SPECIAL FEATURE

ADVANCES IN PLANT DEMOGRAPHY USING MATRIX MODELS

Demographic effects of extreme weather events on a short-lived calcareous grassland species: stochastic life table response experiments

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Summary

1. Life table response experiment (LTRE) analyses have been widely used to examine the sources of differences in the long-term deterministic growth rate ($r = \log \lambda$) of stage-structured populations that live in spatially distinct habitats or under distinct experimental conditions. However, existing methods for LTRE analysis ignore the fact that persistent temporal variation in matrix elements results in a long-term *stochastic* growth rate ($a = \log \lambda_s$) that is different from the deterministic growth rate (r) and thus do not take into account environmental stochasticity.

2. Here, we develop a stochastic extension of LTRE methods that can be used to compare stochastic growth rates among populations that differ in the observed variability of their matrix elements over time. We illustrate our method with actual data and explore a range of questions that may be addressed with these new tools. Specifically, we investigate how variability in weather conditions affected the population dynamics of the short-lived perennial plant species *Anthyllis vulneraria* and examine how differences in stochastic growth rates (a) are determined by contributions of mean matrix elements and variability in matrix elements.

3. We find that, consistent with the life history of the species, differences in mean fertility and growth made the largest contribution to differences in a, whereas in terms of variability fertility made the largest contribution in most populations. However, we also find that in all populations, the magnitude of the total contribution of mean matrix elements outweighed that of variability. Finally, increasing soil depth significantly lowered contributions of variability in matrix elements, but it was not related to contributions of differences in mean matrix elements.

4. *Synthesis.* Stochastic life table response experiment analysis described here provides the first systematic way of incorporating observed differences in temporal variability into the comparison of natural populations. A key finding from this study is that populations occurring on relatively deeper soils were better buffered against climatic variation than populations occurring on shallow soils. We expect this new approach to analyse temporal variability to prove especially useful in the analysis of natural populations experiencing environmental change.

Key-words: *Anthyllis vulneraria*, climate change, life table response experiment (LTRE), population growth, stochastic elasticities

Introduction

Populations of the same species in distinct habitats can differ in structure, stage-transition matrix elements and fertilities, and thus in growth rates and, ultimately, in persistence. A widely used method for identifying the causes of differences in growth rates in terms of the contributions of these differences in projection matrix elements is the life table response experiment (LTRE).

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First used by Birch (1953) to study the effects of different experimental conditions on laboratory insect populations, LTREs have been applied to many biological systems. While early applications focused on environmental toxicology, recent studies address more general ecological and evolutionary questions (Caswell 1996, 2001, pp. 258–277). The standard LTRE examines the sources of differences in the long-term deterministic growth rate ($r = \log \lambda$) of stage-structured populations that live in spatially distinct habitats or under distinct experimental conditions. Standard LTREs have been applied, e.g. to examine the effects of density (e.g. Sibly 1999; Oli, Slade & Dobson 2001; Gustafsson & Ehrlèn 2003), isolation (Schaub *et al.* 2006), fragmentation (Bruna & Oli 2005) and associated changes in land use (Jacquemyn & Brys 2008), competition among predators (Magalhaes *et al.* 2003), prey (Oli & Dobson 2001) or plants (Fréville & Silvertown 2005; Jongejans & de Kroon 2005), nutrient availability in plants (e.g. Gotelli & Ellison 2006) and animals (Cooch, Rockwell & Brault 2001; Dobson & Oli 2001), temperature (e.g. Ramos-Jiliberto & Aranguiz-Acana 2007) and climate (Morrison & Hik 2007). LTREs have also been used to examine wildlife and land management for the conservation of at-risk species and populations (e.g. Gotelli & Ellison 2006; Jäkäläniemi, Tuomi & Siikamäki 2006), invasive species control (e.g. Williams & Crone 2006) and sustainable forestry practices (Zuidema, de Kroon & Werger 2007).

Despite these many applications, a fundamental limitation of LTRE methods is that they ignore environmental stochasticity. Although some LTRE analyses consider patterns of temporal variation in matrix elements (e.g. Horvitz, Schemske & Caswell 1997; Fréville *et al.* 2004; Jongejans & de Kroon 2005; Folk, Holmes & Grand 2007), or identify 'year-effects' on populations (e.g. Angert 2006), they treat temporal variation in the same way as spatial variation. Existing methods for LTRE ignore the fact that persistent temporal variation in matrix elements

results in a long-term *stochastic* growth rate (a) that is different from the deterministic growth rate (r).

When multi-year data reveal temporal variability in the stage-transition matrix elements of a population, no deterministic growth rate will describe the long-term effects of temporal variation (Cohen 1977; Tuljapurkar & Orzack 1980). Instead, population growth in the presence of temporal variability is described by the long-term stochastic growth rate ($a = \log \lambda_S$, Tuljapurkar 1990). In such cases, population statistics, including the stochastic growth rate a, depend upon the temporal sequence of environmental states experienced by a population, so that the effects of conditions in a particular year depend on the entire sequence of years and cannot be studied in isolation. LTREs that report a 'year-effect' (e.g. Angert 2006) treat population data for each year as if they describe a distinct population with its own deterministic growth rate. Differences between years are thus treated in the same way as differences between spatially distinct habitats. Such an LTRE describes the differences between the various years of the study, but not the effects of temporal variability.

We present here a stochastic extension of LTRE methods that can be used to compare stochastic growth rates among populations that differ in the observed variability of their matrix elements over time. The extension we have developed is, naturally, called a stochastic life table response experiment (SLTRE). SLTREs, as illustrated in Fig. 1, describe each 'treatment' population (e.g. populations under distinct management regimes or in distinct spatial habitats) by its particular temporal sequence of habitat states. Each population's temporal sequence creates corresponding stochastic dynamics over time. In SLTREs, 'year' is neither a fixed nor a random effect. It is not a fixed effect because the effect of a given habitat state depends directly on the frequency with which it is experienced and its positions within a sequence of years. It is also not a random effect because a given temporal sequence will always determine a specific stochastic growth rate. Temporal variation
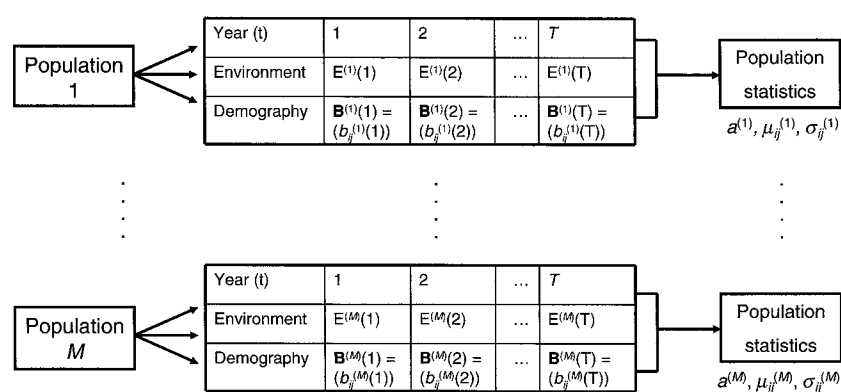
Fig. 1. The design of a stochastic life table response experiment (SLTRE). 'Treatment' m ($m = 1, 2, ..., M$) produces environmental conditions $E^{(m)}(t)$ that vary through time (t) and that affect each of the matrix elements b_{ij}. Thus population m experiences a time series of population matrices $\mathbf{B}^{(m)}(t)$ which can be used to calculate the means (μ_{ij}) and standard deviations (σ_{ij}) for each element (i,j), as well as the stochastic growth rate a ($a = \log \lambda_S$) and stochastic elasticities to mean transition matrix elements (E_{ij}^μ) and to variability in transition matrix elements (E_{ij}^σ). From these statistics, the stochastic reference matrix is computed and the SLTRE performed. Note that in SLTREs, unlike in classic LTREs, population statistics depend directly upon the temporal sequence of conditions experienced by a population. Classic LTRE analysis in this scheme would compare differences in deterministic lambda between years for each population, or between populations for each year. Two-way LTRE analysis would combine these comparisons.

among habitat states may be described by the means and variances of matrix elements, or by a set of matrix elements for each possible habitat along with a model of their temporal sequencing. We note that Caswell (2010) in this issue has independently proposed a similar approach.

This paper develops SLTREs starting from time series of matrix elements for each of several populations. We focus on describing the temporal sequence for each population by (time-averaged) mean values as well as (temporal) variances of matrix elements; in the discussion, we indicate how to carry out an SLTRE in a different way, i.e. one that focuses on habitat-specific matrix elements. Distinct populations may differ in mean matrix elements, in the variances of matrix elements, or in both. In contrast with standard LTREs, the goal of SLTREs is to examine how differences in stochastic growth rates (*a*) are determined by the contributions of mean matrix elements and of variability in matrix elements.

Stochastic life table response experiments may be used to compare two populations or several, as in regular fixed-treatment LTREs (Caswell 2001; Horvitz, Schemske & Caswell 1997). In the latter case, the first step is to define an appropriate reference population, e.g. one whose individual matrix elements are averages of matrix elements across populations. In an SLTRE, there are *T* years of demographic data for each of several populations. Averaging each stage-transition rate across populations within each year results in a time series of matrix elements that describes a (hypothetical) reference population. The stochastic growth rate of the reference population is described by a nonlinear function of each of the means (μ_{ij}) and standard deviations (σ_{ij}) of matrix elements (*i,j*) and therefore may be very different from the average of the stochastic growth rates of the observed populations.

The second step is to calculate differences in μ_{ij} and σ_{ij} between each observed population and the reference population. Next, we compute elasticities of the stochastic growth rate (*a*) for the reference population, with respect to changes in mean matrix values and with respect to changes in the variance of matrix elements (Tuljapurkar, Horvitz & Pascarella 2003). Finally, for each matrix element, we calculate the respective contributions of means and variances to the difference in stochastic growth rate, which are the products of the differences in either means or standard deviations of that rate and their associated stochastic elasticities.

In the following sections, we first describe this new method for conducting SLTRE analyses in detail and then demonstrate the method using actual data. We also explore a range of questions that may be addressed with these new tools. Specifically, we investigated how variability in weather conditions affected population dynamics of the short-lived perennial plant species *Anthyllis vulneraria*. Between 2003 and 2006, at least two major heat waves occurred in our study area and affected the population dynamics of this calcareous grassland species. To investigate whether some populations were better buffered against the observed variation in weather conditions, we first computed for each population the elasticities of the stochastic growth

rates (*a*) *sensu* Tuljapurkar, Horvitz & Pascarella (2003). We were particularly interested in the elasticity to the variance of matrix elements (E_{ij}^{σ}) as a quantitative measure of buffering. Small elasticities may be interpreted as evidence for buffering, as they imply that growth rate is relatively insensitive to changes in the variability of matrix elements. Next, we developed an SLTRE for this species to determine which life stages contributed most to differences in growth rates, in terms of differences in mean matrix elements and in terms of variability in matrix elements. We then investigated whether local environmental conditions (soil depth (cm), cover (%) of bare ground and rock, cover (%) of dominant grass species, litter cover (%) and vegetation height (cm)) were able to buffer populations against the extreme variability in weather conditions. We conclude with a discussion of the significance of our results for the natural populations in the example and highlight the additional information provided by examining the contributions of differential variability in matrix elements.

SLTRE: the essentials

We describe SLTREs in a form applicable to age- or stage-structured populations. We assume that individuals are classified into *P* discrete stages which they move through in discrete time intervals. Stages are denoted by an index *i* or *j*, taking values from 1 to *P*. Population dynamics are described by a ($P \times P$) projection matrix containing estimated matrix elements $b_{ij}(t)$ representing the per capita contributions of individuals in stage *i* in the population at time *t* + 1, made by individuals in stage *j* at time *t*. Temporal variability is described by a time series of matrices $\mathbf{B}(t) = (b_{ij}(t))$ for a given population. Temporal variability in matrix elements is driven by differences, over time, in the environmental conditions that influence fertility and stage transitions. If information about the underlying environmental conditions is available, e.g. climate variables or disturbances such as fire or hurricanes, we can (i) estimate how $\mathbf{B}(t)$ changes with measured environmental factors, and (ii) estimate parameters for a statistical model for temporal change in the environmental factors. For examples, see Tuljapurkar, Horvitz & Pascarella (2003) and Caswell & Kaye (2001).

However, in many cases we only have data on the $\mathbf{B}(t)$, often in the form of short time series. In such cases, we assume that in each year *t* the matrix $\mathbf{B}(t)$ is chosen independently from the same distribution; thus the matrix elements are independent and identically distributed, a phrase we shorten to IID (Tuljapurkar 1990). We take this distribution to be just that of the observed sample, e.g. if we observe $\mathbf{B}(1)$, $\mathbf{B}(2)$, $\mathbf{B}(3)$ and $\mathbf{B}(4)$, then the projection matrix applied in any future year equals each of these with probability 0.25. Of course, if sample periods are short relative to environmental cycles, or if sampling fails to capture rare or infrequent conditions, this assumption may not be robust. Notwithstanding, the IID assumption is widely used (e.g. Boyce 1977; Cohen 1979; Tuljapurkar 1989; Caswell 2001, pp. 377–381; Morris & Doak 2002, pp. 230–232; Morris *et al.* 2008).

CONSTRUCTING SLTRES

A given data set contains observations over T years ($t = 1, ..., T$) for M ($m = 1, ..., M$) populations, with one-period transition probabilities $b_{ij}^{(m)}(t)$ of stage j individuals in population m at time t arriving in stage i at time $t + 1$. For each of the M populations, population means ($\mu_{ij}^{(m)}$) and standard deviations ($\sigma_{ij}^{(m)}$) are calculated across T years for each matrix element ($b_{ij}^{(m)}$) (Table 1). A reference population (K) is constructed by calculating means across the M populations for each matrix element ($b_{ij}^{(m)}(t)$) for each period (t) of the sample data, resulting in reference population transition matrix elements $b_{ij}^{(K)}(t)$ for each of the T years in the data. The mean ($\mu_{ij}^{(K)}$) and standard deviation ($\sigma_{ij}^{(K)}$) of rates for the reference population are calculated across the $b_{ij}^{(K)}(t)$ (Table 1).

As with a deterministic LTRE, three fundamental quantities are examined: *differences, sensitivities/elasticities* and *contributions*. Here, we measure *differences* between an observed population (m) and the reference population (K) on a log scale, rather than as differences between the actual values of matrix elements. Because we are examining changes in the stochastic growth rate a, it is appropriate to work with differences on a log scale and to use elasticities, rather than the sensitivities used in deterministic LTREs. Therefore, we compute the differences as the log-ratios of the mean values of matrix elements ($\log[\mu_{ij}^{(m)}/\mu_{ij}^{(K)}] = \log\mu_{ij}^{(m)} - \log\mu_{ij}^{(K)}$) and of the standard deviations of those matrix elements ($\log[\sigma_{ij}^{(m)}/\sigma_{ij}^{(K)}] = \log\sigma_{ij}^{(m)} - \log\sigma_{ij}^{(K)}$).

Stochastic elasticities (calculated from the reference population K) measure changes in the stochastic growth rate (a) that are proportional to the changes in either the mean values (μ_{ij}) or in the standard deviations (σ_{ij}) of matrix elements ($b_{ij}^{(K)}$). Following Tuljapurkar, Horvitz & Pascarella (2003), we label the elasticity of the stochastic growth rate to changes in matrix elements E_{ij}^s; elasticities to means are labelled E_{ij}^μ ($E_{ij}^\mu = \partial\log\lambda_s/\partial\log\mu_{ij}$) and elasticities to standard deviations are labelled E_{ij}^σ ($E_{ij}^\sigma = \partial\log\lambda_s/\partial\log\sigma_{ij}$). For any given matrix element (b_{ij}), $E_{ij}^s = E_{ij}^\mu + E_{ij}^\sigma$ (Haridas & Tuljapurkar 2005). Furthermore, elasticities sum to unity across all matrix elements within a population such that $\Sigma_{ij}E_{ij}^s = \Sigma_{ij}\{E_{ij}^\mu + E_{ij}^\sigma\} = 1$ (Haridas & Tuljapurkar 2005).

The goal of SLTRE analyses is to examine how differences between populations, in either mean matrix elements (μ_{ij}) or in variability of matrix elements (σ_{ij}), contribute to the observed differences in stochastic growth rates. If a^K and a^m are the stochastic growth rate of the reference population K and an observed population m, respectively, and E_{ij}^μ and E_{ij}^σ are the stochastic elasticities of the reference population, then the basic equation for SLTRE is

$$a^m - a^K \approx \Sigma_{ij}[\log\mu_{ij}^{(m)} - \log\mu_{ij}^{(K)}]E_{ij}^\mu + \Sigma_{ij}[\log\sigma_{ij}^{(m)} - \log\sigma_{ij}^{(K)}]E_{ij}^\sigma. \qquad \text{eqn 1}$$

As in standard LTREs, this equation is a linear approximation that ignores any curvilinear relationship between changes in matrix elements and population growth rate (De Kroon, van Groenendael & Ehrlén 2000). The quantity $C_{ij}^\mu = E_{ij}^\mu(\log\mu_{ij}^{(m)} - \log\mu_{ij}^{(K)})$ is the *contribution* of differences in the mean of matrix element (i,j). The quantity $C_{ij}^\sigma = E_{ij}^\sigma(\log\sigma_{ij}^{(m)} - \log\sigma_{ij}^{(K)})$ is the *contribution* of differences in the variability of the (i,j) element. The different steps in constructing SLTREs are summarized in Appendix S1 in Supporting Information. Script files in Matlab for the methods described here are provided in Appendix S2.

An illustrative example

STUDY SYSTEM

To illustrate our methods, we develop in this section an SLTRE for the calcareous grassland specialist *Anthyllis vulneraria* (Kidney vetch). This species is a short-lived, rosette-forming legume with a complex life cycle, and it is the primary larval host plant of the Red-Listed specialist blue butterfly, *Cupido minimus* (Maes & van Dyck 2001; Krauss, Steffan-Dewenter & Tscharntke 2004). Under glasshouse conditions, *A. vulneraria* behaves like a mono- or dicarpic strict biennial (Sterk *et al.* 1982; Bastrenta & Belhassen 1992). Under natural conditions, however, it remains vegetative during the first year and flowers at least once between its first and fifth year. Hence, the species is considered a semelparous or iteroparous perennial with a delayed time of first reproduction depending on the

Table 1. Array construction of one-period transitions probabilities ($b_{ij}^{(m)}(t)$) for each of M populations and T periods

Population	Year 1	Year 2	...	Mean rates	SD rates
Population 1	$b_{ij}^{(1)}(1)$	$b_{ij}^{(1)}(2)$	...	$\mu_{ij}^{(1)} = (1/T)\Sigma_{t=1}^T[b_{ij}^{(1)}(t)]$	$\sigma_{ij}^{(1)} = \text{std}(b_{ij}^{(1)})$
...	...	...	...	...	...
Population m	$b_{ij}^{(m)}(1)$	$b_{ij}^{(m)}(2)$	...	$\mu_{ij}^{(m)} = (1/T)\Sigma_{t=1}^T[b_{ij}^{(m)}(t)]$	$\sigma_{ij}^{(m)} = \text{std}(b_{ij}^{(m)})$
...	...	...	...	...	...
Reference population (K)	$b_{ij}^{(K)}(1) = (1/M)\sum_{m=1}^M[b_{ij}^{(m)}(1)]$	$b_{ij}^{(K)}(2) = (1/M)\sum_{m=1}^M[b_{ij}^{(m)}(2)]$	...	$\mu_{ij}^{(K)} = (1/T)\Sigma_{t=1}^T[b_{ij}^{(K)}(t)]$	$\sigma_{ij}^{(K)} = \text{std}(b_{ij}^{(K)})$

Population means $\mu_{ij}^{(m)}$ and standard deviations $\sigma_{ij}^{(m)}$ are calculated across the T periods. For the reference population (K), the sequence of one-period matrix elements $b_{ij}^{(K)}(t)$ represents period means across the M populations. Mean matrix elements $\mu_{ij}^{(K)}$ for the reference population are the grand means across M populations and T years, while the standard deviations $\sigma_{ij}^{(K)}$ are calculated across the T years of $b_{ij}^{(K)}$. Std(X) indicates the standard deviation of the observed values of X

environment. Flowering starts early- to mid-June and each mature plant develops between 1 and 20 flowering stalks each with 1–15 flower heads containing 10–25 flowers per head. Fruit and seed set are accomplished within a few weeks after flowering. Fruits are generally one-seeded. Seeds weigh between 1.7 and 2.8 mg (mean: 2.4 mg) (Klotz, Kühn & Durka 2002) and lack specific adaptations for dispersal. The species has no persistent seed bank (Sterk 1975; Sterk *et al.* 1982; Dutoit & Alard 1995).

A total of nine populations were monitored during four consecutive years between 2003 and 2006, resulting in three period transitions and a total of 27 population matrices. A population was defined as all plants occurring in a particular grassland fragment. At the beginning of the monitoring period, population sizes (i.e. the number of flowering individuals) varied between 27 and 50 000. All populations were located in the south-western part of an elongated belt of calcareous grasslands in south-western Belgium (see Honnay *et al.* (2006) and Piessens *et al.* (2009) for more details). The minimum and maximum distances between two populations were 0.5 and 15 km, respectively. Most of these fragments were managed as nature reserves through rotational sheep grazing. The monitoring period was characterized by three extreme weather events: the summer heat wave of 2003 (August to September), the spring drought of 2005 (May to June) and the extreme heat wave of 2006 (June to July and in September) (see Appendix S3 for more details). Within each population, several (4–19) study quadrates were established, depending on the size of the population. During peak flowering, each plant's location and demographic features were recorded. Individuals were assigned to one of four classes based on size, morphological and reproductive traits: seedlings, vegetative adults, small (1–2 flowering stalks) and large (> 3 flowering stalks) generative adults (Fig. 2). Seedlings were easily distinguished from vegetative adults by the presence of withering cotyledons in June.

A total of 2352 individuals were monitored between 2003 and 2006. Population dynamics are described by the life cycle graph and projection matrices as shown in Fig. 2 and Appendix S4. Projection matrices include two non-zero fertility elements (elements (1,3) and (1,4)), three retrogression probabilities (elements (2,3), (2,4) and (3,4)), three stasis probabilities (elements (2,2), (3,3) and (4,4)) and six growth probabilities (elements (2,1), (3,1), (4,1), (3,2), (4,2) and (4,3)). To indicate how the study and reference populations differ, we show in Fig. 3a the distribution of these populations with respect to mean values of the life-history components fertility, stasis and growth. In Fig. 3b, we display the rather different distribution of these populations with respect to the summed variability in these life-history components.

For each population, we also collected biotic and abiotic environmental variables that might affect the demography of the species, including soil depth (cm), cover (%) of bare ground and rock, cover (%) of dominant grass species (*Brachypodium pinnatum* and *Bromus tectorum*), litter cover (%) and average vegetation height (cm). All values were calculated as averages of measured values in the sampled quadrats.
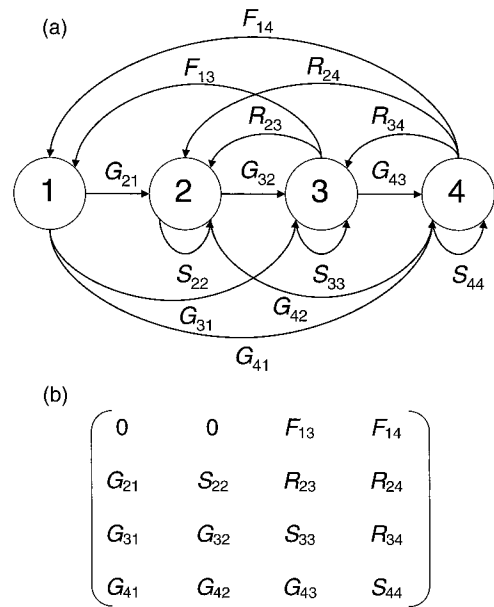

Fig. 2. (a) Life cycle graph for *Anthyllis vulneraria*. Circles correspond to plant stages (1: seedling; 2: vegetative adult; 3: small flowering adult; 4: large flowering adult). Arrows indicate potential transitions between stage classes. Matrix entries are subdivided in fertility (*F*), growth (*G*), stasis (*S*) and retrogression (*R*). (b) Population projection matrix corresponding to the life cycle graph in panel A.

Stochastic elasticities

STOCHASTIC ELASTICITIES BY MATRIX ELEMENT

Stochastic elasticities to mean transition matrix elements (E_{ij}^μ) are always positive, since a change in the mean value of any matrix element will alter the growth rate in the same direction. The distribution of elasticities over elements is broadly similar across the nine populations and the reference population (Fig. 4). Four elements tended to have high E_{ij}^μ: fertility of large reproductive individuals (element (1,4)), rapid growth of seedlings (4,1), stasis of large reproductive individuals (4,4) and fertility of small reproductive individuals (1,3).

Stochastic elasticities to variability in transition matrix elements (E_{ij}^σ) are displayed in Fig. 5 and vary much more among populations than do the E_{ij}^μ. Notice that there are several elements for which E_{ij}^σ is positive; for each population, Fig. 5 shows that the ratio of the sum of all positive E_{ij}^σ to the magnitude of the sum of all negative E_{ij}^σ is generally small, ranging from 0.2% to 18%. These positive E_{ij}^σ are notable, since conventional wisdom holds that, in general, increased variability in matrix elements will negatively influence population growth rates (e.g. Gillespie 1977; Benton & Grant 1996; Pfister 1998). In the reference population, E_{ij}^σ is positive for the variability of stasis for small reproductive individuals (element (3,3)) and of regression for large reproductive individuals (3,4). Increasing the variability in these elements would have (very) slight positive effects on *a*. Each of the study populations also had at least one matrix element for which an increase in the variance would increase *a*, and in one population (E), there were six matrix

(a)

(b)
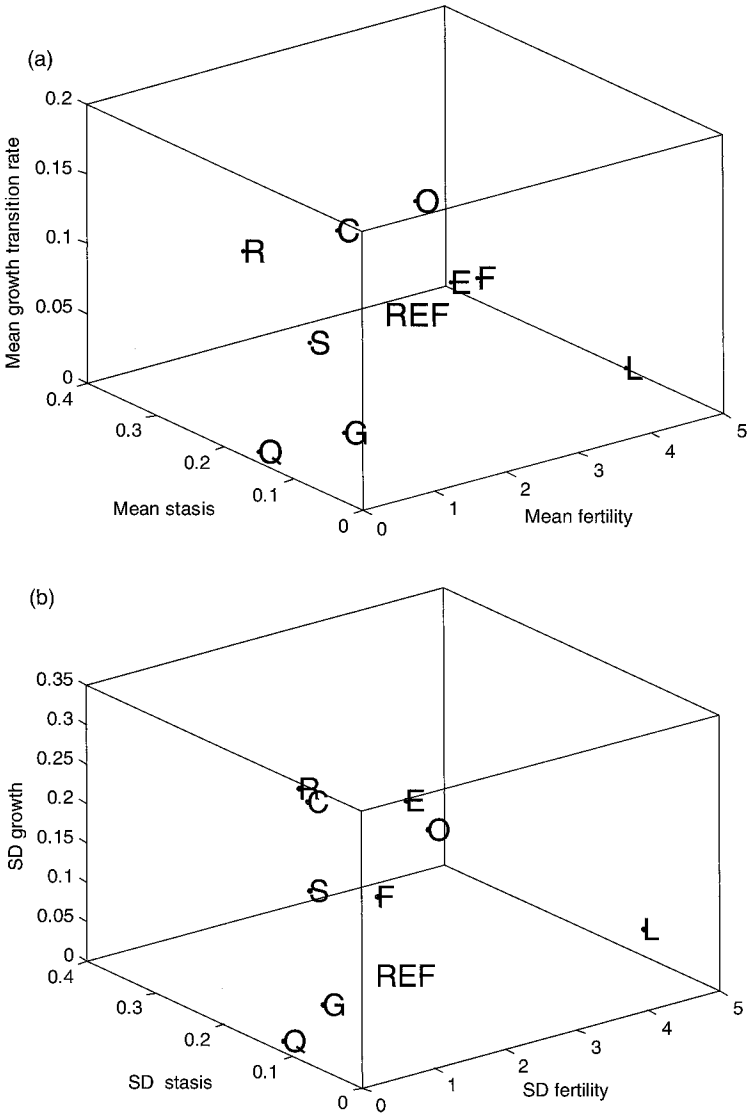
Fig. 3. (a) Differences in mean matrix elements. The nine study populations and the reference populations are indicated by labels showing the values of the mean fertilities (average of elements 1, i for all i), mean stasis (average of elements (i,i) for all i) and growth transitions (average of elements $i + 1, i$, for $i = 1, 2, 3$). (b) Differences in the variability of matrix elements. The nine study populations and the reference populations are indicated by labels showing the values of the standard deviations of fertilities (average for elements 1, i for all i), summed standard deviations of stasis (average for elements (i,i) for all i) and standard deviations (SD) of growth transitions (average for elements $i + 1, i$, for $i = 1, 2, 3$).

elements with positive E_{ij}^σ (Fig. 5). Every non-zero matrix element other than those representing rapid development of seedlings (element (4,1)) and vegetative adults (4,2)) had positive E_{ij}^σ in at least one population. E_{ij}^σ associated with retrogression of large reproductive individuals (element 3,4) were positive in six populations, while those of small reproductive stasis (3,3) were positive in five populations. E_{ij}^σ of small reproductive fertility (1,3) were positive in four populations, while those for growth of small reproductive individuals (4,3) and for stasis of large reproductive individuals (4,4) were positive in three populations each.

ELASTICITIES OF LIFE CYCLE COMPONENTS

Extending the approach of Silvertown *et al.* (1993), elasticities of matrix elements were summed within each of four types of life cycle components: fertility (first row elements $(1, j)$), retrogression ($i < j$), stasis ($i = j$) and growth ($i > j$). These sums, which we will refer to as component elasticities and denote simply by E^μ or E^σ as appropriate, represent the proportional

change in a resulting from a simultaneous and proportional increase of either the mean values or in the variability of all matrix elements of a given transition type.

All else equal, a change in mean values of growth transitions would have the largest effect on a in six of the nine natural populations (C, E, F, G, O, and S) and in the reference population, while changes in fertility would produce the largest effect in two populations, L and Q (Fig. 6). In one population (R), stasis elements had the highest E^μ. In population Q, E^μ for stasis elements was only slightly smaller than that of fertility elements and larger than that of growth elements, while in population S, E^μ of stasis elements was slightly higher than that of fertility, although less than that of growth elements. E^μ of retrogression elements had the smallest composite E^μ in every population, and retrogression E^μ only approached the magnitude of stasis E^μ in two populations (F and O).

Component elasticities to variance were generally negative and much smaller in magnitude than summed E^μ. E^σ was largest (most negative) for the growth component in four
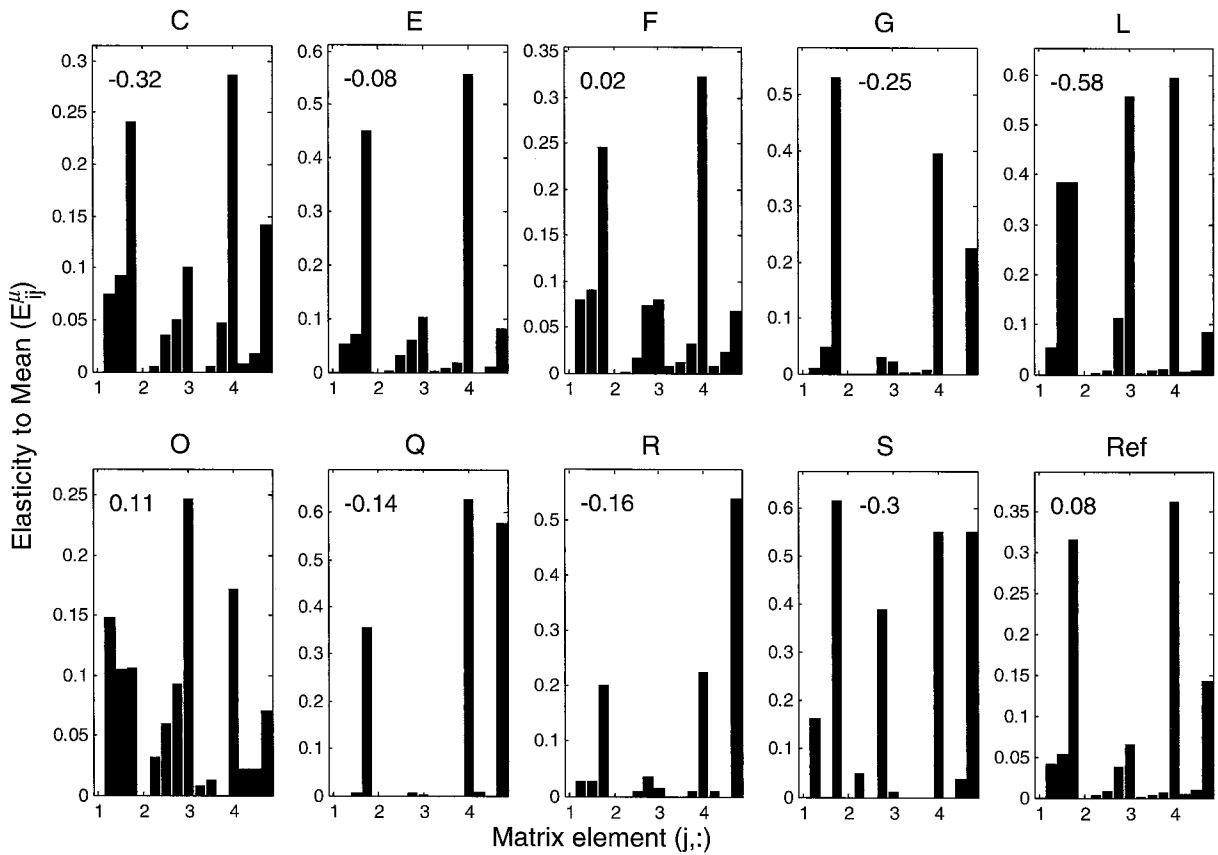
Fig. 4. Elasticities (E_{ij}^{μ}) of stochastic growth rate to changes in the mean values of sixteen matrix elements for nine natural populations of *Anthyllis vulneraria* and for the reference population. Labels on the *x*-axis ($j = 1, 2, 3, 4$) are followed by bars representing transitions from stage j to $i = 1, 2, 3, 4$. Populations are indicated by the letters at the top of each panel of the figure. The number in each panel represents the stochastic growth rate (a) of the population.

populations (C, F, G and S), largest for fertility in three populations (E, L and O) and largest for stasis in two populations (Q and R). A few of the component E^{σ} were positive, but these were generally small and except for retrogression, stasis and components in population E, none exceeded 0.01.

Figure 6 also illustrates the differences in the signs and magnitudes of the E^{σ} values relative to the E^{μ} values. The ratio of the sum of the absolute value of the E_{ij}^{σ} to the sum of the absolute value of the E_{ij}^{μ} was of the order of 0.1 in four natural populations and in the reference population, 0.3 in three other populations (E, Q and S) and over 0.5 in two populations (L and S). Interestingly, the reference population had very small values of elasticities E^{σ} relative to E^{μ}. In the reference population, the highest E_{ij}^{σ} were to variability in large adult fertility (element (1,4)) and large reproductive stasis (4,4), and both were negative.

Stochastic LTRE

We now use the SLTRE decomposition in eqn 1 to examine how differences in element means and variances (see Figs 3a, b) combine with elasticities (of the reference population, Figs 4 and 5) to shape the differences in a between the study and reference populations.

CONTRIBUTIONS OF DIFFERENCES IN MEAN

Although the E_{ij}^{μ} are always positive, the contributions of differences in mean values (C_{ij}^{μ}) to the differences between the stochastic growth rate of a given population (m) and the reference population (K) may be positive or negative. Large reproductive fertility (element (1,4)) had the highest elasticity to the mean and contributed the most to differences in a, followed by rapid growth of seedlings (4,1). However, in many populations contributions of small reproductive individuals' mean fertility (1,3) outweighed those of large reproductive stasis (4,4), even though the former had smaller E_{ij}^{μ} in the reference population. This was because, in 6 out of 10 populations, the magnitude of the differences ($\log \mu_{ij}^{(m)} - \log \mu_{ij}^{(K)}$) for element (1,3) was large enough to overbalance the larger elasticity of element (4,4).

CONTRIBUTIONS OF DIFFERENCES IN VARIATION

We now consider the contributions (C_{ij}^{σ}) of differences in variation of matrix elements. Variance in large reproductive fertility (element (1,4)) made the largest contribution in seven out of nine populations, while variance in large
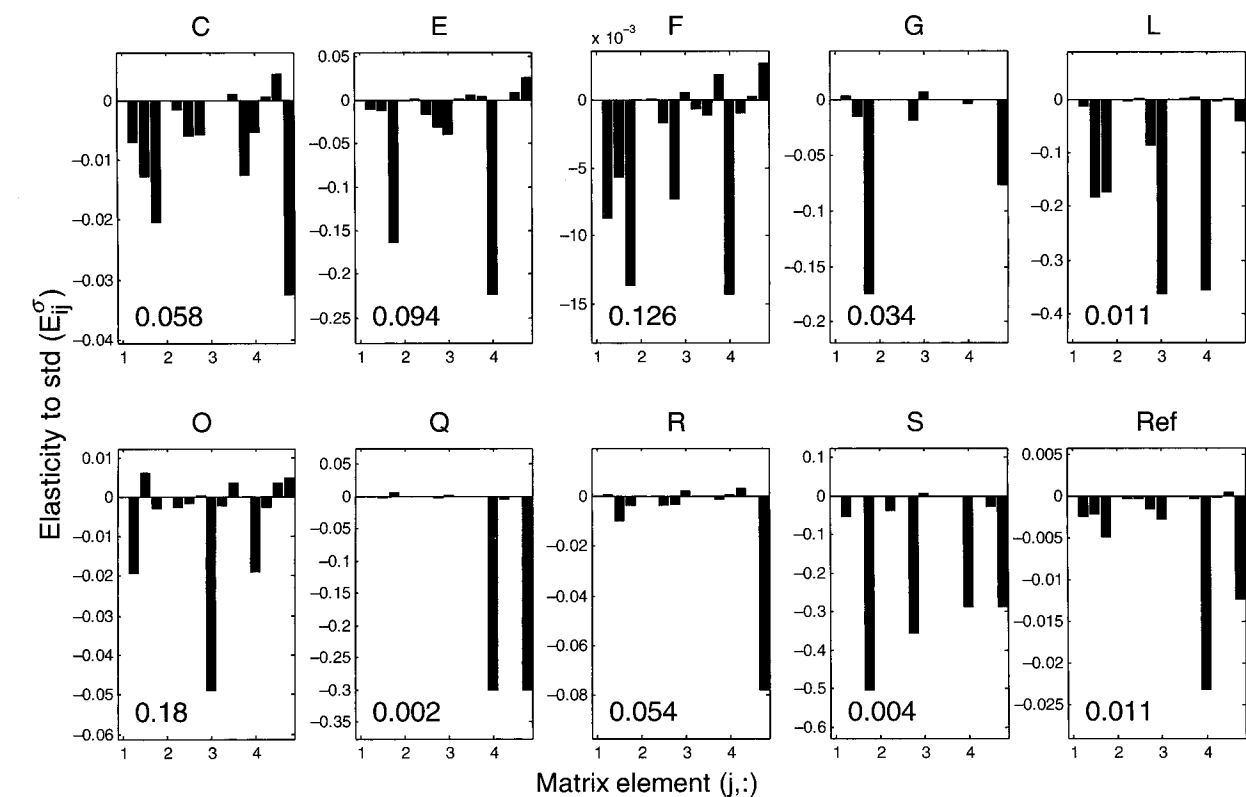
Fig. 5. Elasticities (E_{ij}^σ) of stochastic growth rate to changes in the variation of 16 matrix elements for nine natural populations of *Anthyllis vulneraria* and for the reference population. Labels on the x-axis ($j = 1, 2, 3, 4$) are followed by bars representing transitions from stage j to $i = 1$, 2, 3, 4. Populations are indicated by the letters at the top of each panel of the figure. The number in each panel represents the ratio of the sum of all positive E_{ij}^σ to the magnitude of the sum of all negative E_{ij}^σ.
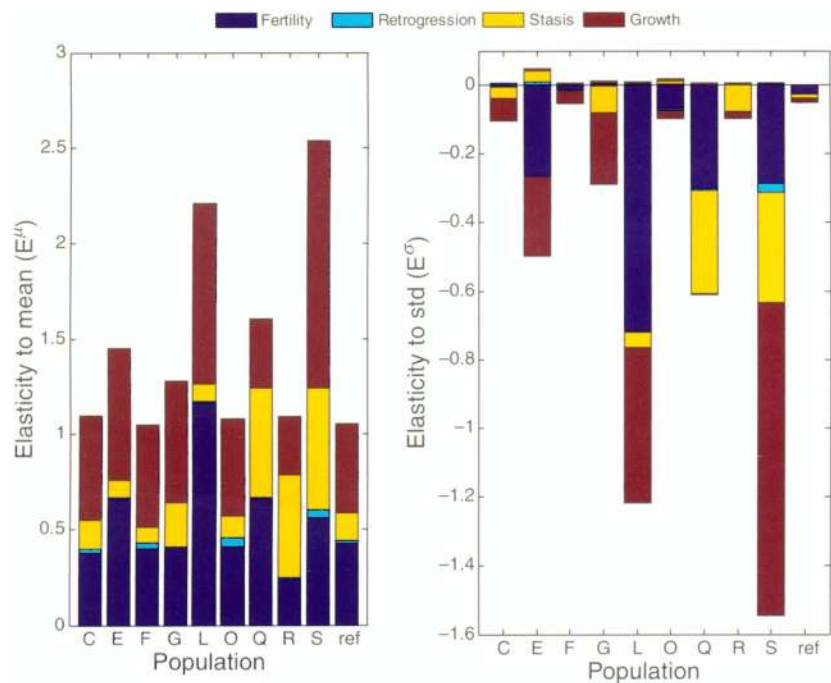

Fig. 6. Stochastic elasticities of four life cycle components for nine natural populations of *Anthyllis vulneraria* and for a hypothetical reference population. Elasticities are summed for each component and compared across populations. The left panel shows elasticity to changes in the mean (E^μ), while the right panel shows elasticity to changes in the variability of matrix elements (E^σ). Note that $E^\mu + E^\sigma = 1$, and the difference in scale between the left and right panel.

reproductive stasis (4,4) made the largest contribution in one population (O). In population Q, the contributions of variability in large reproductive fertility (1,4) and stasis (4,4) were roughly equivalent. Variances in small reproductive fertility (1,3) and variation in seedling growth (elements (2,1), (3,1) and (4,1)) made smaller contributions.
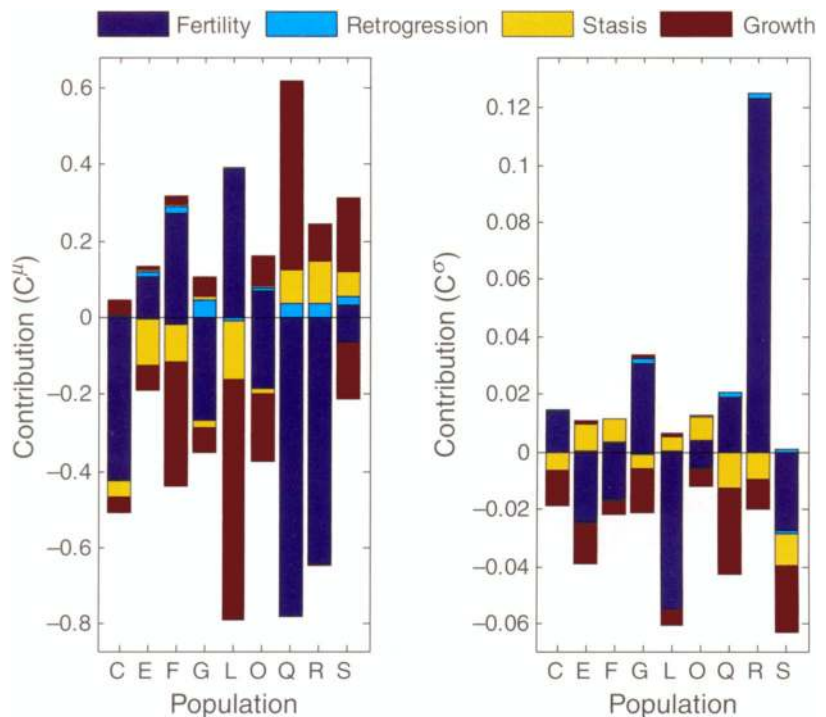
CONTRIBUTIONS OF LIFE CYCLE COMPONENTS

In the same way as we examined the sums of elasticities over all elements of the same transition type, e.g. stasis, we now sum contributions of elements within life-history components. The latter sums exhibit a different pattern than do the component elasticities (compare Fig. 7 with Fig. 6).

Differences in mean fertility made the largest net contribution in five of the nine populations (C, G, O, Q and R), while mean growth made the largest contribution in two populations (F and L) and mean stasis made the largest net contribution in another two (E and S). If we look just at the *magnitudes* of the C^μ for population O, fertility and growth make roughly equal contributions, but the positive and negative contributions within each of these components, which are on balance negative, yield slightly larger net contributions for fertility than for growth. Remarkably, in population S, the combined magnitudes of mean growth contributions are the largest, followed by those of mean fertility, but the negative and positive contributions within each of these two components mostly cancel, leaving stasis with the largest net contribution. Also, contributions from lower mean fertility (in populations Q and R) and growth (in populations F and L) were compensated by higher stasis and growth (Q and R) or higher fertility (F and L). In every population except for S, the largest contributions of mean matrix elements were negative and thus lowered the stochastic growth rate relative to that of the reference population. Contributions of mean retrogression elements were of small magnitude in every population, but after cancelling positive and negative growth contributions, net retrogression contributions ranked second among the C^μ in population G.

In terms of the variability of life cycle components, the ranking of net contributions were fairly consistent across populations. Fertility had the largest net C^σ in every population except two (O and Q) and ranked second in one of these (Q). Growth ranked highest among the C^σ in population Q and second among the C^σ in every other population except F (where net stasis contributions outweighed those of growth). It is noteworthy that in population O, the combined magnitude of fertility contributions outweighed those of stasis and growth, but the positive and negative contributions of fertility resulted in a net contribution smaller than either the mostly positive net contribution of variability in stasis elements or the mostly negative net contribution of growth. Variability in retrogression contributed little in any population.

In every population, variance in retrogression rates of large reproductive individuals (element (3,4)) was greater or equal to that in the reference population, but nevertheless variance in this element increased *a*. This was due to pairing with a positive E_{ij}^σ (in the reference population) to produce contributions (C_{ij}^σ) that raised the stochastic growth rate. This finding goes against the hypothesis that increased variability in vital rates must reduce population growth rates (Pfister 1998).

The magnitude of the total contribution of the standard deviations of matrix elements ($\Sigma_{ij} \left| C_{ij}^\sigma \right|$) did not the exceed 17% of ($\Sigma_{ij} |C^\mu|$) in any population. In three populations (F, O and Q), variability contributed less than 5% of the magnitude of mean contributions, while in two populations (C and L), the magnitude of C_{ij}^σ amounted to 5–10% of ($\Sigma_{ij} |C^\mu|$) and in four populations (E, G, R and S), the magnitude of C_{ij}^σ was between 12% (G) and 17% (R) of the combined magnitude of mean contributions.

Fig. 7. Summed contributions of differences in mean values (C^μ, left panel) and of differences in the variation of matrix elements (C^σ, right panel). Contributions are aggregated into partial contributions of four life cycle components: fertility, regression, stasis and growth. To illustrate opposing contributions within particular life cycle components, positive and negative sums are displayed for each component. Summing positive and negative values of C^μ and C^σ approximates the difference in stochastic growth rate *a* between an observed and the reference population. Note the difference in scale between the left and right panel.

Relationship between contributions of matrix elements and environmental variables

We also examined the relationships between stochastic growth rates and the contributions of different matrix elements on the one hand and a suite of measured environmental characteristics on the other. Although we did not find a direct relationship between stochastic growth rates and any of the measured environmental variables, regressing the summed contributions of differences in mean matrix elements (ΣC^{μ}) and of differential variability in these matrix elements (ΣC^{σ}) against soil depth showed that increasing soil depth significantly lowered the contributions of variability in matrix elements ($F = 13.52$, $P = 0.01$), but was not related to contributions of differences in mean matrix elements ($F = 0.47; P > 0.05$) (Fig. 8).

Discussion

In this article, we have described and illustrated a stochastic LTRE (SLTRE) for species occurring in temporally varying environments. SLTREs add a fundamental dimension (temporal variability) to standard LTREs. SLTREs are useful in at least two ways. First, time series of observations of populations in multiple habitats can be used to examine how differences in the (temporal) means and variances among populations contribute to differences in stochastic growth rates. Second, we can use SLTREs to compare populations in which we have measured environmental variables that are known to drive matrix elements, as illustrated by our analysis of the effects of soil depth across populations of *A. vulneraria*. In such a case, we may (i) develop models relating matrix elements to drivers within each population, and then use stochastic elasticities (Tuljapurkar, Horvitz & Pascarella 2003) to estimate the effect on each population's stochastic growth rate of the mean and variance of each individual environmental driver; (ii) then use SLTREs to examine how differences among populations in the temporal pattern of environmental drivers contribute to differences in matrix elements and in growth rate.

We expect this new approach to analyse temporal variability to prove especially useful in the analysis of natural populations experiencing environmental change. Many have recognized the importance of environmental stochasticity for the persistence of species and populations (see Fieberg & Ellner 2001 for a review of stochastic matrix models in conservation), and the stochastic growth rate (a) is widely used as the appropriate measure of population growth in fluctuating environments (Caswell 2001: 387–401). However, the SLTRE described here provides the first systematic way of incorporating observed differences in temporal variability into the comparison of natural populations.

Our analysis of *A. vulneraria* illustrates the insights gained from an SLTRE. In most populations, differences in fertility and in the transition rate from seedlings to flowering plants made the largest contribution to overall differences in stochastic growth rates. Consistent with the life history of the species, these results indicate that early stages in the life cycle (seed germination and recruitment) had a large impact on stochastic
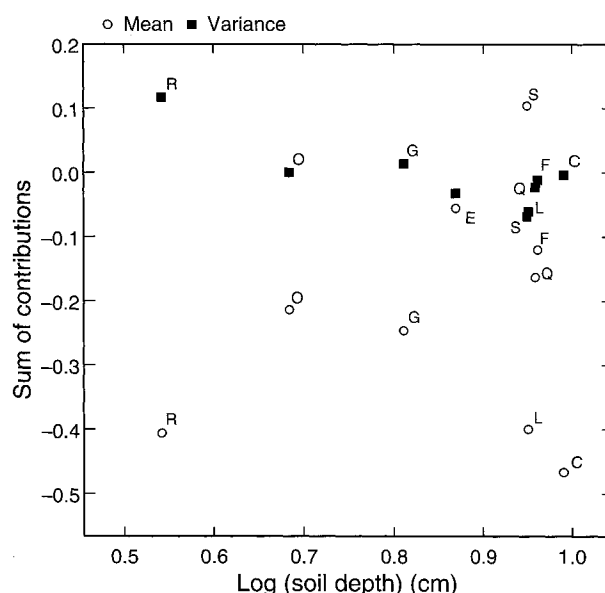

Fig. 8. Summed contributions of differences in mean matrix elements (ΣC^{μ}) and differential variability in these rates (ΣC^{σ}) in relation to soil depth for nine natural populations of *Anthyllis vulneraria*.

population growth rate. The monitoring period was characterized by at least two extreme drought events that differed in intensity, duration and timing during the growing season. Whereas the longest and warmest period occurred from August to September 2003, with only 49% and 25% of the normal amount of precipitation, respectively, this event had little impact on fertility, as it occurred after flowering and seed set. On the other hand, the early drought in May and June 2005, with only 63% and 65% of the normal rainfall, respectively, resulted in massive fruit abortion in 2005, which most probably explains the very low recruitment of seedlings in 2006. Because the species lacks a persistent seed bank, recruitment of seedlings is entirely dependent on seed production in the previous year. In contrast to the high adult survival in the early drought of 2005, the late drought of 2003 appeared to be particularly detrimental for the survival of large reproductive adults. The 2004 season was not unusually dry. The study populations varied significantly in their response to drought. Although the sequence of drought events would suggest that fertility and adult survival might be highest in 2004–2005, in that interval only about half the populations had highest recruitments, and three populations had relatively low survival in that year. As a result, it would be difficult, if not impossible, to translate information on drought directly into changes in matrix elements. For this reason, we conducted an analysis of the relationship between environmental factors and SLTRE contributions.

Our results are consistent with the observation of Morris et al. (2008) that short-lived species are particularly vulnerable to climatic extremes. Given that *A. vulneraria* life expectancy is below 5 years, high matrix element variability was predicted to lead to extremely low stochastic population growth rates. Deterministic analyses using population-mean matrices

predict positive growth rates $(\lambda_0^{(m)})$ for four populations (plus the reference population), while deterministic LTRE analysis predicts positive growth for all but two populations (C and G). This contrasts strongly with stochastic growth rates calculated for these populations. Of the nine populations sampled, only two had a positive stochastic growth rate, indicating that most populations are bound to go extinct under the prevailing (stochastic) conditions. However, populations responded very differently to the same climatic events. In some cases (e.g. population C), low stochastic growth rates were the result of low mean transitions, whereas in others (e.g. populations L and S) large variation in matrix elements led to low stochastic growth rates. These results clearly show that, even within a small geographical area, populations from a single species can exhibit extreme variability in demography (Jongejans *et al.* 2010) and that the processes affecting stochastic growth rates may differ from one population to the next, probably as a result of differences in local abiotic and biotic conditions. Our analyses further suggest that this different response was partly explained by differences in soil depth, given that the relative magnitude of summed contributions of variability in matrix elements declined with increasing soil depth, whereas the relative magnitude of summed contributions of mean matrix elements increased with increasing soil depth. Soil depth thus reduces the impact of a variable environment, e.g. drought. Similar results have been reported for *Purshia subintegra* in Arizona (Maschinski *et al.* 2006) and *Fumana procumbens* in south-Swedish grasslands (Bengtsson 1993).

We did not, however, find a direct relationship between stochastic growth rates and any of the measured environmental variables. Because the dynamics of plant populations are a function of all the demographic rates (i.e. birth, growth and death rates) that in turn determine matrix elements, it might be that other variables (e.g. outcrossing rates, seed predation or timing and intensity of sheep grazing) have been more important than local environmental conditions in determining stochastic growth rates in the studied populations. For example, grazing by sheep during peak flowering strongly reduces seed output and negatively affects seedling establishment in the year following grazing (Bastrenta 1991). Grazing by sheep has most probably contributed to the extreme variation in transition elements and the low stochastic growth rate observed in population L. Nonetheless, it may be clear that in the context of predicted climate change, the observed variation in responses to climatic extremes may be an asset to the species, as not all populations will be swept away simultaneously in a process leading to regional extinction of the species. Although more research is needed to elucidate the exact factors explaining the observed variation in stochastic growth rates between these populations, SLTRE analysis improves our understanding of the life history of *A. vulneraria* in its variable environments.

In the example provided here, we describe how to construct an SLTRE with time-series demographic data and show how stochastic elasticities (as opposed to deterministic elasticities) are employed in decomposing differences in stochastic growth rates. An SLTRE provides new insight into the relative contributions of mean matrix elements vs. variability of matrix ele-

ments in generating such differences. For instance, environmental differences may cause the contributions of mean matrix elements to be negative when the contribution of variability is positive or *vice versa*. In addition, the identification of transition elements with positive elasticities to variability (i.e. $E_{ij}^\sigma > 0$) highlights the importance of qualifying widely held assumptions about the negative role of variability of matrix elements in the regulation of population growth. Although it has been asserted that variability in matrix elements necessarily entails reductions in the stochastic growth rate, many natural populations, including our example species, exhibit positive E_{ij}^σ for at least one transition element (e.g. Tuljapurkar, Horvitz & Pascarella 2003; Haridas & Tuljapurkar 2005). Not surprisingly, transition elements with positive E_{ij}^σ were stasis and retrogression, both of which have been shown to buffer variation in population growth rates (e.g. Jongejans & de Kroon 2005; Salguero-Gómez & Casper 2010). Notably, the only two populations with positive stochastic population growth rates (F and O) had the highest ratio of positive to negative elasticities to the variance (Fig. 4).

Although we have focused on differences in means and variances of matrix elements, our approach is readily extendable to examine habitat-specific differences. For example, if we assume that our data include a year in which all populations experienced drought, and we wanted to know how the resulting differences in matrix elements contributed to observed differences in population growth rates, then, instead of working with the stochastic elasticities of means and variability $(E_{ij}^\mu, E_{ij}^\sigma)$, we can compute habitat-specific elasticities that reveal how changes in matrix elements that only occur in the drought year affect population growth rates. These habitat-specific elasticities E_{ij}^β describe the effects of changes in matrix element (i,j) when the habitat state is β and depend on the environmental sequence (Horvitz, Tuljapurkar & Pascarella 2005). These elasticities sum to unity over all matrix elements and all habitat states. They can be used in an SLTRE to calculate contributions of differences in individual matrix elements in each particular habitat state. For instance, it would allow us to identify how much of the observed differences in stochastic growth rates can be attributed to the effects of drought years. Caswell (2010) provides an alternative stochastic LTRE method, separating contributions of variation in the environment and contribution of population-specific responses of vital rates to these environmental changes.

A particular application of SLTRE would be towards improving our understanding of the ecological and environmental effects of climate change. Global climate models predict changes in the variability of natural environments that meet or exceed predicted changes in mean environmental measures such as temperature or precipitation, as well as predicting increases in the frequency of extreme weather events (e.g. Karl, Knight & Plummer 1995; Bates *et al.* 2008). In light of these findings, there is a clear role for SLTRE in improving insight into the differential responses of populations to environmental variability, whether examining the effects of climate change or studying populations that live in extreme, variable or disturbance-driven habitats.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Constructing a stochastic life table response experiments (SLTRE) with IID rates.

Appendix S2. Matlab code for conducting stochastic LTRE (SLTRE).

Appendix S3. Weather conditions and microclimate in the study area.

Appendix S4. Population matrices for nine *Anthyllis vulneraria* populations sampled annually between 2003 and 2006.

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