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Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area

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Background: High values of specific leaf area (SLA) are generally associated with high maximal growth rates in resource-rich conditions, such as mesic climates and fertile soils. However, fire may complicate this relationship since its frequency varies with both climate and soil fertility, and fire frequency selects for regeneration strategies (resprouting versus seeding) that are not independent of resource-acquisition strategies. Shared ancestry is also expected to affect the distribution of resource-use and regeneration traits.

Aims: We examined climate, soil, and fire as drivers of community-level variation in a key functional trait, SLA, in chaparral in California.

Methods: We quantified the phylogenetic, functional, and environmental non-independence of key traits for 87 species in 115 plots.

Results: Among species, SLA was higher in resprouters than seeders, although not after phylogeny correction. Among communities, mean SLA was lower in harsh interior climates, but in these climates it was higher on more fertile soils and on more recently burned sites; in mesic coastal climates, mean SLA was uniformly high despite variation in soil fertility and fire history.

Conclusions: We conclude that because important correlations exist among both species traits and environmental filters, interpreting the functional and phylogenetic structure of communities may require an understanding of complex interactive effects.

Keywords: chaparral; climate; fire; sandstone; serpentine; soil; specific leaf area

Introduction

Environmental conditions limit the range of viable ecological strategies in a community, creating assemblages in which functionally similar species tend to co-occur (Diamond 1975; Weiher and Keddy 2001; Webb et al. 2002; Cavender-Bares et al. 2009). For example, water or nutrient scarcity may select for species with traits conferring low mean and variance in resource acquisition and growth, such as small thick leaves and high below-ground investment (Grubb 1977; Grime 1979; Diaz et al. 1998; Westoby et al. 2002; Westoby and Wright 2006). For continuous resource-acquisition traits, values are typically measured across single environmental gradients, or in two contrasting habitats, with the expectation that the gradient will filter community composition by limiting the range of trait values found at each site (Knops and Reinhart 2000; Ackerly et al. 2002; Meinzer 2003; Shipley and Almeida-Cortez 2003; Burns 2004; Hoffmann et al. 2005). In turn, such trait filtering leads to the expectation that communities will be phylogenetically clustered along gradients, since close relatives often share trait values (Webb et al. 2002; Cavender-Bares et al. 2009; Willis et al. 2010).

The expectation of close matching between environmental filters, functional traits, and evolutionary

relatedness may not be met, however, when a single trait reflects multiple abiotic factors, such as plant height responding to both light availability and disturbance (McGill et al. 2006); when environmental gradients are not independent of one another, such as correlations among temperature, moisture availability, and fire (Westerling et al. 2006); or when traits are physiologically and/or evolutionarily linked to one another, such as seed mass and seed number (Stearns 1992; Price 1997; Westoby et al. 2002; Vesk and Westoby 2004). Thus, successful interpretation of the environmental filtering of ecological assemblages may depend on understanding the functional, environmental, and phylogenetic relationships among key traits.

One of the most widely studied resource-use traits in plants is specific leaf area (SLA), also known as leaf area/dry mass (Reich et al. 1997; Cornelissen et al. 2003 and references therein). High SLA tends to be associated with high maximal rates of photosynthesis and growth, and thus with high rates of nutrient consumption and leaf turnover. Low SLA tends to reflect the opposing strategy of slow nutrient consumption, low growth rates and slow leaf turnover (Niinemets 2001; Westoby et al. 2002; Wright et al. 2004; Wright et al. 2005; Westoby and Wright 2006; Cornwell and Ackerly 2009; but see Lusk et al. 2010).

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The value of SLA as an indicator of broad resource-use strategies is demonstrated by its negative correlations with water use efficiency, nitrogen per unit leaf mass, photosynthetic capacity, leaf toughness, leaf longevity, leaf dry matter content, and stomatal conductance (Reich et al. 1997; Niinemets 2001; Wright et al. 2002; Reich et al. 2003; Wright et al. 2004; Hoffmann et al. 2005; Wright et al. 2005; Paula and Pausas 2006; Saura Mas et al. 2009). While individuals within species may vary in their SLA (Messier et al. 2010), among-species variation in SLA is generally considerably greater (Cornelissen et al. 2003), especially in heterogeneous environments (Cornwell and Ackerly 2009).

Community assembly along gradients of climatic favourability or soil fertility is expected to be strongly organised by resource-use strategy as measured by SLA. Species expressing higher SLA values should be found at the more favourable ends of these gradients, i.e. in more mesic (abundant rainfall, less extreme temperatures) climates and on more fertile soils (Lamont and Markey 1995; Hopper et al. 1997; Wisheu et al. 2000; Ackerly et al. 2002; Hoffmann et al. 2005; Cornwell and Ackerly 2009). However, these straightforward expectations may be too simplistic if SLA is linked functionally or phylogenetically to other, non-resource traits, or if there is a lack of independence among the environmental gradients selecting for functional traits.

In this article we examined the proposition that the resource-use strategies expressed in chaparral communities, as reflected by the distribution of community-level SLA values along gradients, are shaped not only by climate and soil fertility but also by fire. Chaparral is the Californian term for evergreen shrubland vegetation associated with Mediterranean climates; within these climates it tends to be found on well-drained and nutrient-poor soils such as sandstone and serpentine. Recurrent crown fires are a universal characteristic of chaparral, and chaparral shrubs show alternative strategies for post-fire regeneration (Keeley and Keeley 2000). Obligate resprouters are species that survive fire and re-establish by resprouting from underground roots, rhizomes or aerial buds; obligate seeders are those that are killed by fire and recruit from soil seed banks; and species using both strategies are called 'facultative seeders' (Table 1). These regeneration syndromes are not independent of resource-use strategies. Resprouting, which is favoured by high fire frequency and severity because it permits quick regeneration, comes at the cost of reduced growth because it requires high allocation to below-ground storage. Seeding, which is favoured by lower fire frequency and severity, requires enhanced adaptation to summer drought because of the extremely high mortality at the seedling stage (Keeley and Zedler 1978; Keeley 1981; Keeley et al. 2006; Pausas et al. 2006; Verdú and Pausas 2007). Thus, although SLA is not a fire-adaptive trait per se, fire regimes may affect it indirectly by the post-fire reproductive strategies for which they select (Clarke 2002a; Clarke 2002b; Clarke et al. 2005).

An additional link between fire and resource-use strategies lies in the environmental correlations among climate, soils, and fire. Fire regimes are affected by climate both directly (i.e. fire is more frequent where the dry season is longer and more severe) and indirectly through the effects of climate on plant biomass (i.e. fire may be more frequent or severe where productive climates lead to high fuel loads). Fire regimes may also be affected by soils; for example, plant communities on extremely infertile soils such as serpentine may have less frequent and severe fire because of their lower biomass accumulation and discontinuous canopy cover, leading to a higher prevalence of 'seeder' shrub species on these soils (Safford and Harrison 2004).

In the context of Californian chaparral, we asked whether it is reasonable to expect a dependable matching of a single trait such as SLA to individual environmental filters, or whether interaction terms representing the correlations among traits and among filters are required for a correct interpretation of environmental filtering. We tested the following hypotheses: (H₁) SLA is only affected by climate; (H₂) SLA is only affected by soil fertility; (H₃) SLA is only affected by fire frequency; and (H₄) SLA is affected by an interaction of several or all of these potential environmental filters.

Materials and methods

Study system

We examined 115 plots of chaparral community composition (Figure 1). The plots are from two datasets, referred to as 'McLaughlin' and 'Central Coast'. The McLaughlin plots were sampled on two soils (sandstone and serpentine) and two fire histories (recently burned and unburned); the Central Coast plots were sampled on one soil (sandstone) in two climatic zones (maritime and interior).

The McLaughlin plot data were collected at McLaughlin University of California Reserve, located in Napa, Lake, and Yolo counties, California, USA. The McLaughlin dataset includes 80 plots, each 50 m × 5 m, from two soil types: serpentine ($n = 40$) and sandstone ($n = 40$) (Safford and Harrison 2004). Half of the plots on each soil type burned in an arson fire on 16 October 1999, removing an average of 85% of the original shrub cover; half of the plots did not burn. We refer to these plots as 'recently burned' and 'unburned', respectively.

At McLaughlin, soil fertility is correlated with fire frequency and intensity, where chaparral on relatively fertile sandstone burns significantly more often than chaparral on very infertile serpentine (time since fire 18.6 ± 3.1 years on sandstone vs. 73.7 ± 39 years for serpentine) and with higher severity (Safford and Harrison 2004). Fire is less frequent and severe on serpentine because soil infertility limits biomass accumulation, as shown by positive severity–biomass correlations within soil types. Given their proximity, the plots at McLaughlin do not differ in climate.

The Central Coast data include 35 sandstone plots in the coastal ranges of California, spanning climatic zones

Table 1. Expected characteristics of chaparral species with regard to post-fire regeneration strategy.

Characteristic	Post fire regeneration strategy		
	Resprouter	Seeder	References
<i>Plant level</i>			
Allocation to storage	High	Low	(Pate et al. 1990; Bell et al. 1996; Bell 2001; Langley et al. 2002; Knox and Clarke 2005; but see Chew and Bonser 2009)
Growth rate	Low	High	(Pate et al. 1990; Bell et al. 1996; Bell 2001; Bond and Midgley 2003; Schwilk and Ackerly 2005; but see Chew and Bonser 2009)
Height	Uncertain	Uncertain	(Midgley 1996; Bond and Midgley 2003; Falster and Westoby 2005; Menges 2007)
Rooting depth	Deep	Shallow	(Bell et al. 1996; Bell 2001)
Fecundity	Low	High	(Lamont 1985; Verdú 2000; Bell 2001; Bond and Midgley 2001; Lamont and Wiens 2003)
<i>Ecological strategy</i>			
Fire	Tolerate	Avoid	(Odion and Davis 2000; Clarke 2002a; Clarke 2002b; Clarke and Knox 2002; Russell-Smith et al. 2003; Pausas et al. 2004; Clarke et al. 2005; Franklin et al. 2005; Ojeda et al. 2005; Keeley et al. 2006)
Drought/Aridity	Avoid	Tolerate	(but see Lamont and Markey 1995; Pausas et al. 2004; Clarke et al. 2005; Lloret et al. 2005; Ojeda et al. 2005; Pratt et al. 2008; Saura Mas et al. 2009)
Soil infertility	Avoid	Tolerate	(Lamont and Markey 1995; Wisheu et al. 2000; Safford and Harrison 2004)
Shading	Tolerate	Avoid	(Hawkes and Menges 1996; Menges 2007; Pratt et al. 2008)
Lifespan	Long	Short	(Bond and Midgley 2003; Lamont and Wiens 2003; Chew and Bonser 2009)
Competitive ability	Uncertain	Uncertain	(Schmalzer 2003; Clarke et al. 2005; Schwilk and Ackerly 2005; Chew and Bonser 2009; Clarke and Knox 2009) (Schmalzer 2003; Clarke et al. 2005; Schwilk and Ackerly 2005; Chew and Bonser 2009; Clarke and Knox 2009)

from maritime ($n = 17$) to interior ($n = 18$) (Figure 1). This climate transition integrates decreased presence of a summer marine fog layer, increased temperatures, decreased relative humidity, and decreased summer water availability. Field data from the 35 chaparral plots in summer 2009 showed large differences between maritime and interior (respectively) climate zones in daily average daily leaf wetness (50.2 ± 1.9 vs. $3.8 \pm 0.7\%$), vapour pressure difference (3.3 ± 0.3 vs. 21.4 ± 0.9 kPa), average daily maximum temperature (20.0 ± 0.4 vs. 31.8 ± 0.4 °C), and average daily soil water concentration (12.3 ± 0.1 vs. $2.3 \pm 0.2\%$) (means \pm one standard deviation; Vasey et al., in review).

Fire occurs less frequently in the maritime than the interior climatic zone due to a shorter fire season, associated with cooler, less seasonal temperatures, higher relative humidity, lower evapotranspiration, and higher rainfall (Odion and Tyler 2002). However, chaparral in the maritime climatic zone is found on infertile, shallow, and sandy soils relative to chaparral in the interior climatic zone, because these edaphic factors favour the persistence of chaparral vegetation (Griffin 1978; Sawyer et al. 2009).

Plant community composition and soil variables

At McLaughlin, woody plant community composition and cover was measured in 2002. Visual cover was estimated as

a measure of species abundances for species in each of five 1 m² quadrats spaced evenly along the centre-line of each plot. Cover values were then averaged for each species and each plot. For each plot, 50 g of soil were collected from the centre of each quadrat at 5–10 cm depth, mixed, and then analysed by A & L Western Agricultural Laboratories, Modesto, California, USA, for organic matter, K, Mg, Ca, and Bray P.

At the Central Coast plots, the plant composition and cover of woody plants for each of the 35 plots, each 50 × 20 m, was surveyed between 2003 and 2004 (Vasey et al., in review). Visual cover was estimated in 10 quadrats, each 10 × 10 m, to provide a mean abundance per species, per plot. Soil was collected from each quadrat at 5–10 cm depth, mixed together, and analysed by Brookside Laboratories, New Knoxville, Ohio, USA, for organic matter, K, Mg, Ca, and Bray P.

Climate and fire variables

To obtain climate data for each Central Coast plot, we intersected plot locations with maps of 10 macroclimate variables from the climate mapping system for the United States PRISM (<http://www.prism.oregonstate.edu/>). Variables were based on 30-year averages and had a resolution of 1 km². Variables were relative humidity (%), potential evapotranspiration (cm), annual temperature (°C),

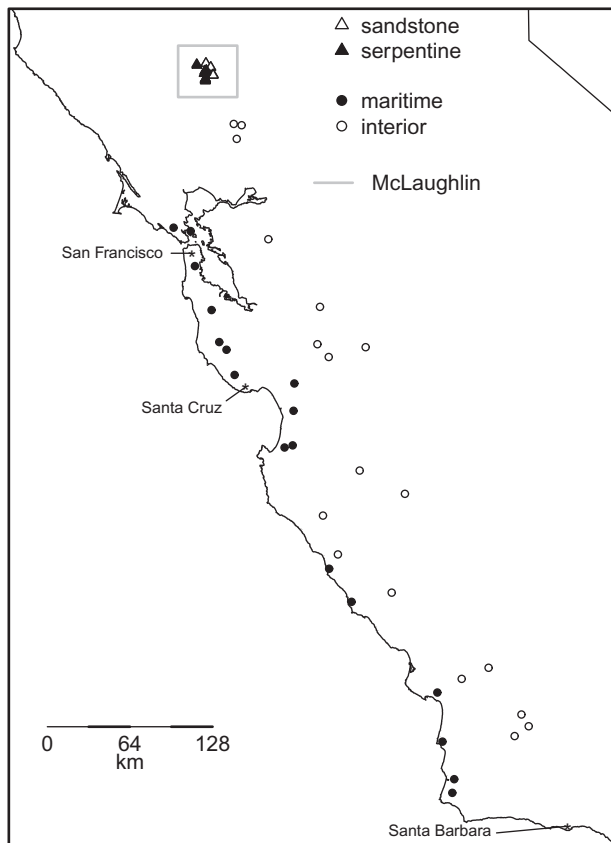


Figure 1. Locations of 115 chaparral study plots in western California. 80 plots were surveyed at McLaughlin, a University of California Natural Reserve, stratified by soil type (sandstone and serpentine) and burn history (recently burned and unburned). In addition, 35 plots were surveyed on sandstone soils in the Central Coast region; these plots were stratified by climatic zone (maritime and interior).

minimum winter temperature ($^{\circ}\text{C}$), maximum summer temperature ($^{\circ}\text{C}$), temperature seasonality (standard deviation), annual precipitation, winter precipitation, summer precipitation, and precipitation seasonality (coefficient of variation).

To obtain data on fire regimes, we intersected plot locations with raster grids (250 m^2) of ‘fuel rank’ and ‘fire rotation’ from the California Department of Forestry and Fire Protection’s Fire and Resource Assessment Program (CDF 2003, Fire Regime and Condition Class, Edition 03_2; <http://frap.cdf.ca.gov/data/frapgisdata/select.asp?theme=5>). Fuel rank is based on topography, vegetative fuel loads, and climate, and varied from -1 for ‘little or no fire hazard’ to 3 for ‘very high fire hazard’. The fire rotation data are also given in classes, and are based on annual acres burned, vegetation type, development status, elevation, and the bioregion; values range from 1 for ‘moderate frequency’ to 3 for ‘high frequency’.

Trait data – SLA and post-fire regeneration strategy

Mean SLA ($\text{mm}^2\text{ mg}^{-1}$) was obtained for the 87 species found in the plots (see Table 1 in Appendix 1) from several sources, primarily from new field measurements.

For 66 of the species, SLA was measured from new field collections, where 10 leaves were collected from each of 10 individuals. Individuals were sampled from at least three unique populations. To account for phenotypic plasticity of SLA with respect to soil, for species occurring on both serpentine and non-serpentine (34 of the 66 species), five individuals were sampled from each soil; for the others, all individuals were sampled from one soil type. Mean SLA per species was determined using a standard protocol (Cornelissen et al. 2003). For nine species, SLA data were available from The Ecological Flora of California (<http://ucjeps.berkeley.edu/efc/>), so new field measurements were not sought. For an additional 12 *Arctostaphylos* that were very geographically rare, we measured SLA using our own dried herbarium specimens. To validate using SLA from dried leaves versus fresh leaves for *Arctostaphylos*, we measured SLA from both dry leaves and from fresh leaves for 20 additional, more common *Arctostaphylos* taxa, and found that the two measures were highly correlated ($r^2 = 0.88$, $n = 20$, $b = 1.01$, intercept = -0.09 , $P < 0.001$). To examine intraspecific variation of SLA by soil type, soil type-specific SLA means were also calculated for the 34 species collected on two soils. In all analyses described below, mean SLA was log-transformed to meet the assumptions of parametric analyses. It is possible that the SLA values we determined for these species would differ if measured in other environments than those selected because genotypes and environments interact to determine phenotypes.

For each of the 87 species, we determined post-fire regeneration strategy using Hickman (1993), published literature, and expert opinion by the authors (primarily JK). We designated each species as an obligate resprouter, obligate seeder, or facultative resprouter (can resprout or recruit from seed following fire). Only 20% of our species can both resprout and post-fire seed, suggesting a negative trade-off between resprouting capacity and propagule persistence (Pausas 2001; Pausas and Verdu 2005).

Analyses

Correlated environmental filters. We tested if field-measured edaphic variables, remotely sensed macroclimate variables, and/or remotely sensed fire attributes differed among climatic zones (interior, maritime) using one-way ANOVA. Relationships of soil fertility, fire frequency and intensity, and recent burn history at McLaughlin, described above, are reported elsewhere (Safford and Harrison 2004), and thus new analyses were not conducted here.

Correlated traits. At the species level ($n = 87$), we tested whether SLA differed by post-fire regeneration strategy, using one-way ANOVA, and also repeated this analysis using a correction for phylogenetic non-independence (comparative analysis by independent contrasts (CAIC); details in Appendix 2).

The percentage of obligate seeders in each plot was calculated; percentages were weighted by abundance to

315 down-weight the relative influence of rare species on
 the description of functional structure. The abundance-
 weighted percentage for each plot was calculated as fol-
 lows: (sum abundance obligate seeders / sum abundance
 of all species) \times 100. We calculated community-level post-
 320 fire strategy with obligate seeders as the numerator because
 both facultative resprouters and obligate resprouters are
 ecologically similar in the sense that they can both resprout.
 For McLaughlin, we tested if the percentage of obligate
 seeders differed by soil type, burn history, and their interac-
 325 tion (two-way ANOVA). Prior to analysis, the percentage of
 obligate seeders was arc-sine transformed. For the Central
 Coast dataset, we tested if the percentage of seeders differed
 among climatic zones using one-way ANOVA.

Environmental correlates of SLA. At the community level,
 we tested if the mean abundance-weighted SLA observed
 330 in each plot at McLaughlin differed by soil type, burn his-
 tory, and their interaction (two-way ANOVA). For each plot,
 the mean abundance-weighted SLA was calculated by sum-
 ming the product of each species' SLA and its proportion
 of total cover in that plot, and then dividing by the number
 335 of species in that plot. We used the proportion of a species
 cover in each plot as our metric of abundance, rather than
 abundance alone. To examine for intraspecific variation in
 SLA by soil type, we compared the SLA of sandstone
 collections with the SLA of serpentine collections for the
 340 34 species collected from both soil types using a paired
t-test. For the Central Coast, we tested if abundance-
 weighted mean SLA differed among climatic zones using
 one-way ANOVA.

Environmental filtering of SLA. To test for filtering of SLA,
 345 the range of SLA for each community was calculated
 (range_{obs}) and compared with a null expectation of the
 range of SLA at the observed level of richness (range_{exp})
 (sensu Cornwell and Ackerly 2009). We randomly sam-
 350 pled the species pool, by data set, 9999 times for each
 level of observed species richness among the plots, and
 calculated the mean range of SLA values for each level of
 species richness. Communities in which a filter is operating
 will have range_{exp} > range_{obs}. We tested if the distribu-
 355 tion of range_{exp} - range_{obs} was significantly greater than
 zero using a one-tailed *t*-test. We then tested if range_{exp} -
 range_{obs} in each plot differed by soil type, burn history, and
 climatic zone using a two-way ANOVA. All analyses were
 performed in R version 12.0 (R Development Core Team
 2010).

360 Results

Correlated environmental filters

365 Serpentine plots had a significantly lower Ca:Mg ratio,
 higher organic matter content, and lower P and K levels
 than the sandstone plots. The less fertile maritime plots
 also had a significantly lower Ca:Mg ratio and lower P level
 than the interior plots (Table 2). There were higher fuel lev-
 els and also more frequent fires in interior plots than in
 maritime plots (Table 2). For the macroclimate variables,
 interior plots were shown to be significantly more arid

than maritime plots (lower relative humidity, higher poten- 370
 tial evapotranspiration, higher summer temperature, lower
 winter temperature, and higher temperature seasonality),
 although precipitation did not differ by zone (Table 2 in
 Appendix 1).

Correlated traits 375

At the species level, mean SLA was significantly higher in
 obligate resprouters than in either facultative resprouters
 or obligate seeders (one-way ANOVA: $F_{2,84} = 16.4$;
 $P < 0.001$) (Figure 2). This relationship was not signif-
 380 icant after correction for phylogenetic non-independence
 ($P = 0.327$) (Appendix 2), demonstrating shared variation
 among higher taxa.

The abundance-weighted percentage of seeders was
 significantly lower on sandstone soils compared to serpen- 385
 tine soils (Figure 3a), but this soil contrast disappeared
 in recently burned plots (two-way ANOVA: soil $F_{1,76} =$
 26.2 , $P < 0.001$; burn history $F_{1,76} = 21.9$, $P < 0.001$;
 soil \times burn history $F_{1,76} = 2.94$, $P = 0.09$; Figure 3a).
 For the Central Coast plots, there was a higher abundance-
 weighted percentage of obligate seeders in the low-fire, 390
 maritime climatic zone compared with the high-fire, inter-
 ior climatic zone (Table 2; Figure 3c). The Central Coast
 compared with McLaughlin had fewer obligate resprouters
 (0.40 vs. 0.54), more obligate seeders (0.38 vs. 0.27),
 and roughly the same proportion of facultative seeders 395
 (0.22 vs. 0.19).

Environmental correlates of specific leaf area

In the McLaughlin plots, abundance-weighted mean SLA
 was significantly higher on sandstone soils compared with 400
 serpentine soils (Figure 3b), regardless of burn history
 (two-way ANOVA: soil $F_{1,76} = 20.3$, $P < 0.001$; burn his-
 tory $F_{1,76} = 1.0$, $P = 0.31$; soil \times burn history $F_{1,76} = 0.3$,
 $P = 0.59$). Abundances were significantly lower on serpen-
 tine soils, but this difference was only present among the
 unburned plots (Figure 3c; two-way ANOVA: soil $F_{1,76} =$ 405
 6.1 , $P = 0.015$; burn history $F_{1,76} = 690.5$, $P < 0.001$;
 soil \times burn history $F_{1,76} = 4.9$, $P = 0.03$). In the Central
 Coast plots, abundance-weighted mean SLA was not signif-
 icantly different between climatic zones (Figure 3e), nor
 was abundance (Figure 3f). 410

Conspecifics had 18% higher mean SLA on sandstone
 than serpentine soil (paired *t*-test: $t = 2.31$, $df = 33$,
 $P = 0.027$). At the community level, in contrast, mean
 unweighted SLA was even greater, with values in sand- 415
 stone plots 32% higher than in serpentine. Thus, variation
 in SLA among communities was due to both compositional
 turnover and intraspecific variation (i.e. phenotypic plastic-
 ity), but species replacement played a larger role, similar
 to previous results for Californian woody plants (Cornwell
 and Ackerly 2009). 420

Environmental filtering of SLA

The range of SLA values for the McLaughlin plots was
 significantly lower than expected under the null model,

Table 2. Environmental differences by soil type (McLaughlin plots; sandstone, serpentine) and climatic zone (Central Coast plots; interior, maritime).

	<i>McLaughlin</i>				<i>Central Coast</i>			
	Sandstone	Serpentine	<i>F</i>	<i>P</i>	Interior	Maritime	<i>F</i>	<i>P</i>
<i>Edaphic</i>								
Ca:Mg ratio	3.4 ± 2.2	0.5 ± 0.5	69.1	< 0.001	6.9 ± 1.6	4.5 ± 3.4	7.2	0.011
Bray P (ppm)	7.0 ± 2.6	3.4 ± 1.8	53.0	< 0.001	37.6 ± 23.6	14.4 ± 33.5	5.5	0.025
K (ppm)	227.8 ± 62.8	128.5 ± 71.3	44.0	< 0.001	221.1 ± 76.7	172.6 ± 88.6	3.0	0.094
Organic matter (%)	4.3 ± 0.9	5.2 ± 1.5	9.5	0.003	5.0 ± 3.8	6.5 ± 1.8	2.2	0.152
<i>Fire</i>								
Fuel rank ¹	na	na	na	na	2.1 ± 0.5	1.6 ± 0.7	6.6	0.015
Fire rotation	na	na	na	na	2.6 ± 0.6	1.5 ± 1.1	15.3	0.001

Notes: Mean ± one standard deviation. *P* values are reported from one-way ANOVA of each variable with soil type or climatic zone. Degrees of freedom for McLaughlin are 1 and 78 for the factor and the residuals, respectively. Degrees of freedom for Central Coast are 1 and 33 for the factor and the residuals, respectively.

¹Higher fuel ranks correspond to higher potential fire hazard.

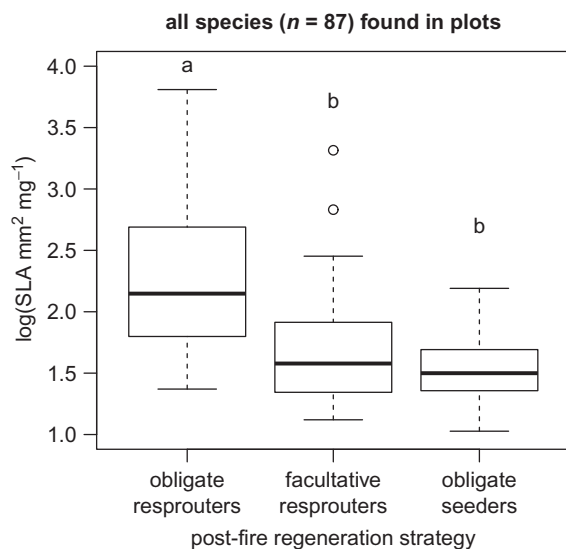


Figure 2. Relationship of SLA and post-fire regeneration strategy among the 87 species considered here. Letters above box-plots indicate significant differences based on a post-hoc Tukey's HSD test. Open circles indicate observations considered to be outliers.

425 indicating environmental filtering (54 of 80 had $\text{range}_{\text{exp}} - \text{range}_{\text{obs}} < 0$; $P = 0.004$) (Figures 4a, b). Filtering strength ($\text{range}_{\text{exp}} - \text{range}_{\text{obs}}$) was significantly higher on sandstone than serpentine (one-way ANOVA: soil $F_{1,78} = 15.7$, $P = 0.0002$; Table 2). Filtering strength was also related to burn history, and soil type × burn history (two-way ANOVA: soil $F_{1,76} = 18.4$, $P < 0.001$, burn history $F_{1,76} = 11.6$, $P = 0.001$; soil × burn history $F_{1,76} = 4.2$, $P = 0.044$). The interaction term reflected that filtering was significant for unburned plots on both soils and for recently burned plots on serpentine, but not recently burned plots on sandstone. 430 The range of SLA values for the Central Coast plots was not significantly lower than expected (17 of 35 had $\text{range}_{\text{exp}} - \text{range}_{\text{obs}} < 0$; $P = 0.378$) indicating a lack of filtering by climatic zone (Table 2, Figure 4c). 435

Discussion

Among Californian chaparral communities varying in climate, soil fertility, and fire histories, we found that SLA, a critical indicator of resource-use strategy, did not follow the simple patterns anticipated from considering individual filters. Within the McLaughlin data, SLA was lower on infertile serpentine soils, as expected, but fire also played a role in broadening the range of SLA present on more fertile sandstone soils (relaxing filtering). Within the Central Coast data, SLA did not follow any simple expectations, being higher neither in more equable maritime climates, nor in the interior where soils are more fertile and fires are more frequent. These results are most consistent with the hypothesis that SLA is affected by an interaction of climate, soil fertility, and fire. Key to understanding this interaction are the correlations we found, at both the species and community levels, between SLA and post-fire regeneration strategies, and also the environmental correlations between climate, soils, and fire frequency. 440 445 450 455

Obligate post-fire seeders had significantly lower SLA than obligate post-fire resprouters (Figure 2). This contradicts the notion that the reduced need for storage of the seeding strategy should lead to relatively higher growth rates and associated higher SLA in seeders (Table 1). The correlation we observed may reflect a physiological trade-off in which obligate seeding imposes strong selection for drought tolerance at the seedling stage (Ackerly 2004). 460 465 Infertile soils may also select for drought-tolerant seeders due to imposing arid conditions (high rock content, high exposure to direct sun, high rates of soil evaporation) (Ojeda et al. 2005; Pratt et al. 2008). While seeders have low allocation to roots and shallow rooting depth, and thus a limited ability to avoid drought by reaching water in lower soil horizons, they may tolerate soil aridity if they have leaf-level strategies, such as low SLA, that provide an advantage under low-resource conditions (Poorter et al. 2009; Saura Mas et al. 2009). Post-fire resprouters, in contrast, avoid drought by having deeper rooting systems (Bell et al. 1996; Bell 2001). 470 475

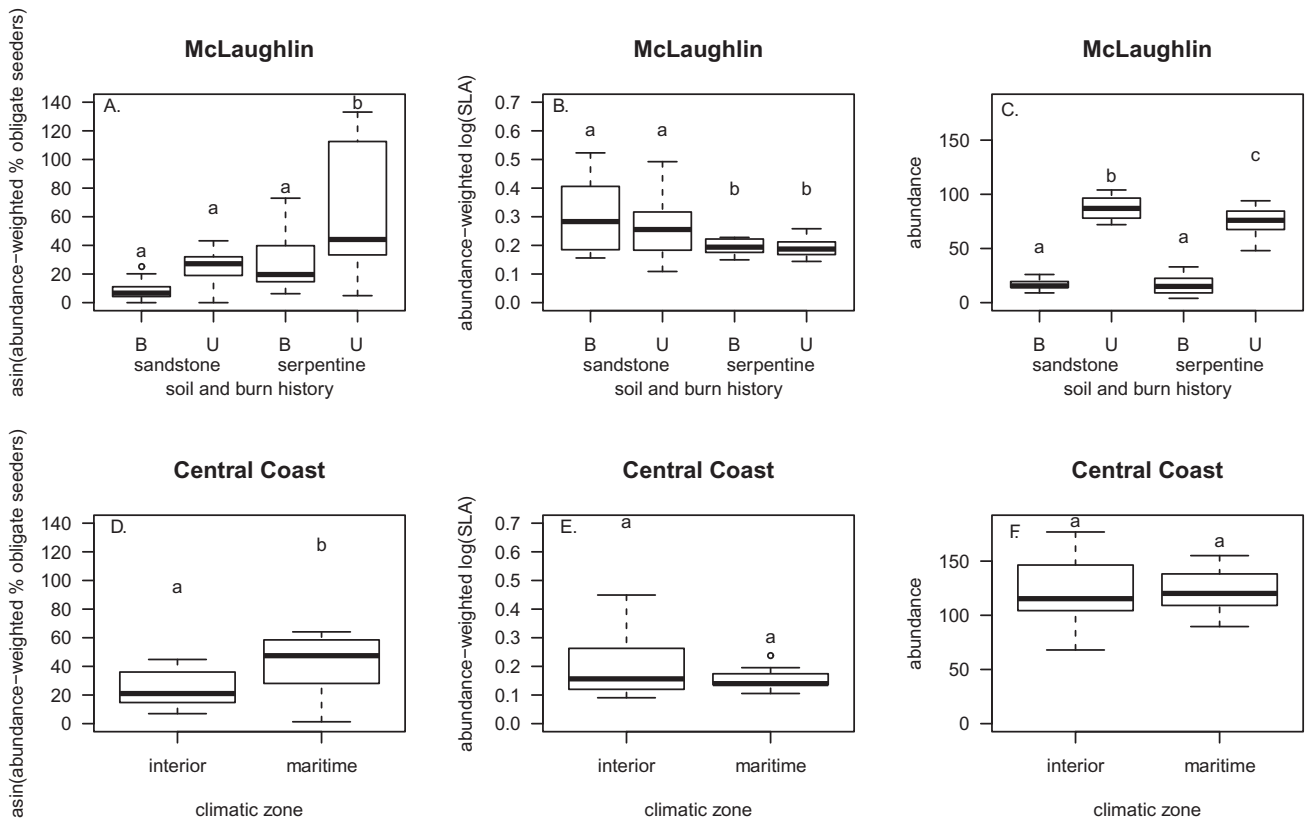


Figure 3. Plant community attributes for serpentine and sandstone soils (a–c) and interior and maritime climatic zones (d–f). Recent fire history is indicated for the McLaughlin data as follows: B = recently burned, U = unburned. Letters above boxplots indicate significant differences based on a post-hoc Tukey’s HSD test. Open circles indicate observations considered to be outliers.

480 The correlation between post-fire regeneration strategy and SLA was not significant in an analysis of phylogenetically independent contrasts, reflecting the influence of species-rich lineages (i.e. *Arctostaphylos* and *Ceanothus*; Appendices 1 and 2) that share particular trait combinations (e.g. post-fire seeding and low SLA) through common inheritance. This means that the observation of low SLA and obligate seeding in a community is in part due to common descent. In other words, an environmental filter may be directly selecting for obligate seeding, and thereby indirectly selecting for the correlated low SLA value, or vice versa. Similarly, a study of 37 plants of the Iberian peninsula showed phylogenetic non-independence among post-fire regeneration strategy and fruit type (Pausas and Verdu 2005). Such patterns of phylogenetic non-independence in traits are well known and form the basis of phylogenetic clustering in community structure (Webb et al. 2002; Anacker 2011).

495 The observed patterns of post-fire regeneration strategy confirmed that fire was more frequent on sandstone relative to serpentine (obligate seeders were more common in serpentine chaparral), and that fire was more frequent in the interior than on the coast (obligate seeders more common in maritime chaparral). In the arid interior, the infertile conditions of serpentine soil limit fuel accumulation, creating local fire refugia and favouring seeders. Along the coast, cool and wet climates limit the length and severity of the

505 fire season and the flammability of fuels, leading to low regional fire frequencies, favouring seeders; low soil fertility is likely important in determining the balance between woodland and chaparral (Griffin 1978; Sawyer et al. 2009), rather than affecting fire regime. Another factor favouring obligate seeding in maritime chaparral is that longer time intervals between fires may increase the severity of fires when they do occur, lowering adult survivorship.

510 Chaparral on serpentine soils at McLaughlin had significantly lower SLA than chaparral on sandstone even immediately following a fire (Figure 3), suggesting that soils play the dominant role in shaping SLA in this setting. However, our observation that low-SLA obligate seeders are much more prevalent on infrequently burning serpentine stands (Figure 3) suggests that fire does interact with soil to determine community-level SLA over longer time periods. In our Central Coast data, SLA did not differ between maritime and interior plots, even though mesic maritime climates should promote high SLA near the coast, while both frequent fire and more fertile soils are predicted to lead to higher SLA in the interior. Abundant evidence from other studies shows that SLA tends to be higher in productive habitats (reviewed in Cornelissen et al. 2003; Westoby and Wright 2006; Poorter et al. 2009), such as our maritime plots where water availability is high. Thus, one of our more striking findings is that the globally predominant role of climate in shaping SLA can be nullified by the

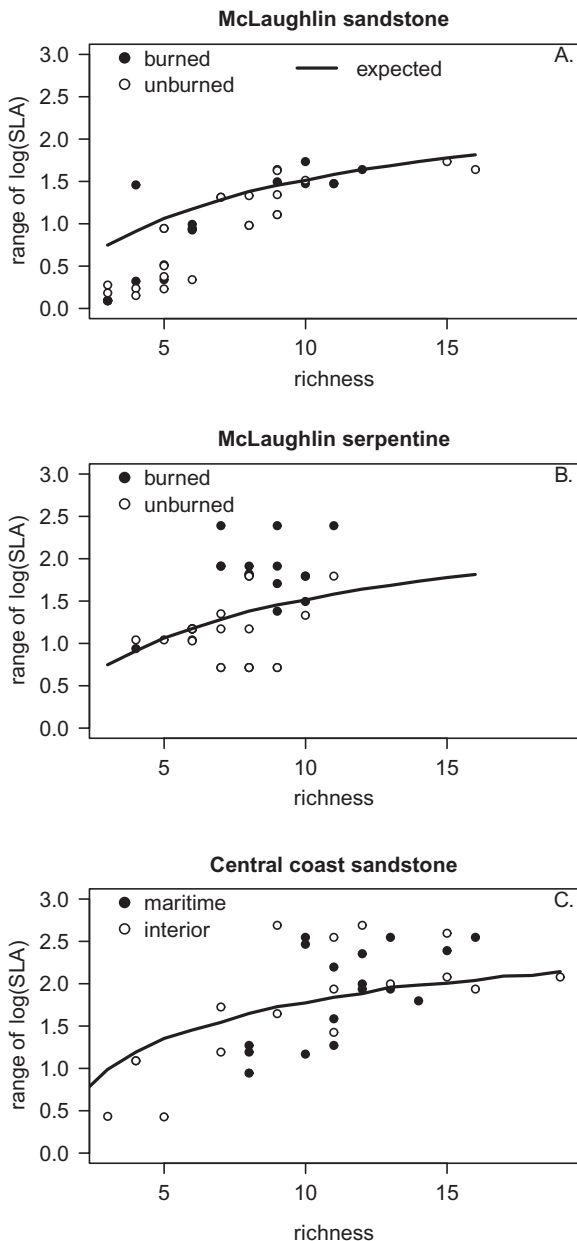


Figure 4. The range of SLA observed in chaparral plots versus null expectation. Points below the line have lower observed ranges than expected by chance.

more localised effects of soil fertility and fire, if these gradients happen to vary in the opposite direction with respect to their effects on SLA.

535 Conclusions

We found that community structure in Californian chaparral is shaped by the environmental filtering of a key resource-acquisition trait – SLA – by the simultaneous effects of climate, soil fertility, and fire. Interactive effects of these three filters arose from two factors: the phylogenetic and functional non-independence of SLA and another critical trait (post-fire regeneration strategy), and the non-independence of the three environmental filters

themselves. Our results provide a clear warning that incorrect inferences about functional and phylogenetic community structure may be reached when either traits or filters are considered in isolation. 545

Notes on contributors

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