

Environmental and dispersal controls of an annual plant's distribution: how similar are patterns and apparent processes at two spatial scales?

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Abstract At scales from microsites to entire ranges, species' distributions reflect limited adaptation and/or limited dispersal. To what extent are specific distribution patterns and processes similar across scales? We investigated environmental effects—presumed because of adaptation—and independent spatial effects—presumed because of dispersal—on distribution at two scales (landscape patches of approximately 1,300 m², sampled along transects, and 4-m² cells, sampled in contiguous grids within popula-

tions) and on individual performance (water status, reproduction) in the California annual, *Clarkia xantiana* ssp. *xantiana*. Because water limitation helps set this species' regional borders, we expected occupancy and performance at smaller scales to correlate with topographic and soil features affecting water relations. At the patch scale, environmental features associated with reduced water stress (i.e., steep slopes that face north; coarse, soft soils; igneous rather than metasedimentary parent rock) predicted occupancy. Spatial aggregation was not detected, but incomplete occupancy of apparently suitable patches indicated that dispersal limits occupancy. At the scale of small cells, relationships between environmental variables, occupancy, density, and performance varied among populations. Associations sometimes resembled those at the patch scale but sometimes opposed them. Spatial aggregation in cell occupancy and/or density occurred in all populations, implying limited dispersal, whereas spatial aggregation of water potential values in some populations might have arisen from spatially structured unmeasured environmental variables. Limited adaptation to drought and limited patch colonization appear to affect patch occupancy in *C. xantiana* ssp. *xantiana*, whereas smaller-scale patterns indicate consistent effects of limited dispersal and somewhat variable environmental effects.

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Introduction

A plant species' geographic distribution is a set of presences and absences at hierarchical scales from microsites, to patches, to landscapes. Individuals occupy a fraction of plant-sized locations (microsites) that can support establishment but are absent where environmental conditions fall outside the limits of adaptation, where propagules have not dispersed, or where chance mortality has occurred (Billings 1952; Harper 1977; Primack and Miao 1992; Eriksson and Ehrlén 1992; Baack et al. 2006; Cheplick 2010; Fig. 1a). At larger scales, sets of individuals occupy landscape patches that contain suitable microsites and other resources (e.g., animal pollinators), that have been colonized, and that have not undergone chance extinction, with sustainable populations occupying one or more patches where the above conditions apply (Quintana-Ascencio and Menges 1996; Ehrlén and Eriksson 2000; Pulliam 2000; Svenning 2001; Jacquemyn et al. 2002; Gaston 2003; Soberón 2007; Fig. 1b). Thus, some combination of limited adaptation, limited dispersal, and stochastic processes is generally expected to control species distributions at multiple spatial scales. To what extent are the specific mechanisms responsible for species' distributions similar across scales? Do the controls and patterns of small-scale distribution mimic or predict those at larger scales (Baack et al. 2006), or do process and pattern vary substantially across scales (e.g., Munzbergova 2004; Karst et al. 2005; Gómez-Aparicio 2008)?

Limited adaptation might not control distributions in exactly the same way at every scale. The set of environmental variables (niche dimensions) and the ranges of those variables that allow individuals to germinate and establish may not be identical to those that allow populations to persist (Grubb 1977; Suzuki et al. 2005; Moore 2009). Some of the same niche dimensions, however, might be critical at multiple scales. In arid landscapes, limited adaptation to drought might prevent species from occupying regions that fall below some threshold in annual precipitation (Hocker 1956; Woodward and Williams 1987; Foden et al. 2007). Within a precipitation-limited range, limited adaptation to drought might restrict populations and individuals to locations where topographic and/or edaphic conditions increase water availability and/or reduce evaporative demand

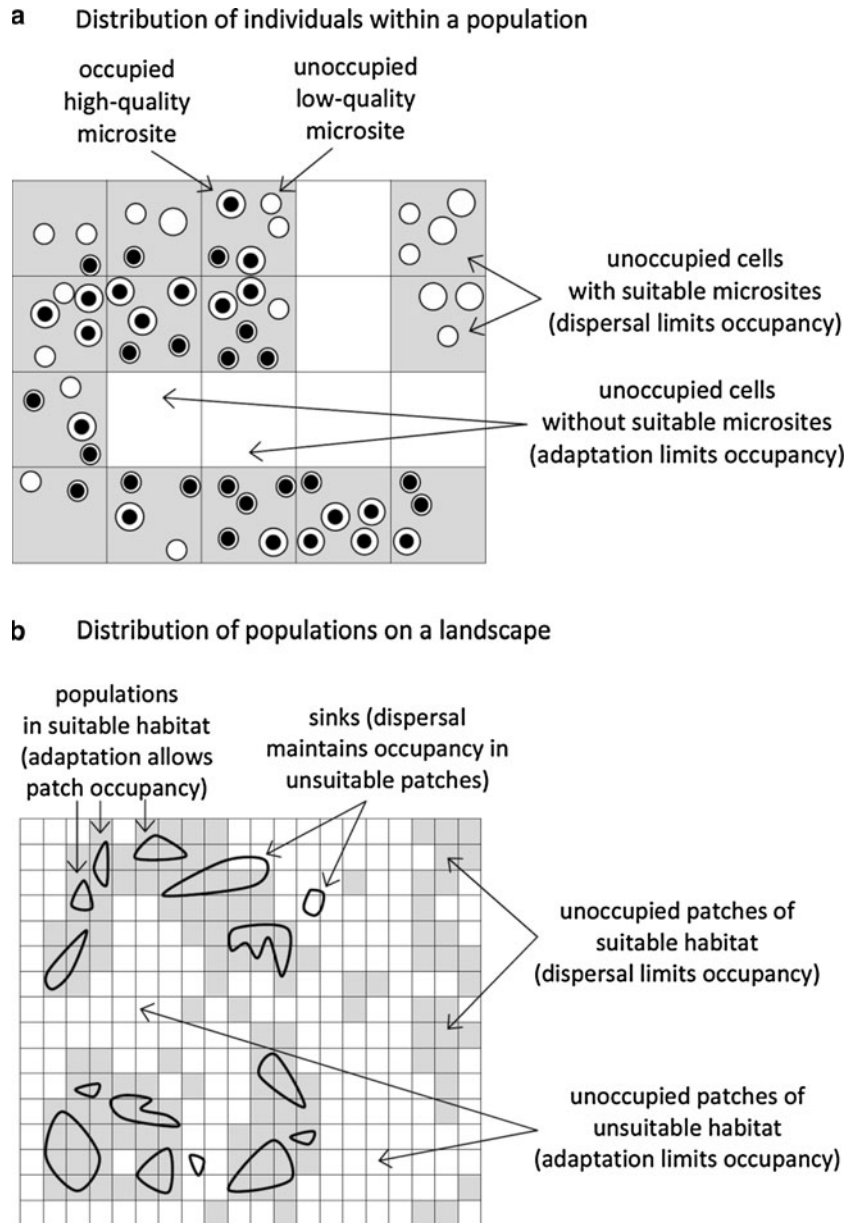
(Shreve 1922; Billings 1952; Holland et al. 1975; Pigott and Pigott 1993; Reynolds et al. 1997; Warren 2008, 2010). In this way, water stress may constrain plant distributions at multiple scales, though the sources of variation in water balance vary.

Dispersal limitation might operate somewhat similarly across scales. The seeds of herbaceous plants that lack dispersal adaptations generally move less than 1 m from parents (Willson 1993; Venable et al. 2008). In such species, restricted dispersal—plus the fact that seeds cannot select habitats—might lead to spatial aggregation within populations at scales close to typical dispersal distances (e.g., Seabloom et al. 2005). Restricted dispersal also might cause spatial clustering of patch occupancy at a larger landscape scale, as the likelihood that a suitable location is colonized (or that patches at risk of extinction are “rescued” by dispersal from others) increases with proximity to existing populations (Ouborg and Eriksson 2004). Thus, at multiple scales, dispersal may cause aggregation that does not match spatial environmental variation, with substantial frequencies of unoccupied suitable habitat (Primack and Miao 1992; Ehrlén and Eriksson 2000; Munzbergova and Herben 2004; Seabloom et al. 2005; Schurr et al. 2007; Samis and Eckert 2009).

The fact that aggregation may stem from limited adaptation in patchy environments or from limited dispersal makes it difficult to determine aggregation's causes (Lichtstein et al. 2002; Diez and Pulliam 2007). One approach to this difficulty is statistical methodology that separates environmental effects from “pure” spatial dependence that does not correlate with environmental variation (Legendre 1993; Dormann et al. 2007; Beale et al. 2010). Additional insight should come from analyzing the spatial distribution of performance: vital rates or finite rates of increase of populations, or the physiological status or fitness components of individuals. Although spatial effects on distribution might arise from local dispersal, similar spatial effects on performance would not generally be expected unless there are spatially correlated environmental factors. Spatially structured performance likely represents spatially variable adaptation, because of environmental variation (Bell et al. 1991; Stratton 1994).

In the California annual *Clarkia xantiana* ssp. *xantiana* A. Gray (Onagraceae), studies of physiology, demography, and species distribution indicate

Fig. 1 Hypothetical controls of plant distribution at contrasting spatial scales. **a** Distribution of individuals (*filled circles*) among small spatial areas (*square “cells”*) within a population, with dimensions of cells approximating mean dispersal distance. *Open circles* depict suitable microsites (plant-sized locations) of low-quality (*small circles*) and high-quality (*larger circles*). Areas outside circles are unsuitable for individual establishment; cells containing at least one suitable microsite are shaded to indicate habitat suitability. Some cells are unoccupied because of limited adaptation (i.e., the absence of suitable microsites), others because of limited dispersal. **b** Distribution of populations (*polygons*) on a landscape divided into patches (*squares*). Shading indicates habitat capable of sustaining demes without immigration through a sufficient density of suitable microsites and other essential resources. Adaptation and dispersal determine patch occupancy as indicated



that the eastern limit of the species’ range is set partly by low and variable precipitation (Geber and Eckhart 2005; Eckhart et al. 2010; Eckhart et al. 2011). Water relations may also influence distribution at smaller scales. Plant water stress appears to be exacerbated in fine-textured, hard soils derived from metasedimentary rock (Eckhart et al. 2010). Within populations, plants experience lower water stress on steep slopes where soils are coarser and softer than on adjacent shallow slopes (Eckhart et al. 2010), possibly because

hill-slopes accumulate soil water (Chamran et al. 2002), because coarse soils hold water with weaker capillary forces (Noy-Meir 1973), and because soft soils provide less resistance to root growth (Passioura 2002).

Here, we analyze distribution at two spatial scales, and performance at the smaller scale, in *C. xantiana* ssp. *xantiana*. We asked two specific questions. First, do topographic variables, soil features, and dispersal limitation influence the occupancy of *C. xantiana* ssp.

xantiana at the level of landscape patches (ca. 1,300 m² areas, sampled along transects at regular intervals)? We predicted that patch occupancy correlates with steep, north- and east-facing slopes and with coarse, soft, igneous soils, with limited dispersal causing aggregation and/or incomplete occupancy of suitable locations. Second, do microtopographic variables, soil resistance, and dispersal limitation affect the occupancy, density, and performance (water status and reproduction) of individuals in small areas (4-m² cells) within populations? We predicted the environmental correlates of cell-scale distribution and performance resemble patterns found at the patch scale, with limited dispersal causing some degree of aggregation in distribution independent of environment.

Methods

Study species

We studied *C. xantiana* ssp. *xantiana* in its region of greatest abundance, on slopes above the Kern River Valley and in the canyons of the Kern River, at elevations from 500 to 1,250 m (Eckhart and Geber 1999; Fig. 2). The most common vegetation there is grassland, dominated by Mediterranean annual grasses (e.g., *Bromus* spp.; *Avena* spp.) but including native bunchgrasses (e.g., *Nasella pulchra*) and low densities of trees (mainly *Aescalus californicus*, *Pinus sabiniana*, *Quercus douglassii*, and *Q. wislizenii*) and shrubs (e.g., *Cercocarpus* spp., *Ephedra* spp., *Eriogonum* spp.).

Like other *Clarkia* (Lewis and Lewis 1955), *Clarkia xantiana* ssp. *xantiana* has a patchy distribution. On an operational definition of a *Clarkia* population (deme) as an aggregation of individuals separated from others by empty areas at scales of 50–100 m (cf. Groom 1998), populations range in area from a few tens of square meters to tens of hectares, and are isolated from others by distances of 50 m to >1 km (Eckhart et al. 2011). Substantial spatial variation in density also occurs within populations (e.g., different 0.5 m² permanent plots within the same population may range from 0 to >100 flowering adults in a given year [unpublished data]).

The study region has a Mediterranean climate, with wet winters and summer drought. The study

species germinates after winter rains and flowers in May and June (Eckhart and Geber 1999; Eckhart et al. 2004; Geber and Eckhart 2005). It is self-compatible but outcrossing (Moore and Lewis 1965; Runions and Geber 2000; Moeller and Geber 2005) and is pollinated by native bees, some of them *Clarkia* specialists (MacSwain et al. 1973; Moeller 2006). The seeds, which passively fall from dead plants in summer and autumn, can survive several years in soil (Eckhart et al. 2011). Field work for this project took place in 2008, a year of high precipitation and high *C. xantiana* ssp. *xantiana* adult abundance (Eckhart et al. 2011). We, therefore, suspect that any failures to find plants in a given patch or cell usually revealed genuine species absences, rather than locations that, in dry years, contain *Clarkia xantiana* ssp. *xantiana* seed banks but no emergent plants (cf. Albrecht and McCarthy 2009; Moore 2009).

Patch occupancy

To determine the occupancy of *Clarkia xantiana* ssp. *xantiana* in representative landscape patches across the range, and to characterize environments at those locations, we surveyed sites: (1) at regular intervals along roughly circular transects surrounding, at a distance, each of five known populations; and (2) along five roughly linear transects along trails or roads (Fig. 2). For each “circular” transect, we used a GPS receiver to circumnavigate the central population (Eckhart et al. 2011) on foot, maintaining a buffer of at least 100 m outside the perimeter. At eight locations along each transect (i.e., at 45° intervals from 0° to 315°), we examined a 20-m radius for the presence of *C. xantiana* ssp. *xantiana* individuals (thus sampling an area of approximately 1,300 m²). Individuals were either obviously present (at least tens of them) or obviously absent from the patch (and from view). We characterized patch topography by estimating overall slope inclination, north aspect (cosine [aspect]), and east aspect (sine [aspect]) (Svenning 2001), with a handheld inclinometer. We estimated soil resistance to penetration at 2.5-cm depth intervals with a SC900 static penetrometer (Spectrum, Plainfield, IL, USA), averaging values for five locations separated by 1 m, along a transect perpendicular to the patch’s aspect. We used mean resistance in MPa at 2.5 cm—the depth for which we had the most complete data—as a soil-

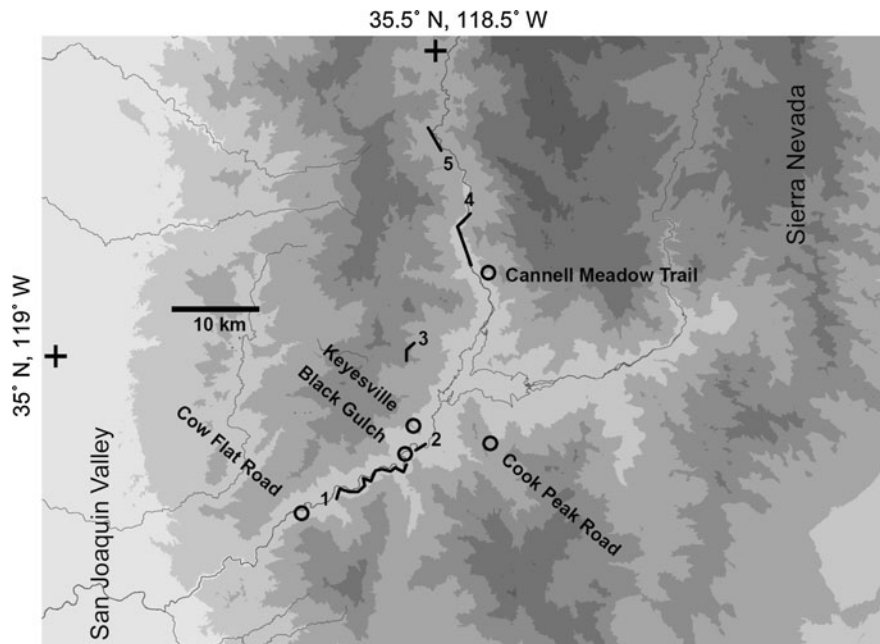


Fig. 2 Map of the study area in the southern Sierra Nevada and adjacent ranges, California, USA, with elevation from $<500\text{ m}$ to $>2,500\text{ m}$ indicated by increasing shading in 500 m intervals. The outlined water body in the center is a reservoir created in the 1950s (Isabella Lake). Labeled circles mark the locations of *circular* transects in the patch-occupancy

study, while numbers from 1 to 5 (from southwest to northeast) mark *linear* transects for that study. The five populations where cell occupancy, density, and performance were analyzed are the populations at the center of each *circular* patch-occupancy transect

resistance index in statistical analyses. We collected five $10 \times 2.5\text{ cm}$ soil cores adjacent to the penetration-resistance locations. Examining rocks and soils in the field and lab, we classified each site's soil parent material as igneous (granodiorite, quartz monzonite, and/or gabbro) or metasedimentary (schist). We classified sites with mixed parent material as metasedimentary. Along "linear" transects, we stopped at regular intervals (0.5 km along trails; 1 km along roads), collecting data as above, recording environmental data at least 20 m from roads and 1 m from trails, to reduce human-disturbance effects.

For soil-texture analysis, we combined three randomly selected soil cores from each site and dried them for 48 h at 65°C . We passed each sample through a 2-mm sieve before shaking it for 8 min at 60 Hz in a Retsch AS200 shaker (Haan, Germany). Sieves of $1, 0.5, 0.25, 0.106,$ and 0.053 mm separated the soil into particle-size fractions, which we weighed. As previous research indicated that the proportion of fine-sand (particles $0.053\text{--}0.016\text{ mm}$ in diameter) by weight was the most spatially variable soil fraction and the most strongly correlated with *C.*

xantiana ssp. *xantiana* performance (Eckhart et al. 2010), we used this fraction as a texture index.

We sampled 71 patches, 40 from circular transects and 31 from linear transects, combining them for analysis. Instrument error caused faulty soil-resistance values in two patches, and two patches were on virtually level ground (with undefined aspects). Thus, the final sample size for patch-occupancy analysis was 67.

Occupancy, density, and performance at the "cell" scale

To assess whether occupancy, density, and performance of individuals in small areas (4-m^2 cells) within populations were influenced by topography and soils, we set up grids of 2-m square cells along a north or east bearing in each of five well-separated populations of *C. xantiana* ssp. *xantiana* (Fig. 2), collecting data at peak flowering. Each grid measured either $50 \times 4\text{ m}$ (50 cells, in three populations) or $32 \times 6\text{ m}$ (48 cells, in two populations). In each cell, we recorded the presence, density, and performance

(water status and potential reproduction) of *C. xantiana* ssp. *xantiana*. We assessed water status as leaf water potential at midday (1,000–1,300 solar time) using a pressure chamber (PMS Model 1000, PMS Instruments, Albany, OR, USA) on one, or if more than one was present, two flowering plants in each cell, averaging when we scored two plants. Lower midday water potential indicates greater water stress and reduced performance (McDowell et al. 2008; Eckhart et al. 2010). We calculated the average number of fruits, flowers, and buds of all individuals within each cell (up to 327 plants per cell) as an estimate of potential individual reproduction. We also scored each cell for physical variables including: (1) slope inclination, averaging measurements at four positions (i.e., the corners of a square with sides of 1.64 m, within the cell) with a Leica Disto A8 laser rangefinder (Leica Geosystems AG, Heerbrug, Switzerland) laid on the soil surface; (2) north aspect and east aspect, averaging four measurements with a handheld compass at the above points; and (3) soil resistance to penetration (as at the landscape-patch scale), averaging two measurements within the cell, and using the average at 2.5-cm depth as an index.

Statistical analysis

At the patch scale, the response variable was *Clarkia xantiana* ssp. *xantiana* occupancy, and the environmental predictors considered were slope inclination (“slope”), north aspect, east aspect, parent material (igneous “1” or metasedimentary “0”), soil penetration-resistance, and soil texture. We characterized the effects of these variables on occupancy, while also estimating the spatial dependence of occupancy independent of environmental variation (presumably because of dispersal), following the approach of Diniz-Filho et al. (2008). We implemented the analysis in SAM (Statistical Analysis in Macroecology) version 4.0 (Rangel et al. 2010). Briefly, we first estimated a spatial autoregressive term for each of the 67 patches, calculated using the matrix of inter-patch distances (Dormann et al. 2007). Then, we ranked the 63 possible ordinary-least-squares models including the spatial term and any combination of the six environmental variables by Akaike’s Information Criterion corrected for small sample sizes (AIC_c) and AIC weights (relative likelihoods of each model) (Burnham and Anderson 2002). We estimated each

variable’s overall contribution by averaging regression coefficients across models by AIC_c weights, identifying significant coefficients as those with 95% confidence intervals that exclude zero (Johnson and Omland 2004; Diniz-Filho et al. 2008). A significant spatial covariate term indicates occupancy patterns independent of environmental variation, positive effects revealing aggregation, negative effects overdispersion. Although the models assumed normal distributions of error, which is not strictly true for binary response variables, spatial autocorrelation in residuals was low and non-significant (Moran’s I was between -0.1 and 0.1 for all lag distances).

At the scale of cells within populations, there were four response variables: *C. xantiana* ssp. *xantiana* occupancy, density, water potential, and potential fruit number. The predictors considered for occupancy and density were slope, north aspect, east aspect, and soil penetration resistance, whereas for water potential and potential fruit number, the predictors also included density, anticipating intraspecific competition. For each response variable in each population, we followed the spatial-regression, model-selection, and model-averaging procedure used for patch occupancy. We expected spatial covariates to affect occupancy and density but not performance, on the hypothesis that our selection of environmental variables accounts for performance variation. Because the models succeeded in accounting for spatial trends, and because ordinary least squares coefficients are reasonably robust to non-normal errors (Kutner et al. 2004), we are confident that the models reveal the effects of predictor variables.

Results

Patch occupancy

Of 67 patches, 14 were occupied. Slope and soil variables appeared frequently in low- AIC_c models of patch occupancy, the single best model including slope, soil parent material, and soil texture (Table 1). Low but significant negative correlations between some environmental variables (slope and soil texture, slope and soil resistance, north aspect and soil resistance, and igneous parent material and soil resistance; Table 2) may account for the approximately adequacy of several models containing combinations of these terms (Table 1).

Table 1 Model selection in least-squares regression analysis of *C. xantiana* ssp. *xantiana* patch occupancy versus six topographic and soil variables and a spatial autoregressive covariate

Model	Environmental predictors	AIC _c	ΔAIC _c	r ²	AIC _c wt
1	SL, IG, TX	67.739	0	0.17	0.096
2	TX	68.149	0.410	0.20	0.078
3	SL, TX	68.162	0.423	0.14	0.077
4	TX, SR	68.412	0.673	0.17	0.068
5	IG, TX	68.491	0.753	0.16	0.066
6	SL, TX, SR	69.287	1.549	0.19	0.044
7	IG, TX, SR	69.635	1.897	0.18	0.037
8	SL, IG, TX, SR	69.784	2.045	0.21	0.034
9	NO, TX	69.846	2.107	0.21	0.033
10	SL, EA, IG, TX	69.894	2.156	0.18	0.033

The ten (of 63 possible) models with the lowest AIC_c values appear above, in increasing order of AIC_c. As models 2–7 have AIC_c values within 2 of model 1, models 1–7 may be considered equally adequate. AIC_c weights (final column) indicate relative likelihoods that each model is the correct one and represents the weighting factors used in the analysis of means and confidence intervals for regression coefficients (Fig. 3)

SL slope, NO north aspect, EA east aspect, IG igneous soil parent material, TX soil texture (weight fraction of particles 0.053–0.106 mm), SR soil resistance to penetration. All models were constrained to include the spatial covariate

Table 2 Correlation coefficients between environmental variables in the analysis of patch occupancy ($N = 67$)

Variable	SL	NO	EA	IG	TX
NO	0.169				
EA	−0.148	−0.106			
IG	0.054	0.187	−0.159		
TX	−0.431	−0.136	−0.014	−0.215	
SR	−0.278	−0.413	−0.044	−0.290	−0.112

Significant coefficients ($P < 0.05$) are in bold. Abbreviations as in Table 1

After model averaging, predictions and findings regarding patch occupancy matched closely (Fig. 3). Overall, patch occupancy correlated with steep north-facing (but not east-facing) slopes, soft, coarse soils, and igneous soil parent material (Figs. 3b and 4). The spatial covariate was not significant; proximity to occupied locations did not predict occupancy. The occurrence of unoccupied patches in environments similar to occupied ones (Fig. 4), however, suggested that dispersal limited occupancy.

Occupancy, density, and performance at the cell scale

The correlates of cell occupancy (ranging from 42 to 60% among populations) and density (averaging from 1.0 to 12.5 individuals m^{−2} among populations) met

expectations less often than for patch occupancy, and they varied substantially among populations (Fig. 5; Online Supplement). Significant effects in expected directions (32 *solid lines* in Fig. 5) were one third more common than significant effects in opposite directions or that were not expected to occur (24 *dashed lines* in Fig. 5). Expected positive effects of slope on occupancy and/or density appeared at three sites (Fig. 5b,c,f), whereas at Keyesville, occupancy correlated with shallow slope (Fig. 5d). Penetration resistance was associated with reduced occupancy and density at Keyesville (Fig. 5d) but with increased occupancy and/or density at Cow Flat (Fig. 5b), Black Gulch (Fig. 5c), and Cook Peak (Fig. 5f). Meanwhile, the spatial covariate was an important and consistent control on distribution, with significant aggregation in occupancy and/or density occurring in all five populations (Fig. 5).

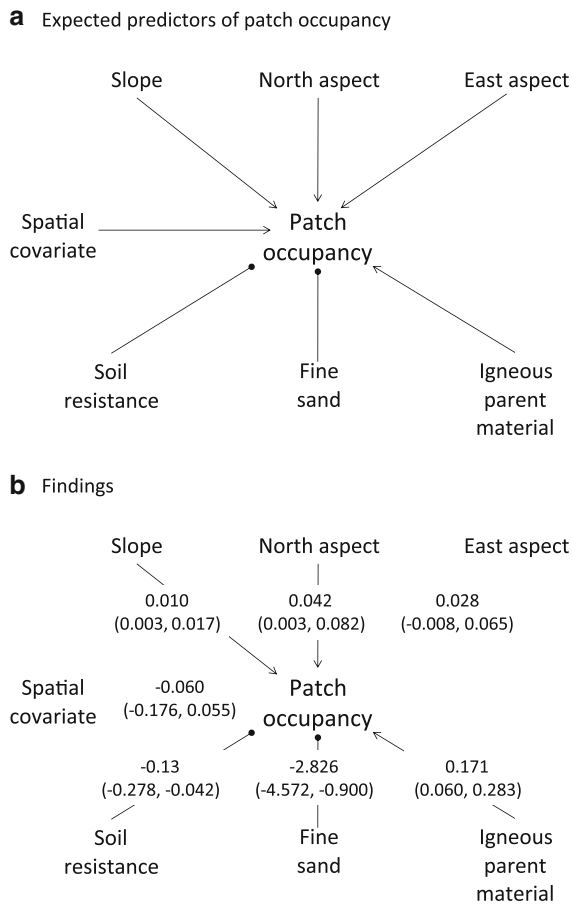


Fig. 3 Topographic and soil controls of the distribution of *Clarkia xantiana* ssp. *xantiana* populations. **a** Predictions, with arrows indicating expected positive effects and blunt-tipped lines indicating expected negative effects. **b** Findings, with lines labeled as in **a**, with AIC_c-weighted averages and 95% confidence limits of coefficients. East aspect and the spatial autoregressive term were not significant and so therefore are not assigned arrows or lines

The correlates of plant performance also varied substantially, sometimes in accord and sometimes in discord with expectations (Fig. 5). Water potential varied at least twofold within each population and ranged overall from -2.4 to -0.8 MPa. It declined with soil resistance, as expected, in four of five populations, and it increased with slope in three of five. Reproduction varied at least fivefold within populations and ranged overall from 1 to 10.8 potential fruits per individual per cell. It increased with east and/or north aspect at three sites, but declined with them at a fourth. Associations between

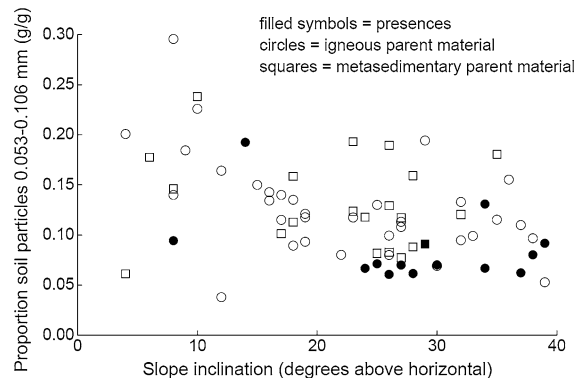


Fig. 4 Scatterplot of proportion fine sand versus slope in the analysis of patch occupancy. Symbol meanings as indicated. Among occupied patches, note the preponderance of circles (igneous parent material) on steep slopes, with little fine sand. Note also that many unoccupied patches exhibit environmental conditions similar to occupied ones

aspect variables and water potential were negative as often as positive.

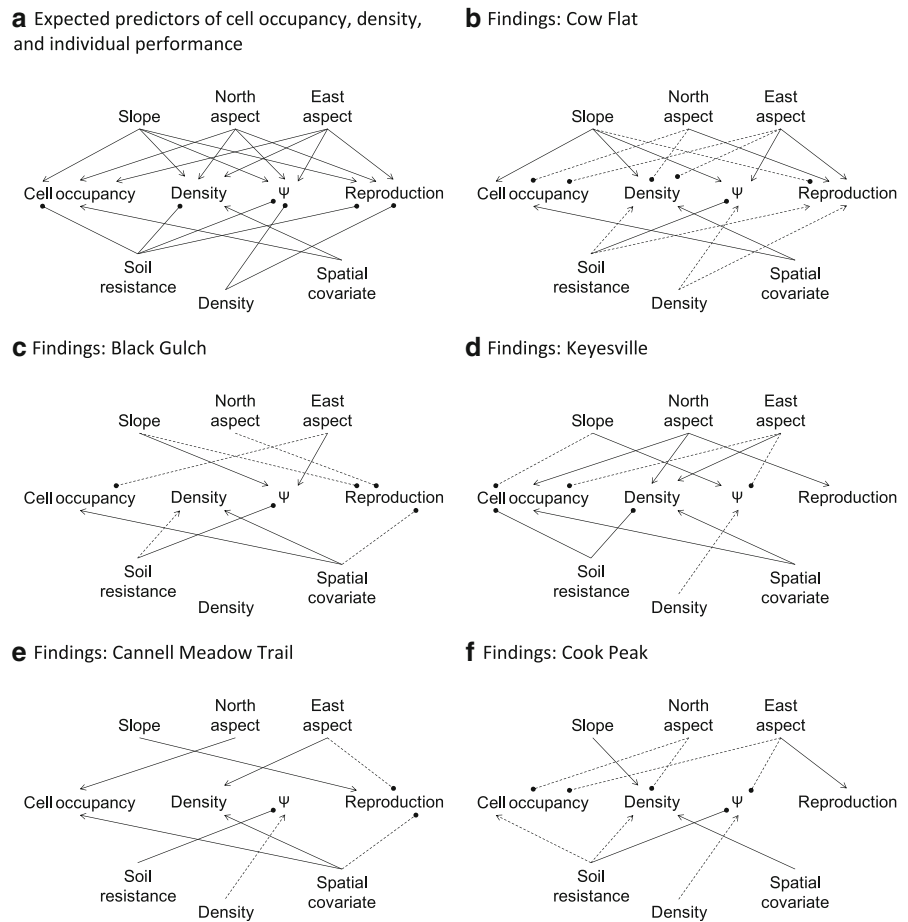
There was no evidence of negative density dependence of performance, but there was unexpected evidence of positive density dependence. Both reproduction and water potential increased with density at Cow Flat (Fig. 5b), and water potential increased with density at Keyesville (Fig. 5d), Cannell Meadow (Fig. 5e), and Cook Peak (Fig. 5f). There was negative spatial dependence of reproduction at Black Gulch (Fig. 5c) and Cannell Meadow (Fig. 5e).

Discussion

Patch occupancy

At the regional scale, (1) associations between precipitation and plant water status (Eckhart et al. 2010), (2) associations between precipitation, vital rates, and population growth rate (Eckhart et al. 2011), and (3) low fitness of transplants in arid areas beyond the eastern species border (Geber and Eckhart 2005; Geber et al. unpublished) point to water limitation of *C. xantiana* ssp. *xantiana* distribution. We, therefore, expected environmental variables associated with lower water stress to predict occupancy of *C. xantiana* ssp. *xantiana* in landscape patches. Patch occupancy correlated with features

Fig. 5 Topographic and soil controls of *Clarkia xantiana* ssp. *xantiana* occupancy, density, and performance (water potential, Ψ , and potential fruit number, “reproduction”) among 4-m² cells within each of five populations. **a** Predicted controls with *arrows* indicating positive effects and *blunt-tipped lines* indicating negative effects. Note that density appears twice: as a response variable, and as a predictor of water potential and reproduction. **b–f** Findings in each of five populations. *Arrows* and *blunt-tipped lines* are only included for those variables that had 95% confidence limits that did not overlap zero (Online Supplement). *Solid lines* depict findings that agree with predictions. *Dashed lines* depict findings opposite to predictions or where unanticipated effects were detected



likely to reduce water stress: steep, north-facing slopes; soft, coarse soils; and igneous rather than metasedimentary soil parent rock. This study joins others that revealed positive effects of coarse soil texture on plant distribution and/or performance in arid areas (Lane et al. 1998; Hamerlynck et al. 2002; Herrera 2002; Hultine et al. 2005; Miller et al. 2006; cf. Pantastico-Caldas and Venable 1993; but see Sperry and Hacke 2002).

We emphasize that topographic features such as slope and aspect are “indirect” environmental variables, correlates of others (conditions such as temperature, wind, and soil structure; resources such as water and sunlight) with direct effects on plants (Austin and Smith 1989; Austin 2007). Additional work, ideally experimentation, is necessary to identify which direct environmental variables are responsible for apparent topographic effects (e.g., Munzbergova 2004; Moore and Elmendorf 2006;

Albrecht and McCarthy 2009; Warren 2010). Our favored hypothesis is that hydrology underlies the slope effect (Eckhart et al. 2010), though slope inclination, per se, may not be the precise terrain feature that matters. Upslope area and slope concavity—that is, a slope’s becoming more gradual down-slope—predict surface water availability as the California dry season progresses (Chamran et al. 2002). On the water-relations hypothesis, we expect topographic effects to vary across *C. xantiana* ssp. *xantiana*’s range, interacting with other larger-scale drivers of water balance, such as precipitation and temperature (Holland et al. 1975; Svenning 2001). Aspect and slope effects should be weaker, for example, in relatively cool moist sections of the range (Holland et al. 1975), such as high-elevation areas.

Patch occupancy in *C. xantiana* ssp. *xantiana* may be influenced by metapopulation dynamics. Absences in patches of apparently suitable habitat suggest that

dispersal limitation and/or stochastic extinction help determine occupancy patterns. (This study did not find another expected signal of metapopulation processes: increasing occupancy with proximity to occupied patches. Perhaps proximity effects occur at scales below our sampling intervals.) Under metapopulation dynamics, geographic declines in the frequency of suitable patches can influence the location of range edges (Holt and Keitt 2000). In *C. xantiana* ssp. *xantiana*, schist soils reduce plant water status (Eckhart et al. 2010), population growth rate (Eckhart et al. 2011), and occupancy (this study), and they are unusually common at the eastern species border (Nadin and Saleeby 2008). Therefore, both the frequency and quality of suitable habitat appear to decline toward the eastern species border.

Occupancy, density, and performance at the cell scale

In contrast to largely successful predictions at the patch scale, predictions about topographic and soil correlates of cell-scale distribution and performance met mixed success. Environmental factors' apparent effects sometimes matched and sometimes contrasted with those found at the larger scale. Slope inclination and soil penetration resistance had cell-scale effects that generally resembled patch-scale effects, suggesting that suitable habitat at the patch scale and the cell scale arises from some of the same factors. In contrast, aspect effects at the cell scale contrasted distinctly among populations. We did not find that water potential and individual reproduction were consistently higher in cells where north- or east-facing slopes might be expected to ameliorate water stress. This finding implies that patch occupancy, which likely depends strongly on past seed production of individuals within patches, does not scale up directly from plant responses to aspect variation at the cell scale. The environmental determinants of distribution appear somewhat decoupled across spatial scales (e.g., Karst et al. 2005; Diez and Pulliam 2007), at least in terms of slope aspect. Meanwhile, spatial autocovariate effects consistently indicated aggregation at the cell-scale, presumably following from short dispersal distances. Previous studies of fine-scale distribution of annuals in California grasslands also indicate substantial spatial patterns

independent of (or despite) patchy environmental variation (Seabloom et al. 2005; Moore 2009).

The apparent partial decoupling of environmental effects across scales may reflect, in part, obscuring influences of unmeasured variables at small scales. The fact that water potential was often superior in high-density cells—after accounting for slope, aspect, and soil resistance—hints that an unmeasured spatially patchy variable increased both survivorship and survivor water status. (Any negative density dependence apparently operates earlier in the life cycle and/or at scales smaller than 4-m² cells, across the range of densities we measured.) Soil texture may be a critical abiotic variable that we did not measure at the cell scale. Nutrient patchiness (Bell et al. 1991) is another possibility. Alternatively, the decoupling may reflect differences in the importance of topography—particularly slope aspect—across scales. Topographic variation among 2-m cells may be largely immaterial to variation in solar radiation, temperature, and water availability in rugged terrain, where topography at somewhat larger scales may dominate what individual plants experience and determine how well they perform. If so, topography at those larger scales may tend to define habitat patches where sets of individuals make sufficient demographic contributions to allow long-term persistence (Fig. 1b).

Spatially variable biotic factors may also have operated at the cell scale. Although we scored cells for other plant species (Kramer and Montgomery unpublished), we left those data out of this analysis because variation in community composition among sites made it difficult to compare (rare) species effects across populations. At Cannell Meadow, however, plants growing within shrub canopies (*Ephedra*, *Erigonum*, or *Yucca*) had significantly lower water potential (-1.70 ± 0.11 , $N = 11$) than those growing away from shrubs (-1.37 ± 0.04 , $N = 12$; $t = -2.84$, $P = 0.015$). This pattern suggests competition for water between *Clarkia* and shrubs. (The difference in potential fruit number between these groups was in the same direction but was not significant [within shrubs 6.0 ± 0.7 ; outside shrubs 8.2 ± 0.28 , $t = 0.76$, $P = 0.462$]). The negative spatial dependence of reproduction found in two populations also may reflect unmeasured variables, either abiotic or biotic.

In summary, limited adaptation to xeric environments appears to explain patch occupancy in *C.*

xantiana ssp. *xantiana* at the landscape scale and may explain occupancy, density, and appears to account for individual performance at the cell-scale in some but not all populations. Dispersal constraints also affect distribution, with incomplete occupancy of suitable sites at the among-patch scale and spatial aggregation at the cell scale. Although some similarities appeared across scales, some degree of scale dependence of the controls of plant species distributions may be the norm in heterogeneous arid landscapes (Gómez-Aparicio 2008).

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