Buffering of Life Histories against Environmental Stochasticity: Accounting for a Spurious Correlation between the Variabilities of Vital Rates and Their Contributions to Fitness

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ABSTRACT: Life-history theory predicts vital rates that on average make large contributions to the annual multiplication rate of a lineage should be highly buffered against environmental variability. This prediction has been tested by looking for a negative correlation between the sensitivities (or elasticities) of the elements in a projection matrix and their variances (or coefficients of variation). Here, we show by constructing random matrices that a spurious negative correlation exists between the sensitivities and variances, and between the elasticities and coefficients of variation, of matrix elements. This spurious correlation arises in part because size transition probabilities, which are bounded by 0 and 1, have a limit to their variability that often does not apply to matrix elements representing reproduction. We advocate an alternative analysis based on the underlying vital rates (not the matrix elements) that accounts for the inherent limit to the variability of zero-to-one vital rates, corrects for sampling variation, and tests for a declining upper limit to variability as a vital rate's fitness contribution increases. Applying this analysis to demographic data from five populations of the alpine cushion plant *Silene acaulis*, we provide evidence of stronger buffering in the vital rates that most influence fitness.

Keywords: demographic buffering, elasticity, environmental stochasticity, sensitivity, *Silene acaulis*.

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Life-history theory consistently predicts that temporal variability in the annual multiplication rate of a genotype will reduce its long-term fitness because long-term fitness is best measured by the geometric, not the arithmetic, mean annual multiplication rate and because temporal variability reduces the geometric mean (Lewontin and Cohen 1969; Gillespie 1974). For perennial organisms, variability in the annual multiplication rate arises from variability in the vital rates (i.e., the rates of survival, reproduction, and growth of different-sized or -aged individuals). However, different vital rates typically make different contributions to the annual multiplication rate. Consequently, the same amount of temporal variability in two different vital rates will not generally reduce long-term fitness to the same degree. The growth rate of a lineage in a randomly varying environment is typically modeled using stochastic projection matrices, the elements of which are functions of the underlying (and temporally varying) vital rates (Caswell 2001). Tuljapurkar (1982) showed that for a lineage described by a stochastic projection matrix, the log of the long-term annual multiplication rate, $\log \lambda_s$, is approximately

$$\log \lambda_s \approx \log \bar{\lambda}_1 - \frac{1}{2\bar{\lambda}_1^2} \sum_{i,j} \mathrm{Var}\,(a_{ij}) S_{ij}^2 - \phi, \qquad (1)$$

where $\bar{\lambda}_1$ is the asymptotic annual multiplication rate predicted by the mean matrix, $\bar{a}_{ij}$ and $\mathrm{Var}\,(a_{ij})$ are the mean and variance of the element in row i and column j of the matrix, and ϕ is a term that involves the covariances between different matrix elements. According to equation (1), temporal variability in matrix element a_{ij} (as measured by $\mathrm{Var}\,(a_{ij})$) reduces long-term fitness only in proportion to $S_{ij} = \partial \bar{\lambda}_1 / \partial \bar{a}_{ij}$, the so-called sensitivity of the annual multiplication rate of the mean matrix to changes in the mean of element a_{ij} (Caswell 1978).

Because the product of the variance and the (squared)

sensitivity of a matrix element appears as a negative term in equation (1), Pfister (1998) predicted that natural selection should favor traits that buffer those matrix elements with the highest sensitivities against temporal environmental variability. More specifically, she predicted that there should be a negative correlation between the variance of a matrix element and its sensitivity. However, Pfister (1998) also noted that as matrix elements representing transitions among size classes are bounded by 0 and 1, whereas elements representing reproduction may be substantially >1, the variances of these different matrix elements may not be directly comparable. Moreover, sensitivities measure the absolute change in the annual multiplication rate in response to an absolute change in a matrix element, but a given absolute change in a matrix element representing survival or growth may be less likely to occur than would the same absolute change in a matrix element representing reproduction, which can vary over a wider range of values (Caswell 2001).

In recognition of these potential limitations of comparing variances and sensitivities, Pfister (1998) also tested for a negative correlation between CV_{ij}, the coefficient of variation (i.e., the standard deviation divided by the mean) of matrix element a_{ij}, and its elasticity, E_{ij}. Elasticities gauge the proportional change in the annual multiplication rate in response to proportional changes in matrix elements and provide relative measures of the influence on the multiplication rate of changes in different matrix elements (de Kroon et al. 1986). Similarly, the coefficient of variation measures the variability of a matrix element relative to its mean. Because $\text{Var}(a_{ij}) = \bar{a}_{ij}^2 CV_{ij}^2$ and $S_{ij}^2 = \bar{\lambda}_1^2 E_{ij}^2/\bar{a}_{ij}^2$, equation (1) can be rewritten as

$$\log \lambda_s \approx \log \bar{\lambda}_1 - \frac{1}{2}\sum_{i,j} CV_{ij}^2 E_{ij}^2 - \phi, \qquad (2)$$

which leads to the prediction that matrix elements with high elasticities should have low coefficients of variation. Using published projection matrices, Pfister (1998) found that both the correlations between the variances and sensitivities and the correlations between the coefficients of variation and the elasticities of matrix elements were skewed toward negative values, as her hypothesis predicted.

However, as we show here, use of the coefficient of variation still does not make levels of variability in different types of matrix elements directly comparable. Moreover, by constructing stochastic matrices at random, we show that spurious negative correlations exist between the coefficients of variation and the elasticities of matrix elements and between their variances and sensitivities, and we explain why these spurious correlations arise. Consequently, a negative correlation between the variances and sensitiv-

ities or between the elasticities and coefficients of variation of matrix elements cannot be unambiguously interpreted as the result of natural selection favoring life-history traits that buffer highly influential demographic processes against environmental variability.

To get around these spurious correlations, we advocate an alternative analysis based on the underlying vital rates themselves rather than the amalgamated matrix elements. We illustrate this analysis using demographic data from five populations of the long-lived alpine cushion plant *Silene acaulis* (Morris and Doak 1998, 2004). Using this analysis, we present stronger evidence that the vital rates with the most influence on the annual multiplication rate are relatively less variable over time.

Apart from avoiding the spurious correlations, there are two more reasons to base a test for demographic buffering on vital rates rather than matrix elements. First, a single vital rate often contributes to several matrix elements, and variation in the vital rates (e.g., the survival and growth probabilities) generates variation in the matrix elements (e.g., the probability an individual undergoes a transition to the next largest size class). Buffering of a survival rate would simultaneously buffer all of the matrix elements influenced by that survival rate. Treating matrix elements as independent when testing for buffering is not justified (but is often the only available option when the amalgamated matrix elements, and not the underlying vital rate values, are the only data published, which was true for most of the demographic studies Pfister [1998] examined). Second, raw estimates of the environmental variability in demographic rates (either vital rates or matrix elements) are typically inflated by sampling variation (Nichols et al. 1996; Gould and Nichols 1998; Kendall 1998; White 2000). Limited sample size would cause estimates of a demographic rate to vary from year to year even if the true rate were constant. Because our goal in assessing buffering is to obtain as accurate an estimate as possible of the environmentally driven variation in demographic rates, we should first discount raw estimates of variability for sampling variation. Existing methods to do so focus on the vital rates (Nichols et al. 1996; Gould and Nichols 1998; Kendall 1998; White 2000).

Finally, we note that a negative rank correlation between the coefficients of variation and the elasticities of vital rates (or between their variances and sensitivities), the statistical indicator chosen by Pfister (1998), is only one way that demographic buffering might manifest itself. Testing for a negative rank correlation presupposes both that highly influential demographic rates will have low variabilities and that low influence rates will be highly variable. However, while it is clear that high levels of variability in highly influential rates should be detrimental to long-term fitness, there is no reason to expect that low variation in demo-

graphic rates with little effect on fitness should be selectively disfavored. In our view, it is more appropriate to test for an upper limit to the levels of variability of demographic rates that declines as their average influence on fitness increases. The existence of a declining upper limit can be evaluated using quantile regression (Cade et al. 1999). In this article, we test for both of these possible manifestations of demographic buffering by using data for *S. acaulis*.

Neither Variance nor Coefficient of Variation Measures Variabilities of Different Types of Matrix Elements on Same Scale

Although the coefficient of variation does measure the variability of each matrix element relative to its mean, both the variance and the coefficient of variation will often be more severely bounded for zero-to-one matrix elements (e.g., those describing transition probabilities among size classes) than they will be for matrix elements that represent reproduction, which often exceed 1. Reproduction elements with a high mean can also have a high temporal variance (and thus a high coefficient of variation). In contrast, zero-to-one matrix elements cannot have both a high mean and a high variance. Perhaps the most flexible and biologically reasonable probability distribution to represent zero-to-one random variables is the β distribution. It is well known that the variance of the β distribution is constrained. If p is the expected value of the β random variable X, the largest variance occurs when the variable takes on the value 1 a proportion p of the time and the value 0 a proportion $1 - p$ of the time (note that the expected value of X is $E\{X\} = 1 \times p + 0 \times (1 - p) = p$). The maximum variance of X is then

$$V_{\max}\{X\} = (0 - p)^2(1 - p) + (1 - p)^2 p = p(1 - p), \quad (3)$$

which is 0 when p is 0 or 1 and attains a maximum of 0.25 when $p = 0.5$ (fig. 1). Therefore, the maximum of the coefficient of variation is

$$\text{CV}_{\max}\{X\} = \frac{\sqrt{V_{\max}\{X\}}}{E\{X\}} = \frac{\sqrt{p(1 - p)}}{p} = \sqrt{\frac{1 - p}{p}}. \quad (4)$$

As p approaches 0, $\text{CV}_{\max}\{X\}$ approaches infinity, and when $p = 1$, $\text{CV}_{\max}\{X\} = 0$ (fig. 1). Thus, both the variance and the coefficient of variation of a zero-to-one matrix element cannot be high if its mean is high.

Because of the upper limit in equation (4), even the coefficient of variation does not place the variabilities of class transition and reproduction elements on the same measurement scale. Another worrisome feature of the co-
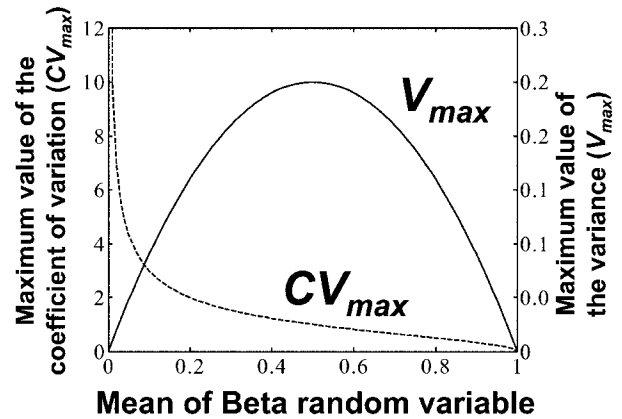

Figure 1: Maximum values of the coefficient of variation and the variance of a β random variable as functions of the mean.

efficient of variation for a zero-to-one matrix element is the fact that it must approach 0 as the mean approaches 1 (fig. 1). For long-lived, slow-growing organisms, the matrix elements with the highest elasticities are typically those that represent stasis (i.e., survival without growth) of individuals in the larger or older classes (Crouse et al. 1987; Silvertown et al. 1993; Doak et al. 1994; Pfister 1998; Heppell et al. 2000; Saether and Bakke 2000; Crone 2001; Oli and Dobson 2003). For such a life history, the means of the stasis elements are often close to 1 and cannot have a high coefficient of variation. These elements have high elasticities in part because, by definition, the elasticity of a matrix element is an increasing function of its mean (specifically, it is the mean multiplied by the sensitivity and divided by the mean annual multiplication rate). Because the elasticity is directly proportional to the mean but the coefficient of variation is inversely proportional to the mean (fig. 1), we expect the elasticities and the coefficients of variation of zero-to-one matrix elements to be negatively correlated if their means differ.

Unlike elasticities, the sensitivity of a matrix element is not an explicit function of the mean (although changing the mean of any matrix element will change all of the sensitivities in complex ways; Caswell 1996). Moreover, the variance of a zero-to-one matrix element is not a strictly decreasing function of the mean (fig. 1). Therefore, in general, we do not expect to see a negative correlation between the variances and sensitivities of zero-to-one matrix elements alone. Nevertheless, because the matrix elements with the highest sensitivities tend to be zero-to-one elements (Pfister 1998) whose variances are therefore constrained (fig. 1), we again expect to see a negative correlation between the variances and sensitivities when both types of matrix elements are included in the analysis.

The preceding arguments suggest that negative correlations between the coefficients of variation (or variances) and the elasticities (or sensitivities) of different matrix elements may not represent a consequence of natural selection favoring traits that buffer the most influential matrix elements against environmental stochasticity. Instead, such correlations may arise from a ceiling on the variance or the coefficient of variation of zero-to-one matrix elements that does not apply to other matrix elements and from the fact that both the coefficient of variation and the elasticity of a zero-to-one matrix element are functions of the mean. To test these conjectures, we constructed projection matrices at random (i.e., with no selection involved) and looked for correlations between measures of the variability of matrix elements and measures of their influence on the annual multiplication rate.

Spurious Negative Correlations between Coefficients of Variation (or Variances) and Elasticities (or Sensitivities) of Matrix Elements

To test for spurious correlations, we generated series of projection matrices from the underlying vital rates, which we varied at random. The key feature of our simulations is that we forced all vital rates of a given type (survival, growth, or fertility) to be equally variable. The resulting matrices thus could not have been shaped by natural selection to buffer variation in any of the vital rates, and any correlation that emerged between the coefficients of variation and the elasticities, or between the variances and sensitivities, would be spurious.

Random matrix series were constructed as follows. We varied the number of size classes from three to 12. For each, we generated 1,000 series of five annual matrices. Parameterizing a series of five projection matrices would require a 6-yr demographic study. Six years was the length of our moss campion study (Morris and Doak 2004) and is toward the long end of the studies examined by Pfister (1998) and indeed of all published demographic studies (see fig. 10.2 in Morris and Doak 2002).

Surviving individuals could either remain in the same size class or grow to the next largest size class. We assumed a postbreeding census of a birth-pulse population (Caswell 2001) so that the reproduction elements in the first row of each matrix included the survival probability for the corresponding adult size class. To illustrate, the matrices with four size classes had the format

$$\mathbf{A}(t) = \begin{bmatrix} p_1(t)[1 - g_1(t)] & p_2(t)f_2(t) & p_3(t)f_3(t) & p_4(t)f_4(t) \\ p_1(t)g_1(t) & p_2(t)[1 - g_2(t)] & 0 & 0 \\ 0 & p_2(t)g_2(t) & p_3(t)[1 - g_3(t)] & 0 \\ 0 & 0 & p_3(t)g_3(t) & p_4(t) \end{bmatrix},$$

(5)

where $p_j(t)$ is the probability that an individual in size class j survives from year t to year $t + 1$, $g_j(t)$ is the probability that a surviving individual in size class j in year t grows into size class $j + 1$ in year $t + 1$, and $f_j(t)$ is the average number of newborns an individual in size class j produces during the birth pulse. To make the matrices biologically realistic, we assumed that the means of $p_j(t)$ and $f_j(t)$ increase linearly and that the means of $g_j(t)$ decrease linearly with size class j (i.e., larger individuals have higher survival, greater offspring production, and slower growth on average than do smaller individuals), but we chose the slopes and intercepts of these linear functions at random (while keeping zero-to-one vital rates properly bounded).

We drew each year's p_j and g_j from β distributions with coefficients of variation equal to 0.1 or 0.3 times the appropriate CV_{max} given each vital rate's mean (see eq. [4]; because the results were qualitatively similar for both levels of variability, we report only results for the lower level). Thus, all of the survival and growth rates had the same degree of relative variability. We drew the fertilities (f_j) from lognormal distributions. Because the variance of the lognormal has no upper limit, it is not possible to set the coefficients of variation of the fertilities as a fixed proportion of their maxima as we did for the survival and growth rates. Instead, we chose their variabilities in two ways, both of which can be seen to make the fertilities equally variable across size classes. First, we assigned all fertilities the same coefficient of variation (0.1 or 0.3). This can be viewed as fixing the relative variability because the standard deviation of fertility increases in direct proportion as the mean fertility increases across size classes, although as a consequence, the variance in fertility increases with size. Alternatively, we assigned all fertilities the same variance (equal to that of the median size class in the first scenario), which implies that the fertilities of the smaller size classes are more variable relative to their means. We discuss the implications of these two approaches in the final section of the paper.

We used the mean of the five random matrices to calculate the matrix element sensitivities and elasticities. For each replicate matrix series, we computed Spearman's rank correlation between the matrix element variances and sensitivities and between the coefficients of variation and the elasticities following Pfister (1998).

Even though our simulations forced all vital rates of a given type to have the same level of variability, the correlations between the coefficients of variation and the elasticities of all matrix elements were skewed toward negative values (see fig. A1*A*, A1*E* in the online edition of the *American Naturalist*), and the confidence interval for the mean rank correlation did not overlap 0 (table 1). This was true for both types of variation in fertilities. The correlations between the variances and sensitivities of all ma-

Table 1: Spearman's rank correlation coefficients between variabilities and importance measures of matrix elements from randomly constructed matrix series

	Raw rank correlations		Partial correlations	
Type of correlation	All matrix elements	Zero-to-one matrix elements only	All matrix elements	Zero-to-one matrix elements only
All fertilities with equal coefficient of variation:				
Coefficients of variation vs. elasticities	**−.1271**	**−.1897**	**−.1357**	**−.0453**[a]
	(−.1331, −.1212)	(−.1966, −.1828)	(−.1415, −.1300)	(−.0522, −.0385)
Variances vs. sensitivities	**−.4790**	**.0268**	.0026[a]	**.1204**[a]
	(−.4826, −.4753)	(.0199, .0337)	(−.0031, .0084)	(.1132, .1276)
All fertilities with equal variance:				
Coeffecients of variation vs. elasticities	**−.0972**	**−.1933**	**−.0976**[a]	**−.0410**[a]
	(−.1036, −.0909)	(−.2003, −.1862)	(−.1038, −.0914)	(−.0479, −.0340)
Variances vs. sensitivities	**−.4686**	**.0327**	**.0183**[a]	**.1251**[a]
	(−.4724, −.4649)	(.0258, .0396)	(.0125, .0241)	(.1178, .1323)

Note: Mean correlations with confidence intervals that do not include 0 are in bold. Means are shown with 95% confidence intervals in parentheses. Partial correlations were used to adjust for shared dependence on the mean. Distributions of raw rank correlations are shown in figure A1 in the online edition of the *American Naturalist*.

[a] In some cases, the rank correlation between the means and either the variances, coefficients of variation, sensitivities, or elasticities equaled 1. As the partial correlation formula would then involve division by 0, partial correlations could not be calculated for these cases.

trix elements were even more strongly negatively biased (table 1; fig. A1*C*, A1*G*). Removing the reproduction elements and basing these correlations only on the zero-to-one matrix elements (i.e., those that are subjected to the variability limit) does not eliminate bias (fig. A1*B*, A1*D*, A1*F*, A1*H*); the correlations between the coefficients of variation and the elasticities are even more negative on average, and the variance-sensitivity correlations have a small but significant positive bias (table 1). Because measures of variability (variance and coefficient of variation) and measures of importance (sensitivities and elasticities) may both be correlated with the means of the matrix elements, Pfister (1998) also computed the partial correlation between them holding the mean constant (using eq. [16.20] in Sokal and Rohlf 1995, p. 649). For our randomly constructed matrices, most of these partial correlations were still significantly biased, the exception being the variance-sensitivity correlation using all matrix elements when all simulated fertilities had the same coefficient of variation. However, note that for some of our random matrix series, these partial correlations could not be computed (table 1).

Thus, there is a spurious negative correlation between the coefficients of variation and the elasticities of all matrix elements, as well as between their variances and sensitivities, that must be taken into account when determining whether demographic processes that contribute the most to the growth rate of a lineage have been selected to be relatively less variable. We now propose a method to largely circumvent these spurious correlations, and we illustrate it using both our simulated demographic data and data on moss campion.

Method to Circumvent Spurious Negative Correlations

Because the coefficient of variation and the variance of zero-to-one random variables have inherent limits, we should test the hypothesis that demographic processes with a high influence on fitness should be less variable using a measure that computes the level of variability relative to its maximum possible value. That is, we should ask whether highly influential rates are less variable than they could be given their means. For example, selection for high longevity may have favored survival rates of larger individuals that are close to 1 on average, with a concomitantly low ceiling on their coefficient of variation (fig. 1). To ask whether selection has also favored low variability in this high-elasticity vital rate, we should ask whether its coefficient of variation (or variance) as a proportion of its maximum possible value given the mean is lower than the corresponding measure for lower-elasticity (or lower-sensitivity) vital rates. As we explained, it makes more sense to base a test for buffering of highly influential components of the life history on the underlying vital rates rather than on the matrix elements themselves.

We advocate a four-step procedure to evaluate whether a nonrandom association exists between the coefficients of variation and the elasticities or between the variances

Table 2: Spearman's rank correlations between variabilities and importance measures of vital rates estimated from randomly constructed matrix series

Type of correlation	Survival and growth rates[a]	Fertilities
All fertilities with equal coefficient of variation:		
Coeffecients of variation vs. elasticities	**−.0073** (−.0136, −.0010)	**−.0116** (−.0221, −.0010)
Variances vs. sensitivities	−.0061 (−.0124, .0001)	**−.2606** (−.2711, −.2501)
All fertilities with equal variance:		
Coeffecients of variation vs. elasticities	4.0353×10^{-4} (−.0059, .0067)	**.2129** (.2021, .2237)
Variances vs. sensitivities	.0016 (−.0047, .0079)	−.0089 (−.0194, .0017)

Note: Mean correlations with confidence intervals that do not include 0 are in bold. See figure A2 in the online edition of the *American Naturalist* for distributions of these correlations.

[a] Variances and coefficients of variation of these zero-to-one vital rates were relativized to their maximum values before computing the correlations with the elasticities and sensitivities, respectively.

and sensitivities of vital rates. Step 1 is to separate the vital rates into zero-to-one rates (e.g., survival and growth probabilities) versus rates without an inherent limit to the level of variability (e.g., fertilities). We will perform separate analyses for these two types of vital rates because there is simply no fair way to compare vital rates that have a limit to their variabilities versus those that do not. Step 2 is to compute the elasticities or sensitivities for the vital rates, not the amalgamated matrix elements. The elasticity (or sensitivity) of a vital rate is easily calculated as the sum across all matrix elements of the elasticity (or sensitivity) of that matrix element times the derivative of the matrix element with respect to the vital rate (Caswell 2001). Whereas the matrix element elasticities and sensitivities are always nonnegative, vital rates that represent reversion to smaller size classes have negative sensitivities and elasticities. However, equations (1) and (2) imply that it is the squares of these sensitivities and elasticities that affect the long-term growth rate of a lineage. Hence, equivalent levels of variation in vital rates whose elasticities or sensitivities have the same magnitude but opposite sign are equally important in reducing long-term fitness. Therefore, the analysis should be based on the absolute values of the vital rate elasticities and sensitivities. Step 3 is to calculate the variance of each vital rate, correct it for sampling variation, and use the corrected variance to compute the coefficient of variation. For vital rates with no inherent limit to variability, we will analyze these corrected variances and coefficients of variation directly. For zero-to-one vital rates, we first compute the relativized variability by dividing the corrected variance or coefficient of variation by the maximum possible value given the mean, as specified in equations (3) or (4). Note that the relativized variance V/V_{max} is simply the square of the relativized coefficient of variation, CV/CV_{max}, so in principle, one could use either measure to compute a rank correlation. Step 4 is to test whether there is a statistically significant relationship between the measures of variability and their influence on fitness.

To test this procedure, we first applied it to the randomly constructed matrix series (with the exception that as we generated the random vital rates directly rather than simulating the fates of individuals, we did not correct for sampling variation). Relativizing the variabilities of the survival and growth rates results in little or no bias in both types of variability-importance correlation (table 2; fig. A2*A*, A2*B*, A2*E*, A2*F* in the online edition of the *American Naturalist*). However, when all fertilities were generated using the same coefficient of variation, the correlations between the coefficients of variation and the elasticities were nearly unbiased (table 2; fig. A2*D*), but the variance-sensitivity correlations were negatively biased (table 2; fig. A2*C*). When all fertilities were generated using the same variance, the variance-sensitivity correlations were unbiased, but the correlations between the coefficients of variation and the elasticities were positively biased (table 2; fig. A2*E*, A2*F*). These biases apparently arose because, in our simulations, the fertility means were positively correlated with size, but both the sensitivities and elasticities were negatively correlated with size (i.e., enhancing reproduction of the smaller size classes would disproportionately increase population growth). With a fixed coefficient of variation, the fertility variances increased with size to keep pace with increasing mean fertility. Therefore, because the fertility variances and sensitivities were directly and inversely proportional to size, respectively, they had to be negatively correlated with one another. Conversely, with the fertility variance fixed, the coefficients of variation decreased with size as mean fertility increased, so the fertility coefficients of variation and elasticities had to be positively correlated with one another. Thus, rather than representing a failure of our proposed method, the biases in table 2 merely point to the fact that when the means, sensitivities, and elasticities of the fertilities are all correlated with size, it may be impossible for both variability measures (the variances and coefficients of variation) to be simultaneously independent of their relevant measures

of influence (sensitivities and elasticities, respectively). We return to this issue in the final section of the article.

Illustration of Method Using Demographic Data from *Silene Acaulis*

Because our proposed method appears to be far less biased than the matrix element approach, we applied it to demographic data on the circumboreal cushion plant moss campion (*Silene acaulis*) to see whether we could find evidence for buffering of influential vital rates. Full details on the study species, the field study, and the methods used

to estimate vital rates are given by Morris and Doak (1998, 2004). Briefly, moss campion inhabits seemingly severe arctic and alpine environments in which temperature, moisture availability, and growing season length can vary considerably from year to year. We quantified moss campion vital rates in five populations arrayed along an elevational gradient in south-central Alaska. Populations are identified with a two-letter site code (CC = Campion Crest, GU = Gulch, PA = Pass, RG = Rock Glacier, and RI = Ridge). We censused each population yearly for 6 yr, yielding five annual estimates for most vital rates for each population. We measured plant size as the two-
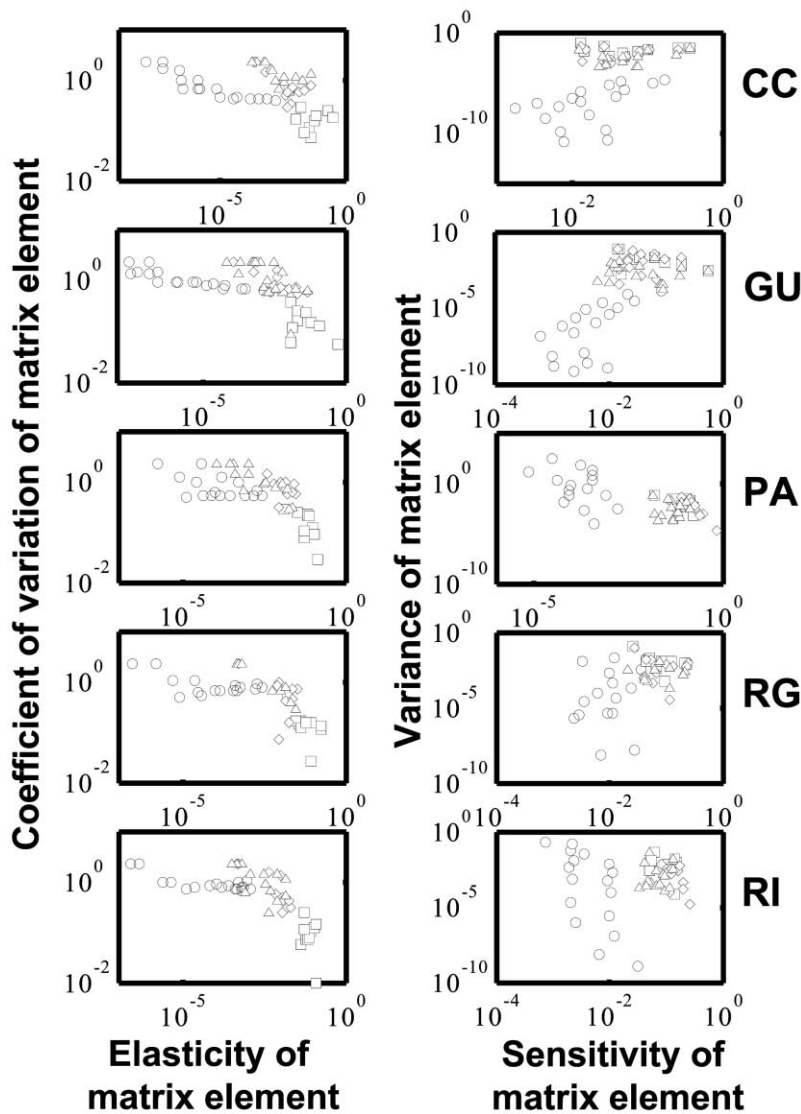

Figure 2: Relationship between the coefficients of variation of matrix elements and their elasticities, and between their variances and sensitivities, for five *Silene acaulis* populations. Symbols indicate different types of matrix elements: *circles*, reproduction; *squares*, probability of stasis; *diamonds*, probability of growth; *triangles*, probability of reversion.

Table 3: Rank correlations between measures of variability versus influence for *Silene acaulis* matrix elements and vital rates

	Coefficients of variation vs. elasticities						Variances vs. sensitivities					
	Matrix elements		Zero-to-one vital rates		Fruit production rates		Matrix elements		Zero-to-one vital rates		Fruit production rates	
Population	r_s	df	r_s	df	r_s	df	r_s	df	r_s	df	r_s	df
CC	−.511***	51	−.407*	27	−1.000***	7	.426	51	−.446**	27	.683	7
GU	−.635***	59	−.474**	27	−.967***	7	.494	59	−.523**	27	.767	7
CC	−.596***	49	−.445**	27	−.452	6	−.536***	49	−.478**	27	−.850**	6
GU	−.663***	44	−.396*	27	−.190	6	.396	44	−.330*	27	.533	6
PA	−.726**	52	−.378*	27	−.517	7	−.106	52	−.324*	27	−.850**	7

Note: Significance levels are for a one-tailed test of the hypothesis $r_s < 0$. For zero-to-one vital rates, coefficients of variation and variances were relativized to their maximum values prior to analysis.

* $.05 < P < .01$.

** $.01 < P < .001$.

*** $P < .001$.

dimensional area of a cushion and divided the populations into 12 size classes. The zero-to-one vital rates we estimated for each size class each year were the probability of surviving, the probability of growing to any larger size class, and the probability of reverting to any smaller size class (plant size frequently decreases as portions of a cushion die back). We also measured the annual fruit production rates for each size class, most of which exceed 1. We were not able to make separate yearly estimates for several other vital rates (i.e., seed germination rate, annual survival rate of seeds in the seed bank, number of seeds per fruit, and probability that a seed lands in a safe site), so we do not include these rates in our analyses. We calculated the raw variance of the five estimates of each vital rate and corrected these variances for sampling variation using the method of White (2000). For zero-to-one vital rates, we then used equations (3) and (4) to convert the corrected variances into measures of relative variability. We calculated the vital rate elasticities and sensitivities from the mean projection matrix for each population.

For the purpose of illustration, we first present an analysis identical to that of Pfister (1998) by using the raw coefficients of variation, elasticities, variances, and sensitivities of the matrix elements, not the underlying vital rates. In each of the five populations, the rank correlation between the coefficients of variation and the elasticities of the matrix elements was highly significantly <0 (fig. 2; table 3). In contrast, the rank correlations between the variances and sensitivities of the matrix elements were significantly negative in only a single population (recall, however, that the matrix element variances are not corrected for sampling variation). The correlations between the coefficients of variation and the elasticities would appear to provide strong evidence in favor of the hypothesis that the most

influential demographic processes are the most buffered against environmental variability. However, this analysis has not taken into account the spurious negative correlation between the coefficients of variation and the elasticities of matrix elements.

The correlations between the relativized coefficients of variation and the elasticities of the zero-to-one vital rates, which circumvent the spurious negative correlation, were less strongly negative than were the correlations between the coefficients of variation and elasticities of matrix elements, but they too were significantly <0 in all five populations (fig. 3; table 3). Moreover, all five of the rank correlations between the relativized variances (now corrected for sampling variation) and the sensitivities of the zero-to-one vital rates were significantly negative (table 3). The mean survival rates of the largest plants (class 12) were extremely high (0.9960, 0.9982, 0.9955, 0.9876, and 0.9921 in the CC, GU, PA, RG, and RI populations, respectively; see Morris and Doak 2004). Consequently, the ranges of potential values of the variance and the coefficient of variation of this survival rate are extremely narrow in all populations (fig. 1). Despite the low values of V_{max} and CV_{max}, the observed variances and coefficients of variation were proportionally lower than for other less influential vital rates. This strongly suggests that in addition to any selection to increase the mean survival rates of large individuals in this long-lived perennial plant, selection has also favored traits that reduce the year-to-year variability in these vital rates.

Although the significant rank correlations in table 3 are consistent with the vital rates that most strongly influence fitness being more highly buffered against environmental variation, we argued at the outset that it is more appropriate to test for an upper limit to the variability of vital
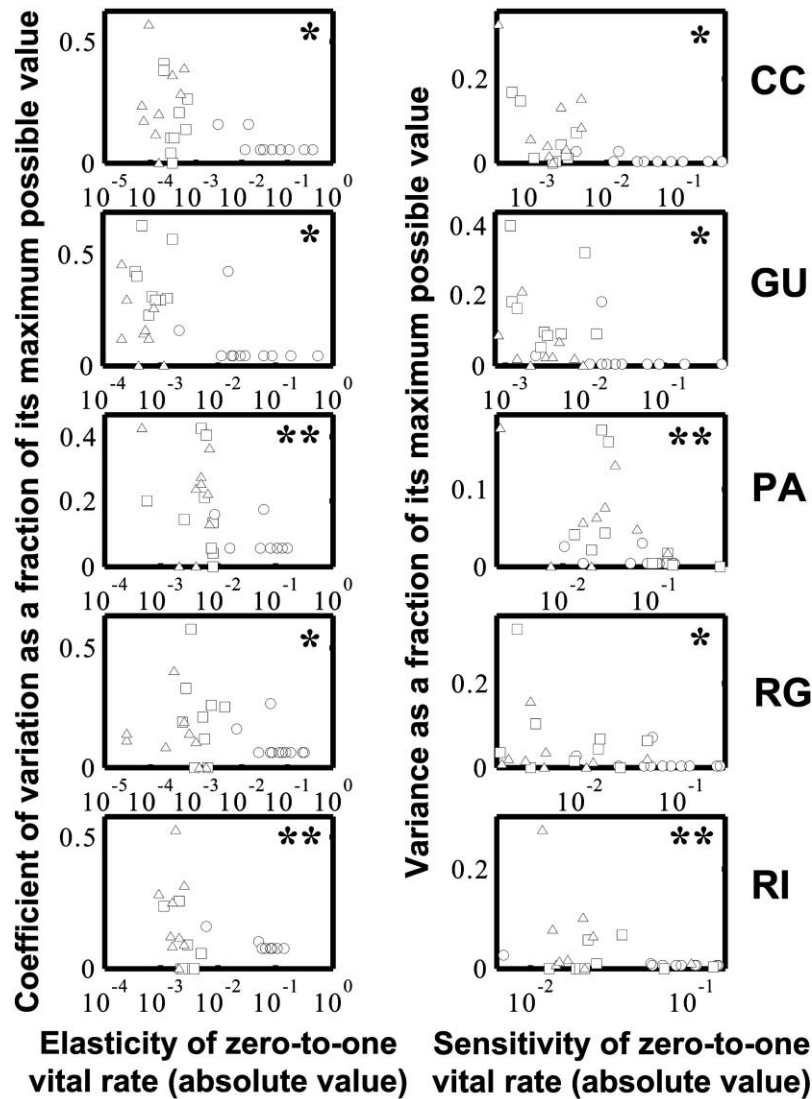
Figure 3: Relationship between the relative variability (i.e., the coefficient of variation or variance as a fraction of the maximum value given the mean; see eqq. [3], [4]) and the influence (elasticity or sensitivity) of zero-to-one vital rates in five *Silene acaulis* populations. The elasticities for the reversion rates are negative. Symbols indicate types of vital rates: *circles*, survival rates; *squares*, growth rates; *diamonds*, reversion rates. Asterisks at the upper right corner of each graph indicate the significance level of quantile regressions. One asterisk indicates $P < .01$ for fiftieth quantile and $P > .05$ for seventieth quantile; two asterisks indicate $P < .05$ for both the fiftieth and seventieth quantile.

rates that declines as their influence on fitness increases. Note that in each plot in figure 3, the data points are concentrated below the diagonal. For example, the survival rates have the highest elasticities, but their relative coefficients of variation are always low, whereas the lower-elasticity growth and reversion rates have relative coefficients of variation that range from high to low. To test for a declining upper limit to variability, we used the Blossom statistical software (Cade and Richards 2001; http://www

.mesc.usgs.gov/products/software/blossom/blossom.asp) to perform quantile regressions of relative coefficients of variation versus elasticities and of relative variances versus sensitivities. Quantile regression fits a linear function below which a specified proportion of the values of the dependent variable are expected to lie conditional on the value of the independent variable. One can then test whether the slope of this function is nonzero by comparing its fit to a function with zero slope using a likelihood ratio
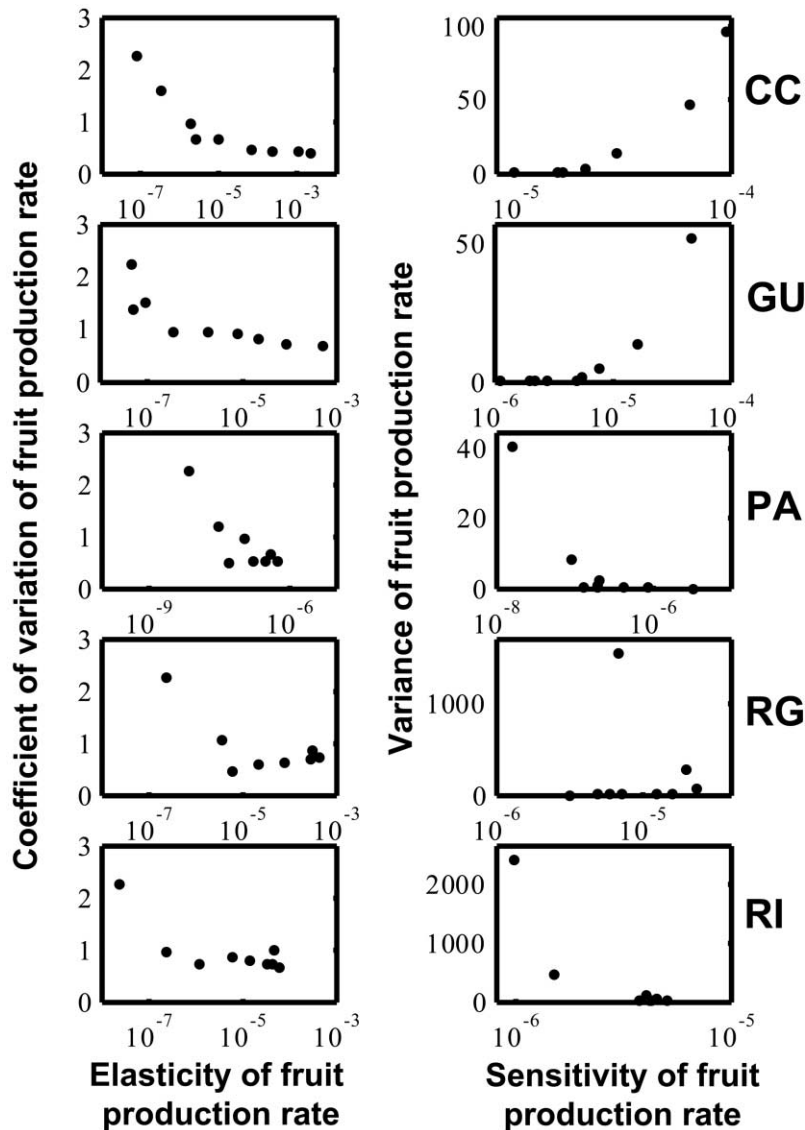
Figure 4: Coefficients of variability versus elasticities and variances versus sensitivities for fruit production rates in five *Silene acaulis* populations

test. In the present context, a significantly negative slope would indicate that the specified quantile of the relative variability declines as a vital rate's influence on fitness increases. To perform a quantile regression, one must first choose a quantile; tests for a nonzero slope of very high (or very low) quantiles often have little power. We chose to fit functions below which 50% or 70% of the values of the dependent variable should lie. In all cases, the slopes of these regressions were negative, significantly so for all of the fiftieth percentile regressions (fig. 3; table A1 in the online edition of the *American Naturalist*). This analysis provides strong support for the hypothesis that zero-to-one vital rates with both a strong effect on fitness and a

high level of relative variability are underrepresented in the data.

The number of fruit production rates we estimated was too small to justify performing quantile regressions, so we calculated rank correlations only. The fruit production rates had substantially lower elasticities and sensitivities than did the survival, growth, and reversion rates (compare the ranges of the X-axes in figs. 3, 4). Moreover, there was no one size class whose fruit production rate had the highest impact on fitness across all populations (e.g., classes 12, 12, 10, 11, and 10 had the highest elasticities for fruit production in the CC, GU, PA, RG, and RI populations, respectively). Despite low degrees of freedom, the rank

correlations between the coefficients of variation and the elasticities were significantly negative in the CC and GU populations (fig. 4; table 3). In contrast, although the variances and sensitivities of the fruit production rates were significantly negatively correlated in two populations, they were actually positively correlated in the other three, in direct opposition to Pfister's (1998) hypothesis. However, the absence of a strong relationship in vital rates with such a weak influence on fitness is not surprising.

Summary, Caveats, and a Final Plea

Our randomly constructed series of projection matrices demonstrate that negative correlations between the variabilities and influence measures of matrix elements may represent spurious evidence that the most influential demographic rates have been selected to be less variable. We can reduce such errors by analyzing zero-to-one and nonzero-to-one vital rates separately and, for the zero-to-one rates, by assessing whether the variabilities of highly influential rates are disproportionately smaller than they could be given the mean rates. By failing to account for the upper limit to the variance or the coefficient of variation of a zero-to-one vital rate (fig. 1), we risk confounding selection to reduce variability with selection to increase the mean. An added benefit of analyzing vital rates rather than matrix elements is that it allows sampling variation to be properly discounted.

Two caveats should be mentioned. First, the hypothesized relationship between the sensitivity or elasticity computed from the mean projection matrix and the degree of variability of a vital rate is motivated by Tuljapurkar's (1982) approximation (eqq. [1], [2]). Tuljapurkar (1982) assumed that annual deviations from the mean matrix are relatively small; if so, the deterministic sensitivities and elasticities calculated from the mean matrix paint a reasonably accurate picture of how the annual multiplication rate will change over the entire ranges of variation in the vital rates (and it is variation in the multiplication rate that reduces long-term fitness). If the annual matrices deviate a great deal from the mean matrix and if the relationship between the annual multiplication rate and the value of a vital rate is nonlinear, the deterministic sensitivity and elasticity will no longer predict how the multiplication rate will vary as the vital rate varies. In this case, it might be preferable to compute the sensitivities and elasticities by stochastic simulation. For the moss campion populations we studied, the long-term multiplication rates computed by stochastic simulation and by Tuljapurkar's (1982) approximation were very close, indicating that the deterministic sensitivities and elasticities accurately predict how much variation in the annual multiplication rate arises from variation in the vital rates. Note

that even if the sensitivity and elasticity are computed by simulation, the variance and coefficient of variation for zero-to-one vital rates should still be expressed as proportions of their maximum values, as we have done here.

The second caveat is that the variance versus sensitivity correlation and the coefficient of variation versus elasticity correlation may not always be similar in magnitude or even in sign (table 3), particularly for vital rates such as fertilities whose variabilities cannot be expressed in relative terms. Moreover, for certain life histories, it may not even be possible for both correlations to be near 0 (fig. A2C, A2D, A2G, A2H). How to interpret such conflicting evidence for demographic buffering as well as the types of life histories for which it is likely to arise are areas for future research.

We end with a plea to population biologists. To make the analysis we have advocated possible, we must have access to estimates of the underlying vital rates. We would have liked to apply our method to the studies analyzed by Pfister (1998), but, unfortunately, most previously published demographic studies have presented only the amalgamated projection matrices (if that) and not the vital rates. Indeed, that is the principal reason why Pfister (1998) was forced to base her analysis on matrix elements when she recognized that it would be preferable to use the vital rates. We implore authors of demographic studies to publish the vital rate estimates so that comparative studies of demographic buffering may be possible in the future. The widespread use of electronic archives by ecology and evolution journals should make it easy to do so.

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