

The effect of geographic range position on demographic variability in annual plants

Katharine L. Gerst^{1*}, Amy L. Angert^{1,2} and D. Lawrence Venable¹

¹Department of Ecology and Evolutionary Biology, University of Arizona, PO Box 210088, Tucson, AZ 85721, USA; and ²Department of Biology and Graduate Degree Program in Ecology, Colorado State University, 1878 Campus Delivery, Fort Collins, CO 80523, USA

Summary

1. The abundant centre model predicts that species abundance will decline from the centre towards the periphery of the geographic range. Thus, we expect to find decreases from the centre towards the edge in variables related to population dynamics such as population density and reproductive output. However, evidence for this pattern is contradictory, suggesting that geographically peripheral sites may not be ecologically peripheral. Populations may thrive in pockets of suitable habitat at the edge of the range or may be locally adapted to peripheral conditions.

2. This study examines how the position of a site within geographic and climatic ranges of 13 species is related to the population dynamics at one common location, The Desert Laboratory at Tumamoc Hill, Tucson, AZ, USA.

3. We used data on survival, fecundity, germination fraction and population density from a 25-year long-term data set on winter annual plants to determine whether there was a relationship between distance to the centre of the range and population dynamics. Geographic distance was calculated by determining the distance from the Desert Laboratory to the centre of the observed range determined from locality records. Climatic distance was calculated using the niche modelling software, MAXENT, and subtracting the mean climatic profile for the species range from that of the Desert Laboratory.

4. There was no relationship between mean population metrics and distance metrics. We found significant relationships between some geographic distance metrics and variance in fecundity, survival and per-germinant fecundity, but not germination fraction or population density. We did not find a relationship with any metric of population dynamic variation and climatic distance.

5. *Synthesis.* Our results indicate that geographic distance from the centre of the range of 13 annual plant species more strongly predicts their population dynamics than climatic distance. This study reinforces the importance of examining vital rates and their variation in order to properly capture the effect of position within a range on population dynamics.

Key-words: abundant centre model, annual plants, demographic variability, geographic range, niche modelling, plant population and community dynamics, Sonoran Desert

Introduction

Elucidating the mechanisms shaping variation in population dynamics across species geographic ranges is the key to understanding what creates geographic range limits and ultimately drives ecological and evolutionary processes such as speciation, extinction and coexistence. The abundant centre model has been invoked as a general rule in biogeography to describe the structure of populations across species geographic distributions (Antonovics 1976; Brown 1984; Kirkpatrick & Barton 1997; Gaston 2003; Guo *et al.* 2005). This model assumes that

the most favourable conditions will be found at the centre of a species range, and thus the centre will support greater abundances than geographically peripheral sites. Several additional predictions arise as corollaries of the abundant centre model. For example, central populations are expected to have high *per capita* fitness and may serve as demographic source populations, whereas peripheral populations may be demographic sinks (Kanda *et al.* 2009) that exhibit more temporally variable population dynamics (Nantel & Gagnon 1999; Williams, Ives & Applegate 2003) and are more prone to extinction (Gargano *et al.* 2007). However, although some species have decreased abundance towards the periphery (Woodward 1997; Alexander *et al.* 2007), many other species do not (Carey, Watkinson

*Correspondence author. E-mail: katgerst@email.arizona.edu

& Gerard 1995; Hodkinson *et al.* 1999), and recent literature reviews raise considerable doubt about the generality of the abundant centre pattern in nature (Sagarin & Gaines 2002; Gaston 2003; Sexton *et al.* 2009).

The lack of consistent evidence for the abundant centre model has caused researchers to question whether geographically peripheral populations are necessarily ecologically or climatically peripheral (Yakimowski & Eckert 2007; Duffy *et al.* 2009; Jarema *et al.* 2009) and to call for the integration of biophysical variables into studies of species geographic range dynamics (Sagarin, Gaines & Gaylord 2006). Traditionally, studies have classified populations as being either geographically central or peripheral. Yet, habitat quality can be patchy throughout a range, and geographically peripheral populations may occupy pockets of locally favourable habitat. Conversely, populations may 'spill over' into ecologically marginal habitat at the geographic range centre. Using geography alone as a surrogate for the degree of ecological peripherality or centrality of a site, relative to the niche requirements of a species, potentially masks the importance of climate and microhabitat in shaping population dynamics. Furthermore, geographically peripheral locations may not be ecologically peripheral if current range limits are not at equilibrium with physiological limits or if geographically peripheral populations are locally adapted to range edge environments.

The kinds of response variables used to test the abundant centre model may also limit our ability to infer population dynamic differences across the geographic range. Previous tests of the abundant centre model have focused on snapshot estimates of abundance (Enquist, Jordan & Brown 1995; Samis & Eckert 2007; Krasnov *et al.* 2008) or performance (Jump & Woodward 2003; Kluth & Bruehlheide 2005). Such measurements do not necessarily capture the appropriate range of temporal variation in population dynamics. Although *mean* environmental conditions may be suitable at the geographic periphery, climatic extremes could exceed the species' tolerance in occasional years (Olmsted, Dunevitz & Platt 1993; Bowman *et al.* 2005). This would result in equivocal patterns of abundance or performance during most short-term studies, but greater variance at the geographic periphery over longer time periods. The data necessary to quantify demographic variability over meaningful temporal scales are difficult to attain. Most examples to date rely on harvest records (e.g. hunting licenses, fisheries stocks) or large-scale national surveys (e.g. North American Breeding Bird Survey; Coelho *et al.* 1994; Curnutt, Pimm & Maurer 1996; Mehlman 1997; Williams, Ives & Applegate 2003). These studies are valuable for examining patterns over broad spatial scales and for large numbers of species, but in most cases they are unable to provide detailed demographic information such as variation in vital rates. Moreover, few studies have integrated variation in multiple vital rates across the life cycle (Nantel & Gagnon 1999; Kluth & Bruehlheide 2005; Angert 2009).

In this study, we ask, how does long-term demographic performance relate to the position of a species within its geographic and climatic range? We have examined long-term population dynamics at one location for multiple species of Sonoran Desert

winter annual plants that vary in their distances from their range centres. This approach enables us to look for patterns across species using detailed demographic data from a single site. Moreover, cross-species comparisons can suggest how biogeography influences local dynamics and species coexistence (Ackerly 2003; Chesson *et al.* 2004). Desert annuals are characterized by high inter-annual population fluctuations driven by unpredictable and highly variable precipitation (Schwinning & Sala 2004; Bowers 2005). Although the population dynamics of all species are variable, species differ significantly in the magnitude of that variability (Venable 2007).

We hypothesized that differences among species in long-term mean and variance of survival, fecundity, per-germinant fecundity, germination fraction and population density are related to differences in species positions within their geographic and climatic ranges. Specifically, we predicted that species for which our study site is geographically and climatically central would have higher means and lower temporal variances in our measures of population dynamics than species for which our study site is farther from the species' geographic range centre or climatic average. Because pockets of climatically suitable habitat may be found at the geographic periphery and unsuitable habitat may occur near geographic centres, we predicted that climatic variables would explain greater variance than geographic variables.

Materials and methods

LONG-TERM DEMOGRAPHIC PERFORMANCE

Data on demographic performance (means and variability) come from a 25-year study of winter annuals at The University of Arizona Desert Laboratory on Tumamoc Hill, initiated in 1982 with fourteen 1.2-m² plots. Forty-two additional plots were added in 1992, and 20 in 1995, for a current total of 72 plots, half of which are in the open and half under shrubs. These plots have been visited every year following each autumn and winter rain event to document winter annual seed germination. Individual plants have been mapped at germination and followed until death for four to seven censuses per year to quantify lifetime survival and reproduction. The average number of seeds produced per survivor was determined as a pre-dispersal fecundity estimate (either direct count of seeds or of reproductive structures later multiplied by the mean seed number per reproductive structure) of up to five individuals per species per cohort per plot. Dormant seeds were counted each year in 180 soil cores located on adjacent plots starting in 1990 (see Venable & Pake 1999 for methods). Several species were recorded only occasionally, so we restricted the analysis to 13 native species with consistent presence throughout the study period: *Daucus pusillus* (Apiaceae), *Eriophyllum lanosum*, *Evax multicaulis*, *Monoptilon bellioides*, *Stylocline micropoides* (Asteraceae), *Eucrypta micrantha*, *Pectocarya recurvata*, *Lappula redowskii* (Boraginaceae), *Draba cuneifolia* (Brassicaceae), *Erodium texanum* (Geraniaceae), *Plantago insularis*, *Plantago patagonica* (Plantaginaceae) and *Vulpia octoflora* (Poaceae). For each species, these observations quantify the population density (seedlings plus dormant seeds m⁻²), germination fraction (proportion of dormant seed bank that germinated each year) and lifetime per-germinant fecundity, *lb* (calculated by multiplying the average survival from germination to reproduction, *l*, by the average number of seeds produced by survivors, *b*) for every

germinated seedling for the past 25 years. Population density and germination fraction data cover 17 years rather than the entire 25-year study span, as the soil cores quantifying the seed bank were started in 1990. We calculated the long-term mean and variance in demographic success for each demographic parameter. We calculated the variabilities for mean survival (l) and germination fraction as relative standard deviations of means [standard deviation/(mean*(1 - mean))], which is appropriate for these binomially distributed variables (Morris & Doak 2004). Mean fecundity, per-germinant fecundity and population density were ln-transformed. Standard deviations of these values were then transformed back to their original scale to calculate the geometric standard deviation of lb .

DISTRIBUTION RECORDS AND MODELLING

We compiled collection records from multiple online data bases and regional herbaria (see Appendix S1 in Supporting Information). We discarded all records without latitude and longitude coordinates, and duplicate records of the same locality, resulting in 370–1752 records per species (Table 1). We used these collection records to model the probability distributions of species occurrences using the maximum entropy ecological niche modelling program MAXENT v. 3.2.19 (Phillips, Anderson & Schapire 2006). This program requires only presence data and has been determined to perform well compared with other niche modelling methods (Elith & Graham 2009). We created a probability distribution of species occurrences based on known presence records and 19 'bioclim' climatic variables taken from the Worldclim data set (<http://www.worldclim.com>, see Appendix S2). Climate variables are based on climatic conditions averaged over the period between c. 1950 and 2000. MAXENT was run for 500 iterations per species. The convergence threshold was set to 1×10^{-5} , a recommended value based on the North American breeding bird survey data and small mammal data from Latin America (Phillips, Anderson & Schapire 2006). The accuracy of the niche models was evaluated by constructing the model using 70% of presence records as training points, with the remaining 30% used to validate the data set as testing points. Model accuracy was determined using a receiver operating characteristic (ROC) analysis (Phillips, Anderson & Schapire 2006). The area under the ROC curve (AUC) of the resulting plot of sensitiv-

ity vs. (1 - specificity) provides a measure of model performance. An optimal model that perfectly predicts a species' occurrence would have an AUC of 1.0, whereas a model that predicted species occurrences at random would have an AUC of 0.5. After creating models for all 13 species using all 19 bioclim variables, we selected nine variables that were consistently the most influential in determining the distributions of all 13 species and then constructed reduced models using the same procedure outlined above. The nine variables used in reduced models were Bio1, Bio2, Bio3, Bio5, Bio6, Bio9, Bio11, Bio16 and Bio18 (see Appendix S2 for descriptions).

GEOGRAPHIC AND CLIMATIC DISTANCES BETWEEN THE DESERT LABORATORY AND SPECIES RANGES

We calculated several metrics of the position of the Desert Laboratory in each species' range as follows:

Climatic distance

We summarized climate profiles for each species following the methods described in Evans *et al.* (2009). We calculated the mean of each bioclim climate variable within the species' range, weighted by the species' predicted probability of occurrence. This was performed by multiplying the bioclim value of each grid cell by the corresponding occurrence probability from the reduced-variable MAXENT model, then summing these and dividing by the total number of grid cells. We then calculated the distance between the Desert Laboratory and the species' distribution in multivariate climate space using Mahalanobis distance. Each Mahalanobis distance calculation incorporates the difference between the climate mean for the range and the climate at the Desert Laboratory across the 19 bioclim variables. These values were calculated by multiplying the inverse covariance matrix describing the covariances among the 19 bioclim variables with the array of arithmetic differences between each bioclim variable and the Desert Laboratory. Since this multivariate metric takes into account the covariation between climate values, it was preferred over a multivariate Euclidean distance calculation.

Geospatial distance

We calculated the distance between the Desert Laboratory and the location of each species' geometric range centre. We estimated the range centre as the centroid of the minimum convex polygon surrounding observed collection records using DIVA GIS Version 7.1 (Hijmans *et al.* 2005). For statistical analyses, we took the natural log of these distance values.

Geographic distance

For each species, we calculated differences between the latitude of the Desert Laboratory and the mean latitude of the set of observed collection records. We also calculated analogous differences using longitude values. We used latitude and longitude separately because these may capture different gradients across species ranges (e.g. temperature vs. precipitation). This allowed us to better quantify the relative importance of directionality in determining the role that distance from the centre of a range plays in influencing demography.

RANGE SIZE

To determine whether range size had a potentially confounding effect on range position at the Desert Laboratory, we calculated the size of

Table 1. Species used for this study, number of points used for model generation, AUC (area under ROC curve) and range size

Species	Number of occurrence points used to generate MAXENT model	MAXENT AUC	Observed range area (km ²)
<i>Daucus pusillus</i>	1369	0.972	6 146 300
<i>Draba cuneifolia</i>	1256	0.967	4 145 200
<i>Eriophyllum lanosum</i>	380	0.997	433 700
<i>Erodium texanum</i>	671	0.990	1 905 800
<i>Eucrypta micrantha</i>	370	0.940	1 004 900
<i>Evax multicaulis</i>	371	0.989	1 582 500
<i>Lappula redowskii</i>	721	0.968	7 894 000
<i>Monoptilon bellioides</i>	414	0.998	399 600
<i>Pectocarya recurvata</i>	504	0.998	458 900
<i>Plantago insularis</i>	783	0.996	2 165 900
<i>Plantago patagonica</i>	1205	0.974	6 384 600
<i>Stylocline micropoides</i>	298	0.997	705 500
<i>Vulpia octoflora</i>	1752	0.955	11 161 900

ROC analysis (receiver operating characteristic) was used to determine model accuracy (Phillips, Anderson & Schapire 2006).

each species' observed range. This was performed by calculating the area of the minimum convex polygon around all observed collection records using DIVA GIS 7.1. For statistical analyses, we took the square root of range area measured in square kilometres.

STATISTICAL ANALYSIS

Relationships between explanatory variables (geographic and climatic distances, range size) and response variables (mean and variance in per-germinant fecundity, fecundity, survival, germination fraction, and population density at the Desert Laboratory) were analysed with simple linear regression in SAS version 9.1 (SAS Institute, Cary, NC, USA). We then used hierarchical partitioning analysis to calculate the independent effects of correlated distance metrics (geographic centroid distance, climate distance and range size) on measures of population dynamic variance. Variables in which zero-order correlations were near zero were excluded from this analysis (Murray & Conner 2009).

Results

There were no significant relationships between the mean metrics of population dynamics [per-germinant fecundity (lb), survival (l), fecundity (b), germination fraction and population density] and any geographic or climatic distance metric (all $P > 0.1$, Table 2). The following results all relate to the variance of population dynamic metrics.

DEMOGRAPHIC VARIATION AND CLIMATIC DISTANCE FROM MEAN OF RANGE

MAXENT model results performed well (AUC ranging from 0.940 to 0.998; Table 1) with the reduced nine-climate-variable model (see Appendix S3 for a brief description of model results and Fig. S1 for modelled distribution maps). We found no relationship between any metric of population dynamics (all $P > 0.09$) and the climatic distance (Mahalanobis distance) between the Desert Laboratory and the mean climate for the

species ranges (Table 2). The Mahalanobis climatic distance had a positive relationship with the geospatial distance from the centre of the range to the Desert Laboratory (slope = 4.58, intercept = -18.4, $R^2 = 0.656$, $P = 0.008$).

DEMOGRAPHIC VARIATION AND GEOGRAPHIC POSITION WITHIN RANGE

We found a significant positive relationship between variance in lb (per-germinant fecundity) and the geographic distance between the Desert Laboratory and the centre of a species range (the centroid of a polygon around the observed and the predicted range) (slope = 3.8, intercept = -14.9, $R^2 = 0.339$, $P = 0.037$; Fig. 1). We also found a significant positive relationship between variance in l (survival) and the geographic distance ($R^2 = 0.359$, $P = 0.030$), as well as a

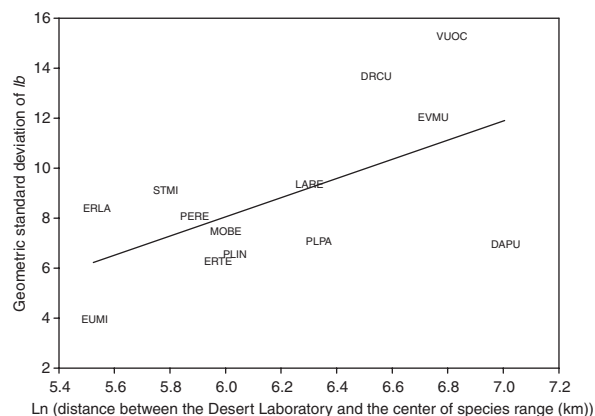


Fig. 1. Variation in per-germinant fecundity (lb) increases with greater distance between the Desert Laboratory and the centroid of the species' range based on observed records [$SD(lb) = -14.9 + 3.8(\text{distance})$, $R^2 = 0.339$, $P = 0.037$]. Each four-letter code represents one species coded by the first two letters of the species and genus name. See Table 1 for a full species list.

Table 2. Linear regression statistics for relationships between distance metrics and demographic variables [per-germinant fecundity (lb), survival (l), fecundity (b), germination fraction and population density]. Bold values represent significant regression statistics ($P \leq 0.05$)

	Climate distance		Geographic centroid distance		Mean latitude distance		Mean longitude distance		Range area	
	R^2	P	R^2	P	R^2	P	R^2	P	R^2	P
Mean										
lb	0.009	0.976	0.002	0.897	0.012	0.723	0.002	0.893	0.021	0.640
l	0.105	0.280	0.045	0.485	0.053	0.449	0.005	0.918	0.175	0.153
b	0.008	0.769	0.008	0.759	0.008	0.761	0.010	0.700	0.004	0.825
Germination fraction	0.049	0.466	0.163	0.171	0.026	0.593	0.202	0.123	0.041	0.505
Population density	0.000	0.997	0.078	0.349	0.154	0.184	0.129	0.226	0.008	0.768
Variance										
lb	0.150	0.191	0.339	0.037	0.007	0.779	0.372	0.027	0.202	0.123
l	0.237	0.090	0.359	0.030	0.049	0.467	0.295	0.055	0.336	0.038
b	0.076	0.363	0.278	0.064	0.049	0.468	0.464	0.010	0.099	0.293
Germination fraction	0.006	0.798	0.021	0.637	0.109	0.271	0.035	0.540	0.068	0.387
Population Density	0.001	0.896	0.058	0.428	0.154	0.184	0.074	0.370	0.026	0.600

marginally significant relationship between variance in b (fecundity) and the geographic distance ($R^2 = 0.278$, $P = 0.064$, Table 2). There were no relationships between germination fraction variance or population density variance and distance from the range centre (Table 2).

Differences between the Desert Laboratory and observed latitude and longitude of species ranges show that some species at the Desert Laboratory had distributional peaks that were more central along the latitude axis but not longitude (e.g. *Eriophyllum lanosum*), some species were more central along longitude but not latitude (e.g. *Lappula redowskii*), and others did not have distributions that peaked at the Desert Laboratory on either axis (e.g. *Plantago insularis*; Figs 2 and 3). Furthermore, although the Desert Laboratory was closer to the southern periphery of the distribution for some species, such as *Eucrypta micrantha*, it was closer to the northern periphery of the distribution of others, such as *Evax multicaulis* (Fig. 2). Likewise with longitude, the Desert Laboratory was

closer to the western periphery of the distribution for some species (e.g. *Evax multicaulis*) but closer to the eastern periphery of the distribution for others (e.g. *M. bellioides*) (Fig. 3). So although any two species may both be peripheral at the Desert Laboratory relative to the centre or edge of their distributions and hence spatial marginality can encompass different ranges of climatic marginality. There were no species for which the Desert Laboratory represented a central point along both longitudinal and latitudinal axes.

There were no significant relationships between differences in the latitude of the Desert Laboratory relative to the mean latitude of the species range and variance in lb , l , b , germination fraction or population density (Table 2). There was a significant positive relationship between lb variation and the distance of the Desert Laboratory from species' mean observed longitude ($R^2 = 0.372$, $P = 0.027$). When analysed separately, there was also a marginally significant positive relationship

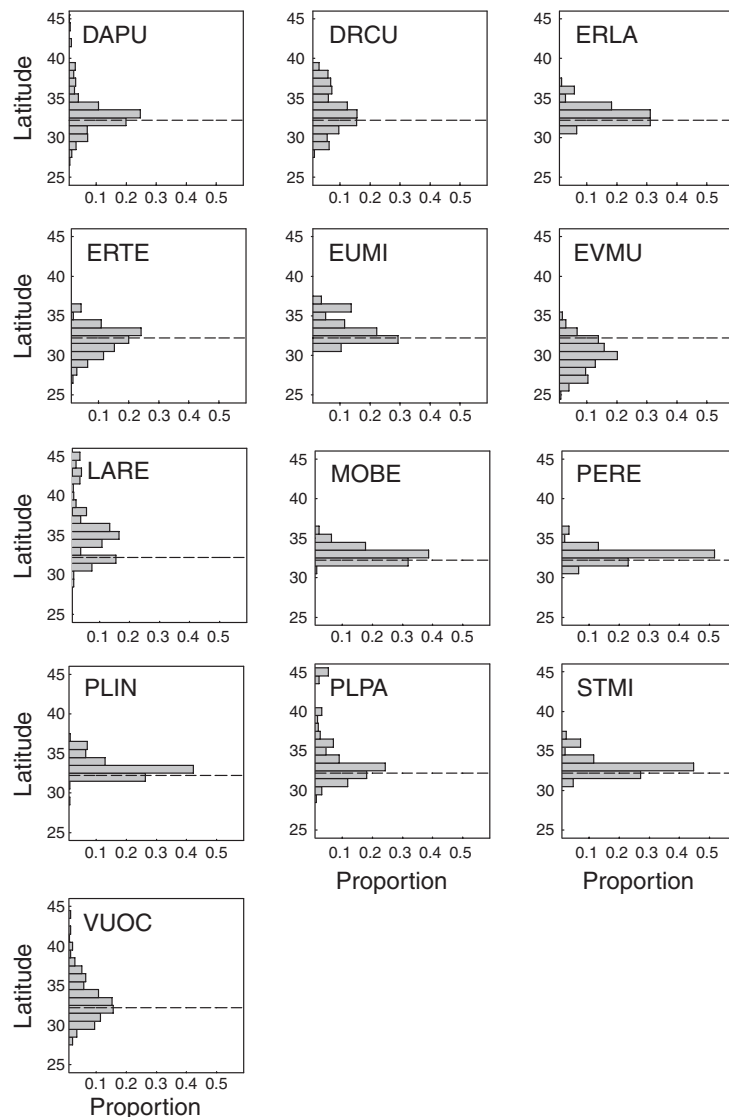


Fig. 2. The relative frequency of presence records at different latitudes. Dotted line represents the latitude for the Desert Laboratory. Each four-letter code represents one species coded by the first two letters of the species and genus name. See Table 1 for a full species list.

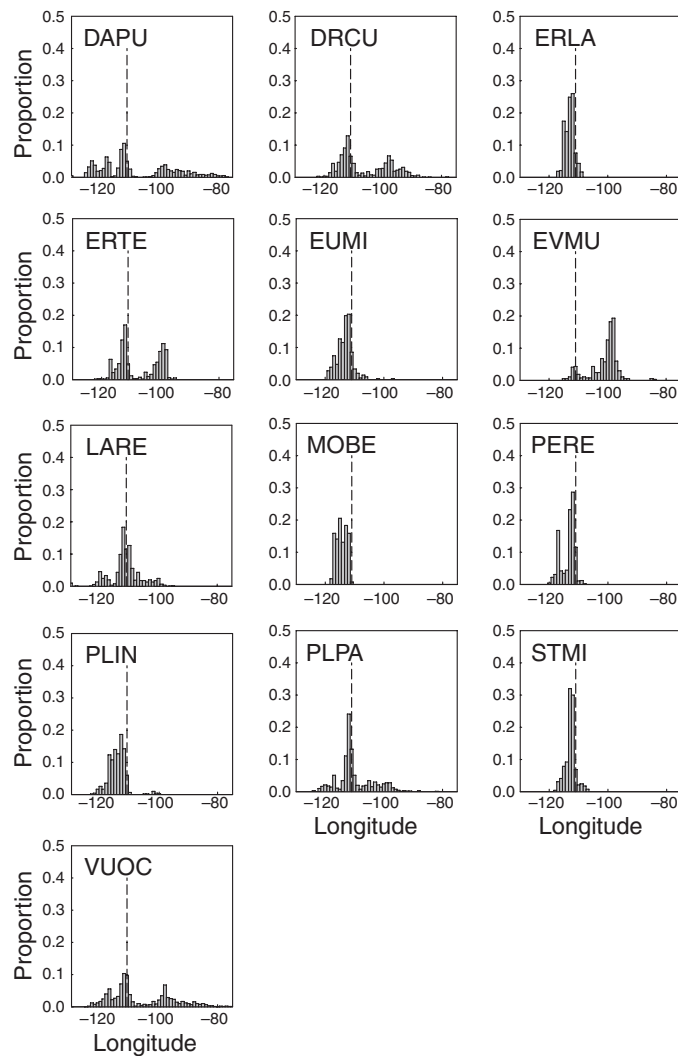


Fig. 3. The relative frequency of presence records at different longitudes. Dotted line represents the longitude for the Desert Laboratory. Each four-letter code represents one species coded by the first two letters of the species and genus name. See Table 1 for a full species list.

with variance in l ($R^2 = 0.295$, $P = 0.055$) and a significant positive relationship with variance in b ($R^2 = 0.464$, $P = 0.010$) (Table 2). That is, there is an increase in variation in survival, fecundity and per-germinant fecundity as observed species distributions are more eastward relative to the Desert Laboratory. There was no significant relationship between variance in germination fraction or population density and longitudinal distances of the observed range (Table 2).

RANGE SIZE

Observed species distributions (Table 1) ranged from small and restricted to south-western deserts (i.e. 399 600 km², *M. bellioides*) to large, covering much of North America (11 161 900 km², *V. octoflora*) (see Fig. S1 for distribution maps). Species with the largest ranges had range centres (the centroid of minimum convex polygons) farthest from the Desert Laboratory (slope = 1411.5, intercept = -7111.4, $R^2 = 0.544$, $P = 0.004$). There was a significant positive relationship between range size and variance in l

($R^2 = 0.336$, $P = 0.038$, Table 2). However, there were no significant relationships between range size and variance in lb , b , germination fraction or population density (Table 2).

HIERARCHICAL PARTITIONING OF VARIANCE

No hierarchical partitioning was performed on variables related to germination fraction or population density since all had near-zero correlations. The factor that had the strongest independent contribution to variance in lb was geographic distance (59.7% independent contribution to variance in lb), followed by range size (22.2% independent contribution) and climate distance (18.1% independent contribution). Likewise, the factor that had the strongest independent contribution to variance in l was geographic distance (42.2% independent contribution to variance in l), followed by range size (36.9% independent contribution) and climate distance (20.9% independent contribution). Lastly, the factor that had the strongest independent contribution to variance in b was geographic distance (71.2% independent contribution to variance in b),

followed by climate distance (16.4% independent contribution) and range size (12.4% independent contribution).

Discussion

We found no relationships between mean metrics of population dynamics (lb , l , b , germination fraction and population density) and distance between the Desert Laboratory and the centre of a species range. This is perhaps not unexpected because species may have innate differences in their population structure or life histories that make interspecific comparisons difficult. For example, different species may have different characteristic population densities or fecundities (although we log-transformed mean values to minimize differences in scale).

We found the predicted positive relationship between variance in per-germinant fecundity (geometric standard deviation of lb) at the Desert Laboratory and the geographic distance to the centre of each species ranges. When analysed separately, variance in survival (l) was also related to geographic distance and variance in fecundity (b) was marginally related to distance from the range centre. Thus, as the distance between the Desert Laboratory and the centre of species ranges increases, the inter-annual variability in both survival and fecundity at the Desert Laboratory becomes greater. This indicates that species may be buffered against mortality effects and extreme plastic responses in fecundity if they are near the centre of their range. Conversely, if they are farther from the centre of their range, species may be more likely to have relatively larger survival and fecundity responses in favourable years and poor responses in other years, suggesting that they may not be as locally adapted to this site. Again, our metrics of variance are standardized to reflect proportional deviations from each species' mean and thus permit comparisons across species. We did not detect a relationship between variance in germination fraction and any measure of geographic distance. However, although seed dormancy is a trait influenced by climate and affecting fitness, variation in this trait more likely reflects a bet-hedging strategy than a poor response to environmental conditions. Likewise, we did not detect a relationship between variance in population density and any measure of geographic distance. This is noteworthy, as population density is predicted to be more variable towards the edge of a range, and density is the most commonly used measure of population dynamic differences between central and peripheral populations (Brown, Mehlman & Stevens 1995; Krasnov *et al.* 2008; Fuller, Harcourt & Parks 2009). The lack of associations detected for population density variation suggests that variation in per-germinant fitness does not necessarily match variation in population density over time. However, this is not necessarily surprising as population density is strongly correlated with the history of previous years, whereas per capita measures are not. Also, these species make long-lived seed banks, which buffer population density against year-to-year variation in reproductive success. Thus, our results highlight the importance of studying vital rates (in this case, survival, fecundity and per-germinant fecundity) in addition to population density in order

to accurately describe the effects of range position on population dynamics. Since this approach utilizes a long-term data set of population dynamics rather than a snapshot, we have been able to maximize our ability to quantify the overall demographic characteristics of these species at this site.

Our separate analyses of mean latitudinal and longitudinal axes relative to the Desert Laboratory indicate that variation in fecundity, survival and per-germinant fecundity is associated with longitudinal, but not latitudinal, distance from the geographic range centre. Specifically, the further east a species' centre of distribution is from the Desert Laboratory the greater the l , b and lb variation. This result suggests that species with more mesic centres of distribution have greater demographic variance when growing at the more arid Desert Laboratory site. Interestingly, this tends to support the climatic distance hypothesis.

We originally hypothesized that climatic distance would be a stronger indicator of demographic variation than geographical distance, but our analysis of climatic distance using a multivariate descriptor of climate did not support this, despite the previously described indirect support from the longitudinal analysis above. In the multivariate analysis, no significant relationships were found between population dynamic variation and climatic distance. However, it should be noted that, in this study, geographic and climatic distances were highly correlated and their overall trends were similar. The hierarchical partitioning analysis suggested that climate distance had an independent effect on the l , b and lb variation that was less than half that of geographic distance. It is possible that our relatively coarse quantification of climate may have weakened our ability to detect a pattern. A site that is considered peripheral in either a geographical or a macroclimatic sense could still potentially be in a favourable microhabitat (Dinsdale, Dale & Kent 2000; Lee *et al.* 2009). Alternatively, our result could be due to local adaptation to differing environmental conditions (Conover & Schultz 1995; Gonzalo-Turpin & Hazard 2009) throughout the range. These possibilities could be further explored through transplant studies and comparative studies on physiological tolerances throughout ranges (Angert 2006; Kimball & Campbell 2009). Furthermore, other aspects of climate, such as the maximum differences between climate layers, might better capture the climatic distance between the Desert Laboratory and a species range as whole.

The location of the Desert Laboratory within North America has an interesting effect on these results. Species with a large range cannot have the Desert Laboratory close to their range's longitudinal centre due to the proximity of the Desert Laboratory to the west coast. Hence, by default, the Desert Laboratory is at the western but not necessarily the northern or southern periphery of a large species range. Another consequence of the Desert Laboratory's location is that climatic variation within the range increases with range size: Small ranges can be included within the desert south-west, whereas larger ranges necessarily include additional biomes. Thus, desert endemic species have smaller ranges and are closer to their centres of distribution than widespread species, for which the desert is a peripheral environment within their range. Species

with small ranges may be more likely to have less absolute variation in the climatic characteristics within their range, and be more able to adapt to them and buffer variation (Maliakal-Witt, Menges & Denslow 2005). Widespread species, on the other hand, are more likely to occupy a large range of environments and thus may be more likely to be demographically variable in any one environment. This, of course, depends on the degree to which a wide-ranging species achieves its broad distribution via generalization, plasticity and local adaptation to particular habitats within its diverse range (Gaston, Blackburn & Lawton 1997; Pandit, Kolasa & Cottenie 2009). However, with the exception of variation in survival, range size was generally not important in contributing to the relationships driving demographic variation.

To our knowledge, this is the first effort to utilize niche modelling to quantify the climatic peripherality of a site and how that relates to spatiotemporal population dynamic variation. However, this work is complementary to recent studies elucidating the environmental and genetic components of range dynamics in migrating tree populations (Wang, O'Neill & Aitken 2010). Additionally, a niche modelling approach is being increasingly used to study biological invasions and the potential demographic consequences of niche specialization in potential invaders (Rodder & Lotters 2009; Medley 2010). The results presented here suggest that geography plays a strong role in generating patterns of survival, fecundity and per-germinant fecundity variation, but not germination fraction or population density variation, within this guild of desert annual plants.

Acknowledgements

The authors thank D. Hearn for assistance in analysing MAXENT output and J. Donohue for GIS assistance. We also thank S. Felker, E. Larios, J. Horst, S. Kimball, J. Paul and S. Sheth for comments on an earlier version of the work, as well as two anonymous referees. Funding was provided by NSF Grants BSR 9107324, DEB 9419905 (LTREB), DEB 0212782 (LTREB) DEB 0717466 (LTREB) and 0817121 (LTREB) to D.L.V.

References

- Ackerly, D.D. (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, **164**, S165–S184.
- Alexander, H.M., Price, S., Houser, R., Finch, D. & Tourtellot, M. (2007) Is there reduction in disease and pre-dispersal seed predation at the border of a host plant's range? Field and herbarium studies of *Carex blanda*. *Journal of Ecology*, **95**, 446–457.
- Angert, A.L. (2006) Growth and leaf physiology of monkeyflowers with different altitude ranges. *Oecologia*, **148**, 183–194.
- Angert, A.L. (2009) Biogeography, Changing Climates, and Niche Evolution Sackler Colloquium: the niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proceedings of the National Academy of Science of the USA*, **106**, 11641–11645.
- Antonovics, J. (1976) Nature of limits to natural selection. *Annals of the Missouri Botanical Garden*, **63**, 224–247.
- Bowers, J.E. (2005) El Niño and displays of spring-flowering annuals in the Mojave and Sonoran deserts. *Journal of the Torrey Botanical Society*, **132**, 38–49.
- Bowman, J., Holloway, G.L., Malcolm, J.R., Middel, K.R. & Wilson, P.J. (2005) Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. *Canadian Journal of Zoology*, **83**, 1486–1494.
- Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.
- Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.
- Carey, P.D., Watkinson, A.R. & Gerard, F.F.O. (1995) The determinants of the distribution and abundance of the winter annual grass *Vulpia-ciliata* ssp *Ambigua*. *Journal of Ecology*, **83**, 177–187.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A. & Weltzin, J.F. (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, **141**, 236–253.
- Coelho, M.L., Stobberup, K.A., Odor, R. & Dawe, E.G. (1994) Life-history strategies of the squid, *Illex-Illecebrosus*, in the Northern Atlantic. *Aquatic Living Resources*, **7**, 233–246.
- Conover, D.O. & Schultz, E.T. (1995) Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution*, **10**, 248–252.
- Curnutt, J.L., Pimm, S.L. & Maurer, B.A. (1996) Population variability of sparrows in space and time. *Oikos*, **76**, 131–144.
- Dinsdale, J.M., Dale, M.P. & Kent, M. (2000) Microhabitat availability and seedling recruitment of *Lobelia urens*: a rare plant species at its geographical limit. *Seed Science Research*, **10**, 471–487.
- Duffy, K.J., Scopece, G., Cozzolino, S., Fay, M.F., Smith, R.J. & Stout, J.C. (2009) Ecology and genetic diversity of the dense-flowered orchid, *Neotinea maculata*, at the centre and edge of its range. *Annals of Botany*, **104**, 507–516.
- Elith, J. & Graham, C.H. (2009) Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, **32**, 66–77.
- Enquist, B.J., Jordan, M.A. & Brown, J.H. (1995) Connections between ecology, biogeography, and paleobiology – relationship between local abundance and geographic-distribution in fossil and recent mollusks. *Evolutionary Ecology*, **9**, 586–604.
- Evans, M.E.K., Smith, S.A., Flynn, R.S. & Donoghue, M.J. (2009) Climate, niche evolution, and diversification of the “bird-cage” evening primroses (Oenothera, sections Anogra and Kleinia). *American Naturalist*, **173**, 225–240.
- Fuller, H.L., Harcourt, A.H. & Parks, S.A. (2009) Does the population density of primate species decline from centre to edge of their geographic ranges? *Journal of Tropical Ecology*, **25**, 387–392.
- Gargano, D., Fenu, G., Medagli, P., Sciandrello, S. & Bernardo, L. (2007) The status of *Sareopoterium spinosum* (Rosaceae) at the western periphery of its range: ecological constraints lead to conservation concerns. *Israel Journal of Plant Sciences*, **55**, 1–13.
- Gaston, K. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.
- Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Interspecific abundance range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579–601.
- Gonzalo-Turpin, H. & Hazard, L. (2009) Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of Ecology*, **97**, 742–751.
- Guo, Q.F., Taper, M., Schoenberger, M. & Brandle, J. (2005) Spatial-temporal population dynamics across species range: from centre to margin. *Oikos*, **108**, 47–57.
- Hijmans, R.J., Guarino, L., Jarvis, A., O'Brien, R., Mathur, P., Bussink, C., Cruz, M., Barrantes, I. & Rojas, E. (2005) DIVA-GIS Version 5.2. Manual. <http://www.diva-gis.org>.
- Hodkinson, I.D., Bird, J., Miles, J.E., Bale, J.S. & Lennon, J.J. (1999) Climatic signals in the life histories of insects: the distribution and abundance of heather psyllids (*Strophingia* spp.) in the UK. *Functional Ecology*, **13**, 83–95.
- Jarema, S.I., Samson, J., McGill, B.J. & Humphries, M.M. (2009) Variation in abundance across a species' range predicts climate change responses in the range interior will exceed those at the edge: a case study with North American beaver. *Global Change Biology*, **15**, 508–522.
- Jump, A.S. & Woodward, F.I. (2003) Seed production and population density decline approaching the range-edge of *Cirsium* species. *New Phytologist*, **160**, 349–358.
- Kanda, L.L., Fuller, T.K., Sievert, P.R. & Kellogg, R.L. (2009) Seasonal source-sink dynamics at the edge of a species' range. *Ecology*, **90**, 1574–1585.
- Kimball, S. & Campbell, D. (2009) Physiological differences among two *Pentstemon* species and their hybrids in field and common garden environments. *New Phytologist*, **181**, 478–488.
- Kirkpatrick, M. & Barton, N.H. (1997) Evolution of a species' range. *American Naturalist*, **150**, 1–23.

- Kluth, C. & Bruehlheide, H. (2005) Central and peripheral *Hornungia petraea* populations: patterns and dynamics. *Journal of Ecology*, **93**, 584–595.
- Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S., Vinarski, M., Korralo-Vinarskaya, N. & Poulin, R. (2008) Geographical patterns of abundance: testing expectations of the 'abundance optimum' model in two taxa of ectoparasitic arthropods. *Journal of Biogeography*, **35**, 2187–2194.
- Lee, J.E., Janion, C., Marais, E., van Vuuren, B.J. & Chown, S.L. (2009) Physiological tolerances account for range limits and abundance structure in an invasive slug. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **276**, 1459–1468.
- Maliakal-Witt, S., Menges, E.S. & Denslow, J.S. (2005) Microhabitat distribution of two Florida scrub endemic plants in comparison to their habitat-generalist congeners. *American Journal of Botany*, **92**, 411–421.
- Medley, K.A. (2010) Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Global Ecology and Biogeography*, **19**, 122–133.
- Mehlman, D.W. (1997) Change in avian abundance across the geographic range in response to environmental change. *Ecological Applications*, **7**, 614–624.
- Morris, W.F. & Doak, D.F. (2004) Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. *American Naturalist*, **163**, 579–590.
- Murray, K. & Conner, M.M. (2009) Methods to quantify variable importance: implications for the analysis of noisy ecological data. *Ecology*, **90**, 348–355.
- Nantel, P. & Gagnon, D. (1999) Variability in the dynamics of northern peripheral versus southern populations of two clonal plant species, *Helianthus divaricatus* and *Rhus aromatica*. *Journal of Ecology*, **87**, 748–760.
- Olmsted, I., Dunevitz, H. & Platt, W.J. (1993) Effects of freezes on tropical trees in Everglades National Park, Florida, USA. *Tropical Ecology*, **34**, 17–34.
- Pandit, S.N., Kolasa, J. & Cottenie, K. (2009) Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology*, **90**, 2253–2262.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Rodder, D. & Lotters, S. (2009) Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Global Ecology and Biogeography*, **18**, 674–687.
- Sagarin, R.D. & Gaines, S.D. (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137–147.
- Sagarin, R.D., Gaines, S.D. & Gaylor, B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution*, **21**, 524–530.
- Samis, K.E. & Eckert, C.R.G. (2007) Testing the abundant center model using range-wide demographic surveys of two coastal dune plants. *Ecology*, **88**, 1747–1758.
- Schwinnig, S. & Sala, O.E. (2004) Hierarchy of responses to resource pulses in and semi-arid ecosystems. *Oecologia*, **141**, 211–220.
- Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology Evolution and Systematics*, **40**, 415–436.
- Venable, D.L. (2007) Bet hedging in a guild of desert annuals. *Ecology*, **88**, 1086–1090.
- Venable, D.L. & Pake, C.E. (1999) Population ecology of Sonoran Desert annual plants. *Ecology of Sonoran Desert Plants and Plant Communities* (ed. R. Robichaux), pp. 115–124. University of Arizona Press, Tucson.
- Wang, T.L., O'Neill, G.A. & Aitken, S.N. (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications*, **20**, 153–163.
- Williams, C.K., Ives, A.R. & Applegate, R.D. (2003) Population dynamics across geographical ranges: time-series analyses of three small game species. *Ecology*, **84**, 2654–2667.
- Woodward, F.I. (1997) Life at the edge: a 14-year study of a *Verbena officinalis* population's interactions with climate. *Journal of Ecology*, **85**, 899–906.
- Yakimowski, S.B. & Eckert, C.G. (2007) Threatened peripheral populations in context: geographical variation in population frequency and size and sexual reproduction in a clonal woody shrub. *Conservation Biology*, **21**, 811–822.

Received 19 May 2010; accepted 1 December 2010

Handling Editor: Pieter Zuidema

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Sources of locality data.

Appendix S2. Wordclim variables derived from monthly data between c. 1950 and 2000.

Appendix S3. MAXENT model results and important variables.

Fig. S1. MAXENT generated maps showing predicted ranges based on occurrence records.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.