

Elasticity of population growth with respect to the intensity of biotic or abiotic driving factors

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Abstract. Demographic analysis can elucidate how driving factors, such as climate or species interactions, affect populations. One important question is how growth would respond to future changes in the mean intensity of a driving factor or in its variability, such as might be expected in a fluctuating and shifting climate. Here I develop an approach to computing new stochastic elasticities to address this question. The linchpin of this novel approach is the multi-dimensional demographic difference that expresses how a population responds to change in the driving factor between two discrete levels of intensity. I use this difference to design a perturbation matrix that links data from common empirical sampling schemes with rigorous theory for stochastic elasticities. Although the starting point is a difference, the products of this synthesis are true derivatives: they are elasticity with respect to the mean intensity of a driving factor, and elasticity with respect to variability in a driving factor. Applying the methods to published data, I demonstrate how these new elasticities can shed light on growth rate response within and at the boundary of the previously observed range of the driving factor, thus helpfully indicating nonlinearity in the observed and in the potential future response. The stochastic approach simplifies in a fixed environment, yielding a compact formula for deterministic elasticity to a driving factor.

Key words: climate change; demography; population growth; species interactions; stochastic elasticity.

INTRODUCTION

Demographic analysis is a powerful tool for elucidating the factors that influence age-, stage-, or size-structured populations. Examples range from life-history evolution (e.g., Coulson et al. 2010) to species interactions (e.g., Kalisz et al. 2014) and conservation and management (e.g., Morris and Doak 2002). Much of the power of demographic analysis lies in its ability to decompose population responses into distinct contributions from individual life-history transitions. Sensitivity and elasticity are long-established, widely used tools for pinpointing influential individual demographic rates in this way (e.g., Crouse et al. 1987). Decomposition approaches can leave some important questions unanswered, however. Awareness of underlying driving factors (by which I mean any factor that influences the value of at least one demographic transition rate) is rising in ecology (e.g., Crone et al. 2013, Ehrlén et al. 2016). Such drivers often affect multiple rates simultaneously, with the magnitude of effect differing between rates. Examples of drivers having such multifaceted effects include fire (Menges and Quintana-Ascencio 2004, Emery and Gross 2005), species interactions (Maron and Crone 2006, Evans et al. 2012), changes in temperature or moisture (Doak and Morris 2010, Benavides et al. 2013), management activities such as livestock tending or vegetation

thinning (Giroldo and Scariot 2015), road density (Boulanger and Stenhouse 2014), or distance from a forest edge (Flaspohler et al. 2001). In such cases, the composite population response to the driving factor may play a prominent role in potentially urgent management questions as well as in basic questions in ecology and evolution. For instance, how can the growth rate of a focal population be expected to respond to continued gradual increases in temperature, in abundance of a novel species, or in road construction?

Demography provides useful tools to quantify the effect of driving factors or interactions on population growth. Ehrlén et al. (2016) identify 136 plant studies conducted in the past 20 years that investigate how changes in a driving factor affect the population growth rate predicted from a parameterized demographic model. Many of these studies take advantage of naturally occurring variation in the driving factor (and commonly involve a linear regression of population growth rate on the factor), whereas others manipulate the driver experimentally. Maron's and Crone's (2006) review of 30 studies that quantify the effects of animal consumption on future plant abundance also includes many that take such an experimental approach, comparing the asymptotic population growth rate in plots where consumers are present to the rate in plots where consumers are absent.

Useful as it is to quantify changes in the population growth rate, more detailed analysis requires additional quantitative tools. One such tool is the life table response experiment (LTRE), which decomposes observed differences in population growth rate into contributions from

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individual demographic rates (e.g., Caswell 2010, Davison et al. 2010). This retrospective analysis explains which rates are most important to an observed difference in growth rate, but does not address future and/or additional change. To attack that problem, researchers may attempt to describe the relationship between individual demographic rates and the driving factor. When combined with sensitivities, which describe how population growth would respond to change in individual demographic rates, this approach can, in principle, describe how the population growth rate would respond to change in the driving factor. This reasoning is an expression of a total derivative using the chain rule, which, briefly, is $d\lambda/dF = \sum_i (\partial\lambda/\partial v_i)(\partial v_i/\partial F)$, where the population growth rate is λ , and where the demographic rates v_i depend upon a shared driving factor, F .

Though reasonable in principle, application of chain-rule-type approaches to specific systems can involve difficulties. The core of the concept is to break the total derivative into two component derivatives. Rigorous standard methods are available for computing the individual sensitivities $\partial\lambda/\partial v_i$, but determining the derivatives $\partial v_i/\partial F$ can be another matter. One can regress a demographic rate on the driving factor, and if the rate is a linear function of the driver, then the desired local derivative is merely the slope of the linear relationship. It can be reasonable to assume that rates depend linearly on driving factors, at least within some range of interest (e.g., Baxter et al. 2006, Vitt et al. 2009, Adler et al. 2012). In general, however, there no reason to expect linearity, and because rates are positive and in many cases are also bounded above, a strong effect of a driver would imply eventual nonlinearity (e.g., Morris and Doak 2002:337). In some cases, nonlinearity can be dramatic (e.g., Gotelli and Ellison 2006). Nonlinearity can substantially complicate the empirical assessment of local derivatives. The resolution with which the driving factor is sampled affects the accuracy with which the local slope of a nonlinear function can be estimated: for instance, barring an *a priori* hypothesis regarding functional form, at least three levels of the driving factor are necessary to detect any nonlinearity, and experimental manipulation in particular may contrast only two distinct levels of the driver. Furthermore, regression requires quantification of the driving factor. Such quantification may not always occur, and may be particularly challenging in cases where a species interaction has been experimentally manipulated, such as in consumer exclusion and control plots, for instance. Finally, regression must be performed for each rate that responds to the driver, so the method becomes more cumbersome the more multifaceted the effect of the driver. Although they do not always constitute an obstacle, these potential issues can unfortunately limit the generality with which chain-rule-type approaches can rigorously be applied.

The potential issues with chain-rule-type approaches revolve around the extraction of derivatives from demographic data. These data are collected at different levels of the driving factor and are therefore fundamentally

discontinuous. I propose that theoretical development would be helpful to shift some emphasis away from how to manipulate discontinuous data to infer an underlying continuous function and toward what useful and interesting questions it might be possible to address by leveraging the discontinuous demographic data in hand. Here, I focus on the empirical difference in demography that occurs between just two given levels of a driving factor. This demographic difference is multidimensional if it involves multiple rates simultaneously. Barring further empirical work to sample the driving factor with greater resolution, this difference is the best available expression of how demography responds to a change in the intensity of the driver between these two levels. Therefore, *given the limitation of the resolution of the discontinuous data*, to ask what the proportional effect on population growth would be of a slight proportional increase in this multidimensional response is equivalent to asking what the effect would be of a slight proportional increase in the intensity of the driver. It is this proportional local derivative that I develop here as the elasticity, E_F , of population growth with respect to the intensity of the driving factor, or driver elasticity for short.

To obtain this derivative, I begin with theory for producing a standard elasticity, by which I mean the elasticity of population growth with respect to a single demographic rate, all others being held constant. I first generalize this theory to enable computation of the elasticity of population growth with respect to multiple, simultaneously changing demographic rates. I then propose a novel design to a key element of this theory to incorporate information about the multidimensional demographic effects of driving factors, such as would be available from empirical protocols commonly used to quantify how the driver affects growth rate. Thus, from two tools with two distinct purposes, one theoretical and one empirical, I synthesize a new, integrative method for quantifying the response of population growth to a small increase in the intensity of an abiotic or biotic driving factor. It is efficient no matter how many rates the driver affects. Because it eliminates the intermediate step of determining relationships between individual demographic rates and the driving factor, it works even in situations where the driver has not been quantified or has been sampled at fewer than three levels. In such cases, it is not possible to determine nonlinearity in how demographic rates depend on the driver, but I show below that the resulting elasticity can nevertheless reveal nonlinearity in how growth rate depends on the driving factor within the range in which the driving factor has been observed, as well as at the boundary (and therefore immediately outside) of the observed range. Boundary information is critical to predictions regarding the possible effects of environmental change beyond what has already occurred.

Many ecologically important driving factors vary substantially through time. Prominent examples include climate and species interactions. Furthermore, fluctuation in additional factors can influence a focal population

along with the driving factor of interest, resulting in background variation in demographic rates and/or context dependency in the response to the driving factor (e.g., Maron et al. 2014). Therefore, it is desirable that measures of elasticity of population growth with respect to a driving factor also accommodate temporal variability. To my knowledge, this is not a feature explicitly addressed by other approaches to the demographic effects of driving factors (although computer simulation should usually be an option). The approach presented here is rigorously stochastic, and highlights the effects of variation in the driver while also accounting for additional, background fluctuation. It can separate the influence of change in the mean effect of a driving factor from the influence of change in the variability in the effect of a driving factor. In a constant environment, the approach simplifies to a single, compact, easy-to-apply formula.

As a final note, the methods described here address situations where a driving factor affects the numerical values of demographic rates. These situations are distinct from ones where the driving factor affects the sequence of demographic transition rates, such as when hurricanes or fires alter the sequence of environments that plants experience (e.g., Quintana-Ascencio et al. 2003, Tuljapurkar et al. 2003). In such systems, the methods developed here would be appropriate for investigating changes not in hurricane or fire frequency, but in the intensity of the successional or regrowth processes that drive subsequent vegetation change. Also distinct, and not addressed here, are situations where a driving factor such as disease or an interacting species participates in population structure (e.g., Ettl and Cottone 2004, Lee and Inouye 2010).

METHODS

In an environment that does not vary, the basic equation for change in a structured population is

$$\mathbf{n}(t) = \mathbf{A}\mathbf{n}(t-1), \quad (1)$$

where the vector $\mathbf{n}(t)$ contains the abundances of each demographic class (age, stage, size, etc.) at time t , and the constant projection matrix \mathbf{A} contains the rates at which members of each class transition into every class during one time interval (e.g., Caswell 2001). The total abundance of such a population eventually changes at constant rate, λ . The proportional response in this asymptotic growth rate that results from a proportional change in one element a_{ij} of the matrix \mathbf{A} is the elasticity, E_{ij} , of the growth rate with respect to that matrix element, defined as $E_{ij} = (\partial\lambda/\lambda)(a_{ij}/\partial a_{ij})$ (e.g., Caswell 2001).

When the environment changes from year to year, the projection matrix also varies:

$$\mathbf{n}(t) = \mathbf{A}(t)\mathbf{n}(t-1). \quad (2)$$

In a variable environment, a population does not achieve a constant rate of change, but instead approaches a long-run average growth rate, $\log \lambda_s = \lim_{t \rightarrow \infty} (1/t) \log [N(t)/N(0)]$,

where $N(t)$ is the sum of the elements of $\mathbf{n}(t)$ (Tuljapurkar 1990). This growth rate responds to changes in the elements of the projection matrix, but in a variable environment, a given demographic transition is described not by a single value, a_{ij} , but rather by a set of values, $a_{ij}(t)$. There are different ways to perturb a set of values, and Tuljapurkar et al. (2003) examine the different ways in which it is meaningful to define elasticity of the stochastic growth rate, $\log \lambda_s$, in light of this fact. They distinguish between the proportional response of the long-run growth rate to change in only the mean value of a matrix element, which they call $E^{S\mu}$, the response to change in only the variability around the mean, $E^{S\sigma}$, and the response to change in the mean and variability simultaneously (called E^S for historical reasons). Tuljapurkar et al. (2003) provide a single, compact expression for determining these different elasticities (given here as Eq. 3) by substituting in the appropriate perturbation matrix, as I will discuss in greater detail.

It is possible, and frequently desirable, to express projection matrix elements as functions of underlying vital rates such as survival, growth or retrogression, or fecundity (e.g., Morris and Doak 2002). Haridas and Tuljapurkar (2005) adapt the perturbation matrices presented in Tuljapurkar et al. (2003) to compute elasticities with respect to the mean or variability of a single underlying vital rate, with all other rates held constant; Morris et al. (2008: appendix B) describe this approach in greater detail.

To develop a new elasticity, I first note that the key to the flexibility of the approach of Tuljapurkar et al. (2003) is a perturbation matrix $\mathbf{C}(t)$. This matrix prescribes changes to the elements of the projection matrix $\mathbf{A}(t)$, with different choices for this perturbation matrix leading to different elasticities. For example, Tuljapurkar et al. (2003) let $C_{ij}(t) = \mu_{ij}$, where $\mu_{ij} = a_{ij}(t)$, the mean of the i, j th matrix entry of the projection matrix, and let all other elements of the perturbation matrix $\mathbf{C}(t)$ be 0. This choice perturbs a single matrix element in isolation, in proportion to the mean of that matrix element in every time step. This changes the mean of the distribution of the i, j th projection matrix element without changing its variability; substituting this matrix into Eq. 3 yields the stochastic elasticity $E_{ij}^{S\mu}$ of the long-run growth rate with respect to the mean of the i, j th matrix element. To obtain the stochastic elasticity $E_{ij}^{S\sigma}$ of the long-run growth rate with respect to the higher moments (variability) of $a_{ij}(t)$, Tuljapurkar et al. (2003) let $C_{ij}(t) = a_{ij}(t) - \mu_{ij}$, with other elements of $\mathbf{C}(t)$ being 0. This choice adds a larger amount in years when the rate is farther above its mean, and subtracts a larger amount in years when the rate is farther below its mean, changing the variability of the distribution of the i, j th element without changing its mean.

The perturbation matrix plays the same key role in stochastic elasticities to underlying vital rates such as survival (Haridas and Tuljapurkar 2005). For instance, following Haridas and Tuljapurkar (2005), Morris et al. (2008: appendix B) choose $\mathbf{C}_x(t) = \bar{v}_x(\partial\mathbf{A}(t))/(\partial v_x)$, where the matrix derivative is the matrix of derivatives of individual projection matrix elements with respect to v_x .

These derivatives are determined by how matrix elements involve v_x , which depends upon the structure of the projection matrix. The result of this matrix perturbation is $E_{v_x}^{S\mu}$, the stochastic elasticity of the long-run growth rate with respect to the mean of vital rate v_x . Using instead $C_x(t) = (v_x(t) - \bar{v}_x)(\partial \mathbf{A}(t)) / (\partial v_x)$ yields $E_{v_x}^{S\sigma}$, the stochastic elasticity of the long-run growth rate with respect to variability around the mean in vital rate v_x .

In order to move beyond elasticity with respect to individual matrix elements or vital rates, I now note that the perturbation matrix $C_x(t)$ can accommodate simultaneous, correlated perturbations of multiple matrix elements. In fact, it already does so in the case of elasticity with respect to vital rates, where multiple matrix elements change, and where correlations between matrix elements arise due to shared dependence of multiple matrix elements on individual vital rates as described by the projection matrix. Nothing about the methods of Tuljapurkar et al. (2003) or Haridas and Tuljapurkar (2005), however, constrains the perturbation matrix to changes arising from single demographic rates, and indeed, the original derivation in Tuljapurkar (1990) is general. One can in principle specify *whatever matrix perturbation one desires*, and use it in Eq. 3, to apply the perturbation to any demography and to compute the elasticity that reports the resulting effect on the stochastic growth rate. The crucial point is to specify perturbations that are biologically meaningful. To obtain elasticity with respect to a driving factor, I develop a new perturbation matrix that encapsulates the multifaceted changes to the projection matrix that arise from change in an underlying driving factor or interaction. I approach the determination of this new perturbation matrix empirically, as the matrix response to perturbation of a driving factor will vary between different biological systems.

To assess demographic responses to driving factors, one must monitor demographic rates under at least two levels of driver intensity. Possible treatment pairs include, for example, herbivore exclusion treatment and untreated control, plots beneath a rainout shelter and controls, control plots and artificially warmed plots, and so on. Plots could also be arranged along an environmental gradient. Such empirical protocols are already in widespread use to quantify the demographic effects of biotic or abiotic driving factors (e.g., Ehrlén et al. 2016). They are also the basis for LTRE studies (Caswell 2001, Davison et al. 2010), where the goal is to decompose the effect of change in the driving factor into contributions from individual demographic transitions.

For the remainder of this paper, I assume the minimum necessary two levels for the driving factor. Because two levels are inadequate to infer nonlinearity in the response of demographic rates to the driver through nonlinear regression, this assumption will help to illustrate in the next section how elasticity to driving factors can nevertheless indicate nonlinearity in the response of population growth to the driver. In the treatment where the driving factor is lesser, I label rates with a minus sign, and

in the treatment where the factor is greater, I use a plus sign. Thus, $v_x^-(t)$ is the value (averaged across replicates) of the x th vital rate in year t in the treatment where the factor is lesser, and $v_x^+(t)$ is its value in the treatment where the factor is greater. Then in year t , the response of the x th vital rate to manipulation of the driving factor is $\Delta_x(t) = v_x^+(t) - v_x^-(t)$. Across T years, the mean response of the x th rate is the mean treatment difference, $\bar{\Delta}_x = (1/T)\sum_{t=1}^T \Delta_x(t)$.

I assemble all vital rates into a projection matrix for each year, one for each level of the driving factor. This yields a series of yearly projection matrices in each treatment. As do the individual measured vital rates, each matrix element has an empirical response to manipulation in each year, which is the difference between treatment levels in a given year: $\Delta_{ij}(t) = a_{ij}^+(t) - a_{ij}^-(t)$. Each matrix element also has a mean response across years, $\bar{\Delta}_{ij} = (1/T)\sum_{t=1}^T \Delta_{ij}(t) = E\{\Delta_{ij}(t)\}$. These are the differences that express the multifaceted effects on demography of change in the driving factor.

Now, I wish to perturb simultaneously every projection matrix element that has a nonzero response to the driving factor in at least 1 year. The key novel operational feature of elasticity with respect to a driving factor is to perturb each matrix element in proportion not to its mean or to its deviation from the mean, as in previous approaches, but in proportion to its *mean response to treatment* or to a given year's *deviation from the mean treatment response*. I let each perturbation matrix element be the mean treatment response of the corresponding projection matrix element, $C_{ij}(t) = \bar{\Delta}_{ij}$, to obtain elasticity of the stochastic growth rate with respect to change in the mean demographic response to the driving factor, $E_F^{S\mu}$. I let each perturbation matrix element instead be the deviation in each period from mean treatment response in the corresponding projection matrix element, $C_{ij}(t) = \Delta_{ij}(t) - \bar{\Delta}_{ij}$, to obtain elasticity with respect to variability in the demographic response to the driving factor, $E_F^{S\sigma}$. These choices for the design of the perturbation matrix single out the multifaceted response to the driving factor against a background of other potential sources of demographic variation. Because this perturbation is derived from the difference between treatment pairs, the values of the demographic rates to which the perturbation is applied are free to vary according to background fluctuation. The resulting slight perturbation to the projection matrix is proportional to the observed multidimensional response to the driver, including all correlations between vital rates due to shared dependence on the driving factor.

With new perturbation matrices in hand, we are now prepared to compute elasticities. As detailed in Tuljapurkar et al. (2003), Haridas and Tuljapurkar (2005), and Morris et al. (2008: appendix B), given a specific choice for the perturbation matrix $\mathbf{C}(t)$, the elasticity of the long-run stochastic growth rate is

$$E^S = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^T \frac{\mathbf{v}'(t)\mathbf{C}(t)\mathbf{u}(t)}{\lambda(t)\mathbf{v}'(t)\mathbf{u}(t+1)}. \tag{3}$$

Here, the vectors $\mathbf{u}(t)$ and $\mathbf{v}'(t)$ are a sequence of population age structures and reproductive value vectors, respectively, associated with the demography at a given level of the driving factor, and $\lambda(t)$ is the corresponding period-specific rate of population growth. Tuljapurkar (1990) defines these three quantities; note that the realized, time-dependent vectors $\mathbf{u}(t)$ and $\mathbf{v}'(t)$ are not the constant eigenvectors denoted using the time-independent notation \mathbf{u} and \mathbf{v} , and that the period-specific growth rate $\lambda(t)$ is similarly distinct from an eigenvalue, λ . To compute these quantities, one generates a long sequence of projection matrices to be perturbed, $\mathbf{A}(t)$, using independent and identically distributed draws from any set of projection matrices observed through time. Projecting the population forward through this sequence of matrices from an arbitrary initial population structure yields a corresponding sequence of population age structures, $\mathbf{u}(t)$, and period-specific growth rates $\lambda(t) = \|\mathbf{A}(t)\mathbf{u}(t)\|$, where the magnitude notation on the right-hand side indicates that vector elements should be summed. Projecting backward through the same $\mathbf{A}(t)$ from an arbitrary final reproductive value yields the $\mathbf{v}'(t)$. Initial and final segments of these sequences are discarded to avoid transients. Letting $C_{ij}(t) = \bar{\Delta}_{ij}$ in this expression yields the elasticity of population growth with respect to the mean demographic response to the driving factor; letting $C_{ij}(t) = \Delta_{ij}(t) - \bar{\Delta}_{ij}$ yields elasticity with respect to the variability in demographic response to the driver.

This development of elasticity works solely with demographic data, not with an underlying driving factor itself. This is a strength of the approach, because the data directly concern demography only: inference (such as nonlinear regression) is necessary to involve the driver. Up to this point, I have assumed that demography has been assessed at only two levels of driver intensity, and have not needed to assume that the value of the driving factor has been quantified at these levels. Finally, as described in the *Introduction* section, the demographic differences Δ_{ij} are the best available estimates of the effect of changes in the driver on the population. Eq. 3 accepts them as a multidimensional demographic difference and rigorously produces proportional local derivatives in the long-time limit (Tuljapurkar 1990, Steinsaltz et al. 2011). The resulting derivatives are the proportional change in long-run population growth with respect to the mean or variability of the observed multidimensional difference. Because the observed demographic change is functionally equivalent, given the resolution of the data, to a change between two levels of the intensity of the underlying driving factor, henceforward I refer to these derivatives as the elasticity of stochastic growth with respect to the mean intensity of a driving factor, E_F^{Stoch} , or the variability in the intensity of the driving factor, E_F^{Var} . For brevity, I refer to them collectively as driver elasticities.

Calculation of a deterministic driver elasticity could be desirable when sampling through time is insufficient for a stochastic analysis. By analogy with the stochastic approach, if one were to project the population repeatedly

through a single, constant projection matrix, the population would achieve a stable growth rate λ , which can be computed directly as the dominant eigenvalue of the projection matrix, and a stable age structure vector \mathbf{u} and reproductive value vector \mathbf{v}' , the right and left eigenvectors associated with the dominant eigenvalue, respectively. Then the deterministic elasticity is

$$E_F = \frac{\mathbf{v}'\mathbf{C}\mathbf{u}}{\lambda\mathbf{v}'\mathbf{u}} \quad (4)$$

where the perturbation matrix for a driving factor is $C_{ij} = \Delta_{ij}$; this single possible choice yields a single elasticity E_F , as there is no variability in the response to the factor. The values of this elasticity should be the same as through use of the chain rule with a linear relationship between each vital rate and the driving factor.

Both the stochastic and the deterministic elasticities are local derivatives, and they apply at the level of demography used to generate the series of projection matrices $\mathbf{A}(t)$ in Eqs. 3 and 4. Thus, the perturbation matrix approach enables one to compute elasticities any level of intensity of the driving factor at which demography has been observed. In the next section, I use a worked example to illustrate the application and interpretation of these elasticities.

EXAMPLE AND RESULTS

This section walks through the calculation and interpretation of driver elasticities using data from Jacquemyn et al. (2012); Matlab code for calculation appears as Appendix S1. Jacquemyn et al. (2012) present a stochastic LTRE to determine the long-term population effects of cattle grazing on the grassland herb *Primula veris*. They contrast grazed plots with fenced controls that were mowed once a year, monitoring two populations in both treatments for 10 yr to obtain a series of nine projection matrices for each population-by-treatment combination. They establish four stage classes (seedlings, juveniles, vegetative individuals, and flowering individuals); demographic rates are survival, growth conditional on survival, probability of flowering, and a fecundity term, which is the product of average number of flowers, average number of seeds per fruit, and proportion of seeds germinating and establishing as seedlings. Jacquemyn et al. (2012: Eq. 1) provide the structure of the transition matrix, along with the values of each rate in each year in their appendix A1. I use this information to compute elasticities of the long-run growth of *P. veris* with respect to grazing.

The mowing treatment removes plant biomass, but other aspects of grazing are absent. I designate mown plots the low-grazing treatment (–), and the cattle-access plots the high-grazing treatment (+). Following Jacquemyn et al. (2012), I first average across the two replicate populations in each treatment. I use Eq. 1 from Jacquemyn et al. (2012) to assemble the demographic rates into nine yearly projection matrices in each treatment level. For instance, the (2, 1) matrix element a_{21} describes

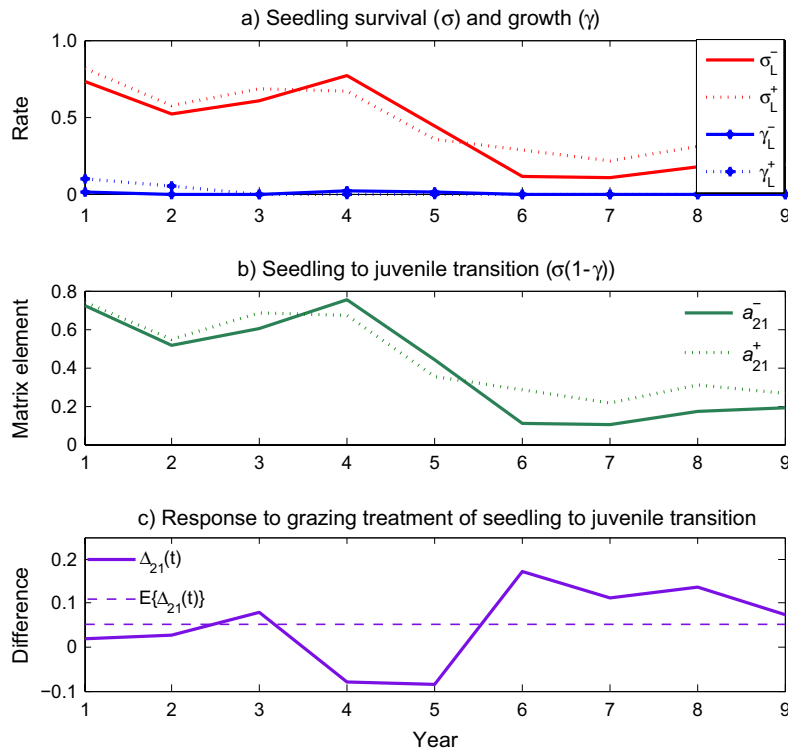


FIG. 1. Calculation of the response of a matrix element to a driving factor, for use in the perturbation matrix. Data for *Primula veris* in mown control (–) and grazed treatments (+), from Jacquemyn et al. (2012). (a) Seedling survival (σ_L) and growth (γ_L) to vegetatively reproducing individuals. (b) The matrix element ($a_{21} = \sigma_L(1 - \gamma_L)$) describing transition from seedling to juvenile, in both control and grazing treatment. (c) The empirical response to grazing in this matrix element, $\Delta_{21}(t)$, is the difference between its values in the two treatments; the dashed line shows the mean through time. [Color figure can be viewed at wileyonlinelibrary.com]

the rate of transition from seedlings (column 1) into juveniles (row 2), and is a product involving seedling survival (σ_L , using the notation of Jacquemyn et al. (2012)) and seedling growth into the vegetatively reproductive stage (γ_L): $a_{21} = \sigma_L(1 - \gamma_L)$. Fig. 1a shows the values through time for each of the two underlying vital rates (σ_L and γ_L) in each treatment. Fig. 1b shows the resulting values through time of the (2, 1) matrix element in each treatment. Because growth rates of seedlings into vegetatively reproductive individuals are very low (Fig. 1a), their complements ($1 - \gamma_L$) are near 1, and as a result the matrix element largely reflects seedling survival rates (compare top and middle panels). Fig. 1c shows how the difference between treatments in the (2, 1) matrix element ($\Delta_{21}(t) = a_{21}^+(t) - a_{21}^-(t)$) fluctuates around its mean. This is the treatment response of the element in each year.

Fig. 2 summarizes the treatment response shown in Fig. 1c for all 16 matrix elements. The first four elements are transitions from the seedling class to every other class, the second four are transitions from juveniles, the third four are from vegetative individuals, and the last four from flowering individuals. The 13th element, a_{14} , which is the only one that can take on values (and hence also treatment response values) greater than 1, is the fecundity element. The most negative responses to treatment occur in transitions from vegetative (12th element, a_{43}) or

flowering (16th element, a_{44}) individuals to flowering individuals, whereas reproduction (13th element, a_{14}) and transitions from flowering to vegetative individuals (15th, a_{34}) respond most positively. These treatment responses are detrimental to population growth except for reproduction (a_{14}), which increases due to an increase in seedling establishment (Jacquemyn et al. 2012).

I generate $T = 10,000$ matrices $\mathbf{A}(t)$ using independent and identically distributed draws from the nine observed grazed projection matrices. I form driver perturbation matrices as described in the previous section, and use them in Eq. 3 to obtain elasticities. Using the observed grazed projection matrices to generate structure and reproductive value vectors produces derivatives at the treatment level of grazing. This asks, “What would the response in long-term population growth be if grazing intensity increased by a slight proportion, such that the demographic response increased by a slight proportion?” I also compute elasticities using the observed mowing control matrices for the long series of projection matrices. This asks, “What would be the response if only a slight proportion of grazing intensity applied, such that the demographic response was only a slight proportion of what actually was observed?”

The stochastic growth rates I compute from these long series are $\log \lambda_s = 0.1019$ in the mown control and \log

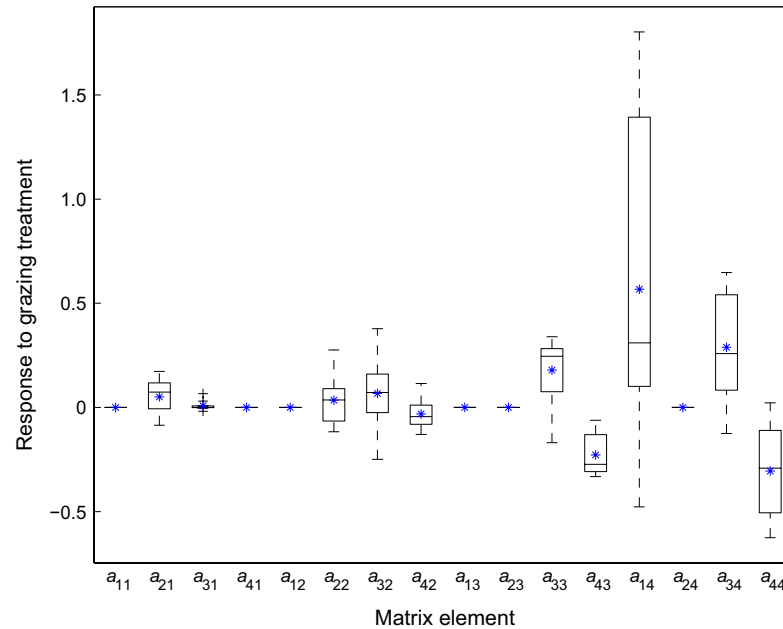


FIG. 2. Box plots showing the distribution of the response of each matrix element to the driving factor. Counting from the left, elements 1–4 are transitions from seedling to each of the seedling, juvenile, vegetative, and flowering stages. Elements 5–8 are transitions from juveniles to each possible stage, elements 9–12 are transitions from vegetative individuals, and elements 13–16 are transitions from flowering individuals. For each element, an asterisk indicates the mean treatment response, and the horizontal line within each box is the median. Box edges indicate the 25th and 75th percentiles, and the whiskers encompass remaining non-outlying points. Outliers (Element 3) are plotted individually using (+) signs. [Color figure can be viewed at wileyonlinelibrary.com]

$\lambda_s = 0.0183$ in the grazing treatment; these accord well with Jacquemyn et al. (2012). The elasticities in grazed plots are $E_F^{S\mu} = -0.1543$ with respect to the mean response to grazing, and $E_F^{S\sigma} = -0.0001$ with respect to the variability in response to grazing. In the mown control, the elasticities are $E_F^{S\mu} = -0.0390$ and $E_F^{S\sigma} = 0.0003$.

These driver elasticities illuminate how long-run population growth in *P. veris* depends on grazing, and they do so in a unique way that complements the analyses in Jacquemyn et al. (2012). In the course of their stochastic LTRE, Jacquemyn et al. (2012) calculate stochastic growth rates, elasticities with respect to vital rates, and contributions of vital rates to observed differences in growth rate. These enable Jacquemyn et al. (2012) to make many valuable inferences regarding the biology of the study species and its demographic responses to grazing. The only quantitative information about specifically how long-run population growth responds to grazing, however, are the values of the population growth rate in control and treatment plots. What is added by the driver elasticities is information about shape of the full relationship between the long-run stochastic growth rate and grazing, particularly immediately outside the range of grazing intensity that was actually observed.

In the mown control, the elasticity with respect to the mean intensity of grazing is $E_F^{S\mu} = ([\partial \log \lambda_s] / [\log \lambda_s]) (F / \partial F) = -0.0390$. This is the proportional change in the long-run growth rate, $\log \lambda_s$, due to a small change in demography that is proportional to the observed response

to grazing. Multiplying this with the population growth rate in the mown control, $\log \lambda_s = 0.01019$, reveals that the absolute change in population growth is -0.0040 . In the grazed treatment, the absolute change is -0.0028 ; the elasticity ($E_F^{S\mu} = -0.1543$) is greater at the higher level of grazing, but it is a greater proportion of a much smaller long-run growth rate ($\log \lambda_s = 0.0183$), resulting in a smaller absolute change. Because I applied the same demographic perturbation in the two treatments, we can directly compare the two absolute changes in growth rate, and infer from the difference between them that the negative effects of grazing pressure decrease at higher levels of grazing intensity. This implies a nonlinear relationship between population growth and grazing, which must be due to different responses of population growth to the same demographic change (because with only two treatment categories, no nonlinearity can be inferred between demographic rates and grazing). Fig. 3 illustrates one simple possibility for the relationship between population growth and grazing.

Thus, the driver elasticities suggest increasing resilience to grazing on the part of *P. veris* under higher grazing pressure. Using stochastic LTRE, Jacquemyn et al. (2012) identified that the primary mechanism through which grazing reduces population growth is lowered flower and seed production. They also identified, however, that grazing increases seed establishment in *P. veris*, and suggest that treading by cattle opens microsites for seedling germination, increases light penetration

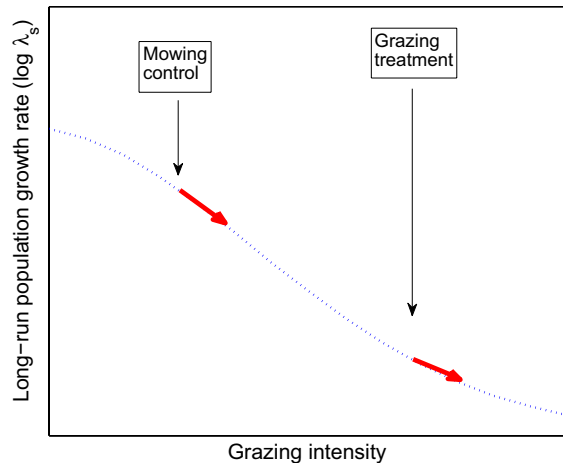


FIG. 3. Schematic diagram illustrating how driver elasticities can illuminate the shape of the relationship between long-run population growth and a driving factor. Bold arrows show information from driver elasticities; they originate at the value of the stochastic growth rate in each treatment (see *Example and results* subsection for details). Lesser change at higher grazing intensity implies that population growth depends nonlinearly on the driver. The dotted curve shows one possibility for this relationship that is consistent with the elasticity information. [Color figure can be viewed at wileyonlinelibrary.com]

for seedling growth, and decreases density dependence among seedlings. The addition of the present elasticity analysis suggests that under more intense grazing than was experimentally applied, these positive effects could more effectively counteract the negative effects of decreased fecundity, and that further increases in grazing pressure therefore would not be as detrimental to *P. veris* as one might suppose based upon only the change in population growth between treatments.

The elasticities to variability in herbivory are two to four orders of magnitude smaller than the elasticities to mean herbivory intensity, so the effect of variability in herbivory is essentially negligible in this system. Little explicit information on variability in cattle grazing appears in Jacquemyn et al. (2012), although the mean density is 15 cows/ha. It is not clear whether the observed year-to-year variability in the response of *P. veris* to herbivory is due primarily to changes in cattle abundance and/or condition, or to other factors, such as rainfall, which could affect plant response to grazing in addition to other independent or interactive stochastic effects on plant demography. All told, whether the minor effect of variability in response to a driving factor is specific to this study or is likely to hold in other biological systems is an interesting question for future study.

DISCUSSION

I have presented a novel approach to obtaining elasticity of population growth rate with respect to a driving biotic or abiotic factor. It readily accepts data from a familiar empirical design in the form of the different effects of the

driver on multiple demographic rates, including any between-rate correlations that arise as a result. In a variable environment, this approach separates the effect of the mean demographic response to the driving factor from effects of the variability in response, and can do so against a background of additional variability. Interpreted as a local proportional derivative, driver elasticities enable extrapolation beyond observed levels of the driving factor, in a way that can capture nonlinearity in the relationship between growth rate and driver. The approach works in cases where the driving factor is manipulated experimentally, as in the *Primula veris* example here, or in cases where demography is documented under at least two naturally occurring levels of a driving factor.

The methods described here should generalize to other study systems where demography has been quantified for at least two levels of driver intensity. Where there are only two levels, as in the example here, there is a single treatment response, and a small proportion of this single response can be applied to both levels. The situation would be more complex given more levels of the driving factor. In general, monitoring demography at L levels of the driving factor yields up to $L - 1$ different treatment responses (more if differences are taken between non-neighboring levels), any of which could be applied as a prospective perturbation to as many as all L levels of observed demography. For instance, given three levels of the driver, one can choose from two single-segment multidimensional differences to perturb the central level. Generally speaking, if the multidimensional treatment response changes with the intensity of the driving factor, then at least some demographic rates depend nonlinearly on the driver, which could contribute additionally to nonlinearity in the response of population growth to the driver. Beyond this, one must clarify which calculated elasticities result from which demographic perturbations, and take care in the interpretation of different elasticities. Depending on the biological system and the questions asked, it could be reasonable to apply the same perturbation to all levels in order to be able to compare them all, for instance, and/or to apply a proportion of each treatment response to its associated endpoints only, in order to compare neighboring points using their shared treatment response.

In some cases, the effects of multiple drivers are present in the same dataset. To calculate multiple driver elasticities, one would confront a choice of assessing each driver independently by pooling across a second driver when determining the treatment response to a first, or of assessing the treatment response to each driver only at a given level of the other to reveal interactions. As in the case of multiple treatment levels, this choice and associated inferences would likely depend upon the questions being asked of a particular study system; several possibilities could be informative if stated clearly and applied in a way consistent with desired comparisons.

In the *P. veris* example, elasticities predict that increasing the variability of response to herbivory would

have little effect on population dynamics. It would be interesting to know whether elasticities to driver variability would also be small in other systems, especially ones where the driver is conspicuously variable. Examples of such drivers include insect herbivore abundances or climatic variables, which can sometimes fluctuate dramatically. Because elasticities to a driving factor single out one source of demographic variability against a potentially variable background of other factors, they represent a useful addition to the ecological toolbox for understanding how natural populations could respond to changing conditions.

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