and elasticity analyses are sometimes used to make recommendations about which stage class conservation managers should focus on in order to increase the population growth rate of an endangered species.

Transition matrices To set up a matrix model we start with a population partitioned into m stage classes. Let $t \in \mathbb{N} = \{0, 1, 2, \dots\}$ be time, measured discretely, and let $\mathbf{n}(t)$ be the population column vector

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

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

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t), \tag{1}$$

where $\mathbf{A} = (k_{ij})$ 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

$$n(i, t+1) = \sum_{j=1}^{m} k_{ij} n(j,t), \quad i = 1, \dots n. \tag{2}$$

The entry k_{ij} determines how the number of stage j individuals at time t affects 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 $\mathbf{A}$ are survivorship probabilities and fecundities. What we call a Leslie matrix has the form

$$\mathbf{A} = \begin{pmatrix} f_1 & f_2 & \cdots & f_{m-1} & f_m \\ p_1 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & \cdots & 0 & 0 \\ \vdots & 0 & \ddots & 0 & 0 \\ 0 & \cdots & \cdots & p_{m-1} & 0 \end{pmatrix},$$

where p_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 stage 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 may appear in any entry of the m x m matrix $\mathbf{A}$.

For any matrix $\mathbf{A}$ and $t \in \mathbb{N}$, let $\mathbf{A}^t$ denote the tth power of $\mathbf{A}$ for any natural number t. It follows from (1) that

$$\mathbf{n}(t) = \mathbf{A}^t \mathbf{n}(0). \tag{3}$$

The long-term behavior of $\mathbf{n}(t)$ is determined by the eigenvalues and eigenvectors of $\mathbf{A}$. We say that $\mathbf{A}$ is nonnegative if all of its entries are nonnegative, and that $\mathbf{A}$ is primitive if for some $t \in \mathbb{N}$, all entries of $\mathbf{A}^t$ are positive. 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 nonnegative and primitive, thus the following theorem is extremely useful [**23**, Section 1.1]:

PERRON-FROBENIUS THEOREM. *Let* $\mathbf{A}$ *be a square, nonnegative, primitive matrix. Then* $\mathbf{A}$ *has an eigenvalue,* λ*, known as the dominant eigenvalue, that satisfies:*

1. λ *is real and* $\lambda > 0$*,*
2. λ *has right and left eigenvectors whose components are strictly positive,*
3. $\lambda > |\tilde{\lambda}|$ *for any eigenvalue* $\tilde{\lambda}$ *such that* $\tilde{\lambda} \neq \lambda$*,*
4. λ *has algebraic and geometric multiplicity* 1.

This theorem is important in the analysis of population models because the dominant eigenvalue is the asymptotic growth rate of the modeled population, and its associated eigenvector is the asymptotic population structure. To see this, assume that $\mathbf{A}$ is primitive. Let $\mathbf{n} = [n_1, n_2, \ldots, n_m]$, and $\|\mathbf{n}\|$ denote the ℓ_1 norm:

$$\|\mathbf{n}\| = |n_1| + |n_2| + \ldots |n_m|. \tag{4}$$

Denote the unit eigenvector associated with λ by $\mathbf{v}$, so

$$\lim_{t\to\infty} \frac{\|\mathbf{n}(t+1)\|}{\|\mathbf{n}(t)\|} = \lambda \quad \text{and} \quad \lim_{t\to\infty} \frac{\mathbf{n}(t)}{\|\mathbf{n}(t)\|} = \mathbf{v}. \tag{5}$$

Thus as time goes on, the growth rate approaches λ and the stage structure approaches $\mathbf{v}$. In particular, the dynamics of a long-established population is described by λ and $\mathbf{v}$.

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. As mentioned previously, if stage classes are defined in such a way that there is at least one class in which the life history parameters vary considerably, then it might not be possible to accurately describe individuals in that stage class, which might result in erroneous predictions. Easterling [**8**] and Easterling et al. [**9**] give an example of such a "bad" partition of the population.

Fortunately it is often possible to decompose a particular population in a biologically sensible fashion. Vandermeer [**24**] and Moloney [**18**] have crafted algorithms to minimize errors associated with choosing class boundaries. Such algorithms help to derive more reasonable matrices, but for many populations they cannot altogether eliminate the sampling and distribution errors associated with discretization. For instance, for many plants size is the natural stage variable, and no decomposition of

size into discrete stage classes will adequately capture the life history variations. Furthermore, sensitivity and elasticity analyses have both been shown to be affected by changes in stage class division, Easterling, et al. [**9**].

Regardless of how well the population is decomposed 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.

For many populations, these difficulties can be overcome by analyzing a continuum of stages, which is discussed in the next section.

Integral projection models

An alternate approach to discretizing continuous variables such as size is to use Integral Projection Models. These models retain much of the analytical machinery that makes the matrix model appealing, while allowing for a continuous range of stages. Easterling [**8**] and Easterling et al. [**9**] show how to construct such an integral projection model, using continuous stage classes and discrete time, and they provide sensitivity and elasticity formulas analogous to those for matrix models. In Ellner and Rees [**10**] 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 that 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, they have, so far, not used integral models widely. Stage structured IPMs of the type considered in this paper have appeared in the scientific literature since around ten years ago [**5, 6, 8, 9, 10, 11, 21, 22**]. There is a large literature on integral models for spatial spread of a population [**12, 13**]. The structure of the integral operators describing spatial spread can be very different from those for IPMs. For instance, the integral operators discussed in this paper are compact, while the operators describing spatial spread might not be compact. Compact operators have many properties that are similar to those of matrices [**1**, Chapter 17], and these properties make the spectral analysis, and hence the asymptotic analysis, more analogous to matrix models.

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, if m_s is the minimum size, and M_s is the maximum size, as determined by field measurements, then $x \in [m_s, M_s]$ would be the size of an individual.

The analogue of the matrix entries $k_{i,j}$ 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 kernel is time-independent, which is analogous to the time-independent matrix entries. The time unit $t = 1$ represents a time interval in which data is naturally measured; in the example in this paper the unit of time is a year. The analogue of (2) is

$$n(y, t+1) = \int_{m_s}^{M_s} k(y, x) n(x, t)\, dx, \quad y \in [m_s, M_s]. \tag{6}$$

In particular, the kernel determines how the distribution of stage x individuals at time t contributes 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 contributes to stage i at time $t + 1$.

The kernel is determined by statistically derived functions for life history parameters such as survival, growth, and fecundity. At first the construction of an integral operator model might seem more difficult than the construction of a matrix model. However, the life history functions are assumed to have a particular distributional form, often with only a few parameters to be determined for each function. Hence the total number of parameters to be estimated can be smaller than the number of matrix entries. This of course would not work if the life history functions did not have an appropriate distributional form. Fortunately, ecologists have a toolbox of functional forms for different biological parameters. For instance, size is usually described by a lognormal distribution or truncated normal distribution. TABLE 2 shows all of the life history functions needed to construct the kernel for a particular integral projection model for the Platte thistle [**22**]. An advantage of the integral approach is that data over the entire distribution can be used to estimate the parameters of the life-history functions, thus minimizing parameter uncertainty. In contrast, the transitions between life history stages in matrix models are estimated from subsets of the data.

The stage variable x need not be a scalar, but the range of stage variables should be a compact metric space. In cases 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 [**10**] 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 a complete normed linear space (that is, a *Banach space*). For every $t > 0$, the

TABLE 2: Life history functions for the Platte thistle [**22**], where variables x and y are in ln(crown diameter)

Demography	Equation
Survival	$s(x) = \dfrac{e^{-0.62+0.85x}}{(1+e^{-0.62+0.85x})}$
Flowering Probability	$f_p(x) = \dfrac{e^{-10.22+4.25x}}{(1+e^{-10.22+4.25x})}$
Growth Distribution	$g(x, y) =$ Normal Distribution in y with $\sigma^2 = 0.19$ and $\mu(x) = 0.83 + 0.69x$
Individual Seed Set	$S(x) = e^{0.37+2.02x}$
Juvenile Size Distribution	$J(y) =$ Normal Distribution with $\sigma_f^2 = 0.17$ and $\mu_f = 0.75$
Germination Probability	$P_e = .067$ density independent or $P_e = S_T(t)^{-0.33}$ density dependent where $S_T(t)$ is the total seed set

population distribution $n(\cdot, t)$ is in $L^1(m_s, M_s)$, and the total population is $\|\mathbf{n}(t)\|$. 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 $\mathbf{n}(t) = n(\cdot, t)$; we refer to $\mathbf{n}(t)$ as a "vector" in $L^1(m_s, M_s)$. Define the operator $\mathbf{A} : L^1(m_s, M_s) \to L^1(m_s, M_s)$ by

$$(\mathbf{A}\mathbf{v})(\cdot) := \int_{m_s}^{M_s} k(\cdot, x)\mathbf{v}(x)\, dx.$$

It is not hard to show that $\mathbf{A}$ is bounded on $L^1(m_s, M_s)$. In fact, since

$$\int_{m_s}^{M_s} \int_{m_s}^{M_s} |k(x, y)|^2\, dx\, dy < \infty,$$

it is well known that $\mathbf{A}$ is compact [**1**, p. 403], which implies that $\mathbf{A}$ has nice spectral properties, in a certain sense [**1**, Ch. 21]. Then (6) is equivalent to

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t), \tag{7}$$

which is analogous to (1).

Ellner and Rees [**10**] show that for a large class of kernels k, the integral operator $\mathbf{A}$ satisfies an analog of the Perron-Frobenius Theorem for matrices. In particular, for a certain class of operators discussed [**10**, Appendix C], $\mathbf{A}$ has a dominant real eigenvalue λ that is the asymptotic growth rate and an associated unit eigenvector $\mathbf{v}$ that is the stable stage distribution. In this case the eigenvectors are functions in $L^1(m_s, M_s)$, rather than vectors in $\mathbb{R}^m$. Additionally

$$\lim_{t\to\infty} \frac{\|\mathbf{n}(t + 1)\|}{\|\mathbf{n}(t)\|} = \lambda \quad \text{and} \quad \lim_{t\to\infty} \frac{\mathbf{n}(t)}{\|\mathbf{n}(t)\|} = \mathbf{v},$$

where the convergence of the second equation is interpreted as $L^1(m_s, M_s)$ convergence.

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 density of probability that an individual of size x will survive to be an individual of size y in one time step. Therefore, for each $y \in [m_s, M_s]$,

$$\int_{m_s}^{M_s} p(y, x)\, dx \le 1.$$

The function $f(y, x)$ is the distribution for the number of offspring of size y that an individual of size x will produce in one time step. 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 is virtually zero.

Estimating the kernel for Platte thistle We now show how a specific model is constructed, using a modification of the model for Platte thistle *(Cirsium canescens)* found in Rose et al. [**22**]. Platte thistle is an indigenous perennial plant in the midgrass sand prairies of central North America. The species is in decline in its native environment, possibly due to a biocontrol agent introduced to manage a different thistle, that is considered invasive. The time unit in this example is one year. It is strictly monocarpic, meaning that plants die after reproducing, so the flowering probability must be incorporated into the kernel. The Platte thistle lives 2–4 years [**17**]. In this model, the continuous class variables x and y are the natural log of the root crown diameter (measured in mm). The maximum and minimum root crown diameter are taken as $m_s = \ln(.5)$ and $M_s = 3.5$, respectively; we found that making M_s larger does not appreciably change the results. 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.

We start with some component life-history functions. These are estimated from the data using standard statistical methods. For instance, logistic regression analysis can be used to describe survival as a function of size. Below is a description of these functions, and formulas are given in TABLE 2. All functions are defined for $x \in [m_s, M_s]$.

- $s(x)$ is the probability that a size x individual survives to the next time step. It is statistically fit to the logistic curve

$$s(x) = \frac{e^{ax+b}}{1 + e^{ax+b}},$$

  where $b < 0$.
- $f_p(x)$ is the probability that a size x plant will flower in one time step. This function is chosen to have the same logistic form as $s(x)$.
- $g(y, x)$ is the density of probability that an individual of size x will have size y at the next time step. This can describe both the probability of growing to a larger size and the probability of shrinking to a smaller size. The growth function $g(y, x)$ is a normal distribution in the variable y.
- $S(x)$ is the number of seeds produced on average per plant of size x. It is assumed to be an exponential function.
- $J(y)$ is the distribution of offspring sizes. It is assumed to be a normal distribution.
- P_e is the average probability that a seed will germinate. This is also known as the *recruitment probability*. We first assume that it is constant, but in a more realistic model it will be a function of the number of seeds.

Growth and survival kernel: To construct the growth and survival kernel, note that the probability that a size x individual does not flower is $1 - f_p(x)$. Since the Platte thistle dies after reproduction, the probability that a size x individual survives to the next time step is the survival probability $s(x)$ times the probability of not flowering, or $s(x)(1 - f_p(x))$. Hence the growth and survival kernel is

$$p(y, x) = s(x)(1 - f_p(x))g(y, x).$$

Fecundity kernel: Each plant will produce seeds, and these seeds must germinate for an offspring to be included in the next population count. For a Platte thistle to produce seeds, it must survive through a year and flower. Thus, each plant of root crown diameter size x will produce $s(x) f_p(x) S(x)$ seeds on average, so the total number of

seeds resulting from a population distribution of $n(x,t)$ at time t is

$$S_T(t) = \int_{m_s}^{M_s} s(x) f_p(x) S(x) n(x,t) dx \tag{8}$$

and the total number of germinated seeds at time t is $P_e S_T(t)$. Finally, we also need to distribute the offspring into the various sizes by $J(y)$. The distribution of offspring at time $t+1$ resulting from a population distribution of $n(x,t)$ at time t is

$$P_e J(y) S_T(t) = P_e J(y) \int_{m_s}^{M_s} s(x) f_p(x) S(x) n(x,t)\, dx.$$

Therefore the fecundity kernel is

$$f(y,x) = P_e J(y) s(x) f_p(x) S(x). \tag{9}$$

FIGURE 1 shows a graph of the total kernel

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

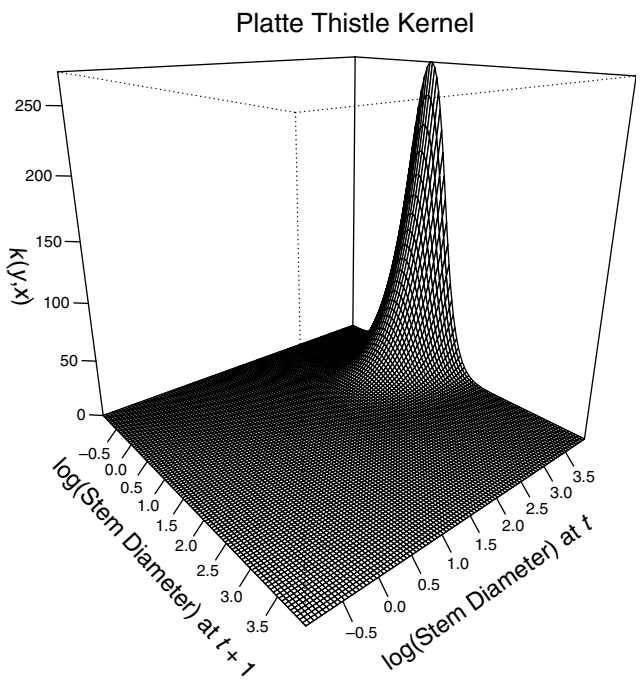

Figure 1 The kernel for the Platte thistle integral projection model

Numerical solution of the integrodifference equation Analytic evaluation of the integral operator is difficult if not impossible to perform. Thus, we use numerical integration to obtain an estimate of the population. A conceptually easy and reasonably 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

$$(\mathbf{An})(y,t) = \int_{m_s}^{M_s} k(y,x) n(x,t)\, dx \approx \frac{M_s - m_s}{N} \sum_{j=1}^{N} k(y,x_j) n(x_j,t). \tag{10}$$

Let

$$k_{ij} = \frac{M_s - m_s}{N} k(x_i, x_j) \text{ for } i, j = 1, 2, \ldots N, \quad \mathbf{A}_N = (k_{ij})$$

and

$$\mathbf{n}_N(t) = [n(x_1, t), n(x_2, t), \ldots n(x_N, t)]^T.$$

Then $\mathbf{n}_N(t)$ is a discrete approximation of $n(x, t)$, $\mathbf{A}_N$ is a discrete approximation of the integral operator $\mathbf{A}$, and

$$\mathbf{A}_N \mathbf{n}_N = \frac{M_s - m_s}{N} \sum_{j=1}^{N} k(x_i, x_j) n(x_j, t).$$

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

This matrix model can be analyzed much like a traditional matrix model. Since the dominant eigenvalue λ_N of $\mathbf{A}_N$ converges to the dominant eigenvalue λ of $\mathbf{A}$ as $N \to \infty$ [**10, 8**], the long term growth rate is easily estimated. FIGURE 2 shows this convergence of λ_N to $\lambda = 1.325$ as N increases. The leading eigenvalue of $\mathbf{A}_5$ is 1.332, so we see that fairly small dimensional approximations of $\mathbf{A}$ lead to very good approximations of the long-term growth of the system.

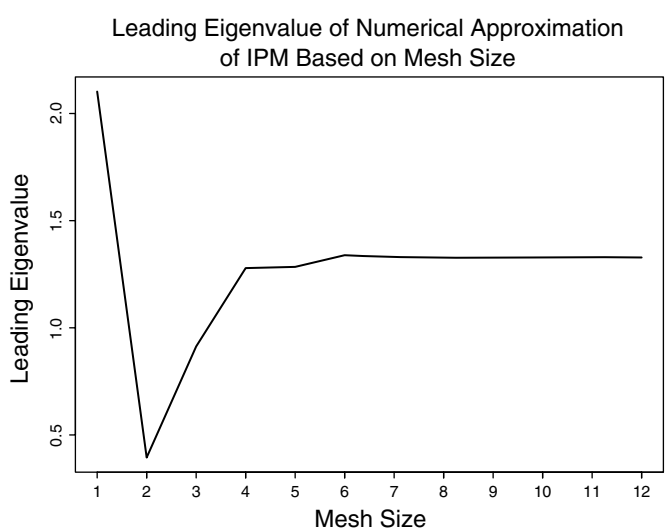

Figure 2 The leading eigenvector of the numerical approximation of the integral projection model as a function of number of subintervals in the Riemann sum

We should emphasize the difference between a PPM and the matrix model obtained from an IPM. In the former every nonzero entry is estimated directly; a large matrix of this type is not intended to approximate an IPM, and is subject to the discretization problems we described above. In the latter, the life history functions are estimated, giving rise to a kernel, and this kernel is used to obtain a matrix that approximates the integral operator for large N. As indicated above, an IPM is often preferable to a PPM, and in these cases the matrix model based on the IPM is also preferable to a PPM.

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 $\mathbf{A}$, and normalizing it so that it has $L^1(m_s, M_s)$ norm of 1. This eigenvector is the curve labeled "Density Independent" in FIGURE 3. Note that the x-axis is in mm rather than ln(mm). The curve is obtained by computing the unit leading eigenvector of $\mathbf{A}_N$ for large N, and noting that this is a good approximation of the unit leading eigenvector [**10**].

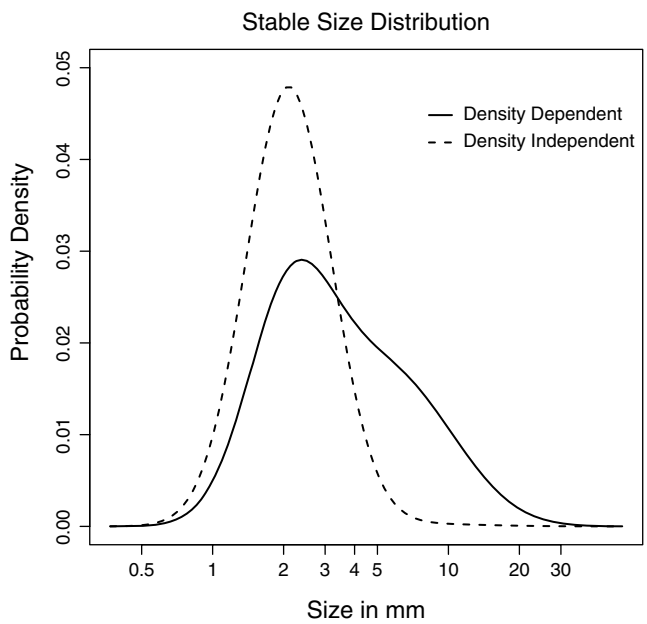

Figure 3 Stable state population densities of Platte thistle

Density dependence In the Platte thistle model above, we made the simplifying assumption that the germination probability, P_e, is constant, and obtained a *density independent* model. By "density independence" we mean that $\mathbf{n}(t+1)$ is a linear function of $\mathbf{n}(t)$, or equivalently, that the operator $\mathbf{A}$ does not depend upon $\mathbf{n}(t)$. Using the average germination probability, the growth rate of 1.325 we obtain from this model does not match the observed data. In particular, the data in Rose et al. [**22**] does not indicate that there is a constant growth rate, but rather shows a leveling off of the population over time. Furthermore, ecologists consider density dependent recruitment more realistic, since as the total number of seeds increases, the chance that each individual seed will germinate declines. Therefore, the germination probability is taken to be a nonlinear function of $S_T(t)$, the total number of seeds produced at time t, instead of a constant. Since the number of seeds produced depends on $n(x,t)$, the resulting system will be density dependent. In [**22**] the germination probability is modeled by $P_e(t) = (S_T(t))^{-.33}$. The resulting nonlinear system is

$$\begin{aligned} n(y,t+1) &= \int_{m_s}^{M_s} p(y,x)n(x,t)\,dx + J(y)(S_T(t))^{-.33}\int_{m_s}^{M_s} s(x)f_p(x)S(x)n(x,t)\,dx \\ &= \int_{m_s}^{M_s} p(y,x)n(x,t)\,dx + J(y)(S_T(t))^{.67}. \end{aligned}$$

The solutions to the resulting nonlinear system matches the data better than the solutions to the linear system.

This nonlinearity substantially changes the qualitative and quantitative nature of the model. For instance, as discussed above, in the linear model an asymptotic growth rate is determined by the leading eigenvalue and a stable age structure is determined by the eigenvector associated with the leading eigenvalue. We prove in another paper that for this nonlinear model the solutions $n(\cdot, t)$ converge in $L_1(m_s, M_s)$ as $t \to \infty$, and that this limit is independent of the initial population vector (provided that the initial population vector is nonzero) [**20**]. We denote the limit by $\mathbf{w}(\cdot)$, and the normalized limit $\mathbf{v}(\cdot) = \mathbf{w}(\cdot)/\|\mathbf{w}(\cdot)\|$. This latter vector is the stable age distribution for this system, and is shown by FIGURE 3 (the "Density Dependent" curve). It follows from the Dominated Convergence Theorem that the total population $N(t) = \|n(\cdot, t)\|$ converges to $\|\mathbf{w}\|$ 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.

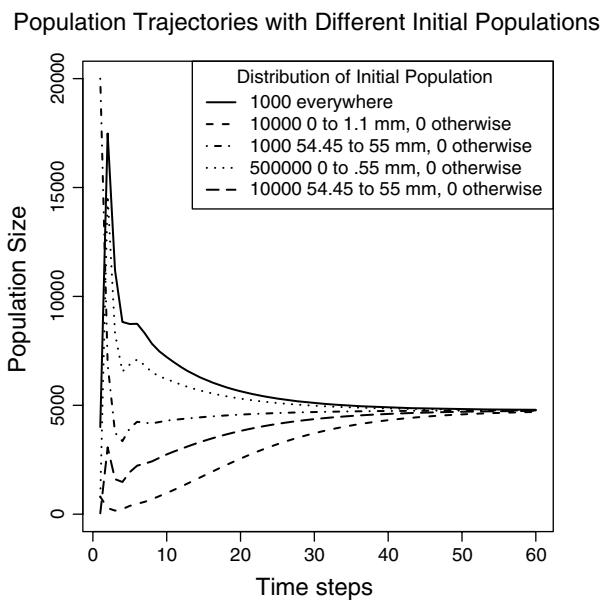

Figure 4 Asymptotic behavior of the total population

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Summary A single species is often modeled as a structured population. In a matrix projection model, individuals in the population are partitioned into a finite number of stage classes. For example, an insect population can be partitioned into egg, larva, pupa and adult stages. For some populations the stages are better described by a continuous variable, such as the stem diameter of a plant. For such populations an integral projection model can be used to describe the population dynamics, and might be easier to use or more accurate than a matrix model. In this article we discuss the similarities and differences between matrix projection models and integral projection models. We illustrate integral projection modeling by a Platte thistle population, showing how the model is determined by basic life history functions.

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