Using Population Viability Analysis to Predict the Effects of Climate Change on the Extinction Risk of an Endangered Limestone Endemic Shrub, Arizona Cliffrose

JOYCE MASCHINSKI,*† JOANNE E. BAGGS,†‡ PEDRO F. QUINTANA-ASCENCIO,§ AND ERIC S. MENGES**

*Fairchild Tropical Botanic Garden, 11935 Old Cutler Road, Miami, FL 33156, U.S.A., email jmaschinski@fairchildgarden.org
†The Arboretum at Flagstaff, Flagstaff, AZ 86001, U.S.A.
‡U.S. Forest Service, Humboldt-Toiyabe National Forest, 1200 Franklin Way, Sparks, NV 89431, U.S.A.
§Department of Biology, University of Central Florida, 4000 Central Florida Boulevard, Orlando, FL 32816-2368, U.S.A.
**Archbold Biological Station, P.O. Box 2057, Lake Placid, FL 33862, U.S.A.

Abstract: *The threat of global warming to rare species is a growing concern, yet few studies have predicted its effects on rare populations. Using demographic data gathered in both drought and nondrought years between 1996–2003 in central Arizona upper Sonoran Desert, we modeled population viability for the federally endangered* Purshia subintegra *(Kearney) Henrickson (Arizona cliffrose). We used deterministic matrix projection models and stochastic models simulating weather conditions during our study, given historical weather variation and under scenarios of increased aridity. Our models suggest that the* P. subintegra *population in Verde Valley is slowly declining and will be at greater risk of extinction with increased aridity. Across patches at a fine spatial scale, demographic performance was associated with environmental factors. Moist sites (patches with the highest soil moisture, lowest sand content, and most northern aspects) had the highest densities, highest seedling recruitment, and highest risk of extinction over the shortest time span. Extinction risk in moist sites was exacerbated by higher variance in recruitment and mortality. Dry sites had higher cumulative adult survival and lower extinction risk but negative growth rates. Steps necessary for the conservation of the species include introductions at more northern latitudes and in situ manipulations to enhance seedling recruitment and plant survival. We demonstrate that fine spatial-scale modeling is necessary to predict where patches with highest extinction risk or potential refugia for rare species may occur. Because current climate projections for the 21st century imply range shifts at rates of 300 to 500 km/century, which are beyond even exceptional examples of shifts in the fossil record of 100–150 km, it is likely that preservation of many rare species will require human intervention and a long-term commitment. Global warming conditions are likely to reduce the carrying capacity of many rare species' habitats.*

Key Words: drought, endangered species, global warming, population viability analysis, *Purshia subintegra*

Utilización de AVP para Predecir los Efectos del Cambio Climático sobre el Riesgo de Extinción de *Purshia subintegra*, un Arbusto Endémico en Peligro

Resumen: *La amenaza del calentamiento global a las especies raras es una preocupación creciente, a pesar de ello pocos estudios han predicho sus efectos sobre poblaciones raras. Utilizando datos demográficos obtenidos en años con y sin sequía entre 1996 y 2003 en el centro de Arizona en el desierto de Sonora, modelamos la viabilidad poblacional de* Purshia subintegra *(Kearney) Henrickson, federalmente en peligro.*

Utilizamos modelos determinísticos de proyección matricial y modelos estocásticos que simularon las condiciones del tiempo durante nuestro estudio, considerando la variación climatológica histórica y bajo escenarios de aridez creciente. Nuestros modelos sugieren que la población de P. subintegra *en Valle Verde está declinando lentamente y estará en mayor riesgo de extinción con la aridez creciente. En una escala espacial fina, el funcionamiento poblacional se asoció con factores ambientales. Los sitios húmedos (parches con la mayor humedad del suelo, menor contenido de arena y con los aspectos más norteños) tuvieron las densidades más altas, el mayor reclutamiento de plántulas y el mayor riesgo de extinción en el plazo más corto. El riesgo de extinción en los sitios húmedos fue exacerbado por la mayor variación en el reclutamiento y la mortalidad. Los sitios secos tuvieron mayor supervivencia acumulativa de adultos y menor riesgo de extinción pero tasas negativas de crecimiento. Los pasos necesarios para la conservación de las especies incluyen introducciones en latitudes más al norte y manipulaciones in situ para reforzar el reclutamiento de plántulas y la supervivencia de plantas. Demostramos que el modelado a escala espacial fina es necesario para predecir donde pueden ocurrir parches con mayor riesgo de extinción o como refugios para especies raras. Debido a que las actuales proyecciones climáticas para el siglo veintiuno implican cambios en los rangos de distribución a una tasa de 300 a 500 km/siglo, que exceden aun a los ejemplos de cambios excepcionales de 100-150 km en el registro fósil, es probable que la preservación de muchas especies raras requiera de la intervención humana con un compromiso a largo plazo. Las condiciones del calentamiento global probablemente reducirán la capacidad de carga de los hábitats de muchas especies raras.*

Palabras Clave: análisis de viabilidad poblacional, calentamiento global, especies en peligro, *Purshia subintegra*, sequía

Introduction

Global meta-analyses, dendrochronological records, and recent climate records substantiate the idea that global climate change threatens biodiversity (IPPC 2001; Parmesan & Yohe 2003), yet few studies have documented the effects of climate change on rare populations. Most of the knowledge of species' responses to climatic change has come from historical or prehistoric records on common species or from physiological-based models of well-studied common species (i.e., Beerling et al. 2001; Davis & Shaw 2001; Rehfeldt et al. 2001). Because rare species have populations that are small, fragmented, restricted to fine-scale geologic formations and/or have limited dispersal ability, extreme climatic shifts could significantly decrease population size, increase extinction risk, and alter the distribution of species (Davis & Shaw 2001; McCarty 2001; Parmesan & Yohe 2003).

Models incorporating parameters from common plant species suggest that southern latitudes of North America will most likely have higher temperatures and drying trends, which will probably have negative impacts on species at the southern edge of their range (Rehfeldt et al. 2001).

Hotter and drier conditions are predicted for interior continents, with semiarid ecosystems being the most sensitive (Risser 1995; Allen & Breshears 1998). Recent observations support these predictions. Within the past 7 years severe drought has caused up to 70% mortality of some pinyon pine (*Pinus edulis* Engelm.) populations in northern Arizona (Ogle et al. 2000). Although rare species in the southwestern United States evolved with drought, recent changes in temperature, rainfall patterns, and El

Niño oscillations present stressful conditions of magnitudes greater than any they faced historically and raise the question of whether rare species can persist through this period (e.g., Davis & Shaw 2001).

In the face of climatic change, conservation efforts should be focused on parts of the landscapes and populations with highest risk and highest conservation value, or on areas where species' recovery is likely (Hannah et al. 2002; Lavendel 2003). Interannual variation in moisture influences regional recruitment and mortality of tree populations in the Southwest over fairly large scales (Betancourt et al. 1993; Savage et al. 1996; Swetnam & Betancourt 1998). Yet, even at finer scales, vital rates vary significantly depending on fire history and patch characteristics (Quintana-Ascencio et al. 1998; Quintana-Ascencio & Menges 2000; Menges & Quintana-Ascencio 2004). Therefore, certain patches within a population may have greater probabilities of persistence and greater conservation value in the face of major climatic events. Relatively small areas may have an important role to play in protecting species and ecosystems by providing refugia that in turn can be sources of propagules for future natural or human-assisted expansion (Pulliam 1988; Lavendel 2003). Identifying areas of high conservation value is a priority for preserving biodiversity.

Using demographic data gathered in both wet and dry years between 1996 and 2003, we modeled population viability and extinction risk for the federally endangered *Purshia subintegra* (Kearney) Henrickson (Arizona cliffrose) under current and 100-year past conditions and under two scenarios of increased aridity. We hypothesized that the predicted climate change of higher temperatures and lower precipitation would negatively affect

population viability. Furthermore, we hypothesized that fine-scale structure would influence viability and conservation strategies for the species. The southwestern United States has undergone extreme drought within the past 7 years; therefore, this is a model system for addressing the following conservation questions: How does population viability of *P. subintegra* in the Verde Valley, Arizona, change under historical, current, and increasingly arid conditions? Does population demography vary across different patches such that some sites have greater susceptibility to climate change than other sites? Are there some patches of higher conservation value? Is demography related to environmental variables and is there spatial variation in these factors across the landscape? How would conditions of increasing aridity influence extinction risk and spatial distribution of the species?

Methods

Study Site and Organism

The federally endangered shrub *P. subintegra* occurs on limestone outcrops in four disjunct populations in central Arizona (USFWS 1994). Occupied area ranges from 1.2 km^2 near Bylas to 3.5 km^2 each at Burro Creek and Horseshoe Lake to 9 km^2 in the Verde Valley, where we conducted our study. Verde Valley is approximately 10 km north of Cottonwood, Arizona (34°44.381′N, 111°59.026′W). From 1971 to 2000, mean annual precipitation was 32 cm and mean high and low temperatures were 26.8° C and 8.6° C, respectively. Temperature extremes from 1994 to 2004 were 47° C and −8.3° C, and precipitation was below average in 7 of 10 years by 3–46% (NOAA 2003). Vegetation is the Upper Sonoran Desert scrub community, part of the *Larrea tridentata-Canothia holacantha* association (Brown 1982). Four rare limestone endemics co-occur with *P. subintegra* (Baggs 1998).

Usually <2 m tall, *P. subintegra* is a xeric rosaceaeous nonclonal evergreen shrub with pale yellow flowers and entire leaves that lack glands. Adult plants bloom from late March through early June (Fitts et al. 1993; Baggs & Maschinski 2000). Seeds disperse from July through August and seed germination occurs the following spring from March through June, depending on temperature and rainfall. In dry years, plants may not produce any viable seed and there may be no seedling recruitment (Baggs & Maschinski 2000).

In the Verde Valley, *P. subintegra* hybridizes with *P. stansburiana* (Torr.) Henrickson (Stansbury cliffrose), a widespread species in the western United States that has lobed leaves and glands on the hypanthium, young stems, and leaves (Baggs & Maschinski 2001*b*). Morphologically there are distinctions within the hybrid swarm in which some plants have "pure" *P. subintegra* and *P. stansburi-ana* characters and others have a blend of both. Plants with pure morphological characters have unique phenology, relative growth rates, and distinct root:shoot allocation patterns even when grown under common garden conditions (Baggs & Maschinski 2001*b*; Maschinski et al. 2002; J.E.B., unpublished data). We monitored and modeled morphologically pure *P. subintegra*. Investigations of the hybrid swarm are ongoing.
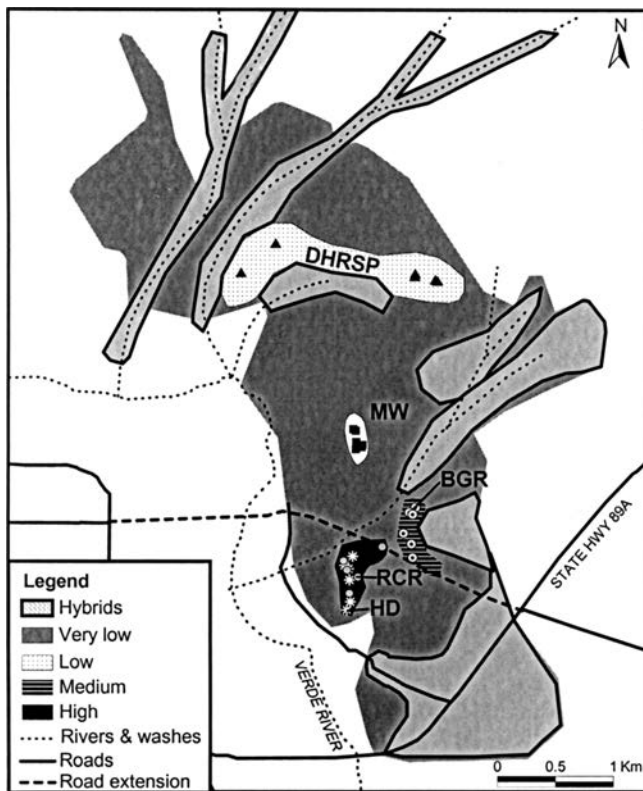
Demography

To determine the demographic patterns of *P. subintegra* growing in the Verde Valley, in 1996 we established 30, 4 × 10 m plots. We randomly selected 6 plots in each of four patches that span the species' 5-km range within the valley. We systematically selected 6 plots in HD patch, where we observed high densities of relatively young *P. subintegra* (HD, Fig. 1). All plots were located on similar geologic strata (limestone outcrops) and had similar Sonoran Desert scrub vegetation. We quantified environmental characteristics of each plot.

In October and November 1996, we established all plots and monitored each in late spring (April through June) from 1997 through 2001. For each individual, we measured height, perpendicular canopy widths, basal diameter, and total seeds. We determined canopy volume (Ludwig et al. 1975), which proved to be a reliable character for classifying stages. Each year we classified individuals into four nonoverlapping stages: seedlings, juveniles, vegetative adults, and reproductive adults. Seedlings had cotyledons present and fewer than six true leaves. Seedlings retained green cotyledons for approximately 2 months. In greenhouse and field studies, we never observed seedlings retain cotyledons for more than 1 year. Juveniles had more than six true leaves, canopy volume ≤550 cm^3, and basal diameter ≤4 mm. We never observed smaller plants flowering. Vegetative adults had canopy volume >550 cm^3 and produced no viable seed in the observation year, and reproductive adults had canopy volume >550 cm^3 and produced viable seed in the observation year. Because seeds can persist in the seed bank and germinate up to 3.5 years following release from reproductive adults, we included a persistent seed-bank stage in the model and used mean values from the studies described below to estimate seed-bank parameters.

Seed Bank

From 1997 to 2003, as part of a larger experiment, we examined germination and longevity of 1600 *P. subintegra* seeds sown into 240 cages in an experimental seed bank near a dry patch in the Verde Valley (BGR, Fig. 1; Maschinski et al. 2004). We calculated average seedling emergence in each year.

Figure 1. Map of demographic plots in Verde Valley, Arizona, showing relative locations of HD, RCR, MW, DHRSP, and BGR patches used to generate population viability analysis. The HD and RCR patches were moist and MW, DHRSP, and BGR patches were dry as determined by discriminant analysis. Field trials of seed germination occurred near the BGR patches. The legend refers to areas where hybrids are present and areas with varying densities of P. subintegra *(very low, ≤4 plants/40 m²; low, ≤10 plants/40 m²; medium, ≤20 plants/40 m²; high, ≤70 plants/40 m²). Delineation of boundaries between densities and hybrids are marked for graphic clarity but are less abrupt in nature.*

To assess the longevity of seeds in the seed bank, in 2001 we retrieved seeds from a subsample of 57 cages (with 1140 of the seeds sown in 1996) and counted the number of whole seeds with intact seed coats and seed fragments remaining in the seed bank. Using methods of Baggs and Maschinski (2001a), we stratified seeds for 4 weeks and quantified the germination of whole seeds with intact seed coats for 34 days in a greenhouse. Thus we quantified the mean proportion of fresh seeds germinating from one transition year to the next, the mean survival of seeds in the seed bank, and the mean proportion of seeds germinating from the seed bank for 3.5 years. We used these values to derive seed bank and reproductive values in the projection matrices.

Environmental, Demographic, and Spatial Factors

To determine whether plant demography was related to environmental factors and whether there was spatial differential in environmental factors and demography, we measured environmental attributes of plots: elevation, slope, aspect, gravimetric soil moisture, total N, total P, total K, soil particle size distribution, and bulk density. We determined elevation with an altimeter and slope with a clinometer. From each plot we collected three 0- to 10-cm soil cores and combined them for analysis of soil chemistry, gravimetric soil moisture, and soil composition (g/10 cm³) in April 1997. We repeated soil moisture measurements in April 1999. To determine gravimetric soil moisture, we passed soil through a 2-mm sieve and dried it to a constant weight at 105° C. We report results as percent oven dry weight, determined from grams of water lost in drying per gram of oven-dry soil × 100. Determining concentrations of total N, P, and K required a Kjeldahl digestion on soil subsamples. We determined soil particle size with a mechanical sieve method (Day 1965).

Using a Garmin GPS12 (Olathe, Kansas, U.S.A.), we recorded the global positioning satellite (GPS) locations of demographic plots to determine spatial location of *P. subintegra* patches (Fig. 1). For each patch we determined density of plants per square meter and used these to project population densities for scenarios of global warming. We determined patterns of environmental and demographic attributes in plots with stepwise discriminant analysis (SPSS 2001). We summarized demographic factors by quantifying total *P. subintegra* density in 1997, total seedling recruitment in 1997, and cumulative seedling and adult survival in plots from 1996 to 2003. Before analysis we examined variables for autocorrelations. None had correlations >0.8; therefore we used all variables. Using only variables that met tolerance limits, we examined patterns of environment and demography separately.

Population Viability Analysis

We developed a five-stage model: (1) seed bank, (2) seedling, (3) juvenile, (4) vegetative adult, and (5) reproductive adult. All stages except seedlings had stasis and all stages had transitions to larger class. Reproductive adults could transition back to vegetative adults and were the only stage that contributed to the seed bank and seedling stages.

We classified patches into either dry or moist sites based on discriminant analysis of environmental data and conducted analyses on each site for 7 transition years. We used conservative realistic estimates to model uncertainty. When any matrix cell was zero, we pooled data across years, excluding the transition 1998–1999, which had considerably higher precipitation than the other transition years. When mortality was not detected in a given

year, we adjusted cells based on calculations of cumulative survival of cohorts within a site. When no juveniles or reproductive plants changed stage, we decreased stasis transitions by 0.001 and added this value to the corresponding growth cell. In general transects in the dry site had much less recruitment and mortality than transects in moist sites; therefore they had more transitions with estimated values included in the matrices.

We estimated fertility terms, seed-bank survival, and germination from the seed bank with data either from the seed-bank experiment or from observed seedling recruitment and reproductive adults. We validated the fit of the fecundity values by comparing model and observed trajectories with chi-square tests (Sokal & Rolhf 1995). In years that had no seedlings or seeds we used the lowest nonzero combination of values for dry or moist sites. We adjusted for seed predation by multiplying all four reproductive matrix elements by 0.26, which represented seed losses estimated in an arid system (Chambers 2001). Details are available from www.thearb.org.

Model Scenarios for Current Conditions, Historical Conditions, and Increased Aridity

To determine the relative climatic condition of any transition year, we used climatic data from Tuzigoot National Monument, Arizona, a weather station 4 km from the field site. We determined yearly and seasonal precipitation patterns from 1994 to 2003 (NOAA 2003). We classified the observation transition years as wet or dry based on mean 1994–2003 precipitation (1997–1998 and 2000–2001 were wet transition years; all others were dry).

To determine precipitation patterns over a longer time scale, we used region-wide climatic data. Tree-ring records from El Malpais in northwestern New Mexico indicate that within the past 2129-year dendrochronological record a number of severe droughts have spanned decades (Grissino-Mayer 1996; Kipfmueller 2003). At the turn of the century there was a severe decade-long drought (Sheppard et al. 2002; NOAA 2003), yet the century that followed was relatively wet. Between 1903 and 2003, 43 years had average or above average precipitation. In 7 of the last 10 years there has been moderate to extreme drought. The most extreme occurred in 1999–2002, with precipitation 57% below average (Kipfmueller 2003). Thus, the 100-year-historical model had a greater percentage of years with above average precipitation than the random model, which encompassed precipitation patterns from 1996 to 2003.

To assess *P. subintegra* population viability under historical and simulated conditions of global warming, we generated population viability analysis (PVA) models separately for dry and moist sites in four different scenarios: (1) random, where each matrix for transition years 1996–2003 had equal probability of selection (0.143); (2) 100-year past, imitating actual precipitation probabilities

of dry years and wet years in the past 100 years (dry years 0.104; wet years 0.24); (3) 20% increased aridity (dry years 0.144; wet years 0.14); and (4) 40% increased aridity (dry years 0.184; wet years 0.04). We randomly selected matrices from wet or dry years to include in the models according to the proportional probabilities estimated for increased aridity. The matrix selection technique preserves life-history correlations and avoids unrealistic combinations of life-history traits (e.g., Menges & Quintana-Ascencio 2004). It evaluates a more limited sample of the range of parameter variation and covariation, however, and may underestimate the stochasticity in the system and extinction risks. Matrix and element selection produce highly correlated population growth rates and robust rankings of populations; therefore it is unlikely that using the matrix selection technique altered the relative ranks of scenarios or the predictions for management needs of the species (Kaye & Pyke 2003; McCarthy et al. 2003).

We used the stochastic simulation program POPPROJ (Menges 1990) to generate models with 1000 simulations over 150 years. For dry-site simulations we used an initial vector of [692227 0 0 121 0] and for moist site simulations we used [717 0 51 500 0]. Model predictions included final population sizes and probabilities of extinction (populations falling below a threshold of 1 individual). We calculated median stochastic λ values for each scenario following methods of Caswell (2001).

We verified the final random model predictions against 8 years of actual population numbers in the moist and dry sites with maximum likelihood tests (Sokal & Rolhf 1995). Models closely approximated the actual population numbers and were not significantly different (dry χ^2 = 3.87, $p > 0.05$; moist $\chi^2 = 5.9$, $p > 0.05$).

To assess the change of *P. subintegra* distribution in the Verde Valley under global warming scenarios, we used GIS to derive a map of the spatial change based on observed densities and model outcomes.

Results

Seed Bank

Purshia subintegra emerged from our experimental seed bank for 3.5 years after sowing. The first germination occurred 6 months after sowing; therefore estimates of initial germination and survival were based on 6 months in the first year and then 12 months in subsequent years. The greatest germination (387 of 1600 seeds) occurred in the first season after sowing, spring 1998 (a wet year). In subsequent years, few seeds germinated (1999, 2 seeds; 2000, 1 seed; 2001, 1 seed), and no new seedlings emerged in 2002 or 2003.

For the subset of cages used to quantify seed bank properties, 13% (148 of 1140 seeds) germinated within the first

6 months. By 2001 we retrieved 24 whole seeds and 388 seeds with split seed coats. We assumed that the seeds with split seed coats (34%) had begun to germinate but did not emerge. None of the 24 whole seeds we recovered from the seed bank germinated when exposed to misting in the greenhouse after 1 month of cold stratification. Because no seeds recovered from the seed bank in 2001 germinated, we assumed the longevity of seeds in the seed bank was 3.5 years for estimates in the PVA. We could not account for 51% of the seeds in the original cohort. These may have been lost to herbivory or some other factor.

Demography across Patches and Relationship to Environmental Factors

Discriminant analysis indicated that patches had distinct environmental characteristics that grouped into two clusters (Fig. 2). Plots were correctly classified into appropriate patches 73% of the time. Patches HD and RCR grouped distinctively from patches MW, DHRSP, and BGR, based on relatively high soil moisture and total P content and low sand content. For the population viability analysis, we therefore pooled the 12 HD and RCR plots and henceforth refer to them as the "moist" sites (Fig. 1). Similarly, we pooled 18 MW, DHRSP, and BGR plots for PVA and refer to them as the "dry" sites. Moist designation is only
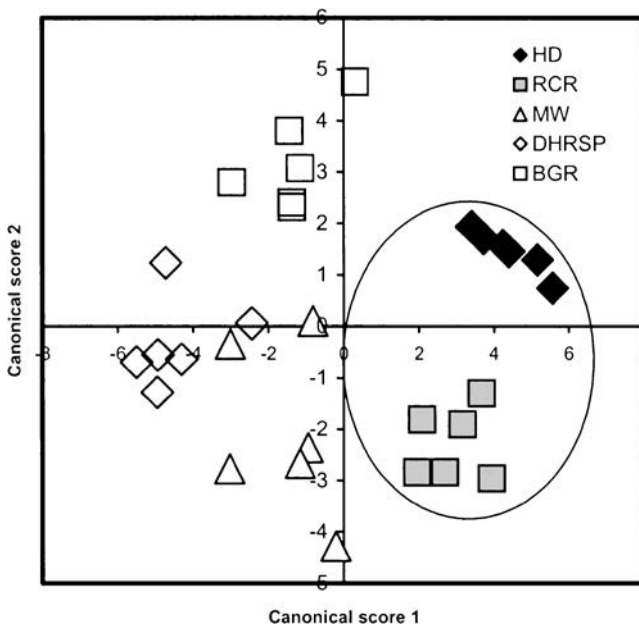
Figure 2. Discriminant analysis of environmental characters examined in group demographic plots (HD, RCR, MW, DHRSP, BGR, see Fig. 1): soil moisture measured in 1997 and 1999, total N, total P, total K, pH, proportion gravel, sand, silt/clay, elevation (m), slope, aspect, and bulk density. Soil moisture 1997, total P, sand, and northern aspect were significant factors. Circle encloses the moist site plots.

relative to the dry sites and should not be construed to mean mesic.

Discriminant analysis of demographic data indicated that patches with the highest soil moisture, lowest sand content, and greatest northern aspect tended to have high seedling recruitment and densities, whereas plots with the lowest soil moisture had the highest cumulative adult survival. Environmental characteristics had better classification resolution than demographic characteristics.

Population Viability of *Purshia subintegra*

Moist and dry sites had similar yearly fluctuation patterns and population growth corresponding to variation in seedling recruitment and mortality. The moist site had densities 2- to 4.5-fold higher than the dry site. In 1996 the dry site had 121 plants, whereas moist sites had 515 plants. In 1998 and 2001 many seedlings recruited in both moist and dry sites, but mortality was high in 1999, 2002, and 2003. In both dry and moist sites the highest mortality occurred in the smallest individuals, either seedlings or juveniles in the driest years. For example, between 2000 and 2001, dry sites had 86% juvenile mortality, whereas moist sites had 60%. In 2001–2002 only 2% and 3% of seedlings survived to the juvenile stage in dry and moist sites, respectively. No seedlings recruited in either moist or dry sites in 1996 or 2002. The 2003 recruitment of 77 seedlings we observed must have come largely from the persistent seed bank because only five seeds were produced on a single adult in the moist site in 2002. Despite recruitment in some years, the number of plants at the moist and dry sites continued to decline precipitously by 2003. Vegetative adult mortality was notably high in 2002–2003, especially in moist sites.

Based on random selection of matrices, projections suggest that *P. subintegra* will slowly decline in both dry ($\lambda = 0.983$, Fig. 3) and moist sites ($\lambda = 0.970$, Fig. 4). Variability was higher in moist than dry sites. Median population size of the moist site fell to 100 individuals within the 150 years, with a 20% extinction probability within 150 years (Fig. 3). Although the dry site had no extinctions within 150 years, median population size decreased to <20 individuals in 150 years (Fig. 4).

For models based on climate records in the last 100 years, when there were more years with above average precipitation, there was a much slower decline of population size and lower extinction risk in both dry ($\lambda = 0.988$, Fig. 3) and moist sites ($\lambda = 0.981$; Fig. 4). Dry sites had no extinctions within 150 years, whereas the moist site had a 2% probability of extinction within that time span. As was true with the random model, the moist site had higher population size and much greater variation than the dry site.

Elasticity analyses indicated that seed production did not contribute significantly to population growth. Even huge seed production (2 million seeds in 1997) in dry sites
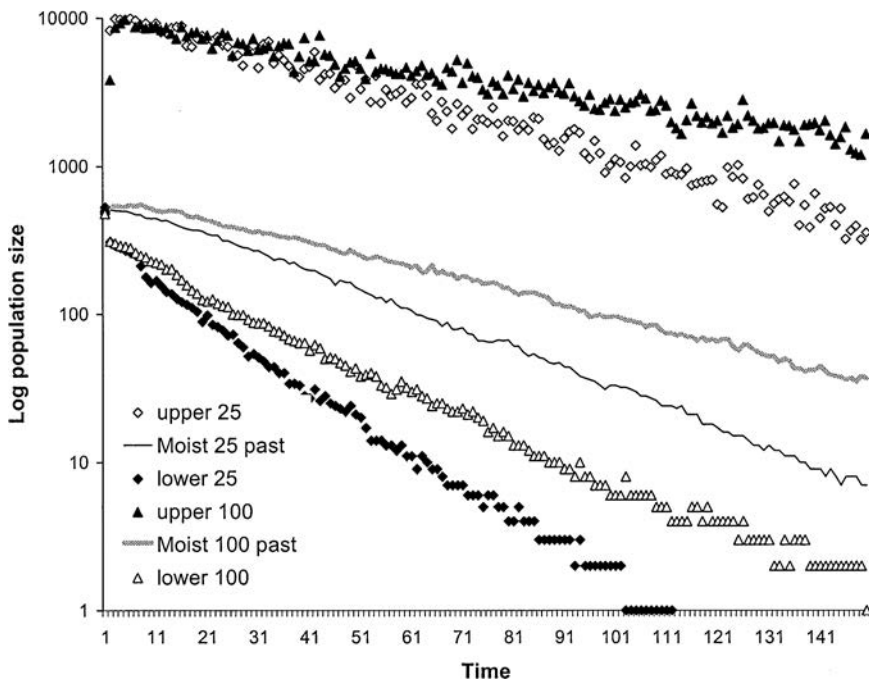
Figure 3. Projected population size of P. subintegra *in the moist site based on population viability models generated with 1000 simulations run for 150 years under random and 100-year past scenarios. Random models had equal probability of transition matrix entry, whereas 100-year models had probabilities of 0.104 for dry years and 0.24 for wet years. Upper and lower 95% confidence limits are indicated for each scenario.*

did not result in sustained population increases because seedling survival ranged from 2%–17.5%, depending on transition year. Seed bank and adult fecundity matrix elements had inconsequential elasticities. Stasis elements for vegetative adults in moist and dry sites contributed most to λ in most transition years. Exceptions occurred in 1996–1997 and 1999-2000, when reproductive adult stasis was the most important element.

Extinction Risk under Increasingly Arid Conditions

Under increasing arid conditions, extinction risk accelerated for both dry (20% λ = 0. 979; 40% λ = 0. 973, Fig. 5) and moist sites (20% λ = 0.970; 40% λ = 0. 964; Fig. 6). Population size declined more slowly at the dry site than at the moist site; there were no extinctions within 150 years. Variance and uncertainty increased dramatically in
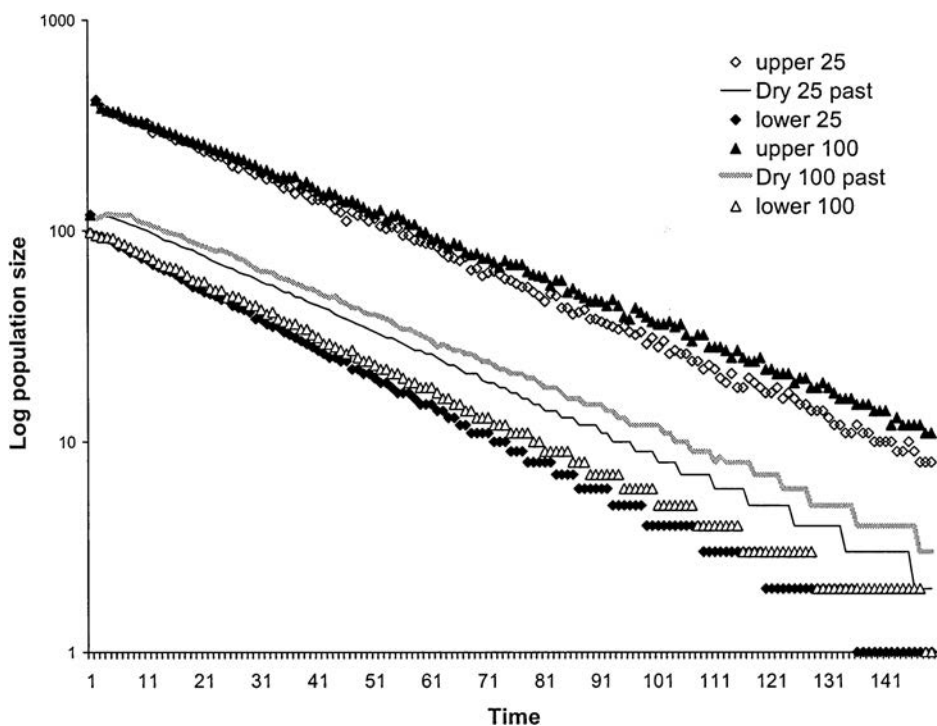

Figure 4. Projected population size of P. subintegra *in the dry site based on population viability models generated with 1000 simulations run for 150 years under random and 100-year past scenarios. Random models had equal probability of transition matrix entry, whereas 100-year models had probabilities of 0.104 for dry years and 0.24 for wet years. Upper and lower 95% confidence limits are indicated for each scenario.*
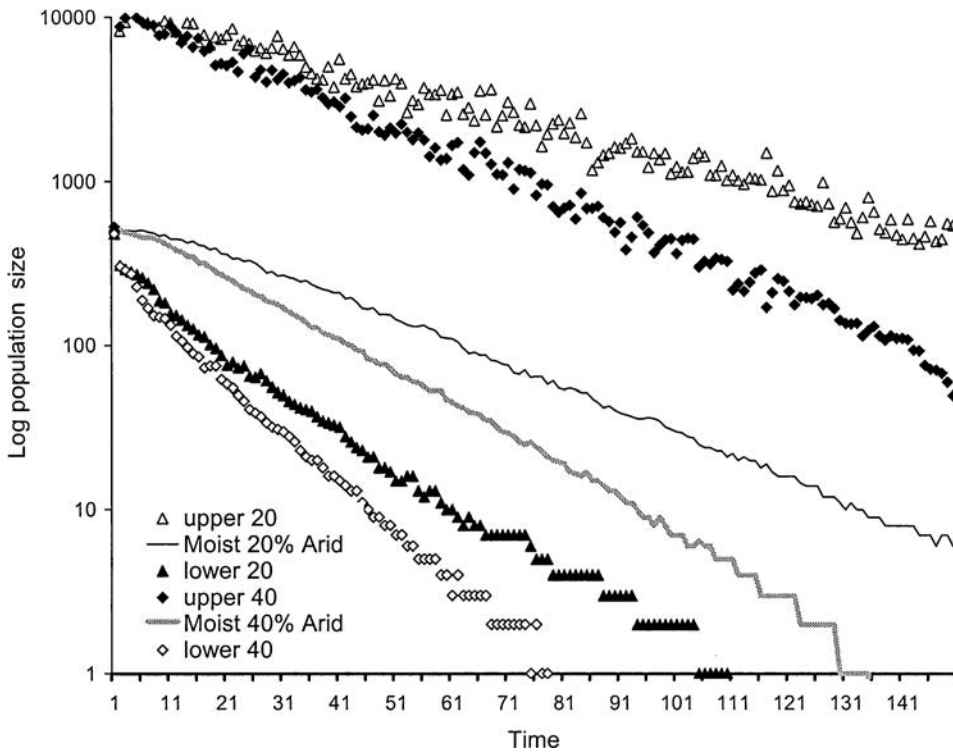
Figure 5. Projected population size of P. subintegra *in the moist site based on population viability models generated with 1000 simulations run for 150 years with 20% and 40% increased aridity scenarios. Models of 20% increased aridity had probabilities of matrix selection as 0.144 for dry years and 0.14 for wet years. Models of 40% increased aridity had probabilities of matrix selection as 0.184 for dry years and 0.04 for wet years. Upper and lower 95% confidence limits are indicated for each scenario.*

the moist-site models (Fig. 6), such that predicted population size between 75 and 105 years for the 20% and 40% arid models ranged from 0 to 10,000. Within 105 years, the probability of extinction at the moist site increased to 19% for the 20% arid model and to 63% for the 40% arid model.

In the face of increased aridity, these models suggest that patches of *P. subintegra* would shrink to extinction at varying rates (Fig. 1). The moist site, which encompassed approximately 20% of the total population density, had a higher probability of suffering loss in a shorter time span than the dry sites.
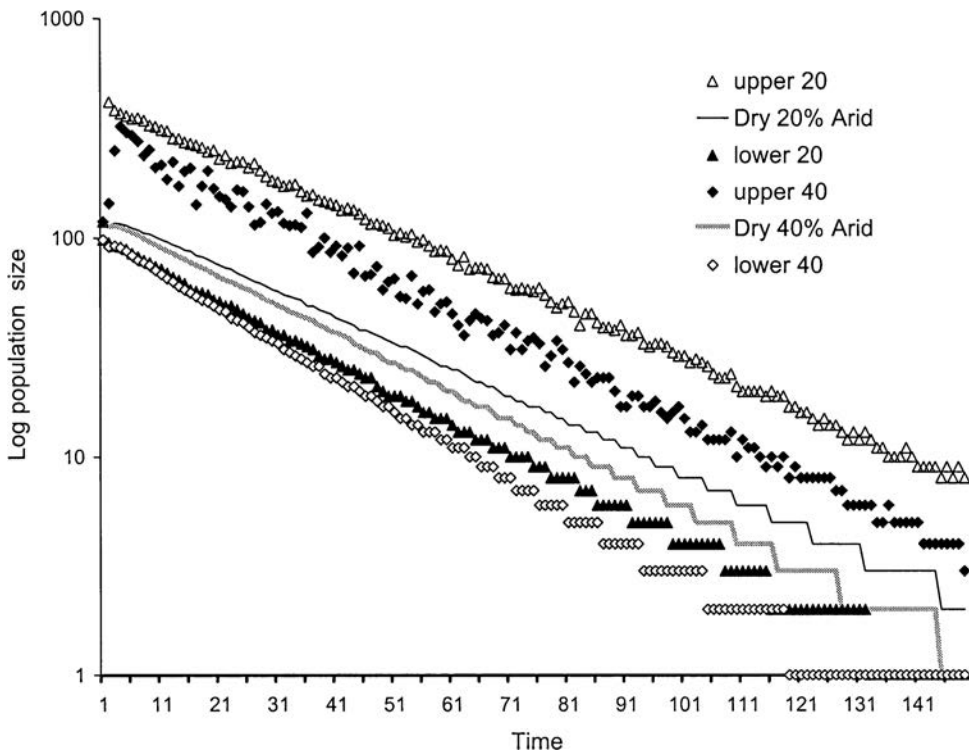

Figure 6. Projected population size of P. subintegra *in the dry site based on population viability models generated with 1000 simulations run for 150 years with 20% and 40% increased aridity scenarios. Models of 20% increased aridity had probabilities of matrix selection as 0.144 for dry years and 0.14 for wet years. Models of 40% increased aridity had probabilities of matrix selection as 0.184 for dry years and 0.04 for wet years. Upper and lower 95% confidence limits are indicated for each scenario.*

Discussion

The threat of global climate change to rare species has been a growing concern that calls for novel approaches to conservation management of rare species (McCarty 2001; Lavendel 2003). Capturing demographic behavior of *P. subintegra* during drought and nondrought years provided us valuable data for building population viability models under historical and hypothetical conditions of increased aridity. Our models suggest that the *P. subintegra* population in Verde Valley is slowly declining and will be at greater risk of extinction with global warming.

Other models of climate change in temperate North America that incorporate increased temperature and drought predict reductions of forest stands, mortality of small-stature plants (seedlings and saplings), gradual changes in species composition (Hanson & Weltzin 2000), loss of several key species (Bugmann et al. 2001; Iverson & Prasad 2002), and change in species ranges (Iverson & Prasad 2002). These models focus on widespread species. Our models of the endangered *P. subintegra* suggest similar outcomes—reduced population size and higher mortality of small plants. With decreasing population size, the risks of genetic erosion and extinction increase, and these risks become even higher when habitat is fragmented (Young & Clarke 2000).

Further, our models suggest that within the *P. subintegra* population in the Verde Valley there is differential demographic behavior across patches at a fine spatial scale. The moist site had greater densities and recruitment, greater variance of population size, greater stand diversity, and higher risk of extinction than patches in dry sites. Under global warming, our models suggest that *P. subintegra* could experience loss from the moist and dry sites or a contraction of range, as has been predicted by other models incorporating climate change (Iverson & Prasad 2002), and it is probable that extinction would occur more rapidly at moist sites than at dry sites (Fig. 1).

The spatial pattern of demography was related to aspects of soil moisture, northern aspect, and P and sand content in soils. It is likely that underlying geomorphic structure influences the patterns we saw among soil water content, plant performance, and demography (McAuliffe 1994; Hamerlynck et al. 2002). In other desert shrubs there is evidence that geomorphology is correlated with demography and the spatial distribution of species (McAuliffe & McDonald 1995; Hamerlynck et al. 2002). Sites in the Verde Valley supporting the most seedlings and juveniles of *P. subintegra* had the greatest surface soil moisture in a wet (1997) and dry year (1999), but they still sustained high mortality of seedlings and juveniles in the driest years (2001 and 2002). In contrast, the driest sites tended to have the fewest seedlings and juveniles but the largest, most fecund reproductive adults. This pattern is consistent with an underlying soil structure that retains water at depths which can support large shrubs but not small individuals (e.g., Hamerlynck et al. 2002).

Conservation of the species will require population enhancement within and outside currently occupied habitat. As has been observed in other long-lived species, surviving *P. subintegra* adults have the largest elasticity values, but the major threat to this species' persistence is lack of recruitment (Maunder et al. 2002; Schwartz 2003; Kwit et al. 2004). Vital rates with high elasticities are not necessarily the most productive targets for management because frequently they have low variation (Pfister 1998; de Kroon et al. 2000; Brigham & Schwartz 2003; Schwartz 2003; but see Pico et al. 2003) and therefore may have limited impact on population growth.

Although restoring the population with adults is possible, this strategy will require a long-term commitment for cultivation and irrigation after introduction (Baggs & Maschinski 2001*a*). Further, it is the most technically difficult and resource-intensive approach and has proven less successful than introductions of seeds unless plants are irrigated over the long term (Maschinski 2006). Introduced adult *P. subintegra* with 6 months of weekly irrigation had 98% mortality after 5 years; those with weekly irrigation for 2 years, however, had 14% mortality (Maschinski 2006; S. Murray, unpublished data).

Enhancing seedling recruitment and plant survival is essential and will require different strategies in moist and dry habitats. Moist sites had the greatest seedling recruitment and high episodic mortality, which suggests that human intervention could be most effective at this site. Given the high plant densities and higher extinction risk at this site more immediate active management is needed. We recommend enhancing survival of seedlings with protective caging (Maschinski et al. 2004). Dry sites have sparse stands of adults with little recruitment. Experiments are needed to determine whether introduced seeds will germinate and survive at dry sites with the lowest densities.

Enhancing the population with seeds in both moist and dry sites could increase our understanding of the seed bank, which is the least-understood part of the life cycle. Storing seeds from dry and moist habitats is recommended to preserve genetic diversity and to provide sources for introductions during wet years (e.g., Guerrant et al. 2004). Our observations showed that seedling recruitment in 2003 was reasonably good following the severe drought of 2002, when few seeds were produced, suggesting that seeds in the seed bank rapidly responded to favorable precipitation. Seed-bank responses (both natural and human assisted) may prove to be an important hedge against extinction for many rare species.

Because it is possible that the Verde Valley habitat may not be able to sustain larger numbers of *P. subintegra* under conditions of increased aridity, experimental attempts to introduce the species to higher moister sites are recommended. This solution is complicated by the presence of a

common congener, *P. stansburiana*, that grows at higher elevation and is known to hybridize with *P. subintegra.*

Imagining where it is likely that a rare species could achieve successful establishment under conditions of global warming is particularly difficult when habitats are restricted and disjunct or if the species' physiological tolerance thresholds may prohibit its survival at higher latitudes. Because current climate projections for the 21st century, which necessitate range shifts at rates of 300 to 500 km per century, are beyond even exceptional examples of fossil record shifts of 100–150 km (Davis & Shaw 2001), it is likely that preservation of many rare species will require human intervention and a long-term commitment. Human-assisted translocations of genetically diverse founder populations would improve the probability for survival in new ambient conditions.

Our findings demonstrate that modeling the effects of global warming on rare species requires a fine scale to predict where possible refugia lie. By the nature of their rarity, rare species cannot be considered in large spatial or community scale because they are, as Gaston (1994) suggests, statistically problematic. Nevertheless, if we are to understand the implications of climate change on biodiversity and meet the objectives of the 1992 Convention on Biological Diversity (Heywood & Watson 1995), it is important to examine rare species too. Through fine-scale examination one can come closer to predicting shifts in ranges of individual species and communities and the interactions between effects of climate change and habitat fragmentation (Kappelle et al. 1999).

Acknowledgments

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