

Matrix Dimensions Bias Demographic Inferences: Implications for Comparative Plant Demography

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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 7×7 , 5×5 , 4×4 , and 3×3 matrices and (ii) into 5×5 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 con-

firmed 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 (Lefkovich 1965) or a mixture of these variables (e.g., Ehrlén 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., Lefkovich 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

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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; Shimatani 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 *Ari-*

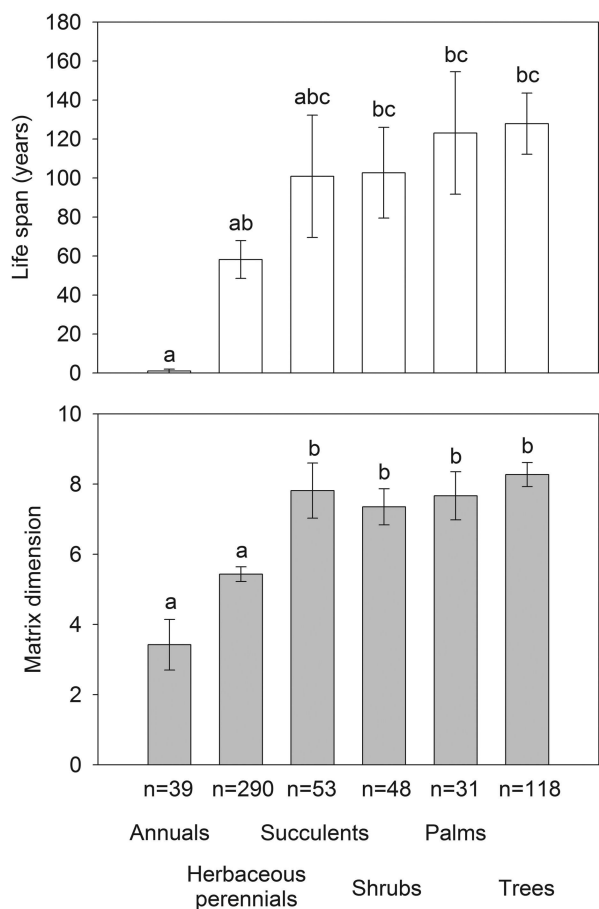


Figure 1: Life span (mean \pm SE, gray bars) and matrix dimension (mean \pm SE, white bars) by growth form, collated from 475 published projection matrices of plant species. Letters indicate significant differences among groups (Tukey-Kramer HSD test).

saema 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 interest in comparative studies (Silvertown et al. 2001). We examine an overlooked algorithm that allows the reduction of matrix dimension without using raw data and without altering the inferred population growth rate, reproductive output, or stable class distribution (Hooley 2000). We apply this algorithm to the projection matrices of nine plant species with different growth forms and longevities in order to (i) study the dissimilarities in the inferred elasticities of demographic processes in collapsed matrices and (ii) evaluate Enright et al.'s (1995) collapsing criteria, as well as (iii) propose alternative collapsing criteria that minimize the differences in elasticity values between the original and the collapsed matrices. We demonstrate that matrix dimension affects the estimation of all parameters of interest, particularly in herbaceous perennial species, and that such relationships are not always monotonic. We discuss the limitations of Hooley's (2000) algorithm regarding stable stage distribution of the population. Finally, we conclude with some suggestions for implementing meaningful comparative demographic studies based on projection matrices.

Implementation of the Collapsing Algorithm in Size- and Developmental Stage-Based Models

The algorithm of Hooley (2000) describes a method to reduce 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 regress (e.g., Bruna and Oli 2005; Lucas et al. 2008).

Briefly, three steps must be taken to reduce a projection matrix of n dimensions, $\mathbf{A}_{n \times n}$, to one of m dimensions, $\mathbf{C}_{m \times m}$: (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 $\mathbf{A}_{n \times n}$ into a new class k' in the collapsed matrix $\mathbf{C}_{(n-1) \times (n-1)}$, we first add the matrix elements $a_{k,j} + a_{k+1,j}$ along the k and $k + 1$ rows. The resulting intermediate matrix $\mathbf{B}_{(n-1) \times n}$ 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' ;

abrupt changes in size and development, typically expressed by some plant species, may lead individuals to leap over several classes over one time interval. For age-, size-, or developmental stage-based models, the collapsed vector that can be obtained from the intermediate matrix $\mathbf{B}_{(n-1) \times n}$ will report only the total number of individuals in the collapsed class and not the breakdown in the number of individuals coming from each class involved. Thus, in order to collapse the columns, we must assume that the population was close to equilibrium during the field censuses. In this case, it is possible to take the elements of the stable class distribution (w) as the weighting factors to construct the new collapsed class. Consequently, we define the weighting factors $r_k = w_k / (w_k + w_{k+1})$ and $r_{k+1} = w_{k+1} / (w_k + w_{k+1})$, which are the proportions of the merged classes that we expect to form from the original class k and class $k + 1$, respectively. Column k' in the collapsed matrix \mathbf{C} is made of entries that are the weighted averages, using weighting factors r_k and r_{k+1} , respectively, of columns k and $k + 1$ of the partially collapsed matrix \mathbf{B} . The stable class distribution is an intrinsic parameter of the projection matrix that can be obtained with a two-line command in Matlab: the right eigenvector associated with the dominant eigenvalue. This knowledge regarding the stable class distribution is critical because it can free us from needing the raw field data to be able to quantify matrix entries in collapsed matrices (app. D, in the online edition of the *American Naturalist*, describes whether our techniques are robust when the assumption of stable equilibrium is violated).

Matrix Algorithm Implementation

Mechanistically, the collapsing algorithm can be applied to almost any (see “Discussion”) projection matrix following the calculation:

$$\mathbf{P}_{m \times n} \cdot \mathbf{A}_{n \times n} \cdot \mathbf{Q}_{n \times m} = \mathbf{C}_{m \times m}, \tag{1}$$

where \mathbf{P} is a matrix of $m \times n$ dimensions containing dummy holders (“1”) on the elements that are to be collapsed ($a_{k',k}$ and $a_{k',k+1}$), with the rest of the matrix being formed by identity submatrices \mathbf{I} ,

$$\mathbf{P} = \begin{bmatrix} \mathbf{I}_{k-1} & 0 & 0 & 0 \\ 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & \mathbf{I}_{n-k-1} \end{bmatrix}_{m \times n}, \tag{2}$$

and \mathbf{Q} is a matrix of $n \times m$ dimensions that contains the weighting factors for the elements in the columns k and $k + 1$ that are to be collapsed, with the rest of the matrix elements characterized by identity submatrices,

$$\mathbf{Q} = \begin{bmatrix} \mathbf{I}_{k-1} & 0 & 0 \\ 0 & r_k & 0 \\ 0 & r_{k+1} & 0 \\ 0 & 0 & \mathbf{I}_{n-k-1} \end{bmatrix}_{n \times m}. \tag{3}$$

This algorithm also allows us to collapse multiple classes into a single class or into fewer, separated classes in just one step, which saves a significant amount of time when dealing with projection matrices of high dimension in large databases. The steps when dealing with multiple collapses are the same: normalize the elements on the merging columns by calculating the weighted average of the appropriate 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

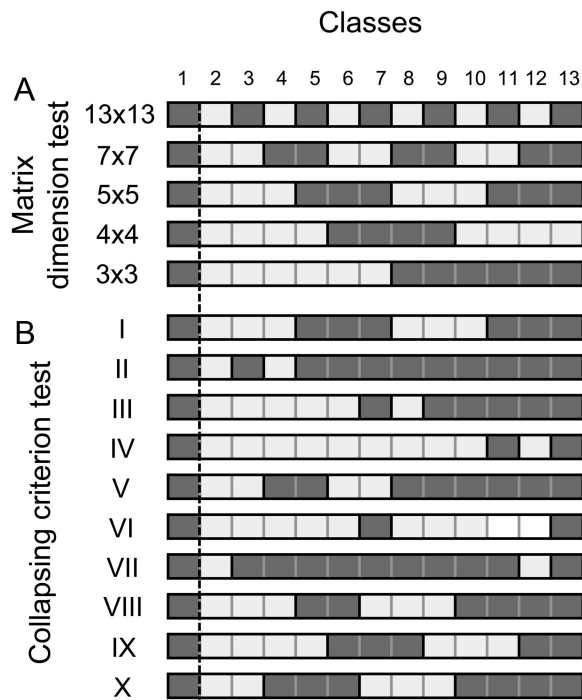


Figure 2: Collapsing approaches used to reduce the dimensions of 13×13 projection matrices. Adjacent classes represented with the same color were collapsed. The first class was kept unaltered because it contains reproduction probabilities that are not to be merged with transition probabilities. **A,** The original 13×13 matrix was collapsed evenly into 7×7 , 5×5 , 4×4 and 3×3 matrices to study the effect of decreasing matrix dimension on its elasticity structure. **B,** The original 13×13 matrix was collapsed into 5×5 matrices in different ways to evaluate the effect of several collapsing criteria on the matrix elasticity structure. Criteria are (I) collapsing an even number of classes, resulting in the structure {1, 2–4, 5–7, 8–10, 11–13}; (II) leaving unaltered the first three {1, 2, 3, 4, 5–13}; (III) the middle two {1, 2–6, 7, 8, 9–13}, or (IV) the last three classes {1, 2–10, 11, 12, 13}; (V) collapsing every two classes for the first six classes and collapsing the remaining classes into a large class {1, 2–3, 4–5, 6–7, 8–13}; (VI) leaving unaltered the middle and last class and collapsing the remaining classes {1, 2–6, 7, 8–12, 13}; (VII) collapsing the central classes and leaving unaltered the first and last two classes {1, 2, 3–11, 12, 13}; and collapsing classes so that the newly formed classes will keep their respective stasis probabilities (VIII), residence times (IX), and mortality probabilities (X) similar for each new class. Collapsing criteria VIII–X are species specific (the example here presented is for *Cryptantha flava*; fig. A2, in the online edition of the *American Naturalist*).

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 matrix dimensions are typically too small for us to implement any reduction with a meaningful outcome (fig. 1).

We chose an original, uncollapsed dimension of 13×13 in order to study the dissimilarities of elasticities in collapsed matrices, starting from a matrix of a dimension that

falls within the range typically reported in the literature. For collapsing purposes, we treated the original 13×13 matrices as $(1 + 12) \times (1 + 12)$ matrices in which the first 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 $a_{1i} \in (0, \infty)$ (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 13×13 . For those species whose original dimensions were higher than 13×13 (*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 (*Rourea induta*) was already of a 13×13 dimension. All other species had matrix dimensions below 13×13 (*Calathea ovandensis*, *Viola frimbriatula*, *Pterocereus gaudereri*, *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 Forbis 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 13×13 or of reduced size, we calculated the population growth rate λ , the stable class distribution w , 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 (λ) due to a proportional change in a group of matrix cells

Table 1: Description of species used in this study, ranked by life span

Species	Family	Architectural type	Life span (years)	Population growth rate (λ)	Matrix dimension	Source
<i>Cryptantha flava</i>	Boraginaceae	Herbaceous	14	.86	13 ^a	Lucas et al. 2008
<i>Calathea ovandensis</i>	Marantaceae	Herbaceous	20	.99	8	Horvitz and Schemske 1995
<i>Ulex minor</i>	Fabaceae	Shrub	21	1.31	16	Stokes et al. 2004
<i>Viola frimbriatula</i>	Violaceae	Herbaceous	23	1.22	11	Solbrig et al. 1988
<i>Pterocereus gaumerii</i>	Cactaceae	Succulent	31	1.00	10	Méndez et al. 2004
<i>Neobuxbaumia macrocephala</i>	Cactaceae	Succulent	41	1.03	10	Esparza-Olguín et al. 2005
<i>Rourea induta</i>	Connaraceae	Shrub	52	.99	13	Hoffmann 1999
<i>Thrinax radiata</i>	Arecaceae	Palm	136	1.13	9	Olmsted and Alvarez-Buylla 1995
<i>Araucaria cunninghamii</i>	Araucariaceae	Tree	256	1.02	17	Enright and Ogden 1979

^a Original matrix dimensions in the publication were 7×7 , but we used the raw data to recalculate the matrix on the basis of a life cycle of 13 stages.

corresponding to a demographic process, while vital-rate elasticity measures proportional changes in λ 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 13×13 -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 7×7 , 5×5 , 4×4 , and 3×3 . 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 13×13 matrices into 5×5 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 5×5 . 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 5×5 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 13×13 matrices (app. B), as guaran-

teed 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 3×3 . When even collapsing to produce 7×7 , 5×5 , or 4×4 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), *Pterocereus 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 5×5 matrices, decreased for the 4×4 matrices.

When the matrices were further collapsed to a dimension of 3×3 , 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 3×3 matrices. Nonetheless, this behavior was not consistent across all species. In the case of the vital-rate elasticities, survival decreased from 4×4 matrices to 3×3 matrices, not only in *C. ovandensis* and *T. radiata* but also in *Viola fimbriatula*, *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 [7×7 , 5×5 , 4×4 , 3×3] \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_4-k_{13} into class $k_{3'}$ (fig. 2B, criterion II) resulted in the smallest dissimilarity between the associated elasticities of the 13×13 original and 5×5 collapsed matrices (fig. 5). Such dissimilarity was particularly small for the comparison based on vital-rate elasticities ($\bar{x}_{\text{criterion II}} = 0.07$).

The criteria that formed 5×5 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) < V (0.17) < IX (0.20) < III (0.20) < VIII (0.20) < VI (0.20) < I (0.21) < VII (0.23) < X (0.23) < 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 flava* and *C. ovandensis*, all collapsing criteria separated nonreproductive and reproductive classes, but the criterion that collapsed classes k_5-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_3-k_{11} 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 ($t_{1,8} = 6.14$, $P = .104$) and was borderline significant for vital-rate elasticities ($t_{1,8} = 5.15$, $P = .057$), 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

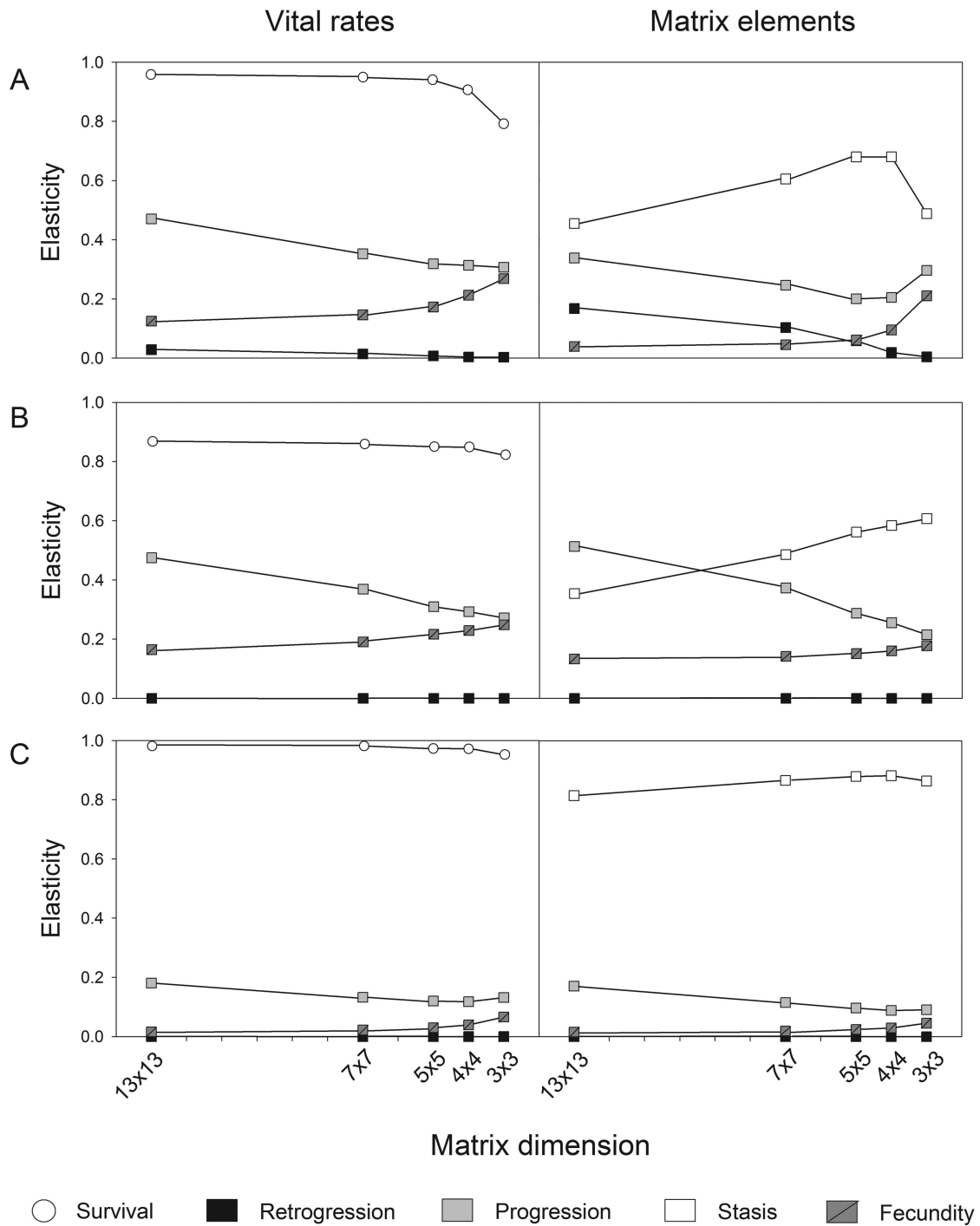


Figure 3: Effects of matrix dimension on the elasticity of vital rate- and matrix element-based demographic processes for three of the nine species our study: *Calathea ovoidensis* (A), *Ulex minor* (B), and *Thrinax radiata* (C). In each case, the original 13×13 projection matrix was collapsed by combining two, three, four, or six adjacent classes, to produced 7×7 , 5×5 , 4×4 , and 3×3 matrices, respectively. Retrogression vital-rate elasticities are represented as absolute values to fit into the positive axis, but they are negative.

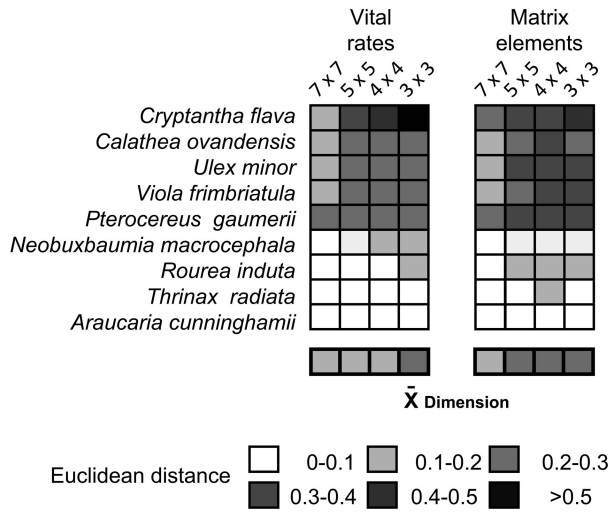


Figure 4: Euclidean distance ($\bar{x}_{\text{dimension}}$) between the elasticities of the original 13×13 matrix and the elasticities of the 7×7 , 5×5 , 4×4 , and 3×3 matrices for each species (using criteria described in fig. 2A). Species are ranked from top to bottom by increasing life span.

5×5 dimension via the previously established optimum criterion (criterion II; fig. 2B; $t_{1,64} = 18.49$, $P < .001$, $R^2 = 22.4\%$; fig. 6). Furthermore, the correlation between dissimilarity and life span was growth form specific ($F_{5,60} = 7.45$, $P < .001$; growth form as covariate: $F_{4,60} = 5.02$, $P < .001$), and it was primarily driven by the significant life span–dissimilarity correlation of herbaceous perennials ($t_{1,36} = 17.95$, $P < .001$); this correlation was non-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., 3×3) 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-

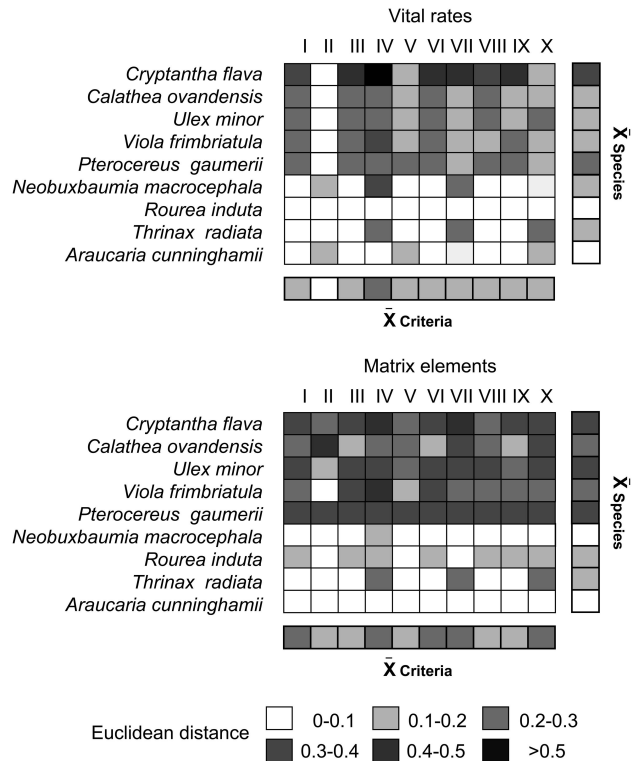


Figure 5: Euclidean distance between the elasticities of the original 13×13 matrix and the elasticities of the 5×5 collapsed matrices obtained with the various collapsing criteria described in figure 2B. Overall Euclidean distances are averaged per species (\bar{x}_{species}) and per criterion ($\bar{x}_{\text{criteria}}$).

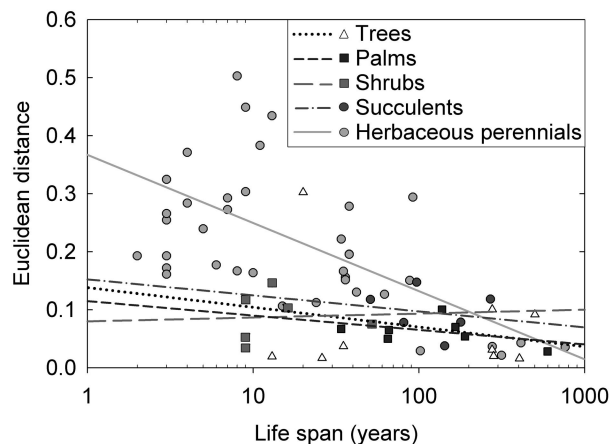


Figure 6: Euclidean distance between the elasticities of the original and the 5×5 collapsed matrices (using collapsing criterion II in fig. 2B) as a function of life span for 66 plant species: 38 herbaceous perennial, 6 succulent, 6 shrub, 7 palm, and 9 tree species.

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

We also found some inconsistencies with previous works on the robustness of vital-rate versus matrix-element elasticities 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 increasing 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. Nevertheless, vital-rate elasticities seem more relevant for the study of ecological patterns because they reflect independent 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 scenario, field censuses would be extensively temporarily rep-

licated so that they comprise all biotic and abiotic phenomena that are inherent to the species' life cycle. Doing so would approximate the mean observed class distribution 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 incorporate 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 elasticities 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 retrogression 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 attribute the unexpected increase in matrix-element progression elasticities in small matrices of some herbaceous perennials and succulent species, and the subsequent decrease in stasis elasticity, to the high degree of phenotypic plasticity of these growth forms and their fast demographic dynamics (Chien and Zuidema 2006). Furthermore, studies 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 implications for comparative studies. We have shown that the apparent importance of fecundity, stasis, progression,

retrogression, and survival is highly sensitive to the dimensions of the projection matrix. Consequently, demographic comparisons of species based on elasticities must carefully account for the varying matrix dimensions.

For comparative work based on published projection matrices, we suggest two alternatives: either account for matrix dimension with a nonlinear analysis or collapse matrices into an equal dimension, at least for the herbaceous perennials, whose elasticities are most sensitive to matrix dimension (fig. 6). Surprisingly, most recent comparative studies using projection matrices have not used matrix dimension as a covariate (Franco and Silvertown 2004; Bruna et al. 2009). On the other hand, a trade-off emerges between the matrix dimension cutoff and how many studies to include for comparative purposes because (i) matrix collapsing will mean that species with fairly dissimilar traits will be treated as equals from a demographic standpoint (e.g., Crouse et al. 1987; Cochran and Ellner 1992); (ii) decreasing dimension, regardless of the collapsing criteria, will tend to artificially promote the apparent importance of stasis and fecundity, compared to progression and retrogression; and (iii) an extreme decrease in the number of classes will not allow for the study of processes such as class-specific mortality rates, time to maturation, senescence, clonal growth, or vegetative dormancy. In the extreme, a very small matrix will inevitably merge transition probabilities for stasis, progression, and/or retrogression $p_{ij} \in (0, 1)$ with sexual and/or clonal reproduction $a_i \in (0, \infty)$, which makes little biological sense. Based on the results of our matrix-dimension test, in which the elasticities exhibited unexpected behaviors for dimensions smaller than 4, we suggest dimensions of at least 5 in complex and 4 in simple life cycles for comparative studies, despite the fact that this rules out a large number of published projection matrices with smaller dimensions ($n = 107$; R. Salguero-Gómez, unpublished data) for demographic comparisons. Finally, our results suggest an optimum criterion for choosing which stages to collapse in a projection matrix (criterion II; fig. 2B): keeping the first few life-cycle classes unaltered and collapsing all other older/larger/more developed classes, regardless of whether that means merging nonreproductive and reproductive classes or keeps the residence times constant in the newly collapsed classes.

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