Matrix Dimensions Bias Demographic Inferences: Implications for Comparative Plant Demography

Roberto Salguero-Gómez* and Joshua B. Plotkin

Biology Department, University of Pennsylvania, Philadelphia, Pennsylvania 19104

Submitted December 8, 2009; Accepted August 12, 2010; Electronically published October 22, 2010

Abstract: While the wealth of projection matrices in plant demography permits comparative studies, variation in matrix dimensions complicates interspecific comparisons. Collapsing matrices to a common dimension may facilitate such comparisons but may also bias the inferred demographic parameters. Here we examine how matrix dimension affects inferred demographic elasticities and how different collapsing criteria perform. We analyzed 13 × 13 matrices representing nine plant species, collapsing these matrices (i) into even, , , and matrices and (ii) into matrices using different criteria. Stasis and fecundity elasticities increased when matrix dimension was reduced, whereas those of progression and retrogression decreased. We suggest a collapsing criterion that minimizes dissimilarities between the original- and collapsed-matrix elasticities and apply it to 66 plant species to study how life span and growth form influence the relationship between matrix dimension and elasticities. Our analysis demonstrates that (i) projection matrix dimension has significant effects on inferred demographic parameters, (ii) there are better-performing methods than previously suggested for standardizing matrix dimension, and (iii) herbaceous perennial projection matrices are particularly sensitive to changes in matrix dimensionality. For comparative demographic studies, we recommend normalizing matrices to a common dimension by collapsing higher classes and leaving the first few classes unaltered.

Keywords: collapsing, comparative plant demography, elasticity, matrix dimension, population growth rate (λ), projection matrix models.

Introduction

Although most ecologists carry out specific experiments with a limited set of study species, their ultimate goal is to discover general rules, often by compiling and comparing studies. Indeed, most general ecological rules (e.g., exponential growth potential and regulated population growth, the principle of competitive exclusion, robust coexistence, life-history trade-offs) arose and have been confirmed through the extensive application of standardized, comparative methodologies.

In the case of demography, projection matrix models have become a widely used, powerful tool for studying ecological and evolutionary questions. A matrix model classifies individuals in a population according to a discrete range of ages (Leslie 1945), sizes, or developmental stages (Lefkovitch 1965) or a mixture of these variables (e.g., Ehrlein et al. 2005; Jacquemyn et al. 2005). The projection matrix quantifies three fundamental processes for each of the classes that together determine the life cycle of the species: (i) the probability of survival of its individuals, (ii) their probability of staying in the same class (stasis) or transition to another class (progression to higher classes or retrogression to lower classes), and (iii) their contributions with newborns to the population (fecundity). Matrix models have been used to project population growth (e.g., Lefkovitch 1965; Marrero-Gómez et al. 2007) and to examine the relative contributions of the different demographic processes to the population growth rate (e.g., Bierzychudek 1999; van Mantgem and Stephenson 2005) using elasticity analysis (de Kroon et al. 1986). Matrix models have also been used to explore the importance of alternative life-history strategies (e.g., Moloney 1988; Morris and Doak 1998), to identify the most vulnerable classes of a life cycle for the purposes of population management (Werner and Caswell 1977; Lubben et al. 2008), and to establish exploitation regimes that are compatible with long-term demographic viability (Nault and Gagnon 1993; Freckleton et al. 2003).

A great potential for comparative demographic studies has emerged from the large body of literature based on population projection matrices. Such matrices have now been estimated from data and published for more than 475 plant species (R. Salguero-Gómez, unpublished data), whose life spans range across four orders of magnitude (e.g., Namkoong and Roberds 1974; Dostal 2007). Because these demographic dynamics are compiled in the same format—a matrix—the data can, in principle, be used to...
examine broad ecological and evolutionary questions about demographic dynamics.

Studies using large numbers of projection matrices have allowed for linkage between specific demographic processes and stages along ecological succession gradients (Silvertown et al. 1992); for the establishment of methodologies to study the responses of populations to ecotones (Angert 2006), herbivory (Maron and Crone 2006), or habitat fragmentation (Bruna et al. 2009); and for comparing demographic dynamics of native and invasive plant species (Ramula et al. 2008), phylogenetic relationships of life-history strategies (Burns et al. 2010), or relationships between short-term (transient) and long-term (asymptotic) population dynamics (Stott et al. 2010). The number of demographic studies based on projection matrices is growing rapidly (fig. A1, in the online edition of the American Naturalist). Consequently, matrix models will likely serve an important role in future studies of broad ecological and evolutionary questions.

Using published projection matrices for comparative studies is attractive, but it is complicated by the fact that these matrices vary in the number of classes employed, or matrix dimension (fig. 1). The dimension of projection matrices influences the apparent demographic processes of a specific class, such as per capita fecundities (de Matos and Silva Matos 1998), as well as other parameters derived from the matrix, such as population growth rates (Lamar and McGraw 2005; Ramula and Lehtilä 2005); transient dynamics (Tenhumberg et al. 2009; Stott et al. 2010); elasticities of matrix elements (Silvertown et al. 1993; Enright et al. 1995) and vital rates (Zuidema 2000; Salguero-Gómez and Casper 2010); elasticities of demographic pathways (Salguero-Gómez and Casper 2010), as analyzed by loop analysis (van Groenendael et al. 1994); and demographic relationships based on phylogeny (Burns et al. 2010; Stott et al. 2010). This is a nontrivial issue because matrix dimension varies a great deal, from two (Sohn and Policansky 1977) to 24 (Meagher 1982). Although several algorithms have been proposed to determine optimum criteria to establish cutoffs for classes in constructing the original matrices (Vandermeer 1978; Moloney 1986; Shimmatani et al. 2007), thus offering some standardization, most plant demographers still classify systems on the basis of the specific biology of the species and the question being asked (Caswell 2001).

Concerns about matrix dimension were first addressed by Enright et al. (1995), who suggested ways to overcome the problem of variation in dimension among projection matrices. First, they proposed keeping the number of classes proportional to the life span of each species. However, populations of many short-lived herbaceous species are usually classified using many life stages (e.g., 15 classes in Allium tricoccum [Nault and Gagnon 1993] and 17 in Aris- saea serratum [Kakehashi and Kinoshita 1990]; fig. 1). It would be laborious and probably meaningless from a biological perspective to follow the suggestion of Enright et al. (1995) and enforce a correspondingly higher number of life stages for longer-lived herbaceous, shrub, palm, and tree species (Ebert 1999; Caswell 2001). On the other hand, decreasing the number of classes for shorter-lived species matrices would blur the study of their demographic dynamics. Alternatively, Enright et al. (1995) recommended collapsing matrices to the same dimension for all species of a comparative study. However, we know of no comparative plant demographic study that has adopted this suggestion (but see Salguero-Gómez and Casper 2010), perhaps because this would require raw census data for each species, which are frequently unavailable.
Currently, comparative demographic studies either do not control for varying matrix dimensions (Silvertown et al. 2001; Franco and Silvertown 2004; Bruna et al. 2009) or treat dimension as a covariate in the analysis (Ramula et al. 2008; Burns et al. 2010; Stott et al. 2010), which is inappropriate unless the residuals are normally distributed with linear effects on inferred parameters. Integral projection models (IPMs; Easterling et al. 2000), on the other hand, offer an appealing alternative for demographic comparisons because they are more robust to life-cycle complexity than classical projection matrices (Ramula et al. 2008; Zuidema et al. 2010). However, we know of only a dozen plant species that have been studied with IPMs. For classical projection matrices, Enright et al. (1995) suggested specific collapsing criteria to minimize alterations to demographic inferences. These criteria include forming collapsed classes of similar residence times (the average time spent by an individual in a given class) and not merging nonreproductive and reproductive classes, because they are biologically different. However, no study has explicitly evaluated whether these collapsing criteria minimize associated changes to demographic inferences drawn from the collapsed matrix.

In this article, we explore the inferred demographic parameters associated with matrices of different dimensions with the goal of providing rational guidelines for interspecific comparative studies. Specifically, we evaluate how the relative importance of each demographic parameter (elasticity) varies as a function of matrix dimension. We pay special attention to the population growth rate and elasticities because they are of primary importance unless the residuals are normally distributed or treated as a covariate in the analysis (Ramula et al. 2001; Franco and Silvertown 2004; Bruna et al. 2009), reducing the dimension of a projection matrix, once it has been decided which classes to collapse. In its original form, Hooley’s algorithm was intended for age-based models. These models provide poor descriptions of plant demographic patterns because plants are often difficult to age and because age is usually not the best predictor of plant demographics (Harper 1977; Werner and Caswell 1977; Ebert 1999). Here, we expand Hooley’s algorithm to size-and developmental stage–based matrix models. Such models allow individuals not only to advance several classes per unit time but also to retrogress (e.g., Bruna and Oli 2005; Lucas et al. 2008).

Briefly, three steps must be taken to reduce a projection matrix of $n$ dimensions, $A_{n \times n}$, to one of $m$ dimensions, $C_{m \times m}$: (1) choose classes to collapse according to some specified “collapsing criteria,” (2) collapse rows of those classes in the matrix, and (3) collapse the respective columns. Choosing the appropriate classes to collapse (i.e., specifying the collapsing criteria) is a nontrivial decision, and we discuss it below. Collapsing rows is performed by a simple element-by-element addition. Collapsing the columns is the most complex step of the process because, without the raw data, we do not know the proportion of individuals of the original classes that will contribute to forming the matrix elements $a_{ij}$ of the newly collapsed class.

In the simplest case possible, that of collapsing the two classes $k$ and $k + 1$ of an $n$-dimensional matrix $A_{n \times n}$ into a new class $k'$ in the collapsed matrix $C_{(n-1) \times (n-1)}$, we first add the matrix elements $a_{ij} + a_{i+1,j}$ along the $k$ and $k + 1$ rows. The resulting intermediate matrix $B_{(n-1) \times (n-1)}$ is then collapsed for columns $k$ and $k + 1$. For age-based models, determining the entries in column $k'$ of the new collapsed matrix is rather intuitive: simply calculate the proportion of individuals in class $k - 1$ who survive, and consequently age, entering class $k$ after one transition period, as well as the proportion of individuals who survive from class $k$ and will automatically age into class $k + 1$. Surviving individuals from class $k + 1$ do not represent a challenge for this calculation because they will transition into another class that is not collapsed in this example.

The calculation of the entries of column $k'$ for size- and developmental stage–based models is somewhat challenging, because it involves the calculation of survival for the individuals in the two classes to be collapsed ($k$ and $k + 1$), transition probabilities with which the individuals in either class will not leave the collapsed class, and transition probabilities with which the individuals from all other classes (e.g., $k - 1$, $k + 2$) may enter the collapsed class $k'$;
matrices differ because the demographic dynamics are inappropriate stable class distributions.

**Methods: Illustration of the Matrix Dimension–Collapsing Algorithm in Nine Plant Species**

We applied Hooley’s algorithm to population projection matrices of nine different plant species, in order to examine the dissimilarities between the elasticities of demographic processes in matrices of different dimensions and to establish the optimum collapsing criteria. The elasticity is a widely used measurement of the importance of a demographic process in a population; elasticity reflects the proportional change in population growth rate as a function of a proportional change in a part of the projection matrix (de Kroon et al. 1986). Specifically, we explored (i) how the inferred elasticities are influenced by matrix dimension when a fixed collapsing criterion is used (“even collapsing”; see below) and (ii) how collapsing a large matrix into a fixed, smaller dimension in different ways (i.e., using different collapsing criteria; fig. 2) influences the associated elasticities. We refer to the first of these studies as the “matrix-dimension test” and the second as the “collapsing-criterion test.” We then investigated how the elasticities of the collapsed matrices had changed relative to the elasticities of the original, uncollapsed matrices. We used these comparisons to determine guidelines for optimal collapsing (i.e., guidelines for both the size of the collapsed matrices and for the collapsing criteria that minimize the dissimilarities between the inferred elasticities).

We chose nine plant species of different growth forms and longevities for which size- or developmental stage–based projection matrices with relatively high dimension were available in the literature (table 1). These species’ matrices differ because the demographic dynamics are strongly influenced by the growth forms and life histories of the species (Silvertown and Franco 1993). For instance, herbaceous species display a higher fluctuation in sizes and developmental stages because they may skip over more than one class, in both positive (progression) and negative (retrogression) directions, after one annual transition. By
contrast, the dynamics of longer-lived shrubs and trees are “slower” because biomass decreases or dramatic increases occur rarely. We did not include annuals because their “slower” because biomass decreases or dramatic increases occur rarely. We did not include annuals because their

class was never merged with other classes so as to avoid mixing the transition probabilities $p_{ij} \in (0, 1)$ with the per capita contributions of fecundity $a_{ij} \in (0, \infty)$ (fig. 2). Note that in some projection matrix models, per capita contributions such as seed bank, seedling recruitment, and clonal reproduction can expand beyond the first row (e.g., Eriksson 1988; Cipollini et al. 1994; but this is not the case for any of the species in table 1) and that, likewise, these classes should not be merged with those that contain transition probabilities.

Because the matrix dimensions of the chosen species were not identical (table 1), we slightly modified them to produce matrices of initial dimension $13 \times 13$. For those species whose original dimensions were higher than $13 \times 13$ (Ulex minor and Araucaria cunninghamii), we used Hooley’s algorithm to collapse the higher classes to form a life cycle of 13 classes. For one species (Cryptantha flava), we recalculated its projection matrix on the basis of a 13-class life cycle, using the available raw data (B. Casper, personal communication). The matrix of another species (Rouea induta) was already of a $13 \times 13$ dimension. All other species had matrix dimensions below $13 \times 13$ (Calathea ovandensis, Viola frimbriatula, Pterocereus gaumerii, Neobuxbaumia macrocephala, and Thrinax radiata), and here we expanded the number of classes by replicating the matrix elements of the last classes and readjusting the transition probabilities and per capita reproductive contributions to resemble the dynamics described by the original matrices. In all cases, we calculated the primary demographic parameters (life span, population growth rate, stable stage distribution, and elasticities) before and after the readjustment to make sure that the modification did not alter their demographic traits (app. B, in the online edition of the American Naturalist). Nevertheless, we emphasize that our goal is not to study the precise details of these particular species but rather to explore the effects of matrix dimension on the demographic dynamics of realistic exemplars of a range of plant species. Life spans were calculated as described in Forbes and Doak (2004). We calculated the demographic parameters using Matlab, version 7.1 (MathWorks 2001), and PopTools, version 3.0 (Hood 2003).

For every projection matrix, either $13 \times 13$ or of reduced size, we calculated the population growth rate $\lambda$, the stable class distribution $v$, the reproductive output $v$, and the elasticities of the demographic processes involved. We calculated two types of elasticities: matrix-element elasticities and vital-rate elasticities. Matrix-element elasticity measures the proportional change in the population growth rate ($\lambda$) due to a proportional change in a group of matrix cells.
corresponding to a demographic process, while vital-rate elasticity measures proportional changes in $\lambda$ based on proportional changes of the underlying demographic processes that correspond to each projection matrix element, such as survival (Franco and Silvertown 2004).

To examine the effect of matrix dimension on the inferred elasticities (hereafter “matrix-dimension test”), we collapsed the $13 \times 13$-class life cycle into new classes of even size, with the exception of the first class, which was not collapsed. This resulted in matrices of dimensions $7 \times 7$, $5 \times 5$, $4 \times 4$, and $3 \times 3$. We then calculated the dissimilarities between the elasticity structure of the original and the sequentially collapsed matrices. In order to explore how different ways of collapsing the matrices affects differently the elasticities and to establish an optimum criterion (“collapsing-criterion test”), we collapsed the $13 \times 13$ matrices into $5 \times 5$ matrices (the median dimension in demographic studies; fig. A3), using various collapsing criteria. We then calculated the dissimilarity between the elasticities of the original and its respectively collapsed matrices; the collapsing criterion that resulted in the lowest dissimilarity was then established as the optimum criterion. We performed the matrix-dimension test and the collapsing-criterion test for both matrix-element elasticities and vital-rate elasticities. We carried out a principal-component analysis (PCA) on the elasticities of survival, stasis, retrogression, progression, and fecundity to calculate elasticity dissimilarities. The PCA reveals relationships and measures of proximity based on Euclidean distances (Davidson 1975). The comparisons of elasticities based on Euclidean distances were carried out for both matrix-element elasticities and their underlying vital-rate elasticities.

In the collapsing-criterion test, we applied 10 different collapsing criteria to produce collapsed matrices of dimension $5 \times 5$. Briefly, these criteria involved collapsing classes evenly (I), collapsing a large number of classes together but in different positions of the life cycle (II–IV), collapsing irregularly (V–VII), and collapsing so that the mean stasis probabilities (VIII), residence times (IX), and mortality rates (X) were as similar as possible for each new class (see fig. 2 for a detailed description of these criteria). For criterion IX, the class-specific residence times were calculated according to Caswell (2001, p. 112). The last three collapsing criteria (VIII–X) are species specific because of the species’ different demographic life histories (app. B). Similarly, because each species has to pass through a different number of classes before attaining maturity, the criteria that separate nonreproductive and reproductive classes (an approach suggested by Enright et al. [1995]), are also species specific, although there was for each species at least one criterion that fulfilled such a condition (fig. A2).

Finally, we also measured the dissimilarity of the elasticity structures before and after collapsing the population projection matrices of a large database as a function of their growth form and life span. We applied the optimum collapsing algorithm that was identified from the collapsing-criterion test to a set of 66 species’ projection matrices. We calculated the Euclidean distance between the elasticities before and after collapsing each original matrix to a $5 \times 5$ matrix. We then performed linear regressions to study how life span and growth form correlate with these Euclidean distances, using R (R Development Core Team 2009).

Results

The collapsed matrices for the matrix-dimension and collapsing-criterion tests of the nine species had the same or extremely similar asymptotic growth rates and life spans as their respective $13 \times 13$ matrices (app. B), as guaran-
ted by the Hooley algorithm. Their stable class distributions and reproductive outputs were also the same, with the exception of the collapsed classes, whose class distribution and reproductive outputs were equal to the sum of the classes that were merged (not shown).

Matrix-Dimension Test: How Does Matrix Dimension Affect the Estimation of Elasticities?

Matrix dimension affected the matrix-element elasticities consistently across all species in our study for matrices collapsed to dimensions of more than $3 \times 3$. When even collapsing to produce $7 \times 7$, $5 \times 5$, or $4 \times 4$ matrices, the matrix-element elasticities of stasis and fecundity increased, whereas the elasticities of retrogression and progression decreased. The relationships between matrix dimension and inferred elasticities were not always linear (fig. 3). A similar pattern was detected for the vital-rate elasticities, except for Calathea ovandensis (fig. 3A), Pterocephus gaumerii, and Neobuxbaumia macrocephala (app. C, in the online edition of the American Naturalist), where the matrix-element elasticities of stasis, after having reached a maximum value in $5 \times 5$ matrices, decreased for the $4 \times 4$ matrices.

When the matrices were further collapsed to a dimension of $3 \times 3$, an unexpected behavior was detected. In the case of the matrix-element elasticities of the herbaceous C. ovandensis and the palm Thrinax radiata (fig. 3), the elasticity of stasis decreased drastically in the $3 \times 3$ matrices. Nonetheless, this behavior was not consistent across all species. In the case of the vital-rate elasticities, survival decreased from $4 \times 4$ matrices to $3 \times 3$ matrices, not only in C. ovandensis and T. radiata but also in Viola fimbrifolia, N. macrocephala, and Araucaria cunninghamii (app. C). In these five species, the decreases in the vital-rate elasticity of survival (C. ovandensis: $-17\%$; T. radiata: $-3\%$; all other species experienced a less drastic decrease of survival, between $0\%$ and $1\%$), and the increases in fecundity (C. ovandensis: $+435\%$ and $+115\%$; T. radiata: $+317\%$ and $+197\%$, for element matrix and vital-rate elasticities, respectively) were rather steep.

The effects of collapsing matrix dimension on inferred elasticities were typically smaller for vital-rate elasticities than for matrix-element elasticities. In particular, the Euclidean distances between the collapsed and original elasticities were smaller for vital-rate elasticities than for matrix-element elasticities in 29 out of 36 cases (four matrix dimensions $[7 \times 7, 5 \times 5, 4 \times 4, 3 \times 3] \times$ nine species; $P < .001$, binomial test; fig. 4).

Collapsing-Criterion Test: What Is the Best Criterion for Specifying Which Classes to Collapse?

The collapsing criterion that did not modify the first four classes and collapsed classes $k_{13}$ into class $k_5$ (fig. 2B, criterion II) resulted in the smallest dissimilarity between the associated elasticities of the $13 \times 13$ original and $5 \times 5$ collapsed matrices (fig. 5). Such dissimilarity was particularly small for the comparison based on vital-rate elasticities ($\bar{x}_{\text{criteria, II}} = 0.07$).

The criteria that formed $5 \times 5$ matrices such that the stasis probabilities (VIII), residence times (IX), or mortality probabilities (X) of each collapsed class were similar did not rank among the most optimal collapsing criteria. The Euclidean distances ranked the collapsing criteria as follows when based on matrix-element elasticities: II (Euclidean distance $= 0.16$) $<$ IX $<$ V (0.20) $<$ III (0.20) $<$ VIII (0.20) $<$ VI (0.20) $<$ I (0.21) $<$ VII (0.23) $<$ X (0.25) $<$ IV (0.27); the criteria were ranked as follows when based on vital-rate elasticities: II (0.07) $<$ V (0.13) $<$ VIII (0.16) $<$ X (0.16) $<$ IX (0.16) $<$ I (0.17) $<$ III (0.17) $<$ VI (0.18) $<$ VII (0.19) $<$ IV (0.27); see figure 2B.

The collapsing criteria that separated nonreproductive and reproductive classes (fig. A2) did not systematically result in lower dissimilarities between the elasticity structures of the original and the collapsed matrices. For instance, for Cryptantha flav a and C. ovandensis, all collapsing criteria separated nonreproductive and reproductive classes, but the criterion that collapsed classes $k_{13}$ (fig. 2B, criterion II) performed the best, in that the dissimilarity between the elasticities of the original and collapsed matrices was lowest. A cursory evaluation of the results in figure 5, contrasted with figure A2, would suggest that this criterion (criterion II; fig. 2B) is the optimum one because it splits nonreproductive and reproductive classes in five of the nine species in our study. However, the same is true of the criterion where classes $k_{13}$ were collapsed (criterion VII; fig. 2B), and yet it performed relatively poorly. Furthermore, the criterion that collapsed only the last classes into a new class (criterion II; fig. 2B) was the best approach even for those species in which this criterion did not separate reproductive and nonreproductive classes (e.g., P. gaumerii, N. macrocephala, T. radiata, and A. cunninghamii).

We found that collapsing matrices had a larger effect on inferred elasticities for shorter-lived species. While the linear regression between life-span and dissimilarity measurements of the nine study species was not significant for matrix-element elasticities ($t_{1, s} = 6.14, P = .104$) and was borderline significant for vital-rate elasticities ($t_{1, s} = 5.15, P = .057$), this relationship was highly significant when a more extensive study of 66 species was used, in which their projection matrices had been collapsed to a
Figure 3: Effects of matrix dimension on the elasticity of vital rate– and matrix element–based demographic processes for three of the nine species our study: Calathea ovandensis (A), Ulex minor (B), and Thrinax radiata (C). In each case, the original $13 \times 13$ projection matrix was collapsed by combining two, three, four, or six adjacent classes, to produce $7 \times 7$, $5 \times 5$, $4 \times 4$, and $3 \times 3$ matrices, respectively. Retrogression vital-rate elasticities are represented as absolute values to fit into the positive axis, but they are negative.
The American Naturalist

Figure 4: Euclidean distance (\(\bar{x}_{\text{dimension}}\)) between the elasticities of the original 13 \(\times\) 13 matrix and the elasticities of the 7 \(\times\) 7, 5 \(\times\) 5, 4 \(\times\) 4, and 3 \(\times\) 3 matrices for each species (using criteria described in fig. 2A). Species are ranked from top to bottom by increasing life span.

\[5 \times 5\text{ dimension via the previously established optimum criterion (criterion II; fig. 2B; } t_{1,40} = 18.49, \ P < .001, \ R^2 = 22.4\%; \text{ fig. 6). Furthermore, the correlation between dissimilarity and life span was growth form specific (} F_{5,60} = 7.45, \ P < .001; \text{ growth form as covariate: } F_{5,60} = 5.02, \ P < .001), \text{ and it was primarily driven by the significant life span–dissimilarity correlation of herbaceous perennials (} t_{1,40} = 17.95, \ P < .001); \text{ this correlation was not significant for succulent, shrub, palm, and tree species.}

Discussion

Our study offers insights into how and why the dimension of projection matrices influences the estimation of fundamental demographic parameters. Using an overlooked algorithm (Hooley 2000) for collapsing matrix dimension without relying on raw field data, we have (i) established collapsing criteria better than those previously suggested (Enright et al. 1995); (ii) found that the effect of matrix dimension on the associated elasticity structure is often nonmonotonic and not always lower on vital-rate elasticities than on matrix-element elasticities, as previously reported (Zuidema 2000); (iii) observed unexpected behavior for very small matrices (e.g., 3 \(\times\) 3) that allows us to establish a dimension threshold for comparative plant demographic studies; and (iv) found a negative relationship between life span and the robustness of elasticities to matrix dimension in herbaceous perennials.

Our results indicate that collapsing a population projection matrix by similar residence times leads to a large difference in elasticities between the original and collapsed matrices, contrary to the suggestion of Enright et al. (1995). Specifically, we found that for all species in this study, keeping the first life-cycle classes unaltered (criterion II; fig. 2B) resulted in the lowest effect on the inferred elasticities. This likely occurs because individuals of younger/smaller/less developed classes are usually more susceptible to changes in the environment and thus typically exhibit distinct, class-specific vital rates (Harper 1977). These conclusions are further supported by the fact that while the criterion that grouped the first classes and left the last four classes unaltered (IV, the opposite of II; fig. 2B) was the worst performer, the criterion where the first classes were collapsed only two at a time, in a form very similar to criterion II, always ranked in the second position.

Our results are also supported by a study that suggests ways to save time, resources, and field effort while constructing projection matrices from small populations of threatened species (Ramula and Lehtilä 2005).

Our findings suggest that fecundity or age at first reproduction are not the most important biological pro-
Figure 6: Euclidean distance between the elasticities of the original and
the 5 × 5 collapsed matrices (using collapsing criterion II in fig. 2B) as
a function of life span for 66 plant species: 38 herbaceous perennial, 6
succulent, 6 shrub, 7 palm, and 9 tree species.

cesses on which to base the classes chosen for matrix
construction and collapsing. Enright et al. (1995) rec-
commended against merging nonreproductive and repro-
ductive classes because trade-offs between reproduction,
growth, and survival would result in distinctive demo-
graphic dynamics in both life-cycle stages. However, we
show that collapsing criteria that violate this suggestion
can produce more robust elasticities than collapsing cri-
teria that differentiate nonreproductive from reproductive
classes.

We also found some inconsistencies with previous works
on the robustness of vital-rate versus matrix-element elas-
ticities to varying matrix dimension. Zuidema and Zagt
(in Zuidema 2000) studied the effect of matrix dimension
on inferred elasticities and found that progression and retrogression matrix-element elasticities decreased with in-
creasing dimension, consistent with our results. However,
they also reported that the vital-rate elasticities were more
robust to varying matrix dimension than their matrix-
element counterparts. Our results generally agree with
theirs, but in 20% of the cases (n = 9 species) in our
study, vital-rate elasticities were more robust than matrix-
element elasticities to changes in matrix dimension. Nev-
evertheless, vital-rate elasticities seem more relevant for
the study of ecological patterns because they reflect indepen-
dent demographic processes and allow for the separation
of the survival vital rates (e.g., Bruna et al. 2009).

Although the collapsing algorithm we have analyzed
here has the virtue of preserving population growth rates,
stable class distributions, and reproductive output, this
algorithm assumes demographic stability. In an ideal sce-
nario, field censuses would be extensively temporarily rep-
licated so that they comprise all biotic and abiotic phe-
nomena that are inherent to the species’ life cycle. Doing
so would approximate the mean observed class distribu-
tion to the stable class distribution. We suggest that class
distributions be calculated and compared to the stable class
distribution as a prerequisite to deciding whether to in-
corporate a given annual transition for later interspecific
comparison. Applying methods to do so (Keyfitz’s Δ, in
Caswell 2001, p. 101), we have found evidence that Hooley’s algorithm provides reliable collapsed projection
matrices for at least one population subjected to extreme
weather events (app. D). We also recommend averaging
the control transition matrices for as many sites and years
as there are data available to reduce the effect of abnormal
biotic and abiotic fluctuations.

Intuition behind the Impact of Matrix Dimension
on Elasticities

Although we cannot provide a mechanistic explanation for
all the specific details of our results on the nine plant
species, there is a simple intuition for the general effects
of collapsing dimension on associated elasticities. The elas-
ticities of fecundity tend to increase as matrix dimension
is reduced because the merging of nonreproductive and
reproductive classes inevitably makes reproductive status
attainable in a shorter period of time by the faster-growing
individuals in the population (Enright et al. 1995). Faster
demographic processes have been shown to have greater
elasticities (Zuidema et al. 2009). Similarly, the elasticity
of stasis also increases because, with fewer classes in a
collapsed matrix, the amount of stasis is again augmented.
Since stasis elasticity increases while the overall population
growth rate λ is kept constant, the elasticities of retro-
gression and progression must decrease. Although there is
some variation across species and some aberrant behavior
at very small dimensions, this simple intuition explains
most of the general patterns we have observed. We at-
tribute the unexpected increase in matrix-element pro-
gression elasticities in small matrices of some herbaceous
perennials and succulent species, and the subsequent de-
crease in stasis elasticity, to the high degree of phenotypic
plasticity of these growth forms and their fast demographic
dynamics (Chien and Zuidema 2006). Furthermore, stud-
ies of herbaceous perennials often suffer from small sample
sizes in large size classes.

Guidelines for Comparative Demographic Studies

Our results on the relationship between matrix dimension
and inferred demographic properties have important im-
portations for comparative studies. We have shown that
the apparent importance of fecundity, stasis, progression,
Acknowledgments

We thank B. Casper, M. Franco, B. Waring, and P. Zuidema for valuable comments on the manuscript. Thanks are also due to R. Lucas and B. Casper, who made available the raw demographic data for Cryptantha flava. The manuscript also greatly benefited from useful comments from two reviewers. J.B.P. acknowledges support from the Burroughs Wellcome Fund, the David and Lucile Packard Foundation, the James S. McDonnell Foundation, and the Alfred P. Sloan Foundation. R.S.-G. was supported by a Dissertation Research Fellowship of the University of Pennsylvania.

Literature Cited


Ehrlén, J., K. Syrjanen, R. Leimu, M. B. Garcia, and K. Lehtila. 2005,


Cryptantha flava (Boraginaceae), in full bloom in Utah, frequently undergoes drastic changes in size between years. Photograph by Roberto Salguero-Gómez.