The Geography of Demography: Long-Term Demographic Studies and Species Distribution Models Reveal a Species Border Limited by Adaptation

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ABSTRACT: Potential causes of species' geographic distribution limits fall into two broad classes: (1) limited adaptation across spatially variable environments and (2) limited opportunities to colonize unoccupied areas. Combining demographic studies, analyses of demographic responses to environmental variation, and species distribution models, we investigated the causes of range limits in a model system, the eastern border of the California annual plant *Clarkia xantiana* ssp. *xantiana*. Vital rates of 20 populations varied with growing season temperature and precipitation: fruit number and overwinter survival of 1-year-old seeds declined steeply, while current-year seed germination increased modestly along west-to-east gradients in decreasing temperature, decreasing mean precipitation, and increasing variation in precipitation. Long-term stochastic finite rate of increase, λ_s, exhibited a fourfold range and varied among geologic surface materials as well as with temperature and precipitation. Growth rate declined significantly toward the eastern border, falling below 1 in three of the five easternmost populations. Distribution models employing demographically important environmental variables predicted low habitat favorability beyond the eastern border. Models that filtered or weighted population presences by λ_s predicted steeper eastward declines in favorability and assigned greater roles in setting the distribution to among-year variation in precipitation and to geologic surface material. These analyses reveal a species border likely set by limited adaptation to declining environmental quality.

Keywords: geographic range, species borders, demography, population projection matrixes, species distribution modeling.

Introduction

Understanding limits to species' geographic distributions is fundamental to biology (Grinnell 1917; MacArthur 1972; Brown and Lomolino 1998; Gaston 2003; Geber 2011) and critical for conservation and predicting biotic

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responses to climate change (Parmesan et al. 2005). Potential sources of distribution limits fall into two broad classes that may act alone or in combination (reviewed, e.g., in Sexton et al. 2009; Holt and Barfield 2011): (1) limits to adaptation across spatially variable environments, caused by trade-offs and/or inadequate or maladaptive genetic variation in species-border populations (Antonovics 1976; Hoffmann and Blows 1994; Kirkpatrick and Barton 1997; Bridle et al. 2007), and (2) limited opportunity to colonize patches of suitable habitat, caused by various forms of dispersal constraints (Holt and Keitt 2000; Keitt et al. 2001; Paul et al. 2009). At present, the operation of limited adaptation is supported by considerable evidence (Gaston 2003), while limited opportunity clearly defines ranges during rapid expansions (Ibañez et al. 2009) and also appears to operate over longer ecological (Munguía et al. 2008; Samis and Eckert 2009) and evolutionary time scales (Paul et al. 2009). Comprehensive studies that consider multiple sources of range limits in the same system, however, are very rare, making it difficult to explain particular cases, let alone draw general conclusions (Gaston 2009).

Understanding geographic variation in demography is the key to discerning the causes of range limits. If dispersal constraints are weak, one would expect species' geographic borders to correlate closely with the environmental variation that distinguishes regions where populations can persist (i.e., where the finite rate of increase, λ, is 1 or greater) from regions where they cannot (Brown et al. 1996; Pulliam 2000; Soberón 2007; Godsoe 2009). Covariance across the range between population performance and environmental factors confirmed to affect performance would implicate limited adaptation (e.g., Carey et al. 1995; Purves 2009). If variation in population performance is independent of range position (e.g., Samis and Eckert 2007) or if performance increases at the border (Prince and Carter

1985; Angert 2009), then limited dispersal may be the chief factor defining range limits.

When there is evidence of limited adaptation in defining a species border, identifying the environmental conditions that enable population persistence is challenging, given that population performance may be highly variable in time and space and population growth may vary in sensitivity to different life-cycle transitions (de Kroon et al. 1986; Caswell 2001). Multiyear multipopulation studies that follow populations throughout the life cycle—and that use projection models to make realistic estimates of long-term population growth (e.g., Morris and Doak 2005)—are therefore necessary to properly characterize demographic variation across the species' range (Jongejans et al. 2010). Such studies should also provide insight into the life stages and environmental factors that most strongly limit adaptation. Most existing demographic studies of species' ranges either record the geography of population census size, rather than the geography of population growth rate and the vital rates that drive it, or estimate population growth rate in a small number of populations (reviewed in Gaston 2009).

In this analysis, our approach to distinguishing the sources of range limits is to combine (1) estimates of vital rates and population growth rates in many populations over a substantial portion of a species' range, (2) analyses of the environmental factors that correlate with variation in demography, and (3) species distribution modeling (Peterson 2001; Latimer et al. 2006; Austin 2007; Elith and Leathwick 2009; Franklin 2009). Most species distribution models are purely correlative, taking species presence and absences—or presences alone—plus large numbers of georeferenced environmental variables as input to create statistical predictions of suitable habitat (potential geographic range) as output. An alternative approach is to use mechanistic models of individual or population performance specific to an organism, to identify threshold levels of environmental conditions that enable a specified level of performance (ideally, sustained population growth), and to map locations that lie above those thresholds (Kearney and Porter 2009; Buckley et al. 2010; Kearney et al. 2010). Our protocol, which uses field studies of demography to guide the selection of environmental variables and population points in correlative models of species distribution, combines aspects of both approaches (see also Morin and Thuiller 2009).

In the core range of the California annual plant *Clarkia xantiana* ssp. *xantiana*, we estimated vital rates over 4 years in 20 populations. We used estimates of vital rate to create population-projection matrices and estimate each population's long-term stochastic finite rate of increase, λ_s (Tuljapurkar et al. 2003). Assembling abiotic environmental data for each site and for the region enabled us to char-acterize how environmental variables may affect individual vital rates and λ_s. We used the environmental variables that were identified as important drivers of population performance as predictors in maximum entropy modeling of the species distribution (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011). We also applied two schemes to give high-performing populations greater influence in the models: (1) restricting models to populations that exhibit $\lambda_s \geq 1$ and (2) weighting populations by λ_s. We expected models that account for population performance to make superior predictions of habitat suitability and potential range. We interpreted our findings in light of the above expectations and in light of a simultaneous study of historical demography and population genetic structure of *C. xantiana* ssp. *xantiana* (Moeller et al. 2011).

Material and Methods

Study Organism

Clarkia xantiana ssp. *xantiana* A. Gray (Onagraceae), a winter annual endemic to central and southern California, has been the subject of a substantial history of evolutionary and ecological research (e.g., Moore and Lewis 1965; Mazer et al. 2004; Moeller 2004, 2006; Dudley et al. 2007; Eckhart et al. 2006, 2010). Its evolutionary sister is the smaller, earlier-flowering, and strongly self-fertilizing (as opposed to the highly outcrossing *C. xantiana* ssp. *xantiana*) *C. xantiana* ssp. *parviflora* (Eastw.) Harlan Lewis, which has a parapatric range. As the latter taxon is distinct phenotypically (Lewis and Raven 1992; Eckhart and Geber 1999; Runions and Geber 2000; Mazer et al. 2004; Eckhart et al. 2004), ecologically (Geber and Eckhart 2005), and genetically (Moore and Lewis 1965; Gottlieb 1984; D. A. Moeller and P. Tiffin, unpublished data), we treat the range limits of *C. xantiana* ssp. *xantiana* as species borders.

The setting for this study, the lower Kern River drainage (fig. 1), where *C. xantiana* ssp. *xantiana* is most abundant, is a climatically and biologically complex region where diverse taxa reach their geographic range limits (Grinnell 1917; California Department of Fish and Game 2003). Populations of *C. xantiana* ssp. *xantiana* occur here on slopes (mostly between elevations of 500 and 1,250 m), in sandy soils of igneous (mostly granodiorite or gabbro) or metasedimentary (mostly schist) origin (Lewis and Lewis 1955; Eckhart and Geber 1999; Eckhart et al. 2010).

Limited adaptation to low water availability appears to play a role in setting the eastern border of the range of *C. xantiana* ssp. *xantiana* in the study area. Rainfall tends to decline to the east in this part of the range (Western Regional Climate Center 2010; Eckhart et al. 2010). In a previous transplant experiment, lifetime fitness of *C. xantiana* ssp. *xantiana* was approximately tenfold lower at an
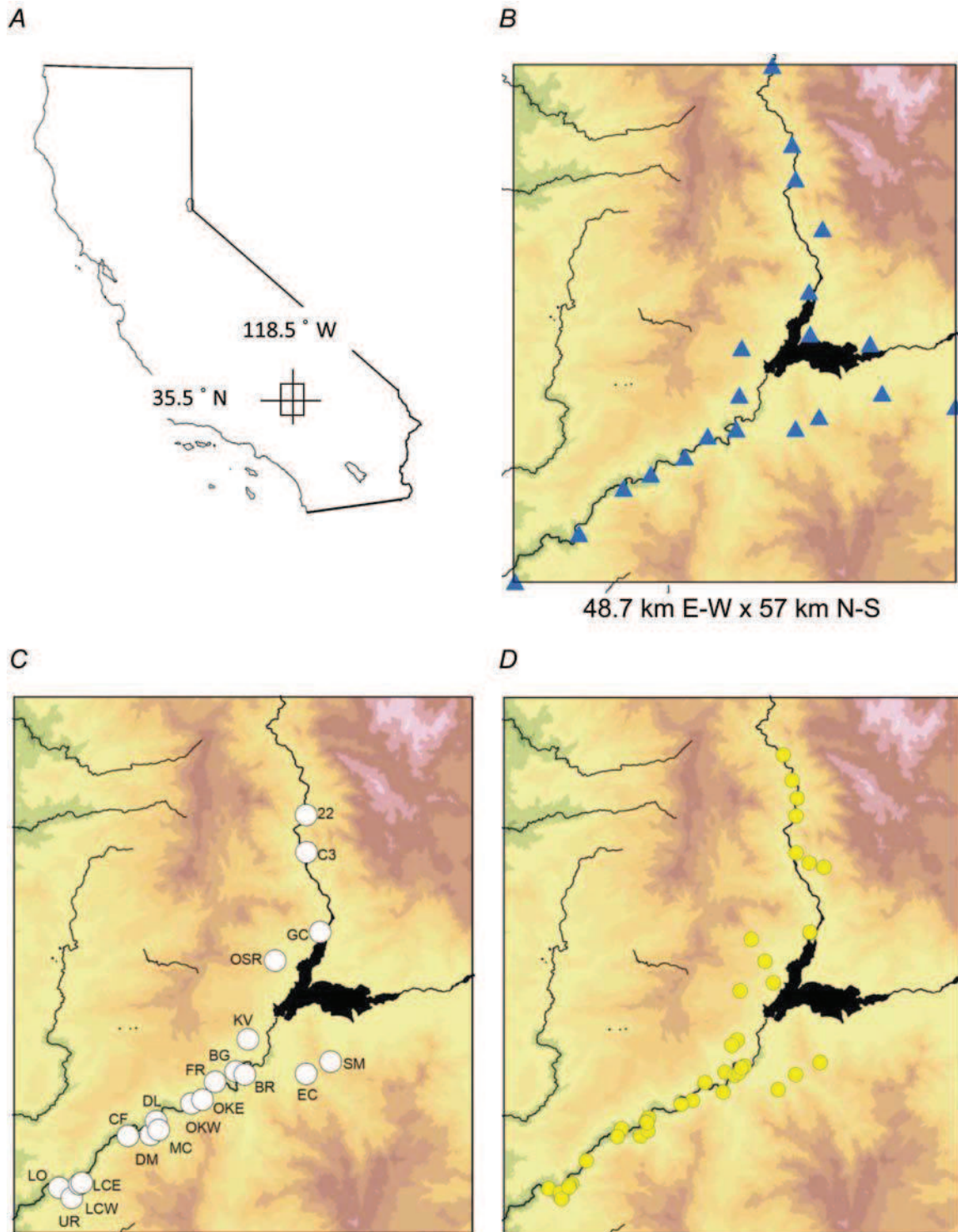
Figure 1: Details of the study area. *A*, Location within California. *B*, Blue triangles indicate weather stations; color shading shows elevations in 250-m intervals from the deepest canyons in the southwest (green, 250–500 m) to the highest peaks in the northeast (white, >2,500 m). *C*, White symbols indicate the 20 populations of *Clarkia xantiana* ssp. *xantiana* subjected to detailed demographic studies. *D*, Yellow symbols indicate the 20 focal populations in *C*, plus 21 additional populations with demographic data.

arid site beyond the eastern border than at sites within the species range, and within-sites fitness differences between a wet growing season and a dry growing season were even larger (Geber and Eckhart 2005). In a separate study, declines among populations in plant water status and fruit number mirrored declining annual precipitation and appeared to be exacerbated in areas of metasedimentary surface rocks along the eastern border, rocks that generate fine-textured soils that may increase water stress compared with coarser, igneous soils common elsewhere in the range (Eckhart et al. 2010). We therefore predicted (1) that one or more vital rates are sensitive to variation in seasonal precipitation and soil parent rock within the range (and likely also sensitive to temperatures, expected to decline with elevation) and (2) that population growth rates decline toward the eastern border. Environmental variables capable of causing such clinal variation in demography and limits to species' ranges would be expected to exhibit west-to-east gradients. Our sampling of environments and populations (see below) was designed to capture variation along this west-to-east axis rather than to investigate all range limits comprehensively.

Environment

Geologic data for the study area came from a combination of direct field observations and publicly available information. We noted the majority surface rock type for each study population (see below) by inspection and determined it for other parts of the landscape with a digitized geologic surface map (U.S. Geological Survey [USGS]; and see Nadin and Saleeby 2008). A digital elevation model (USGS) allowed us to estimate slope inclination, slope aspect, and potential solar radiation (the latter used for temperature modeling) with ArcGIS Spatial Analyst extension (ESRI, Redlands, CA).

Area climate data that were obtained during the study period came from a network of 21 weather stations (Onset Computer Corporation, Bourne, MA), where data loggers monitored temperature and precipitation beginning in October 2005 (fig. 1*B*). By replacing batteries and damaged (e.g., gun-shot) or stolen sensors and stations, we maintained a network of eight to 18 active stations that were separated from each other by ~5 km. To estimate precipitation somewhat beyond the geographic range, we placed four stations 2–13 km beyond the eastern border and obtained data from two additional locations beyond the range of the study populations to the west and to the north that provided web-published daily rainfall data (California Department of Water Resources 2010). We used spatial interpolation (kriging in ArcGIS 9.3 Spatial Analyst [ESRI], with default parameters and with grid cells of 1 ha, close to the mean size of *C. xantiana* ssp. *xantiana* population

areas; table A1 in the online edition of the *American Naturalist*) to estimate accumulated precipitation over specified ranges of dates and within a 48.7 × 57.0-km rectangle defined by the limits of the weather station network.

Temperature was expected to decline with elevation and increase on slopes receiving abundant solar radiation. Thus, to estimate seasonal temperatures over the landscape, we submitted our weather-station data to linear models, with year as a categorical variable and elevation, potential estimated solar radiation (on the winter solstice, vernal equinox, or summer solstice, depending on the time period being modeled), and linear azimuth (the absolute value of angular deviations from true south of slope aspect) as covariates. We used the Raster Calculator function of ArcGIS 9.3 to estimate temperature variables for grid cells, using the coefficients of the linear models.

For the analyses below, we calculated the following summary climate data: cumulative precipitation and the average daily mean, maximum, and minimum temperatures for selected multiple-month periods corresponding to the life-cycle transitions of the demography analysis (see below). In addition to calculating the means (across years) of all variables, we also calculated the coefficients of variation (CVs) in seasonal precipitation across years. We extracted values of climate variables for each focal population and evaluated relationships between climate and the eastward positions of populations, and we mapped climate variables and other physical features across the entire landscape that were used in species distribution modeling (see below).

Demography

We estimated age-specific seed survival and germination, seedling survival to fruiting, fruit production, and seeds per fruit for 20 *C. xantiana ssp. xantiana* populations from 2005 to 2009 (fig. A1 in the online edition of the *American Naturalist*; table A1). Focal populations were distributed from the western edge of the study area in the lower Kern Canyon, upriver in the Kern Canyon toward Isabella Lake (a reservoir created in the 1950s), and at the eastern range edge along the North Fork of the Kern River and on the south side of the reservoir (fig. 1*C*). We performed an annual census of fruiting adults for an additional 21 populations (fig. 1*D*; for methods, see Eckhart et al. 2010; Moeller et al. 2011).

In October 2005, we established at each of the 20 focal populations 30 permanent 1 × 0.5-m plots distributed among four to six transects, depending on site configuration. Plots were spaced 2.5 m apart along transects. Beginning in January 2006 and continuing each January until 2009, we recorded the number of *C. xantiana* ssp. *xantiana* seedlings in each plot. In June–July of each year, we re-

corded the number of fruiting plants and the number of fruits per plant for up to 15–20 plants per 0.5-m² plot. We collected one fruit from each of 20–30 haphazardly selected plants distributed across each population (but in outside plots, to avoid influencing seed input within them) to estimate the mean number of seeds produced per fruit. For each year, these data provided us with estimates of seedling survivorship to fruiting (σ), the number of fruits produced per plant (F), and the number of seeds produced per fruit (φ).

Also in October 2005, we placed at each site 30 5 × 5-cm nylon mesh bags, each containing 100 seeds collected at the site in June–July 2005. We positioned a seed bag closely adjacent to each permanent plot, affixing the bag to the ground with a steel fencing staple and covering it lightly with soil. In January 2006, we removed 10 bags at random from each site, counted the numbers of germinated seedlings and intact seeds in each bag, returned ungerminated seeds to the resealed bags, and returned the bags to their field positions 1 day later. In October 2006, we retrieved the same 200 bags to count the number of intact seeds and test them for viability (see protocol in box 1). This first set of seed bags provided estimates of seed survivorship (s_1) and germination (g_1) between November and January—the period when most germination occurs in response to winter rains—and of survival of ungerminated seeds from January to October (s_2) for seeds produced in the current year. In January 2007, we collected a second random sample of 10 bags for each of the 30 sites, counted germinants and intact seeds as above, and returned bags of intact seeds to their original sites. We retrieved this second set of bags permanently in October 2007 to perform viability tests. On the assumption that, during their first year, seeds in this second set of bags survived and germinated at the same rates as seeds in the first set of bags, we used our counts of germinants and intact seeds from the second set to estimate October–January survivorship (s_3), germination of 1-year-old seeds (g_2), and January–October survivorship of ungerminated 1-year-old seeds (s_4). The final set of 10 bags at each site was scored in January 2008 for intact seeds and germinants and then retrieved in October 2008 for tests of seed viability. From these data, we obtained estimates of October–January survivorship and germination (s_5 and g_3, respectively) and January–October survivorship (s_6) of 2-year-old seeds.

We repeated the seed-bag experiment twice. The first repeat began in October 2006, with 20 bags placed at each site for a second set of estimates of seed vital rates for current-year (s_1, s_2, and g_1) and 1-year-old (s_3, s_4, and g_2) seeds. The second repeat began in October 2007, with 10 bags per site for a third set of estimates of s_1, s_2, and g_1.

Seed survival over a time interval is the number of viable

seeds at the end of the interval (e.g., in January for s_3) divided by the number of viable seeds at the beginning (e.g., in October for s_3). Estimating seed-related vital rates required that some calculations be performed on raw data from seed bags. Because we did not unearth bags and estimate viability directly between every life-cycle transition, we estimated unmeasured survival rates by interpolation. For example, when estimating rates of seed survival to the germination season (s_1, s_3, and s_5) and germination rates (g_1, g_2, and g_3), we used October seed-viability estimates to incorporate loss of viability from October to January. As some seeds that appeared to be intact in October proved on lab testing to be inviable, the same was likely true of seeds that appeared to be intact in January (when no viability tests were performed). Therefore, we estimated seed viability in January by interpolating between the preceding and succeeding October viability estimates. For example, the viability of seeds in January of their second year was calculated as $V_1(V_2/V_1)^{1/3}$, where V_1 is the viability of seeds from that same cohort as estimated in the preceding October (when they had been in the field for 1 year) and V_2 is the viability of seeds from that same cohort as estimated in the succeeding October (when they had been in the field for 2 years), and thus V_2/V_1 is the fraction of viability remaining after the passage of the year from the cohort's first October to its second. (If this resulted in an estimate greater than 1, then we set it equal to 1.) The 1/3 exponent accounts for the fact that the period from October to January is one-third of that year. We thus assumed that viability declined exponentially. We also assumed that all seeds were viable when they were placed in the field, making the viability of seeds in their first January simply $(V_1)^{1/3}$. Because seeds are naturally dispersed in July but seed bags were placed in the field in October, the bag experiments did not provide a direct estimate of s_0, seed survival from July through October of the seeds' first year. Hence, we estimated s_0 as $(s_2)^{3/8}$, where 3 accounts for the 3 months from July to September and $(s_2)^{1/8}$ is the estimated monthly survival of ungerminated seeds from the previous cohort in the period from the end

of January to the beginning of October. Finally, we adjusted s_0 because initial estimates often predicted more seedlings than we observed. Inferring that using the seed bags underestimated or reduced sources of seed mortality from June to October (e.g., seed predation just before or shortly after dispersal), we adjusted s_0 by multiplying it by the ratio of observed seedlings to expected seedlings. We based expected numbers on seed production of the previous year and the survival and germination rates of bagged first-year seeds, ignoring, for simplicity, much smaller contributions from older seeds.

We used the estimates of vital rates for each population to construct annual projection matrices, assuming a census in October (i.e., at the time the seed bags were placed in the field, when only seeds are present). Seeds at each census were classified into three stages: age 0 (produced in the current year), age 1 (produced in the preceding year), and age 2+ (produced two or more years previously). In terms of the underlying vital rates, the matrices have the form

$$\begin{bmatrix} s_1 g_1 \sigma F \phi s_0 & s_3 g_2 \sigma F \phi s_0 & s_5 g_3 \sigma F \phi s_0 \\ s_1(1-g_1)s_2 & 0 & 0 \\ 0 & s_3(1-g_2)s_4 & s_5(1-g_3)s_6 \end{bmatrix},$$

where vital rates are described above (fig. A1). Here we have assumed that plants experience the same aboveground vital rates, regardless of seed age at germination, and that belowground vital rates do not change with seed age past age 2 because, in both cases, we lacked the data necessary to do otherwise. Because we had four estimates of σ, F, and φ, we constructed four matrices for the years 2006–2009, using corresponding yearly values of the other vital rates if they were available or the mean values if they were not. To account for the effects of environmental stochasticity on population growth, we calculated the long-term stochastic growth rate, λ_s, for each population using the standard random matrix selection method described by Caswell (2001). We assumed that all annual projection matrices for a population were equally likely to be chosen each year in long-term projections.

We placed confidence limits on λ_s for each population using a parametric bootstrap. Specifically, we obtained random values of each vital rate from its sampling distribution (binomial for survival and germination rates, normal for mean number of fruits per plant and mean number of seeds per fruit) in each year, used each set of random annual vital rates to estimate a set of annual projection matrices, and used them to numerically compute the stochastic population growth rate. We repeated this procedure 2,000 times and chose the 2.5th and 97.5th percentiles of the bootstrap distribution as the lower and upper 95% confidence limits.

Analysis of Environmental Effects and Geographic Patterns in Demography

For those vital rates with more than one yearly estimate per population (i.e., s_1–s_4, g_1–g_2, σ, F, and φ; fig. A1), we investigated relationships between demography and environment by selecting among generalized linear mixed models, using the lmer function in R (R Development Core Team 2005). All models considered included population as a random effect to account for variation among populations due to unmeasured factors. We considered models with measures of accumulated precipitation and mean daily temperatures (alone and in combination) during the period(s) over which the vital rate was estimated (November–January for s_1, s_3, g_1, and g_2; February–October for s_2 and s_4; and because soils remain moist for weeks to months after winter rains [V. M. Eckhart, unpublished data], both November–January and February–June for σ, F, and φ). As temperature variables within time periods tended to be highly correlated with one another, we included in each regression only the single temperature variable (daily mean, minimum, or maximum) that had the strongest individual effect on the vital rate being modeled. After investigating a series of models for each vital rate in this way, we selected for each the model with the minimum value of Akaike's Information Criterion (AIC). Model uncertainty was generally low (Burnham and Anderson 2002; Richards 2005), the AIC of the minimum model being more than 15 units below that of the closest alternative for six of nine vital rates, with exceptions as noted below. We assumed that fruits per plant and seeds per fruit were Poisson distributed and all other vital rates were binomially distributed. We analyzed geographic variation in demographic variables using ordinary linear regression (assuming normal errors) in Minitab 16 (Minitab, State College, PA), with demographic variables on easting (eastward geographic position).

Species Distribution Modeling

For modeling we used MaxEnt, version 3.3.3 (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011), which estimates habitat favorability (as probability of presence) on a landscape according to observed species points and the values of gridded environmental variables from files with equal pixel size and spatial extent, with models chosen according to the criterion of least information (maximum entropy) remaining in residual variation. We ran MaxEnt mainly with default parameters, except we specified 75% of presences for training and 25% for testing, generating the mean of 50 pseudoreplicate models with bootstrapping, and, for simplicity, considering only linear and quadratic response functions for continuous environmental

variables. We considered the area under the receiver-operator curve (AUC; minimum value = 0.5 [predictions no better than random], maximum value = 1) for test data as an indicator of model accuracy, a better indicator of the MaxEnt models' ability to correctly discriminate presences and absences than the customary AUC with training data (Warren and Seifert 2011).

All models included the same eight environmental variables. Five were climate features selected because of their associations with demography (see below): (1) mean February–June ("spring") temperature and (2, 3) the means and (4, 5) CVs of accumulated precipitation both during the November–January ("winter") germination season and during the spring growth and reproduction season. We did not include mean winter temperature because it correlated closely with mean spring temperature. The other three variables were geological: (6) surface material, (7) slope inclination, and (8) slope aspect. The two topographic variables, slope inclination and slope aspect, have been shown to be important in other studies of local distribution and individual performance. (Occurrence and performance correlate with steep north- and east-facing slopes; Eckhart et al. 2010; Kramer et al. 2011.) Note that this application of species distribution modeling was not a search for a best-performing or most parsimonious model, made by winnowing down a large set of hypothetical predictor variables. Instead, our approach was to use predictors shown by independent evidence to affect plant performance (excluding variables that correlated very closely with others) and to view the output as predictions of habitat suitability, with the hypothesis that those variables control distribution. For all models, estimates of the relative contributions of individual variables to models and response curves of probability of presence versus each variable appear in the appendix in the online edition of the *American Naturalist*. Species distribution model applications often visualize potential range by partitioning model output into within-range and outside-range portions, selecting a discriminatory threshold value (Liu et al. 2005; Franklin 2009). Because we wished to analyze quantitative variation in suitability across a species border, our purposes were better served by visualizing continuous variation in habitat suitability (Freeman and Moisen 2008), but output based on an example threshold also appears in the appendix.

Before modeling, we trimmed the geographic extent of the focal study region by selectively "masking" areas in two categories: (1) areas distant from our extensive searches for populations, which also correspond to areas where kriging estimated precipitation with lower confidence, and (2) areas with surfaces clearly unsuitable for *C. xantiana* ssp. *xantiana* (Elith et al. 2011). We accounted for category 1 by masking all areas at elevations above 1,500 m plus rectangular areas in the northwest and southeast corners of the region. We masked the area within Isabella Lake's maximum water line to account for category 2. We did not mask developed areas, because *C. xantiana* ssp. *xantiana* populations can occur on roadsides (V. Eckhart, personal observation).

We generated three distribution models that differed in the population presences they used and therefore in interpretation. The first model ("unweighted"), a baseline, included the 41 population points where we performed adult censuses (fig. 1D). We could have used larger sets of presences (e.g., Eckhart and Geber 1999), but the sample of 41 includes complete coverage of the easternmost populations of which we are aware and has a similar geographic extent to the focal sample of 20 populations, thus facilitating comparisons between models. The second and third models represent two ways of modeling the geographic distribution of areas that allow long-term population persistence. The second model ("filtered") used as presences only populations where $\lambda_s \geq 1$ ($N = 15$). MaxEnt performs well even with sample sizes this small (Pearson et al. 2007). The third model, "weighted," used 50 "pseudopresences" in which the 20 focal populations were weighted by their quartiles of the λ_s distribution. In other words, populations in the lowest quartile were considered single presences, those in the second quartile were considered two presences, and so on. For the weighted model, we turned off MaxEnt's "remove duplicates from analysis" option, thus increasing the likelihood (proportional to the weighting factor) that high-performing populations would be selected for training and testing data sets.

Results

Environment

Moving eastward among the 20 focal populations, mean temperatures declined, mean spring precipitation declined, and seasonal CVs in precipitation increased significantly (fig. 2). Across the range and beyond, west-east gradients in temperature are not very striking (fig. 3A, 3B) but gradients in seasonal precipitation are, with declining means and increasing CVs to the east (fig. 3C–3F). A different pattern appears moving north along the North Fork of the Kern River, where both precipitation means and CVs increased. Geologic surfaces also show west-east change, with the frequencies of alluvium and metasedimentary rocks being particularly high at the border and east of it (fig. 3G). Slopes of diverse inclination (fig. 3H) and aspect (fig. 3I) appear throughout the range and beyond; as would be expected, however, areas north of the Kern River and Isabella Lake have high frequencies of south-facing slopes,
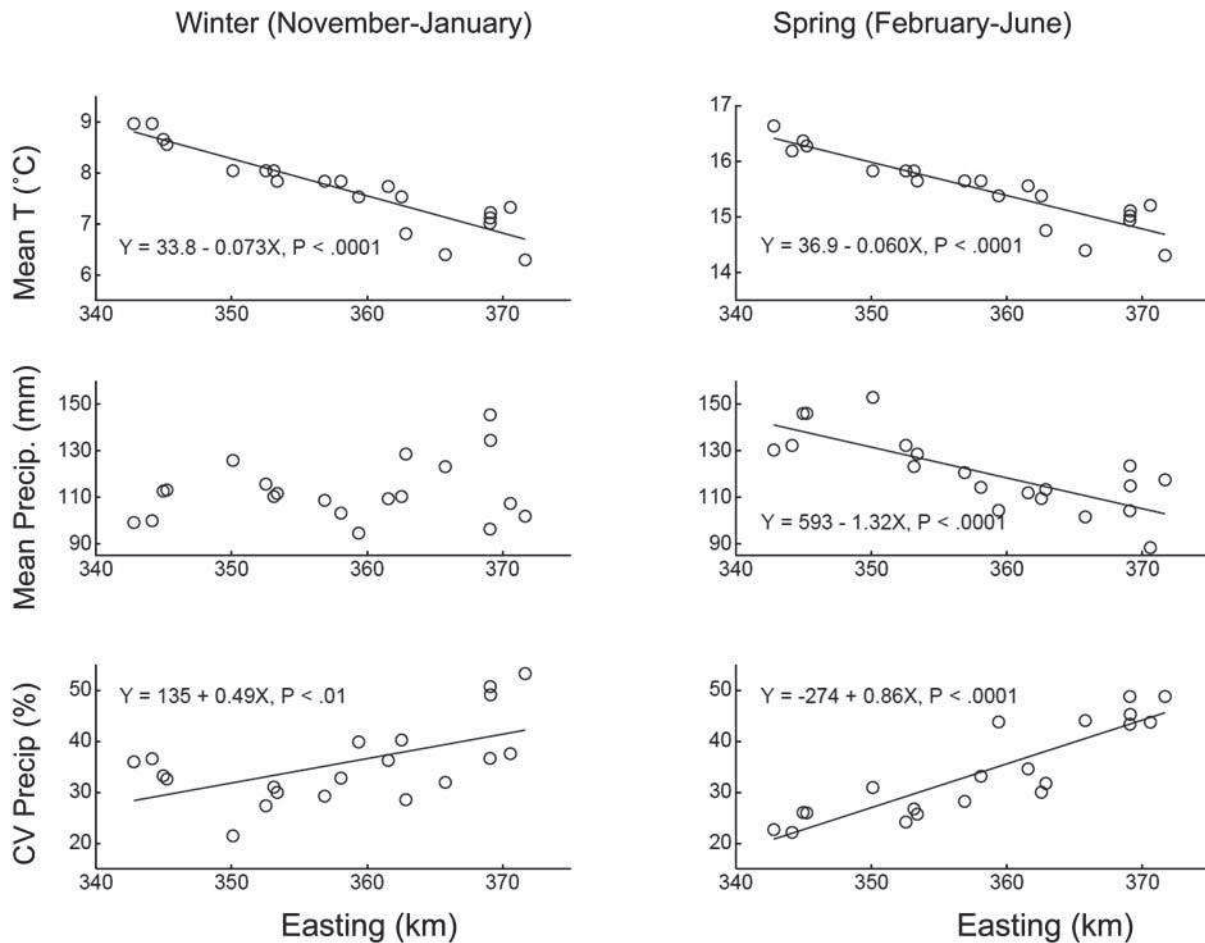
Figure 2: Scatterplots of climatic variables versus easting (UTM NAD 27, zone 11 north) for the 20 focal populations of *Clarkia xantiana* ssp. *xantiana*. *Left*, winter values; *right*, spring values. Lines are significant linear regressions. CV, coefficient of variation.

and the terrain in the Kern River Valley, east of Isabella Lake, is flat.

Demography

The apparent sensitivity of vital rates to climate drivers varied with season and life cycle component. Patterns appear in the signs of the coefficients and in the sets of variables that were included in minimum-AIC models (table 1). Winter precipitation suppressed seed bank survival, enhanced germination and seedling survival, and reduced fruit and seed production. Spring precipitation, in contrast, enhanced all three "aboveground" rates. High winter temperatures increased seed bank survival, suppressed germination, and reduced seedling survival. High February–October mean temperatures enhanced survival of 2-year-old seeds. Low winter minimum temperatures reduced germination of older seeds. High spring temperatures in-

creased seedling survival, fruit production, and seed production. The population term remained present in all models. Thus, for all vital rates, substantial variation was associated with population, in addition to any variation accounted for by the above climate variables.

Most mean vital rates did not show linear relationships with easting, but three of the 13 showed strong ones (fig. 4). Survival of seeds through their first winter, s_1 (fig. 4A), and fruit number, F (fig. 4B), declined approximately threefold from the original values from west to east. Germination of first-year seed, g_1, increased modestly to the east, but with a tight correlation (fig. 4A). The sensitivity of these vital rates to climate variables (table 1) and the distribution of climate variables among sites (fig. 2) suggest that the eastward decline in seed survival and the increase in first-year seed germination were due to an eastward decline in winter temperature, while the decline in fruit
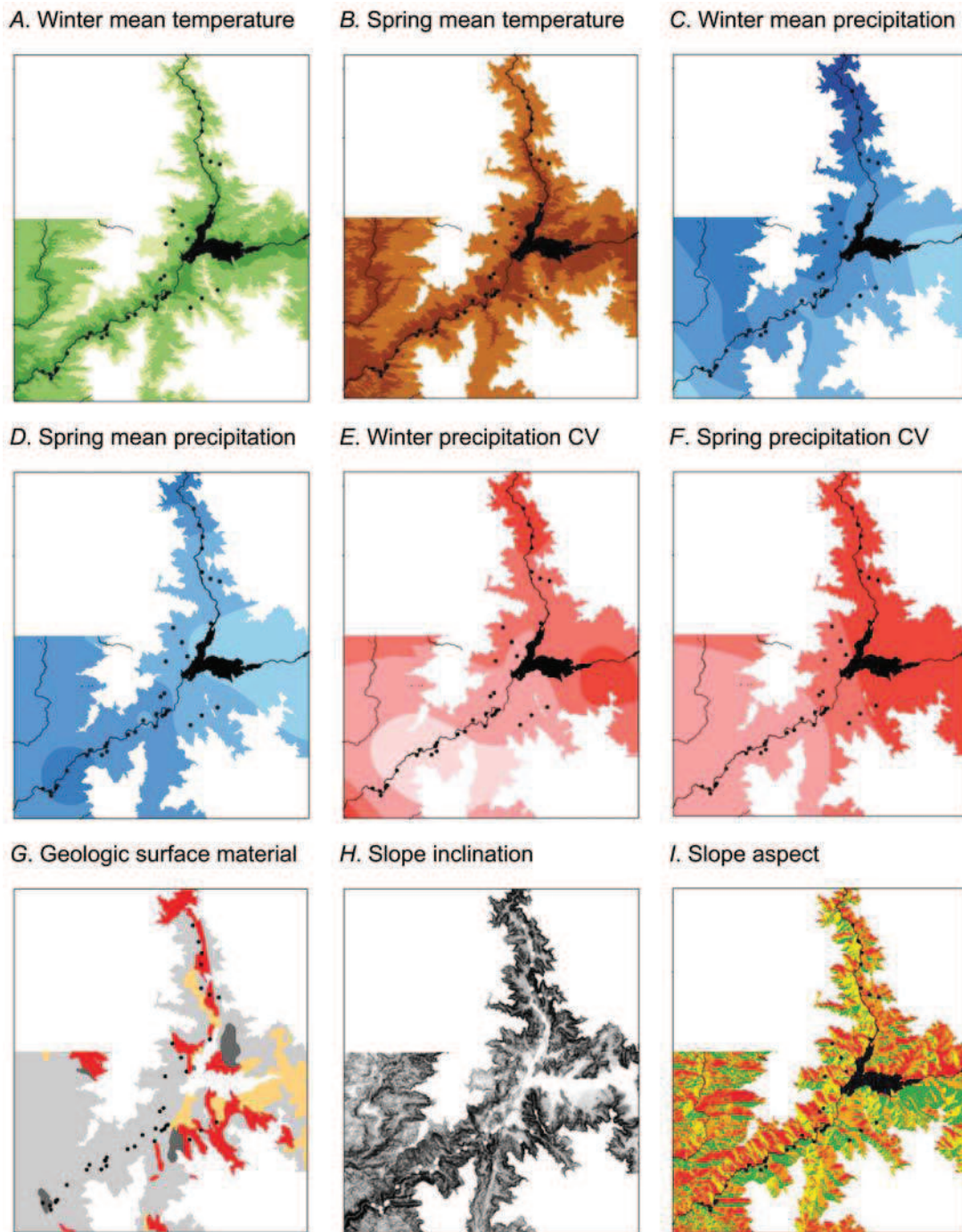
Figure 3: Environmental variation in the study area. Areas that were masked from species distribution models are white (elevations >1,500 m and northwest and southwest corners) or black (within the high-water line of the reservoir). Circles indicate 41 *Clarkia xantiana* ssp. *xantiana* populations. *A*, Mean daily temperature, November–January, from <4°C (palest green) to >8°C (deepest green). *B*, Mean daily temperature, February–June, from <12°C (palest brown) to >16°C (deepest brown). *C, D*, Mean precipitation for November–January and February–June, respectively, from <60 mm (palest blue) to >160 mm (deepest blue). *E, F*, Coefficient of variation in precipitation for November–January and February–June, respectively, from <20% (palest red) to >50% (deepest red). *G*, Geologic surface material. Igneous surfaces are gray (granodiorite, pale gray; gabbro, dark gray), metasedimentary surfaces are red, and alluvium is tan. *H*, Slope inclination in shades of gray from 0%–53%. *I*, Slope aspect (north [315°–45°], green; east [45°–135°], yellow; south [135°–225°], red; west [215°–315°], orange).

Table 1: Regression coefficients from minimum Akaike Information Criterion (AIC) models of vital rates versus climate variables

Model, vital rate	Seed survival				Germination		σ^c	F	φ
	s_1	$s_2{}^a$	$s_3{}^b$	$s_4{}^a$	g_1	g_2			
Intercept (population)	−17.4	−13.8	−7.08	−3.45	7.20	.73	−2.51	−6.25	−2.14
Precipitation:									
Nov–Jan total	−.02	.0004	−.005	−.002	.005		.006	−.004	−.001
Feb–Jun total							.010	.006	.003
Temperature:									
Nov–Jan maximum	1.26		.66		−.59				
Nov–Jan minimum						−1.61			
Nov–Jan mean							−.73	.33	.135
Feb–Jun mean							.29	.33	.287
Feb–Oct mean		.76		.24					

Note: σ, seedling survival; F, fruit number; φ, seeds per fruit.

[a] An alternative model omitting the precipitation variable was within 2 AIC units.

[b] An alternative model omitting the precipitation variable was within 8 AIC units.

[c] An alternative model using Nov-Jan minimum temperature was within 2 AIC units.

number followed from an eastward decline in spring precipitation.

Stochastic long-term growth rate varied fourfold among populations, from nearly 0.7 to more than 2.8. Fifteen of 20 populations had values greater than 1.0, 11 significantly so, while five had values that were significantly less than 1.0 (table A2 in the online edition of the *American Naturalist*). Growth rate increased with winter temperature and (the closely correlated) spring temperature (fig. 5). It also increased with mean spring precipitation while declining with the CV of spring precipitation (fig. 5). Populations on igneous substrates had higher λ_s values (mean ± SE, 1.46 ± .13) than populations on metasedimentary or mixed substrates (0.80 ± 0.13; $t_{[7]} = 2.73$; $P = .007$).

Population growth rate declined significantly from west to east (fig. 6). Populations in the far west had the highest values, with three of the four westernmost populations having λ_s values well above 1.0 and the fourth having a high value (>2) but a broad confidence interval. Meanwhile, three of the five easternmost populations had values below 1.

Species Distribution Models

The three models performed similarly well (unweighted model mean $AUC_{testing}$ ± SE for 50 runs, 0.86 ± 0.01; filtered model, 0.87 ± 0.01; weighted model, 0.86 ± 0.01) and made several qualitatively similar predictions (figs. 7, A2 in the online edition of the *American Naturalist*). All predicted high favorability at lower elevations in canyons west of Isabella Lake and in the next major drainage north of the Kern River (Poso Creek), and all predicted low favorability east of the range edge. All pre-

dicted some areas of high suitability deep in the Kern Canyon, fully to the western edge of the study region. All predicted declines in suitability with increasing elevation.

There were also clear differences between the unweighted model (figs. 7A, A2A) and the two models adjusted according to demographic findings (figs. 7B, 7C, A2B, A2C). The filtered and weighted models indicated broader elevation ranges of high suitability in the west, diminished extents of highly suitable habitat at and beyond the border, and steeper overall declines in suitability from west to east, patterns especially strong in the filtered model (fig. A3B in the online edition of the *American Naturalist*). The two demography-adjusted models predicted low suitability along the North Fork of the Kern River. Thus, accounting for demography drew the predicted distributions of highly suitable habitat westward and southward. We confirmed that the differences between model predictions are due not to sample size differences in the models but to the geographic and environmental distributions of populations (fig. A4 in the online edition of the *American Naturalist*).

The models also differed somewhat in contributions from environmental variables. In the unweighted model, the four most important contributors were (1) a positive effect of winter temperature, (2) a negative effect of the CV of winter precipitation, (3) a negative effect of mean winter precipitation, and (4) variation among geologic surfaces, with alluvium and metasedimentary rock associated with lower favorability than igneous rocks (table A3; fig. A5 in the online edition of the *American Naturalist*). Temperature was also the strongest contributor in the two adjusted models (in fact, its effect here was somewhat stronger than in the unweighted model), but in the filtered model the second-ranking CV of winter precipitation was
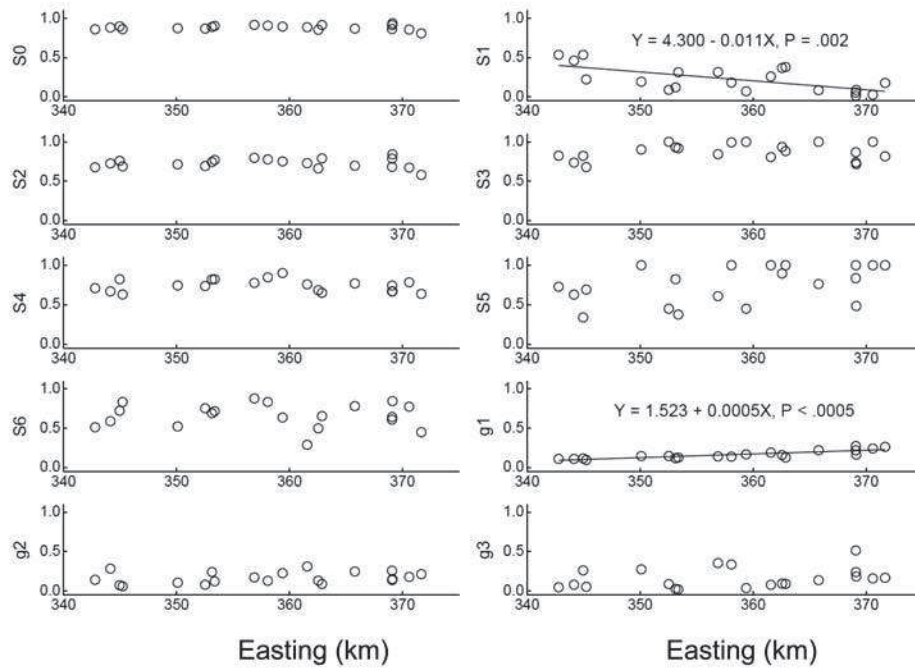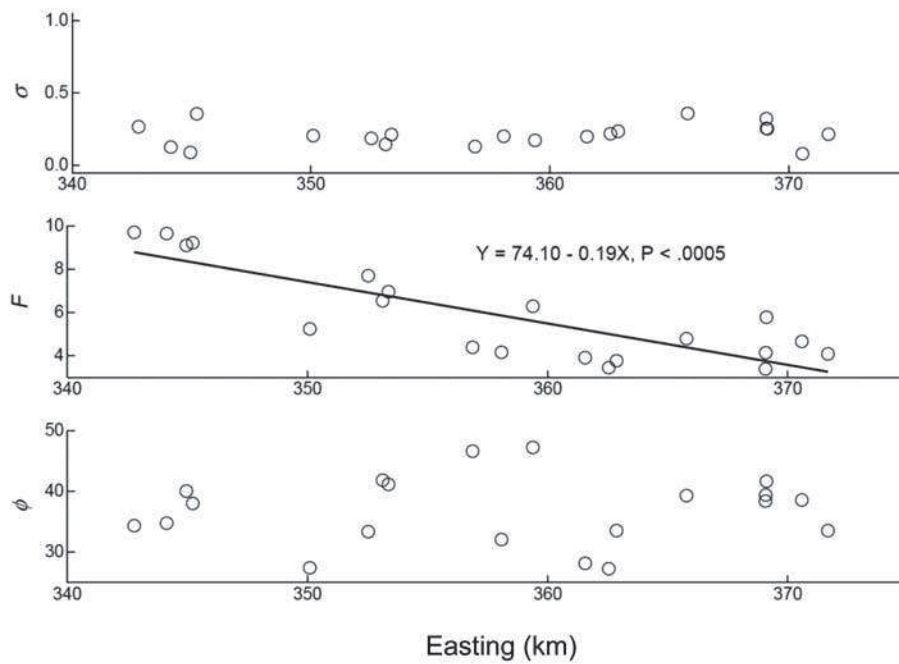
Figure 4: Scatterplots of vital rates versus easting for 20 *Clarkia xantiana* ssp. *xantiana* populations. Lines are significant linear regressions. *A*, Seasonal and age-dependent seed survival (s_i) and germination (g_i). *B*, "Aboveground" vital rates: seedling survival (σ), per-capita fruit number (F), and seeds per fruit (φ).
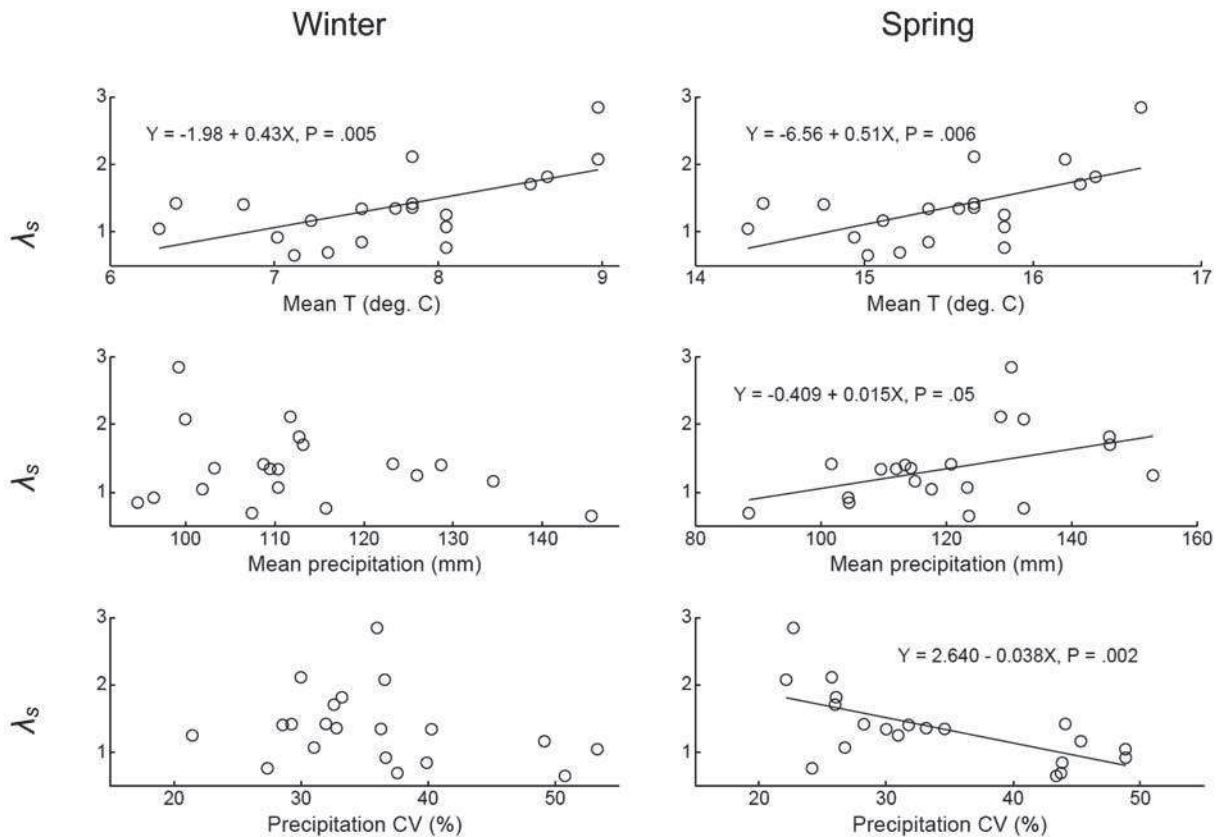
Figure 5: Scatterplots of λ_s versus climatic variables for 20 *Clarkia xantiana* ssp. *xantiana* populations. *Left*, winter variables; *right*, spring variables. Lines are significant linear regressions.

much more influential, while surface material ranked second in importance in the weighted model (table A3; figs. A6, A7 in the online edition of the *American Naturalist*). Effects of topography were generally weak compared with other variables at this spatial scale (table A3; figs. A6–A8 in the online edition of the *American Naturalist*).

Discussion

Demographic Structure of the Geographic Range

When limited adaptation is the chief constraint at a species border, one would expect environment-dependent declines in individual and population performance from the range center to the border (Caughley et al. 1988; Brown et al. 1996), a pattern not expected for borders set chiefly by limited dispersal (e.g., Norton et al. 2005). Our novel analysis of environmental variation, demography, and species distribution models suggests that the eastern border of *Clarkia xantiana* ssp. *xantiana* in the Sierra Nevada fits the expectations of an adaptation-limited range edge, one that reflects the spatial distribution of the fundamental

niche (Grinnell 1917; MacArthur 1972; Pulliam 2000; Holt et al. 2005; Soberón 2007).

All estimated vital rates varied with seasonal temperature and/or precipitation. Two—winter seed survival and fruit production—declined dramatically from west to east, apparently in response to low temperatures and low precipitation, respectively. Long-term stochastic population growth rate varied with climate and surface rock, and it declined significantly toward the eastern border, falling below 1.0 in three of the five easternmost populations. Species distribution models predicted that the limits of highly suitable habitat occur at or within a few kilometers of the current border. Demographically adjusted models predicted steeper eastward declines in habitat quality and indicated larger roles for highly variable precipitation and geological surfaces in defining favorable habitat. According to the unweighted and weighted models, the most extensive area of predicted highly suitable habitat east of the known populations is along the north shore of Isabella Lake. Dispersal limitation (possibly influenced at present by the reservoir) may account for this lack of occupancy
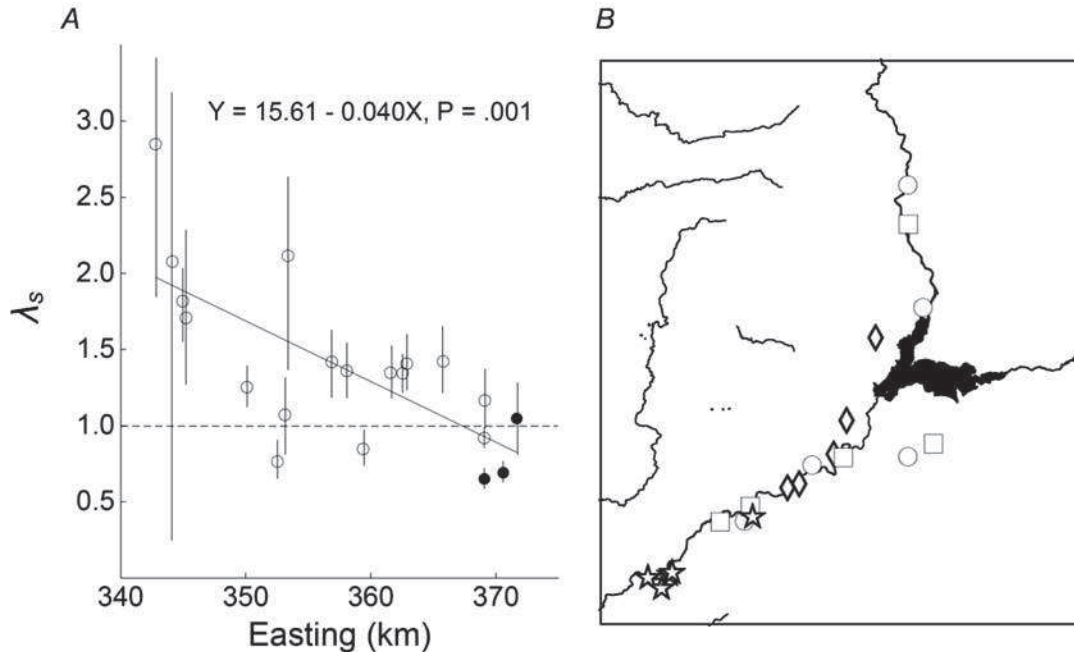
Figure 6: Geographic variation in population growth rate. *A*, Scatterplot and linear regression of long-term stochastic growth rate, λ_s, versus easting for 20 populations of *Clarkia xantiana* ssp. *xantiana*. Open circles represent populations on igneous substrates; filled circles represent populations on metasedimentary substrates. Error bars are 95% confidence intervals. Dashed line indicates zero growth. *B*, Locations of the populations in *A*, with quartiles of the λ_s distribution shown by contrasting symbols (circles, $0.65 \leq \lambda_s \leq 0.92$; squares, $0.93 \leq \lambda_s \leq 1.34$; diamonds, $1.35 \leq \lambda_s \leq 1.42$; stars, $1.71 \leq \lambda_s \leq 2.85$).

or, if the filtered model is indeed the best indicator of habitat quality, this area may not actually be highly suitable. Although biotic factors (i.e., pollination and herbivory) also affect performance and vary geographically in *C. xantiana* ssp. *xantiana* (Geber and Eckhart 2005; Moeller 2006; D. A. Moeller, M. A. Geber, V. M. Eckhart, and P. Tiffin, unpublished data), and although topography influences distribution and performance at smaller scales (Eckhart et al. 2010; Kramer et al. 2011), climate and soils appear to have dominant effects in defining the eastern limit, likely via their roles in water stress (Eckhart et al. 2010).

The gradual eastward decline in λ_s, together with genetic evidence of historical population expansion in the range center of *C. xantiana* ssp. *xantiana* (Moeller et al. 2011), suggests two hypotheses. One is that range-edge populations are demographic sinks maintained by dispersal from growing populations farther west (Pulliam 2000). The absence of obvious dispersal adaptations in *Clarkia* (although long-distance seed movement might occur in ungulate guts; see Dullinger et al. 2011) cast doubt on this idea, and population genetics data indicate historical stability of border populations over the long term, and not the bottlenecks or fluctuations that might be expected on the

source-sink hypothesis (Moeller et al. 2011). A second hypothesis is that the distribution of species' suitable habitat has recently begun to contract westward. Recent changes in regional climates have created clines in population growth rate (Jiguet et al. 2010), increases in mortality in newly stressful areas (Foden et al. 2007; van Mantgem et al. 2009), and changes in elevation range (Lenoir et al. 2008) in diverse organisms and locations, including some montane plants in California and adjacent Oregon (Kelly and Goulden 2008; Damschen et al. 2010; Crimmins et al. 2011). In the near future, in what is projected to be a warmer and drier California climate, the range of *C. xantiana* ssp. *xantiana* might shift toward wetter areas (Kueppers et al. 2005; Loarie et al. 2008).

The above findings and interpretations apply to a restricted part of the geographic range of *C. xantiana* ssp. *xantiana*, the eastern border in the Kern River Valley. We can make a few comments on other limits, one being a caveat about high-elevation predictions. The positive effects of temperature on some vital rates and on predicted habitat favorability suggest that low temperature sets upper-elevation limits. The importance of temperature in distribution models, however, may be somewhat overestimated because our sample of populations for demo-
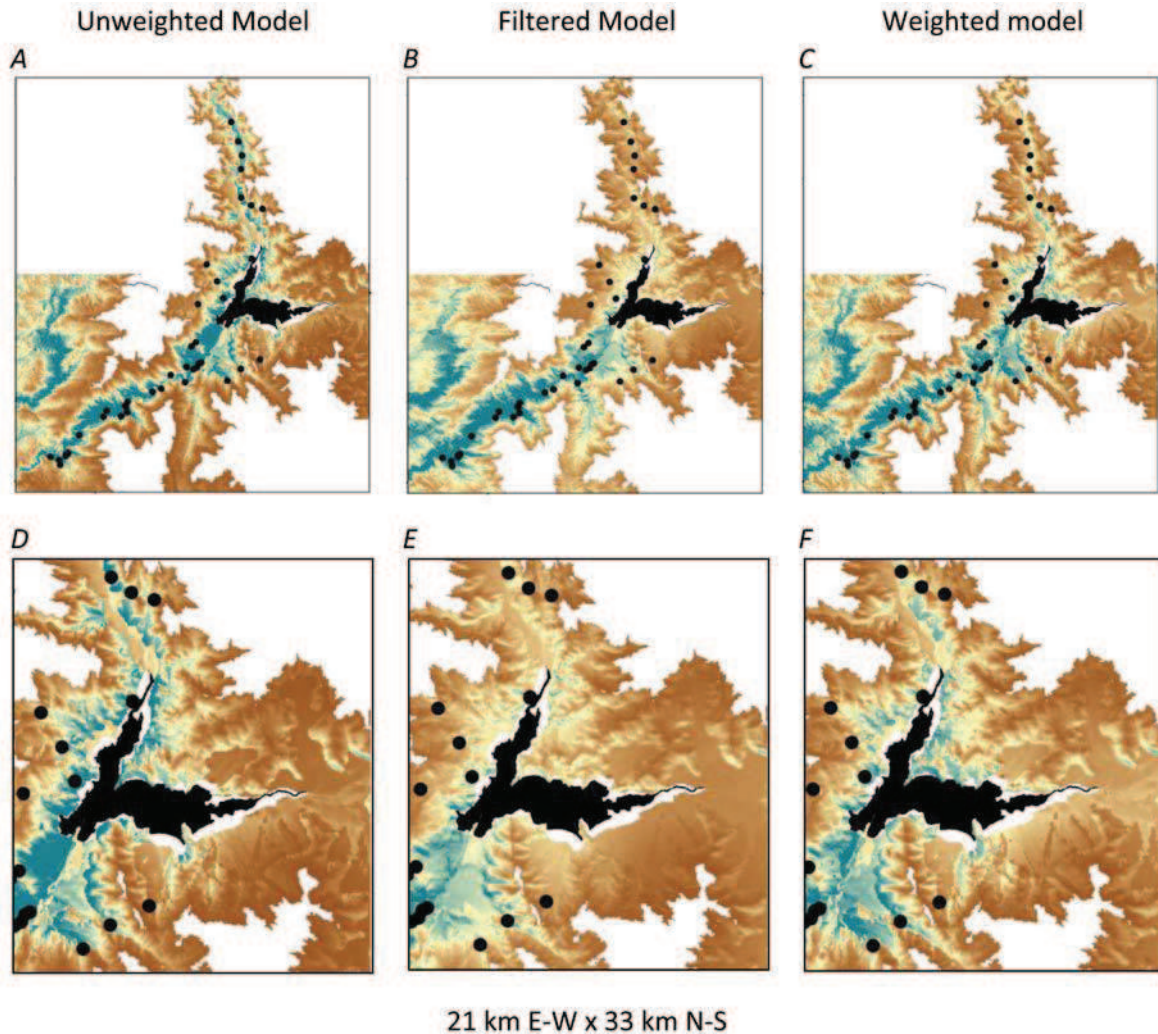
Figure 7: Species distribution models for *Clarkia xantiana* ssp. *xantiana* in the Kern River drainage. Circles represent 41 populations. Columns from left to right correspond to the three models: unweighted (using 41 populations), filtered (using 15 populations, where $\lambda_s \geq 1$), and weighted (weighting 20 populations by four categories of λ_s as if there were 50 presences). Color coding shows MaxEnt logistic output on a common logarithmic scale, from deepest brown (lowest values, least suitability/probability of presence) to deepest green (highest values, greatest suitability/probability of presence). *A–C*, Entire modeled area; *D–F*, detail in the vicinity of the eastern species border in the Kern River Valley.

graphic study did not include some known high-elevation populations west of the range edge. Including some of these populations extends the predicted highly suitable habitat to higher elevations (though not eastward [fig. A4C], so our interpretations regarding the eastern border appear robust). It also is worth noting that populations within 5 km of the western border performed exceptionally well. The intensively urbanized, agricultural, alluvium-filled, flat San Joaquin Valley, approximately 15 km to the west of our study area, may represent an absolute western limit, but populations are also absent from less-disturbed areas adjacent to the Valley (Eckhart and Geber 1999). We cannot yet assess whether limited adaptation to very steep environmental gradients (e.g., in precipitation) and/or dispersal opportunity constrains the western border.

Mechanisms That Might Limit Adaptation

If the eastern border of *C. xantiana* ssp. *xantiana* is set by limited adaptation, what specific mechanisms might be responsible? Those posited by theory (reviewed in Gaston 2003, 2009; Holt and Barfield 2011; Moeller et al. 2011;

Overgaard et al. 2011) include three nonexclusive candidates: (1) low genetic variance in fitness in marginal populations, stemming from genetic drift and/or strong selection; (2) maladaptive, asymmetric gene flow from interior populations to edge populations; and/or (3) strong trade-offs between traits that contribute to adaptation along environmental gradients.

Our analysis of mechanisms is ongoing, but we can make some early assessments. Regarding genetic variation, there is slightly less (e.g., fewer private alleles at microsatellite loci) in eastern-border populations than in central populations (Moeller et al. 2011). Average adult population size over the study period was independent of easting (and of λ_s), however (fig. A8), and genetic data indicate historically large populations in the east (up to hundreds of thousands), which is too large for dramatic loss of variation by drift to occur (Moeller et al. 2011). Thus, constraints due to reduced genetic variation at the border may apply, but genetic drift is not likely to be responsible for any such constraints. With family-structured transplant experiments, we are comparing genetic variance in fitness among populations from different parts of the range.

For maladaptive gene flow to limit adaptation, it requires geographic variation in selection plus asymmetric gene flow from interior populations to border populations. The necessary preconditions for this scenario seem to apply. There are differences in selection, with, for example, large size and late flowering favored to the west and early flowering favored to the east (Geber and Eckhart 2005; M. A. Geber and V. M. Eckhart, unpublished data). Genetic data indicate net-eastward gene flow: long-term demographic and genetic contributions from central populations to eastern-border populations (Moeller et al. 2011). We are addressing whether maladaptive gene flow reduces fitness in border populations via transplant experiments with interpopulation hybrids.

Finally, what traits and trade-offs might limit adaptation at the edge? Low, variable precipitation may generate the advantage of early flowering in the east, as it allows plants to escape drought (Bennington and McGraw 1995; Stanton et al. 2000; Geber and Eckhart 2005; Franks 2011). A trade-off between the benefits of early flowering and the benefits of large plant size and fruit production may contribute to the eastern limit of *C. xantiana* ssp. *xantiana* (Geber and Eckhart 2005) just as it contributes to the northern limit of invasive *Lythrum salicaria* in North America (Colautti et al. 2010). Similar constraints on the evolution of early flowering in stressful range-edge environments might commonly underlie adaptation-limited ranges in herbaceous plants (e.g., Griffith and Watson 2005). Bet-hedging traits such as seed dormancy might also be favored by uncertain precipitation (Phillipi 1993; Venable 2007). A possible biotic constraint in the present case is the scarcity of pollinators near the range edge, which may favor floral traits that facilitate self-pollination at the border (Fausto et al. 2001; Geber and Eckhart 2005; Moeller 2006).

In conclusion, along with a companion population genetics study (Moeller et al. 2011), this article represents an unusually comprehensive investigation of the reasons species borders occur where they do, responding to calls to integrate multiple kinds of relevant information (Pulliam 2000; Gaston 2009). Studies of environment and demography, species distribution modeling, and analyses of population-genetic structure support the hypothesis that limited adaptation to abiotic factors places the eastern range border of *C. xantiana* ssp. *xantiana* where it is, leaving us to identify the mechanisms that limit adaptation.

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