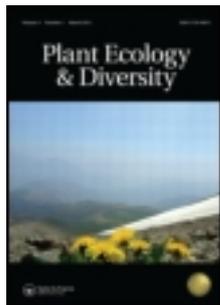


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Little evidence for local adaptation to soils or microclimate in the post-fire recruitment of three Californian shrubs

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Background: Seedling recruitment following fire is an infrequent yet critical demographic transition for woody plants in Mediterranean ecosystems.

Aims: Here we examine whether post-fire seedling recruitment of three widespread Californian chaparral shrubs is affected by local adaptation within an edaphically and topographically complex landscape.

Methods: We reciprocally transplanted 6-month-old seedlings of *Adenostema fasciculatum*, *Ceanothus cuneatus* and *Eriodictyon californicum* to serpentine and sandstone soils, and cool northerly and warm southerly slopes.

Results: At the age of 2 years, none of the species manifested higher survival or growth on 'home' compared with 'away' soils or slopes, indicating an absence of local adaptation with respect to seedling recruitment in these environments. Seedlings of all species manifested lower survival and relative growth on serpentine soils regardless of seedling source, as well as a variety of other destination and source effects.

Conclusions: The ability of these three species to recruit in new environments, such as in restoration settings or in response to shifting climates, is unlikely to be impeded by a need for seeds from sources that closely match their edaphic or topographic destination.

Keywords: chaparral; ecotypic differentiation; fire; local adaptation; reciprocal transplant; seedling recruitment; serpentine; topography

Introduction

Local adaptation, in which individuals in their 'home' environments show higher fitness than conspecifics from 'away' environments, is of fundamental importance in evolution, ecology, conservation, and restoration (Kawecki and Ebert 2004; Leimu and Fischer 2008; Wright and Stanton 2011). Local adaptation is classically detected using reciprocal transplant experiments, and a recent meta-analysis of such studies found significant local adaptation in 71% of cases (Leimu and Fischer 2008). Plants may be locally adapted to macroclimate (e.g. Turesson 1922; Clausen et al. 1948; Hall et al. 2010) microclimate (Joshi et al. 2001; McKay et al. 2001), salinity (Lowry et al. 2009), or infertile soils such as serpentine (e.g. Kruckeberg 1951; O'Dell and Rajakaruna 2011; Wright and Stanton 2011). Local adaptation offers opportunities to study parallel and convergent evolution (Rajakaruna et al. 2003a), the genetic and environmental mechanisms of natural selection (von Wettberg and Wright 2011), and incipient ecological speciation (Kay et al. 2011). Local adaptation is also significant as a possible constraint on the dispersal potential of species within heterogeneous environments. To the extent that seemingly generalist species are actually mosaics of locally adapted genotypes, this may inhibit the potential for ecological restoration (McKay et al. 2005), range shifts under natural and human-caused climate change (Walther et al. 2002;

Ackerly 2003; Parmesan 2006), and assisted migration (McLachlan et al. 2007; Aitken et al. 2008).

Local adaptation is expected to be less common in long-lived plants because longevity results in a greater potential for gene flow to homogenise populations (Leimu and Fischer 2008). However, the vast majority of local adaptation studies has been on herbs (including all the 35 cases reviewed by Leimu and Fischer 2008), so the actual frequency of local adaptation in other life forms is not well known. One life-history group that has been less studied than others with respect to local adaptation is Mediterranean-climate shrubs that recruit in response to fire (but see Pausas et al. 2012 for a study of local adaptation to fire regime in *Ulex parviflorus* Pourr.). In Mediterranean shrubland vegetation, fire is a predictable and defining – although usually infrequent – event, generally occurring on multi-decadal time scales, but with very large variance in recurrence times (Cody and Mooney 1978; Naveh and Whittaker 1979; Barbour and Minnich 1990). Reproduction by seed for many shrubs occurs primarily or exclusively in the first few growing seasons after a fire, at which time mass germination from the dormant seedbank may be followed by high initial seedling mortality from drought stress during the first several post-fire summers (Jacks 1984; Kummerow et al. 1985; Mills 1986; Moreno et al. 2011). Once adults are established, their

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mortality and recruitment rates may be low, and change in community composition may be relatively modest until the next fire (Keeley and Bond 1997; Keeley et al. 2006; Rutherford et al. 2011; Pérez-Ramos et al. 2012). Years to decades may elapse between fires, with tremendous spatial and temporal variability due to macro- and microclimate, topographic position, vegetation composition and density, and the large element of chance in weather and ignitions. The relative rarity and unpredictability of fire events and the high natural mortality of seedlings make it very challenging to study shrub demography (but see Clemente et al. 1996 for an example), including the role (if any) of local adaptation in shrub recruitment in heterogeneous environments.

We took advantage of a wildfire to test for local adaptation to soil and microclimate in seedlings of three widespread shrubs of Californian chaparral, *Adenostema fasciculatum* Hook. & Arn., *Ceanothus cuneatus* (Hook.) Nutt. and *Eriodictyon californicum* (Hook. & Arn.) Torr. These were the three most common species at our site that met the two necessary criteria for our study: soil generalism and post-fire seeding. Each species is found on serpentine, which is an infertile soil (low Ca:Mg ratio, low primary nutrients, often low water availability, sometimes high levels of Ni and other metals; Kruckeberg 1984) and is often associated with a flora associated with local adaptation, and sandstone, which is nutritionally more balanced and chemically 'normal'. Each species is also found on cool north-facing and warm south-facing slopes. In such 'generalist' chaparral shrubs, individuals growing on serpentine compared with sandstone soils may differ in functionally important morphological traits (e.g. specific leaf area; Anacker et al. 2011) and physiological traits (e.g. water potential, water use-efficiency, nutrient relations; N. Rajakaruna and D. Ackerly, unpublished data); however, to what extent these differences are genetically based is unknown. In pairs of congeneric shrub species that are specialised to either of these soils, the serpentine species often maintain higher foliar Ca:Mg when grown on serpentine, suggesting that the ability to regulate cations at the root-shoot boundary is an important adaptation to serpentine soils (O'Dell et al. 2006; O'Dell and Rajakaruna 2011). These between-soil trait differences provide clear evidence for heterogeneity in the environmental demands faced by 'generalist' chaparral shrubs depending on which soil they grow on. However, to our knowledge no previous studies have investigated the potential for local adaptation to affect the post-fire recruitment of these soil-generalist chaparral shrubs.

Chaparral shrub recruitment is a subject of ever-increasing importance, since the frequency of large and severe fires in North America has increased in recent decades, with a climatic warming playing a detectable role (Gillett and Weaver 2004; Westerling et al. 2006). Increased fire frequency in southern California has contributed to the widespread conversion of chaparral rich in native species to exotic-dominated grasslands (Keeley and Footheringham 2001; Minnich 2001). Chaparral growing

on serpentine soils, which has a distinctive mix of endemic and widespread shrub species, tends to burn in a patchier and less intense fashion, but to recover considerably more slowly after fire than non-serpentine chaparral (Safford and Harrison 2004). In a recent study in southern California, chaparral shrubs were found to be dying off at the lower margins of their elevational ranges as predicted under a warming climate; at the same time the upper elevational limits of these shrubs were not expanding (Kelly and Goulden 2008). These impacts on chaparral ecosystems make it timely to examine whether seedling recruitment of common shrubs is constrained by local adaptation in complex landscapes.

Materials and methods

Study site and species

Walker Ridge is a rugged area managed by the US Bureau of Land Management in Lake and Colusa Counties, California, USA (39° 05' 09" N, 22° 29' 08" W). Major vegetation types include chaparral dominated by chamise (*Adenostema fasciculatum* Hook. & Arn., Rosaceae) on sandstone soils, chaparral dominated by leather oak (*Quercus durata* Jeps., Fagaceae) on serpentine soils, and several other plant communities not considered in this study (e.g. *Quercus douglassi* Hook. & Arn. woodlands on fine-textured sedimentary soils, and *Hesperocyparis macnabiana* (A. Murray bis) Bartel (Cupressaceae) forests on higher-elevation serpentine soils).

We studied three shrub species that are common in chaparral on both serpentine and sandstone soils and on both north- and south-facing slopes: chamise, yerba santa (*Eriodictyon californicum* (Hook. & Arn.) Torr., Boraginaceae) and buckbrush (*Ceanothus cuneatus* (Hook.) Nutt., Rhamnaceae). They are insect-pollinated, and their seed dispersal has not been well characterised, although long-distance seed dispersal is generally considered rare in chaparral shrubs (Minnich and Bahre 1995). *A. fasciculatum* and *C. cuneatus* are 'facultative seeders', which are capable of resprouting, but also produce abundant seedlings after fire; *E. californicum* is an 'obligate seeder' whose mature adults are killed by fire and whose seed very seldom germinates, except in response to fire (Keeley 1991).

The 5867 ha Indian Valley Fire occurred in August 2008 at Walker Ridge, burning large areas on serpentine and non-serpentine soils. Seedlings of our study species appeared in April 2009, simultaneously with the last rains of the year. Newly germinated shrub seedlings thus faced a 'race against time' to develop roots in rapidly drying soils, as is typical in chaparral shrubs (Kummerow et al. 1985).

Experimental set-up

In late April and early May 2009, we collected newly emerged seedlings from serpentine and sandstone soils, and within each soil, from both north and south aspects with slopes of 21–44%. For each species, we collected

120 seedlings from each of the four source types, for a total of 1440 seedlings. We collected and pooled them from several different locations of each source type over an area of several km² within the burned area to ensure that the collected seedlings were random with respect to source location. We did not use seedlings showing any visible herbivorous insect damage. The seedlings were collected by carefully shovelling out a block of soil containing their roots, which were generally 2–4 cm in length with few lateral roots. They were gently shaken to remove dry soil from the roots. To ensure proper drainage, they were then planted into a 50:50 mixture of their home soil and uniform coarse sand in tubular 164 ml pots. The seedlings were kept for 6 months in a shade house and transplanted in winter 2009–2010. They were watered two to three times per week. Due to two hot days in Davis and water system failure in August 2009, >50% of seedlings died in the shade house, leaving 294 *A. fasciculatum*, 193 *C. cuneatus* and 154 *E. californicum*.

Nonetheless, keeping the seedlings in the shade house proved to be a good strategy to hedge against excessive losses of experimental seedlings. In a first trial we transplanted seedlings into the field directly after collection. Over 95% of them died in the first year, most likely due to rootlet damage that exacerbated drought stress.

For transplantation we chose two replicate destination sites on serpentine and two on sandstone, well interspersed along a 10 km unpaved road traversing the burned area. Sites were chosen by looking for adjacent N and S aspects within each soil, with relatively steep slopes (21–44%), and accessible (50–500 m distant) from the road. Each site consisted of two plots, one on the north and the other on the south slope, for a total of eight destination plots (Table 1).

At each plot we planted up to 96 seedlings (three species × four sources × five to eight replicates) at randomly assigned locations in a 10 m × 12 m rectangular grid with a spacing of 1 m. We controlled for differences in initial seedling size by randomly assigning seedlings to treatments, as well as by using relative rates as our focal variables (see below). To minimise damage to the roots, which by then were generally 10–15 cm long, the seedlings were transplanted without attempting to wash off the home soil and sand mix. Since we studied these

seedlings for 3 years, during which they grew substantially in size and root depth, we believe there is little possibility that their growth was strongly affected by the small amount of original soil mix clinging to the roots at transplantation. Naturally occurring seedlings within a 30 cm radius around the transplanted seedlings were periodically removed during the first year.

Measurements. We monitored seedlings for two years after transplantation. Survival was measured by censusing seedlings every 2 months in the first year and every 6 months in the second year. Seedling height (ground to apex) was measured 3 weeks after transplantation and twice per year thereafter (in spring and autumn). Growth, as relative increase in height, was calculated as $\ln(\text{final height}/\text{initial height})$.

Survey of natural seedling populations

To monitor natural (un-transplanted) seedlings, we chose 36, 1 m × 1 m² quadrats adjacent to the transplant sites and at one additional soil/slope combination, each containing at least 15 naturally occurring individuals of one target species (i.e. three species × four soil/slope combinations × three replicate sites). For *E. californicum*, 1 m × 2 m² quadrats were sometimes necessary to capture 15 seedlings. We recorded numbers of seedlings and the height of five randomly chosen individuals in these quadrats for three growing seasons (spring 2009–2011).

Habitat conditions

To confirm the classifications of our sites, we collected soil and temperature data. In each of the eight destination plots we collected two samples of 50 g soil from 10–30 cm depth in spring 2009. Samples were air dried, ground, and analysed by A & L Western Agricultural Laboratories, Modesto, California, for cation exchange capacity, organic matter, pH, exchangeable K, Mg, Zn, Mn, Fe, Cu, B, Ca, SO₄²⁻, NH₄⁺, Na, total N and Bray P. To quantify the effect of slope and aspect on microclimate, in each destination plot we also measured above- and below-ground temperatures in summer 2009. For above-ground

Table 1. Characterisation of the replicated plots at each destination combination. Destination plots were located on serpentine soil (Serp) on north- and south-facing slopes (N, S) and on sandstone soil (Sand) on north- and south-facing slopes (N, S).

Transplant destination	Sand N		Sand S		Serp N		Serp S	
	1	2	1	2	1	2	1	2
Soil type	sandstone		sandstone		serpentine		serpentine	
Ca:Mg	2.6	1.3	3.9	0.7	0.4	0.4	0.2	0.5
pH	6.1	6.1	7	6.5	6.8	6.7	7.1	7.1
Org. matter (ENR)	127	110	116	104	193	175	123	148
Slope	25 %	21 %	43 %	44 %	27 %	27 %	38 %	37 %
Elevation (m)	840	850	820	850	840	850	850	850

measurements we placed temperature loggers (i-buttons, Maxim, Sunnyvale, USA) in white PVC pipes with open ends (pipe length: 150 mm, diameter: 50 mm) laid perpendicular to the slope at the upper right and lower left corner of each plot. For below-ground temperature we buried one temperature logger per plot 10 cm deep in the soil, at the centre of each plot. Temperature was recorded every 2 h from late June until early September 2009.

To evaluate whether our experimental years were typical in terms of key growing-season climatic conditions, we compared 2009 and 2010 values with 26-year means of water-year precipitation (i.e. from fall to spring) and spring and summer temperatures (Table S1, available online). We used climate data for 1986–2011 from the McLaughlin University of California Natural Reserve, located 21 km south of the study area (38°51'N, 123°30'W).

To test for local adaptation with respect to survival, we analysed individual survival curves. We chose the non-parametric Cox proportional hazard model, which uses an unspecified baseline hazard function and depends on the ranks of survival times (Crawley 2007). The model for each species included destination soil (sandstone, serpentine) and destination slope (N, S), source soil (sandstone, serpentine) and source slope (N, S) and their two-way interactions. Site was included as a factor to account for destination-specific differences at the plot level.

The proportion of seedlings surviving in natural populations was analysed using generalised linear models (GLM). Due to the non-normal error distribution of the proportion data we used models with binomial error distribution.

To test for local adaptation with respect to growth, we did a multifactorial analysis of variances (ANOVA) with the different source and destination combinations and their two-way interactions as factors. Site was included as a factor to account for destination site-specific differences.

All analyses were conducted in R 2.10.1 (R Development Core Team 2007) and survival analyses

were made using the package Survival (Therneau and Lumley 2011).

Results

Survival

Experimental populations. Survival curves for all three species decreased most on serpentine destination soils regardless of source, and survival for one species (*E. californicum*) was lower on S-facing than on N-facing destination slopes (Table 2; Figure S1, available online). The survival analysis did not show any significant source–destination interactions indicative of local adaptation (Figure 1; Table 2).

Natural populations. In naturally occurring seedlings over the same timespan as the experiment, survival was higher on N-facing slopes than on S-facing slopes in *A. fasciculatum* seedling populations, but only on sandstone soils (GLM with binomial error distribution on proportion: soil type, $z = 1.4$, $P = 0.15$; aspect, $z = 6.5$, $P < 0.001$; interaction, $z = -4.1$, $P < 0.001$; Figure 2A). Percent survival was higher on N-facing than on S-facing slopes in *C. cuneatus* populations on sandstone soils, and higher on S-facing than on N-facing slopes on serpentine soils (soil, $z = 5.5$, $P < 0.001$; slope, $z = 4.8$, $P < 0.001$; interaction, $z = -5.9$, $P < 0.001$; Figure 2B). Mean percentage survival was unaffected by soil or slope in *E. californicum* (soil, $z = -0.9$, $P = 0.3$; slope, $z = 1.1$, $P = 0.3$; interaction, $z = -0.4$, $P = 0.7$; Figure 2C).

Growth

Experimental populations. Initial height of transplanted seedlings, measured 3 weeks after they were transplanted in winter 2009/2010, varied significantly among the different source soil and slope combinations for all three species,

Table 2. Cox proportional survival analysis of transplants over 2 years. Analyses were made for each species separately. In the survival analysis Likelihood ratio-, Wald- and Score (logrank)- test were significant for all three species (*A. fasciculatum*: $N = 268$, 11 df, $P < 0.001$; *C. cuneatus*: $N = 175$, 11 df, $P < 0.001$; *E. californicum*: $N = 144$, 11 df, $P < 0.05$).

Factor	<i>A. fasciculatum</i>		<i>C. cuneatus</i>		<i>E. californicum</i>	
	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>	<i>z</i>	<i>P</i>
Destination						
Soil	3.5	<0.001	4.9	<0.001	2	0.045
Slope	-1.6	0.106	1.5	0.125	2	0.040
Soil × slope	0.9	0.377	-2.7	0.008	-2	0.052
Source						
Soil	-0.3	0.767	-0.3	0.743	0	0.995
Slope	0.2	0.877	1.5	0.134	-0.6	0.544
Soil × slope	1.7	0.083	1.4	0.171	1.1	0.256
Source × destination						
Matching source and destination soil	-0.6	0.561	0.2	0.837	0	0.998
Matching source and destination slope	-0.1	0.910	-1.3	0.181	0.4	0.680
Source slope × destination soil	-0.7	0.461	-1.4	0.161	0.6	0.516
Source soil × destination slope	-0.2	0.819	0.8	0.415	-0.7	0.454
Site	-4.3	<0.001	-4.1	<0.001	-2.1	0.039

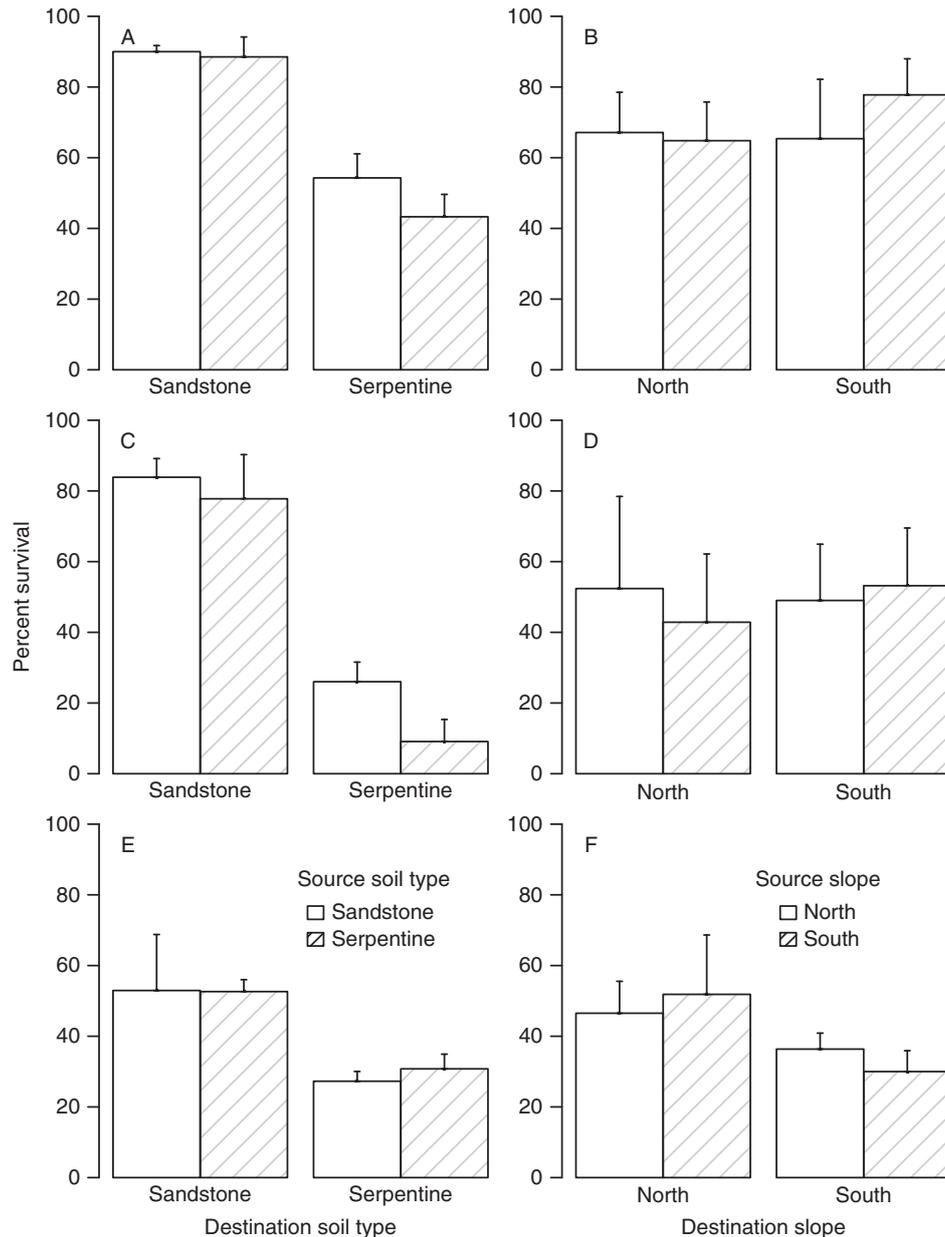


Figure 1. Mean percent survival (\pm SE) over replicated experimental populations for *A. fasciculatum* (A, B), *C. cuneatus* (C, D) and *E. californicum* (E, F). Percent seedlings surviving per source and destination combination was calculated by dividing the number of surviving seedlings after 2 years with the number of initially transplanted seedlings. Panels A, C and E show survival depending on source and destination soil type. Panels B, D and F show survival depending on source and destination slope.

even though seedlings had been kept under constant conditions in the shade house for more than 6 months. In all three species, seedlings from serpentine sources were significantly smaller compared with those from sandstone sources, and seedlings from S-facing slopes were smaller compared with N-facing slopes (Table 3; Figure S2, available online).

Relative height increase in *A. fasciculatum* and *C. cuneatus* was smaller for seedlings in serpentine than sandstone destinations, and larger for seedlings from serpentine than sandstone sources (Table 4; Figure 3A and 3C). Relative height in *A. fasciculatum* was larger for seedlings from serpentine sources in sandstone destinations than in

seedlings from sandstone sources (Table 4). However, relative height increase never showed any source–destination interactions in a direction indicative of local adaptation (Table 4; Figure 3).

Natural populations. Seedling height of *A. fasciculatum* and *E. californicum* in spring 2009 was greater on S-facing than on N-facing slopes, possibly due to earlier germination on the S slopes. However, relative height increase in these species was not influenced by slope. Relative height increase in *A. fasciculatum* was larger on serpentine than on sandstone soil. Relative height increase in *E. californicum* was larger on S compared with N slopes on sandstone, but

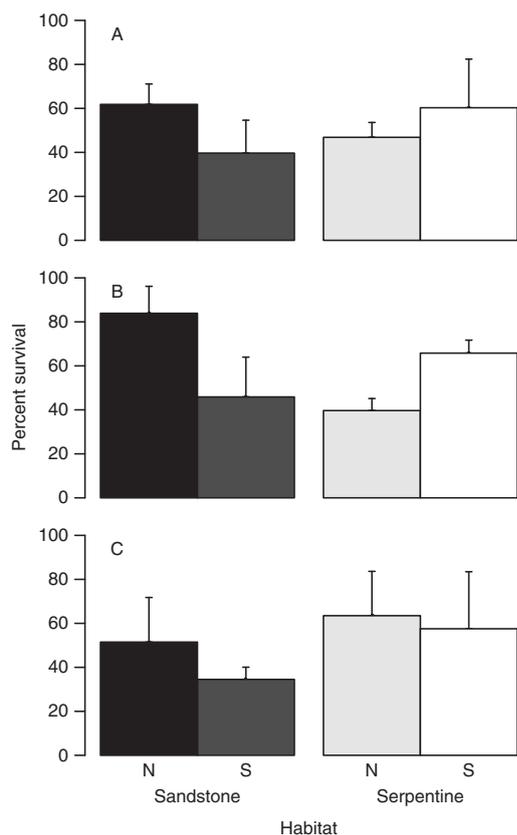


Figure 2. Mean percent survival (\pm SE) of replicated natural populations of *A. fasciculatum* (A), *C. cuneatus* (B), and *E. californicum* (C). Densities of naturally emerged seedling populations were censused over three growing seasons (starting at the time of seedling collection for the transplant experiment) and survival was calculated by dividing final with initial density. Survival on sandstone north- and south-facing slopes and serpentine, respectively, are shown.

Table 3. Analysis of variance (ANOVA) on log-transformed initial height of all three species (measured 3 weeks after transplantation) depending on source soil type and slope.

Factor	<i>A. fasciculatum</i>		<i>C. cuneatus</i>		<i>E. californicum</i>	
	F _(1,264)	P	F _(1,171)	P	F _(1,138)	P
Soil	48.0	<0.001	89.5	<0.001	11.0	0.001
Slope	5.5	0.020	7.4	0.007	4.6	0.034
Soil \times slope	6.1	0.014	0.3	0.558	0.9	0.358

larger on N compared with S slopes on serpentine. Initial height and height increase in *C. cuneatus* were relatively little influenced by slope, soil, or their interaction (Table 5; Figure S3, available online).

Habitat characteristics

Confirming our microclimate classifications, above-ground temperatures (daily maxima) were warmer on S-facing than N-facing slopes, and the S-facing slopes on serpentine were the warmest (Figure S4, available online). Below-ground temperatures showed more muted results, showing

highest daily maxima on N-facing serpentine and warmer daily minima on S-facing slopes on both soils (Figure S5, available online). In agreement with the expected differences between serpentine and sandstone soils, serpentine soils at the transplant locations contained significantly less exchangeable Ca (mean serp = 1086 ppm \pm 133 SE, mean sand = 3112 ppm \pm 708 SE, $P < 0.05$), more Ni (mean serp = 34.7 ppm \pm 9.4 SE, mean sand = 0.7 ppm \pm 0.2 SE, $P < 0.001$) and more exchangeable Mg (mean serp = 2454 ppm \pm 258 SE, mean sand = 1124 ppm \pm 387 SE, $P < 0.05$) compared with sandstone soils. Exchangeable Ca:Mg was $\ll 1.0$ on serpentine (mean = 0.48 \pm 0.1 SE) and $\gg 1.0$ on sandstone (mean = 3.6 \pm 0.7 SE). Soil pH and organic matter were slightly higher on serpentine than sandstone (Table 1). No differences were found between soils in cation exchange capacity, soluble salts, SO_4^{2-} , B, Fe, Cu, Mn, K, NH_4^+ , Na, total N and Bray P, nor did any soil properties differ significantly between N and S slopes within soil types (MANOVA on ln transformed data).

Growing-season climatic conditions in 2009 and 2010 were largely typical (i.e. all variables < 1 SD from their 26-year means), except that spring 2010 mean and maximum temperatures were slightly cooler (1.6 and 1.3 SD below their 26-year means; Table S1, available online).

Discussion

Our results reinforce the observation that chaparral shrubs survive and recruit in a challenging fitness landscape. Survival of young seedlings averaged 51–62% in natural un-manipulated seedlings from a few weeks after germination to an age of 2.5 years (figures that omit additional mortality at earlier stages); moreover, both our experimental transplants and the natural seedlings manifested substantial environmental variation in survival and growth. Survival was up to 60% lower on serpentine than sandstone soils, and up to 15% lower on south than north-facing slopes, while relative growth rates were up to 32% lower on serpentine than sandstone soils. Strong variation in shrub species composition has been observed across soils and slopes in Californian chaparral communities (Franklin 1998, Moody and Meentemeyer 2001, Ackerly et al. 2002), and recruitment differences such as those we observed have the clear potential to contribute to this variation. *A. fasciculatum* and *C. cuneatus*, for example, are considerably less abundant in serpentine than sandstone chaparral (Harrison 1997), but within sandstone chaparral, both of these species are relatively prevalent across varying slopes, paralleling the strong soil effects and weaker slope effects on the seedling recruitment of these species that we found in this experiment.

Despite the strong direct effects of soils and slopes that we observed, we found no evidence for local adaptation to these environments at the seedling stage in our focal species. The general causes of lack of local adaptation include high gene flow and the absence of fitness trade-offs between environments (Endler 1973; Slatkin

Table 4. Analyses of variances (ANOVA) of growth (relative increase in height, ln-transformed) in the transplanted seedlings over 2 years. Analyses were carried out for each species separately.

Factor	<i>A. fasciculatum</i>			<i>C. cuneatus</i>			<i>E. californicum</i>		
	df	F	P	df	F	P	df	F	P
Destination									
Soil	1	24.3	<0.001	1	5.9	0.019	1	2.3	0.140
Slope	1	19.1	<0.001	1	3.3	0.071	1	0.3	0.579
Soil × slope	1	5.3	0.022	1	0.1	0.793	1	0.1	0.769
Source									
Soil	1	19.5	<0.001	1	23.2	<0.001	1	0	0.903
Slope	1	1.8	0.187	1	1.1	0.292	1	3.1	0.086
Soil × slope	1	0.7	0.398	1	0.3	0.594	1	1.1	0.299
Source × destination									
Matching source and destination soil	1	0	0.907	1	0.4	0.521	1	2.9	0.098
Matching source and destination slope	1	3.2	0.078	1	0.7	0.391	1	0.3	0.594
Source slope × destination soil	1	0.6	0.446	1	3.3	0.073	1	2.3	0.136
Source soil × destination slope	1	0.1	0.736	1	0.5	0.504	1	0.2	0.696
Site	1	2.4	0.120	1	2.1	0.154	1	0.9	0.343
Residuals	179			75			46		

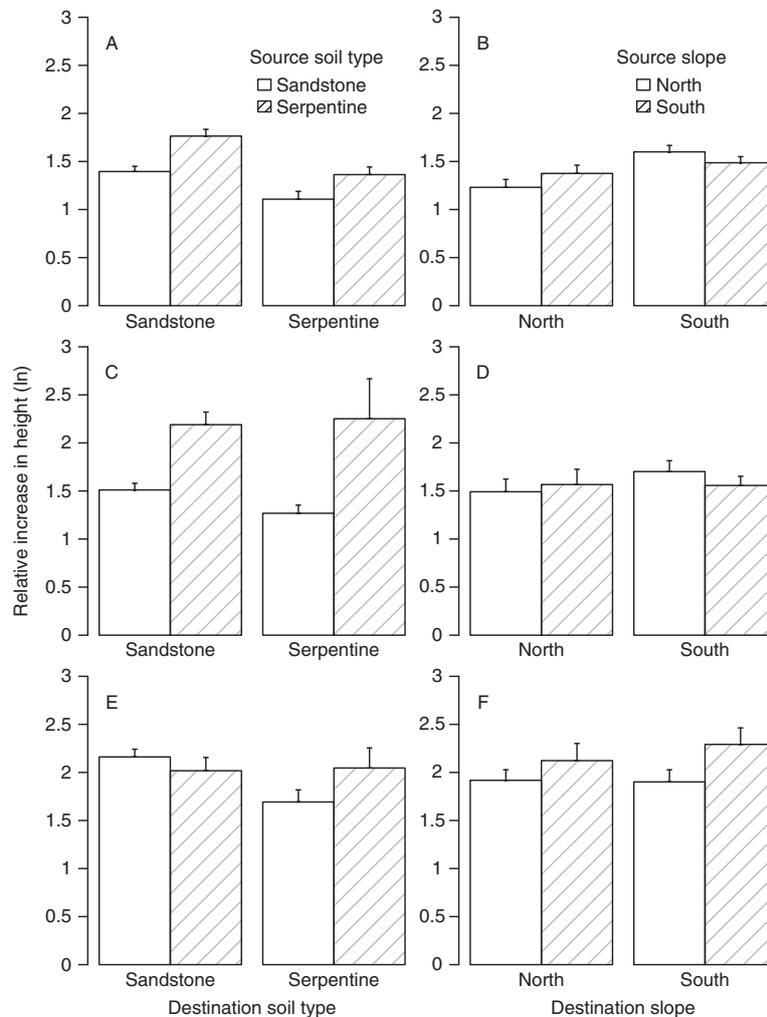


Figure 3. Mean relative growth rates (\pm SE) over 16 months of replicated experimental populations of *A. fasciculatum* (A, D), *C. cuneatus* (B, E) and *E. californicum* (C, F). The panels show soil effects (A, B, and C) and slope effects (D, E, F). Relative growth rates were ln-transformed and calculated dividing final with initial height.

Table 5. Analysis of variance (ANOVA) for initial height and growth (relative height increase: final/initial height) over 2 years of natural seedling populations.

Initial height	<i>A. fasciculatum</i>		<i>C. cuneatus</i>		<i>E. californicum</i>	
	F _(1,56)	<i>P</i>	F _(1,56)	<i>P</i>	F _(1,56)	<i>P</i>
Soil	9.4	0.003	3.6	0.065	1.7	0.196
Slope	6.3	0.015	0.5	0.491	8.4	0.005
Soil × slope	0.0	0.846	0.3	0.607	0.1	0.785
Growth	<i>A. fasciculatum</i>		<i>C. cuneatus</i>		<i>E. californicum</i>	
	F _(1,56)	<i>P</i>	F _(1,56)	<i>P</i>	F _(1,56)	<i>P</i>
Soil	8.5	0.005	0.0	0.979	3.6	0.063
Slope	0.2	0.662	1.1	0.295	2.6	0.112
Soil × slope	0.9	0.340	1.6	0.211	7.6	0.008

1985). We cannot determine from our results which of the two is more important here. In ‘bodenvag’ species, species that can grow commonly on and also off of serpentine, those showing no evidence for local adaptation have been described as having ‘general-purpose genotypes’ (Kruckeberg 1951). In a recent review, O’Dell and Rajakaruna (2011) found evidence for local adaptation to serpentine in 31 of 35 herbs, but only four of 14 grasses and two of seven trees that have been studied, suggesting that the prevalence of soil generalism is higher in some functional groups than others. Although the specific mechanisms for serpentine-tolerant general-purpose genotypes have not been elucidated, O’Dell and Rajakaruna (2011) speculated that the cell wall structure of grasses makes them less sensitive than forbs to the calcium deficiency of serpentine soils.

Our results do not, of course, rule out local adaptation at either earlier or later life stages than those we were able to study in our experiment. Local adaptation may be more likely to be expressed in reproductive traits, since vegetative traits are so strongly shaped by direct effects of the environment (Nagy and Rice 1997). In the case of local adaptation to serpentine, for example, reduced reproductive effort may arise as a consequence of selection for increased below-ground allocation (Rajakaruna and Bohm 1999; Rajakaruna et al. 2003b). However, Raabová et al. (2007) detected local adaptation in transplanted seeds but not in transplanted adults of a perennial herb, indicating that early life stages may also be important in the expression of local adaptation. In any case, seedling survival is likely to be a highly critical life-history transition for postfire-seeding chaparral shrubs, perhaps exerting larger effects on the distributions of these species than the survival or seed production of mature adults (see Menges 2007 for a discussion of plant demography in the context of fire).

We found differences in seedling heights among the different habitat types in the first weeks after transplantation, even after keeping them in the shade house for more than 6 months, suggesting lasting effects of the maternal and/or early seedling environment. Maternal effects are a well-known problem in studies of local adaptation,

especially in long-lived perennials, for which it is seldom practical to grow individuals in a common garden and cross them to obtain F1 seedlings (Wright 2007; Wright and Stanton 2011). A partial solution is to run an experiment long enough so that the effects of maternal environment on offspring phenotype are diminished relative to the lifelong effects of genotype and the current environment (Roach and Wulff 1987; Donohue et al. 2005; Wright et al. 2006); however, this is not an option when studying seedling survival and growth, as in our study. If we had found evidence supporting local adaptation, we would have to consider maternal effects as an alternative explanation; our negative results, however, are unlikely to have been caused by maternal effects. Also, we acknowledge that our statistical power was limited by high seedling mortality. In retrospect, our power to detect relatively small effects would have been strengthened by studying only one species, but this would have also limited the generality of the results.

We conclude that with respect to seedling recruitment, our three focal species are habitat generalists showing no evidence for intraspecific adaptation to soils or slopes. While this may not be particularly surprising, given the relatively fine-grained mosaic of soils and slopes within which they occur, it is significant negative evidence considering the widespread interest in documenting patterns and mechanisms of local adaptation (Leimu and Fischer 2008; Coop et al. 2010; Anderson et al. 2011). With respect to the accelerating environmental changes affecting Mediterranean shrublands, including increasingly severe droughts, frequent fires, atmospheric nutrient deposition and habitat conversion, a positive outcome from this study is that successful seedling recruitment of our focal species does not appear to depend on close matching between source and destination habitats.

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