The genealogical decomposition of a matrix population model with applications to the aggregation of stages

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ABSTRACT

Matrix projection models are a central tool in many areas of population biology. In most applications, one starts from the projection matrix to quantify the asymptotic growth rate of the population (the dominant eigenvalue), the stable stage distribution, and the reproductive values (the dominant right and left eigenvectors, respectively). Any primitive projection matrix also has an associated ergodic Markov chain that contains information about the genealogy of the population. In this paper, we show that these facts can be used to specify any matrix population model as a triple consisting of the ergodic Markov matrix, the dominant eigenvalue and one of the corresponding eigenvectors. This decomposition of the projection matrix separates properties associated with lineages from those associated with individuals. It also clarifies the relationships between many quantities commonly used to describe such models, including the relationship between eigenvalue sensitivities and elasticities. We illustrate the utility of such a decomposition by introducing a new method for aggregating classes in a matrix population model to produce a simpler model with a smaller number of classes. Unlike the standard method, our method has the advantage of preserving reproductive values and elasticities. It also has conceptually satisfying properties such as commuting with changes of units.

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1. Introduction

Many simple models in population biology take the following form: a non-negative vector gives the current abundances of types within the population; then, to determine the abundances of types at some future time, one multiplies this vector by a non-negative matrix capturing the interconversion and reproductive rates of the types. Examples include models of deterministic mutation–selection balance in population genetics (where the types correspond to genotypes, Nagylaki, 1992 Chapter 2; Bürger, 2000 Chapter 3) and models of spatially structured populations (where the types correspond to demes, Rousset, 2004). The most common use of such models is in the ecological and demographic literature, where the types correspond to age ranges or developmental stages. In this last context, such models are commonly known as "matrix population models" and they play a critical role in both ecological theory and applications to population management (Caswell, 2001).

In the ecological or demographic context, the entries in the update or projection matrix are typically estimated based on observations from some natural population (Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016). To better understand the dynamics of the population, one then calculates various descriptors of the resulting model such as the asymptotic growth rate of the population, the generation time, the asymptotic distribution of type frequencies, etc. (for a more complete list, see e.g. Cochran and Ellner, 1992; Caswell, 2001). Here, we provide a method to move in the opposite direction: given certain descriptors of the population, we construct the corresponding projection matrix. Besides providing a means to construct projection matrices with specified properties, our method provides a unifying perspective on the theory of matrix population models by clarifying the relationships between various commonly used descriptors.

The key idea is that any matrix population model is completely determined by the specification of (1) its asymptotic growth rate, (2) its stable stage distribution and (3) a Markov chain describing the sequence of classes visited when we consider the lineages of

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individuals within the population. While this viewpoint is perhaps implicit in the classical literature (Demetrius, 1974, 1975; Tuljapurkar, 1982, 1993), its power has not been sufficiently appreciated because the strength of the connections between this genealogical Markov chain and other population descriptors has only recently come to light. In particular, recent work has revealed that certain hitting times on this genealogical Markov chain determine the generation time (Bienvenu and Legendre, 2015; Lehmann, 2014), while the asymptotic frequencies of the transitions of this Markov chain give the elasticities of the asymptotic growth rate with respect to the entries of the projection matrix (Bienvenu and Legendre, 2015). Since an ergodic Markov chain is uniquely specified by the asymptotic frequencies of its transitions, this means that if we specify the asymptotic growth rate, stable stage distribution and matrix of eigenvalue elasticities, we can immediately write down the unique projection matrix with these desired characteristics.

This construction provides a great deal of clarity, particularly concerning the interpretation and biological meaning of eigenvalue elasticities. Indeed, merely recognizing that the matrix of elasticities is given by the asymptotic transition frequencies of the genealogical Markov chain makes several facts obvious that are otherwise rather mysterious from a classical perspective (Bienvenu and Legendre, 2015). For instance, one can show that the total of the entries of the elasticity matrix must sum to one by either direct calculation (de Kroon et al., 1986) or by an appeal to Euler's Theorem for homogeneous functions (Mesterton-Gibbons, 1993). However, recognizing the elasticities as the asymptotic transition frequencies of a Markov chain make it obvious that they sum to one, since the asymptotic frequencies of the transitions form a probability distribution (the chain must always transition from one state to another). Similarly, the row sums of the matrix of elasticities equal its column sums (van Groenendael et al., 1994) due to the simple fact that at stationarity the probability of arriving in a state must equal the probability of exiting that state. Furthermore these row and column sums are just the class reproductive values, which when appropriately normalized are themselves just the asymptotic frequencies of the classes visited by the genealogical Markov chain.

The present work shows how a Markov chain perspective can be carried further to illuminate other aspects of the theory of matrix population models. For instance, it is helpful to classify descriptors of the matrix population models in terms of their dependencies on the triple of growth rate, stable stage distribution, and genealogical Markov chain: in our parametrization, elasticities depend only on the genealogical Markov chain, whereas the sensitivities of the asymptotic growth rate to perturbations in the entries of the projection matrix do not depend on the asymptotic growth rate but do depend on both the genealogical Markov chain and the stable stage distribution. Similarly, whereas matrix population models most frequently track the number of individuals in a given class, they can also be written in terms of other units such as the biomass present in each class. It turns out that specifying the stable stage distribution is equivalent to making a choice of units, so that, for example, the matrix of sensitivities depends on the choice of units whereas the matrix of elasticities does not. Indeed, the genealogical Markov chains arise by expressing the matrix population model in units of reproductive value, so that the choice of stable stage distribution can be fruitfully viewed as determining the conversion factor between reproductive value and number of individuals. That is, two models can have the same genealogical Markov chain and asymptotic growth rate but different stable stage distributions because of different choices concerning how reproductive value is packaged into individuals.

To demonstrate the power of this approach, we present a new solution to the problem of how to aggregate states in a matrix population model. This problem is important for two reasons. First, it

has long been known that estimates of various population descriptors depend on the number of organismal states used in the matrix population model (Silvertown et al., 1993; Enright et al., 1995; Benton and Grant, 1999; Ramula and Lehtilä, 2005; Salguero-Gómez and Plotkin, 2010; Picard and Liang, 2014). As a result, when comparing matrix projection models of different species, the dimensionality of the projection matrix is sometimes reduced by aggregating or "collapsing" multiple states into one so that the dimensionality is the same for all species being compared (Enright et al., 1995; Salguero-Gómez and Plotkin, 2010). Second, because one needs to observe multiple transitions between pairs of classes to accurately estimate vital rates, there is a trade-off between error in estimating the vital rates and the degree of within-state heterogeneity that is neglected by the model (Vandermeer, 1978; Moloney, 1986; Caswell, 2001). Thus, some degree of collapsing necessarily arises in the construction of matrix population models, a defect which in part motivated the proposal of integral projection models (Easterling et al., 2000).

The standard method for collapsing states in matrix population models was proposed by Enright et al. (1995) and generalized by Salguero-Gómez and Plotkin (2010). It essentially assumes that the population is at its stable stage distribution and then aggregates a group of classes by considering what we would observe if we did not distinguish between classes within this collapsed group. Remarkably, this procedure preserves both the asymptotic growth rate and the stable stage distribution (Hooley, 2000; Salguero-Gómez and Plotkin, 2010). However, its effects on reproductive values and elasticities are poorly characterized and can be substantial (Enright et al., 1995; Benton and Grant, 1999; Ramula and Lehtilä, 2005; Salguero-Gómez and Plotkin, 2010; Picard and Liang, 2014).

Here we show that this behavior arises because the standard method, while preserving the stable stage distribution and asymptotic growth rate, fails to preserve the genealogical Markov chain. By applying our decomposition to the projection matrix, we propose a method wherein the stable stage distribution and genealogical Markov chain are collapsed separately and subsequently recombined to construct the collapsed projection matrix. This method optimally preserves reproductive values, the genealogical Markov chain, the matrix of elasticities, and the generation time in addition to the stable stage distribution and the asymptotic growth rate. The method is also independent of the units used to describe the population in the sense that, unlike the standard collapsing method, it commutes with changes of units. We return to the practical applicability of this new collapsing method in the Discussion.

2. Genealogical Markov chains associated with matrix population models

A matrix population model is given by a non-negative matrix $\mathbf{A} = (a_{ij})$. The model assumes that if there are $n_j(t)$ individuals in the population of class j at time t, these individuals will make a contribution of $a_{ij} n_j(t)$ individuals to the total number of individuals of class i at time $t + 1$. That is, the dynamics of the population are governed by the matrix equation

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

where $\mathbf{n}(t) = (n_i(t))$ is the vector giving the number of individuals in each class at time t.

While Eq. (1) describes the dynamics of the size and composition of the population, it is also sometimes useful to consider the sequence of classes occupied by a particular individual, its ancestors, and descendants. We begin by reviewing the features of two Markov chains that capture the dynamics along such lineages. These ideas are due to Demetrius (1974, 1975), and have been further exploited in Tuljapurkar (1982, 1993).