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The use of the vec-permutation matrix in spatial matrix population models

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Abstract

Matrix models for a metapopulation can be formulated in two ways: in terms of the stage distribution within each spatial patch, or in terms of the spatial distribution within each stage. In either case, the entries of the projection matrix combine demographic and dispersal information in potentially complicated ways. We show how to construct such models from a simple block-diagonal formulation of the demographic and dispersal processes, using a special permutation matrix called the vec-permutation matrix. This formulation makes it easy to calculate and interpret the sensitivity and elasticity of λ to changes in stage- and patch-specific demographic and dispersal parameters.

Keywords: Matrix population model; Spatial model; Metapopulation; Multiregional model; Dispersal; Movement; Sensitivity; Elasticity

1. Introduction

A spatial population model describes a finite set of discrete local populations coupled by the movement or dispersal of individuals. Human demographers call these multiregional populations (Rogers, 1968, 1995), ecologists call them multisite populations (Lebreton, 1996) or metapopulations (Hanski, 1999). The dynamics of metapopulations are determined by the patterns of dispersal among the local populations and the demographic conditions experienced by the local populations.

If each local population is described by a stage-classified matrix population model (see Caswell, 2001), a spatial matrix model describing the metapopulation can be written as

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

The population vector, **n**, includes the densities of each stage in each local population (which we will refer to here as a patch). The projection matrix, **A**, includes both demographic processes, (which generally differ among patches) and dispersal processes (which generally differ among stages). The asymptotic population growth rate, λ, is the dominant eigenvalue of **A**, and the stable stage × patch distribution and the reproductive values are given by

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the corresponding right and left eigenvectors **w** and **v**.

The elements of **A** are combinations of demographic rates and dispersal probabilities. It can be challenging to formulate these elements, and difficult to analyze the role of particular parameters. This can be especially problematic for perturbation analyses. The sensitivity and elasticity of λ to the elements of **A** are of little interest, because a change in a_{ij} has no simple biological interpretation. Instead, attention focuses on the effects of changes in demography and dispersal separately.

Here we describe a method for constructing spatial matrix population models that keeps demographic and dispersal parameters clearly distinguished and separates their effects in perturbation analysis. It permits the inclusion of complicated seasonal patterns of dispersal. We describe model construction and the formulation of sensitivity and elasticity analyses, and apply the method to two simple examples.

2. Spatial model construction

Constructing a spatial matrix model requires specifying the state of the metapopulation, the demographic characteristics of each patch, and the dispersal of individuals among the patches. To describe the state of the metapopulation let p be the number of patches and s be the number of stages. The state of the metapopulation can then be described by the matrix

$$\mathbf{N}(t) = \begin{pmatrix} n_{11} & n_{12} & \cdots & n_{1p} \\ n_{21} & n_{22} & \cdots & n_{2p} \\ \vdots & \vdots & \ddots & \vdots \\ n_{s1} & n_{s2} & \cdots & n_{sp} \end{pmatrix}(t) \quad (2)$$

where $n_{ij}(t)$ is the density of stage i in patch j at time t. The population vector **n** in (1) can be written in two ways. Let $\mathbf{n}_{i\cdot}$ = row i and $\mathbf{n}_{\cdot j}$ = column j of **N**, then

$$\mathbf{n}_{\text{patches}} = \begin{pmatrix} \mathbf{n}_{\cdot 1} \\ \hline \vdots \\ \hline \mathbf{n}_{\cdot p} \end{pmatrix} \quad \text{or} \quad \mathbf{n}_{\text{stages}} = \begin{pmatrix} \mathbf{n}_{1\cdot}^{\mathsf{T}} \\ \hline \vdots \\ \hline \mathbf{n}_{s\cdot}^{\mathsf{T}} \end{pmatrix} \quad (3)$$

In the first arrangement ($\mathbf{n}_{\text{patches}}$), the subvectors give the stage distribution within each patch. In the second arrangement ($\mathbf{n}_{\text{stages}}$) the subvectors give the spatial distribution of each stage. Note that in general it is not possible to write a model in which the matrix $\mathbf{N}(t)$ replaces the vector $\mathbf{n}(t)$ in Eq. (1) and is projected by multiplication by a matrix (Logofet, 2002).

To model demography without dispersal, it would be convenient to organize the population by patches. Let $\mathbf{B}_i$ be the $s \times s$ demographic projection matrix for patch i, such that $\mathbf{n}_{\cdot i}(t+1) = \mathbf{B}_i \mathbf{n}_{\cdot i}(t)$. Then, without dispersal, the metapopulation would be projected by a block diagonal matrix $\mathbb{B}$

$$\begin{pmatrix} \mathbf{n}_{\cdot 1} \\ \hline \vdots \\ \hline \mathbf{n}_{\cdot p} \end{pmatrix}(t+1) = \underbrace{\left(\begin{array}{c|c|c|c} \mathbf{B}_1 & 0 & \cdots & 0 \\ \hline 0 & \mathbf{B}_2 & \cdots & 0 \\ \hline & & \ddots & \\ \hline 0 & 0 & \cdots & \mathbf{B}_p \end{array}\right)}_{\mathbb{B}} \begin{pmatrix} \mathbf{n}_{\cdot 1} \\ \hline \vdots \\ \hline \mathbf{n}_{\cdot p} \end{pmatrix}(t) \quad (4)$$

To model dispersal without demography, it would be more convenient to organize the population by stages. Let $\mathbf{M}_h$ be the $p \times p$ dispersal matrix for stage h, so that $m_{ij}^{(h)}$ is the probability that an individual of stage h moves from patch j to patch i. Then dispersal would be described by a block diagonal matrix $\mathbb{M}$

$$\begin{pmatrix} \mathbf{n}_{1\cdot}^{\mathsf{T}} \\ \hline \vdots \\ \hline \mathbf{n}_{s\cdot}^{\mathsf{T}} \end{pmatrix}(t+1) = \underbrace{\left(\begin{array}{c|c|c|c} \mathbf{M}_1 & 0 & \cdots & 0 \\ \hline 0 & \mathbf{M}_2 & \cdots & 0 \\ \hline & & \ddots & \\ \hline 0 & 0 & \cdots & \mathbf{M}_s \end{array}\right)}_{\mathbb{M}} \begin{pmatrix} \mathbf{n}_{1\cdot}^{\mathsf{T}} \\ \hline \vdots \\ \hline \mathbf{n}_{s\cdot}^{\mathsf{T}} \end{pmatrix}(t) \quad (5)$$

Constructing a spatial model that incorporates both demography and dispersal has previously required sacrificing one or both of these block-diagonal forms. Our goal is a method of model construction that maintains them both.

As many other authors have done, we assume that demography and dispersal can be treated as operating sequentially within the projection interval (e.g., Hastings, 1992; Bravo de la Parra et al., 1995, 1997; Sanz and Bravo de la Parra, 1999, 2000; Lebreton and Gonzalez-Davila, 1993), although either process may be seasonal and they may occur in any order. Then, constructing a model that maintains the block diagonal forms of the demography and dispersal matrices in (4) and (5) requires converting a population vector organized by patches into a population vector organized by stages and vice versa. This conversion is accomplished by noting that

$$\mathbf{n}_{\text{patches}} = \text{vec}(\mathbf{N}) \tag{6}$$

$$\mathbf{n}_{\text{stages}} = \text{vec}(\mathbf{N}^{\mathsf{T}}) \tag{7}$$

where the vec operator, vec(·), stacks the columns of a matrix one on top of the other (this is implemented with the command `N(:)` in MATLAB). The vectors (6) and (7) are related by a special permutation matrix, **P**, called the *vec-permutation matrix*; i.e.,

$$\text{vec}(\mathbf{N}^{\mathsf{T}}) = \mathbf{P}\,\text{vec}(\mathbf{N}) \tag{8}$$

Henderson and Searle (1981) reviewed the properties and derivation of the vec-permutation matrix. It has dimension ($sp \times sp$) and is given by

$$\mathbf{P}(s, p) = \sum_{i=1}^{s} \sum_{j=1}^{p} \mathbf{E}_{ij} \otimes \mathbf{E}_{ij}^{\mathsf{T}} \tag{9}$$

where $\mathbf{E}_{ij}$ is an $s \times p$ matrix with a 1 in the (i, j) position and zeros elsewhere and $\otimes$ denotes the Kronecker matrix product. As with any permutation matrix, $\mathbf{P}^{\mathsf{T}} = \mathbf{P}^{-1}$.

Suppose that, within each projection interval, demographic change occurs within each patch and then dispersal redistributes individuals among patches. If we organize **n** by patches we can use the vec-permutation matrix to write

$$\begin{pmatrix} \mathbf{n}_{\cdot 1} \\ \hline \vdots \\ \hline \mathbf{n}_{\cdot p} \end{pmatrix} (t+1) = \mathbf{P}^{\mathsf{T}}\,\mathbb{M}\,\mathbf{P}\,\mathbb{B} \begin{pmatrix} \mathbf{n}_{\cdot 1} \\ \hline \vdots \\ \hline \mathbf{n}_{\cdot p} \end{pmatrix} (t) \tag{10}$$

The projection matrix **A** in (1) is then $\mathbf{A} = \mathbf{P}^{\mathsf{T}}\,\mathbb{M}\,\mathbf{P}\,\mathbb{B}$. In this case, **A** first applies the block-demography matrix $\mathbb{B}$ to the population vector organized by patches, then permutes the result to reorganize the population vector by stages, applies the block-dispersal matrix $\mathbb{M}$, and then permutes the result back to the original organization of the population by patches.

Table 1
The projection matrix **A** and the sensitivity matrices $\mathbf{S}_{\mathbb{B}}$ and $\mathbf{S}_{\mathbb{M}}$ as a function of the arrangement of the population vector (by patches or by stages) and the order of demography and dispersal within the projection interval

Population vector arrangement			
By patches		By stages	
Demography then dispersal			
(a)	$\mathbf{A} = \mathbf{P}^{\mathsf{T}}\mathbb{M}\mathbf{P}\mathbb{B}$	(b)	$\mathbf{A} = \mathbb{M}\,\mathbf{P}\,\mathbb{B}\,\mathbf{P}^{\mathsf{T}}$
	$\mathbf{S}_{\mathbb{B}} = \mathbf{P}^{\mathsf{T}}\mathbb{M}^{\mathsf{T}}\mathbf{P}\mathbf{S}_{\mathbf{A}}$		$\mathbf{S}_{\mathbb{B}} = \mathbf{P}^{\mathsf{T}}\,\mathbb{M}^{\mathsf{T}}\,\mathbf{S}_{\mathbf{A}}\,\mathbf{P}$
	$\mathbf{S}_{\mathbb{M}} = \mathbf{P}\mathbf{S}_{\mathbf{A}}\,\mathbb{B}^{\mathsf{T}}\,\mathbf{P}^{\mathsf{T}}$		$\mathbf{S}_{\mathbb{M}} = \mathbf{S}_{\mathbf{A}}\mathbf{P}\mathbb{B}^{\mathsf{T}}\mathbf{P}^{\mathsf{T}}$
Dispersal then demography			
(c)	$\mathbf{A} = \mathbb{B}\,\mathbf{P}^{\mathsf{T}}\,\mathbb{M}\,\mathbf{P}$	(d)	$\mathbf{A} = \mathbf{P}\,\mathbb{B}\,\mathbf{P}^{\mathsf{T}}\,\mathbb{M}$
	$\mathbf{S}_{\mathbb{B}} = \mathbf{S}_{\mathbf{A}}\,\mathbf{P}^{\mathsf{T}}\,\mathbb{M}^{\mathsf{T}}\,\mathbf{P}$		$\mathbf{S}_{\mathbb{B}} = \mathbf{P}^{\mathsf{T}}\,\mathbf{S}_{\mathbf{A}}\,\mathbb{M}^{\mathsf{T}}\,\mathbf{P}$
	$\mathbf{S}_{\mathbb{M}} = \mathbf{P}\,\mathbb{B}^{\mathsf{T}}\,\mathbf{S}_{\mathbf{A}}\,\mathbf{P}^{\mathsf{T}}$		$\mathbf{S}_{\mathbb{M}} = \mathbf{P}\,\mathbb{B}^{\mathsf{T}}\,\mathbf{P}^{\mathsf{T}}\,\mathbf{S}_{\mathbf{A}}$

In all cases, the elasticity matrices satisfy $\mathbf{E}_{\mathbb{B}} = \mathbb{B} \circ \mathbf{S}_{\mathbb{B}}/\lambda$ and $\mathbf{E}_{\mathbb{M}} = \mathbb{M} \circ \mathbf{S}_{\mathbb{M}}/\lambda$.

If dispersal is followed by demography and we arrange **n** by stages, we would have

$$\begin{pmatrix} \mathbf{n}_{1\cdot}^{\mathsf{T}} \\ \hline \vdots \\ \hline \mathbf{n}_{s\cdot}^{\mathsf{T}} \end{pmatrix} (t+1) = \mathbf{P}\,\mathbb{B}\,\mathbf{P}^{\mathsf{T}}\,\mathbb{M} \begin{pmatrix} \mathbf{n}_{1\cdot}^{\mathsf{T}} \\ \hline \vdots \\ \hline \mathbf{n}_{s\cdot}^{\mathsf{T}} \end{pmatrix} (t) \tag{11}$$

In this case, the projection matrix is $\mathbf{A} = \mathbf{P}\,\mathbb{B}\,\mathbf{P}^{\mathsf{T}}\,\mathbb{M}$.

The four possible combinations of arrangements of **n** and sequences of a single demography and a single dispersal event lead to the four projection matrices shown in Table 1. Each of these projection matrices can be obtained from any of the others by a cyclic permutation of the matrices making up the product. Hence their eigenvalue spectra are identical (Horn and Johnson, 1990, Theorem 1.3.20; see Caswell, 2001 p. 350), as are the sensitivities and elasticities of λ to the entries of $\mathbb{B}$ and $\mathbb{M}$ obtained from each.

3. Sensitivity analysis

Eqs. (10) and (11) describe population growth in a periodic environment that alternates between episodes of demography and dispersal. The sensitivity and elasticity of λ to changes in demography or dispersal at any point in the projection cycle can be calculated using results of Caswell and Trevisan (1994) and Lesnoff et al. (2003). In general, let $\mathbf{A} = \mathbf{D}_m \cdots \mathbf{D}_1$ be any matrix product. The sensitivity matrix of **A** (i.e., the matrix whose (i, j) entry is $\partial\lambda/\partial a_{ij}$) is

$$\mathbf{S_A} = \frac{\mathbf{v}\mathbf{w}^{\mathsf{T}}}{\langle \mathbf{w}, \mathbf{v} \rangle} \tag{12}$$

To calculate the sensitivity of λ to the entries of one of the matrices in the product, say $\mathbf{D}_k$, write $\mathbf{A} = \mathbf{F}_k\mathbf{D}_k\mathbf{G}_k$ where

$$\mathbf{F}_k = \begin{cases} \mathbf{D}_m \cdots \mathbf{D}_{k+1} & k \neq m \\ \mathbf{I} & k = m \end{cases}$$

$$\mathbf{G}_k = \begin{cases} \mathbf{D}_{k-1} \cdots \mathbf{D}_1 & k \neq 1 \\ \mathbf{I} & k = 1 \end{cases} \tag{13}$$

Then the sensitivity and elasticity matrices for $\mathbf{D}_k$ are

$$\mathbf{S}_{\mathbf{D}_k} = \left(\frac{\partial\lambda}{\partial d_{ij}^{(k)}} \right) = \mathbf{F}_k^{\mathsf{T}}\, \mathbf{S_A}\, \mathbf{G}_k^{\mathsf{T}} \tag{14}$$

$$\mathbf{E}_{\mathbf{D}_k} = \left(\frac{d_{ij}^{(k)}}{\lambda} \frac{\partial\lambda}{\partial d_{ij}^{(k)}} \right) = \frac{\mathbf{D}_k}{\lambda} \circ \mathbf{S}_{\mathbf{D}_k} \tag{15}$$

where $\circ$ denotes the Hadamard product (Caswell and Trevisan, 1994; Lesnoff et al., 2003). Table 1 shows the sensitivity matrices resulting from applying (14) to each of the four projection matrices. In each case, the elasticity matrices are given by

$$\mathbf{E}_{\mathbb{B}} = \frac{1}{\lambda}\mathbb{B} \circ \mathbf{S}_{\mathbb{B}} \tag{16}$$

$$\mathbf{E}_{\mathbb{M}} = \frac{1}{\lambda}\mathbb{M} \circ \mathbf{S}_{\mathbb{M}} \tag{17}$$

The sensitivities and elasticities relevant to demographic and dispersal transitions appear in the $s \times s$ diagonal blocks of $\mathbf{S}_{\mathbb{B}}$ and $\mathbf{E}_{\mathbb{B}}$, and the $p \times p$ diagonal blocks of $\mathbf{S}_{\mathbb{M}}$ and $\mathbf{E}_{\mathbb{M}}$. This makes the interpretation of the results particularly clear.

4. Examples

In this section we present two examples of the use of the vec-permutation matrix in constructing and analyzing spatial matrix models for metapopulations.

4.1. The peregrine falcon

Wootton and Bell (1992) presented a matrix model for the peregrine falcon, *Falco peregrinus anatum*, in California. The model describes a population in two patches (northern and southern California) with two stages (juveniles and adults). This case is simple enough that the projection matrix can be written down directly (as Wootton and Bell did), but shows clearly how the block-demography and block-dispersal matrices can be used in such analyses.

Wootton and Bell arranged the population by patches. They assumed dispersal happens before demography, so the survival of dispersing birds depends on their destination. Only juveniles disperse, and they assume that the probability of juvenile dispersal is d regardless of direction. Thus, the dispersal matrices for juveniles and adults are

$$\mathbf{M}_1 = \begin{pmatrix} 1-d & d \\ d & 1-d \end{pmatrix} \tag{18}$$

$$\mathbf{M}_2 = \mathbf{I} \tag{19}$$

Demography in patch i is described by

$$\mathbf{B}_i = \begin{pmatrix} 0 & f_i \\ p_i & q_i \end{pmatrix} \tag{20}$$

where f_i is fertility, p_i is juvenile survival, and q_i is adult survival in patch i (1 = north, 2 = south). From (9), the vec-permutation matrix is

$$\mathbf{P}(2,2) = \begin{pmatrix} 1&0&0&0 \\ 0&0&1&0 \\ 0&1&0&0 \\ 0&0&0&1 \end{pmatrix} \tag{21}$$

Constructing the block-diagonal matrices $\mathbb{B}$ and $\mathbb{M}$ and combining these with $\mathbf{P}$ gives the metapopulation projection matrix

$$\mathbf{A} = \mathbb{B}\mathbf{P}^{\mathsf{T}}\mathbb{M}\mathbf{P} = \left(\begin{array}{cc|cc} 0 & f_1 & 0 & 0 \\ (1-d)p_1 & q_1 & \mathrm{d}p_1 & 0 \\ \hline 0 & 0 & 0 & f_2 \\ \mathrm{d}p_2 & 0 & (1-d)p_2 & q_2 \end{array} \right) \tag{22}$$

Table 2
Parameter values for the northern and southern peregrine falcon populations (from Wootton and Bell, 1992)

Parameter	Northern	Southern
f	0.26	0.19
p	0.72	0.72
q	0.77	0.77
d	0.27	0.27

Parameter values from Wootton and Bell (1992) are shown in Table 2. Only fertility differed between the two populations. The resulting metapopulation projection matrix is

$$\mathbf{A} = \left(\begin{array}{cc|cc} 0 & 0.2556 & 0 & 0 \\ 0.5256 & 0.77 & 0.1944 & 0 \\ \hline 0 & 0 & 0 & 0.1908 \\ 0.1944 & 0 & 0.5256 & 0.77 \end{array}\right) \tag{23}$$

In the absence of dispersal, the northern population, which has higher fertility, would have a higher growth rate ($\lambda_{\mathbf{B}_1} = 0.961$) than the southern population ($\lambda_{\mathbf{B}_2} = 0.919$). The growth rate of the metapopulation is $\lambda_{\mathbf{A}} = 0.943$. Although all these growth rates are less than 1, the precision of the parameter estimates is unknown (and probably not high); and for the purposes of this example only the relative values of λ are relevant.

From (12), the sensitivity matrix for $\lambda_{\mathbf{A}}$ is

$$\mathbf{S_A} = \left(\begin{array}{cc|cc} 0.1062 & 0.392 & 0.0623 & 0.3082 \\ 0.1567 & 0.5781 & 0.0919 & 0.4544 \\ \hline 0.0835 & 0.3082 & 0.049 & 0.2422 \\ 0.0919 & 0.3392 & 0.0539 & 0.2666 \end{array}\right) \tag{24}$$

The sensitivity and elasticity matrices for the demography and dispersal components are given in Table 1(c). The sensitivity and elasticity of λ to the demographic matrices are

$$\mathbf{S}_{\mathbb{B}} = \left(\begin{array}{cc|cc} 0.0944 & 0.392 & - & - \\ 0.1392 & 0.5781 & - & - \\ \hline - & - & 0.0583 & 0.2422 \\ - & - & 0.0642 & 0.2666 \end{array}\right) \tag{25}$$

$$\mathbf{E}_{\mathbb{B}} = \left(\begin{array}{cc|cc} 0 & 0.1062 & - & - \\ 0.1062 & 0.4719 & - & - \\ \hline - & - & 0 & 0.049 \\ - & - & 0.049 & 0.2177 \end{array}\right) \tag{26}$$

The off-diagonal blocks of $\mathbf{S}_{\mathbb{B}}$ and $\mathbf{E}_{\mathbb{B}}$ are of no interest because they show the results of perturbations to elements of $\mathbb{B}$ that are inherently zero. The elasticity matrix shows that λ is most elastic to changes in adult survival. The sums of the diagonal blocks of $\mathbf{E}_{\mathbb{B}}$ give the proportional contributions of the northern and southern populations to the metapopulation growth rate (0.68 and 0.32, respectively).

The sensitivity and elasticity of λ to the dispersal matrices are

$$\mathbf{S}_{\mathbb{M}} = \left(\begin{array}{cc|cc} 0.1128 & 0.0662 & - & - \\ 0.0662 & 0.0388 & - & - \\ \hline - & - & 0.5454 & 0.4287 \\ - & - & 0.3200 & 0.2515 \end{array}\right) \tag{27}$$

$$\mathbf{E}_{\mathbb{M}} = \left(\begin{array}{cc|cc} 0.0873 & 0.0189 & - & - \\ 0.0189 & 0.0301 & - & - \\ \hline - & - & 0.5781 & 0 \\ - & - & 0 & 0.2666 \end{array}\right) \tag{28}$$

where again the off-diagonal blocks are irrelevant. The columns of the $\mathbf{M}_1$ must sum to 1. Thus we are interested only in perturbations in which a change in any entry is compensated by changes elsewhere in that column. We do this by calculating the sensitivity to the dispersal probability d, treating d as a lower-level parameter (Caswell, 2001).

$$\begin{aligned} \frac{\partial\lambda}{\partial d} &= \sum_{i,j} \frac{\partial\lambda}{\partial m_{ij}^{(1)}} \frac{\partial m_{ij}^{(1)}}{\partial d} \\ &= \frac{\partial\lambda}{\partial m_{12}^{(1)}} + \frac{\partial\lambda}{\partial m_{21}^{(1)}} - \frac{\partial\lambda}{\partial m_{11}^{(1)}} - \frac{\partial\lambda}{\partial m_{22}^{(1)}} \\ &= -0.02 \end{aligned} \tag{29}$$

where $m_{ij}^{(1)}$ is the i, j element of $\mathbf{M}_1$. Thus, an increase in d, which would increase dispersal from the high quality patch to the low quality patch and vice-versa, would reduce λ. Numerical calculations show that $\partial\lambda/\partial d$ becomes more negative as the difference in fertility between the northern and southern populations increases, as intuition would suggest.

4.2. The black-headed gull

Many formulations of spatial matrix models in the literature can be written using the vec-permutation matrix. For example, Lebreton (1996) presents a spatial model for the black-headed gull (*Larus ridibundus*) in two patches, one of good quality and one of poor quality, in central France. Five age classes are distinguished, with demographic matrices and population growth rates

$$\mathbf{B}_1 = \begin{pmatrix} 0 & 0.096 & 0.160 & 0.224 & 0.320 \\ 0.80 & 0 & 0 & 0 & 0 \\ 0 & 0.82 & 0 & 0 & 0 \\ 0 & 0 & 0.82 & 0 & 0 \\ 0 & 0 & 0 & 0.82 & 0.82 \end{pmatrix},$$

$$\lambda = 1.011 \qquad (30)$$

$$\mathbf{B}_2 = \begin{pmatrix} 0 & 0.100 & 0.160 & 0.200 & 0.200 \\ 0.80 & 0 & 0 & 0 & 0 \\ 0 & 0.82 & 0 & 0 & 0 \\ 0 & 0 & 0.82 & 0 & 0 \\ 0 & 0 & 0 & 0.82 & 0.82 \end{pmatrix},$$

$$\lambda = 0.968 \qquad (31)$$

Only age class 1 disperses, so

$$\mathbf{M}_1 = \begin{pmatrix} 0.75 & 0.375 \\ 0.25 & 0.625 \end{pmatrix} = \begin{pmatrix} 1-p & q \\ p & 1-q \end{pmatrix} \qquad (32)$$

and $\mathbf{M}_2 = \mathbf{M}_3 = \mathbf{M}_4 = \mathbf{M}_5 = \mathbf{I}$. The metapopulation projection matrix, given by Table 1(d), is

$$\mathbf{A} = \left(\begin{array}{cc|cc|cc|cc|cc} 0 & 0 & 0.096 & 0 & 0.160 & 0 & 0.224 & 0 & 0.320 & 0 \\ 0 & 0 & 0 & 0.100 & 0 & 0.160 & 0 & 0.200 & 0 & 0.200 \\ \hline 0.60 & 0.30 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.20 & 0.50 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0.82 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.82 & 0 & 0 & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 0 & 0.82 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.82 & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 0 & 0 & 0 & 0.82 & 0 & 0.82 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.82 & 0 & 0.82 \end{array}\right) \qquad (33)$$

with $\lambda = 0.997$. The non-zero blocks in $\mathbf{A}$ can be labelled as

$$\mathbf{A} = \left(\begin{array}{c|c|c|c|c} \mathbf{F}_1 & \mathbf{F}_2 & \mathbf{F}_3 & \mathbf{F}_4 & \mathbf{F}_5 \\ \hline \mathbf{P}_1 & 0 & 0 & 0 & 0 \\ \hline 0 & \mathbf{P}_2 & 0 & 0 & 0 \\ \hline 0 & 0 & \mathbf{P}_3 & 0 & 0 \\ \hline 0 & 0 & 0 & \mathbf{P}_4 & \mathbf{P}_5 \end{array}\right) \qquad (34)$$

which replicates, in block form, the generalized Leslie matrix format of $\mathbf{B}_1$ and $\mathbf{B}_2$.

The sensitivity and elasticity of λ to $\mathbb{B}$ and $\mathbb{M}$ are obtained from Table 1(d). As in the peregrine falcon example, the elasticities of λ to $\mathbb{B}$ show that most (77%) of λ is contributed by the high quality patch. The columns of $\mathbf{M}_1$ must sum to 1 so we calculate the sensitivity of λ to p and q directly

$$\frac{\partial\lambda}{\partial p} = \frac{\partial\lambda}{\partial m_{21}^{(1)}} - \frac{\partial\lambda}{\partial m_{11}^{(1)}} = -0.043 \qquad (35)$$

$$\frac{\partial\lambda}{\partial q} = \frac{\partial\lambda}{\partial m_{12}^{(1)}} - \frac{\partial\lambda}{\partial m_{22}^{(1)}} = 0.0173 \qquad (36)$$

This formulation has useful theoretical properties, because $\mathbf{A}$ is a block matrix version of the age-classified Leslie matrix. Lebreton (1996), extending the earlier work of Le Bras (1971) and Rogers (1974), showed this form can be analyzed with a block-matrix generalization of the age-classified renewal equation, and applied the approach to the evolution of dispersal (Lebreton et al., 2000; Khaladi et al., 2000).

5. Discussion

The vec-permutation matrix provides a framework for constructing spatial matrix models that incorporate demography and dispersal. Because it yields a matrix product in which dispersal and demography appear as block-diagonal matrices, it makes perturbation analysis particularly simple, permitting straightforward calculation of the sensitivity and elasticity of λ to changes in demography and dispersal at any point in the annual cycle and for any stage.

Although the cases we have examined here include only a single episode each of dispersal and demography, it also applies to situations that include seasonality of demography or dispersal, multiple episodes of dispersal, and dispersal of different stages at different times of year. Any number and any order of demography and dispersal events, connected by the appropriate vec-permutation and reverse permutation matrices, can be included in the projection matrix **A**. This construction is particularly apt for species in which dispersal occurs at particular seasons within the year, but is not restricted to this case. Nor is it restricted to populations classified by stage and location; it can be applied to populations stratified by other pairs of factors, such as age and size. In a subsequent paper we will examine such cases that require more complex structures to incorporate the biology of dispersal.

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