Demography in an increasingly variable world

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Recent advances in stochastic demography provide unique insights into the probable effects of increasing environmental variability on population dynamics, and these insights can be substantially different compared with those from deterministic models. Stochastic variation in structured population models influences estimates of population growth rate, persistence and resilience, which ultimately can alter community composition, species interactions, distributions and harvesting. Here, we discuss how understanding these demographic consequences of environmental variation will have applications for anticipating changes in populations resulting from anthropogenic activities that affect the variance in vital rates. We also highlight new tools for anticipating the consequences of the magnitude and temporal patterning of environmental variability.

'The use of deterministic rather than stochastic models can only be justified by mathematical convenience.' J. Maynard Smith [1].

Introduction

Demography is the study of how vital rates, such as fecundity and survival, influence population processes. Although the original theory of demography was deterministic (i.e. non-random), all natural populations experience stochastic (i.e. random) variation in vital rates, the effects of which can be considered only in the context of stochastic demography (see Glossary). Because of the mathematical difficulty of the stochastic theory, only recently have we acquired the tools to examine the consequences of random variation in vital rates in structured populations [2,3]. Several studies have shown that stochastic demographic models can yield results that are substantially different from those of traditional deterministic models [2,4,5].

Variation in vital rates significantly affects the outcome of stochastic demographic models, with important ramifications for estimates of population growth rate [4], persistence [6,7] and average size [8]. Several sources of evidence suggest that the amplitude and probability distribution of environmental variability is changing in response to anthropogenic impacts; thus, it is important that we understand the effect of variance in stochastic demography. General circulation models (GCMs) predict increased climatic variability over much of the planet [9,10], from mesoscale (2–2000 km) temperature and precipitation to disturbances such as hurricanes [11,12].

Glossary

Diffusion process: the logarithm of the population size $\log N(t)$, at time t, is approximately normally distributed when t is large, with mean and variance increasing linearly with time [3]. A diffusion approximation makes use of this fact to express the change in size in a small unit of time (growth rate) as a time-dependent random variable with a mean (an infinitesimal mean) and variance (an infinitesimal variance) [7].

Elasticity: the proportional change in a population property, such as growth rate or population size, given a proportional perturbation in a vital rate. For example, perturbing a rate in every environmental state such that its mean changes but its variance is constant, we obtain the elasticity with respect to the mean of that rate, $E^{s\mu}$ (Box 2).

General circulation model: these divide the globe into grid boxes $\sim 3°$ latitude and longitude on a side, and calculate motions of the atmosphere (potentially coupled with oceanic processes) from physical equations and parameterizations for sub-grid-scale processes. Under different scenarios of emissions, land use and regulation, simulations of these models are used to anticipate changes in the means and variances of climate variables, including temperature and precipitation, for each grid box. Regional circulation models (RCM) and statistical downscaling methods are alternatives for more fine-grained projections.

Lyapunov exponent: a measure of the rate at which initially nearby trajectories of a system converge toward or move away from each other. The deviation at time t in the trajectories generated by two initial vectors $P_1(0)$ and $P_2(0)$ is given by $|x(t)| = |P_1(t) - P_2(t)|$, where $|u|$ denotes the length of a vector $u = (u_1, u_2, \ldots u_k)$, often taken as $|u| = \sum_i |u_i|$. The (dominant) Lyapunov exponent λ_1 is usually defined as the long-term average growth rate of the logarithm of this deviation when the difference $|x(0)|$ between the two initial population vectors decreases to zero [3].

Sensitivity: the change in a population property in response to a perturbation in a vital rate; similar to elasticity [2,3] although changes are not proportional.

Stochastic demography: the study of age- or stage-structured populations in temporally varying environments, with states of the environment given by some stochastic process [2]. This process could be independent and identically distributed (i.i.d.), where independent draws from the same distribution determine the state of the process at each time. Examples of correlated processes, where the state at each time step depends on the states in the preceding time steps, include Markov processes and auto-regressive moving average (ARMA) processes [3].

Vital rate: here, any age- or state-specific demographic rate, such as survival or fecundity. An element of a population projection matrix (Box 2) is also a vital rate, even though it might be a function of other rates [3].

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Observations indicate increases in seasonal variability (e.g. changes in mesozooplankton communities in the Indian Ocean in recent years, driven by expanding oxygen minimum zones [13]) and in the frequency of previously rare events (e.g. mass mortalities of marine organisms owing to epidemics, exotic invasions, algal blooms, pollution and other consequences of anthropogenic impacts [14]). These changes could all increase the variability (i.e. variance, covariance and autocorrelation) in vital rates, as individual organisms respond to their changing environments.

In some systems, anthropogenic alterations of the environment can reduce environmental variance. Dams, flood-control projects and other activities change the hydrological character of stream environments, thus altering the variability of stream flow. Decreases in extreme flow events (e.g. floods and droughts) are common in altered streams, with demographic consequences for assemblages of species adapted to the natural magnitude, frequency, seasonal timing, predictability, duration and rate of change of flow conditions [15]. However, hydropower dams operated to meet peak-load electrical demand can increase flow variability by occasionally releasing water in high-frequency, large-magnitude pulses, which affect the survival and reproduction of many species, ultimately altering the composition of stream species [16].

Stochastic demography can help us to anticipate how vital rate variation *per se* will influence future populations [2,4]. Here, we identify examples where variation affects demography, and highlight new tools for anticipating the consequences of the magnitude and temporal patterning of environmental variability. We conclude with suggestions for future research that might shed light on population responses to changing climatic variability.

Variation influences population growth and fitness

Standard deterministic approaches in demography provide a framework for modeling structured populations in which growth, death and birth rates depend on age, size or developmental stage. A vector of the numbers of individuals in each age or stage class describes the population in each time step, and a matrix operates on this vector to project the population forward in time. The elements of the projection matrix are the rates of transition between ages or stages, and comprise combinations of vital rates, such as survival, growth and fecundity. The long-term growth rate of the population, $\log \lambda_0$, is a function of the projection matrix [3]. In an evolutionary context, this growth rate serves as a fitness parameter [2,3]. The change in $\log \lambda_0$ that results from changing one projection matrix element by a given proportion is called the elasticity of λ_0 with respect to that element. Elasticities are measures of the importance to the population growth rate of matrix elements and the vital rates that comprise them.

This theoretical framework for structured populations does not include temporal variability. If empirical estimates of the projection matrix differ annually, owing to environmental variation, sampling variation, or other factors, the elements of the matrix can be averaged across years to obtain a mean projection matrix. The theory of stochastic demography, by contrast, is based on population projection matrices that vary randomly through time as the environment varies (Box 1). This conceptually simple modification has several important implications. The long-run growth rate of a population now depends on a complete series of projection matrices. Because the environment varies randomly, correlations become possible: the sequence of matrices might exhibit temporal correlation, and matrix elements or vital rates might be correlated with each other. The concept of elasticity must be extended to cover matrix elements and vital rates that are no longer constants, and which have means, variances and covariances associated with them. Stochastic demographic theory provides the tools to analyze population growth and fitness while taking these important consequences of variability into account. Box 2 provides technical details of the mathematical framework of stochastic demographic theory.

The expected long-run growth rate of structured populations in varying environments is the stochastic growth rate, $\log \lambda_S$. The value of the stochastic growth rate can be comparable to the deterministic long-term growth rate, $\log \lambda_0$, which is obtained from the average projection matrix [17]. Two recent studies, however, find substantial differences between $\log \lambda_0$ and $\log \lambda_S$ ([4,5]; Box 1). In Box 2, we present an approximation for the value of $\log \lambda_S$ that shows its relationship to $\log \lambda_0$, the elasticities of λ_0 to the elements of the mean matrix, the variability of the elements and the correlations between those elements. Generally, $\log \lambda_S$ is less than $\log \lambda_0$ [2,5]. Because the growth rate is a function of all the vital rates in the projection matrix, anticipating the effects of environmental variation for a given population will require understanding how the environment influences particular vital rates. Increasing environmental variation generally changes the variability of vital rates. It can also change the means of vital rates (Box 3). How can we understand the impact of these changes on $\log \lambda_S$?

As in the deterministic case, elasticities provide information about how growth rates depend on changes in vital rates. However, in stochastic environments, more changes to vital rates are possible than in a constant environment. As a result, several stochastic elasticities can be calculated. As with deterministic and stochastic growth rates, deterministic and stochastic patterns of elasticities can be similar [17] or strikingly different [4,5,18]. In Box 4, we illustrate these elasticities with data from an understorey shrub in a hurricane-perturbed forest.

Changes in environmental variability can include changes in the pattern of environments experienced, as well as changes in the magnitude of the variation. For instance, greater climatic variability might result from more frequent or longer-lasting unfavorable conditions for individual species, or longer sequences of favorable years, rather than increases in the maximum favorability or decreases in the minimum [9]. Such increases in the temporal correlation of environmental variation can decrease time to extinction, as demonstrated by comparative analyses of long-term data on population abundances [19] and an experimental manipulation of clonal

Box 1. Stochastic versus deterministic population growth

Analysis of the mean environment does not always capture demographic dynamics in randomly varying environments. Figure Ia shows a sequence of environmental states determined by two independent random variables, one represented by color and the other by pattern. Yellow squares are years with favorable weather and blue squares are unfavorable years; the probability of a good year is $q=0.5$. Years with favorable opportunities for growth, characterized by lessened competition owing to natural disturbance or other factors independent of the weather, are hatched, whereas years in which opportunities are lacking are unhatched; opportunities are also shown occurring with probability $p=0.5$. There is no temporal correlation between years. Figure Ib shows the average environment occurring each year, as assumed by standard deterministic demographic analysis. The two approaches to environmental variability can result in very different assessments of long-term growth rate. Figure Ic (adapted with permission from [5]) shows the long-term growth rates calculated from the two models for transgenic oilseed rape *Brassica napus*, for a range of frequencies of favorable competitive opportunity (the probability of a good year is fixed at $q=0.5$). The growth rate computed from the stochastic model, $\log \lambda_S$, for this example is always less than the deterministic rate, $\log \lambda_0$, and the two are so dissimilar in some environments that the stochastic model predicts population decline whereas the mean model predicts growth. The effects of variable environments thus can be profound, and stochastic demographic theory is necessary to anticipate the consequences of the variability.
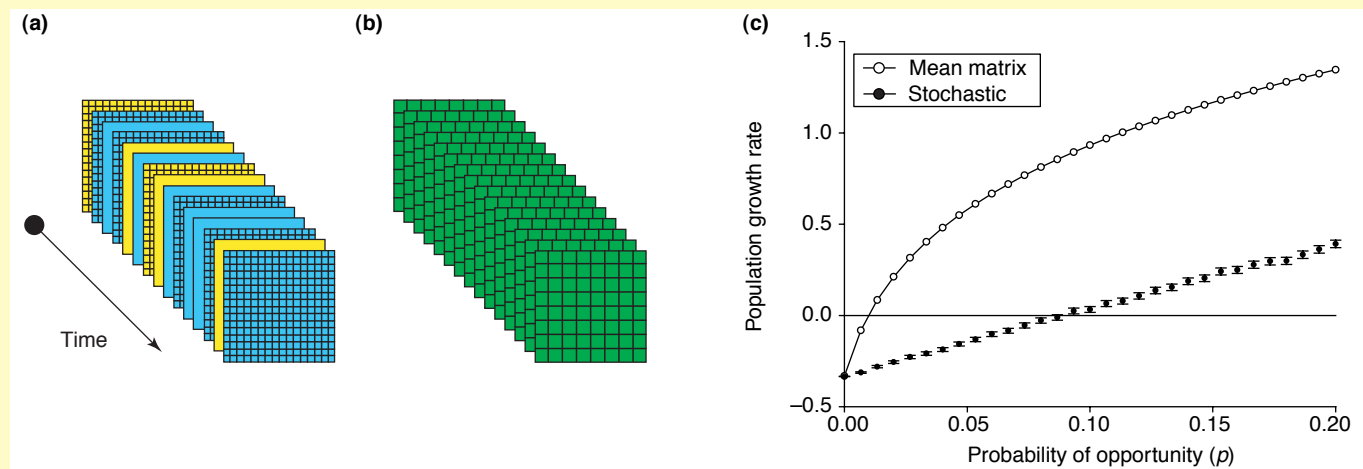

Figure I.

populations of the collembolan *Folsomia candida* [20]. Autocorrelation of the environment might change the mean and variance of disturbance frequency, which can have profound effects on population growth rates and elasticities. For instance, if longer sequences of warm years increase the frequency of hurricanes, the demographic response of a tropical understorey shrub could be dramatic [4]. Climate change might also shift the season of disturbance. For example, droughts earlier in the year or serial drought years might alter the seasonal fire regime, which can have dramatic effects on population and community dynamics [21].

Covariances among vital rates are the final important aspect of environmental variation that we consider here. Covariances can have a large effect on population growth and elasticities. In a comparative study of five ecological situations, covariation among vital rates accounted for between one-third and one-half of the observed variation

Box 2. Stochastic structured population models

The basic population model [3] for demography in stochastic environments is Equation I:

$$\boldsymbol{P}(t) = \boldsymbol{X}(t)\boldsymbol{P}(t-1) \qquad \text{[Eqn I]}$$

where $\boldsymbol{P}(t)$ is the population vector at time t and $\boldsymbol{X}(t)$ is the random population projection matrix at time t. Variation in the matrix $\boldsymbol{X}(t)$ represents the responses of the population to variation in the environment. The long-term stochastic growth rate of the population, $\log \lambda_S$, is a function of the sequence of environments, as filtered through the vital rates of the population. When environments are independent and identically distributed (i.i.d.) and variation in matrix elements is small, an approximation for $\log \lambda_S$ can be written as Equation II [2]:

$$\log \lambda_s \approx \log(\lambda_0) + \frac{1}{2}T^\sigma, \qquad \text{[Eqn II]}$$

where (Equation III):

$$T^\sigma = -\sum_{ij}\sum_{kl} e_{ij}e_{kl}c_{ij}c_{kl}\rho_{ij,kl}, \qquad \text{[Eqn III]}$$

λ_0 is the dominant eigenvalue of the mean matrix $\overline{X} \equiv E[\boldsymbol{X}(t)]$, e_{ij} is the elasticity of λ_0 with respect to the (i,j) element of $\overline{X}$ [3], c_{ij} is the coefficient of variation (CV) of the (i,j) matrix element and $\rho_{ij,kl}$ is the correlation coefficient between the (i,j) and (k,l) elements. Equation II shows how the means of demographic rates and their variance–covariance structure influence fitness.

Elasticities capture the effects on λ_S of proportional perturbations, K_{ij}, in matrix elements [4]. We can perturb $X_{ij}(t)$, the (i,j) element of $\boldsymbol{X}(t)$, by an amount proportional to $K_{ij}(t)$. With $K_{ij}=\mu_{ij}$, we obtain the elasticity $E_{ij}^{S\mu}$ of λ_S with respect to the mean μ_{ij} of $X_{ij}(t)$. This is the proportional change in λ_S for a proportional change in μ_{ij}, keeping σ_{ij} fixed. With $K_{ij}=X_{ij}-\mu_{ij}$, we obtain $E_{ij}^{S\sigma}$, the proportional change in λ_S for a proportional change in σ_{ij} when the mean is unchanged. These two elasticities separate the effects of changes in means and in variability of demographic rates. With $K_{ij}=X_{ij}$, we obtain E_{ij}^{S}, the proportional change in λ_S for equal proportional changes in μ_{ij} and σ_{ij}. The above elasticities are related via a sum rule [55] (Equation IV):

$$E_{ij}^{S\mu} + E_{ij}^{S\sigma} = E_{ij}^{S} \qquad \text{[Eqn IV]}$$

Box 3. Responses of mean vital rates to changed environmental variability

Vital rates are functions of environmental variables, such as temperature and rainfall. If the mean of the environmental variable stays the same, but the variance increases, will this affect the mean vital rate? Jensen's inequality [56] tells us that if x is an environmental variable (e.g. temperature) and $f(x)$ is the function relating a vital rate (e.g. survival) to the environmental variable, then the relationship between the mean vital rate in the variable environment ($E[f(x)]$) and the vital rate in the mean environment ($f(E[x])$) is as follow (Equations I–III):

$$E[f(x)] \geq f(E[x]) \text{ if } \frac{d^2 f}{dx^2} > 0 \qquad \text{[Eqn I]}$$

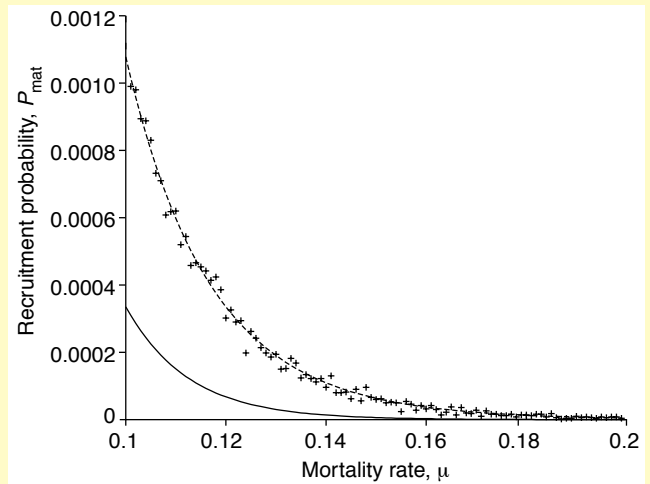$$E[f(x)] = f(E[x]) \text{ if } \frac{d^2 f}{dx^2} = 0 \qquad \text{[Eqn II]}$$

$$E[f(x)] \leq f(E[x]) \text{ if } \frac{d^2 f}{dx^2} < 0 \qquad \text{[Eqn III]}$$

In other words, whether environmental fluctuations increase or decrease the mean vital rate depends on the sign of the second derivative (convex if positive, concave if negative) of the function relating the vital rate to the environment [57]. If environmental fluctuations are approximately normally distributed, then the magnitude of the change is linearly related to the environmental variance.

Pitchford *et al.* [58] illustrate this result with a study of survival rates in larval fish. In their model, the probability that a larva survives to maturity is a convex function of time, $P_{mat} = e^{(-\mu t)}$. Under conditions that are generally unfavorable for the larvae, the average probability of reaching maturity is greater when the time to maturity is a random variable than when it is fixed at its mean value [58] (Figure I). In the notation above, this case demonstrates that $E[f(x)] > f(E[x])$.

Responses to environmental variability can also depend on the current mean value of a vital rate. For example, if a vital rate in the mean environment is low, variation in environmental conditions will probably increase the mean vital rate because bad years cannot get much worse, but good years can get much better. A long-lived organism that can tolerate years of no reproduction can benefit from this effect on fecundity. However, if this results in zero survival in the bad years, the increase in mean survival will amount to nothing for a population that has gone extinct. By contrast, when survival in the mean environment is close to one, environmental variation can only make things worse [45].

Figure I. The influence of nonlinearity on vital rate response to environmental variability. The probability that a larval fish survives until maturity can be greater when the environment varies than when it is constant. The probability of reaching maturity, P_{mat}, is shown as a function of the mortality rate, μ, for foraging at a constant rate (solid line) and foraging subject to white noise (line with crosses). Model parameters are representative of fish larvae reaching maturity in ~80 time units, with mean growth rate and variability of the same order. Adapted, with permission, from [58].

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in population growth for two ungulate species [22]. A study of the endangered desert tortoise *Gopherus agassizii* showed that strong and consistent positive correlations between important vital rates dramatically enhance elasticities to those rates, whereas negative correlations can reverse them [23]. Covariation between vital rates can be generated by genetic constraints, which lead to tradeoffs [24,25]; by density dependence, where increasing density decreases individual performance and thus affects several vital rates in the same direction [26]; and by shared environmental drivers [27]. Increased environmental variance could increase the strength of covariation between vital rates: for example, years of inclement weather or food shortage might reduce survival and fecundity for all age or stage classes in a population. Thus, environmental variability affects population growth and fitness in several interrelated ways, and stochastic demographic theory provides the tools for their systematic analysis.

Variation influences resilience and population size

A central aim for population ecologists is to determine how density dependence varies with environmental variance. In other words, what limits and regulates the size of natural populations? Recent studies have shown that environmental variation interplays with density dependence in a large range of species

and ecosystems (terrestrial birds [28], marine birds [29], crab and salmon [30], small mammals [31] and large terrestrial herbivores [22,27]). The basic modeling framework that we presented in the previous section, however, does not include density dependence. Although projection matrices can be modified to represent density-dependent processes [3], the stochastic population growth rate and its elasticities become uninformative: when density-dependent processes regulate population size, the long-term growth rate, $\log \lambda_S$, is 0, and perturbations to vital rates generally do not change this long-run behavior. We must therefore seek better measures than elasticities of λ_S to analyze the effects of environmental variability in the presence of density dependence. There are three approaches for dealing with stochastic variation in density-dependent models.

Stochastic simulation with estimated parameters

The first uses stochastic simulation of a population model with estimated parameters [8,32]. At low numbers, population behavior is described by a Lyapunov exponent and density dependence can have a substantial effect on elasticities of this exponent to vital rates. Even with short time series, we can approximate the elasticities of the Lyapunov exponent for small population numbers using either (i) the growth rate computed from a matrix of time-averaged vital rates [8,32], or (ii) a low-density growth
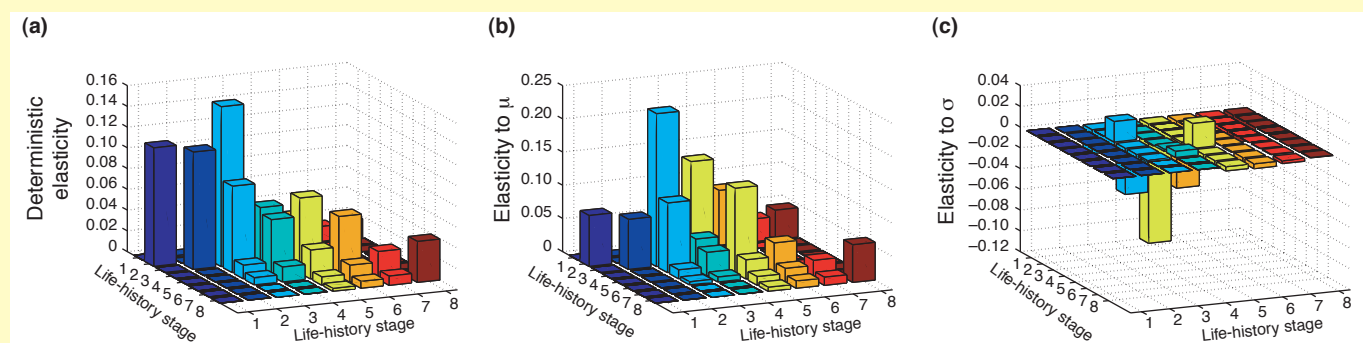
Box 4. Stochastic elasticities

Elasticity measures the importance of vital rates to population growth rate. Deterministic elasticities are calculated with respect to proportional perturbations of the values of individual fixed vital rates. In stochastic environments, each projection matrix element can take different values as the environment changes, so that multiple perturbations of each element are possible, each with potentially different effects on log λ_S. For example, one can perturb a vital rate in every environment so that its mean changes, but its variance does not; the reciprocal perturbation, where the variance changes but the mean does not, is also possible (Box 1).

Because these two perturbations provide an extremely useful decomposition of the contribution of different vital rates to the stochastic growth rate, it is essential to distinguish elasticity to the mean value of elements from elasticity to the variability of elements. Stochastic elasticities to changes in mean elements can be qualitatively and quantitatively different from deterministic elasticities calculated

from a mean projection matrix. Figure Ia and Ib illustrate this difference for an understorey shrub, *Ardisia escallonioides*, in a hurricane-disturbed ecosystem in Florida: each bar is elasticity for a transition between the life-history stage on the *x* axis to the stage on the *y* axis [59]. There are large differences in elasticities of the (1,1) and (2,2) elements. Figure Ic, for the same example, shows how elasticity to variability changes in magnitude and sign between matrix elements. Interestingly, increased variability in some elements can increase the population stochastic growth rate. More generally, stochastic elasticity can also describe the population consequences of changes in the covariance among matrix elements, or the temporal patterning of environmental states. Another useful elasticity describes the response of the growth rate to a change in a matrix element in a single state of the environment, termed 'habitat-stage elasticity' [59]. Together, these new tools provide means to explore population consequences of changes in the temporal patterning and variability of the environment.

Figure I. Stage elasticities influenced by variability. Deterministic and stochastic elasticities can differ dramatically. The elasticities shown are the proportional effect on the long-term growth rate (z axes, note changes in scale) of the understorey shrub *Ardisia escallonioides* to changes in transitions between eight life-history stages. Transitions are made from stages on the y axes to stages on the x axes. **(a)** Elasticities of the deterministic growth rate to changes in mean transition rates. **(b)** Elasticities of the stochastic growth rate to changes in the means of transition rates, holding the variances constant. **(c)** Elasticities of the stochastic growth rate to changes in the variances of the transition rates, holding the means constant. Adapted with permission from {59}.

rate of a mutant type, with some vital rate perturbed, given that the original type is at its equilibrium value [33]. This second approximation works well except when density dependence leads to complex (cyclical, aperiodic, or chaotic) dynamics. Elasticities of average population size to changes in vital rates have also been computed [32], and similar computation of elasticities of extinction probability or of variance in population size would be useful.

Population variability, equilibrium levels and density-dependent regulation

The second approach is related to the first, and analyzes population variability around equilibrium levels that are set by density-dependent regulation. Here, the mathematical properties that characterize resilience of the structured population model (e.g. the 2nd eigenvalue) can give insight into density-dependent population behavior. Likewise, average population size can be affected by environmental variation [8].

Divergence between neighboring trajectories

A final approach considers divergence between neighboring trajectories, measured by local or global Lyapunov exponents [34]. This approach was developed to analyze population time series, but has also been applied to

stochastic nonlinear models of plankton dynamics and nitrogen cycling [35]. Local exponents describe short-time predictability, whereas global exponents describe the long-run effects of initial conditions. Lyapunov exponents have been used primarily as indicators of chaos in deterministic nonlinear systems and are, as yet, poorly understood in stochastic models [36]. Further work on the interplay among density dependence, environmental variability and population structure would significantly advance the study of stochastic demography.

Variation influences extinction risk

Stochasticity is a major factor in models designed to estimate the probability of persistence [i.e. population viability analysis (PVA)]. Most PVAs have been done using computer simulations using software, such as RAMAS [37], that can accommodate density dependence, age and/ or stage structure, spatial structure and covariance among vital rates. Analytical methods have been developed to include demographic variance based on variation in fecundity and survival among individuals [38], and environmental variance characterized by among-year variation in projection matrices [5]. If variance is modest, the stochastic model can be approximated by a diffusion process with only three parameters: (i) growth rate of the expected projection matrix; (ii) environmental

variance; and (iii) demographic variance [6]. The effect of demographic variance on extinction risk can be substantial when population size is small, whereas environmental variance can be a major determinant of extinction risk even for larger populations.

Although seldom considered in PVAs, the temporal sequencing of variation in the environment and, thus, variation in vital rates can have a large influence on extinction risk (autocorrelated environments are more risky) [19,20]. Estimating population parameters for PVA remains a major challenge, especially for threatened and endangered species for which limited data are available [39].

Variation influences spatial processes and community composition

Temporal variation can interact with spatial processes, such as dispersal and population expansion. Dynamic models show that environmental variation affects the rates of spread [40] and population declines of invasive species [41]. For metapopulations, where asynchrony among subpopulations might be essential for regional persistence, the possibility for climate change to increase synchrony in climate and population dynamics is ominous; however, in some species, population dynamics might remain asynchronous in spite of a correlated climate [42].

Temporal variability has an important role in promoting competitive coexistence. Environmental fluctuations provide temporal niche opportunities, so that species that are too similar to coexist in a fixed environment can coexist stably in a varying environment. For instance, rainfall pulses might enable species to differ in which pulses they use or in the timing with which they use a given pulse [43]. This temporal differentiation (together with the presence of a persistent life-history stage and covariance between the responses of species to the environment and responses to competition) enables species to coexist via the temporal storage effect [43]. A distinct coexistence mechanism, relative nonlinearity of competition, also requires temporal variability to operate [44]. Changes in environmental variability can influence the operation of these mechanisms and change community composition as a result. These potential effects of variation on regional species composition can complicate the application of stochastic demography to particular populations.

Demographic buffering to environmental variation

Variation in the environment does not always translate into variation in vital rates. Reducing the variance of vital rates that contribute strongly to population growth rate is demographic buffering and there is some evidence that natural populations do buffer changes in population growth by reducing the sensitivity of population growth to more variable vital rates [23,45,46]. Documenting how such adaptations might occur requires increased understanding of the connections between demography and genetics.

The genetic variances and correlations that underlie vital rate distributions can change through selection [24,47]. Evolution of vital rate distributions in response

to increased environmental variation, however, is constrained by life-history tradeoffs at the physiological and behavioral level or even in basic protein structure [25,48]. As a general rule, limitations of time or resources constrain growth and traits associated with survival and reproduction, thus creating obvious tradeoffs among vital rates. In extreme environments, the limitations are expected to be more acute. When the entire time or resource budget (including foraging and life-history traits) functions as a unit [49], constraints and associated tradeoffs might be apparent only in extreme or variable environments [50]. However, theoretical work has shown that the magnitude of environmental change can be so large relative to standing phenotypic and/or genetic variation that it is impossible for the population to adapt and survive the new environment [51].

In extreme environments, in which probabilities of survival and/or reproduction approach zero, bet-hedging traits, such as seed dormancy [52] and self-pollination in plants [53], are favored. Such traits can delay the time to extinction [54] and their maintenance within populations is counterbalanced by the fitness cost of having such traits in benign environments. The frequency of poor environments experienced by a population can determine the selective benefits versus costs of such traits.

Past climate has shaped the life histories that we currently see, suggesting that organisms have suites of life-history traits that reduce variability in population growth rate. Although the demographic buffering hypothesis requires more extensive testing, it raises provocative questions about how climate will affect variation in population growth. As climate changes, will demographic buffering continue to dampen fluctuations in population growth rate? Or will climate change result in suites of life-history traits that exacerbate variation in population growth rate? The answer will depend upon which aspects of the life history of a species are affected by climate change. For those vital rates that typically vary little, but have a large effect on population growth rate (such as adult survivorship of relatively long-lived species), climate changes that drive novel adult survivorship patterns can have profound effects on population growth rate and, thus, extinction risk. Therefore, to be predictive about the effects of climate change, we need to know how an aspect of climate (e.g. temperature or precipitation) is linked to the vital rates with disproportionate effects on population growth rate and the correlation structure of all vital rates in the life history.

Anticipating climate change

Climate change is expected to alter environmental variability [9–11], with consequences for the variance in vital rates. To anticipate the effect on populations, we propose several areas for future research.

First, it is essential to know how the drivers of vital rates are linked to climate changes predicted by GCMs. For example, do GCMs predict increased or decreased variability in rainfall over the geographical range of a set of target species? What is the relationship between rainfall and survival for these species? Armed with predictions from these models, we then can proceed to document

patterns of elasticities for the target species. If projected climate change increases variability in a vital rate, we need to know whether the elasticity structure for that species is likely to result in an amplified versus dampened stochastic population growth rate ($\log \lambda_S$) (Box 4). Estimating the elasticity of λ_S to changes in the mean versus the variance of target vital rates predicts whether population growth rates are likely to be influenced by increasing environmental variance. Similarly, in populations with density dependence, estimating elasticities of resilience of the projection matrix is largely unexplored and fertile ground for study. Additional analytical work could develop methods for estimating directly the elasticities relative to environmental parameters. A third direction is to determine the extent to which the composite elasticities, variances and correlations among vital rates contribute to the variability in $\log \lambda_S$ given structural life-history constraints on the elasticities of these quantities [18,55].

These proposed future directions could show how climate change is related to future patterns of population change only if we link GCM predictions to detailed demographic analyses of multiple taxa. Only by understanding the demographic responses to environmental variability will we be able to anticipate the population consequences of global change in an increasingly variable world.

Acknowledgements

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