

Research Article

Contrasting soil-texture niches facilitate coexistence of two congeneric plants that differ in competitive ability

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Abstract. Whether close evolutionary relatives can coexist is expected to depend on evolutionary divergence in niches relative to divergence in competitive abilities. We investigated how plant species' responses to soil texture might affect coexistence by analysing distributions, seedling emergence and performance, and competitive abilities of the winter annuals *Clarkia speciosa* ssp. *polyantha* and *C. xantiana* ssp. *xantiana*. A landscape survey showed that the species have distinct associations with soil texture, *C. speciosa* presence correlating with fine soil and *C. xantiana* correlating with coarse soil. At the scale of population presences, the species co-occur less often than would be expected at random. On small scales within sites where they do co-occur, each species was negatively associated with the other. *Clarkia xantiana* presence and/or density also correlated positively with coarse soil texture and steep, poleward slopes, suggesting limitation by water availability. Lab experiments that varied substrate texture and imposed drought revealed contrasting species' fundamental niches at the seed and seedling stages. In coarse substrates, *C. xantiana* seedlings emerged at several-fold higher rates than *C. speciosa*, and, unlike *C. speciosa*, emerged when seeds were buried 0.5 cm. *Clarkia speciosa* seedlings had superior drought tolerance, independent of substrate. Competition coefficients estimated in a response surface experiment in artificial substrates predicted competitive exclusion of *C. speciosa* by *C. xantiana* in coarse substrate, with possible founder control of competitive outcome in fine substrate. Species' differences in responses to soil texture generate spatial segregation that likely facilitates coexistence, despite competitive ability differences that oppose it.

Keywords: *Clarkia speciosa* ssp. *polyantha*; *Clarkia xantiana* ssp. *xantiana*; competition; geographic distribution; niche differences; seedling emergence; soil texture; species coexistence.

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Introduction

Closely related species often belong to the same regional species pool (Anacker and Strauss 2014; Zobel 2016) and possess similar niches (Ackerly 2003; Burns and Strauss 2011; Anacker and Strauss 2016), giving them the opportunity to co-occur within communities. Whether opportunities to co-occur become long-term coexistence, however, requires species having evolved some degree of niche differences, relative to differences in competitive ability, since their lineages diverged (Mayfield and Levine 2010; Weber and Strauss 2016). Large niche differences generally favour coexistence, but large competitive ability differences combined with relatively small niche differences make coexistence unlikely (Chesson 2000) and competitive exclusion rapid (Carmel et al. 2017). Of studies of plant species coexistence that estimate differences in both niches and competitive abilities (e.g. Chu and Adler 2015, and references therein), few explicitly compare co-occurring close relatives. A recent example (Staples et al. 2016) found coexistence of close relatives is likely enabled by substantial niche differences combined with minimal competitive ability differences. More such studies should reveal some of the mechanisms that underlie phylogenetic patterns in community assembly (Mayfield and Levine 2010).

In plants, soil texture may be an important niche dimension related to coexistence (Fernandez-Illescas et al. 2001). In arid environments, water availability can vary according to the inverse soil-texture effect, whereby higher infiltration, lower losses to evaporation and weaker capillary forces binding water to soil particles in coarse-textured soils can lead to greater plant-available water (Noy-Meir 1973). Partly via this effect, texture gradients in arid lands can create substantial variation in plant performance (Barnes and Harrison 1982; Rosenthal et al. 2005; Eckhart et al. 2010; Fensham et al. 2015). Plant species frequently respond differently along such hydrologic gradients (Silvertown et al. 2015). Soil texture also affects plant performance and creates opportunities for niche differences in ways besides water relations. For example, seedling establishment can be texture-dependent, independent of water availability, possibly because fine-textured soils are hard for some species' roots to penetrate (Tsuyuzaki et al. 1997). Coarse soil texture can increase seed burial depth (Benvenuti 2007), especially of small seeds (Chambers et al. 1991). Deep burial, in turn, can reduce seed germination and emergence, due to reduced availability of light and other germination cues (Bliss and Smith 1985; Benvenuti et al. 2001; Grundy et al. 2003; Guillemin and Chauvel 2011; Hoyle et al. 2013). Moreover, soil texture can interact with burial depth. As soil texture becomes finer, light penetration declines (Bliss and Smith 1985).

Perhaps as a result, germination often declines with depth, but species' responses to burial depth and to texture can vary substantially (Benvenuti 2003; Guillemin and Chauvel 2011; Berti and Johnson 2013; Hoyle et al. 2013). Thus, in environments that vary in soil texture, contrasting species' responses to texture might favour coexistence. Meanwhile, species with similar soil-texture niches might be unlikely to coexist, especially if they differ in competitive ability.

Here we analyse factors potentially affecting coexistence in landscapes that vary in soil texture, for range-sharing annual plants in the same genus, *Clarkia speciosa* ssp. *polyantha* and *C. xantiana* ssp. *xantiana* (Onagraceae). Combining field studies with growth chamber and greenhouse experiments, we compared these species': (i) realized soil-texture niches (i.e. spatial distributions with respect to variation in soil texture at the levels of populations on landscapes and of individuals within populations); (ii) fundamental niches (i.e. responses of seeds and seedlings to experimental manipulation of substrate texture and water availability); and (iii) competitive abilities in contrasting substrate textures (i.e. intra- and interspecific competition coefficients, estimated by a response surface experiment). Our findings indicate that the soil-texture niche differences these species exhibit may be critical to their coexistence, as their competitive abilities predict competitive exclusion.

Methods

Study system

The study species are winter annuals endemic to California that share much of their geographic distributions (Lewis and Lewis 1955; Baldwin and Goldman 2012), which are centred in the Kern River drainage of the southern Sierra Nevada and adjacent ranges. Here most populations of *Clarkia xantiana* (including all in this study) are *C. xantiana* ssp. *xantiana* (hereafter, *xantiana*), and all populations of *C. speciosa* are *C. speciosa* ssp. *polyantha* (hereafter, *speciosa*). The range of *xantiana* also extends ca. 100 km south of this area, into the Transverse Ranges north of Los Angeles, while *speciosa*'s extends ca. 50 km north along the Sierra Nevada foothills (Lewis and Lewis 1955).

Found mainly at low to moderate elevations (ca. 500–1600 m) in grasslands and savannas (often with free-ranging cattle in the growing season), and in openings of chaparral and woodland, both study taxa germinate when winter rains arrive and flower with the onset of annual drought in late spring and early summer, in the region's Mediterranean climate (Lewis and

Lewis 1955). Like most other *Clarkia*, the study species share a set of specialist and generalist bee species as pollinators (MacSwain et al. 1973; Moeller 2004). Seeds disperse passively in late summer and fall, as persistent capsules dehisce from the apex (Lewis and Lewis 1955). The species' seed morphologies are similar: cylindrical segments with slanted ends, 1–2 mm long and <1 mm in diameter, with rough surfaces.

In *xantiana*, water limitation constrains individual performance, population success and geographic distribution (Geber and Eckhart 2005; Eckhart et al. 2010; Eckhart et al. 2011; Kramer et al. 2011). The soil texture of the region predicts soil water characteristic curves—finer soils having lower water potential for a given water content—and plants in coarser soils have higher water status (Eckhart et al. 2010). Coarse soil texture is a strong predictor of *C. xantiana* ssp. *xantiana* population presence (Kramer et al. 2011). Soil texture effects on *speciosa* distribution and performance have not been reported.

Distributions

A field survey taken at a coarse grain and large spatial extent revealed associations of *xantiana* presences and absences with topography and soil variables (Kramer et al. 2011), also generating previously unpublished data on *speciosa* distribution. Here we analysed soil-texture associations of both species and applied Veech's (2013) metric of the probability of species co-occurrence. For full details of data collection, see Kramer et al. (2011). In June 2008, we sampled 66 representative patches (ca. 20 × 20 m) at regular intervals along roads, trails and cross-country transects, dispersed throughout the species' ranges in the Kern River drainage [see Supporting Information—Table S1, Fig. S1], scoring species presence or absence and several environmental variables, and collecting several soil cores for lab analysis. Soil-texture analysis began with drying bulked site samples in a forced-air oven for at least 48 h at 65 °C. We passed each dry sample through a 2 mm sieve prior to shaking it for 8 min at 60 Hz in a Retsch AS200 shaker (Haan, Germany). Stacked sieves separated soil into particle size fractions of 1000–2000 µm, 500–1000 µm, 250–500 µm, 106–250 µm, 53–106 µm, and <0.053 µm. The smallest size fraction, which is minimal in these soils, combines silt and clay. An index of soil texture with known physical and biological consequences is the 53–106 µm weight fraction, the finest class of sand (Eckhart et al. 2010). Here we subtracted this weight fraction from 1, so that higher values indicate coarser-textured soil. We performed logistic regression of each species' presence on this soil-coarseness index, with a binomial response and logit-link function, using Minitab version 17.3 (Minitab,

State College, PA, USA) for this and other analyses, except where noted.

Within populations, *xantiana* presence, density and performance correlate with spatial position, microtopography and soil penetration resistance (Kramer et al. 2011). At this scale it is not known whether *xantiana* associates with soil texture or with *speciosa*, and *speciosa*'s distributional correlates are unknown. We collected distribution and environmental data during flowering in June 2011, at five sites where *xantiana* and *speciosa* individuals do occur together (discovered by earlier searches for *xantiana* populations [Eckhart and Geber 1999]): different locations than studied by Kramer et al. (2011) [see Supporting Information—Fig. S1]. At three sites, we set up a transect 100, 108 or 120 m long (constrained by terrain) and 12 m wide, positioned deliberately to capture environmental variation (the 'gradsect' approach of Austin and Heyligers 1989). At the other sites, the terrain compelled us to set up two shorter transects extending at an obtuse angle from a common origin. At one of these locations, Site 63 [see Supporting Information—Fig. S1], plants were small, and many had finished flowering and had lost their leaves at the time of the census. Probably for these reasons, we occasionally misidentified senescent plants at that site. Discovering these identification errors later (when cultivating seeds collected at the sites; see below), we therefore omitted field data from Site 63 from the field distribution analysis. Species identifications were accurate elsewhere.

Sampling and analysis were as follows. We scored *xantiana* and *speciosa* density within transects in a 3 m × 3 m grid, using a 0.5 m × 1 m quadrat frame. Excluding positions covered by boulders or large, dense shrubs, we sampled 130–162 positions per site. Densities ranged from 0 to 398 m⁻² in *speciosa* and 0 to 416 m⁻² in *xantiana*. At the centre of each quadrat, we also measured slope inclination, slope aspect (converted to linear azimuth [degrees' deviation from south]) and proportion vegetative cover in quartiles (later converted to binary presence or absence of bare ground). Finally, we collected a soil sample ~7 cm deep by 7 cm wide (ca. 350 mL). We determined soil texture in the lab as above.

In addition to wide ranges of density, there were many zeros in the data set: 352 quadrats with no *speciosa* individuals and 320 with no *xantiana*, out of 562 total grid positions. Following the recommendations of O'Hara and Kotze (2010) for zero-inflated counts, we applied zero-inflated negative binomial regression to analyse species' presences and, where present, their densities. We used the function `zeroinfl` in the `pscl` package, implemented in R 3.4.1 (R Core Team 2017), to evaluate models with site, soil-coarseness index, bare ground, slope inclination, slope linear azimuth and the other species'

density as predictors. This method provides predictor coefficients in each of two models: (i) a ‘counts model’ that estimates predictors’ influence on non-zero counts, assuming a negative binomial distribution and using a log link; and (ii) a zero-inflation model that analyses contributions to absences (zeros), assuming a negative binomial distribution and using a logit link. Spatial autocorrelation of species presence was negligible among neighbouring sampling points within sites at this scale (S. Mizuno, Grinnell College, unpubl. data).

Responses to experimental variation in substrate texture and to drought

To isolate the effects of soil texture on plant performance, we carried out controlled environment experiments for which we created substrates of contrasting texture (i.e. particle size distributions) but similar chemical composition. First we compared seed germination and seedling emergence of *xantiana* and *speciosa* from two depths, in sand of contrasting textures, in a growth chamber. The seed source was a bulked sample of 10 randomly selected maternal families of each species from the Mill Creek site. We sieved commercial ‘play sand’ to create coarse (1:1 [v/v] 2000–4000 μm and 500–2000 μm particles) and fine (1:1 [v/v] 500–2000 μm and 125–500 μm particles) substrates. Taking two 25 \times 50 cm plastic nursery flats filled with 48-cell inserts, we filled 24 cells each with one of the following: 63 mL coarse sand; 49 mL coarse sand; 63 mL fine sand; and 49 mL fine sand. We dispersed treatments in a ‘checkerboard’ pattern in each tray. We irrigated the sand carefully and levelled it in each cell. Into 12 cells of each substrate and volume, we sowed four seeds of one or the other species on the surface. Carefully adding 14 mL of the appropriate sand texture to each 49 mL cell created 12 replicates of each species sowed on the surface or 0.5 cm deep, in coarse or fine sand. Automatic misting watered the flats overnight. We then moved the flats to a growth chamber set to a cycle of 12 h of 18 °C light and 12 h of 13 °C darkness, checking seedling emergence daily until no new seedlings emerged. We analysed emergence on Day 9 (when emergence had ceased) with logistic regression and a logit-link function, with categorical factors species, depth and texture, plus all interactions. We dropped terms from the full model until finding one with minimal AIC_c. Interaction terms involving species estimate niche differences.

In a second experiment, we imposed drought on *xantiana* and *speciosa* seedlings transplanted into two distinct textures of calcined clay, scoring survival. Seeds came from five randomly selected maternal families of each species from Mill Creek and Site 63 (15 seeds per family). We scattered seeds on fine vermiculite in

nursery flats, covered them with plastic domes after watering and placed them in a growth chamber as above. After 2 weeks, we moved flats to a greenhouse (daytime temperatures 24 \pm 3 °C, night-time temperatures at 15 \pm 3 °C; daytime light supplemented with metal-halide lamps; pests managed with bio-control), watering daily. We fertilized seedlings once with 150 mL per cell of Jack’s Classic 20:20:20 with Micronutrients (JR Peters Inc., Allentown, PA, USA), 0.34 g L⁻¹, 2 weeks after sowing. Two weeks later we transplanted seedlings into ‘Deep Pots’ (top diameter 5 cm, height 25 cm; Stuewe and Sons, Tangent, OR, USA), lined with cheesecloth, filled with calcined clay (Turface MVP, Profile Products, Buffalo Grove, IL, USA) with 8 treatments (2 species \times 2 sites \times 2 soil textures) and 10 replicates, organized in a checkerboard design. The coarse substrate consisted of unmodified fritted clay (59 % particles > 200 μm and 41 % particles 1000–2000 μm ; estimated as for field soils). The fine substrate contained 90 % unmodified Turface plus 10 % (v:v) Turface that had been ground in batches in an electric coffee grinder, creating a substrate we found (with sieve analysis, as above) to consist of 79 % particles > 1000 μm , 11 % particles 500–1000 μm , 4 % particles 250–500 μm , 4 % particles 106–250 μm and 2 % particles 53–106 μm .

After transplanting seedlings, we watered each pot to saturation daily. Irrigation ceased 20 days after transplanting, after which water potential declined faster in the finer substrate [see Supporting Information—Section S1]. We analysed survivorship 17 days after irrigation ceased with χ^2 analysis. Species identification errors among seeds from Site 63 (see above) modified sample sizes to 13 *speciosa* individuals in each treatment, and to 25 and 28 *xantiana* individuals in coarse and fine substrate, respectively.

Competitive abilities

To estimate intra- and interspecific competition coefficients in coarse and fine substrates, we employed a response surface design, varying species’ densities and frequencies (Inouye 2001). Emulating a similar experiment (Thompson et al. 2015), we assigned plants of each species to one of three densities: 2, 4 and 6 per 12.5 \times 12.5 \times 12 cm plastic pot. In other words, pots designated for a single species had 2, 4 or 6 plants in each, while pots designated for both species had six target combinations of densities and species frequencies (2 plants of each species; 2 plants of one and 4 of the other [and the reverse]; and 2 plants of one and 6 of the other [and the reverse]; see Supporting Information—Section S2). In pots containing both species, we positioned plants to ensure that an individual of one species neighbored an individual of the other.

To launch the experiment, we prepared seedlings to transplant into pots. The seed source was bulked seed of 20 maternal families from all the field sites except Site 22 [see Supporting Information—Fig. S1]. We used the same germination protocol and environmental setting as above, this time giving seedlings an additional week in the greenhouse before transplanting. We transferred seedlings into pots filled with coarse- or fine-textured substrate. In this experiment, the fine-textured substrate consisted of a mixture of 12.5 % (by weight) 45–90 μm glass sandblasting beads (Potter's Industries, Valley Forge, PA, USA), 43.75 % Turface MVP and 43.75 % Pro-Mix PGX potting soil (Hummert International, Earth City, MO, USA). The coarse-textured treatment was identical except that the glass beads were 212–300 μm . These choices mimicked differences in fine-sand fraction found in field soils, though other substrate constituents (e.g. organic matter content) differed from them. Substrates with smaller glass particles exhibited faster water potential declines during drought [see Supporting Information—Section S2]. We watered the plants every 2 days for the first 4 weeks after transplanting. Afterwards, until harvest, we attempted to induce water stress by irrigating when ~50 % of plants were wilting.

We varied the positions of treatment replicates in space and time to distribute environmental variation. We set out the 96 pots on a single greenhouse bench in four sets of 24, each containing one replicate from the 24 treatment combinations. After an initial random assignment of positions within blocks, we rotated the locations of the pots in each block systematically, every week thereafter.

We measured performance as per capita shoot biomass 11 weeks after sowing. To estimate shoot biomass, we harvested plants by cutting from the point where they breached the soil surface, ignoring fallen leaves. At harvest, many individuals of both species had well-developed flower buds, but none had begun to flower. We put individuals of the same species from the same pot into separate envelopes, oven drying them at 70 °C for 48 h. We estimated for each pot the per capita shoot biomass of each species by dividing by that species' density. There was no mortality.

Due to the previously mentioned seed collection errors at Site 63, species densities and frequencies deviated slightly from the intended design [see Supporting Information—Section S2]. Fifteen of 96 pots contained a frequency that was slightly off-target (e.g. two of four pots intended to contain two *speciosa* and four *xantiana* actually contained three individuals of each). As the regression-based method (see below) is robust to such modestly unbalanced data, pots with mistaken identities were reclassified correctly and kept in the analysis.

To estimate absolute intra- and interspecific competition coefficients for each species in each soil texture, we employed linear regression of the (\log_{10}) reciprocal of each species' mean individual shoot biomass on number of neighbours of each species (Spitters et al. 1989; Thompson et al. 2015). The regression coefficients represent either intraspecific competition coefficients (if the response is to the number of neighbours of the same species) or interspecific competition coefficients (if the response is to the number of neighbours of the other species). Because we used the reciprocals of the performance variables as responses, positive coefficients represent declines in performance with density. As y -intercepts estimate individual biomass without neighbours, and as the units are \log_{10} reciprocal biomass, lower y -intercepts imply greater shoot biomass in the absence of competition.

Results

Distributions

At the scale of population presences on the landscape, the species showed contrasting associations with soil texture (Fig. 1). Across the range of increasing soil coarseness (i.e. a 7-fold range in declining proportion of fine sand), the predicted probability of *speciosa* presence declined approximately linearly, more than 5-fold ($\chi^2 = 6.83$, $P = 0.009$; deviance $r^2 = 0.10$; Fig. 1). Meanwhile, the probability of presence of *xantiana* increased steeply as soils became coarser, with a predicted presence of zero and no observed presences across the lower two-thirds of the range ($\chi^2 = 26.35$, $P < 0.000001$; deviance $r^2 = 0.42$; Fig. 1). The soil-texture range over which *speciosa* occurred overlapped with almost all of *xantiana*'s range, but *speciosa*'s range extended to much finer soils (Fig. 1). The species had similar prevalence (15 sites occupied by *speciosa*, 12 by *xantiana*) but co-occurred at only one site in this sample, a highly unlikely outcome ($P < 10^{-20}$) by Veech's (2013) method.

At sites where the species do occur together [see Supporting Information—Fig. S1], their small-scale distributions responded differently, with *xantiana* responding strongly to coarse soil texture and both species showing negative associations with the other. In grid cells where *speciosa* occurred, its density varied significantly among sites and correlated with bare ground and steep slopes but was independent of soil texture (Table 1, counts model). Despite the association of high counts with steep slopes, *speciosa* densities of 0 were more likely on steep slopes; the strongest predictor of the absence of *speciosa* was a high density of *xantiana* (Table 1, zero-inflation

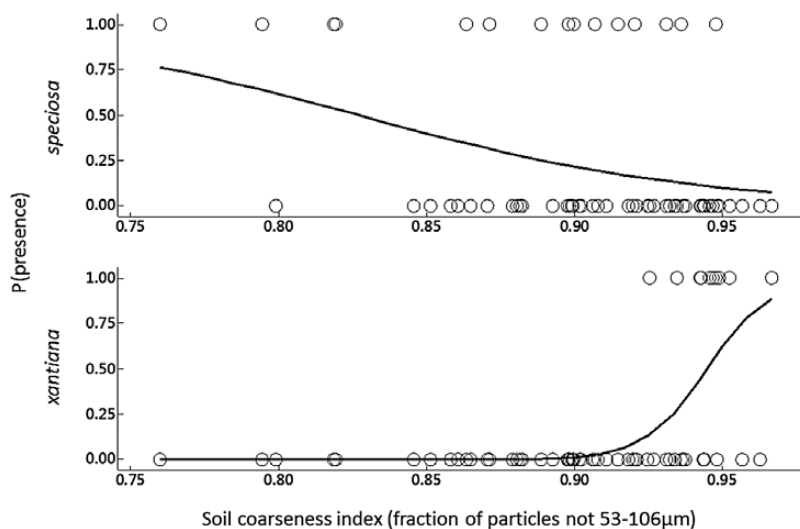


Figure 1. Scatterplots of presence and absence of two *Clarkia* species against an index of coarse soil texture, with fitted logit functions. $N = 66$. (Upper) *Clarkia speciosa* presence = $\exp(14.62 - 17.66[\text{soil coarseness index}]) / (1 + \exp(14.62 - 17.66[\text{soil coarseness index}]))$. (Lower) *Clarkia xantiana* presence = $\exp(-90.5 + 95.8[\text{soil coarseness index}]) / (1 + \exp(-90.5 + 95.8[\text{soil coarseness index}]))$.

Table 1. Zero-inflated negative binomial regression of density at sites where species co-occur. In the zero-inflation model, coefficients are with respect to the probability that density is 0. $N = 562$. IN, intercept; SI, site; SC, soil coarseness; BG, bare ground; SL, slope inclination; LA, linear azimuth; *xan*, *xantiana*; *spe*, *speciosa*.

	<i>speciosa</i> , count model			<i>speciosa</i> , zero-inflation model		
	Coeff ± SE	Z	P	Coeff ± SE	Z	P
IN	3.31 ± 3.75	0.88	0.38	-2.56 ± 6.35	-0.40	0.69
SI	-0.76 ± 0.20	-3.75	<0.0005	-0.21 ± 0.32	-0.67	0.51
SC	-1.22 ± 3.77	-0.33	0.74	0.006 ± 6.7	0.001	0.99
BG	0.96 ± 0.40	2.42	0.016	0.35 ± 0.73	0.47	0.28
SL	0.038 ± 0.014	2.81	0.005	0.089 ± 0.026	3.39	0.0007
LA	0.003 ± 0.002	1.25	0.21	-0.006 ± 0.005	-1.07	0.28
<i>xan</i>	0.025 ± 0.018	1.33	0.18	0.056 ± 0.013	4.29	<0.0005
	<i>xantiana</i> , count model			<i>xantiana</i> , zero-inflation model		
IN	-19.21 ± 3.84	-4.99	<0.0005	13.56 ± 5.44	2.49	0.013
SI	-0.66 ± 0.19	3.55	<0.0005	-0.111 ± 0.180	-0.62	0.53
SC	24.07 ± 3.95	6.09	<0.0005	-9.78 ± 5.71	1.71	0.087
BG	0.273 ± 0.197	1.39	0.16	-0.476 ± 0.283	-1.68	0.093
SL	0.014 ± 0.009	1.47	0.14	-0.121 ± 0.016	-7.56	<0.0005
LA	0.001 ± 0.004	0.37	0.72	-0.007 ± 0.003	-2.03	0.043
<i>spe</i>	-0.007 ± 0.002	-3.58	<0.0005	-0.007 ± 0.004	-1.57	0.117

model). Where *xantiana* was present, density varied among sites, increased with soil coarseness, and declined with *speciosa* density (Table 1, counts model). Densities of 0 in *xantiana* were more likely to occur on shallow, more southerly facing slopes, and there were hints of associations of zero counts with fine-textured

soil and highly covered ground (Table 1, zero-inflation model).

Responses to experimental variation in substrate texture and to drought

The emergence of seedlings from contrasting substrate textures and depths distinguished *speciosa* and

xantiana, with *xantiana* being superior at emerging from depth and from coarse substrate. The lowest AIC_c logistic regression model ($\Delta\text{AIC}_c = 3.63$) included the three main factors and the 2 two-way interactions involving depth. Emergence from the surface was similar between species (coefficient \pm SE: 0.34 ± 0.29 , $\chi_1^2 = 1.34$, $P = 0.25$) and independent of texture (0.17 ± 0.29 , $\chi_1^2 = 0.34$, $P = 0.56$). About 50 % of surface seeds produced seedlings (Fig. 2). Emergence from 0.5 cm depth, however, was significantly reduced overall (-1.86 ± 0.48 , $\chi_1^2 = 18.13$, $P < 0.0005$), occurring in only about 25 % of seeds (Fig. 2). In coarse substrate reduced emergence at depth occurred only in *speciosa*, a significant depth by species interaction (1.90 ± 0.55 , $\chi_1^2 = 13.55$, $P < 0.0005$). Emergence from depth was higher, overall, in the coarse substrate (depth by texture interaction: -1.63 ± 0.50 , $\chi_1^2 = 11.51$, $P < 0.001$).

Species, but not soil texture, affected seedling survival under drought, with *xantiana* experiencing much higher mortality. After 17 days' drought, 25 of 26 *speciosa* seedlings survived, while only 28 of 53 *xantiana* seedlings did ($\chi_1^2 = 18.27$, $P < 0.0001$). In *xantiana*, survivors were rather evenly divided between the coarse (14 survivors of 28) and fine substrates (11 survivors of 25).

Competitive abilities

Density effects on shoot biomass revealed highly significant intraspecific competition and interspecific competition. Across soil treatments, *xantiana* had 1.5–2.5 times the per capita effect on itself ($\alpha_{\text{xantiana,xantiana}}$ estimates of 0.093 and 0.086, in fine and coarse soil, respectively) and on *speciosa* ($\alpha_{\text{speciosa,xantiana}}$ estimates of 0.137 and 0.132) that *speciosa* had on itself ($\alpha_{\text{speciosa,speciosa}}$ values of 0.045 and 0.073) or on *xantiana* ($\alpha_{\text{xantiana,speciosa}}$ values of 0.057 and 0.056) (Table 2). While interspecific competition coefficients were very similar between soil textures, as

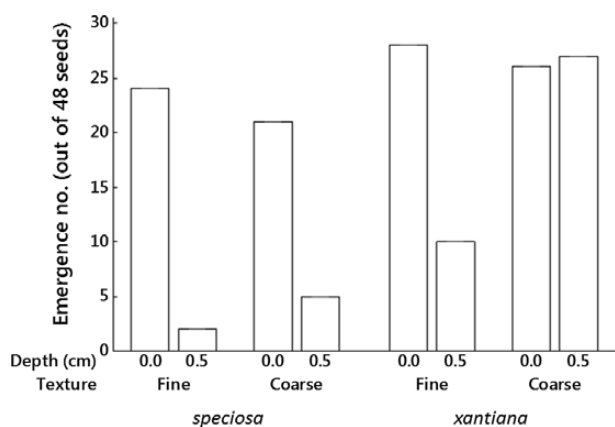


Figure 2. Counts of emerged seedlings 9 days after sowing *speciosa* and *xantiana* seeds, on the surface or buried 0.5 cm, in substrates of fine or coarse sand. $N = 48$ seeds per treatment combination.

were intraspecific coefficients in *xantiana*, *speciosa* suppressed its own performance about 60 % more strongly in coarse substrate than in fine ($\alpha_{\text{speciosa,speciosa}}$ of 0.073 versus 0.045) (Table 2). In both substrates, y-intercepts were higher in *speciosa* (-0.048 and -0.014 , in fine and coarse, respectively) than *xantiana* (-0.396 and -0.357) (Table 2), implying that *speciosa*'s shoot biomass would be considerably smaller than *xantiana*'s in the absence of competition. Calculating shoot biomass from the intercepts gives estimates for *speciosa* without competition as 0.72 g ($10^{0.144}$ g) and for *xantiana* without competition as 2.27 g ($10^{0.357}$ g). In fine soil, these estimates would be 0.89 and 2.49 g, respectively.

Discussion

We found that two annual plants in the same genus differed in field distributions along soil texture and other gradients and responded differently to experimental variation in soil texture, drought and intra- and interspecific density. As we detail below, our findings indicate that coexistence of these species is enabled by the niche differences they exhibit, as their competitive abilities predict competitive exclusion.

Distributions

The species' overlapping geographic ranges may reflect their shared phylogenetic and geographic history (Lewis and Lewis 1955), specialist pollinators (Moeller 2004), and possibly niche conservatism and habitat filtering in response to large-scale climate variation. Within the range, however, at the larger scale studied here, the species appear to co-occur less frequently than expected at random, and soil texture appears to be one niche axis along which they segregate. The data are consistent with the idea that the species differ in their probability of population establishment and/or persistence along soil-texture gradients, with fine soils strongly limiting *xantiana* and coarse soil more modestly limiting *speciosa*. Relative contributions of niche differences and competition to the rarity of co-occurrence at this scale cannot be determined by survey data alone (Ulrich et al. 2017). The data do suggest, however, that many sites suitable to one or the other species in terms of soil texture are unoccupied. Absence from apparently suitable sites may reflect species' other environmental tolerances, other species interactions, dispersal limitation and/or frequent chance extinction (Pulliam 2000).

Within sites where the species do co-occur, we also found correlational evidence of niche differences and/or competition. The small-scale distribution of *xantiana* clearly appears to reflect variation in water availability. This species' presence was more likely on steeper (and

Table 2. Regression analysis of species' $\log_{10}[1/(\text{per capita shoot biomass})]$ on neighbour densities, in fine and coarse substrates. Coefficients appear ± 1 SE.

Substrate	Species <i>i</i>	<i>N</i>	Intercept	Intraspecific competition coefficient (α_i)	Interspecific competition coefficient (α_j)	<i>r</i> ²
Fine	<i>speciosa</i>	39	-0.048 \pm .058 <i>t</i> = -0.83 NS	0.045 \pm 0.016 <i>t</i> = 2.92 <i>P</i> = 0.006	0.137 \pm 0.016 <i>t</i> = 8.83 <i>P</i> < 0.0005	0.686
	<i>xantiana</i>	35	-0.396 \pm 0.038 <i>t</i> = -10.41 <i>P</i> < 0.0005	0.093 \pm 0.011 <i>t</i> = 8.86 <i>P</i> < 0.0005	0.057 \pm 0.010 <i>t</i> = 5.89 <i>P</i> < 0.005	0.727
Coarse	<i>speciosa</i>	41	-0.144 \pm 0.063 <i>t</i> = -2.30 <i>P</i> < 0.027	0.073 \pm 0.170 <i>t</i> = 4.25 <i>P</i> < 0.0005	0.132 \pm 0.018 <i>t</i> = 7.45 <i>P</i> < 0.0005	0.608
	<i>xantiana</i>	35	-0.357 \pm 0.055 <i>t</i> = -6.45 <i>P</i> < 0.0005	0.086 \pm 0.016 <i>t</i> = 5.25 <i>P</i> < 0.0005	0.056 \pm 0.014 <i>t</i> = 4.01 <i>P</i> < 0.0005	0.503

more poleward-facing) slopes, and, where present, its densities were higher on coarser-textured soils, where soil and plant water potentials are higher (Eckhart et al. 2010). Though, where present, *speciosa*'s density increased with slope, its presence was associated with shallow slopes. Adjusting for physical environment responses both species showed evidence of negative associations with their congener, *speciosa* at the level of presence versus absence, *xantiana* both in presence and, where present, in abundance. Mutually negative effects suggest competition, subject to the caveat that we may have missed one or more critical environmental controls (such as plant–soil feedbacks; Brandt et al. 2013).

Fundamental niches

Experiments supported the hypothesis that contrasting individual responses to soil texture (and to water stress, its likely correlate) underlie some of the field distribution differences. One finding was that *speciosa* had distinctly lower emergence from seeds buried in coarse soil. Increased emergence from coarse soil may, in dry environments, be due in part to greater water availability in coarse soil (Zhu et al 2014), and/or partly due to enforced dormancy. A pilot study found that burial depths of 1, 2 and 3 cm completely suppress emergence of both species (M. R. Howland, unpubl. data). Evidence exists in other systems (e.g. *Ambrosia* [Asteraceae]; Guillemain and Chauvel 2011) that poor emergence of buried seeds helps explain distribution limits. In this system, investigating natural seed burial depths across soil-texture gradients might be informative, as might studies of seed dormancy and germination. The second

finding was that *speciosa* seedlings are superior at surviving drought. In the experiment, the finer substrate texture did not exacerbate drought mortality, but in the field *speciosa* would be expected to experience greater water stress in the fine-textured soils it sometimes occupies.

Competitive abilities

The study species differed substantially in competitive ability, with effects of soil texture that align with species' distributions and niche differences. Stable coexistence of two species requires that each can increase when rare (invade) when the other is common, which is expected when the suppressing effect of each species on itself is greater than the suppressing effects of the interspecific competitors (i.e. when intraspecific competition exceeds interspecific competition) (Chesson 2000). Taking the experimental findings at face value, *xantiana* would be predicted to invade *speciosa* in coarse soil ($\alpha_{\text{speciosa,speciosa}} > \alpha_{\text{xantiana,speciosa}}$; $0.073 > 0.056$) but not in fine soil ($\alpha_{\text{speciosa,speciosa}} < \alpha_{\text{xantiana,speciosa}}$; $0.045 < 0.057$), while *speciosa* should be unable to invade *xantiana* in either coarse ($\alpha_{\text{xantiana,xantiana}} < \alpha_{\text{speciosa,xantiana}}$; $0.086 < 0.132$) or fine soil ($\alpha_{\text{xantiana,xantiana}} < \alpha_{\text{speciosa,xantiana}}$; $0.093 < 0.137$). A critical caveat is that invasion also depends on species' intrinsic differences in vital rates (Chesson's [2000] 'fitness differences'), which are unknown (though *xantiana*'s greater shoot biomass may underlie its strong competitive effects as well as reflect higher intrinsic fitness). An experiment with artificial substrates and growing conditions, and which scored pre-reproductive shoot biomass as a

performance metric, is not a complete nor realistic model of competition in nature. Nevertheless, the competition experiment suggests the testable hypotheses that: (i) *xantiana* can competitively exclude *speciosa* from coarse-soiled patches; and (ii) each species is resistant to invasion in its ‘preferred’ soil. Collectively, our findings suggest that these species’ contrasting responses to spatial variation in soil texture make intraspecific competition more frequent than interspecific competition via spatial storage effects: patches of high performance for each species (Sears and Chesson 2007; Staples et al. 2016).

Our results suggest that the outcome of the competition in fine soil depends on which species becomes established in a patch first (founder control), with competitive exclusion of *speciosa* likely in patches with coarse soils. A field experiment comparing competitive abilities of two closely related species in the *Erythranthe guttata* complex (Phrymaceae) revealed a similar pattern, with founder control predicted in habitats intermediate in water availability between those where each species dominates (Peterson et al. 2013).

Conclusions

The present study uncovered contrasts between annual plant species’ distributions, fundamental niches and competitive abilities, mediated by variation in soil texture. In addition to showing that soil texture can affect species interactions and coexistence, these findings raise at least two questions. First, what traits and trait values confer adaptation to restricted ranges of soil texture? Some possibilities are likely, others less certain. Variation in the sensitivity of seedling emergence to texture—and associated burial depth—may follow from variable germination requirements for light and/or fluctuating temperatures experienced near soil surfaces, or from resource-based limits to the depth from which seedlings can emerge (Saatkamp et al. 2014). In seedlings and mature plants, it is likely that some soil-texture adaptations are familiar drought-tolerance adaptations, such as deep rooting, water-conserving leaf physiology, and resistance to leaf turgor loss or xylem cavitation (Kooyers 2015). Other traits, such as the architecture and activity of roots, might influence water uptake or anchorage in soils of different textures, but these functional relationships are less well understood (Hamer et al. 2016). A second question is whether adaptation to soil textures involves functional trade-offs that affect species coexistence, not just in the present case but also generally. We speculate that because fine-textured soils in arid lands limit growth partly by water stress, trade-offs between

growth potential and drought tolerance create spatial storage effects, similarly to how such trade-offs create temporal storage effects in communities of annuals with high year-to-year variation in climate (Angert et al. 2009).

Supporting Information

The following additional information is available in the online version of this article—

Table S1. Position and coarse soil texture index of 66 patches surveyed for the presence (1) and absence (0) of *Clarkia speciosa* ssp. *polyantha* (“*speciosa*”) and *C. xantiana* ssp. *xantiana* (“*xantiana*”).

Figure S1. Five sites at which *Clarkia speciosa* ssp. *polyantha* and *C. xantiana* ssp. *xantiana* co-occur in the lower Kern River drainage of California, USA. Inset at left shows location and N latitude and W longitude. Colors at right show elevations ranging from 500 (palest yellow) to 2500 m (white). The large body of water (black polygon) is Isabella Lake, a reservoir on the Kern River (black line).

Section S1. Descriptions and findings in support of experimental studies of fundamental niches.

Section S2. Descriptions and findings in support of experimental study of competitive abilities.

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Contributions by the Authors

V.M.E. conceived the overall research plan, assisted data collection, carried out the final data analyses and prepared the completed manuscript, tables, figures and supporting information files. M.R.H. designed, carried out the major portion and drafted text to communicate the research for the sections entitled, ‘Responses to experimental variation in substrate texture and to drought’ and ‘Fundamental niches’, along with associated supporting information. K.J., B.K.K. and D.M.M. designed, carried out the major portion and drafted text to communicate the research for the sections entitled, ‘Distributions’, along with associated supporting information. Y.Y. designed, carried out the major portion and drafted text to communicate research for the sections entitled, ‘Competitive abilities’, with associated supporting information. M.A.G. helped conceive the overall research plan and assisted the design and data

collection for ‘Distributions’ studies. All authors edited early manuscript drafts.

Conflicts of Interest

None declared.

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