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2 **Running head:** Demography and CWM trait turnover

3 **Title: Functional traits predict species responses to environmental variation in a Cali-**
4 **fornia grassland annual plant community**

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9 **Authors:** Gaurav S. Kandlikar^{1,2}, Andrew R. Kleinhesselink¹, Nathan J.B. Kraft¹

10 ¹ Dept. of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA.

11 ² Present address: Division of Biological Sciences, University of Missouri, Columbia, MO.

12 **Author for correspondence:**

13 Gaurav Kandlikar: gaurav.kandlikar@gmail.com

14 **Coauthor contact information:**

15 Andrew R. Kleinhesselink: arklein@ucla.edu

16 Nathan J.B. Kraft: nkraft@ucla.edu

17 **Abstract**

- 18 1. Turnover in species composition and community-wide functional traits across environmental
19 gradients is a ubiquitous pattern in ecology, and is generally assumed to reflect shifts in trait optima
20 across these gradients. However, the demographic processes that give rise to these trait turnover
21 patterns at the community level remain unclear.
- 22 2. We asked whether shifts in the community-weighted means of three key functional traits across an
23 environmental gradient in a southern California grassland reflect variation in the trait-performance
24 relationship across the landscape.
- 25 3. We planted seeds of 17 annual plant species in cleared patches with no competitors, and quantified
26 the lifetime seed production of 1360 individuals. We then asked whether models that included
27 trait-environment interactions help explain interspecific variation in demographic responses to the
28 environment. This allowed us to evaluate whether observed shifts in community-weighted mean
29 traits matched the direction of any trait-environment interactions detected in the plant performance
30 experiment.
- 31 4. Our results indicate that commonly-measured plant functional traits help explain variation in
32 species responses to the environment – for example, high-SLA species had a demographic advantage
33 in soils with high soil Ca:Mg levels, while low-SLA species had an advantage in low Ca:Mg soils. We
34 also found that shifts in community-weighted mean traits often reflect the direction of these
35 trait-environment interactions, though not all trait-environment relationships at the community level
36 reflect interactive effects of traits and environment on species performance.
- 37 5. Our results support the value of plant functional traits for predicting species responses to
38 environmental variation, and highlight a need for more detailed evaluation of how
39 trait-performance relationships change across environments to improve such predictions.

40 Introduction

41 Understanding how environmental variation shapes the diversity and dynamics of plant communities is a
42 fundamental challenge in ecology . In addition to variation in species composition (Whittaker 1960; Janzen
43 1967), turnover in the functional traits of plant communities across abiotic gradients has emerged as a
44 ubiquitous pattern across ecosystems (Cavender-Bares et al. 2004; Hulshof et al. 2013; Bjorkman et al.
45 2018; Jardine et al. 2020). These functional traits reflect key physiological and life history strategies of
46 plants, which ultimately determine variation in plant fitness across different environments (Violle et al.
47 2007; Reich 2014). One of the most common ways for plant ecologists to study trait-environmental
48 relationships has been to quantify variation in community-weighted mean (CWM) of functional traits
49 across landscapes. CWM trait values are calculated as species' trait values weighted by their relative
50 biomass or cover, and reflect the functional properties of the dominant plant species growing in a
51 community (Grime 1998; Garnier et al. 2004). Across ecosystems, communities with less harsh abiotic
52 conditions (e.g. lower drought stress, higher resource availability) tend to be dominated by plants with
53 functional traits that generally reflect resource-acquisitive strategies (e.g. higher specific leaf area or leaf N
54 concentrations (Reich 2014)), and vice-versa in environments that are less favorable for plant growth.
55 Shifts in CWM traits are often assumed to reflect variation in trait optima across environmental gradients,
56 with species whose traits closely match CWM expected to have highest fitness (Ackerly 2003; Shipley et al.
57 2006; Enquist et al. 2015).

58 Although shifts in the functional traits of plant communities across environmental gradients is
59 well-documented, the demographic processes driving these pattern remain unclear (Salguero-Gomez et al.
60 2018; Laughlin et al. 2020). As a result, predicting how variation in species functional traits drives
61 variation in community composition – one of the key promises of functional trait ecology (McGill et al.
62 2006; Westoby and Wright 2006)– remains a challenge. For example, Muscarella and Uriarte (2016) found
63 that a substantial portion of tree species in a tropical forest were more abundant in sites where their traits
64 were more dissimilar from the site's CWM, contrary to predictions of the hypothesis that CWM shifts
65 reflect shifts in trait optima. Part of the challenge is that we lack a clear understanding of whether CWM
66 trait shifts reflect variation in the relationship between functional traits and the vital rates
67 (e.g. germination rate, fecundity, survival rate) that ultimately determine species performance across
68 landscapes (Shipley et al. 2016).

69 One path forward is to pair observed shifts in CWM traits with analyses that evaluate the interactive
70 effect of traits environments on species' demographic rates (Laughlin and Messier 2015; Swenson et al.
71 2020). For example, in one of the few studies that has investigated whether CWM trait shifts reflect
72 variation in trait optima, Laughlin et al. (2018) found CWM shifts in leaf, root, and reproductive functional
73 to be unreliable predictors of how traits influence survival rates of plants in a pine forest system, also
74 contradicting the predictions of the idea that CWM trait shifts reflect shifting trait optima. It is important

75 for such analyses to quantify species fitness based on their vital rates or population growth rates rather
76 than species abundance measured at a single time point, which can be influenced multiple abiotic and
77 biotic processes (e.g. dispersal, competition, natural enemies) and is thus a poor proxy for intrinsic fitness
78 (e.g. Fox 2012; McGill 2012).

79 The impact of changing trait-performance relationships on CWM traits can be expected to take one of a
80 number of forms, some of which are illustrated in Fig. 1. If trait-performance relations remain constant
81 across an environmental gradient (Fig. 1B), any observed CWM trait shifts likely reflect the effects of
82 species interactions or other processes rather than shifting trait optima in terms of species' intrinsic
83 responses to the landscape. Trait-performance relationships may differ in magnitude but not in sign across
84 a gradient in a way that matches observed shifts in CWM traits (Fig. 1C). Such trait-performance
85 relationships with the same sign across the environmental gradient would not by themselves result in
86 differential distribution of traits across the landscape, but provide weak support that CWM trait shifts
87 reflect shifting trait optima. The strongest evidence that CWM trait shifts reflect shifting trait optima
88 would be if the sign of the trait-performance relationship changes across the gradient in a way that is
89 consistent with the CWM trait patterns (Fig. 1D). It is also possible that we find strong trait-environment
90 interactions when looking at the vital rates even when there are no observed CWM trait shifts. This might
91 indicate that other processes obscure underlying trait-performance relationships. A major challenge in
92 testing for concordance between CWM trait shifts and variation in trait-performance relationships has
93 been that quantifying how trait variation influences species demography across landscapes is very
94 data-intensive, requiring plant performance data across large temporal and spatial gradients. Although
95 such data are becoming increasingly available for a wide range of perennial plants (e.g. Salguero-Gomez et
96 al. 2014), short-lived plant communities, where we can quantify relevant vital rates on fairly short time
97 scales, offer an ideal system in which to test for concordance between trait-performance relationships and
98 CWM trait shifts.

99 In order to address this longstanding question of how whether trait shifts at the community level
100 reflect variation in trait optima across the landscape, here we compared CWM trait shifts to the interactive
101 effects of traits and environment on species' fitness in a southern California serpentine annual grassland
102 community. We surveyed the plant community at sites that captured a wide range of variation in soil
103 Ca:Mg, sand content, and depth – three axes of abiotic variation that are known to be important in such
104 serpentine communities. To capture various dimensions of plant ecological strategies, we quantified
105 community-wide variation in one leaf trait (specific leaf area), one root trait (specific root length), and one
106 whole-plant trait (maximum height). In a parallel experiment, we quantified the intrinsic fitness (lifetime
107 fecundity of individuals growing without competitors) of 17 annual plant species that naturally occur in
108 this community and that capture a wide range of functional variation. We then asked whether observed
109 CWM trait shifts reflect trait-environment interactions that shape variation in species' fecundity across this

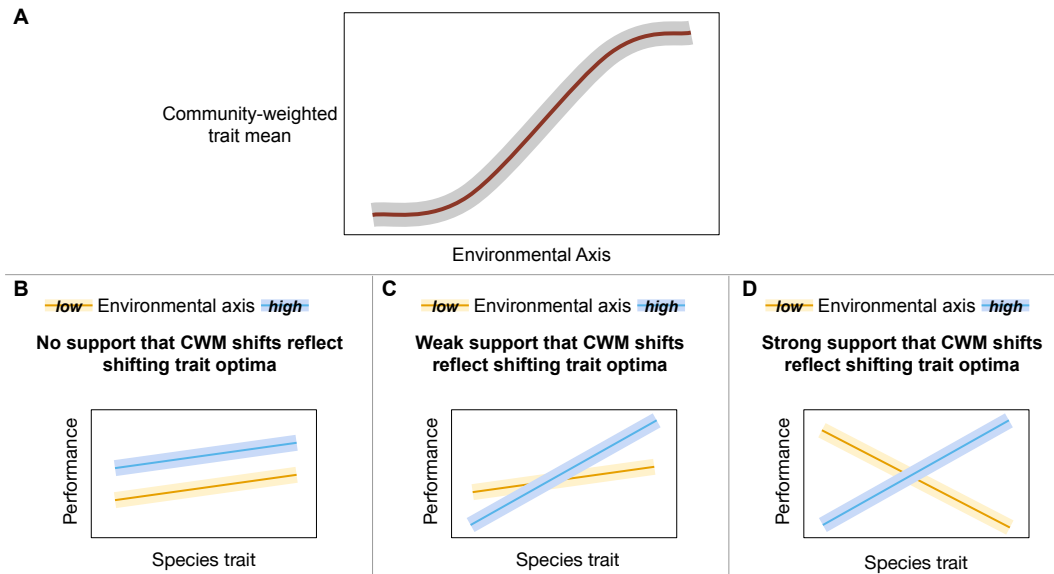


Figure 1: A) Variation in community-weighted mean (CWM) functional traits across gradients is a common pattern in plant communities, though whether or not such variation in CWM traits reflects shifts in trait optima across environmental gradients. Here we evaluate whether CWM shifts in plant functional traits reflect shifts in trait-performance relationships across key environmental gradients. Panels B-D illustrate how trait-performance relationships might vary across environments. B) The trait-performance relationship may be identical at opposite ends of the environmental gradient, indicating that other factors (e.g. dispersal limitation) might drive observed shifts in CWM traits. We interpret this as a lack of evidence that CWM trait-environment relationships reflect variation in trait optima across the environment. C) The trait-performance relationship may change across the environmental gradient in a direction that is consistent with observed CWM shifts, but the sign of the trait-performance relationship may be the same at either end of the gradient. We interpret this as providing weak evidence that CWM shifts reflect changing trait optima. D) The sign of the trait-performance relationship may change across the gradient, such that species with low trait values have a relative advantage at the low end of the environmental gradient, and vice versa at the high end of the gradient. We interpret this as strong evidence that CWM shifts reflect changing trait optima.

110 gradient. Our results show that shifts in CWM traits can provide valuable information into how trait
111 optima shift across gradients, but also caution against predicting species responses to environmental
112 variation on the basis of shifts in CWM traits alone.

113 **Methods**

114 **Study system**

115 We studied trait-environment relations in the grassland community at the University of California
116 Sedgwick Reserve in southern coastal California. This region experiences a Mediterranean climate of cool,
117 wet winters and long, dry summers. Plant phenology in this system is driven largely by the rainfall
118 regime: seeds of plants germinate with early-season rain storms in November and December, and plants
119 begin to reproduce and senesce with the onset of summer droughts (though there is substantial variation
120 in the timing of reproduction among species (Godoy and Levine 2014; Kraft et al. 2015)). The reserve
121 encompasses significant topographic and edaphic heterogeneity, including oak-savanna, coastal sage
122 scrub, and California grassland communities. Our study focused on a part of the reserve with
123 serpentine-derived soils that are dominated by invasive *Avena* and *Bromus* spp. In this area, rocky
124 serpentine outcrops (“hummocks”) are embedded within a matrix of deep, clay soil. The outcrops are
125 considerably less vegetated than the matrix soils, and act as spatial refuges for several native plant species
126 (Gram et al. 2004). We studied trait-environment interactions at 16 sites on this landscape, with 10 sites
127 located on serpentine hummocks and 6 in the matrix.

128 **Quantifying species performance across the landscape**

129 In November 2015, before the first major rain storm of the season, we cleared all existing vegetation in 2m
130 X 3m plots at each of our 16 focal sites. At each site, we sowed five replicate plots with the equivalent of
131 20-60 viable seeds each of our 17 focal species (Table S2) on a grid with 15 cm spacing between each
132 species. We collected seeds from hundreds of plants growing across Sedgwick Reserve in the spring prior
133 to this study, and seeds were homogenized among sources before planting to ensure that local adaptation
134 (Rajakaruna and Bohm 1999) or maternal effects (Germain and Gilbert 2014) did not systematically drive
135 variation in plant performance across sites in our experiment.

136 In February 2016, we counted the number of germinants of each focal species in our experimental plots,
137 and thinned each plot to leave only two individuals of each focal species. In March, we further thinned
138 each point down to a single individual of each species, and weeded around this focal individual to ensure
139 that it was not competing with other plants in a 15cm radius. Between April-June 2016, we quantified the
140 total seed output of each focal individual in our experiment, for a total of 1360 individuals (17 species * 16
141 sites * 5 plots per site) tracked across the environment (see Appendix S1 for details on how we estimated
142 total seed output). This design let us quantify the germination rate and the per-germinant seed production

143 (fecundity) in the absence of competitors for each species at each site. Both of these vital rates are known
144 to be important determinant of annual plant demography in this community (Levine and HilleRisLambers
145 2009), but we focus only on fecundity as a measure of species performance in the remainder of this study
146 because the functional traits we measured most clearly relate to the growth of plants after germination.

147 **Measuring compositional turnover across the landscape**

148 In Spring 2017 (the year after the experimental assessment of plant performance), we surveyed five
149 undisturbed plots (0.5x0.5m) adjacent to the experimental plots at each of our 16 sites to characterize the
150 vascular plant community composition. These community survey plots were spaced evenly on a 10m
151 transect located alongside the cleared plots in which we had experimentally quantified plant performance
152 in the prior year. In each plot, we visually estimated the total (absolute) cover of each of species in early
153 April, and again in early June.

154 **Functional trait measurement**

155 Kraft et al. (2015) had previously measured 11 functional traits (Table S1) that to capture ecologically
156 important variation in leaf, root, whole-plant, and reproductive functioning of plant species for most
157 species in our demography experiment (12 out of 17 species; note that *U. lindelyi* was misidentified
158 *Agoseris heterophylla* in that study). In Spring 2016, we measured the same set of traits for the five species in
159 our experiment that were not part of Kraft et al. (2015)'s study: *Bromus madritensis*, *Chaenactis glabriuscula*,
160 *Hordeum murinum*, *Micropus californica*, and *Vulpia microstachys*. We followed the protocols detailed in Kraft
161 et al. (2015) to measure traits from 5-8 individuals growing in 0.7*0.7m plots at three of the matrix sites in
162 our experiment, which we had sowed with seeds of all 17 annual plant species for a total sowing density
163 of 8g viable seeds/m². In Spring 2017, we measured the same set of functional traits on the 38 of the most
164 common annual plant species encountered within the community composition plots (of the species for
165 which we could not measure at least one of the focal traits, mean cover of these species in sites where they
166 were present was < 5%).

167 Our analysis focuses on three traits that capture distinct dimensions of plant ecological strategies and
168 that were largely uncorrelated in a principal components analysis of the traits we measured (Fig. S1):
169 specific leaf area (SLA), specific root length (SRL), and maximum height. SLA, the ratio of leaf area to dry
170 mass, is strongly linked to species' position along the leaf economics spectrum (Wright et al. 2004) and at a
171 global scale is positively correlated to photosynthesis and growth rate (Adler et al. 2014). SRL, the ratio of
172 fine root length to dry mass, reflects the area over which roots can uptake resources relative to biomass
173 investment, is an important component of the root economics spectrum (Laliberte 2016; Weemstra et al.
174 2020). At both a global scale (Weemstra et al. 2016) and within our study (Fig. S1), SRL is largely
175 uncorrelated with SLA. Species with higher SRL tend to have superior nutrient acquisition capability, but

176 are generally more susceptible to attack by pathogenic microbes (Eissenstat 1992; Laliberte et al. 2014).
177 Maximum height is a globally relevant trait (Díaz et al. 2016) that integrates across various dimensions of
178 ecological strategy and can indicate the ability of adult plants to preempt and intercept light (Westoby et
179 al. 2002). The 17 focal species of our performance experiment reflected a wide range of variation observed
180 across the plant community for these three traits (Fig. S2)

181 **Environmental sampling**

182 We quantified various soil chemical and physical characteristics to identify the primary axes of
183 environmental variation among our study sites. We measured gravimetric water content ((weight of fresh
184 soil - weight of dry soil)/weight of dry soil) in the early- and mid- growing season (March and April,
185 respectively), and summarized across these measurements to estimate the average soil moisture at each
186 site. At each site, we also collected soil for analysis by A&L Western Agricultural Laboratories (Modesto,
187 CA) for a variety of soil chemical and physical properties: soil organic matter, P (Weak Bray and Olsen
188 methods), K (ppm), Mg (ppm), Ca (ppm), Na(ppm), pH, CEC, NO₃, SO₄, NH₄, and soil texture (sand, silt,
189 and clay content). We collected the soil for these analysis from three points arranged in between the five
190 experimental plots, and homogenized within site prior to analysis. We also programmed iButtons (Maxim
191 Integrated) to log temperature at 2-hr intervals, and used these data to quantify the average daily
192 maximum temperature at each site. To avoid direct solar radiation on iButtons, we placed them in
193 anchored PVC tubes with holes for airflow. Based on a PCA of all environmental variables (Fig. S3), we
194 focus on soil Ca:Mg, soil sand content, and soil depth as biologically relevant and largely uncorrelated
195 environmental variables that capture the primary axes of abiotic variation among our study sites.

196 **Analysis**

197 *Quantifying community-weighted trait turnover across the landscape*

198 We used the community composition and functional trait measurements to calculate the
199 community-weighted mean (CWM) trait values, which represent the mean trait value of all species
200 growing at a site, weighted by the species' relative cover. We calculated the CWM for each trait (t) at each
201 of our 16 sites (s) by averaging across the CWM of the five plots p at each site as follows:
202 $CWM_{t,s} = \frac{1}{5} \sum_{p=1}^5 \sum_{i=1}^n t_i c_{i,p}$, where n is the number of species found in each plot, t_i is the mean trait value
203 of species i , and $c_{i,p}$ is the relative cover of species i in the plot p . We then evaluated whether CWM traits
204 vary across the environmental gradient in our study with simple bivariate linear regressions between each
205 of the three focal traits and each of the three focal environmental characteristics ($\alpha = 0.05$). We also tested
206 for evidence of nonlinear trait-environment relations by including a quadratic term in the predictor
207 (environmental) variables.

208 *Quantifying the functional trait basis for variation in species performance across the environment*

209 We next asked whether observed CWM trait shifts across the environmental gradients in our study reflect
210 variation in the trait-performance relationship in the demography experiment. We used `glmmTMB` (Brooks
211 et al. 2017) to fit a generalized linear mixed effects model with each focal individual's seed production as
212 the response variable, and with the three focal environmental variables, three focal functional traits, and
213 nine pairwise trait-environment interaction terms as predictors. The model also included random effects
214 for species identity and site, and was fit with a zero-inflated negative binomial error structure. We
215 log-transformed all functional trait values, and scaled all parameters to help with model convergence. We
216 used `performance` (Lüdecke et al. 2020) to quantify model fit and to ensure that the model did not suffer
217 from collinearity of predictors (variation inflation factors < 2), and used `DHARMA` (Hartig 2020) to evaluate
218 the model residuals. We also compared the AICc of the model with all trait-environment interaction terms
219 to a null model and one with only the main trait and environment effects as predictors to verify that the
220 interaction terms were supported ($\Delta\text{AICc} > 2$ in favor of the model with trait-environment interactions).
221 Finally, we used `effects` (Fox and Weisberg 2018) to evaluate the trait-performance relationship at the
222 highest and lowest value of the environmental gradient in our study based on the marginal effects of the
223 model. We considered trait-environment interactions that were significant in the model, but whose slope
224 did not change sign across the environmental gradient, as weak evidence that CWM trait shifts reflect
225 shifts in trait optima across the landscape (Fig. 1C). If the sign of the trait-performance sign shifted in the
226 direction predicted by CWM trait shifts, we considered this as strong evidence that CWM trait shifts
227 reflect shifts in trait optima across the landscape (Fig. 1D).

228 We conducted all analyses in R v. 3.6.3 (R Core Team 2020) and provide code to recreate all analyses in
229 appendix S2. All data are available as supplementary files and will be deposited in to an archival
230 repository prior to publication.

231 Results

232 Community-wide trait turnover at Sedgwick

233 The plant species in our study system vary considerably in their functional traits. Across the 55 species we
234 observed across the landscape, there was 3 fold variation in SLA (5th percentile = $124.83\text{cm}^2/\text{g}$, 95th
235 percentile = $433.8\text{cm}^2/\text{g}$), 9 fold variation in SRL (5th percentile = $32.26\text{m}/\text{g}$, 95th percentile = $290.67\text{m}/\text{g}$),
236 and 10 fold variation in Maximum Height (5th percentile = 11.38cm, 95th percentile = 108.7cm). This trait
237 variation was strongly structured along various environmental axes in our study. We observed strong
238 positive relationships between CWM SLA and soil Ca:Mg and soil depth (Fig. 3A-B), a strong negative
239 relationship between CWM SRL and soil sand content (Fig. 3C), and a strong positive relationship
240 between CWM max height and soil depth (Fig. 3D). We also found evidence that CWM SRL tends to be
241 highest at intermediate values of Ca:Mg (Table S3).

242 Environmental and functional trait drivers of variation in species performance

243 The fixed effects of our GLMM with all the main and interactive effects explained 18% of the variation in
244 seed production (Marginal $R^2 = 0.18$), and the random effects of species and site explained an additional
245 19% of the variation (Conditional $R^2 = 0.37$). The model included significant positive main effects of soil
246 Ca:Mg ($p = 0.016$) and soil depth ($p = 0.016$), indicating that seed production was higher in sites with
247 higher Ca:Mg and deeper soils, irrespective of plant traits (Fig 2). The main effect of maximum height was
248 also significant and positive ($p = 0.005$), indicating higher seed output from larger-statured plants across
249 the environmental gradient (Fig 2).

250 The model also provided evidence that three out of the four significant relationships between CWM
251 traits and environmental variables reflect variation in trait-performance relations across the environmental
252 gradient. We found strong evidence that the positive relationship between CWM SLA and soil Ca:Mg (Fig.
253 3A) reflects a shift in the trait-performance relationship on this landscape. Seed production was shaped by
254 a significant positive interaction between SLA and soil Ca:Mg, which caused the sign of the
255 SLA-performance relationship to shift from negative in the lowest-Ca:Mg site to positive in the highest
256 Ca:Mg site (Fig 3E). We found similarly strong evidence that the negative relationship between CWM-SRL
257 and soil sand content (Fig. 3C) reflects shifts in trait-performance relationships. Seed production was
258 shaped by a significant negative interaction between SRL and soil sand content, which caused the sign of
259 the SRL-performance to shift from positive in the least sandy site, to negative in the most sandy sites in
260 our study (Fig 3G). The model also provided weak evidence that the positive relationship between CWM
261 max height and soil depth (Fig. 3D) reflects shifts in trait-performance relationships. Seed production was
262 shaped by a significant positive interaction between maximum height and soil depth, though this
263 interaction only reflected a more positive max height-performance relationship in deeper than in
264 shallower soils, rather than a change in the sign of the trait-performance relationship across the soil depth
265 gradient (Fig. 3H). The model did not provide any evidence that the negative CWM SLA-soil depth
266 relationship (Fig. 3B) reflected a change in the SLA-performance relationship across the soil depth
267 gradient in our study (Fig. 3F). Finally, in no case did the model identify a trait-environment interaction in
268 the demography experiment for which we did not also find a corresponding relationship in the CWM trait
269 analysis (Fig. S4).

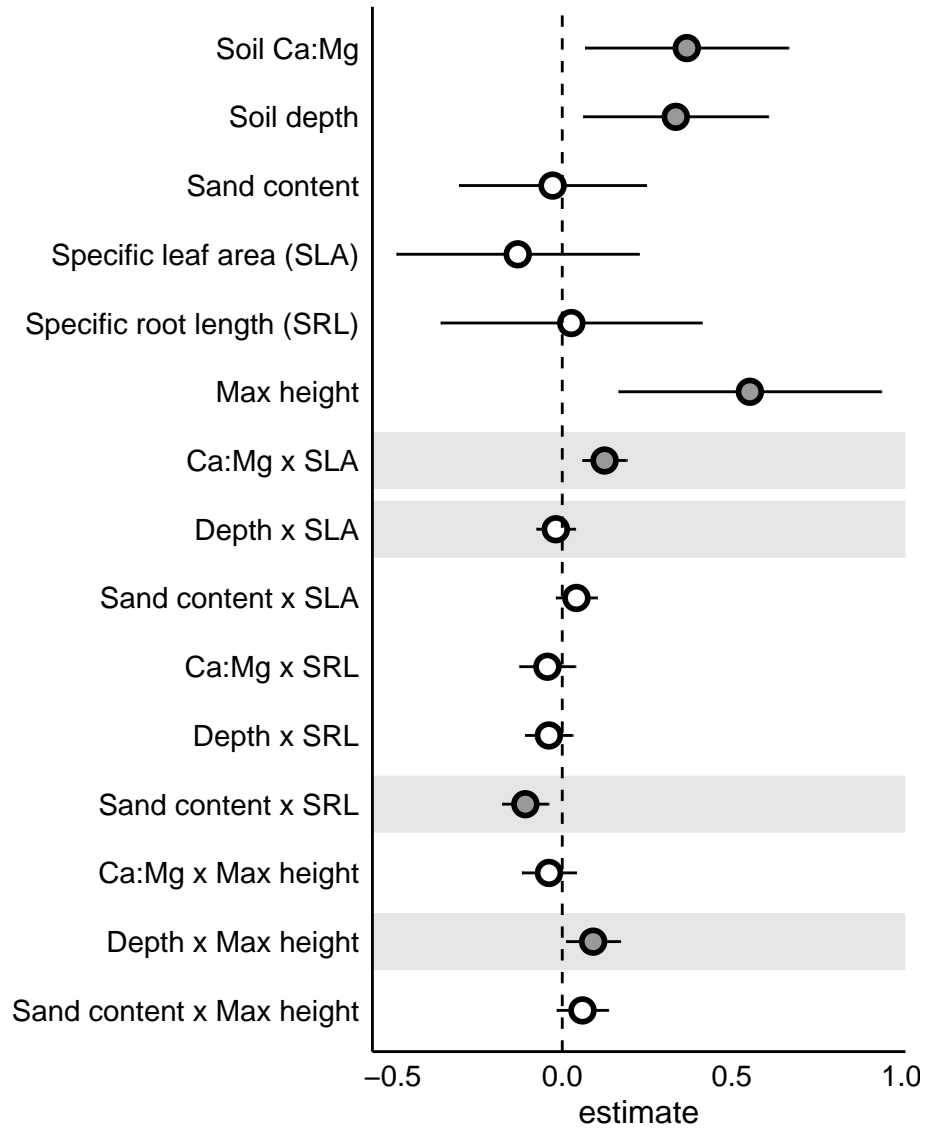


Figure 2: Standardized effects of environmental variables, functional traits, and their interactions on seed production. Grey points indicate those effects whose 95% confidence intervals (indicated by thin bars) do not overlap zero. Horizontal grey bars indicate the four significant trait-environment relations we observed in the CWM trait analysis.

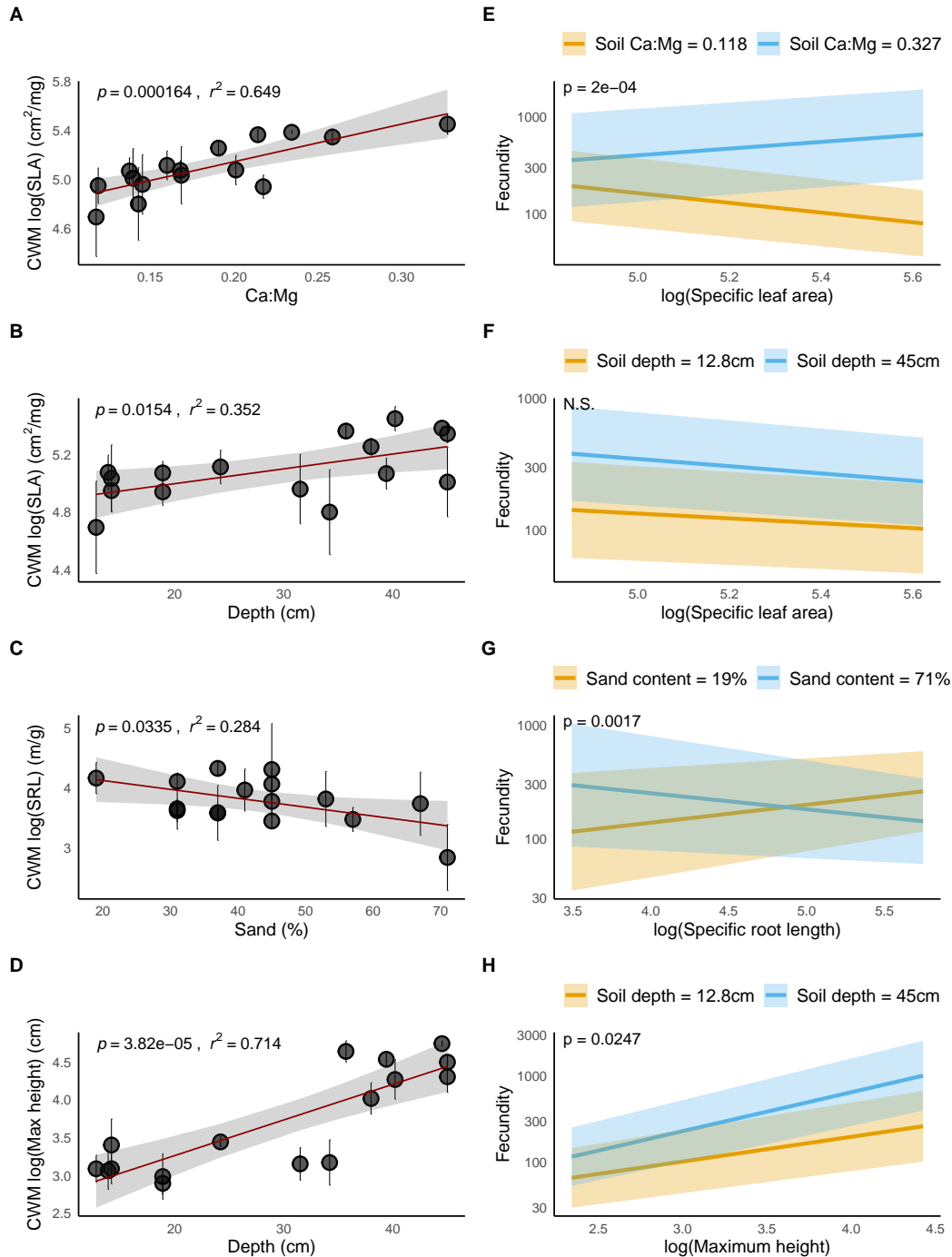


Figure 3: Plots A-D show the four significant relationships we observed between environmental variables and community weighted mean traits (points indicate means and bars show the 95% confidence interval at each site). Panels E-H show the corresponding trait-environment interactions from our GLMM, with yellow lines showing the trait-performance relationship at the lowest value of the environmental variable observed in our study, and the blue lines at the highest. Translucent bands in all panels represent the 95% confidence intervals. Note that model predictions were made with scaled values of trait and environmental predictors, which were back-transformed onto their original scale for visualization. Plots of all non-significant trait-environment relationships are available in Fig. S4, and 3D surfaces for each interaction in Fig. S5.

270 Discussion

271 Turnover in community-weighted trait means across environmental gradients is a ubiquitous pattern in
272 nature, but whether these patterns reflect shifts in trait-performance relations across environmental
273 gradients remains poorly understood (Shipley et al. 2016). As a result, predicting plant species'
274 demographic responses to environmental variation on the basis of their functional traits remains
275 challenging (Laughlin and Messier 2015). Quantifying trait-performance relations across environmental
276 gradients at the community level is a key step in improving our ability to project how plant communities
277 will respond to environmental change. Here, we asked whether patterns of community-weighted mean
278 trait turnover in three key functional traits reflect variation in the trait-performance relationships across
279 three abiotic gradients in a southern California serpentine grassland community. We found evidence that
280 three out of the four significant trait-environment relationships at the community level reflect shifts in
281 trait-performance relationships across the gradients. Quantifying how traits mediate species'
282 demographic responses across their life remains a key step in improving our ability to use functional traits
283 to predict plant community responses to environmental variation.

284 We found three trait-environment interactions structuring both the whole plant community as well as
285 variation in the seed production of focal species in our experiment on this landscape. The positive
286 relationships between CWM SLA and soil Ca:Mg is consistent with other studies that have found lower
287 CWM SLA in serpentine soils than in soils with weaker serpentine characteristics (Fernandez-Going et al.
288 2013), and with the general finding of increasing CWM SLA in more fertile soils (e.g. Cornwell and
289 Ackerly 2009). Our GLMM analysis of the focal species' seed production suggests that this
290 community-level pattern may arise in part because the value of SLA that confers the optimal fitness
291 (measured here as the intrinsic fecundity of plants when not facing competitors) shifts along the Ca:Mg
292 gradient. Our model included a significant positive main effect of soil Ca:Mg, indicating that all plants
293 performed better in high-Ca:Mg than low-Ca:Mg soils, irrespective of their traits. However, the magnitude
294 SLA-Ca:Mg interaction term indicates that lower SLA was associated with higher intrinsic fitness at soils
295 with low-Ca:Mg, and vice-versa in high-Ca:Mg soils (Fig. 3E). This is consistent with the general
296 expectation of lower SLA being correlated with a suite of traits that confer plants greater tolerance of
297 abiotic stress, at the cost of a relative disadvantage when abiotic stress is less limiting (Wright et al. 2004;
298 Sterck et al. 2006). For example, lower SLA was correlated with higher water use efficiency (Fig. S1),
299 which may give low-SLA species a relative advantage in low-Ca:Mg sites, which also tended to have
300 lower soil moisture in this system (Fig. S3).

301 We also found a negative relationship between CWM SRL and sand content (Fig. 3C). This relationship
302 is contrary to Laughlin et al. (2018), who found a positive CWM SRL-soil sand content relationship and a
303 positive interactive effect of SRL and soil sand content on plant survival in a pine-dominated forest in
304 Arizona. This discrepancy may have arisen in part because in our system, soil sand content was generally

305 much higher on serpentine hummocks that were also characterized by low soil moisture and organic
306 matter (Fig. S3). In this context, the negative relationship between CWM SRL and sand content is
307 consistent with the more general expectation of low SRL indicating a resource-conservative strategy that
308 allows plants outperform species with resource-acquisitive strategies in more stressful conditions (Reich
309 2014). Moreover, our analysis of trait and environmental predictors of seed production provides strong
310 evidence that this community-level pattern is in part driven by low-SLA species having higher intrinsic
311 fecundity in sandy soils, and vice-versa in soils with low sand content (Fig. 3C). Understanding the
312 drivers of variation in trait-environment interactions among different plant communities remains a key
313 challenge in building towards a more predictive trait ecology (Funk et al. 2016), and may be achieved with
314 more studies that couple observational studies at the community level with species-level analyses of
315 trait-environment interactions.

316 The third trait-environment interaction for which we found evidence for in both the observational
317 study and in our demography experiment was the positive interaction between soil depth and maximum
318 height (Fig. 3D). This finding of a positive CWM max height-soil depth relationship is consistent with the
319 distribution of plant height along soil depth gradients in other Mediterranean grassland communities
320 (Bernard-Verdier et al. 2012). This community-level pattern may be driven by a positive interactive effect
321 of maximum height and soil depth on intrinsic fecundity (Fig. 3H). However, this interaction term
322 provides only weak evidence that the turnover in CWM max height across soil depth reflects a shifting
323 trait-performance relationships, because seed production was also influenced by a significant positive
324 main effect of species' max height. In other words, even though the relative advantage to taller species is
325 diminished in shallower vs. deeper soils, tall species had higher intrinsic fecundity than short species
326 across the depth gradient. Although the interactive effect of maximum height and soil depth on intrinsic
327 fecundity alone may not be sufficient to drive trait shifts across the landscape, trait-performance
328 relationships in other vital rates may compound this effect to give rise the community-wide trait turnover
329 in maximum height. For example, Kraft et al. (2015) previously found that taller species have a
330 competitive advantage over shorter species in a pairwise competition experiment conducted on matrix
331 soils in this landscape. Shallower soils on serpentine hummocks are also characterized by lower density of
332 vegetation (Gram et al. 2004) and potentially less severe light competition, which could provide a
333 competitive advantage to shorter species if there is a tradeoff in aboveground vs. belowground
334 competitive ability (DeMalach et al. 2016). Future studies that investigate trait-performance relationships
335 in various demographic processes will be critical for understanding how plant traits determine overall
336 population growth rates and this influence community assembly processes across landscapes.

337 Although three three of the four CWM trait-environment correlations in this study seem to at least
338 qualitatively reflect the direction of the trait-environment interaction in terms of species' intrinsic
339 fecundity, we did not find such evidence for the positive CWM SLA-soil depth correlation (Fig. 3B,F). This

340 raises the question of what might drive the community-level association between species' SLA and soil
341 depth. It is possible that the rather than influencing how intrinsic fecundity of species responds to
342 variation in soil depth, SLA might instead mediate the response of other vital rates to this environmental
343 gradient. It is also possible that the CWM SLA-depth relationship arises due to trait-environment
344 interactions between other correlated traits or environmental variables which are not reflected in our
345 analysis of intrinsic fecundity (Marks and Lechowicz 2006; Laughlin and Messier 2015). In general, that
346 the CWM SLA is strongly correlated with soil depth even though SLA does not appear to mediate
347 variation in intrinsic fecundity across the soil depth gradient highlights the potential pitfalls in predicting
348 species' demographic responses to environmental gradients on the basis of community-wide patterns of
349 trait turnover.

350 Our analysis also allows us to ask whether any trait-environment interactions mediate variation in
351 species performance but do not appear to turn over across the environmental gradient at the community
352 level. We did not find any evidence for trait-environment interactions influencing species performance
353 that did not manifest in CWM trait turnover (Fig. S4). This suggests that in our annual grassland system,
354 trait-environment interactions that shape variation in species' intrinsic fecundity in different environments
355 do manifest in trait turnover at the community level. In comparison, Laughlin et al. (2018) found a strong
356 negative interactive effect of SLA and soil C:N on plant survival, but did not observe a negative CWM
357 SLA-C:N relationship at the community level. It is possible that community patterns in annual-dominated
358 communities are more sensitive to underlying species-level trait-environment interactions than the
359 perennial system in Laughlin et al. (2018)'s study. Coupling empirical studies with simulations of
360 community dynamics in systems dominated by plants of differing life histories will help to build a more
361 general understanding of the mapping between species- and community-level trait-environment
362 interactions.

363 Our overall finding that shifts in CWM traits across environmental gradients often reflect shifts in
364 trait-performance relations but are not perfect predictors of trait optima is consistent with other studies
365 that have investigated variation in CWM traits and species performance on a landscape (Muscarella and
366 Uriarte 2016; Laughlin et al. 2018). However, our study also had some important limitations. First, the 17
367 species we used in our experiment to quantify intrinsic fecundity across the landscape did not include
368 several of the most dominant species in our observational community composition plots (e.g. *Avena fatua*,
369 *A. barbata*, *Bromus diandrus*, *Microseris douglasii*, and *Lolium perenne* each achieved >50% cover in at least
370 one 1x1 plot across the 16 sites, but were not part of the experiment). Moreover, the functional traits of
371 some of the most dominant species were beyond the range of functional traits captured by the 17 species
372 in our demography experiment (e.g. all five of the aforementioned dominant species had SRL values
373 below those of the 17 species in the experiment, Fig. S2). As CWM trait values are intrinsically reflective of
374 dominant species' responses to the landscape, it is possible that including more species that captured a

375 wider range of the trait variation found in our community would reveal trait-environment interactions
376 that drive trait turnover patterns at the community level.

377 A second limitation of our study is that we were unable to account for the possibility that intra-specific
378 trait variation (ITV) driven by local adaptation, phenotypic plasticity, or maternal effects – processes that
379 are known to be important in similar serpentine systems (Rajakaruna and Bohm 1999; Baythavong 2011;
380 Germain and Gilbert 2014) – mediate trait-environment relations at either the community or individual
381 scale. However, our finding that trait-performance relationships do change across the environmental
382 gradient generate predictions for future studies about how ITV may be structured on this landscape. For
383 example, our result finding that the optimal value of SLA shifts from low to high with an increase in soil
384 Ca:Mg (Fig. 3E) suggests that ITV may be structured such that individuals of the same species growing in
385 soils with higher Ca:Mg build higher-SLA leaves than conspecific individuals on low-Ca:Mg soils.
386 Understanding how the spatial structure of ITV differs between species may be critical for predicting
387 variation between species in their demographic responses to environmental gradients (Swenson et al.
388 2020).

389 **Conclusion**

390 Understanding and forecasting how species and communities respond to environmental variation is a
391 fundamental challenge in ecology. Predicting variation in species-level demographic processes based on
392 patterns in trait turnover across whole communities is a promising approach, but most methods to do so
393 have relied on the assumption that variation in community-weighted mean (CWM) traits reflect shifts in
394 trait optima over landscapes. Our study found consistent evidence that variation in CWM traits across
395 environmental gradients reflect the effects of changing trait-performance relationships, but they our
396 results caution against inferring likely demographic responses of plants to environments on the basis of
397 CWM traits alone. Future efforts that link plant traits to variation in population growth across variable
398 environments rates will help build towards more predictive trait-based models of plant community
399 dynamics.

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526 **Supplemental figures**

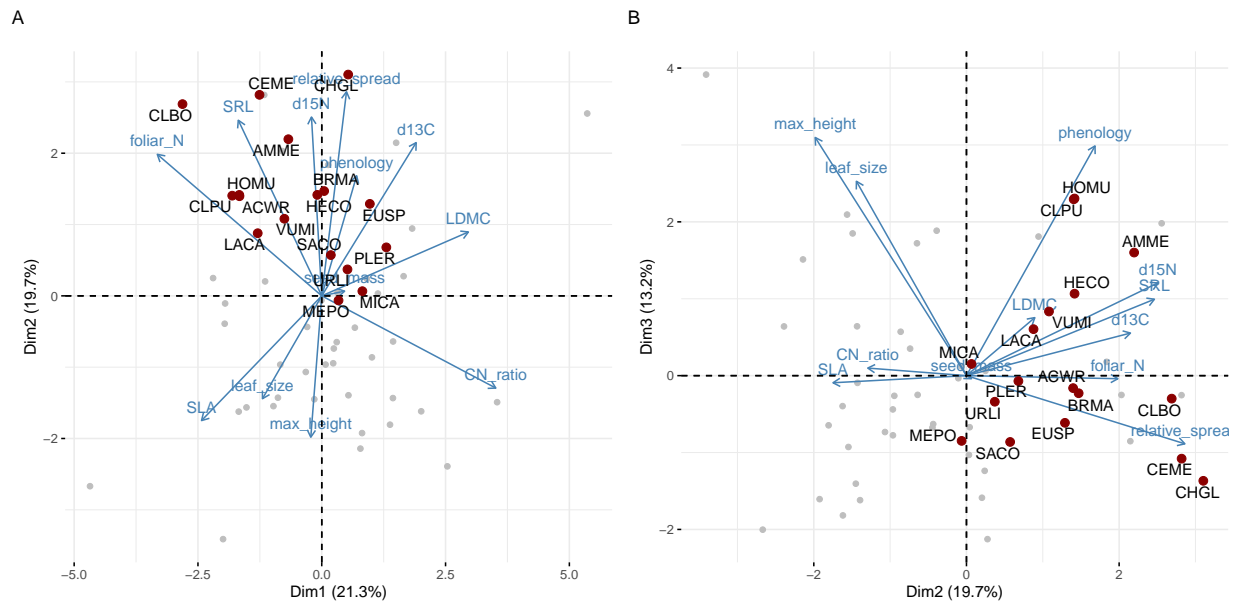


Figure S1: Biplots of axes 1/2 (Panel A) and axes 2/3 (Panel B) from a PCA of the functional traits measured for this study. Light grey points indicate the position of the species found across the community (N = 55), and red points indicate the position of each of the focal species of the demography experiment (N = 17)

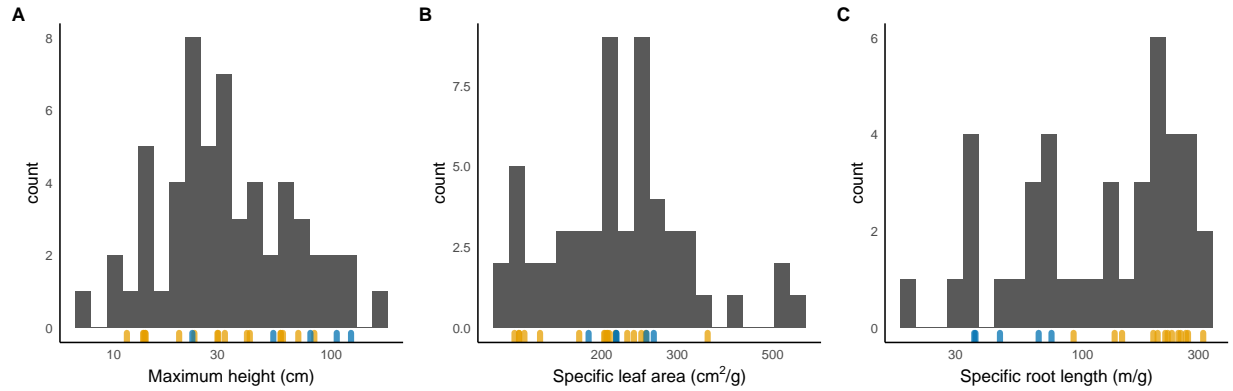


Figure S2: Histograms of the three focal for all species encountered in the Serpentine grassland at Sedgwick Reserve. Each blue tick at the bottom of the histograms indicates the trait value for one of the focal species in the demography experiment, and the orange ticks indicate trait values of species that were dominant in the community (relative cover > 50 in at least one site) but absent in our experiment. Note the log-transformed X-axis in each panel.

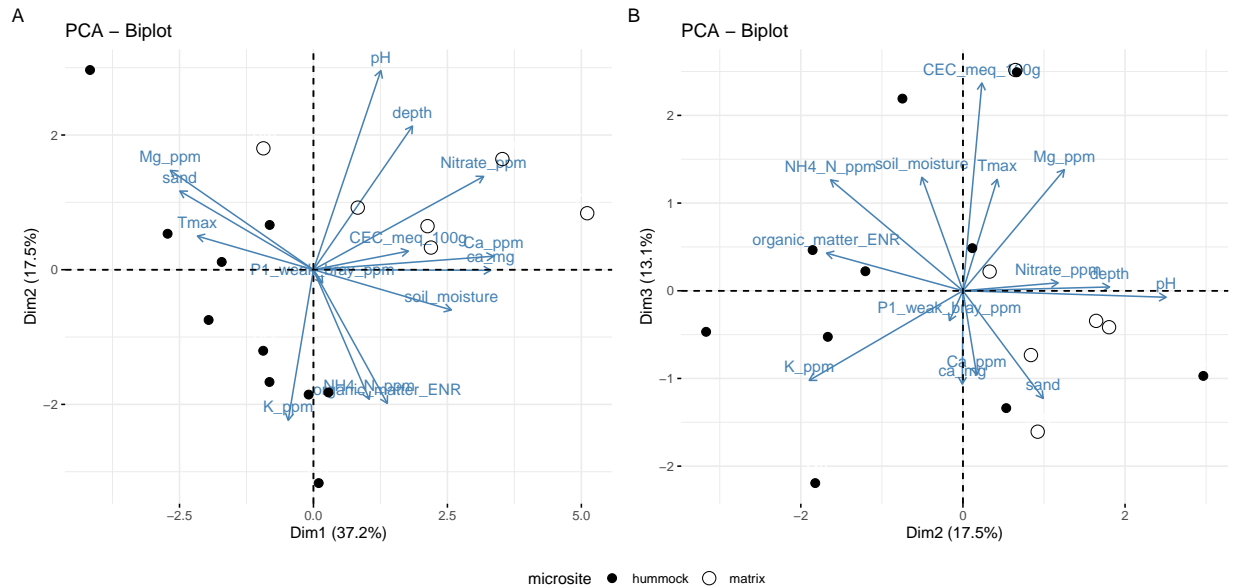


Figure S3: Biplots of axes 1/2 (Panel A) and axes 2/3 (Panel B) from a PCA of the environmental gradients measured for this study.

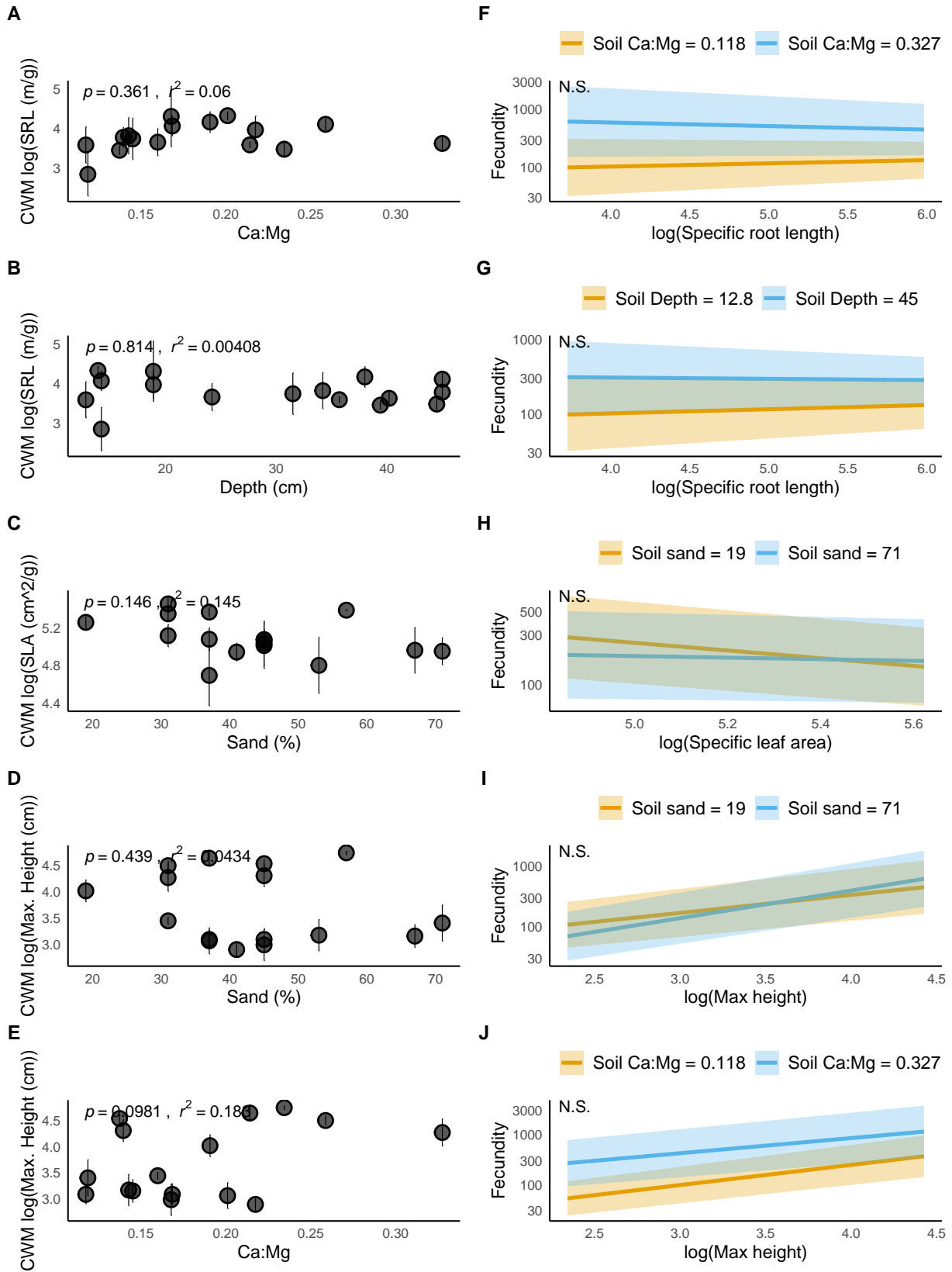


Figure S4: Panels A-E are biplots of CWM trait values and environmental variables for the five pairwise comparisons that were non-significant. Panels F-J show the corresponding trait-environment interactions in the model of seed output as a function of trait and environmental predictors.

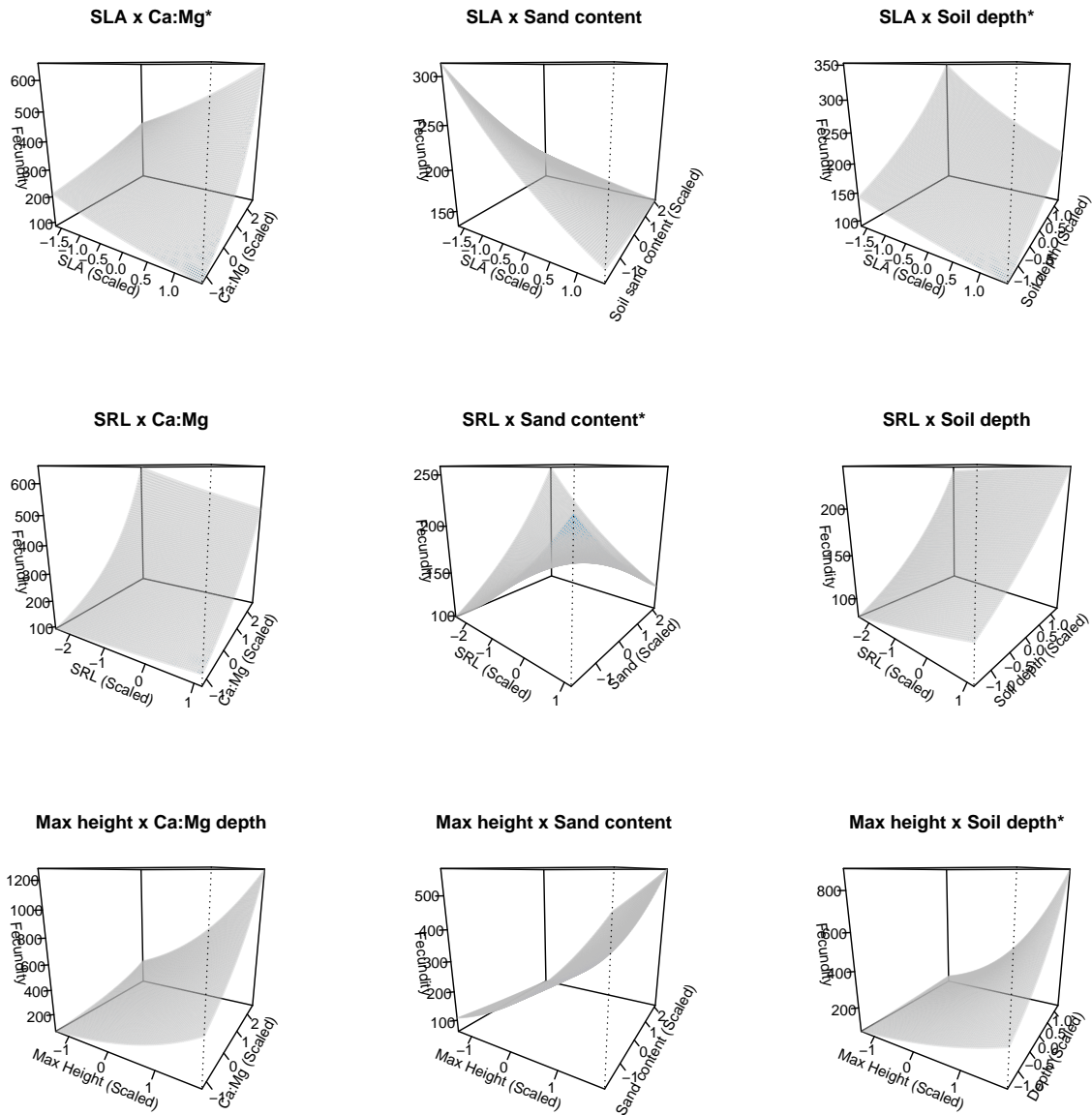


Figure S5: 3D interaction surfaces for all nine trait-environment interactions in our GLMM of seed production as a function of trait and environment predictors. Plots labeled with an asterisk indicate significant interaction terms.

Table S1: List of traits measured for this study

Organ	Trait	Units
Whole plant	Max. height	cm
	Canopy shape index	dimensionless
	Carbon isotope composition (dC13)	dC13
	Phenology	day of year
	Seed mass	mg
Leaf	Leaf size	cm ²
	Specific leaf area	g/cm ²
	Leaf dry matter content	mg/g
	C:N ratio	dimensionless
	Leaf N concentration	mg/g
Root	Specific root length	m/g

Table S2: Species used in the demography experiment.

Family	Species	Name in Kraft et al. 2015
Asteraceae	<i>Centaurea melitensis</i>	same
	<i>Chaenactis glabriuscula</i>	N/A
	<i>Hemizonia congesta</i>	same
	<i>Lasthenia californica</i>	same
	<i>Micropus californica</i>	same
	<i>Uropappus lindleyi</i>	<i>Agoseris heterophylla</i>
Boraginaceae	<i>Amsinckia menziesii</i>	same
Euphorbiaceae	<i>Euphorbia spathulata</i>	<i>Euphorbia peplus</i>
Fabaceae	<i>Acmispon wrangelianus</i>	<i>Lotus wrangelianus</i>
	<i>Medicago polymorpha</i>	same
Lamiaceae	<i>Salvia columbariae</i>	same
Onagraceae	<i>Clarkia bottae</i>	N/A
	<i>Clarkia purpurea</i>	same
Plantaginaceae	<i>Plantago erecta</i>	same
Poaceae	<i>Bromus madritensis</i>	N/A
	<i>Hordeum murinum</i>	N/A
	<i>Vulpia microstachys</i>	N/A

Table S3: Model output for quadratic relationships between CWM traits and environmental variables

trait	environment	term	estimate	std.error	statistic	p.value
SLA	Ca:Mg	Intercept	4.1710630	0.3810	10.9473	0.0000
SLA		Linear	6.7997132	3.7945	1.7920	0.0964
SLA		Quadratic	-8.8295749	8.8486	-0.9978	0.3366
SLA	Depth	Intercept	4.8685302	0.3669	13.2676	0.0000
SLA		Linear	0.0039068	0.0296	0.1322	0.8968
SLA		Quadratic	0.0001119	0.0005	0.2187	0.8302
SLA	Sand	Intercept	5.6767840	0.5039	11.2652	0.0000
SLA		Linear	-0.0211202	0.0225	-0.9375	0.3656
SLA		Quadratic	0.0001628	0.0002	0.6820	0.5072
SRL	Ca:Mg	Intercept	1.3091538	0.9470	1.3824	0.1901
SRL		Linear	24.1034774	9.4310	2.5558	0.0239
SRL		Quadratic	-53.0592298	21.9926	-2.4126	0.0313
SRL	Depth	Intercept	3.7116730	0.8014	4.6316	0.0005
SRL		Linear	0.0093611	0.0645	0.1450	0.8869
SRL		Quadratic	-0.0001975	0.0011	-0.1768	0.8624
SRL	Sand	Intercept	3.6723606	0.7948	4.6207	0.0005
SRL		Linear	0.0207823	0.0355	0.5849	0.5686
SRL		Quadratic	-0.0003831	0.0004	-1.0175	0.3275
Max. Height	Ca:Mg	Intercept	2.9756663	1.9356	1.5373	0.1482
Max. Height		Linear	2.8657993	19.2769	0.1487	0.8841
Max. Height		Quadratic	5.5585773	44.9527	0.1237	0.9035
Max. Height	Depth	Intercept	3.4516879	0.7104	4.8586	0.0003
Max. Height		Linear	-0.0486766	0.0572	-0.8508	0.4103
Max. Height		Quadratic	0.0016727	0.0010	1.6891	0.1150
Max. Height	Sand	Intercept	4.4618081	1.7386	2.5663	0.0235
Max. Height		Linear	-0.0246015	0.0777	-0.3165	0.7566
Max. Height		Quadratic	0.0001513	0.0008	0.1837	0.8571

527 **Appendices**