

THE STATE OF THE ART OF POPULATION PROJECTION MODELS: FROM THE LESLIE MATRIX TO EVOLUTIONARY DEMOGRAPHY

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ABSTRACT

Population projection models have received much attention in ecology and made important theoretical advances in the last 50 years. They represent vital tools for improving conservation strategies and management actions. Here we attempt to join some of theoretical advances made in the field of population projection modelling, briefly revise the history and present some applications derived from population matrix models in ecological and evolutionary studies.

Keywords: Elasticity; life cycle; sensitivity; selection; vital rate.

RESUMO

O ESTADO DA ARTE DE MODELOS DE PROJEÇÃO POPULACIONAL: DA MATRIZ DE LESLIE À DEMOGRAFIA EVOLUTIVA. Os modelos de projeção populacional receberam muita atenção na Ecologia e tiveram importantes avanços teóricos nos últimos 50 anos. Eles representam uma ferramenta vital para uma melhoria nas estratégias de conservação e ações de manejo. Nesta revisão, abordamos a história do desenvolvimento dos modelos de matrizes populacionais, seus avanços teóricos, e também apresentamos algumas aplicações dos modelos em estudos ecológicos e evolutivos.

Palavras-chave: Elasticidade; ciclo de vida; sensibilidade; seleção; taxa de vida.

RESUMEN

ESTADO DEL ARTE DE LOS MODELOS DE PROYECCION POBLACIONAL: DESDE LA MATRIZ DE LESLIE A LA DEMOGRAFIA EVOLUTIVA. Los modelos de proyección poblacionales han recibido mucha atención en ecología y han generado importantes avances teóricos en los últimos 50 años. Representan herramientas vitales para mejorar las estrategias de conservación y las acciones de manejo. Aquí intentamos reunir algunos de los avances teóricos hechos en el campo de los modelos de proyección poblacional, revisar brevemente la historia y presentar algunas aplicaciones derivadas de los modelos poblacionales matriciales en estudios ecológicos y evolutivos.

Palabras clave: Elasticidad; ciclo de vida; sensibilidad; selección; tasa vital.

INTRODUCTION

Demographic studies have evolved to be essential to the understanding of evolutionary outcomes of natural populations (Fisher 1930, Cole 1954, Caswell 2001, Coulson *et al.* 2010, Jonzén *et al.* 2010,

Tuljapurkar 2010, Carslake *et al.* 2008), yet prior to the 1930s, demography was still a discrete discipline in relation to evolution. Important connections between demographic and evolutionary fields were established using matrix population models (ex. van Tienderen 2000) since they establish a bridge

between population fitness, an evolutionary feature, and population demographic rates, which influence this fitness. This method is not new, dating back to Leslie (1945), but it is a demographic analysis tool of animal populations that has been transformed by an impressive number of improvements and modifications, rendering it an indispensable modern tool for ecological analysis. Here we attempt to combine some theoretical and analytical developments made in the field and present some applications derived from population matrix models in ecological and evolutionary studies after the initial appearance of population matrix modelling.

POPULATION PROJECTION MODELS

Population projection models (PPMs) represent a vital tool for planning conservation strategies and improving the management of endangered plant and animal species by identifying critical vital rates, or those that can most effectively cause an increase in population size (Baxter *et al.* 2006, Heppell 1998, Caswell 2001, Van der Voort & McGraw 2006); however, the same analysis might be used to decelerate the growth rate of an invasive or exotic species, or be applied for biological control purposes (Shea *et al.* 2005, Neubert & Caswell 2000). PPMs have been used for studying human populations as well (ex. Cohen 1979). The beauty of PPMs lies in the change in focus from the individual to the population's state, by presuming that a population can be meaningfully classified into stages (or classes), where individuals of the same stage (or class) share equal demographic parameters. Such a model is typically represented by the following equation:

$$x(t+1) = Ax(t) \quad (1)$$

where A represents the population projection matrix (PPM), *i.e.* a matrix containing the transition rates between life-cycle stages (or age classes). When $i=3$, the equation 1 is equivalent to:

$$\begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} (t+1) = \begin{pmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} (t) \quad (2)$$

In this case, where individuals are classified according to age classes, the elements denoted as 0 represent the impossible transitions and the matrix in equation 2 is called the Leslie matrix (Leslie 1945). The F_i elements correspond to fecundity rates and the P_i elements to probabilities of surviving from one class to the other. A more general case where all the transitions (including reverse) between stages are possible, since the classification is established based on the organism's life stages, is referred to as the Lefkovich matrix (Lefkovich 1965). In a species where $n_{i,t}$ individuals are classified into i life stages at a certain time t , the number of individuals in time t can be projected to the following interval $t+1$ and the system of equations describing this may be joined into the following generic matrix notation:

$$\begin{pmatrix} a_{1,1} & a_{1,2} & \cdots & a_{1,s} \\ a_{2,1} & a_{2,2} & \cdots & a_{2,s} \\ \vdots & \vdots & \ddots & \vdots \\ a_{s,1} & a_{s,2} & \cdots & a_{s,s} \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_s \end{pmatrix}_t = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_s \end{pmatrix}_{t+1} \quad (3)$$

where s is the maximum number of stages, x_i is the number of individuals in each stage in either time t or $t+1$, and $a_{p,i,t}$ are the coefficients of matrix A , representing the transitional rates between stages (p stands for a specific stage) (Lefkovich 1965). Such a matrix is more appropriate for organisms where an individual can regress in a state, which is impossible when classified according to age. Some organisms are difficult or even impossible to classify according to age. Therefore size may be a more appropriate classificatory criterion, especially in organisms where vital rates, such as survival and fecundity, are less related to age and more to the size of an individual.

In the PPMs, time is incorporated by the variable t , and it is usually measured in years or reproductive intervals, depending on the species studied. Yet, the nature of the PPMs can vary and the different PPMs grade the matrix population models into distinct classes (Figure 1): if PPM A is constant, the resulting population projection model is a time-invariant linear system of difference equations (1). This means that survival and reproduction are constant parameters. Such a model is also autonomous, since it incorporates no exogenous variables (McCarthy *et al.* 2008). If A is not constant (which is a more realistic scenario for natural populations), the variation in its transition rates

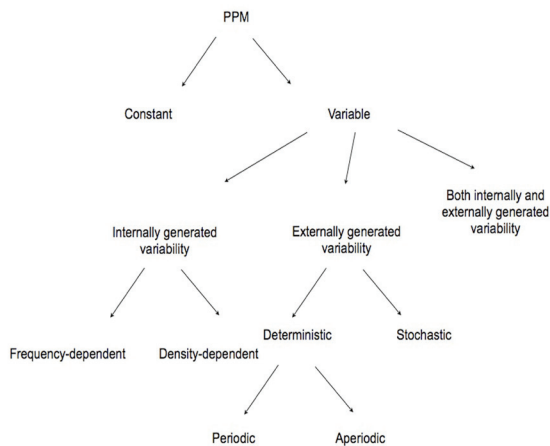


Figure 1. Matrix population models resulting from the different types of variability included in the population projection matrix (PPM) (from Caswell 2001, pp 9).

may be due to endogenous effects of a population on itself (where a factor affects the population while it is being affected by the population as well) or due to exogenous factors, external to the population (such as the climate conditions, for example). The corresponding matrix population model for incorporating an external factor would thus include environmental variation, which can be deterministic or stochastic, but the model still remains a linear model. In this model, each transition between life-cycle stages within the matrix can vary as a function of time. However, there are different types of external variations that an exogenous factor may cause: 1) deterministic (predictable) and 2) stochastic (unpredictable), which can be further separated into 3) periodic (fluctuating), and 4) aperiodic (Figure 1).

A linear PPM assumes that a population under study has constant demographic parameters and that the population growth is not dependent upon the population abundance or density at any time. Such models can be useful in a constant environment (Caswell 2001), and for example in some populations where population size is below the carrying capacity. Such a scenario is advocated especially for endangered species, since, if supposing their population size is reduced, the endogenous factors would be less likely to be operating (Grant & Benton 2000), as compared to large sized populations reaching their carrying capacity, where such a factor would be more likely to operate. The importance of endogenous factors in population dynamics has been a point of strong debate among ecologists (Sibly *et al.* 2005); however,

the main reason for the rare incorporation of them into demographic models is probably the difficulty in obtaining demographic data that can detect their functioning (Grant & Benton 2000).

A model becomes non-linear when variation caused by endogenous factors is included, which allows for the transition rates of the PPM to be a function of the population itself (vector x in eq. 1). The equation of the PPM that contains an endogenous factor can be represented as:

$$x(t+1) = A_x x(t) \quad (4)$$

Where A_x denotes that the matrix A is a function of a factor endogenous to the population. However, in many animal (and plant, as well as in human) populations the vital rates can depend on the sex, rather than on density of the whole population. It is not rare that males present higher mortality rates than females, and in such cases, the frequency-dependence can be incorporated into the PPM in a similar manner as functioning of an endogenous factor. It depends entirely upon the function to which you constrain matrix A ; however, usually including such factors of any kind results in complex dynamics, which are difficult to interpret.

Throughout the 20th century, two approaches have held sway in ecology: the first propose density-dependent factors and processes (ex. intra-specific competition for resources) as the main driving forces for population dynamics (Nicholson 1933), and the second propose the density-independent factors (ex. climate) as the principal population regulatory forces (Andrewartha & Birch 1954). New revisions of anterior concepts based on empirical evidence joining the two previous approaches have emerged, proposing a synergism of endogenous and exogenous factors in studies of population dynamics (Murdoch 1994, Turchin 1995, Leirs *et al.* 1997, Grenfell *et al.* 1998, Lima *et al.* 2001a, Lima *et al.* 2001b, Lima *et al.* 2002). PPMs conveniently offer an alternative of integrating both types of factors into a system of non-homogeneous non-linear equations:

$$x(t+1) = A_{x,t} x(t) \quad (5)$$

but may sometimes be difficult to interpret (Caswell 2001).

APPLICATIONS OF POPULATION PROJECTION MODELS

Two pioneers in the use of the population projection models were E.G. Lewis (1942), contributing to a discussion on population growth rate, and P.H. Leslie (1945) commonly given even more credit for studying fertility and mortality patterns through projection models. As a legacy to the latter, the name of the quadratic matrix, representing the growth of an age-structured population where only the first row (fertilities) and the sub-diagonal elements (survival probabilities) are non-zero, was named the Leslie matrix. Both Lewis and Leslie independently introduced the idea of projecting a structured population size in discrete steps in the future. Some extensions of the use of PPMs were published in 1959 by Williamson, Usher (1966) and some years later, Lefkovich (1965) added an important attribute by grouping individuals by stage categories (rather than by age as in the Leslie matrix), since his study objects were insects. Bosch (1971) extended the use of Lefkovich matrices in tree populations.

Another gratifying characteristic of the population projection models is equalizing the dominant eigenvalue of the PPM with the population growth rate, λ . If population growth is described by a PPM A ,

the eigenvalues $\lambda^{(i)}$ and the right and left eigenvectors ($\mathbf{w}^{(i)}$ and $\mathbf{v}^{(i)}$, respectively) of matrix A should satisfy

$$\begin{aligned} A \mathbf{w}^{(i)} &= \lambda^{(i)} \mathbf{w}^{(i)} \\ \mathbf{v}^{(i)CCT} A &= \lambda^{(i)} \mathbf{v}^{(i)}, \end{aligned}$$

Where CCT stands for a complex conjugate transpose of vector x (Caswell 1996). Among i eigenvalues, the highest real positive value (the dominant eigenvalue) represents the rate at which a population grew in a defined time interval.

The long-term population growth rate is frequently a desirable variable to estimate, and at this point we should note that there are different ways of representing the PPM and solving the system of linear equations, which makes the method even more accessible. Here, the life-cycle graph analysis turned out to be a useful analytical expansion since a PPM can be easily transformed into a self-explanatory life-cycle graph, which represents the probability of transitions between stages or age classes equally (Hubbell & Werner 1979, Ebert 1999). An example of a Leslie matrix (2) transformed into a three-node life cycle for a hypothetical three age-class organism is represented in Figure 2. Transitions a , and b correspond to survival from class 1 to class 2 and class 2 to class 3, respectively, while transitions c , d , and e correspond to fecundity rates, F_i in the matrix of equation 2.

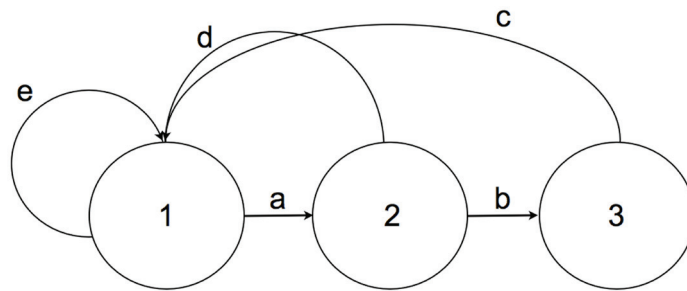


Figure 2. A life cycle derived from a 3x3 Leslie matrix for a hypothetical organism. Transitions a and b correspond to survival parameters, and transitions c , d and e to fecundity parameters.

For example, the element in the matrix position [1,3] (first line third column, F_3 in this case) will represent an incoming transition to the first class from the third class, and is represented in Figure 1 as the transition c .

A life-cycle graph is especially useful for complicated life cycles, and all the transitions can be

seen, whereby all the time intervals must be compatible between each other (equal or proportional) – which is an important premise of any PPM as well (Caswell 2001). Through a life-cycle graph a characteristic polynomial equation for the population growth rate may be derived. The same equation may be obtained by rearranging the Euler equation (Ebert 1999):

$$1 = \sum_x l_x m_x e^{-rx}$$

If we have, for example, a four age class organism, $x=1,2,3,4$, and $e^r=\lambda$, then the characteristic equation may have a form of

$$\lambda^4 - P_0 P_1 m_2 \lambda^2 - P_0 P_1 P_2 m_3 \lambda - P_0 P_1 P_2 P_3 m_4 = 0$$

where the l_x are the products of P_i . Once we have the characteristic equation for λ , we can distinguish those components of the life-cycle graph that have the highest first partial derivatives with respect to population growth rate. In other words, to which component (or matrix element) the dominant eigenvalue (λ) is most sensitive to. Each matrix entry has a positive effect on the population rate of increase, λ (Caswell 2001). So, sensitivities, $\delta\lambda/\delta a_{ij}$, represent the first-order derivatives of the population growth rate with respect to each matrix element (a_{ij}), and as such, quantify the impact of changes in a_{ij} on λ .

Another important measure for population analysis is the elasticity (Kroon *et al.* 1986), which can be obtained as:

$$Ea = \left(\frac{a_{ij}}{\lambda} \right) \left(\frac{\partial \lambda}{\partial a_{ij}} \right)$$

or

$$\frac{\partial \log \lambda}{\partial \log a_{ij}}$$

These measures are scaled and quantify the proportional increase of λ with an increase of a certain character a_{ij} . Allowing proportional comparisons between survival and fecundity makes elasticities particularly useful (de Kroon *et al.* 2000), because fecundity data normally does not fall within the 0-1 interval. Such comparison would not be possible without a relative measure (Ebert 1999). Also, a life-cycle graph has an additional practical characteristic: it can be further subdivided into separate loops, each one representing reproduction events at different stages of age classes (van Groenendaal *et al.* 1994). As such, a characteristic elasticity can be identified for each loop, which permits us to identify those reproductive loops that are proportionally most influential on a population growth rate.

Sensitivity and elasticity analysis have been frequently used for plants (ex. Ramula 2008, Ehrlén

2003) and have also been commonly used with animals, for turtle demography (Heppel 1996, 1998), fish (Bronikowski *et al.* 2002), birds (Steen & Erikstad 1996, Clark & Martin 2007, Wisdom *et al.* 2000) and mammal populations (Heppel *et al.* 2000, Zeoli *et al.* 2008, Gerber *et al.* 2004, Nilsen *et al.* 2009, Brault & Caswell 1993, Gaillard & Yoccoz 2003).

THE APPLICATION OF PPMs IN THE CONTEXT OF EVOLUTIONARY DEMOGRAPHY

Sensitivities reveal important demographic information; however, they assume no correlation between elements in the Leslie matrix, and are as such, described by Stearns (1992) as *direct* selection pressures. Elasticity analysis can provide insights into the strength of direct selective pressures on age-specific vital rates (van Tienderen 2000, Benton & Grant 2000, Rose *et al.* 2002), but Caswell (2001) argues that selective pressures should not be represented by elasticities, but rather by sensitivities, which are represented by partial derivatives of population growth rate. "Sensitivities, not elasticities, appear in the evolutionary calculations" (Caswell 2001, p. 295) and taking elasticities as selection gradients can result in erroneous interpretations of the roles that certain vital rates or traits have in the life history of an organism, since elasticities would consider any vital rate with value of 0.00 as selectively neutral, which may not always be the case. For example, future fecundity for most animals has a value of 0.00, thus, a resulting zero elasticity, but may have non-zero sensitivity, and thus may not be selectively neutral.

One of the measures of the population's fitness is its rate of increase, λ (Caswell 2001) and the sensitivity of λ to a certain trait can be interpreted as the intensity of selection on that trait. However, the strength of selection pressure acting on a given life history trait is determined by all "surrounding" life history traits and by phenotypic relationships among them (Stearns 1992). Thus, the sensitivities can be called *situational* (in the sense that they ignore the surrounding traits and their correlation) and hence, second derivatives of finite population growth rate are biologically interesting to calculate (Caswell 1996).

Second-order derivatives permit distinguishing between the different types of selection acting on a certain trait. The self-partial derivative of form $\partial^2\lambda/\partial a_{ij}^2$ represents the relationship between the sensitivity of a matrix element ($\partial\lambda/\partial a_{ij}$) and itself (a_{ij}). If negative, it indicates a concave type of selection, corresponding to a stabilizing selection in the case of a single trait, forcing the trait to remain close to its mean. If positive, it indicates convex selection (corresponding to disruptive selection), forcing the variance in a trait or vital rate to increase (Caswell 2001, McCarthy *et al.* 2008).

However, selection acts on variations of a certain trait as well as on its mean, and any evolutionary demographic analysis should include an analysis of variations of the traits (Benton & Grant 1996, Gaillard & Yoccoz 2003, Tuljapurkar 2010, Phillips & Arnold 1989, Pfister 1998). It may be induced via demographic stochasticity or environmental stochasticity/variability (Kendall 1998, Saether *et al.* 1998, Drake 2005). Valuable contributions of demography population studies, by considering environments random, were made by Tuljapurkar (1989, 2010, Tuljapurkar *et al.* 2003, Tuljapurkar & Orzack 1980). Depending on the environment as well as the species characteristics; deterministic, stochastic, or both population growth rates should be considered, since the stochastic type accounts for the population's growth rate in all possible environments (Tuljapurkar *et al.* 2003). The deterministic formulations can be useful when the stochastic effects are minimized or absent; however, wherever there is some evidence for stochasticity, it can be incorporated into the calculation of population growth rate.

One example of incorporating stochasticity into a population growth rate calculation was shown by Doak *et al.* (2005), where the authors report an approximation of the log stochastic population growth rate, $\log \lambda_s$:

$$\log \lambda_s = \log \bar{\lambda}_1 - \frac{1}{2} \left(\frac{\tau^2}{\bar{\lambda}_1^2} \right)$$

where

$$\tau^2 = \sum_i \sum_j \rho_{vi, vj} \sigma_{vi} \sigma_{vj} \bar{s}_{vi} \bar{s}_{vj}$$

The τ is calculated based on correlations between matrix elements and their standard deviations, rather than covariances. To determine which component of

variation contributes most to the stochastic population growth rate, the sensitivity and elasticity of the growth rate to variation in matrix elements can be obtained, as well as the sensitivity and elasticity of the growth rate to the correlation between matrix elements (Doak *et al.* 2005).

Variability will influence a population's fitness negatively, since the more variable a life history stage is, the less it contributes to population growth rate (Pfister 1998). If variability is selectively disadvantageous (Gaillard & Yoccoz 2003), fitness components with a variation that influences the population growth rate will suffer selection against variation (canalization). The different effects of selection on variation in a trait can be inferred as described by Caswell (2001) through the self-partial derivatives. If we take an example of a single trait, stabilizing selection will reduce the variance of the trait under selective pressure, while a disruptive type of selection will force the variation to increase, leading away from the trait mean (Caswell 2001, Carlslake *et al.* 2008). Disruptive selection after some generations may thus result in divergent phenotypic extremes within the population. However, variation may be induced or prevented by other means too; in some cases species may even respond evolutionarily to human disturbances originating from removal of the population (ex. Mangel 2006).

CONCLUSION

Population matrix models have grown increasingly important in Ecology studies after much development since the first Leslie Matrix. They provide a wide range of applications since they have undergone thorough analytical development and their utility in, for example, conservation biology, is not trivial. When aiming to intervene in the growth rate of a certain population (either to increase or decrease it), the sensitivity and elasticity analysis of population matrix models can contribute to assembling efficient management strategies, since they identify the targets that influence the population growth rate most critically (thus possibly cause most efficient change on the population with less cost) (Caswell 2000). The advantage of modelling a stage (or age) structured population have been extended not only into identifying specific management targets, but also in

a wide spectrum of possible applications, especially in evolutionary demographic research. Evolutionary implications inferred from convex or concave shapes of the growth rate function, taking into account that evolution may occur on a shorter time scale (Stockwell *et al.* 2003). They may also have strong implications for biodiversity conservation, since they provide detailed insight into the life history dynamics of a population under study, and may thus be the basis for well-informed decisions.

ACKNOWLEDGEMENT: We wish to thank A. M. Marcondes for administrative help. The study was financed by CNPq, FAPERJ, CAPES and CAPES/PNPD. AcademicEnglishSolutions.com revised the English.

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Submetido em 01/04/2011

Aceito em 03/10/2011