Alternative Life-History Pathways and the Elasticity of Stochastic Matrix Models

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ABSTRACT: Loop analysis is a powerful tool for analyzing matrix population models. This note shows that the results of loop analysis, which have been proved for constant matrices only, apply to stochastic matrices as well if elasticity is defined as the effect of a proportional perturbation of both mean and variance. Using the ideas of loop analysis, it is shown that the structure of the stochastic matrix in terms of alternative life-history pathways has important consequences for the effect of stochasticity on elasticities. If the life cycle contains nonoverlapping, alternative life-history pathways, the ranking in terms of elasticity of the most critical vital rates may be reversed in stochastic and the corresponding average environments. This has obvious and important consequences for population management because focusing on a deterministic model would lead to an ineffective or counterproductive management strategy.

Keywords: elasticity analysis, life cycle pathways, matrix population models, environmental stochasticity, loop analysis, annual plants.

Recently, Tuljapurkar et al. (2003) provided an example of a stochastic matrix model where elasticities of the stochastic matrix are very different from elasticities of the matrix of average transitions. This result contradicts the prevailing consensus that stochasticity has little effect on elasticity and hence on the relative importance of different vital rates for population growth, which was based on earlier examples showing striking similarities between elasticity analysis of stochastic matrices and their average equivalents (Benton and Grant 1996; Grant and Benton

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2000; Caswell 2001; Caswell and Kaye 2001; Silvertown and Charlesworth 2001).

Demographic studies of stochastic matrix models often focus on the long-term stochastic population growth rate (denoted by $\log \lambda_s$; Caswell 2001) and its elasticity (Fieberg and Ellner 2001). The common definition of stochastic elasticity (denoted by E^S; Tuljapurkar et al. 2003) is the proportional change in $\log \lambda_s$ caused by a proportional perturbation of both the mean and standard deviation of a matrix element. The consensus that stochasticity has little effect on elasticity is based on comparisons of E^S with the elasticity of the average matrix (denoted by E^A).

In their model of a hurricane-dependent shrub species, Tuljapurkar et al. (2003) find a poor fit between E^S and E^A, which they attribute to two aspects of environmental stochasticity that are not taken into account in the average matrix and in E^A: the effects of habitat sequencing and the variance in life-history traits. It remains to be understood, however, how in the earlier examples cited above, which included both these aspects, stochasticity had such small effect on elasticity despite a considerable effect on population numbers. Solving the apparent contradiction between the early and recent findings will advance our understanding of the role of environmental randomness for population dynamics.

The aim of this note is to complement the observation of Tuljapurkar et al. (2003) with a more detailed understanding of what causes differences between stochastic and average matrix elasticities. One factor causing deviation between stochastic and average matrix elasticities is when the level of stochasticity becomes very large (Benton and Grant 1996; Caswell 2001). Tuljapurkar et al. (2003) identify two other factors: first, if there are many possible environmental states and transitions between them are correlated and second, if the demography of the mean matrix converges slowly and cyclically to a stable population structure.

Here it is shown that the structure of the matrix, in terms of life-history pathways or "loops," is critical in determining the fit between stochastic and mean matrix elasticities. First, I show that loop analysis, which was

proved for constant matrices only (van Groenendael et al. 1994), is valid for stochastic matrix models as well. Second, I study the implications of alternative life-history pathways for the effect of environmental stochasticity on (prospective) elasticity.

Tuljapurkar et al. (2003) show that the dynamics of a stochastic matrix model can be characterized by many different types of population growth rates, sensitivities, and elasticities and that each measure has its own interpretation. In addition to E^S, they introduced two other kinds of stochastic elasticity: one that assumes perturbations of the mean only (denoted $E^{S\mu}$) and one that assumes perturbations of the variance only (denoted $E^{S\sigma}$). While my focus is on the original definition (E^S), the validity of the results for the other types is discussed briefly.

Loop Analysis

Consider stochastic matrix population models of the form

$$\mathbf{n}(t + 1) = \mathbf{X}_t\mathbf{n}(t),$$

$$t = 0, \ldots, T, \qquad (1)$$

with population vector $\mathbf{n}(t)$, stochastic matrix $\mathbf{X}_t$, and initial condition $\mathbf{n}(0) = \mathbf{n}_0$. The long-term stochastic population growth rate is denoted $\log\lambda_s$ (defined in the appendix). The most commonly used type of stochastic elasticity measures the effect on $\log\lambda_s$ of a simultaneous and proportional perturbation of the mean and variance of an element of $\mathbf{X}_t$ (appendix, eq. [A4]). The results below apply to this type of stochastic elasticity, unless stated otherwise.

A life-history pathway or loop is a single, closed loop formed by a subset of the arrows (transitions) in the life cycle graph (van Groenendael et al. 1994; Wardle 1998). Each loop can be assigned a loop elasticity, which corresponds to the contribution of this loop to the total population growth rate. The ideas of "loop analysis" are based on two mathematical properties of matrices and are exposed by van Groenendael et al. (1994) and critically reexamined by Wardle (1998). The first property is that "for each stage i in the life cycle graph, the summed elasticity of incoming transitions equals the summed elasticity of outgoing transitions": $\sum_j e_{ij} = \sum_j e_{ji}$ (van Groenendael et al. 1994, p. 2,411). The second property is that all loop elasticities together sum to 1, just like normal elasticities. These properties were proved for deterministic matrices by van Groenendael et al. (1994). In the appendix, I show that the first property holds for a stochastic matrix model as well. Van Groenendael et al.'s (1994) proof of the second property requires that the first property is true and that the sum of all elasticities equals 1. Since the latter is the case for stochastic elasticities (Tuljapurkar 1990), the proof in the appendix ensures that the second property also holds for stochastic matrices.

A consequence of the first property is that within a loop all transitions have the same elasticity, which is termed the characteristic elasticity of that loop. It is denoted c_k where k is an index of the loop. The total loop elasticity equals c_k multiplied by the number of transitions in the loop. The elasticity of a transition rate a_{ij} in matrix $\mathbf{A}$ equals the sum of the characteristic elasticities of all loops that pass through element a_{ij}. Loops link the elasticities of different matrix elements. Stochastic variation in a transition rate a_{ij} hence affects the characteristic elasticity of all loops passing through a_{ij}. Similarly, c_k depends on stochastic variation in all transitions that are part of the kth loop.

Some ideas from loop analysis are illustrated by the following simple examples. Consider a 3 × 3 age-structured Leslie matrix $\mathbf{A}_1$ containing a single loop only, with p_1 and p_2 the survival rates at ages 1 and 2, respectively, and f_3 the fecundity of age 3 (fig. 1a). Because there is only a single loop, it follows from loop analysis that all nonzero elements of $\mathbf{A}_1$ have the same elasticity, equal to the characteristic elasticity c_1. The transition matrix $\mathbf{A}_1$ and the corresponding elasticity matrix $\mathbf{E}_1$ are

$$\mathbf{A}_1 = \begin{pmatrix} 0 & 0 & f_3 \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{pmatrix}, \qquad \mathbf{E}_1 = \begin{pmatrix} 0 & 0 & c_1 \\ c_1 & 0 & 0 \\ 0 & c_1 & 0 \end{pmatrix}, \qquad (2)$$

with $c_1 = 1/3$ irrespective of the values of p_1, p_2, and f_3.

By allowing stage 3 individuals to survive annually with probability s_3, the following (stage-structured) transition matrix and corresponding elasticity matrix is obtained:

$$\mathbf{A}_2 = \begin{pmatrix} 0 & 0 & f_3 \\ p_1 & 0 & 0 \\ 0 & p_2 & s_3 \end{pmatrix}, \qquad \mathbf{E}_2 = \begin{pmatrix} 0 & 0 & c_1 \\ c_1 & 0 & 0 \\ 0 & c_1 & c_2 \end{pmatrix}. \qquad (3)$$

Matrix $\mathbf{A}_2$ contains two loops: 1-2-3-1 and the 3-3 self loop. The two loops are nonoverlapping because they do not share any arrows (transitions) in the life cycle graph (fig. 1b). In consequence, the elasticity of any nonzero matrix element is either c_1 or c_2.

By contrast, by modifying the original matrix by allowing age-2 individuals to reproduce, matrix $\mathbf{A}_3$ with two overlapping loops (fig. 1c) is obtained. The elasticity of the element that belongs to both loops (element a_{21}) is therefore $c_1 + c_2$ and necessarily the largest:

$$\mathbf{A}_3 = \begin{pmatrix} 0 & f_2 & f_3 \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{pmatrix}, \qquad \mathbf{E}_3 = \begin{pmatrix} 0 & c_2 & c_1 \\ c_1 + c_2 & 0 & 0 \\ 0 & c_1 & 0 \end{pmatrix}. \qquad (4)$$
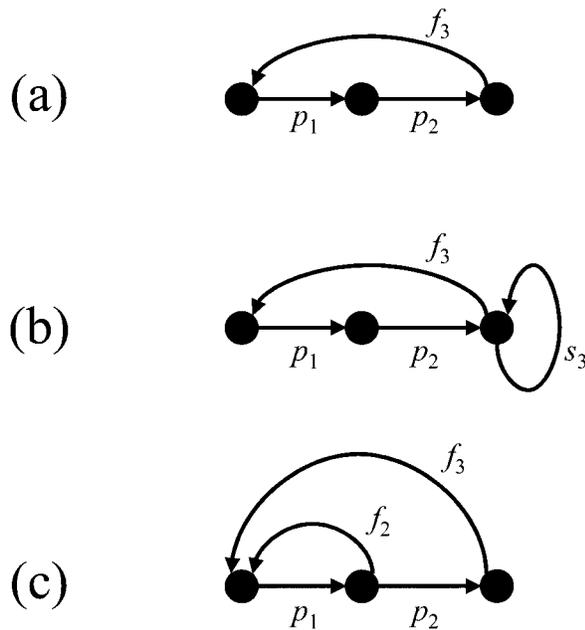
Figure 1: Examples of life cycle graphs with a single loop (*a*), two distinct loops (*b*), and two overlapping loops (*c*).

Here, $\mathbf{A}_3$ is a 3×3 Leslie matrix with $f_1 = 0$. Note that in any Leslie matrix of size $m \times m$ (assuming that the loops are indexed such that the loop that passes through the fertility of the last class is loop 1, of the previous class is loop 2, etc.), the elasticity e_{21} equals $\sum_{k=1}^{m-1} c_k$, while $e_{32} = \sum_{k=1}^{m-2} c_k$, and so forth. This implies that for all the subdiagonal elasticities, $e_{i+1,i} > e_{j+1,j}$ and $e_{i+1,i} \geq e_{1,j}$ for all $j > i$. In other words, owing to the overlap of the loops, the elasticity of p_i exceeds that of all p_j and f_j with $j > i$. Only the elasticity of the 1-1 self loop ($e_{11} = c_m$) can exceed e_{21}, provided that $f_1 > 0$.

The Effect of Environmental Stochasticity

Excluding a number of special cases, a general result is that increasing variability in a matrix element has a negative effect on the population growth rate (Tuljapurkar 1990; Caswell 2001). Loop analysis tells us that increasing variability in one element will affect the elasticity of all elements that share loops with this element. Using the three examples above, I discuss the possible implications of stochasticity depending on the structure of the matrix.

The case of a single loop (eq. [2]) is almost trivial. From the first property, it follows that environmental stochasticity in any or all of the nonzero elements of $\mathbf{A}_1$ simply cannot affect the elasticity matrix because all elasticities must equal c_1. This is true for single-loop matrices of any size. The size of the matrix (or the length of the loop)

affects only the value of c_1, which is $c_1 = 1/L$, where L is the length of the loop.

In the case of two distinct loops as in equation (3), environmental stochasticity can affect elasticity. If only a single element is affected by stochasticity, it will generally decrease the elasticity of the loop it belongs to because the loop's contribution to population growth decreases; it will also increase the elasticity of the other loop because its relative contribution to population growth increases. When elements in both loops are stochastic, the loop that experiences the lowest variability will increase in elasticity while the other one will lose elasticity. This is illustrated with some numerical examples below.

In the case of Leslie matrices with at least one nonreproductive age class ($f_1 = 0$) and at least two reproductive classes such as $\mathbf{A}_3$ (eq. [4]), loop analysis shows that there exists a clear ranking of elasticities in which the survival rates p_i generally have a high elasticity because these transitions belong to many loops. This inherent ranking due to the structure of the matrix implies that there is limited scope for stochasticity to result in rank reversals.

Numerical Examples

Consider the above model (eq. [1]), and assume that at each time step a matrix is selected, randomly depending on the state of the environment. Suppose the environmental conditions can be either "good" or "bad," with probability P and $1 - P$, respectively, and that

$$\mathbf{X}_t = \begin{cases} \mathbf{g}(v) & \text{with probability } P \\ \mathbf{b}(v) & \text{otherwise} \end{cases}, \tag{5}$$

where $\mathbf{g}(v)$ and $\mathbf{b}(v)$ are the matrices for good and bad years, respectively. The parameter $v \in (0, 1)$ is introduced to study the effect of variation. It determines the difference between the two matrices

$$\mathbf{g}(v) = \mathbf{U} + v(\mathbf{G} - \mathbf{U}), \tag{6}$$

$$\mathbf{b}(v) = \mathbf{U} + v(\mathbf{B} - \mathbf{U}), \tag{7}$$

where the average matrix $\mathbf{U}$ is defined as

$$\mathbf{U} = P\mathbf{G} + (1 - P)\mathbf{B} \tag{8}$$

and $\mathbf{G}$ and $\mathbf{B}$ are two distinct matrices. Choosing $v = 1$ gives maximum variation $\mathbf{g}(1) = \mathbf{G}$ and $\mathbf{b}(1) = \mathbf{B}$. In the absence of variability ($v = 0$), the average matrix is obtained, $\mathbf{g}(0) = \mathbf{b}(0) = \mathbf{U}$, and the stochastic elasticity (eq. [A4]) then equals the average matrix elasticity ($E^S = E^A$). Below, stochastic elasticities (eq. [A4]) are computed from observed population structure in simulations with $T = 50{,}000$ using the method of Tuljapurkar et al. (2003).

First, consider model (1) with the following matrices for good and bad years, respectively:

$$\mathbf{G} = \begin{pmatrix} 0 & 0 & 15 \\ 0.3 & 0 & 0 \\ 0 & 0.4 & 0.5 \end{pmatrix}, \qquad \mathbf{B} = \begin{pmatrix} 0 & 0 & 0 \\ 0.2 & 0 & 0 \\ 0 & 0.3 & 0.4 \end{pmatrix}, \quad (9)$$

with $P = .5$. The stochastic matrix $\mathbf{X}_t$ (eq. [5]) has the same structure as $\mathbf{A}_2$ (eq. [3]) and contains two loops, 1-2-3-1 and 3-3. In good years, adult plants (stage 3) have a high fecundity, but in bad years they cannot reproduce. Adults can survive bad years, however, creating the second loop of the life cycle. Figure 2*A* shows the relation between the stochastic elasticities of the nonzero elements of $\mathbf{X}_t$ and v. First, despite elements x_{13}, x_{21}, and x_{32} being subject to different levels of variability, they always have the same elasticity, which corresponds to the characteristic elasticity c_1 of the loop they belong to. Second, note that as v in-

creases, the larger variation in the first loop reduces its characteristic elasticity (c_1), while the relative contribution of the adult-stage self loop ($c_2 = e_{33}$) increases.

Next, consider a life cycle of the structure as in $\mathbf{A}_3$ (eq. [4]), with two loops that overlap in one transition ($x_{21} = p_1$). Based on loop analysis, I expect the elasticity of element x_{21} to be highest, irrespective of the level of stochasticity. To illustrate this, I deliberately choose a large variation in p_1:

$$\mathbf{G} = \begin{pmatrix} 0 & 10 & 5 \\ 0.95 & 0 & 0 \\ 0 & 0.4 & 0 \end{pmatrix}, \qquad \mathbf{B} = \begin{pmatrix} 0 & 0 & 5 \\ 0.05 & 0 & 0 \\ 0 & 0.3 & 0 \end{pmatrix}. \quad (10)$$

Figure 2*B* confirms that the elasticity of element x_{21} is always highest (and equal to the sum of the other two values), as expected from loop analysis (eq. [4]). In addition, figure 2*B* shows that the larger variation in loop
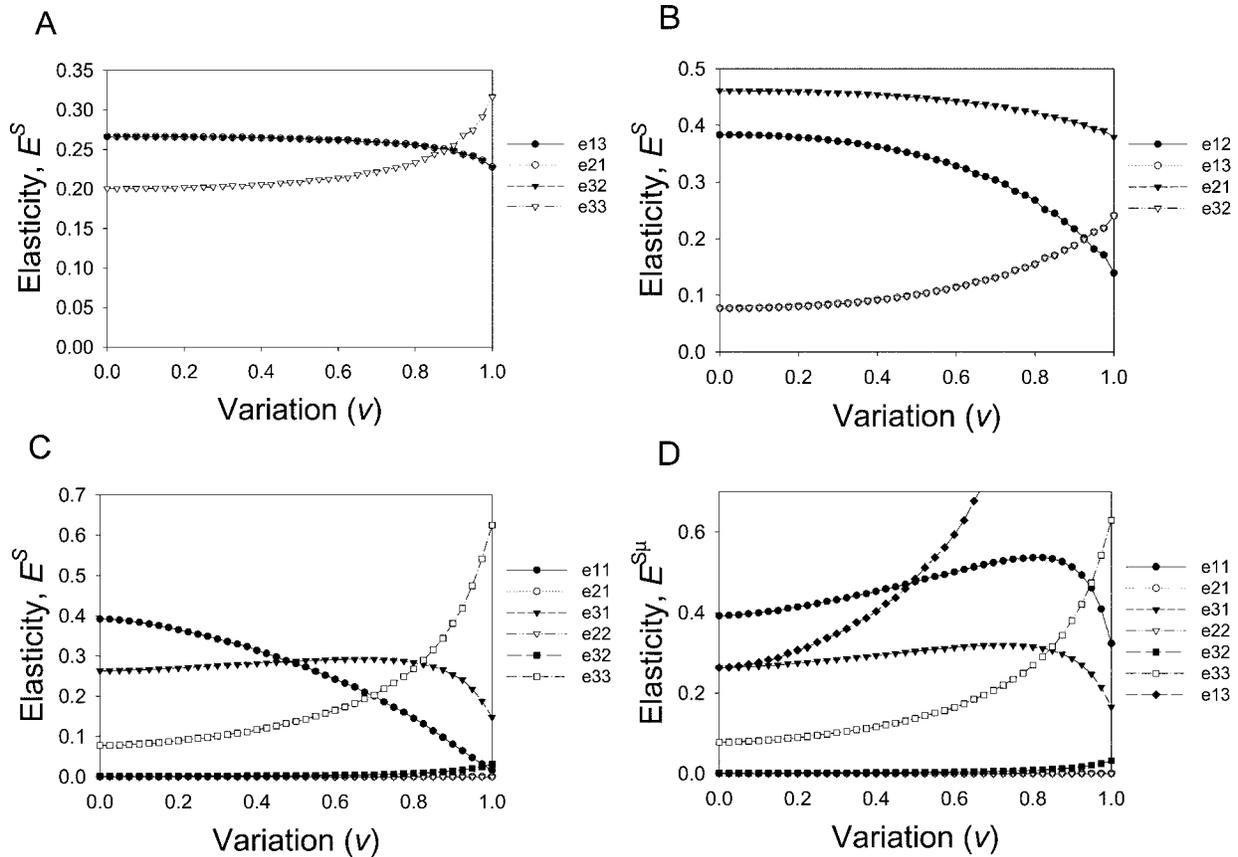

Figure 2: Stochastic elasticities E_{ij}^S (eq. [A4]) as functions of v, computed with simulations using $T = 50,000$. *A*, Life cycle with two distinct loops (eq. [9]). *B*, Life cycle with two overlapping loops (eq. [10]). *C*, Oilseed rape model (eq. [11]). Note that in *A*, *B*, and *C*, $e_{21} = e_{12}$, $e_{31} = e_{13}$, and $e_{32} = e_{23}$. *D*, Alternative stochastic elasticity $E_{ij}^{S\mu}$ for the oilseed rape model (eq. [11]). $E_{ij}^{S\mu}$ is computed using equation (A4) but with $x_{ij}(t)$ replaced by its average, μ_{ij} (Tuljapurkar et al. 2003).

1-2-1 reduces its characteristic elasticity ($c_2 = e_{12}$) while that of loop 1-2-3-1 increases ($c_1 = e_{13}$).

I complement these hypothetical examples with a biologically more realistic one, based on a study of volunteer (weedy) populations of oilseed rape (*Brassica napus*). The life cycle consists of flowering plants (stage 1), seeds in the shallow seed bank (stage 2), and seeds in the deep seed bank (stage 3). The self loop within the flowering plants (1-1) corresponds to the annual life-history pathway, while self loops also exist in the two seed bank stages (2-2 and 3-3). In addition, there are biennial and triennial loops involving exchange between seed bank layers or between flowering plants and the seed bank. The matrices for good and bad years are, respectively,

$$\mathbf{G} = \begin{pmatrix} 14.7 & 0.0029 & 0.042 \\ 1.49 & 0.0012 & 0.017 \\ 970 & 0.78 & 0.57 \end{pmatrix},$$

$$\mathbf{B} = \begin{pmatrix} 0.019 & 0 & 0.0001 \\ 0.89 & 0.0018 & 0.026 \\ 388 & 0.78 & 0.57 \end{pmatrix} \tag{11}$$

(Claessen et al. 2005). Note that there is no variation in survival in the deep seed bank (x_{33}), while there is considerable variation in the annual loop (x_{11}). For volunteer oilseed rape, the difference between good and bad years derives mainly from the probability of a small patch of plants to escape control measures, which I assume to be $P = .1$.

Figure 2*C* shows that for the average matrix ($v = 0$), the annual loop of flowering plants has the highest elasticity. For intermediate v, the highest elasticity is found for elements x_{31} and x_{13}, which make up the 1-3-1 loop between flowering plants and the deep seed bank. Figure 2*C* clearly shows a reversal in the contribution of the 1-1 and 3-3 self loops with increasing v; for $v = 1$, the deep seed bank self loop, which itself is unaffected by stochasticity, contributes most to population growth.

In the numerical examples above (eqq. [9]–[11]), most of the covariances are positive. To check for the effect of covariance, simulations were repeated with negative covariances obtained by swapping matrix elements between **G** and **B**. This had small quantitative but no qualitative effects on the curves in figure 2. Further analysis of the effect of covariances in more complicated matrices is left as a topic for future work.

Discussion

Starting from the observation of Tuljapurkar et al. (2003) that stochastic elasticities can be very different from average matrix elasticities, this note aimed at understanding in more detail the differences between these two kinds of elasticities. For the common definition of stochastic elasticity (E^s), loop analysis yields the following results. First, environmental stochasticity can affect elasticities only if the life cycle graph contains alternative life-history pathways (loops). Second, if life-history pathways overlap, the overlapping transition(s) have a higher elasticity than the nonoverlapping transition(s), irrespective of the level of stochasticity or which elements are subject to stochasticity. This implies that rank reversals of the most important transitions in terms of their elasticity (such as observed in fig. 2*A*, 2*C*) are possible only if the life cycle graphs contain nonoverlapping loops. When loops are overlapping, rank reversals are possible only among less important transitions (such as observed in fig. 2*B*).

Further, the effect of stochasticity on the characteristic elasticity of a loop depends on the level of variability within the loop compared to that level in other loops. Unfortunately, I have not been able to quantify the relevant measure of loop-specific variability to arrive at a more rigorous condition. This remains open to future research. However, the effect of large versus small variability of matrix elements on the relation between elasticity and v is clear in the examples: large variation in loop 1-2-3-1 in equation (9) results in reduction of $c_1 = e_{13}$ with v and an increase in $c_2 = e_{33}$ (fig. 2*A*). The larger variation in loop 1-2-1 in equation (10) results in reduction of $c_2 = e_{12}$ and an increase in $c_1 = e_{32}$ (fig. 2*B*). The absence of variation in loop 3-3 in equation (11) eventually results in the deep seed bank being most critical in the life cycle of volunteer oilseed rape (fig. 2*C*).

Together, these findings suggest that the largest effect of stochasticity on elasticities, in particular in terms of their ranking, is to be expected when the life cycle graph contains alternative life-history pathways and when the loop with highest elasticity in the average matrix is subject to the largest variation. As illustrated by figure 2*C*, this configuration can be expected in models of annual plants with a seed bank because, first, the seed bank is a stable environment that buffers against environmental variability; second, the aboveground processes are likely to be subject to environmental variability; and third, the aboveground processes are essential to population growth. By contrast, life cycles that are abundant in overlapping loops, such as Leslie matrices with multiple adult stages (e.g., eq. [3]), are less likely to be strongly affected by stochasticity because the overlapping transitions will have highest elasticity with or without stochasticity. Note, however, that as stochasticity increases, population numbers will become more variable even if elasticity is not affected (such as in the case of a single loop).

Life cycles in which transitions with high average matrix elasticity are buffered against environmental stochasticity

are predicted to be insensitive to the effect of stochasticity on elasticity because, at most, the effect will be that stochasticity lowers the low-ranking elasticities. Interestingly, Pfister (1998) found a negative correlation between the variance in life-history trait (i.e., matrix element) and its contribution to population growth (i.e., elasticity of the average matrix) in a survey of 17 populations (but see Morris and Doak 2004). If I can take this as a general pattern, then I expect that in many cases of natural populations stochasticity has indeed only a small effect on elasticity.

The question of why the earlier examples cited in the introduction showed a good fit between stochastic and average matrix elasticities can now be addressed with these new findings in mind. In the case of *Arisaema triphyllum* studied by Caswell (2001), the matrix element with highest average matrix elasticity (a_{22}) has practically no variation, while elements with most variation are the ones with the lowest elasticity (cf. Pfister 1998). I hence do not expect stochasticity to affect elasticities significantly. In the model of (Caswell and Kaye 2001), the element with the highest average matrix elasticity (a_{55}) is subject to small variation: the fecundities a_{15} and a_{16} display a >10-fold higher coefficient of variation (CV). However, the effect of stochasticity on the elasticity of these elements is diluted by the much smaller CV of other elements that belong to the same loops (e.g., survival rates up to stage 5). Benton and Grant (1996) studied life cycles of the Leslie type such as equation (3). Due to the large amount of overlap in such life cycles and the implicated ranking of elasticity, it is not surprising that they did not find large discrepancies between stochastic and deterministic elasticities.

Other Kinds of Stochastic Elasticities

The results presented above apply to one specific kind of stochastic elasticity (E^S), which assumes simultaneous perturbation of mean and variance of a matrix element. For the two recently introduced types (denoted by $E^{S\mu}$ and $E^{S\sigma}$; Tuljapurkar et al. 2003), loop analysis is not expected to be valid. First, these elasticities do not sum to 1 ($\sum e_{ij} \neq 1$), and second, the proof in the appendix does not hold for these definitions. My results hence do not generally hold for $E^{S\mu}$ and $E^{S\sigma}$.

I have computed $E^{S\mu}$ and $E^{S\sigma}$ for the examples studied above. There is no apparent relation between $E^{S\sigma}$ and E^S (data not shown). There is more correspondence between $E^{S\mu}$ and E^S. From their definitions (Tuljapurkar et al. 2003), it follows that in the limit of no variation in a matrix element, they are equal ($E_{ij}^{S\mu} = E_{ij}^S$ if $CV_{ij} = 0$). The results

of $E^{S\mu}$ for the oilseed rape model (eq. [11]) are depicted in figure 2D. Comparison of figure 2C and 2C indeed shows that $E^{S\mu} \approx E^S$ for matrix elements with little variation, for example, for e_{33} and e_{31}. Large discrepancies, however, are found for elements with large variation, for example, $E^{S\mu} > E^S$ for e_{11} and e_{31} (note that the CV of elements x_{13} and x_{31} is, respectively, 2.98 and 0.39 if $v = 1$).

The invalidity of loop analysis for $E^{S\mu}$ is most clearly illustrated by the case of a single loop, in which case the E^S values are necessarily all equal to the characteristic loop elasticity, but the $E^{S\mu}$ values of matrix elements with nonzero variation deviate from this value (data not shown). A thorough analysis of the relation between the three types of stochastic elasticity is beyond the scope of this note. Here, I merely note that the results obtained in this note for E^S appear to carry over only to $E^{S\mu}$ and then only in cases with little stochastic variation in all matrix elements.

Conclusions

Tuljapurkar et al. (2003) define and analyze three growth rates and five kinds of elasticities, concluding that, in general, they are different. In particular, their observation that average matrix elasticity is a poor predictor of stochastic elasticity contradicts prevailing ecological consensus. They stress that by using the average matrix, one discards all information on habitat sequencing, which explains the differences between E^A and E^S. Complementary to their general perspective, this note aims at understanding in more detail the relation between two types of elasticity, E^S and E^A, which are the most commonly used types. Using the theory of loop analysis, which I have shown to be valid for stochastic matrices (but only for E^S), I have shown that the structure of the stochastic matrix in terms of alternative life-history pathways has important consequences for the effect of environmental stochasticity on the pattern of elasticities.

APPENDIX

Extension of First Property of Loop Analysis to Stochastic Matrices

Consider model (1). Following Caswell (2001), normalizing the population vector gives us the population structure, $\mathbf{w}(t) = \mathbf{n}(t)/\|\mathbf{n}(t)\|$. The dynamics of $\mathbf{w}(t)$ are

$$\mathbf{w}(t+1) = \frac{\mathbf{X}_t\mathbf{w}(t)}{\|\mathbf{X}_t\mathbf{w}(t)\|}. \tag{A1}$$

The growth factor in year t is defined as $R_t = \|\mathbf{X}_t\mathbf{w}(t)\|$. The reproductive value vectors $\mathbf{v}(t)$ follow

$$\mathbf{v}^{\mathrm{T}}(t-1) = \frac{\mathbf{v}^{\mathrm{T}}(t)\mathbf{X}_{t-1}}{\|\mathbf{v}^{\mathrm{T}}(t)\mathbf{X}_{t-1}\|} \tag{A2}$$

(Caswell 2001), where T denotes transpose. I define the growth factor of the reproductive values from year $t+1$ to t as $Q_t = \|\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{X}_t\|$. The stochastic population growth rate is defined as

$$\log\lambda_s = \lim_{T\to\infty}\frac{1}{T}\sum_{t=0}^{T}\log R_t \tag{A3}$$

(Tuljapurkar 1990). The elasticity of $\log\lambda_s$ to matrix element x_{ij} is defined as

$$e_{ij} = \frac{\partial\log\lambda_s}{\partial\log x_{ij}} = \lim_{T\to\infty}\frac{1}{T}\sum_{t=0}^{T-1}\frac{x_{ij}(t)v_i(t+1)w_j(t)}{R_t\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)}, \tag{A4}$$

which is stochastic elasticity of type E^S (Tuljapurkar et al. 2003). Below I will use the relation

$$\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1) = \mathbf{v}^{\mathrm{T}}(t)\mathbf{w}(t)\frac{Q_t}{R_t}, \tag{A5}$$

which can be proved by substitution of expressions (eqq. [A1], [A2]):

$$\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)R_t = \mathbf{v}^{\mathrm{T}}(t)\mathbf{w}(t)Q_t, \tag{A6}$$

$$\Leftrightarrow \quad \mathbf{v}^{\mathrm{T}}(t+1)\frac{\mathbf{X}_t\mathbf{w}(t)}{\|\mathbf{X}_t\mathbf{w}(t)\|}R_t = \frac{\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{X}_t}{\|\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{X}_t\|}\mathbf{w}(t)Q_t, \tag{A7}$$

$$\Leftrightarrow \quad \mathbf{v}^{\mathrm{T}}(t+1)\mathbf{X}_t\mathbf{w}(t) = \mathbf{v}^{\mathrm{T}}(t+1)\mathbf{X}_t\mathbf{w}(t). \tag{A8}$$

Property 1 of Loop Analysis

To show that

$$\sum_j e_{ij} = \sum_j e_{ji}, \tag{A9}$$

write the left-hand side of equation (A9) as

$$\sum_j e_{ij} = \lim_{T\to\infty}\frac{1}{T}\sum_{t=0}^{T-1}\sum_j\frac{x_{ij}(t)v_i(t+1)w_j(t)}{R_t\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)}. \tag{A10}$$

Denote the innermost summation in equation (A10) by $Z_i(t)$:

$$\sum_j e_{ij} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} Z_i(t), \tag{A11}$$

and rewrite it as follows:

$$Z_i(t) = \sum_j \frac{x_{ij}(t)v_i(t+1)w_j(t)}{R_t \mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)} = \frac{v_i(t+1)}{\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)} \sum_j \frac{x_{ij}(t)w_j(t)}{R_t}. \tag{A12}$$

From equation (A1), it follows that $\sum_j x_{ij}(t)w_j(t)/R_t = w_i(t+1)$, so

$$Z_i(t) = \frac{v_i(t+1)w_i(t+1)}{\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)}. \tag{A13}$$

Similarly, for the expression of the summed outgoing elasticities $\sum_j e_{ji}$,

$$\sum_j e_{ji} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} Y_i(t), \tag{A14}$$

with $Y_i(t)$ defined as

$$Y_i(t) = \sum_j \frac{x_{ji}(t)v_j(t+1)w_i(t)}{R_t \mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)} = \frac{w_i(t)}{\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)} \sum_j \frac{v_j(t+1)x_{ji}(t)}{R_t}. \tag{A15}$$

From equation (A2), it follows that $\sum_j v_j(t+1)x_{ji}(t) = v_i(t)Q_t$, and hence,

$$Y_i(t) = \frac{v_i(t)w_i(t)}{\mathbf{v}^{\mathrm{T}}(t+1)\mathbf{w}(t+1)} \frac{Q_t}{R_t}. \tag{A16}$$

Using equation (A5), this can be rewritten as

$$Y_i(t) = \frac{v_i(t)w_i(t)}{\mathbf{v}^{\mathrm{T}}(t)\mathbf{w}(t)} = Z_i(t-1). \tag{A17}$$

Because $Y_i(t) = Z_i(t-1)$, the long-term averages of Y_i and Z_i (eqq. [A11], [A14]) are the same, and hence equation (A9) is true.

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