Ecology, 89(1), 2008, pp. 19–25
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LONGEVITY CAN BUFFER PLANT AND ANIMAL POPULATIONS AGAINST CHANGING CLIMATIC VARIABILITY

William F. Morris,[1,16] Catherine A. Pfister,[2] Shripad Tuljapurkar,[3] Chirrakal V. Haridas,[3] Carol L. Boggs,[3] Mark S. Boyce,[4] Emilio M. Bruna,[5] Don R. Church,[6] Tim Coulson,[7] Daniel F. Doak,[8] Stacey Forsyth,[9] Jean-Michel Gaillard,[10] Carol C. Horvitz,[11] Susan Kalisz,[12] Bruce E. Kendall,[13] Tiffany M. Knight,[14] Charlotte T. Lee,[3] and Eric S. Menges[15]

[1]*Biology Department, Duke University, Box 90338, Durham, North Carolina 27708-0338 USA*
[2]*Department of Ecology and Evolution, University of Chicago, 1101 E. 57th Street, Chicago, Illinois 60637 USA*
[3]*Biological Sciences, Stanford University, Stanford, California 94305 USA*
[4]*Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada*
[5]*Department of Wildlife Ecology and Conservation and The Center for Latin American Studies, University of Florida, Gainesville, Florida 32611 USA*
[6]*Department of Biology, University of Virginia, Gilmer Hall, Charlottesville, Virginia 22904 USA*
[7]*Division of Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY UK*
[8]*Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95064 USA*
[9]*BIO5 Institute, P.O. Box 210091, University of Arizona, Tucson, Arizona 85721 USA*
[10]*Laboratoire de Biométrie et Biologie Evolutive, Unité Mixte de Recherche N° 5558, Université Claude Bernard Lyon 1, Bâtiment 711, 43 boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France*
[11]*Department of Biology, University of Miami, Coral Gables, Florida 33124-0421 USA*
[12]*Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260 USA*
[13]*Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, California 93106-5131 USA*
[14]*Department of Biology, Washington University in St. Louis, One Brookings Drive, Box 1229, St. Louis, Missouri 63130 USA*
[15]*Archbold Biological Station, P.O. Box 2057, Lake Placid, Florida 33862 USA*

Abstract. Both means and year-to-year variances of climate variables such as temperature and precipitation are predicted to change. However, the potential impact of changing climatic variability on the fate of populations has been largely unexamined. We analyzed multiyear demographic data for 36 plant and animal species with a broad range of life histories and types of environment to ask how sensitive their long-term stochastic population growth rates are likely to be to changes in the means and standard deviations of vital rates (survival, reproduction, growth) in response to changing climate. We quantified responsiveness using elasticities of the long-term population growth rate predicted by stochastic projection matrix models. Short-lived species (insects and annual plants and algae) are predicted to be more strongly (and negatively) affected by increasing vital rate variability relative to longer-lived species (perennial plants, birds, ungulates). Taxonomic affiliation has little power to explain sensitivity to increasing variability once longevity has been taken into account. Our results highlight the potential vulnerability of short-lived species to an increasingly variable climate, but also suggest that problems associated with short-lived undesirable species (agricultural pests, disease vectors, invasive weedy plants) may be exacerbated in regions where climate variability decreases.

Key words: *climate variability; elasticity; longevity; stochastic demography.*

Introduction

Future climate change will be manifested as year-to-year fluctuations about long-term trends. Climatologists' initial predictions about the consequences of elevated atmospheric concentrations of greenhouse gases focused on the trends (Intergovernmental Panel on Climate Change 2007). However, recent climate modeling is providing growing evidence that the degree of climatic variability among successive time periods is also likely to change as a consequence of human activities (Boer et al. 2000, Raisanen 2002, Giorgi et al. 2004, Rowell 2005, Watterson 2005), leading, for example, to greater or lesser contrast than at present between wet and dry or between hot and cold years.

Like climatologists, ecologists have paid more attention to effects on animal and plant populations of changes in climatic averages than to changes in variability (Parmesan et al. 1999, Easterling et al. 2000, Parmesan and Yohe 2003, Root et al. 2003, Thomas et al. 2004, Pounds et al. 2006). But interannual environmental variability is likely to translate into variability in birth and death rates, and a change in the year-to-year variance of the finite rate of population increase (births minus deaths) can have a distinct influence on the long-term population growth rate

Manuscript received 10 May 2007; revised 21 September 2007; accepted 25 September 2007. Corresponding Editor: N. J. Gotelli.
[16] E-mail: wfmorris@duke.edu

relative to a change in the mean rate of increase. For example, if annual population growth is described by the simple model $N_{t+1} = \lambda_t N_t$, where N_t is density in year t and the finite rates of increase (the λ_t's) are independently and identically distributed with mean $\bar{\lambda}$ and variance Var(λ), the log of the long-term population growth rate, λ_s, is approximately

$$\log\lambda_s \approx \log\bar{\lambda} - \mathrm{Var}(\lambda)/(2\bar{\lambda}^2) \quad (1)$$

(Lewontin and Cohen 1969), where the subscript s stands for stochastic. According to Eq. 1, an increase in $\bar{\lambda}$ will increase λ_s, whereas an increase in the year-to-year variability of births and deaths will decrease it. More generally, Eq. 1 illustrates that anticipating the impact of climate change on populations will require that we account for the distinct effects of trends in climate averages vs. trends in climate variability.

Despite its heuristic value, the model underlying Eq. 1 is too simple to describe most populations and environments. In particular, in long-lived species, (1) both means and variances of vital rates (i.e., rates of survival, growth, and reproduction) differ among individuals as a function of their age or size; (2) vital rates contribute differentially to the population growth rate; and (3) vital rates are often temporally correlated both within and among age or size classes. Moreover, environmental conditions often are not independently distributed among years, but instead reflect climatic oscillations with a period >1 year (such as El Niño Southern Oscillation) or long-lasting effects of disturbance by fire or hurricanes. In such cases, environmental conditions tend to be correlated between successive years. Incorporating such features of real populations and environments can lead to predictions that differ from those of Eq. 1. For example, increasing a vital rate's interannual variance can actually increase λ_s when within- and between-year correlations are considered (Tuljapurkar et al. 2003, Doak et al. 2005, Morris et al. 2006).

Predicting population consequences of climate change would ideally use a three-step approach. First, climate models would be used to produce future sequences of climate variables at a population-relevant spatial scale. Second, knowledge of the relationship between vital rates and climate would be used to generate future vital rate sequences. Third, vital rate sequences would be used to project future population size. However, two links currently weaken this chain of inference. First, as general circulation models of Earth's climate utilize a fairly coarse spatial grid, their predictions are more robust at large spatial scales than at the scale of local populations (although downscaling climate projections is an active research area [Intergovernmental Panel on Climate Change 2007]). Second, ecologists' knowledge of the mapping between vital rates and climate is incomplete, primarily because many years of data are often needed to discern such linkages. Thus, the time is not yet ripe to apply this detailed approach to most species.

However, an alternative way to quantify potential population effects of trends in climatic averages and variability is to use existing demographic data to compute elasticities of the long-term population growth rate, λ_s. An elasticity measures the proportional change in λ_s resulting from a proportional change in the mean or standard deviation (SD) of a single vital rate. The elasticity thus serves as the basis for a linear extrapolation of how a change in the mean or SD of a vital rate will affect λ_s. Positive elasticities imply that an increase in the mean or SD of a vital rate will increase λ_s, and vice versa. Moreover, by comparing the elasticity for a vital rate SD to the elasticity for a vital rate mean, we can gauge the relative sensitivity of λ_s to trends in variability vs. averages. A change in the mean of a climate variable may change not only a vital rate's mean but also its variability. For example, survival variability is increasingly bounded as mean survival approaches 0 or 1 (Morris and Doak 2004), so improved average conditions may increase mean survival but decrease survival variability. Similarly, a change in the SD of a climate variable can change a vital rate's variability but also its mean (if the vital rate is a nonlinear function of the climate variable [Drake 2005, Boyce et al. 2006]). Elasticities gauge the population effects of changes in vital rate means and SDs, whether those changes result from changes in climatic means, variabilities, or both.

Here, we compute and compare elasticities of the long-term population growth rate to the vital rate means and SDs using data from multiyear demographic studies of 36 populations of plant and animal species that differ in their life histories and types of environment. We use the elasticities to address four questions. First, how sensitive are populations likely to be to changes in demographic variability relative to changes in mean vital rates? Second, is future population growth more likely to be affected by changes in the variability of certain types of vital rates (e.g., survival) rather than others (e.g., reproduction)? Third, do populations from environments that are correlated between years differ in their sensitivity to changing climatic variability relative to populations from environments that are less obviously autocorrelated? Fourth, do taxonomic differences or differences in life history (in particular, life span) influence the sensitivity of populations to changes in vital rate averages vs. variability? Life history theory supports the general hypothesis that a long life span and iterated reproduction can confer fitness benefits in a stochastic environment (Murphy 1968, Schaffer 1974). However, whether a species will be selected for short vs. long lifespan will be influenced by many factors, including costs of delayed reproduction, degree of variability in different demographic rates, and environmental autocorrelation (Orzack and Tuljapurkar 1989). Rather than asking whether longevity will be favored in a particular environment, here we ask a slightly different

question: comparing species that have evolved short vs. long life spans in their native environments, does current life span help to predict the effects on population growth of future changes in demographic variability?

Methods

We compiled demographic data for 15 plant and 21 animal taxa from our own studies or the literature (Appendix A). Most were north temperate studies, but a few were tropical or arctic. As computing elasticities to vital rate SDs requires estimates of current variability, we only used studies with ≥ 3 (median 6, range 3–73) estimates of most vital rates. In most cases, estimates were made in separate years at a single site (in others, estimates were combined from >1 site to construct a sequence of vital rates vs. time since disturbance). We included the largest or longest-studied population per species, except that for *Cervus elaphus* (elk or red deer) we included two ecologically distinct populations (in North America and Europe).

We classified species as short-lived (insects, annual algae, and *Collinsia verna*, an annual plant with a seed bank in which the life expectancy of a newly dispersed seed is just over 1 year) or long-lived (perennial plants, two birds, one amphibian, and seven ungulates). We also calculated mean life expectancy following Tuljapurkar and Horvitz (2006), assuming an uncorrelated or autocorrelated environment as appropriate for each species. Because high mortality of newborns can strongly curtail their life expectancy even in long-lived species, we computed life expectancy conditional on reaching the second stage in the life cycle.

We treated the yearly environmental states as being either independently and identically distributed (IID) or temporally autocorrelated (Markovian). In the IID case, all yearly sets of vital rates were equally likely to be chosen each year. In our data sets, autocorrelation arose for three reasons (Appendix A): a disturbance/recovery cycle; multiyear fluctuations in density; and environmental drivers with multiyear cycles. We used information about environmental autocorrelation to construct Markovian environmental state transition matrices that governed the choice of successive sets of vital rates.

We computed elasticities of λ_s to means and SDs of vital rates by perturbing the sequence of population projection matrices following Tuljapurkar et al. (2003) and Haridas and Tuljapurkar (2005; details in Appendix B). This method makes no limiting assumptions about the magnitude of variability and allows environmental autocorrelation. For an IID environment, the elasticity to a vital rate SD is computed by increasing the vital rate when it is above and decreasing it when it is below its mean, leaving the mean unchanged. In the autocorrelated case, vital rate variability may have multiple components. For example, a vital rate may fluctuate with time since disturbance or with fluctuations in density, but it may also vary among years at an equivalent disturbance or density phase due to interannual climate variability. For disturbance- and density-driven species, we computed SD elasticities by perturbing each vital rate about the mean specific to each year's disturbance or density phase (which preserves both the phase-specific means and the overall mean). Elsewhere we have examined the effects of increasing the variation in the disturbance phase means about the overall mean (Morris et al. 2006).

The projection matrices for all but one animal species and one annual plant were structured by age or stage and for all remaining plants by size. All matrices include survival and reproductive rates, but size-based matrices also have growth and reversion rates. We compare survival and reproduction elasticities across all species, and we report growth/reversion elasticities for size-classified species in Appendix C. Because the number of survival and reproductive rates differ among species due to differences in the number of classes, we summed separately the survival rate and reproductive rate elasticities for each species. These summed elasticities represent the change in λ_s that would result if the mean or SD of all survival or reproductive rates were simultaneously increased. Across all projection matrix elements, the sums of the mean and SD elasticities add to 1 (Haridas and Tuljapurkar 2005), and because the matrix elements are functions of the vital rates, the total elasticity to the vital rate means and SDs likely also has a limit (not necessarily 1). Thus the summed elasticities to the vital rate means and SDs are not independent. To account for this, we express the relative sensitivity of λ_s to increasingly variable survival or reproduction as the ratio of the summed SD elasticity to the total elasticity (i.e., the sum of the SD and mean elasticities over all rates). For example, for survival we computed the ratio $\Sigma_j E^{\sigma}_{s_j}/\Sigma_i (E^{\mu}_{v_i} + E^{\sigma}_{v_i})$, where $E^{\sigma}_{s_j}$ is the elasticity to the SD of survival rate j and $E^{\mu}_{v_i}$ and $E^{\sigma}_{v_i}$ are the elasticities to the mean and SD of vital rate i; note the numerator sum is over all survival rates and the denominator sum is over all vital rates. We also computed ratios for reproductive rates and for all vital rates combined. These ratios are the fraction of the total elasticity that is due to a change in the variability of a given type of vital rate, and we refer to them as the "relative effect of variability." As the denominator is always positive, a negative ratio indicates that increasing variability depresses λ_s and vice versa. A larger absolute value of the ratio indicates a larger effect of variability on the long-run growth rate relative to the effect of the mean.

Results

For most species, increasing vital rate variability is predicted to decrease long-term population growth, although small predicted increases do occur for some species (Fig. 1). But strikingly, short-lived species are far more negatively impacted by increases in variability than are long-lived species, a difference that is highly significant for survival, reproduction, and all vital rates combined (test results in Appendix C). By comparison,

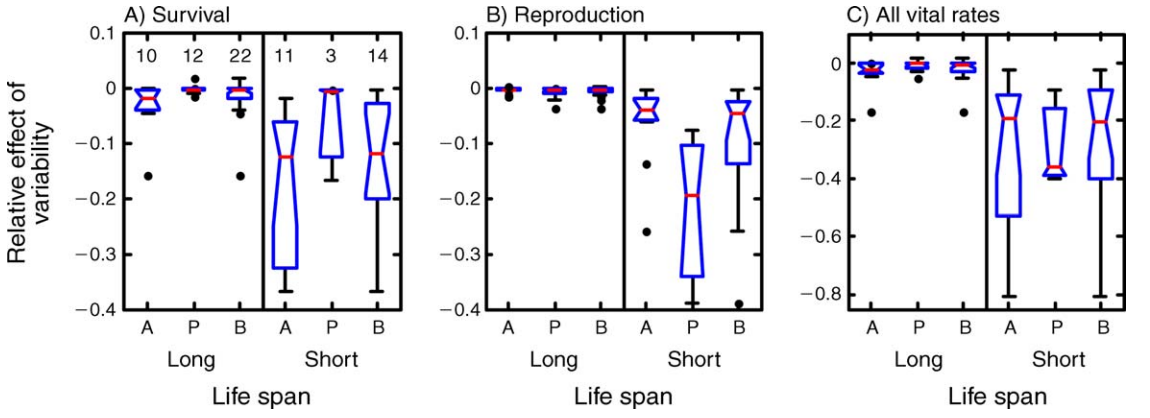

FIG. 1. Relative effect on the stochastic population growth rate, for organisms with short vs. long life spans, of increasing variability of (A) survival rates, (B) reproductive rates, and (C) all vital rates. Negative values indicate that increasing variability depresses long-term population growth. Box plot features are median (red line), inter-quartile range (blue box), most extreme values within 1.5(inter-quartile range) of the median (whiskers), and outliers (dots). Abbreviations are A, animals; P, plants; B, both. Numbers at the top in panel A give the number of studies in each group. For clarity, negative outliers for two univoltine insects were omitted in panels A and C.

taxonomy has a minor influence; the relative effect of variability in all vital rates does not differ between plants and animals in either life span category, but long-lived plants in our sample are less sensitive to variation in survival and short-lived plants are more sensitive to variation in reproduction than are animals of comparable life span. Increasing survival variability depresses λ_s more than does increasing reproduction variability, for both long-lived (median relative elasticities: −0.0048 for survival vs. −0.0013 for reproduction) and short-lived (−0.095 vs. −0.046) species, but not significantly so (Wilcoxon's signed ranks tests, $P = 0.24$ and 0.12, respectively). As all species from autocorrelated environments were long-lived and given the strong effect of longevity in Fig. 1, we used only long-lived species to compare IID vs. Markovian environments. Environmental autocorrelation did not influence significantly the relative effect of increasing variability of survival, reproduction, or all vital rates combined (Appendix C).

To look more closely at the relationship between longevity and the impact of increasing variability, we plotted the absolute value of the relative elasticity against life expectancy (Fig. 2). We used absolute value to compare the magnitudes of the elasticities, regardless of whether variability depresses or enhances λ_s. For survival, reproduction, and all vital rates combined, the relative effect of variability was strongly and negatively correlated with life expectancy. The slope of the relationship between relative elasticity and life expectancy is similar for animals and plants (ANCOVA on log-transformed data in Fig. 2; taxon × longevity interactions are not significant ($P > 0.5$) for survival, reproduction, or all vital rates combined). There is a significant ($F_{1,32} = 10.74$, $P = 0.0025$) main effect of taxon for survival only, indicating that after controlling for the effect of life expectancy, animals had a somewhat higher relative sensitivity to increasing survival variability than did plants (Fig. 2A). For size-classified species, the relative effect on λ_s of variability in growth and reversion rates declined slightly with increasing life expectancy, but not significantly so (Appendix C). Because sensitivity to survival variability declined more steeply (and significantly) with life expectancy in these species, longer-lived species were more sensitive to variability in growth/reversion than in survival (Fig. C3).

DISCUSSION

We found a strong negative relationship between the sensitivity of population growth to increasing interannual variation in vital rates (relative to increasing mean rates) and longevity, which cuts across taxonomic and environmental differences. As a consequence, we expect short-lived species to be more influenced than longer-lived species by climate-driven increases in demographic variability. The potential sensitivity of short-lived species to an increasingly variable climate has important implications for biodiversity and human health. Annual organisms with no seed or propagule bank (annual seaweeds and univoltine insects in this study) are vulnerable to environmental fluctuation because viability of their populations hinges on successful survival and reproduction every year. However, because many important agricultural pests and disease vectors are short-lived insects, and many noxious invasive species are annual or short-lived perennial plants, we may also expect that populations of these undesirable species may decline (or at least grow less rapidly) in a more variable world, thus ameliorating their negative impacts. Of course, if climatic variability decreases in some regions (as climate models predict), a negative elasticity to variability implies that population growth will increase as variability declines; locales with declining climate variability thus may experience increased viability of

short-lived native species but exacerbated problems with pest species.

Our results suggest that we should consider life history features such as life expectancy rather than taxonomic affiliation when we attempt to identify species that will be most sensitive to future changes in climate variability. We did see greater sensitivity to increased variability of survival in animals relative to plants even after accounting for life expectancy (Fig. 2A), but this may reflect methodological rather than true biological differences. We used age-based models for all animal populations but size-based models for most plants. In age-based models, survival probabilities govern the likelihood both of remaining in the population and of advancing to later life-history stages, whereas in size-based matrices, advancement (and reversion) is governed by additional vital rates. Thus variation in survival may be representing more of the total demographic variation for age-classified animal populations.

Although increasing vital rate variability does have a measurable impact, it is important to note that trends in mean vital rates are predicted to have a stronger influence on the population growth rates of all species. Short-lived species showed on average the largest relative effect of increasing variability in all vital rates, a value of −0.2 (Fig. 1C), which implies that the magnitude of the summed elasticity to the vital rate SDs must be about one-sixth the magnitude of the summed elasticity to the vital rate means. Thus climate-driven changes in mean vital rates are clearly important, but their effects may be significantly modified by differences among species in their responses to changing variability as a function of their life histories.

Why are long-lived species more immune to increasing variability of both survival and reproduction? Lower elasticity to survival variability in longer-lived species may reflect in part a constraint on the variance of survival. For a species to be long-lived, survival must be high in most years, so the SD of survival must be low (Morris and Doak 2004). As it is a proportional derivative, the elasticity to a SD can be expressed as the derivative of λ_s with respect to the vital rate SD (the so-called "sensitivity" of λ_s to the vital rate SD) divided by λ_s and multiplied by the SD; consequently, the elasticity will tend to be small when the SD is small. However, the absolute value of the summed sensitivities to the SDs of survival rates is itself strongly and negatively correlated with longevity (Appendix C), reflecting a deeper resilience to changing year-to-year variability in long-lived species. Regarding reproduction, for many species in our database (especially plants that produce many offspring per year), the reproductive rates as a whole are not subjected to the same limit to variability that applies to survival rates, but there is again a negative (albeit weaker) correlation between the summed sensitivities to the reproductive rate SDs and longevity. In long-lived species, the deterministic sensitivities of reproductive rates are usually low relative to survival rate sensitivities (Pfister 1998, Caswell 2001); as a result, we expect increasing variation in reproduction to have a weaker effect on the interannual variation in population growth (and thus on λ_s) than increasing variation in survival if vital rates vary independently (Pfister 1998, Gaillard et al. 2000, Saether and Bakke

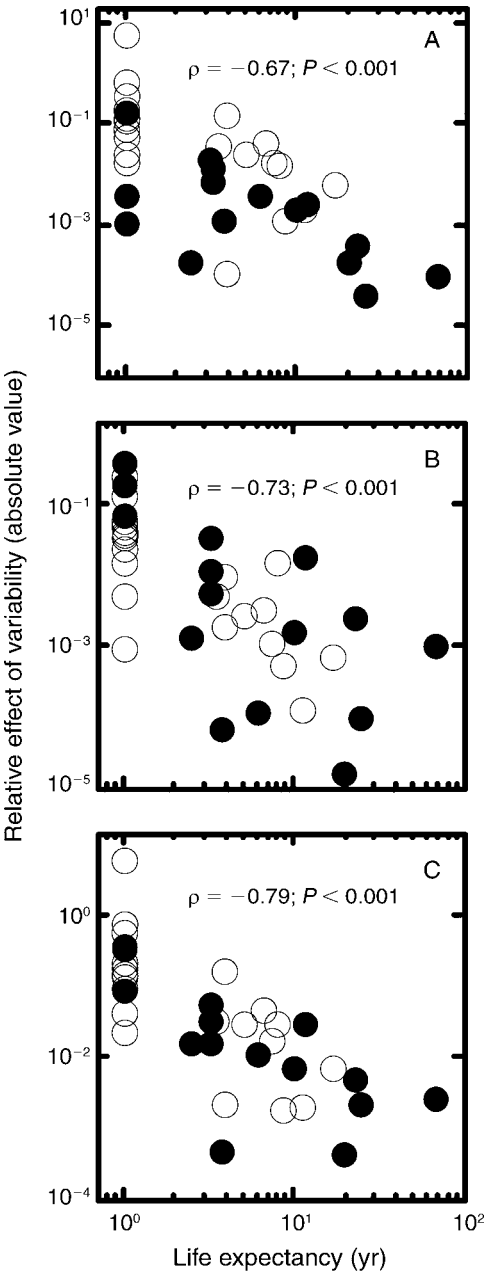

FIG. 2. Longer-lived species are less sensitive to increasing variability in (A) survival rates, (B) reproductive rates, and (C) all vital rates. Open symbols represent animals; solid symbols are plants. Annual species were assigned a life expectancy of 1 year. Spearman's rank correlation, ρ, is given, as well as *P*, the probability from a two-tailed test of the hypothesis that $\rho = 0$. Note the log–log scale.

2000, Morris and Doak 2004). Thus the presence of a persistent adult stage allows long-lived species to better tolerate small increases in the year-to-year variability of both survival and reproduction. In fact, we can show using randomly constructed but biologically realistic sets of vital rates that lower sensitivity to increasing demographic variability is likely to be a general correlate of increasing longevity (Appendix D).

Species in autocorrelated environments show responses to increasing vital rate variability that are similar overall to those of species in IID environments (Appendix C). For some IID cases, subtle environmental autocorrelation may nevertheless exist, but the overall similarity in elasticity patterns suggests that any omission of autocorrelation we may have committed would not have strongly biased our results. But we reiterate that for most species in autocorrelated environments, we modeled increasing variability by perturbing vital rates about the means specific to each phase in a disturbance or density cycle. The only exceptions are the plants *Ardisia elliptica* and *Calathea ovandensis*, for which we modeled increasing variability by perturbing vital rates about their overall means (Appendix A). Interestingly, those are the only two species that have positive elasticities to increasing variability in all vital rates, implying that they would experience slightly higher long-term growth rates in a more variable world. For disturbance-prone species, perturbing the vital rate means specific to each disturbance phase about the overall means can result in elasticities to increasing variability that are more strongly positive, because the precise sequence of life history events may be adapted to exploit the disturbance cycle (Morris et al. 2006). However, an unresolved question is how often (if ever) climate fluctuations will be sufficiently synchronized with the disturbance cycle such that increasing climatic variability would consistently push a vital rate further above its overall mean during disturbance stages in which it is already high and farther below its mean when it is already low. Nonetheless, a generalization that emerges from the analysis we have presented here is that increasing vital rate variability, either over all years in IID scenarios or within stages of a multiyear disturbance or density cycle, as might occur under increased interannual climate variability, most often acts to depress the long-term population growth rate.

Four caveats apply to our results. First, elasticities describe the response of λ_s to small changes in the mean or SD of a vital rate. Second, as the data did not allow us to include density dependence for most species, we have neglected interactions between density and climate (Coulson et al. 2001, Saether et al. 2005, Boyce et al. 2006) and the possibility that declining populations may be rescued by the relaxation of negative density dependence (or further endangered by demographic stochasticity, Allee effects, etc.). Third, in summing elasticities, we assumed that all vital rates experience similar proportional changes, whereas in reality some vital rates may be more environmentally sensitive than others. Finally, for disturbance-prone species in autocorrelated environments, we assumed that the environmental state transition matrix remains constant as the values of the vital rates in each environmental state are perturbed, whereas climate change may also alter the disturbance frequency and thus the state transition matrix. Despite these caveats, in the absence of more detailed data on how climate will change at the scale of local populations, and on how vital rates respond to those changes, comparing elasticity patterns across species, as we have done here, provides an initial glimpse at the likely impacts on populations of trends in both climate averages and climatic variability, and it suggests that life history differences will play a very important role in shaping those impacts.

Acknowledgments

This work was conducted as part of the Stochastic Demography Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0072909), the University of California, and the Santa Barbara campus. We also thank the many people who helped collect the demographic data that made this analysis possible. C. V. Haridas and C. T. Lee were supported by NIA grant PO1 AB 22500 to S. Tuljapurkar and C. C. Horvitz.

Literature Cited

Boer, G. J., G. Flato, and D. Ramsden. 2000. A transient climate change simulation with greenhouse gas and aerosol forcing: projected climate to the twenty-first century. Climate Dynamics 16:427–450.

Boyce, M. S., C. V. Haridas, and C. T. Lee. 2006. Demography in an increasingly variable world. Trends in Ecology and Evolution 21:141–148.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Coulson, T. E., A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Doak, D. F., W. F. Morris, C. Pfister, B. E. Kendall, and E. M. Bruna. 2005. Correctly estimating how environmental stochasticity influences fitness and population growth. American Naturalist 166:E14–E21.

Drake, J. M. 2005. Population effects of increased climate variation. Proceedings of The Royal Society B 272:1823–1827.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–2074.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Giorgi, F., X. Q. Bi, and J. Pal. 2004. Mean, interannual variability and trends in a regional climate change experiment over Europe. II: climate change scenarios (2071–2100). Climate Dynamics 23:839–858.

Haridas, C. V., and S. Tuljapurkar. 2005. Elasticities in variable environments: properties and implications. American Naturalist 166:481–495.

Intergovernmental Panel on Climate Change. 2007. Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, UK.

Lewontin, R. C., and D. Cohen. 1969. On population growth in a randomly varying environment. Proceedings of the National Academy of Sciences (USA) 62:1056–1060.
Morris, W. F., and D. F. Doak. 2004. Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. American Naturalist 163:579–590.
Morris, W. F., S. Tuljapurkar, C. V. Haridas, E. S. Menges, C. C. Horvitz, and C. A. Pfister. 2006. Sensitivity of the population growth rate to demographic variability within and between phases of the disturbance cycle. Ecology Letters 9:1331–1341.
Murphy, G. I. 1968. Pattern in life history and environment. American Naturalist 102:391–403.
Orzack, S. H., and S. Tuljapurkar. 1989. Population dynamics in variable environments. 7. The demography and evolution of iteroparity. American Naturalist 133:901–923.
Parmesan, C., et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583.
Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.
Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences (USA) 95:213–218.
Pounds, J. A., et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161–167.
Raisanen, J. 2002. CO_2-induced changes in interannual temperature and precipitation variability in 19 CMIP2 experiments. Journal of Climate 15:2395–2411.
Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.
Rowell, D. P. 2005. A scenario of European climate change for the late twenty-first century: seasonal means and interannual variability. Climate Dynamics 25:837–849.
Saether, B. E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.
Saether, B. E., et al. 2005. Generation time and temporal scaling of bird population dynamics. Nature 436:99–102.
Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. American Naturalist 108:783–790.
Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature 427:145–148.
Tuljapurkar, S., and C. C. Horvitz. 2006. From stage to age in variable environments: life expectancy and survivorship. Ecology 87:1497–1509.
Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. American Naturalist 162:489–502.
Watterson, I. G. 2005. Simulated changes due to global warming in the variability of precipitation, and their interpretation using a gamma-distributed stochastic model. Advances in Water Resources 28:1368–1381.

APPENDIX A

Descriptions of the demographic studies used in the analysis (*Ecological Archives* E089-003-A1).

APPENDIX B

Methods for constructing projection matrices and computing stochastic elasticities (*Ecological Archives* E089-003-A2).

APPENDIX C

Statistical tables and additional results (*Ecological Archives* E089-003-A3).

APPENDIX D

Sensitivity to increasing variability vs. longevity in randomly constructed life histories (*Ecological Archives* E089-003-A4).