RESEARCH ARTICLE

Functional traits predict species responses to environmental variation in a California grassland annual plant community

Gaurav S. Kandlikar © | Andrew R. Kleinhesselink © | Nathan J. B. Kraft ©

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA

Correspondence
Gaurav Kandlikar
Email: gaurav.kandlikar@gmail.com

Present address
Gaurav S. Kandlikar, Division of Biological Sciences, Division of Plant Sciences & Technology, University of Missouri, Columbia, Missouri, USA

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Abstract

1. Turnover in species composition and the dominant functional strategies in plant communities across environmental gradients is a common pattern across biomes, and is often assumed to reflect shifts in trait optima. However, the extent to which community-wide trait turnover patterns reflect changes in how plant traits affect the vital rates that ultimately determine fitness remain unclear.

2. We tested whether shifts in the community-weighted means of four key functional traits across an environmental gradient in a southern California grassland reflect variation in how these traits affect species’ germination and fecundity across the landscape.

3. We asked whether models that included trait–environment interactions help explain variation in two key vital rates (germination rates and fecundity), as well as an integrative measure of fitness incorporating both vital rates (the product of germination rate and fecundity). To do so, we planted seeds of 17 annual plant species at 16 sites in cleared patches with no competitors, and quantified the lifetime seed production of 1360 individuals. We also measured community composition and a variety of abiotic variables across the same sites. This allowed us to evaluate whether observed shifts in community-weighted mean traits matched the direction of any trait–environment interactions detected in the plant performance experiment.

4. We found that commonly measured plant functional traits do help explain variation in species responses to the environment—for example, high-SLA species had a demographic advantage (higher germination rates and fecundity) in sites with high soil Ca:Mg levels, while low-SLA species had an advantage in low Ca:Mg soils. We also found that shifts in community-weighted mean traits often reflect the direction of these trait–environment interactions, though not all trait–environment relationships at the community level reflect changes in optimal trait values across these gradients.

5. Synthesis. Our results show how shifts in trait–fitness relationships can give rise to turnover in plant phenotypes across environmental gradients, a fundamental pattern in ecology. We highlight the value of plant functional traits in predicting species responses to environmental variation, and emphasise the need for more
1 | INTRODUCTION

Understanding how environmental variation shapes the diversity and dynamics of plant communities is a fundamental challenge in ecology. In addition to variation in species composition (Janzen, 1967; Whittaker, 1960), turnover in the functional composition of plant communities across abiotic gradients is a longstanding pattern in ecology (Schimper, 1898) that continues to motivate new research (Bjorkman et al., 2018; Cavender-Bares et al., 2004; Hulshof et al., 2013; Jardine et al., 2020), especially in the field of trait-based ecology (McGill et al., 2006; Westoby & Wright, 2006). These functional traits reflect key physiological and life-history strategies of plants, which ultimately determine variation in plant fitness across different environments (Adler et al., 2014; Reich, 2014; Violle et al., 2007). One of the most common ways for plant ecologists to study the relationship between functional trait composition and environmental gradients has been to quantify variation in the community-weighted mean (CWM) of functional traits across landscapes. CWM trait values are calculated as species’ trait values weighted by their relative biomass or cover, and reflect the functional properties of the dominant plant species growing in a community (Garnier et al., 2004; Grime, 1998). Across ecosystems, communities with less harsh abiotic conditions (e.g. lower drought stress, higher resource availability) tend to be dominated by plants with functional traits that generally reflect resource-acquisitive strategies (e.g. higher specific leaf area or leaf N concentrations; Reich, 2014), and vice versa in environments that are less favourable for plant growth. Such CWM–environment relationships are often assumed to reflect variation in trait optima across environmental gradients, with species whose traits closely match the local CWM expected to have highest fitness (Ackerly, 2003; Enquist et al., 2015; Shipley et al., 2006).

Although CWM–environment relationships are well documented, the extent to which they arise from shifts in trait effects on species fitness remains unclear (Laughlin et al., 2020; Salguero-Gomez et al., 2018). At the most basic level, trait variation across landscapes can be driven by changes in species demographic rates (e.g. germination, survival, fecundity) across environmental gradients. These demographic (vital) rates influence the capacity of species to establish or persist in different environments, and if there is a functional basis to these demographic changes across gradients (cf. Violle et al., 2007), we expect the resulting communities to show changes in CWM as well. While this is a fairly common expectation, few studies have directly explored whether patterns of CWM trait turnover across gradients consistently reflect shifts in trait–performance relationships (Shipley et al., 2016; but see Laughlin et al., 2018). Furthermore, the link between CWM–environment relationships and underlying shifts in trait optima across gradients may be obscured for a variety of reasons. For example, species with traits that confer high fitness at a given point along an abiotic gradient may be absent in the local community due to dispersal limitation rather than any deterministic effects of the environment (Pinto & MacDougall, 2010). Alternatively, traits associated with high fitness in the absence of biotic interactions may also make species more sensitive to competition and/or natural enemies such that species with high intrinsic fitness may fail to become dominant on a landscape (e.g. Tilman, 1990). In the context of rapid environmental change, mismatches between CWM-environment and trait-performance relationships may also arise due to lags in how quickly demographic processes reshape whole communities (Laughlin et al., 2020). As a result, predicting how variation in species functional traits drives variation in community composition—one of the key promises of functional trait ecology (McGill et al., 2006; Westoby & Wright, 2006)—remains a challenge.

One path forward is to pair observed shifts in CWM traits with analyses that evaluate the interactive effect of traits environments on species’ fitness (Laughlin & Messier, 2015; Swenson et al., 2020). For example, in one of the few studies that has investigated whether CWM trait shifts reflect variation in trait optima, Laughlin et al. (2018) found shifts in CWM leaf, root and reproductive functional traits to be unreliable predictors of how traits influence species’ survival rates in a pine forest system, contradicting the idea that CWM trait shifts reflect shifting trait optima. It is important for such analyses to infer species fitness not solely based on abundance measured at a single time point, which can be influenced by multiple abiotic and biotic processes (e.g. dispersal, competition, natural enemies; Fox, 2012; McGill, 2012), but to rather directly quantify population growth rates or the vital rates that drive population growth (Laughlin et al., 2020; Swenson et al., 2020). As species fitness is driven by multiple processes (e.g. growth, survival, fecundity), it is also important to consider how functional traits relate to integrative measures of fitness rather than focusing only on individual vital rates separately (Laughlin et al., 2020).

The impact of changing trait–performance relationships on CWM traits can be expected to take one of a number of forms, some of which are illustrated in Figure 1. If trait–performance relations remain constant across an environmental gradient (Figure 1b), any observed CWM–environment relationships likely reflect the effects of widespread study of trait–performance relationships to improve predictions of community responses to global change.

KEYWORDS community assembly, community-weighted mean, demography, serpentine grassland, trait–environment interactions, vital rates
species interactions or other processes rather than shifting trait optima in terms of species’ intrinsic responses to the landscape. Trait–performance relationships may differ in magnitude but not in sign across a gradient in a way that matches observed shifts in CWM traits (Figure 1c). Such trait–performance relationships with the same sign across the environmental gradient would not by themselves result in differential distribution of traits across the landscape, but provide weak support that CWM–environment relationships reflect shifting trait optima. Stronger evidence that CWM trait shifts reflect shifting trait optima would be if the sign of the trait–performance relationship changes across the gradient in a way that is consistent with the CWM trait patterns (Figure 1d). It is also possible that we find trait–environment interactions when looking at the vital rates, even when there are no observed CWM–environment relationships. This might indicate that other processes obscure underlying trait–performance relationships. A major challenge in testing for concordance between CWM trait patterns and variation in trait–performance relationships has been that quantifying how trait variation influences species fitness across landscapes is data-intensive, requiring plant performance data across temporal and spatial gradients. Although such data are becoming increasingly available for a wide range of long-lived plants through long-term monitoring efforts (e.g. Davies et al., 2021; Losos & Leigh, 2004), short-lived plant communities, where we can quantify relevant vital rates for many members of the community on fairly short time-scales, offer an ideal system in which to test for concordance between trait–performance relationships and CWM trait shifts.

To address whether functional trait shifts in communities reflect shifting trait–performance relationships across the landscape, we quantified changes in community composition and vital rates across a landscape dominated by serpentine annual grasslands in Southern California. Specifically, we asked if CWM–environment relationships seen in naturally occurring communities on the landscape were consistent with trait–performance relationships seen in naturally occurring communities on the landscape and CWM trait shifts.

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–environment relationships in plant functional traits reflect shifts in trait–performance relationships across the landscape. Panels (b)–(d) illustrate how trait–performance relationships might differ at opposite ends of the environmental gradient in panel (a). (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 evidence that CWM shifts reflect changing trait optima. Note trait–environmental relationships may also be unimodal in nature, and while we explore this possibility at the community level, we are unable to explore nonlinear trait–environment interactions shaping individual species fitness in this paper.

![Figure 1](https://example.com/figure1.png)
community-wide variation in one leaf trait (specific leaf area), one root trait (specific root length), one whole-plant trait (maximum height) and one reproductive trait (seed mass) using species’ mean trait values. In a parallel experiment, we quantified components of the intrinsic fitness (germination rate, lifetime fecundity of individuals growing without competitors and their product) of 17 annual plant species that naturally occur in this community and that capture a wide range of functional variation. We then asked whether observed CWM trait shifts reflect trait–environment interactions that shape variation in species’ fitness across this gradient. Our results show that shifts in CWM traits often provide valuable information into how trait optima shift across gradients, but we also found some discordance between patterns of CWM trait turnover and trait–performance relationships, which cautions against predicting species responses to environmental variation on the basis of shifts in CWM traits alone.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied trait–environment relations in the grassland community at the University of California Sedgwick Reserve in southern coastal California. This region experiences a Mediterranean climate of cool, wet winters and long, dry summers. Plant phenology in this system is driven largely by the rainfall regime: seeds germinate with early-season rainstorms in November and December, and plants begin to reproduce and senescence with the onset of summer droughts (though there is substantial variation in the timing of reproduction among species; Godoy & Levine, 2014; Kraft et al., 2015). The reserve encompasses significant topographic and edaphic heterogeneity, including oak-savanna, coastal sage scrub and California grassland communities. Our study focused on a part of the reserve with serpentine-derived soils that are dominated by invasive Avena and Bromus spp. In this area, outcrops of rocky serpentine soil (‘serpentinite hummocks’) are embedded within more mesic soils that are deeper and have higher soil moisture. The hummocks are considerably less vegetated and act as spatial refuges for several native plant species (Gram et al., 2004). We studied trait–environment relationships at 16 sites on this landscape, of which six were located on serpentinite hummocks.

2.2 | Quantifying species performance (vital rates) across the landscape

In November 2015, before the first major rainstorm of the season, we cleared all existing vegetation in 2 m × 3 m plots at each of our 16 focal sites. At each site, we sowed five replicate plots with 20–100 viable seeds each of our 17 focal species (Table S1) on a grid with 15 cm spacing between each species. We collected seeds from hundreds of plants growing across Sedgwick Reserve in spring 2015, and homogenised seeds among sources before planting to ensure that local adaptation to different soils within the reserve (e.g. Rajakaruna & Bohm, 1999) or maternal effects (e.g. Germain & Gilbert, 2014; Schmitt & Antonovics, 1986) did not systematically drive variation in plant performance across sites in our experiment.

In February 2016, we counted the number of germinants of each focal species in our experimental plots, and thinned each plot to leave only two individuals of each focal species. In March, we further thinned each point down to a single individual of each species, and weeded around this focal individual to ensure that it was not competing with other plants in a 15 cm radius. Between April and June 2016, we quantified the total seed output of each focal individual in our experiment, for a total of 1360 individuals (17 species × 16 sites × 5 plots per site) tracked across the environment (see Appendix S1 for details on how we estimated total seed output). This design let us quantify two vital rates—germination rate (g) and the per-germinant seed production (fecundity) in the absence of competitors (F)—for each species at each site. To capture potential demographic trade-offs between germination rates and fecundity, we also calculated the product of germination rate and fecundity (g × F) at each plot to serve as a more integrative measure of the species’ fitness across the gradient. This product represents population growth rate in the absence of any competition, assuming that ungerminated seeds do not persist in the seedbank. While this term is an incomplete descriptor of the population dynamics on this landscape (e.g. see Levine and HilleRisLambers, 2009; Godoy and Levine (2014) and Kraft et al. (2015) for models for this community that integrate competition and the survival rates of ungerminated seeds), it represents a step towards integrating multiple vital rates to get a more accurate estimate of fitness.

2.3 | Measuring compositional turnover across the landscape

In Spring 2017, we surveyed five undisturbed plots (0.5 × 0.5 m) adjacent to the experimental plots at each of our 16 sites to characterise the vascular plant community composition. These community survey plots were spaced evenly on a 10 m transect located alongside the cleared plots in which we had experimentally quantified plant performance in the prior year. In each plot, we visually estimated the total (absolute) cover of each of species in early April, and again in early June. We calculated each species’ relative cover in each plot by summing over its cover across the two censuses, and dividing by the total cover recorded in the plot.

2.4 | Functional trait measurement

Our analysis focuses on four traits that capture different dimensions of plant ecological strategies: specific leaf area (SLA), specific root length (SRL), maximum height and seed mass. SLA, the ratio of leaf area to dry mass, is strongly linked to species’ position
along the leaf economics spectrum (Wright et al., 2004) and at a global scale is positively correlated to photosynthesis and growth rate (Adler et al., 2014). SRL, the ratio of fine root length to dry mass, reflects the area over which roots can uptake resources relative to biomass investment, and is an important component of the root economics spectrum (Laliberte, 2016; Weemstra et al., 2016). At both a global scale (Weemstra et al., 2016) and within our study (Figure S1), SRL is largely uncorrelated with SLA. Maximum height is a globally relevant trait (Díaz et al., 2016) that integrates across various dimensions of ecological strategy and can indicate the ability of adult plants to preempt and intercept light (Westoby et al., 2002). Seed mass affects population growth through its effect on germination rates (Grubb, 1977), as well as its effects on species’ intrinsic growth and in shaping size asymmetric competition among plants (DeMalach et al., 2018; Simpson et al., 2021).

Kraft et al. (2015) had previously measured these traits for 12 out of 17 species in their demography experiment (Table S1). To measure these traits, Kraft et al. (2015) planted seeds of the focal species in mixed species communities at an intermediate seeding density of 8 g/m², and sampled 8–15 individuals/species to measure leaf and root functional traits. These plots were established in the deeper clay soils away from serpentine hummocks. Maximum height was estimated as the 95%th percentile of heights measured on 40–50 individuals/species, and seed mass was measured for a sample of seed collected from hundreds of individuals across the landscape. In Spring 2016, we measured traits for the five species in our experiment that were not part of Kraft et al. (2015)’s study: Bromus madritensis, Chaenactis glabriuscula, Hordeum murinum, Micropus californica and Vulpia microstachys. Following the protocols detailed in Kraft et al. (2015), we measured leaf and root traits on 5–8 individuals growing in 0.7 × 0.7 m competitive mixtures at three of our non-hummock experimental plots, into which we had sown seeds of all 17 focal plant species. Maximum height and seed mass for these species were also measured as in Kraft et al. (2015). In Spring 2017, we measured the same set of functional traits on 38 of the most common annual plant species encountered within the community composition plots (of the species for which we could not measure at least one of the focal traits, mean cover in sites where they were present was ~5%). For the species that were not included in our performance experiment, we measured traits following the same protocols from 5 to 8 individuals growing in sites where they were relatively abundant; thus, traits were not measured in the identical abiotic and biotic conditions for these species. In all cases, we summarised across measurements within a species to generate a species average for each trait.

2.5 Environmental sampling

We quantified various soil chemical and physical characteristics to identify the primary axes of environmental variation among our study sites. We measured gravimetric water content (weight of fresh soil – weight of dry soil/weight of dry soil) in the early- and mid-growing season (March and April, respectively), and summarised across these measurements to estimate the average soil moisture at each site. At each site, we also collected soil for analysis by A&L Western Agricultural Laboratories (Modesto, CA) for a variety of soil chemical and physical properties: soil organic matter, P (Weak Bray and Olsen methods), K (ppm), Mg (ppm), Ca (ppm), Na(ppm), pH, CEC, NO₃, SO₄, NH₄ and soil texture (sand, silt and clay content). We collected the soil for these analyses from three points arranged in between the five experimental plots, and homogenised within site prior to analysis. We also deployed iButtons (Maxim Integrated) to log temperature at 2-h intervals, and used these data to quantify the average daily maximum temperature at each site. To avoid direct solar radiation on iButtons, we placed them in anchored PVC tubes (2 inch diameter, 6 inch length) with holes for airflow. In the main text, we focus on trait relationships with three soil properties that are known to be important drivers of plant community dynamics across serpentine systems, including at our field site (Alexander et al., 2007; Gram et al., 2004): soil Calcium to Magnesium ratio (Ca:Mg), soil sand content and soil depth. To evaluate trait–environment relationships in the other abiotic gradients on this landscape, we also analysed community patterns and species’ demography with respect to the first two axes of a Principal Components Analysis (PCA) conducted with all environmental variables listed above. Our use of the first two axes was supported by parallel analysis (Adjusted eigenvalues = 3.18 and 1.03 for the first two components, respectively).

2.6 Analysis

2.6.1 Quantifying community-weighted trait–environment relationships across the landscape

We used the community composition and functional trait measurements to calculate the community-weighted mean (CWM) trait values, which represent the mean trait value of all species growing at a site, weighted by the species’ relative cover. We calculated the CWM for each trait $t$ at each of our 16 sites $s$ by averaging across the CWM of the five plots $p$ at each site as follows:

$$CWM_{t,s} = \frac{1}{n} \sum_{p=1}^{5} \sum_{i=1}^{n} tC_i,p,$$

where $n$ is the number of species found in each plot, $t$ is the mean trait value of species $i$ and $C_i,p$ is the relative cover of species $i$ in the plot $p$. We then evaluated whether CWM traits vary across the environmental gradient in our study with simple bivariate linear regressions between each of the three focal traits and each of the three focal environmental characteristics. We also tested for evidence of nonlinear trait–environment relations by including a quadratic term in the predictor (environmental) variables. We evaluated statistical significance at $\alpha = 0.05$. 

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2.6.2 Quantifying functional trait–vital rate relationships across the landscape

We next asked whether observed CWM–environment relationships reflect variation in the trait–performance relationship in the demography experiment. We used glmmTMB (Brooks et al., 2017) to fit three generalised linear mixed effects models with measures of species performance as the response variable (germination rate (g), fecundity (F) or their product, \( g \times F \)). The predictor variables were the three focal environmental variables, four functional traits and their interaction. The models also included random effects for species identity and site, and included an additional zero-inflation parameter. We used a binomial model for germination rate, and a negative binomial model for fecundity and \( g \times F \). We log-transformed all functional trait values, and scaled all parameters to help with model convergence. We used performance (Lüdecke et al., 2020) to quantify model fit and to ensure that the model did not suffer from collinearity of predictors (variation inflation factors <2), and used DHARMa (Hartig, 2020) to evaluate the model residuals. We also compared the AICc of models with all trait–environment interaction terms to corresponding null models and ones with only the main trait and environment effects as predictors to verify that the interaction terms were supported (\( \Delta \text{AICc} > 2 \) in favour of the model with trait–environment interactions). Finally, we used effects (Fox & Weisberg, 2018) to evaluate the trait–performance relationship at the highest and lowest value of the environmental gradient in our study based on the marginal effects of the model.

We conducted all analyses in R v. 4.1.2 (R Core Team, 2021). Data and code to recreate all analyses are archived on Zenodo (https://doi.org/10.5281/zenodo.5796738).

3 RESULTS

3.1 Community-wide trait turnover

The plant species in our study system vary considerably in their functional traits. Across the 55 species we observed across the landscape, there was threefold variation in SLA (5th percentile = 124.83 cm\(^2\)/g, 95th percentile = 433.8 cm\(^2\)/g), ninefold variation in SRL (5th percentile = 32.26 m/g, 95th percentile = 290.67 m/g), 10-fold variation in maximum height (5th percentile = 11.38 cm, 95th percentile = 108.7 cm) and 42-fold variation in seed mass (5th percentile = 2 \times 10^{-4} \text{ mg}, 95th percentile = 0.0083 \text{ mg}). This trait variation was structured according to five significant CWM–environment relationships (horizontal bars in Figure 2). We found positive relationships between CWM SLA and soil Ca:Mg and soil depth (Figure 3a,b), a negative relationship between CWM SRL and soil sand content (Figure 3c), a positive relationship between CWM maximum height and soil depth (Figure 3d) and a positive relationship between CWM seed mass and soil depth (Figure 3e). We also found that CWM SRL tends to be highest at intermediate values of Ca:Mg (Table S2). Each of the four traits also showed significant CWM shifts across at least one of the two first axes from our environmental PCA (Figure S4).

3.2 Environmental and functional trait drivers of variation in species performance

The fixed effects of our GLMM with all the main and interactive effects explained 23% of the variation in germination rates, 20% of variation in fecundity and 16% of variation in \( g \times F \) (see Figure 2 for FIGURE 2 Standardised effects of environmental variables, functional traits and their interactions on fitness components. Panel (a) shows trait and environmental predictors of variation in germination rate, panel (b) shows predictors of fecundity and panel (c) shows the predictors of the integrative fitness measure (\( g \times F \)). Grey points indicate those effects whose 95% confidence intervals (indicated by thin lines) do not overlap zero. Horizontal bars indicate the significant trait–environment relations in the CWM trait analysis, with the four blue bars indicating positive relationships and the red bar indicating negative relationship.
all Conditional and Marginal $R^2$ values). The main effects indicated that germination rates decreased with soil sand content ($p = 0.023$) and increased with seed mass ($p = 0.014$); that fecundity increased with soil Ca:Mg ratio ($p = 0.016$), soil depth ($p = 0.018$) and plant maximum height ($p < 0.001$); and that the product of the two vital rates, $g \times F$, increased with soil Ca:Mg ($p = 0.001$) and seed mass ($p = 0.03$).

Overall, there was mixed evidence that CWM–environment relationships reflect shifting trait optima along the environmental gradients. Specifically, our analyses suggest that three of the five CWM–environment relationships reflect interactive effects of trait and environment on plant fitness. Consistent with the positive CWM SLA-Ca:Mg relationship, we found a positive interaction between SLA and Ca:Mg shaping germination rates and fecundity, and correspondingly, their product ($g \times F$) (Figure 2). Moreover, the sign of the SLA–performance relation changed across the gradient: low-SLA species were predicted to outperform high-SLA species in the site with the lowest Ca:Mg, but high-SLA species had an advantage in high Ca:Mg sites (Figure 3f). Similarly, consistent with the negative CWM SRL–sand content relationship, we found a negative interaction between SRL and soil sand content in shaping species’ fecundity and $g \times F$ (Figure 2). The sign of this relationship also changed across the soil sand content gradient, with high SRL conferring an advantage in less sandy soils, and low SRL conferring an advantage in sandier soils (Figure 3h). Finally, consistent with the positive CWM seed mass–soil depth relationship, we found that fecundity was shaped by a significant positive interaction between seed mass and soil depth (Figure 2b; Figure S6), although we did not find that this interaction influenced $g \times F$ (Figure 3j), the more integrative measure of fitness.

On the other hand, we did not find any evidence that the positive relationships between soil depth and CWM-SLA and CWM-maximum height are driven by trait–vital rate relationships across the landscape. In fact, in the case of soil depth and maximum height, we found an interaction in the opposite direction as would be predicted from the CWM
trait shift. CWM maximum height increased with soil depth (Figure 3d), but we found that a significant negative interaction between these two variables shaped variation in germination rates (Figure 2a; Figure S6D). However, this interaction was not significant when we analysed $g \times F$ as the measure of plant fitness (Figure 3i).

There was also mixed evidence that shifts in trait optima, when they do occur, manifest in CWM–environment relationships. In particular, six trait–environment interactions for which we found no CWM–environment patterns did have statistically significant effects on germination rates (e.g. Ca:Mg-SRL, sand content–maximum height, Figure 2a). However, these effect sizes were generally quite small and in no case led to changes in the sign of the trait–vital rate relationship across the gradients (Figure S7). In only one case was there evidence for a trait–environment interaction in shaping $g \times F$ but no CWM turnover (sand content $\times$ seed mass). Finally, there was similarly mixed concordance between CWM–environment relationships and trait–performance relationships when we evaluated trait relationships with the first two axes of the environmental PCA (Figure S5).

4 DISCUSSION

Turnover in community-weighted trait means across environmental gradients is a common pattern in nature, but whether these patterns reflect shifts in trait–performance relations across environmental gradients remains poorly understood (Shipley et al., 2016). For example, CWM–environment relationships may be poor predictors of trait–fitness relationships if dispersal limitation prevents species with optimal trait values from establishing in certain locations. As a result, predicting plant species’ demographic responses to environmental variation on the basis of their functional traits remains challenging (Funk et al., 2016; Laughlin & Messier, 2015). Quantifying trait–performance relations across environmental gradients at the community level is a key step in improving our ability to project how plant communities will respond to environmental change. Here, we coupled community surveys with a detailed experiment quantifying multiple vital rates of a trait– vital rate interaction in shaping $g \times F$ and their product $g \times F$ shifts along the Ca:Mg gradient. The models for fecundity and $g \times F$ included a significant positive main effect of soil Ca:Mg, indicating that plants generally performed better in high-Ca:Mg than low-Ca:Mg soils, irrespective of their traits. However, the SLA-Ca:Mg interaction term in the model for $g \times F$ indicates that lower SLA was associated with higher fitness at soils with low-Ca:Mg, and vice versa in high-Ca:Mg soils (Figure 3f). This is consistent with the general expectation of lower SLA being correlated with a suite of traits that confer plants greater tolerance of abiotic stress, at the cost of a relative disadvantage when abiotic stress is less limiting (Sterck et al., 2006; Wright et al., 2004). While it is difficult to draw mechanistic links between SLA and variation in germination rates in response to Ca:Mg (Figures 2a; Figure S6A), it is likely that this correlation arises through the suite of resource-acquisitive traits associated with higher SLA.

We also found consistent evidence for a negative relationship between SRL and soil sand content in both the community survey and in the experimental assessment of plant fitness (Figure 3c,h). In particular, the trait–environment interaction was structured such that low-SRL species were predicted to outperform high-SRL species (higher values of $g \times F$) in sandy soils, and vice versa in soils with low sand content. This negative relationship between SRL and soil sand content is contrary to Laughlin et al. (2018), who found a positive CWM SRL–soil sand content relationship and a positive interactive effect of SRL and soil sand content on plant survival in a pine-dominated forest in Arizona. The discrepancy between the two studies may have arisen in part because in our grassland community, soil sand content was generally much higher on serpentine hummocks that were also characterised by low soil moisture and organic matter (Figure S3). In this context, the negative relationship between CWM SRL and sand content is consistent with the more general expectation of low SRL indicating a resource-conservative strategy that allows plants to outperform species with resource-acquisitive strategies in more stressful conditions (Reich, 2014). More broadly, the contrasting CWM SRL–sand content relationship between our study and Laughlin et al. (2018) highlight a gap in our understanding of why trait–environment relationships vary across communities. Addressing this gap is a key step towards achieving a more predictive trait-based ecology, and may be achieved with more studies that couple observational studies at the community level with species-level analyses of trait–environment interactions (Funk et al., 2016).

4.1 Consistencies in CWM–environment and trait–performance relationships

We found three trait–environment interactions with consistent effects on both the whole plant community as well as fitness components of the focal species in our experiment. The first such interaction for which we found evidence in both the community observations and in our experiment was the positive relationship between SLA and soil Ca:Mg. At the community level, this relationship is consistent with other studies that have found lower CWM SLA in serpentine soils than in soils with weaker serpentine characteristics (Fernandez-Going et al., 2013), and with the general finding of increasing CWM SLA in more fertile soils (e.g. Cornwell & Ackerly, 2009). Our GLMM analysis of the focal species’ performance suggests that this community-level pattern may arise in part because the value of SLA that confers the highest fitness (measured here as the germination rate ($g$), fecundity of plants when not facing competitors ($F$) and their product $g \times F$) increases with soil Ca:Mg. SLA in serpentine soils than in soils with weaker serpentine characteristics (Fernandez-Going et al., 2013), and with the general finding of increasing CWM SLA in more fertile soils (e.g. Cornwell & Ackerly, 2009). Our GLMM analysis of the focal species’ performance suggests that this community-level pattern may arise in part because the value of SLA that confers the highest fitness (measured here as the germination rate ($g$), fecundity of plants when not facing competitors ($F$) and their product $g \times F$) increases with soil Ca:Mg. SLA in serpentine soils than in soils with weaker serpentine characteristics (Fernandez-Going et al., 2013), and with the general finding of increasing CWM SLA in more fertile soils (e.g. Cornwell & Ackerly, 2009). Our GLMM analysis of the focal species’ performance suggests that this community-level pattern may arise in part because the value of SLA that confers the highest fitness (measured here as the germination rate ($g$), fecundity of plants when not facing competitors ($F$) and their product $g \times F$) increases with soil Ca:Mg. SLA in serpentine soils than in soils with weaker serpentine characteristics (Fernandez-Going et al., 2013), and with the general finding of increasing CWM SLA in more fertile soils (e.g. Cornwell & Ackerly, 2009). Our GLMM analysis of the focal species’ performance suggests that this community-level pattern may arise in part because the value of SLA that confers the highest fitness (measured here as the germination rate ($g$), fecundity of plants when not facing competitors ($F$) and their product $g \times F$) increases with soil Ca:Mg.
The third trait–environment interaction for which we found some support in both the observational study and in our experimental assessment of plant fitness was the positive relationship between soil depth and seed mass (Figure 3e). This CWM seed mass–soil depth relationship is consistent with larger seeded plants dominating deeper soils and areas with higher water-holding capacity in other Mediterranean grasslands (e.g. Maranon & Grubb, 1993). Our experiment suggested that this pattern reflects a positive interactive effect of seed mass and soil depth on fecundity (Figure 2b). While statistically significant, this interaction term provides only weak evidence that the turnover in CWM seed mass across soil depth reflects a shifting trait–performance relationships, as we did not find an effect of the soil depth–maximum height interaction on the integrative fitness measure \((g \times F, \text{Figure 3j})\). In fact, there was a significant positive main effect of seed mass on \(g \times F\), meaning that larger-seeded species had higher fitness than short species across the depth gradient. Although the interactive effect of seed mass and soil depth on fecundity alone is insufficient to drive trait shifts across the landscape, trait–performance relationships in other vital rates may compound this effect to give rise the community-wide trait turnover in seed mass. For example, higher CWM seed mass in deeper soils may be further driven by larger seeded plants gaining a competitive advantage when soil resources are less limiting because they can be stronger competitors for light (DeMalach et al., 2016, 2018). Future studies that investigate trait-performance relationships in more fitness components will be critical for understanding how plant traits determine overall population growth rates (Laughlin et al., 2020) and thus influence community assembly processes across landscapes.

4.2 | Discrepancies in CWM-environment and trait-performance relationships

Although three of the five CWM trait–environment correlations in this study seem to at least qualitatively reflect the direction of trait–environment interactions in terms of species’ fitness components, we did not find such evidence for the positive CWM SLA–soil depth relationship or the positive CWM maximum height–soil depth relationship (Figure 3b,d). Both of these relationships are consistent with patterns of community-wide trait turnover across soil depth gradients in other Mediterranean grassland communities (Bernard-Verdier et al., 2012), but they do not appear to arise from the interactive effects of the traits and soil depth on germination or fecundity in our experiment. This raises the question of what might drive the observed community-wide correlations. It is possible that the rather than influencing how germination or fecundity of species responds to variation in soil depth, SLA might instead mediate the response of other vital rates to this environmental gradient (Laughlin et al., 2020), or that intraspecific variation among individuals of the focal species blurs observed patterns of how SLA affects species performance across gradients (Bagousse-Pinguet et al., 2015; Violle et al., 2009). It is also possible for discrepancies between individual trait-performance relationships and community-wide patterns to arise due to the fact that population growth rates are simultaneously determined by multiple traits that may or may not covary among species (Laughlin & Messier, 2015; Marks & Lechowicz, 2006). Such trait covariance could, for example, give rise to turnover in a focal trait at the community level even when there is no variation in the trait’s adaptive significance over the landscape (cf. Gould & Lewontin, 1979).

Our analysis also allows us to ask whether any trait–environment interactions mediate variation in species performance but do not turn over across the environmental gradient at the community level. When focusing on the integrative fitness measure \((g \times F)\), we found evidence for one such trait–environment interaction: while a negative interaction between seed mass and soil sand content shaped \(g \times F\), there was no turnover in CWM seed mass with sand content. Coupled with the positive main effect of seed mass on \(g \times F\) (Figure 2c), the negative seed mass × sand content interaction terms meant that the benefit of higher seed mass was diminished in less sandy soils (Figure S7A). We also found six trait–environment interactions with statistically significant effects on germination rates but no turnover at the community level (Figure 2a). While they were statistically significant, these interactions had relatively small effect sizes such that the sign of the trait–performance relationship did not change across the environmental gradients (Figure S7B–G). Such interactive effects of trait and environment on individual fitness components might not manifest at the community level for a variety of reasons. First, it is possible that trade-offs among vital rates erode the interactive effects of traits and environment on population growth rates as a whole (Laughlin et al., 2020). For example, most of the trait–environment interactions shaping germination rates were not significant predictors of fecundity (Figure 2b), indicating that traits that promote germination are not necessarily the same as those that promote high fecundity. When the trait–environment interactions are relatively weak, as in the case of the six significant interactions influencing germination rates, it is also possible for demographic stochasticity or other processes such as dispersal limitation mitigate their effects at the community level (Loranger et al., 2018). In general, the discordance between the turnover in CWM traits across environmental gradients and shifts in adaptive value of traits along those gradients highlights the potential pitfalls in predicting species’ fitness across environmental gradients solely on the basis of community-wide patterns of trait turnover.

4.3 | Study limitations

Our overall finding that shifts in CWM traits across environmental gradients often reflect shifts in trait-performance relations but are not perfect predictors of trait optima is consistent with other studies that have investigated variation in CWM traits and species performance on a landscape (Laughlin et al., 2018; Muscarella & Uriarte, 2016). However, our study also had some important limitations. First, the 17 species we used in our experiment to quantify intrinsic fecundity across the landscape did not include several of
the most dominant species in our observational community composition plots (e.g. *Avena fatua*, *A. barbata*, *Bromus diandrus*, *Microseris douglasii* and *Lolium perenne*) each achieved >50% cover in at least one 1 × 1 plot across the 16 sites, but were not part of the experiment). Moreover, the functional traits of some of the most dominant species were beyond the range of functional traits captured by the 17 species in our demography experiment (e.g. all five of the aforementioned dominant species had SRL values below those of the 17 species in the experiment, and range of the focal species’ SRL covered only 43.7% of the SRL values observed in the community, Figure S2). As CWM trait values are intrinsically reflective of dominant species’ responses to the landscape, it is possible that including more species that captured a wider range of the trait variation found in our community would reveal trait–environment interactions that drive trait turnover patterns at the community level. For example, the negative interaction we detected between seed mass and sand content on *g × F* may not apply as strongly among the dominant plant species on the landscape, which could explain why we do not see any evidence for this relationship at the CWM level. This could arise if, for example, species with high versus low relative abundance occupy distinct different parts of multidimensional trait spaces (e.g. Umaña et al., 2015) and thus respond differently to environmental gradients.

A second limitation of our study is that we were unable to account for the possibility that intraspecific trait variation (ITV) driven by local adaptation, phenotypic plasticity or maternal effects—processes that are known to be important in similar serpentine systems (Baythavong, 2011; Germain & Gilbert, 2014; Rajakaruna & Bohm, 1999)—mediate trait–environment relations at either the community or individual scale. However, our finding that trait–performance relationships do change across the environmental gradient generate predictions for future studies about how ITV may be structured on this landscape. For example, our result finding that the optimal value of SLA shifts from low to high with an increase in soil Ca:Mg (Figure 3e) suggests that ITV may be structured such that individuals of the same species growing in soils with higher Ca:Mg build higher SLA leaves than conspecific individuals on low-Ca:Mg soils. Understanding how the spatial structure of ITV differs between species may be critical for predicting variation between species in their demographic responses to environmental gradients (Swenson et al., 2020). Moreover, while our present study focuses only on evaluating potential drivers of shifts in community-weighted trait means, evaluating how higher moments of community-wide trait distribution (i.e. community-weighted variance, skewness or kurtosis; Bagoussé-Pinguet et al., 2017; Cornwell & Ackerly, 2009) are driven by differential trait–performance relationships will be a fruitful avenue for future research.

5 | CONCLUSIONS

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

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CONFLICT OF INTEREST

We have no conflicts of interest to declare.

AUTHORS’ CONTRIBUTIONS

All authors conceived the ideas, designed the methodology and collected the data; G.S.K. analysed the data; G.S.K. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data and R code to recreate all analyses are archived on Zenodo https://doi.org/10.5281/zenodo.5796738 (Kandlikar, 2021).

ORCID

Gaurav S. Kandlikar https://orcid.org/0000-0003-3043-6780
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