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EXPERIMENTAL STUDIES OF ADAPTATION IN *CLARKIA XANTIANA*. II. FITNESS VARIATION ACROSS A SUBSPECIES BORDER

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Abstract.—Because the range boundary is the locale beyond which a taxon fails to persist, it provides a unique opportunity for studying the limits on adaptive evolution. Adaptive constraints on range expansion are perplexing in view of widespread ecotypic differentiation by habitat and region within a species' range (regional adaptation) and rapid evolutionary response to novel environments. In this study of two parapatric subspecies, *Clarkia xantiana* ssp. *xantiana* and *C. x.* ssp. *parviflora*, we compared the fitness of population transplants within their native region, in a non-native region within the native range, and in the non-native range to assess whether range expansion might be limited by a greater intensity of selection on colonists of a new range versus a new region within the range. The combined range of the two subspecies spans a west-to-east gradient of declining precipitation in the Sierra Nevada of California, with ssp. *xantiana* in the west being replaced by ssp. *parviflora* in the east. Both subspecies had significantly higher fitness in the native range (range adaptation), whereas regional adaptation was weak and was found only in the predominantly outcrossing ssp. *xantiana* but was absent in the inbreeding ssp. *parviflora*. Because selection intensity on transplants was much stronger in the non-native range relative to non-native regions, there is a larger adaptive barrier to range versus regional expansion. Three of five sequential fitness components accounted for regional and range adaptation, but only one of them, survivorship from germination to flowering, contributed to both. Flower number contributed to regional adaptation in ssp. *xantiana* and fruit set (number of fruits per flower) to range adaptation. Differential survivorship of the two taxa or regional populations of ssp. *xantiana* in non-native environments was attributable, in part, to biotic interactions, including competition, herbivory, and pollination. For example, low fruit set in ssp. *xantiana* in the east was likely due to the absence of its principal specialist bee pollinators in ssp. *parviflora*'s range. Thus, convergence on self-fertilization may be necessary for ssp. *xantiana* to invade ssp. *parviflora*'s range, but the evolution of outcrossing would not be required for ssp. *parviflora* to invade ssp. *xantiana*'s range.

Key words.—Fitness components, local adaptation, range boundary, range expansion, range versus regional adaptation, reciprocal transplant.

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A fundamental and long-standing problem in ecology and evolutionary biology concerns the determinants of species' distribution and abundance (Darwin 1859; Wallace 1869; Mayr 1963; Andrewartha and Birch 1954; MacArthur 1972). Central to this problem is an understanding of the forces that determine the location and limits to geographic ranges (Mayr 1963; Brown and Lomolino 1998; Gaston 2003; Holt 2003). Over the short term, range limits do change slightly as peripheral populations go extinct or new ones establish (Gaston 2003). Range boundaries also respond to amelioration of severely limiting environmental factors. Examples include the northward migration of species following the retreat of Pleistocene ice sheets (Davis 1986; Webb and Bartlein 1992) and present-day shifts of species to the north and to higher elevations with rising global temperatures (Parmesan and Yohe 2003; Root et al. 2003). Although these range shifts may occur primarily through dispersal as organisms track permissible environments (Webb and Bartlein 1992), they also may involve evolutionary adaptation to abiotic and biotic changes unrelated to climate (e.g., photoperiod; Geber and Dawson 1993; Travis and Futuyma 1993; Davis and Shaw 2001). Dispersal barriers clearly have played a key role in restricting species' distributions, because the removal of barriers, as in the introduction of non-native species, sometimes leads to spectacular range expansion, which may be enhanced by adaptive evolution (Elton 1958; Williamson and Fitter 1996; Sakai et al. 2001; Lee 2002). Excepting these sorts of boundary shifts, however, why do we not see more frequent and steady range expansions of native species on micro-evolutionary time scales?

The question of what limits adaptive evolution to an expanded range in native species is a puzzle in view of the fact that contemporary populations can evolve rapidly when exposed to novel environments (Bradshaw 1991; Reznick et al. 1997; Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Lee 2002) and in the face of widespread evidence of ecotypic differentiation of populations to different habitats or regions within a species' native range (Turesson 1922; Travis and Futuyma 1993). In the rest of the paper we refer to ecotypic differentiation within a species' range as *regional adaptation*.

Recent theory on limits to range and regional expansion into new habitats identifies a number of constraints (Hoffmann and Blows 1994; Holt 2003) imposed by the shape of the environmental gradient at range and habitat boundaries (Gomulkiewicz and Holt 1995), genetic variation (Gomulkiewicz and Holt 1995; Kirkpatrick and Barton 1997; Kawecki 2000), phenotypic response to novel environments (Conover and Schultz 1995; Eckhart et al. 2004), demographic factors (Kawecki 1995; Keitt et al. 2001), and gene flow (Kawecki 1995; Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997; Holt et al. 2002). In particular, steep environmental gradients resulting in severe fitness reductions across boundaries can impede adaptive evolution as can the absence of appropriate genetic variation for favorable traits or trait combinations (Antonovics 1976; Bradshaw 1991; Hoffmann and

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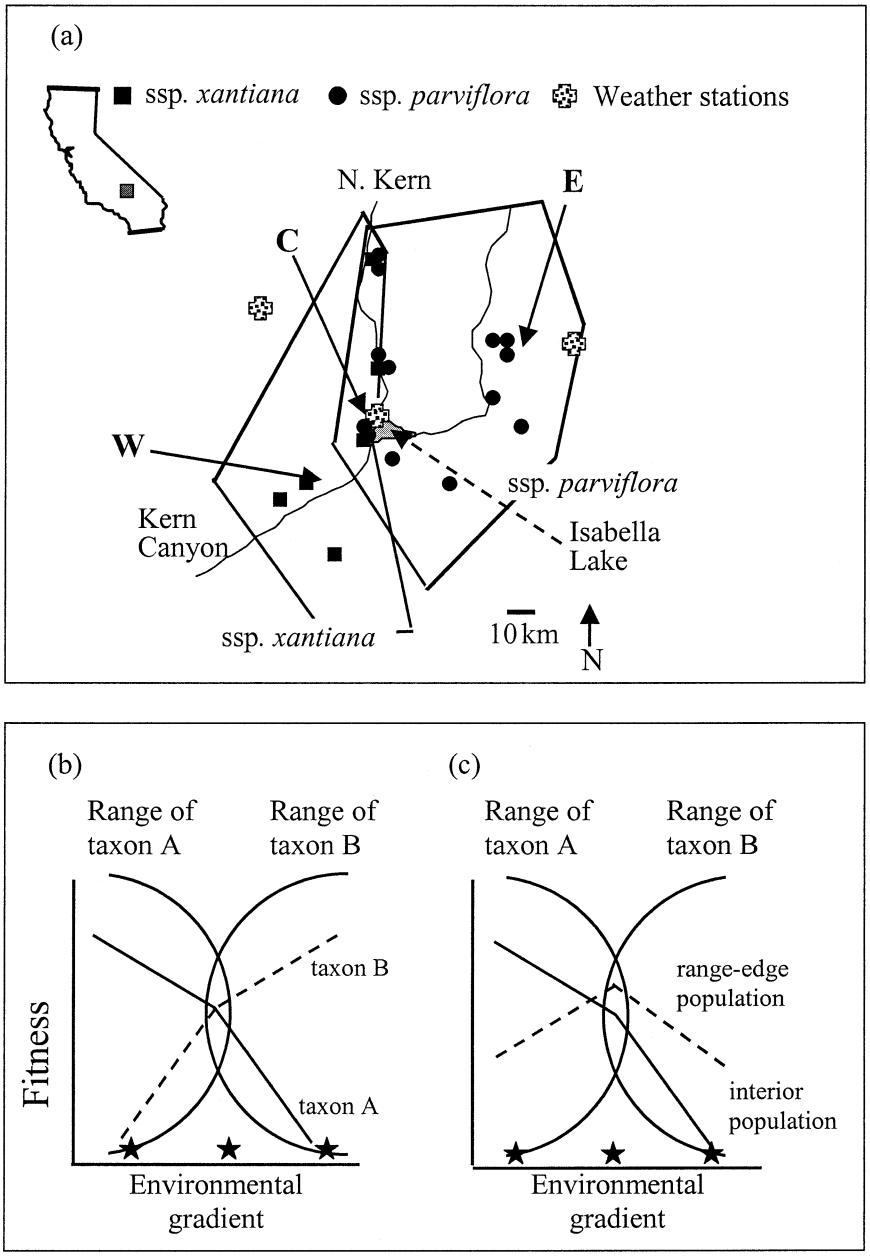

FIG. 1. (a) Range and population sources of the two subspecies of *Clarkia xantiana*; stippled crosses show locations of weather stations (see Materials and Methods). Garden sites are identified as W, western; C, contact-zone; and E, eastern. (b) Expected pattern of fitness for two taxa, A (broken line) and B (solid line), with parapatric geographic distributions (denoted by arcs) in a reciprocal transplant experiment of each taxon's populations into sites (stars) in each other's range and in the shared contact zone. (c) Expected pattern of fitness for populations of taxon B from interior and border regions that are transplanted reciprocally to interior and border regions and to a site in taxon A's exclusive range. The expected fitness pattern for regional populations of taxon A would be a mirror image of those for taxon B.

Parsons 1991). Adaptive evolution can also be retarded by countergradient variation (Antonovics 1976; Eckhart et al. 2004) wherein phenotypic plasticity to novel environments results in trait expression that runs counter to the direction of selection in those environments (Berven and Gill 1983; Conover and Schultz 1995; Eckhart et al. 2004).

In this study, we focus on limits to adaptive evolution caused by severe fitness reductions (i.e., strong intensity of selection) in non-native environments and compare the relative strengths of range versus regional adaptation in two sister subspecies of *Clarkia xantiana* (Onagraceae) that share a common range boundary in the southern Sierra Nevada of California (Fig. 1a; Lewis and Lewis 1955; Eckhart and Geber 1999). Subspecies *xantiana* grows west of the boundary and is replaced by ssp. *parviflora* in the east. The shared range boundary appears to have been stable over the last century (about 100 generations in this annual plant; Eastwood 1903; Lewis and Raven 1992; Eckhart and Geber 1999). In

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the zone of contact, plants of the two subspecies frequently grow intermixed or within a few meters of each other, but maintain distinct phenotypes. Phenotypically hybrid individuals have been noted on occasion in contiguous populations and there is little laboratory evidence of postmating barriers to hybridization (Moore and Lewis 1965; A. Senft and M. A. Geber, unpubl. data). Opportunities for hybridization likely are limited nevertheless by subspecies differences in breeding system and flowering time. For example, in this study, where three sets of contiguous populations of both taxa from the contact zone were grown at the common range boundary, less than 5% of ssp. *parviflora* plants were still flowering when ssp. *xantiana* started flowering.

The species' range spans a west-to-east gradient of declining precipitation (see below) that is reflected in changes in the dominant vegetation from oak-pine grassland in the west to a mixed flora from the Mojave Desert and the Intermountain West in the east. Biotic interactions with pollinators (Fausto et al. 2001; Moeller 2003, 2005a) and herbivores also change along the gradient (see Discussion). For example, the principal pollinators of ssp. *xantian*a are a group of specialist solitary bees that use only *Clarkia* pollen to provision their nests (MacSwain et al. 1973; Moeller 2005b). These specialist bees are absent from ssp. *parviflora*'s exclusive range (Fausto et al. 2001; Moeller 2003).

We sought evidence of limits to range expansion by comparing the fitness of transplants within versus beyond the native range. Range adaptation would be manifested by crossing fitness reaction norms across the shared boundary (Fig. 1b). Regional adaptation within a taxon was examined through fitness comparisons of transplants between regions of the native range; if present, it would show up as crossing reaction norms when populations from interior and border regions are transplanted reciprocally (Fig. 1c). Furthermore, if range expansion is a simple extension of regional adaptation requiring only incremental adaptation of border populations to adjacent environments, we expect range-edge populations of one taxon to have higher fitness than interior populations when transplanted into the non-native range (Fig. 1b versus Fig. 1c) and both forms of adaptation to involve the evolution of similar traits. We measured multiplicative fitness components and cumulative lifetime fitness in all transplants, because the contribution of different fitness components (e.g., survivorship, mating success, fecundity) to lifetime fitness can be helpful in pinpointing the traits and functional mechanisms that underlie adaptation (Kingsolver and Schemske 1991; Geber and Griffin 2003).

We asked three questions: (1) Does each subspecies have higher lifetime fitness and outperform the other in its native range (Fig. 1b)? (2) Do populations within subspecies show regional adaptation, and are range-edge populations better adapted than interior populations to the non-native range (Fig. 1c)? (3) If there is range or regional adaptation, do all fitness components exhibit crossing reaction norms (Fig. 1) or only some of them, and do the same components contribute to both forms of adaptation?

Materials and Methods

Transplant Gardens and Climate Gradient

Reciprocal transplants were conducted at three 900 m^2 common gardens distributed from west to east across the species' range (Fig. 1a). The western transplant site (35°32′N, 118°38′W, 750 m elevation) was in ssp. *xantiana*'s exclusive range, the eastern site (35°46′N 118°04′W, 1350 m) in ssp. *parviflora*'s exclusive range, and the contact-zone site (35°38′N 118°30′W, 800 m) in the zone of overlap. The contact-zone site is 17 km from the western site and 42 km from the eastern site.

On average, 95% of annual precipitation falls between November 1 and June 1 in the region and coincides with *C. xantiana*'s growing season. Rainfall data from three weather stations located at similar longitude and elevation as the transplant sites (Fig. 1a; west: Tule River, Tulare County, 25-year record; contact zone: Isabella Dam, Kern Co., 19-year record, Hawaii Canyon, Inyo Co., 53-year record; National Climatic Data Center [http://www.ncdc.noaa.gov] and the California Department of Water Resources [http://cdec.water.ca.gov]) show that average October to June precipitation declines from west to east across the species' range with the contact-zone transplant site receiving 54–64% (259 mm) and the eastern site 11–34% (88 mm) of the rainfall at the western site (482 mm). In addition, precipitation differed twofold between the two years of our study (see below), with 1997–1998 being exceptionally wet (associated with an El Niño event; west: 883 mm; contact zone: 561 mm; east: 161 mm) and 1998–1999 much drier (west: 424 mm; contact-zone: 259 mm; east: 45 mm). Total precipitation was twice the average for the region in 1997–1998, but was near to, or slightly less than the average in 1998–1999.

Experimental Design

A full account of the experimental design can be found in Eckhart et al. (2004) and is summarized here. A bulked sample of seed from 50–150 maternal plants was collected from each of six populations of ssp. *xantiana* and 12 populations of ssp. *parviflora* the summer before transplanting to the field. Half of the populations of each taxon came from locations in the zone of contact where the subspecies grow in close proximity (Fig. 1a); they are referred to as *range-edge* populations in the remainder of the paper. The other populations came from each subspecies' exclusive range (west for ssp. *xantiana* and east for ssp. *parviflora*; Fig. 1a).

Seeds from each population were sown at the three gardens in October 1997 (Fig. 1a) and again in 1998, before cool-season rains began, in a randomized-complete block design. In each of 10 blocks, seeds were planted into 144 square cells (4 cm^2) in plastic diffusion screens (i.e., flat lattices with square openings, manufactured for fluorescent light fixtures) affixed to the soil surface. Natural vegetation was left undisturbed.

Each population was assigned randomly to eight cells per block, with eight seeds per cell (640 seeds per population and 11,520 seeds per transplant site per year). We planted eight seeds per cell to have sufficient numbers of cells with seedlings. When multiple seeds germinated in a cell, seedling density exceeded natural densities; we therefore thinned seedlings haphazardly down to one per cell in March, after germination was complete. We make the assumption that the fitness of the remaining seedling in a cell is a good approx-

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TABLE 1. Analyses of range adaptation in sequential fitness components and lifetime fitness for the two subspecies of *Clarkia xantiana*. Column entries show: G^2 values for survivorship, F ratios for fixed effects and statistical significance of random effects in remaining fitness measures (df, degrees of freedom for G2 tests, for numerator of F tests, and tests of random effects; df_D, denominator df in F tests). ns, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$. Bold values for fixed effects are statistically significant at $P < 0.05$ after Bonferroni correction. Note that large changes in denominator df between fitness components result from decreasing sample sizes for later fitness components and the unbalanced nature of our data.

Source	df	df_D	Germination	Survivorship	df_D	Flower number	df_D	Fruit set	df_D	Seed set	df_D	Fitness
Site	2	62	**75.8******	**601.3******	93	**6.7****	46	5.0*	96	**7.9*****	25	3.7*
Year	1	62	**299.6******	**436.9******	172	**16.4*****	88	0.7	128	5.4*	25	**39.0******
Subspecies	1	16	2.2	0.5	279	**12.4*****	668	**9.1****	135	**17.6******	16	2.3
Site × year	2	61	**18.8******	**27.1*****	93	0.8	46	1.2	96	0.1	25	2.8
Site × ssp.	2	5335	**8.5*****	**133.9******	1203	3.7*	684	2.3	436	3.8*	4131	**50.1******
Year × ssp.	1	5347	**3.0***	0.0	1062	2.9	668	0.8	397	1.4	4131	2.2
Site × year × ssp.	2	5334	**6.8****	2.9	1202	0.6	684	3.7*	439	2.0	4131	**42.3******
Block (site, year)			****	—		****		ns		ns		**
Population (ssp.)			*	—		ns		ns		ns		ns

imation of any seedling emerging in the cell, when grown at natural densities.

Data were collected monthly from early December to March, and then continuously from April until June or July. At flowering, all flowers in five randomly chosen blocks per transplant site were hand pollinated with intra-subspecific pollen from nearby natural populations. These blocks are excluded from analyses of lifetime fitness and all fitness components that could be affected by supplemental pollination (components 4 and 5 below), because our interest in this paper is to evaluate individual fitness in the natural biotic environment. We consider the role of pollinators as selective agents on floral traits and mating system in another paper (M. A. Geber and V. M. Eckhart, unpubl. data).

We recorded the following sequential fitness components: (1) germination (the fraction of seeds that germinated in a cell); (2) survival to flowering (0 or 1), given successful germination; (3) flower number per surviving plant; (4) fruit set (i.e., number of fruits per flower on flowering plants); and (5) seed set (i.e., number of seeds per fruit on plants with fruit). The actual number of germinants in a cell was calculated as eight times germination (component 1) and average lifetime fitness through female function (i.e., seeds produced per seed planted) was calculated as the number of germinants times the product of the remaining four fitness components.

For strictly self-pollinating taxa, lifetime fitness through female function equals lifetime fitness through both sex functions. However, for outcrossing taxa our estimate of lifetime fitness ignores fitness through male function, unless individuals have equal fitness through both sex functions. Still, in the absence of a seed bank, average lifetime seed production in an annual is equivalent to the annual rate of population growth, and hence is relevant to projecting a population's persistence over time.

Analysis of Range and Regional Adaptation

We performed three sets of analyses, one on the combined data from both subspecies, and separate analyses on the data from each subspecies. In the first analysis, we tested for the effects of transplant site, year, subspecies, and interactions on lifetime fitness and fitness components. In the separate analyses, we used the regional origin of the populations, (i.e., contact or western and eastern allopatric zones of the two subspecies, respectively) as a factor in place of subspecies. We dropped the three-way interaction between site, year, and region in analyses of fitness components 3–5 because of small sample sizes of flowering plants. Range and regional adaptation were revealed by statistically significant interactions involving site and subspecies or region.

Survivorship was analyzed with a log-linear model (Littell et al. 1991; GENMOD procedure in SAS; SAS Institute 2000). Fitness components measured on a continuous scale were analyzed by mixed model analysis of variance (Littell et al. 1996; MIXED procedure in SAS 2000) with the random effect of block nested within transplant site and year and population nested within subspecies or region, using Satterthwaite's approximation for degrees of freedom (Satterthwaite 1946). The MIXED procedure provides traditional type III F tests for fixed effect but computes restricted maximum likelihood estimates of random effects. The statistical significance of random effects is tested by comparing the likelihood ratio of models with versus without the random effect (Littell et al. 1996).

Germination and fruit set were arcsine square-root transformed, and flower number and (lifetime fitness + 1) were $\log_e$ transformed prior to analysis. The effects of independent variables and their interactions on fitness components and fitness were considered statistically significant when $P < 0.05$). We also report statistically significant P-values when the Bonferroni procedure is applied to the tests (Rice 1989; but see Moran 2003). Where analyses indicated statistically significant main effects or interactions, preplanned contrasts were performed to evaluate the source of these effects.

RESULTS

Year and Transplant Site Effects on Fitness

Lifetime fitness and all but one fitness component were significantly higher in the wet (1997–1998) than in the dry (1998–1999) year (Table 1, Fig. 2). Lifetime fitness was 30-fold higher in the wet year (1.7 versus 0.06; Fig. 2a, note log scale of y-axis) and only in this year and in the native range did a subspecies' lifetime fitness exceed one. There was a two- to fourfold difference in germination (0.45 versus

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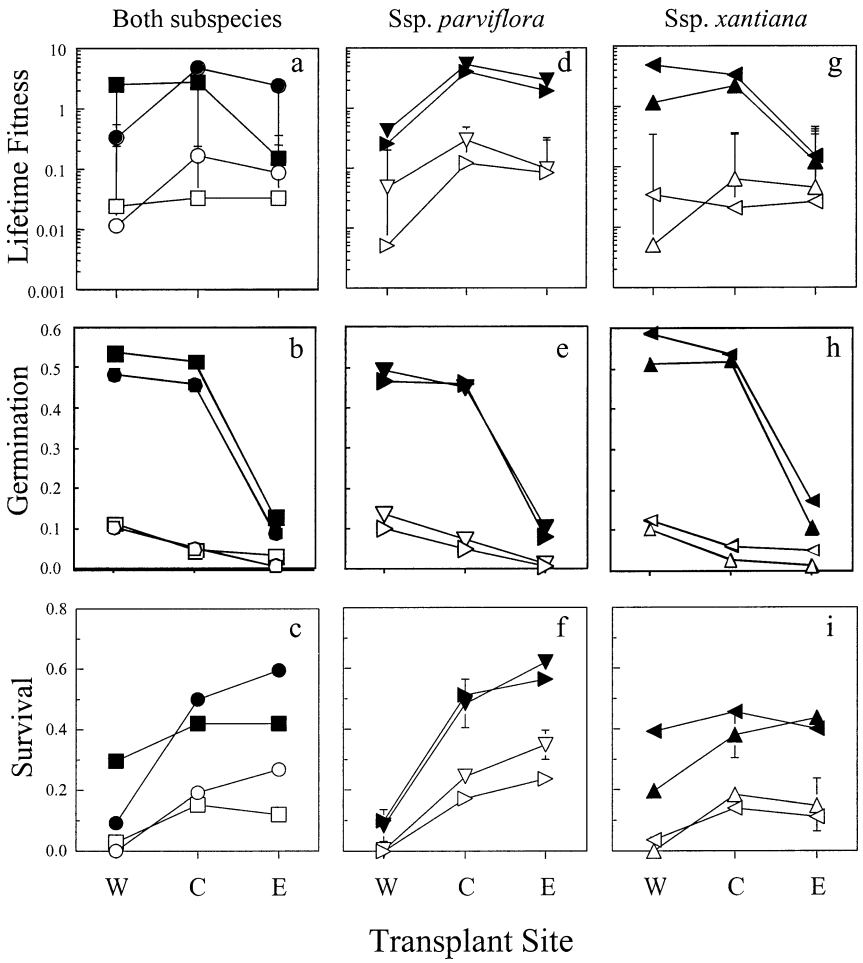

FIG. 2. Least-square means and standard errors of lifetime fitness and early-life fitness components for: (a, b, c) *Clarkia xantiana* ssp. *parviflora* (circles) and ssp. *xantiana* (squares); (d, e, f) range-edge (▽) and eastern (▷) populations of ssp. *parviflora*; and (g, h, i) range-edge (◁) and western (△) of ssp. *xantiana*, transplanted to the western (W), contact-zone (C), and eastern (E) garden sites in 1997–1998 (filled symbols) and 1998–1999 (open symbols). Note that some standard errors are smaller than symbols.

0.11, Fig. 2b), survival (0.39 versus 0.13, Fig. 2c), and flower number (2.4 versus 1.3, Fig. 3a) between years. By contrast, fruit and seed set did not differ between years (Table 1).

Most fitness components differed significantly among transplant sites, but no one site was best for all components (Table 1). Across the two years, germination was two to four times lower in the east relative to the other sites (west versus contact zone versus east: 0.40 versus 0.35 versus 0.21, Fig. 2b). By contrast, survival was three times lower in the west than at other transplant sites (west versus contact zone versus east: 0.10 versus 0.38 versus 0.43, Fig. 2c). Flower number and seed set were significantly lower at the contact-zone site (flower number, west versus contact zone versus east: 2.3 versus 1.3 versus 1.9, Fig. 3a; seeds per fruit: 26.6 versus 10.7 versus 21.0, Fig. 3c).

Range Adaptation in Clarkia xantiana

There was strong evidence of range adaptation in the two subspecies. Each subspecies outperformed the other in its exclusive range (Table 1). In the wet year, ssp. *xantiana* had higher lifetime fitness (2.50 seeds per planted seed) than ssp. *parviflora* (0.34) at the western transplant site ($t_{1,105} = 7.7$, $P < 0.0001$), whereas at the contact-zone and eastern sites, ssp. *parviflora* had higher fitness than ssp. *xantiana* (ssp. *xantiana* versus ssp. *parviflora* at contact zone: 2.89 versus 4.21, $t_{1,106} = -3.5$, $P < 0.001$; eastern site: 0.15 versus 2.38, $F_{1,138} = -8.1$, $P < 0.0001$; Fig 2a). In the wet year, ssp. *xantiana*'s fitness was significantly lower in the east relative to other transplant sites (west versus east: $t_{1,33} = -4.0$, $P < 0.0005$; contact zone versus east: $t_{1,33} = -4.2$, $P < 0.0005$), whereas ssp. *parviflora*'s fitness was significantly lower in the west relative to other sites (west versus contact zone in 1997–1998: $t_{1,26} = -5.5$, $P < 0.0001$; west versus contact zone: $t_{1,27} = -3.5$, $P < 0.005$). There were similar, but nonsignificant, differences in subspecies' fitness across transplant sites in the dry year (Fig. 2a).

Statistically significant range adaptation of each subspecies was reflected in only two fitness components—survival to flowering in both years (Table 1, Fig. 2c) and fruit set in the wet year (Table 1, Fig. 3b). Although survivorship did not differ overall between the subspecies across transplant sites and years (0.28 in ssp. *parviflora* versus 0.27 in ssp. *xantiana*), each subspecies survived better than the other in its exclusive range (ssp. *xantiana* versus *parviflora* at western

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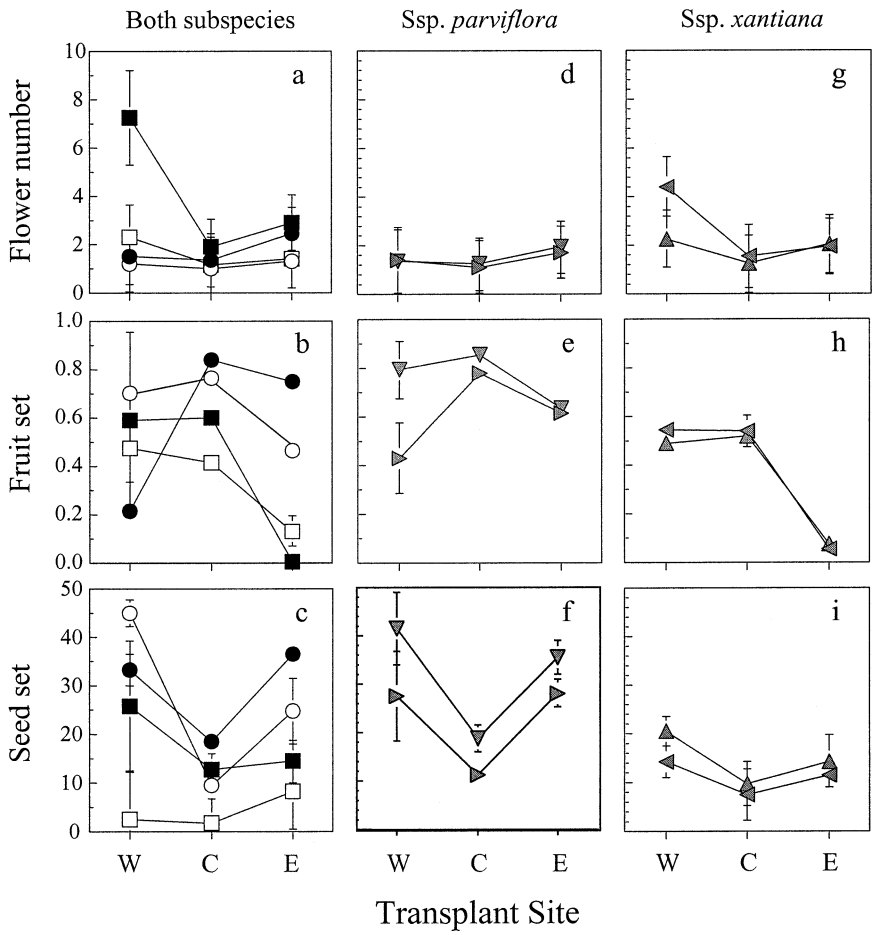

FIG. 3. Least-square means and standard errors of reproductive fitness components at the three transplant sites for the two subspecies of *Clarkia xantiana* in 1997–1998 and 1998–1999 (a, b, c; symbols as in Fig. 2); and for regional populations of ssp. *parviflora* (d, e, f) and ssp. *xantiana* (g, h, i), averaged across the years (gray symbols). Note that some standard errors are smaller than symbols.

site: 0.30 versus 0.09, $G^2 = 95.2$, $P < 0.0001$; at eastern site: 0.60 versus 0.42, $G^2 = 34.4$, $P < 0.0001$). For both subspecies, survivorship was lowest in the west (west versus contact-zone: $G^2 = 297.0$, $P < 0.0001$; west versus east: $G^2 = 247.9$, $P < 0.0001$; contact zone versus west: $G^2 = 1.9$, $P < 0.2$).

Average fruit set across sites and years was more than twice as high in ssp. *parviflora* (0.73) than in ssp. *xantiana* (0.33), but in the wet year, each subspecies had higher fruit set in its exclusive range (Fig. 3b). At the western transplant site in the wet year, ssp. *xantiana* produced more fruits per flower than ssp. *parviflora* (ssp. *xantiana* versus ssp. *parviflora*: 0.59 versus 0.22, $t_{1,723} = 3.1$, $P < 0.002$), and ssp. *parviflora* had higher fruit set than ssp. *xantiana* at the eastern site (ssp. *xantiana* versus ssp. *parviflora* at eastern site: 0.003 versus 0.75, $t_{1,710} = -8.9$, $P < 0.0001$). Also in the wet year, ssp. *xantiana*'s fruit set was lower in the east than at other sites (west versus east: $t_{1,32} = 4.4$, $P < 0.0001$; contact zone versus east: $t_{1,26} = 4.8$, $P < 0.0001$). In ssp. *parviflora*, fruit set was lowest in the west (west versus contact zone: $t_{1,19} = -4.1$, $P < 0.001$; west versus east: $t_{1,21} = -3.4$, $P < 0.005$). There was a similar, but nonsignificant, reversal in fruit set between subspecies across sites in the dry year (Fig. 3b).

Three fitness components were consistently higher in one subspecies or the other (Table 1; Figs. 2, 3). In the wet year, germination was higher in ssp. *xantiana* than in ssp. *parviflora* (0.46 versus 0.45, Fig. 2b). Flower number was always higher in ssp. *xantiana* than in ssp. *parviflora* (flower number: 2.3 versus 1.4, Figs. 3a). By contrast, seed set was always higher in ssp. *parviflora* than in ssp. *xantiana* (seed set in ssp. *xantiana* versus ssp. *parviflora*: 10.9 versus 27.9, Fig. 3c). The magnitude of subspecies' differences in many of these fitness components differed between transplant sites, years or both (Table 1).

Regional Adaptation in Clarkia xantiana

There was no evidence of regional adaptation in ssp. *parviflora* in any fitness measure (Table 2, Figs. 2d,e,f and 3d,e,f). Seed set, the one fitness component that differed between regional populations, was higher in range-edge (31.9) than eastern populations (22.3, Fig. 3f). In contrast to ssp. *parviflora*, there was some evidence of regional adaptation in ssp. *xantiana* (Table 2B). In the wet year, western populations had higher lifetime fitness at the western transplant site than range-edge populations (western versus range-edge populations at western transplant site in 1997–1998: 4.75 seeds per planted seed versus 1.14, $t_{1,1361} = 5.6$, $P < 0.0001$;

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TABLE 2. Analyses of regional adaptation in sequential fitness components and lifetime fitness in (A) *Clarkia xantiana* ssp. *parviflora* and (B) *C. xantiana* ssp. *xantiana*. Column entries show: G^2 values for survivorship, F ratios for fixed effects and statistical significance of random effects in remaining fitness measures (df is degrees of freedom for G^2 tests, for numerator of F tests; df_D is the denominator df in F tests). ns, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$. Bold values for fixed effects are statistically significant at $P < 0.05$ after Bonferroni correction. See Table 1 concerning changes in denominator df between fitness components.

Source	df	df_D	Germination	Survivorship	df_D	Flower number	df_D	Fruit set	df_D	Seed set	df_D	Fitness
(A) ssp. *parviflora*												
Site	2	72	**84.4******	**698.0******	89	**12.7******	39	1.2	58	**14.1******	25	**10.9*****
Year	1	83	**233.6******	**221.9******	351	5.1*	152	0.5	164	0.9	26	**47.7******
Region	1	15	1.2	0.4	67	0.5	476	2.2	346	**6.9***	16	2.0
Site × year	2	71	**11.7******	**18.8*****	89	1.1	39	1.1	59	0.3	25	**7.1****
Site × region	2	3458	0.7	2.7	939	1.3	499	1.5	353	0.5	2739	0.2
Year × region	1	3175	1.9	4.3*	951	4.9*	444	1.0	322	1.1	919	2.8
Site × year × region	2	3457	2.1	2.4		—		—		—	2739	0.4
Block (site, year)			****	—		*		ns		ns		**
Population (ssp.)			*	—		ns		ns		ns		ns
(B) ssp. *xantiana*												
Site	2	71	**60.0******	**37.0*****	79	**6.0****	79	**8.3*****	125	2.9	25	3.3
Year	1	81	**306.3******	**203.8******	103	**19.4******	111	0.1	125	7.3**	25	**16.8*****
Region	1	5	1.3	**10.4****	499	4.5*	206	0.0	125	0.9	1361	**8.3****
Site × year	2	71	**21.7******	**15.2****	77	1.6	76	1.7	125	0.9	25	3.3
Site × region	2	1847	3.4*	**16.2****	474	**6.9****	206	0.1	125	0.6	1361	**4.0***
Year × region	1	1818	0.5	0.6	499	0.0	206	0.7	125	3.5	1361	**8.9****
Site × year × region	2	1847	2.4	3.8		—		—		—	1361	3.1*
Block (site, year)			****	—		***		ns		ns		**
Population (ssp.)			ns	—		ns		ns		ns		ns

Fig. 2g). However, range-edge populations did not have a fitness advantage in the border region (western versus range-edge populations at contact zone in 1997–1998: 3.34 versus 2.15, $t_{1,1361} = 1.1$, $P = 0.28$; Fig. 2g). Furthermore, range-edge populations, which are closer geographically than western populations to ssp. *parviflora*'s range, did not have a fitness advantage in the east (western versus range-edge populations at eastern transplant site in 1997–1998: 0.15 versus 0.12, $t_{1,1361} = 0.1$, $P = 0.9$; Fig. 2g).

For ssp. *xantiana*, two fitness components showed statistically significant evidence of regional adaptation: survival (Table 2B, Fig. 2i) and flower number (Table 2B, Fig. 3g). For both fitness components, western populations performed better than range-edge populations at the western transplant site (survival of western versus range-edge populations at the western site: 0.22 versus 0.14, $G^2 = 24.9$, $P < 0.0001$; flower number: 7.59 versus 3.17, $t_{1,488} = 3.5$, $P < 0.0001$). However, regional populations did not differ at the other two transplant sites (survivorship of western and range-edge populations at contact-zone site; 0.33 versus 0.35, $G^2 = 1.6$, $P = 0.2$; at eastern site: 0.26 versus 0.38, $G^2 = 0.7$, $P = 0.4$; flower number at contact zone: 3.34 versus 1.44, $t_{1,496} = 1.6$, $P = 0.1$; eastern site: 4.44 versus 4.04, $t_{1,497} = -0.3$, $P = 0.8$).

Although germination varied by region and transplant site (site x region interaction; Table 2B), there was no evidence that the reaction norms of regional populations crossed among sites (Fig. 2h). Rather, for each set of regional populations, germination declined from the western to the eastern transplant site, but the magnitude of site-differences varied between regional populations. Fruit set and seed set did not differ between regions (Table 2B).

DISCUSSION

Range and Regional Adaptation

There have been literally thousands of reciprocal transplant studies of species' populations within the confines of their native range, and many find evidence of local adaptation (for a review see Linhart and Grant 1996; but see Parker 1991; Galloway and Fenster 2000). There are many fewer studies of population transplants beyond a species' range boundary (Levin and Clay 1984; see Gaston 2003), and fewer still where sister taxa have been moved into each other's ranges (Clausen et al. 1940; Levin and Schmidt 1985; Schmidt and Levin 1985; Graham et al. 1995; Emms and Arnold 1997; Nagy 1997; Nagy and Rice 1997; Rolán-Alvarez et al. 1997; Wang et al. 1997; Fritsche and Kaltz 2000; Campbell and Waser 2001). These range-boundary studies commonly find evidence of adaptation to the native range, as we did in *C. xantiana* (but see Levin and Schmidt 1985). However, evidence of regional or range adaptation must be interpreted with some caution, because most transplant studies, including our own, have followed transplant performance for less than one to two generations and at only a few transplant sites.

With this caveat in mind, each subspecies of *C. xantiana* had higher lifetime fitness and outperformed the other in its exclusive range. In particular, in the wet year, the fitness of each subspecies in the non-native range was only 5–10% of its fitness in the native range (i.e., ratio of lifetime fitness of a subspecies at the non-native transplant site to its average fitness at the native transplant sites). In the dry year, ssp. *parviflora* experienced a similar reduction in fitness in the non-native versus the native range. By contrast, ssp. *xantiana*

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suffered no fitness reduction outside versus inside its range in the dry year, but only because its fitness was extremely low in the native range in this year (0.02–0.03 seeds per seed planted). Thus, while both subspecies are never successful outside of their native range, regardless of rainfall, ssp. *xantiana* is also relatively unsuccessful at ''home'' in years of average or below average rainfall and in such years does not exhibit range adaptation.

Selection intensities on a subspecies beyond its range edge are very strong and are sufficient to cause extinction of each taxon beyond its range boundary, suggesting that range expansion could only be achieved through stepwise colonization of, and adaptation to, locations progressively farther from the range edge. Our findings of range adaptation support the hypothesis that the sister taxa are adapted to different environments and that selection in response to these environments has shaped divergence in many ecologically important traits (Eckhart and Geber 1999; Eckhart et al. 2004; see also Nagy and Rice 1997).

At the same time, although both subspecies are best adapted to their native range, neither subspecies would be able persist within its range from seeds produced in years of average or below average rainfall. Indeed, it is startling how low population growth rates were for both subspecies in 1998–1999 (0.02–0.16 seeds per planted seed). Therefore, persistence in the native range would depend heavily on seeds produced in years of high precipitation and stored in a seed bank (see below).

Evidence of regional adaptation was considerably weaker. It was found only in the outcrossing ssp. *xantiana* and was restricted to regionally advantaged western populations at the western transplant site. The absence of regional adaptation in ssp. *parviflora* may stem from low levels of genetic variation. Inbreeding, along with small and variable population size across years (M. A. Geber and V. M. Eckhart, pers. obs.), have likely reduced the genetic effective size of its populations (N_e; Wright 1969; Schoen and Brown 1991). Subspecies *parviflora* is less genetically variable than ssp. *xantiana* for 12 developmental, vegetative, and floral traits that were measured over the course of this experiment (Eckhart et al. 2004).

Our findings of strong range and weak regional adaptation parallel those of Levin and colleagues in their pioneering work on the annual *Phlox drummondii* from central Texas (Levin and Clay 1984; Levin and Schmidt 1985; Schmidt and Levin 1985). Namely, fitness declines of transplants away from native sites differ between ecological scales with range boundaries presenting greater barriers to colonization than habitat boundaries within the native range. However, the different ecological scales of adaptive constraint need not reflect geographic scales, since transplants of *P. drummondii* across its range boundary were moved a maximum of 10 km, whereas those between subspecies' ranges and within ranges involved distances of 10 to >300 km, with most being >100 km.

Adaptive constraints at species' or subspecies' boundaries may be more severe if the range edge is associated with a large environmental change or if interior populations have not yet had sufficient time to adapt to this change. Patterns of gene flow could also account for differences in the magnitude of constraint among ecological scales. Gene flow in interior populations is likely to be multidirectional, with alleles coming in from several adjacent habitats. Multidirectional gene flow may lower the degree of local or regional adaptation while, at the same time, expanding the ecological amplitude of populations and their ability to establish in novel environments. Gene flow in peripheral populations, however, may be largely unidirectional and introduce alleles adapted to interior regions but not to conditions beyond the boundary (Hoffmann and Blows 1994; Kirkpatrick and Barton 1997). As a result, adaptation to novel environments beyond the range edge is made more difficult, and, in addition, the boundary will appear as if it is associated with an abrupt environmental change (Kirkpatrick and Barton 1997). Studies of the magnitude and directionality of gene flow in interior and range-edge populations of the two subspecies are needed to evaluate the relevance of this hypothesis to *C. xantiana*.

Fitness Components

Variation in three of five fitness components (germination, flower number, and seed set) did not account for regional or range adaptation, as they did not exhibit crossing reaction norms across the subspecies' border.

Germination was always higher in ssp. *xantiana* than ssp. *parviflora*, even in the east, suggesting higher fitness of the outcrosser than the selfer with respect to this fitness component. However, subspecies differences in seed germination may simply reflect stronger seed dormancy in ssp. *parviflora*. Seed dormancy can evolve as a bet-hedging strategy (i.e., sacrificing single-year performance for the sake of reduced variance in performance across years) in unpredictable environments, such as North American deserts that experience highly variable precipitation among years (Brown and Venable 1986; Philippi and Seger 1989). Across this experiment's precipitation gradient, annual rainfall not only declines but also becomes more variable from west to east (estimated coefficient of variation among years: western transplant site 52%, contact-zone site 53%, eastern site 74%). Thus, over time scales longer than a single year, geographic variation in seed germination in *C. xantiana* may actually contribute to range and regional adaptation (see also Schmidt 1982). Seed dormancy is clearly required for population persistence in both subspecies of *C. xantiana*, along with large seed inputs to the seed bank during years of favorable climate.

Subspecies *xantiana* always had more flowers because it is both a more robust plant and may have experienced pollinator selection for larger floral displays (Table 2B; Schoen and Dubuc 1990; Fishbein and Venable 1996). Conversely, seed set was always higher in ssp. *parviflora* (Table 1), reflecting perhaps lower pollinator limitation to reproduction in the selfer than in the outcrosser (Moeller 2003; M. A. Geber and V. M. Eckhart, unpubl. data). Higher seed set in ssp. *parviflora* also may be due to its having more ovules per ovary than ssp. *xantiana* (A. Senft and M. A. Geber, unpublished data), a characteristic of selfing taxa in which there has been selection to increase investment in female reproduction (Charlesworth and Charlesworth 1981; Johnston et al. 1998).

Three fitness components did exhibit fitness crossing reaction norms but survivorship was the only component to

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contribute to both range and regional adaptation. Fruit set affected only range adaptation, while flower number affected only regional adaptation in ssp. *xantiana*. Field observations on sources of mortality suggest that the low survivorship of ssp. *xantiana* in the east was attributable, in part, to end-of-season drought that caused plants of this late-flowering taxon to wilt and die. Equally important, however, was mortality from small mammal herbivory. Herbivory increased in severity from west to east (percent of plants attacked by small mammals in west: 0.12; contact zone: 0.15; east: 0.32) and was stronger on ssp. *xantiana* than on ssp. *parviflora* at the contact zone and eastern transplant sites (contact-zone site: 0.28 versus 0.08; eastern site: 0.40 versus 0.27; site-by-subspecies interaction: $G^2 = 34.6$, df = 2, $P < 0.001$), most likely because small mammals seemed to prefer plants that had not yet senesced (correlation, in wet year, between flowering date and attack rate by small mammals at contact-zone: $r = 0.80$, $P < 0.0001$; east: $r = 0.85$, $P < 0.0001$). For ssp. *parviflora*, competition likely contributed to low survivorship in the west. Vegetation cover, particularly of grasses, is higher on the wetter western slope of the Sierra Nevada than in the east and, at the western site, survivorship increased with plant size in both years (1997–1998: $G^2 = 266.5$, df = 1, $P < 0.0001$); 1998–1999: $G^2 = 31.2$, df = 1, $P < 0.0001$). Subspecies *parviflora*, the smaller of the two subspecies (total leaf area in ssp. *xantiana* versus *parviflora* in March 1998: 1.41 versus 1.17 cm^2, $P < 0.0004$), is a weaker competitor against these grasses (Y. B. Lindahl and V. M. Eckhart, unpubl. data). In addition, in the first El Niño year of our study, both subspecies were infected with a fungal rust at the western garden, but the frequency and severity of infection were higher on ssp. *parviflora* (M. A. Geber and V. A. Eckhart, pers. obs.), either because it is less well defended or because its position below the grass canopy kept it in a wetter environment. Mortality from fungal attack between the onset of flowering and fruiting also contributed to ssp. *parviflora*'s low fruit set in the west. Regional differences in plant size in ssp. *xantiana* also may account for the higher survivorship and flower production of western compared to range-edge populations at the western transplant site. Plants from western populations are larger (average leaf area of western versus range-edge populations in March 1998: 1.97 versus 1.36 cm^2, $F = 19.1$, df = 1, 1630, $P < 0.0001$) and likely more competitive and less exposed to fungal attack than range-edge populations.

The importance of biotic agents of selection across *C. xantiana*'s entire range is of note because abiotic factors, either directly or indirectly through food resources, are often thought to be important determinants of range limits in harsh environments (e.g., high latitude, elevation, desiccation, salinity), while biotic interactions are considered important in setting range limits in more benign environments factors (Darwin 1859; MacArthur 1972; Woodward 1987; Gross and Price 2000; Grace et al. 2002; Harley 2003; but see Callaway et al. 2002). The drought-prone eastern end of *C. xantiana*'s range typically would be considered harsher than the western end, and yet herbivores and pollinators played important roles in the poor performance of ssp. *xantiana* in the east, just as competition and fungal attack affected ssp. *parviflora*'s fitness in the west.

In sum, differing abiotic (precipitation) and biotic factors (competition, pathogen, and small mammal herbivory) appear to operate as selective agents across the west-to-east gradient. Still, many aspects of regional and range adaptation are related to variation in plant size. Even small-mammal herbivory on ssp. *xantiana*, although a function of delayed phenology, also was associated with plant size because late flowering prolongs the period of vegetative growth (correlation, in wet year, between flowering date and plant size at contact-zone: $r = 0.83$, $P < 0.0001$; in east: $r = 0.48$, $P < 0.07$). An exception is the low fruit set of ssp. *xantiana* in the east that is more likely due to the absence of specialist bee pollinators and scarcity of generalist bees in ssp. *parviflora*'s range (Fausto et al. 2001; Moeller 2003). Thus, evolutionary adaptation to an expanded range is likely to require modifications in both vegetative development (size, growth) and floral characters related to breeding system. All of these characters are genetically variable in one or both subspecies (Eckhart et al. 2004) and studies of population differentiation in *C. unguiculata* (Jonas and Geber 1999) and developmental studies of *C. xantiana* (Runions and Geber 2000) indicate that the traits are not genetically correlated through pleiotropy and can evolve independently. Interestingly, were one subspecies to invade the other's range, adaptive evolution would lead to convergence in vegetative size and development: large size and long development in the west, small size and rapid development in the east. Pollinator scarcity in the east could also select for convergence on mating system were ssp. *xantiana* to invade ssp. *parviflora*'s range. However, convergence in breeding system (i.e., evolution from a selfing to an outcrossing flower form) would not be required for ssp. *parviflora* to invade ssp. *xantiana*'s range, as reproduction of the former taxon is assured whether pollinators are present or absent.

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