

RESEARCH ARTICLE

Functional Ecology



Voles mediate functional trait diversity along a resource gradient

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Abstract

1. Disentangling the effect of multiple ecological processes on plant trait composition is complicated by the fact that both top-down and bottom-up processes may affect similar traits.
2. We examined the interacting role of resource variation and vole herbivory on functional trait patterns in an annual California grassland. We manipulated vole herbivory via exclosures at eight grassland sites along a steep resource gradient and measured plant composition and functional traits over 3 years.
3. Plants with resource acquisitive functional traits were favoured at sites with increasing resources. Vole herbivory influenced community-weighted mean (CWM) leaf nitrogen (N) and seed mass, suggesting these traits may mediate plant susceptibility to vole herbivory. After 3 years, CWM leaf N increased in the absence of the voles, as did CWM seed mass, although this increase in CWM seed mass only occurred at higher resource sites. Vole exclusion at high-resources sites also increased the functional diversity of leaf N and seed mass by the end of the experiment.
4. Overall, environmental filtering primarily structured the dominant plant trait strategies, but vole herbivory also influenced the functional diversity of traits that influence herbivore susceptibility, particularly at resource-rich sites.
5. Thus, habitat filtering and herbivory can operate on different dimensions of plant functional composition to influence the species and functional composition of communities.

KEYWORDS

bottom-up, competition, context dependency, herbivory, top-down

1 | INTRODUCTION

Historically, research on plant community assembly has focused on evaluating how the abiotic environment acts a 'filter' selecting for those species and traits that are best suited for particular environments. Although much work has evaluated trait-abiotic environment relationships (Cornwell & Ackerly, 2010; Kraft et al., 2011; Spasojevic & Suding, 2012), fewer studies have examined how herbivores may mediate these effects (Eskelinen et al., 2012; Maron et al., 2019). The

little work that has been performed has focused on large grazers. Ungulate grazers, by suppressing competitive dominants, can often increase taxonomic diversity and shift the dominant functional strategy in high-resource plant communities (Eskelinen et al., 2012; Hillebrand et al., 2007). These dynamics arise because higher-resource availability selects for the same set of plant traits (e.g. lower leaf C:N in Eskelinen et al., 2012, greater height in Diaz et al., 2007) that are favoured by herbivores. In contrast, these effects can be more muted at locales with lower-resource availability, where plant functional traits suggestive of

a more stress-tolerant strategy are favoured. Whether other types of herbivores have similar effects on plant functional traits that are mediated by shifts in resource availability is unclear.

In many Northern Hemisphere temperate grasslands, voles are the numerically dominant vertebrate herbivore. At high abundance, these animals can have substantial impacts on plant productivity, species composition and richness (Batzli & Pitelka, 1970; Fraser & Madson, 2008; Questad & Foster, 2007). Yet, voles may select for different plant traits, life stages and community characteristics than do large grazers, suggesting that their impacts on plant functional traits at the community level may be different. Furthermore, if voles influence a separate set of traits than those that are selected by the abiotic environment, or differentially influence subdominant species, their impacts may influence functional diversity or richness, metrics that are often interpreted as being influenced by competitively driven niche differentiation (Maire et al., 2012). In other words, it is important to disentangle whether ecological processes affect different axes of functional specialization (Funk et al., 2017; Maire et al., 2012) and assess what aspects of traits [e.g. community-weighted mean (CWM), functional diversity, evenness] are sensitive to herbivory.

These effects, however, may not only vary spatially across resource gradients but also temporally, due to the highly dynamic nature of vole populations. Spatially, voles numbers can vary based on the productivity of habitats; voles prefer locales with high litter cover (Ostfel et al., 1985) and lower livestock grazing pressure (Fehmi & Bartolome, 2002). Temporally, vole numbers spike and crash across years (Batzli & Pitelka, 1970, 1971), with population peaks sometimes coinciding with high rainfall years that stimulate greater plant community biomass (Cockburn & Lidicker, 1983). Therefore, disentangling how these herbivores influence community structure and plant functional traits must involve understanding how spatiotemporal variation in the abiotic environment selects for particular plant traits, and then how these may be influenced by vole herbivory.

Here, we take a multi-trait approach to evaluate the impacts that generalist voles have on plant community trait composition and to examine whether there are trade-offs between traits that influence final community structure. To do this, we experimentally excluded voles from grassland communities along a steep environmental resource gradient in soil inorganic nitrogen and primary productivity. We sampled plant species composition and functional traits within our experimental plots over three growing seasons. Based on common trait trade-offs observed with large ungulate grazers where competitive dominant species with resource acquisitive traits are more vulnerable to herbivory (Eskelinen et al., 2012), we tested the following predictions. First, we predict that at high-resource sites, plants with resource acquisitive strategies (e.g. high SLA and height) should dominate in the absence of voles. Second, if foraging preferences by voles mirror those of larger herbivores, then voles should suppress resource acquisitive species in favour of species with more resource conservative strategies. However, vole populations are dynamic and often fluctuate greatly among years. Thus, we anticipate these predictions primarily hold true in years when vole numbers are

high (i.e. high rainfall years). In years where voles are less abundant, variation in the resource environment should have primacy in affecting community trait patterns.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted our experiment in the annual grasslands at the University of California Sierra Foothill Research Extension Center (SFREC), located in Browns Valley, California, USA (39°15'N, 121°17'W). These communities are dominated by non-native annuals with low abundances of native species. The most abundant species included *Avena barbata*, *Elymus caput-medusae*, *Festuca perennis*, *Bromus hordeaceus* and *Erodium botrys* (nomenclature follows Baldwin et al., 2012). The climate is Mediterranean with cool wet growing seasons (September–May) and hot dry summers (June–August). Growing season rainfall increased over the course of our study more than doubled from 454 mm to 625 mm to 978 mm for the 2014–2015, 2015–2016 and 2016–2017 growing seasons, respectively. The dominant small mammal consumer is *Microtus californicus*, a small meadow vole that prefers habitat with a standing litter layer (Batzli & Pitelka, 1970; Ostfeld et al., 1985). Other small mammal species at our study site predominantly reside in the more heavily cattle grazed pastures (Block & Morrison, 1990). Therefore, our design below reflects predominantly the effects of voles.

2.2 | Sites

We conducted our experiment at eight experimental sites that spanned a steep resource gradient. We described this gradient (hereafter resource gradient) using a principal component analysis (PC1 which described 47.6% of the variation in environmental variables; Appendix S1, Figure S1). At one end of the gradient were low productivity sites (as characterized by above-ground primary productivity) with low soil nitrogen (N), but high micronutrients (i.e. magnesium, sodium and calcium). At the other end of the gradient, sites had high productivity and soil N. We observed within-site variation in soil resources such that in some of our sites, despite our paired design, the soil resources within and outside of the enclosure differed.

2.3 | Experimental design

To evaluate the effects of voles on plant trait composition, in the summer of 2014, we initiated a field experiment where we manipulated the presence of voles. At each site, we established a set of paired plots (9 × 9 m), one fenced to exclude small mammals and one unfenced control to allow small mammal access. The enclosures were constructed of 0.64 cm welded wire dug 60 cm into

the ground around the perimeter of the plot. The fence extended about 90 cm aboveground and was topped with galvanized sheet metal with a 20 cm face to prevent voles from climbing over the fence. Within each of the paired plots, we randomly established a set of six 0.5 m × 0.5 m subplots to assess the effects of voles on plant trait composition. We additionally set up an electric fence around the 14 m × 25 m experimental area at each site to exclude cattle.

2.4 | Plant traits

To examine the distribution of functional traits in communities, we sampled 5–10 individuals of the dominant and subdominant resident species across the sites for plant functional traits (following Pérez-Harguindeguy et al., 2013). The samples were collected from within the non-cattle grazed experimental area but not from within any experimental plots. Samples were collected at peak biomass from April to May in 2015 and 2016. We measured maximum plant vegetative height, SLA (leaf area/dry leaf mass), leaf water content (LWC; $1 - \text{leaf dry weight/leaf fresh weight}$) and seed mass. The sampled leaves were additionally processed for tissue carbon and nitrogen content to estimate leaf N content and carbon to nitrogen ratios. These traits are strong indicators of resource use and plant growth. SLA is positively correlated with a species relative growth rate and tissue N (Reich et al., 1997; Westoby et al., 2002); leaf water content is negatively correlated to water stress (Farooq et al., 2009); plant height is often indicative of competitive interactions for light (Westoby, 1998); and greater leaf N and lower carbon to nitrogen ratios can be linked to higher food quality (Westoby, 1999). To account for potential trait differences in species that occurred across the environmental gradient, we sampled individuals for as many species as possible at both the low and high end of the gradient. To estimate a species' seed mass, we first took 10 samples with the same number of seeds (i.e. the number of seeds was either 50 or 75 seeds for a species, depending on seed availability). For each sample, we calculated the average seed weight by dividing the total weight of the sample by the number of seeds. The species-level average was then the average of those 10 estimates (all species trait data are available in Table S1). In total, we sampled traits on 54 different grassland species (24 of these in both habitat types), which made up on average 98% of the species composition in a given plot (mean, range of species cover: 2015:99.25 (89–100), 2016:98.9 (93.5–100), 2017:98.75 (84–100)).

2.5 | Community sampling

From 2015 to 2017, at peak biomass (April–May), we sampled the plant species composition within each subplot. To estimate vole activity, in 2016 and 2017, we recorded the frequency of vole activity (i.e. runways, burrows and droppings), along eight 10 m long transects within each larger control plot at each site. For each subplot,

we then calculated the CWM for each individual plant trait and the functional dispersion of each trait. CWM is measured as the mean of species trait values present in the community, weighted by the relative abundance of each species (Lavorel et al., 2008). Functional richness (FRic) estimates the dispersion of species in trait spaces without accounting for species abundance and is estimated as the convex hull volume (Villéger et al., 2008). Functional dispersion (FDis) is the average distance to the centroid in multivariate trait space that is weighted by species relative abundances (Laliberté & Legendre, 2010). For those species that occurred across the environmental gradient, we used the species-level trait data for a plot that best matched its position along the environmental gradient for these calculations.

2.6 | Analyses

We first evaluated vole activity (i.e. the average number of vole runways) using ANCOVA, where environment and year were fixed factors and block was a random factor.

To assess the effects of small mammals on plant communities and how these impacts change across space and time, we used repeated measures ANCOVAs with the fixed effects of vole exclusion and year and environment (as characterized by PCA axis 1 of environmental variables) as a covariate. We first assessed the effects on plant taxonomic diversity (species richness and Shannon's diversity). We estimated effects using maximum likelihood estimations to better account for the lack of independence among our sampling plots over time (Everitt & Hothorn, 2011). We additionally used Kenward–Roger approximations for degrees of freedom as these are more appropriate for repeated measures data (Littell et al., 2006). All models were mixed effect models with vole treatment nested within site as a random factor and the repeated measures were estimated with subplot nested within 'vole × site'.

To evaluate trade-offs in species traits, we ran a principal components analysis on the mean trait value for each species. Plants within the grasslands we studied possessed functional traits that fell along two distinct axes relating to resource acquisition and herbivory vulnerability (Figure S2). Carbon to nitrogen ratios decreased as total leaf N and seed mass increased, along the first axis (explaining 31.7% variation, Figure S2). The second axis was described by the classic resource use functional traits of height, leaf area, LWC and SLA such that as leaf area and height increased, SLA and LWC decreased (23.8% variation explained). To simplify interpretation, we only present results for those traits that loaded more strongly on a given PCA axis (e.g. PC1: Leaf N, seed mass; PC2: SLA, Height).

To disentangle the effects of voles on plant functional strategies and the diversity of those strategies, we used the same repeated measures ANCOVA model as above with the CWM of each individual functional trait and that trait's functional diversity as response variables. We additionally ran models with multivariate functional richness and diversity, estimated as FRic and FDis,

respectively, as a response variable to provide a more integrated functional trait response. These models were similarly mixed effect models with vole treatment nested within site as a random factor and the repeated measures were estimated with subplot nested within 'vole × site'.

To evaluate whether the functional patterns we were observing were resulting in trait convergence or dispersion, we conducted null modelling where we randomized species composition within a subplot while maintaining abundance and richness within each plot. For each of 999 iterations, we calculated multivariate and individual functional diversity trait metrics for the null community to generate the mean null $FDis_{\text{null}}$ for a subplot and its associated 95% confidence intervals. We took the difference between the $FDis_{\text{observed}}$ from $FDis_{\text{null}}$ to create an adjusted functional diversity metric, where positive values indicate greater functional diversity than expected by chance (i.e. overdispersion) and negative values indicate lower (i.e. convergence, Spasojevic & Suding, 2012). Our study began towards the end of California's multi-year drought, and we observed that interactive effects of voles and the environment developed over multiple years. These three-way interactive effects were primarily observed in 2017; therefore, we focused our null modelling on data from this year. We ran a simplified ANCOVA with vole exclusion as a fixed effect and environment as a covariate to assess the effects on the adjusted functional diversity with the same random effect structure as above. We additionally ran contingency tests (either Chi-squared or Fisher's exact depending on observed counts) to evaluate whether dispersion patterns (over, under and neutral) were independent of vole treatments (exclosures, open). The PCA and all functional diversity calculations were conducted in R (R Core Team, 2017), with the *STATS* and *FD* packages (Laliberté et al., 2014), respectively, and statistical analyses were run in statistical analysis were run using SAS® software, version 9.4.

3 | RESULTS

3.1 | Vole dynamics

Vole activity more than doubled between 2016 and 2017 with the average number of runways per transect increasing from 1.89 to 4.75 (Figure 1, year $F_{1,6} = 7.16$, $p < 0.05$). Vole activity also increased with increasing productivity and soil N along the resource gradient, but this effect was not dependent on year (env $F_{1,6} = 11.08$, $p < 0.05$, env × year $F_{1,6} = 0.61$, $p = 0.46$, Figure 1). In contrast to our observations outside exclosures, we never observed signs of vole activity inside the exclosures.

3.2 | Vole and environment effects on taxonomic composition

The relationship between plant species richness and the resource gradient, changed during the study and within the vole treatments in 2016 and 2017 (Figure 2A; env × vole × year $p = 0.02$; Table 1A; Table S2A). Specifically, plant richness did not differ along the gradient in 2015 when voles were present or absent but decreased at sites with greater resource availability in 2016 and 2017 and decreased more in the absence of voles than in their presence. Species diversity increased slightly along the resource gradient in 2015 and 2016; however, this relationship changed in the higher rainfall year of 2017 with diversity slowly decreasing with increasing resources (Figure 2B; Table 1A; env × year, $p = 0.007$, Table S2A). Diversity increased in the presence in voles only in 2016 (Figure 2C; Table 1A; vole × year, $p < 0.05$; Tukey, post-hoc $p < 0.05$), but the effects of voles on diversity across the environmental gradient did not vary across years (Table 1A; env × vole × year, $p = 0.39$).

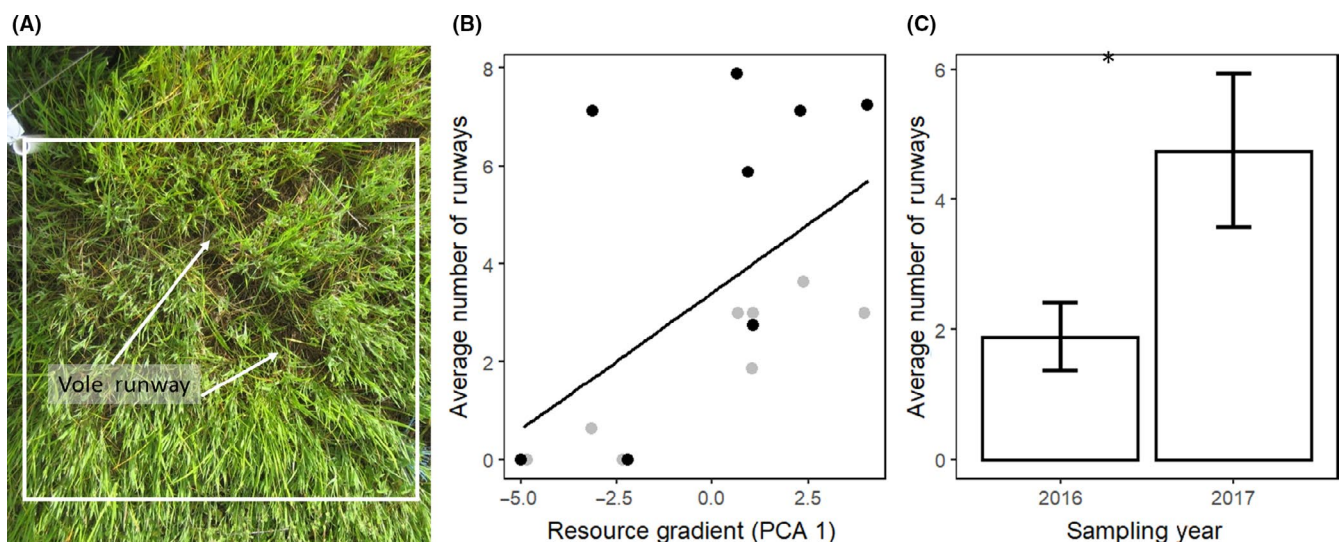


FIGURE 1 Active vole runways (A), changes in the average number of vole runways across the resource gradient from lower to higher productivity/resource sites, 2016, grey circles, 2017, black circle (B) and between years (C). Line and * indicate significant relationships at $p < 0.05$

FIGURE 2 Taxonomic species richness patterns along the resource gradient (i.e. from lower to higher productivity/resource sites) in the presence or absence of voles (orange versus blue, respectively) over the three growing seasons (A). The orange and blue fitted lines in A depict the differential relationship between richness and the resource gradient in the presence or absence of voles, respectively. Plant richness did not differ along the gradient in 2015 when voles were present or absent but decreased at sites with greater resource availability in 2016 and 2017 and decreased more in the absence of voles than in their presence (A). Taxonomic diversity increased similarly along the resource gradient in 2015 and 2016 but decreased in 2017 (B). Voles effects on taxonomic diversity were observed only in 2016 (C). Lines and letters indicate significant relationships and differences, at $p < 0.05$, respectively

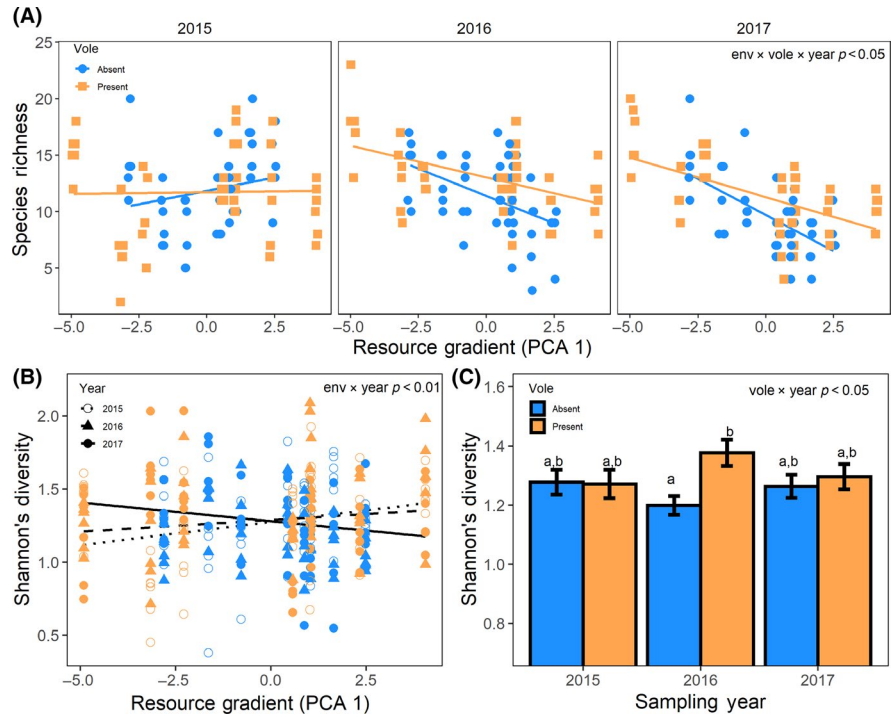


TABLE 1 Statistics for main and interactive effects of resource gradient, herbivory, and time on taxonomic and functional community diversity (A) as well as the trait composition (B) and diversity of individual trait metrics (C). F statistics and degrees of freedom are reported based on Kenward–Roger approximations in Appendix S1, Table A2. + indicates a positive significant interaction, while – indicates a non-significant different. Italics indicates response variables that were natural log transformed prior to analysis

Response variables	Predictor variables						
	Env	Vole	Year	Env × Vole	Env × Year	Vole × Year	Env × Vole × Year
A. Community taxonomic diversity							
Species Richness	+	–	+	–	+	+	+
Diversity (H')	–	–	–	–	+	+	–
B. Community-weighted means							
SLA	+	–	+	+	+	–	–
Height	+	–	+	–	+	–	–
Total N	+	–	+	–	+	+	–
Seed mass	+	–	+	–	+	+	+
C. Single trait diversity							
SLA	–	–	+	–	+	+	–
Height	+	–	–	–	–	–	–
Total N	+	–	+	–	+	+	+
Seed mass	+	–	+	–	–	+	+
D. Community functional diversity							
FRichness	+	–	+	–	+	+	–
FDiversity	+	–	+	–	–	+	+

† $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.3 | Vole and environment effects on functional composition

Resources had a strong effect on the dominant plant functional strategies such that CWM SLA, CWM height, CWM leaf N and

CWM seed mass all increased from lower- to higher-resource sites (Figures 3 and 4; Table 1B; Table S2B). Voles mediated this relationship for CWM SLA, resulting in the CWM being slightly higher at the low end of the resource gradient when voles were present, regardless of the year (Figure 3A; Table 1B; env × vole $p < 0.05$).

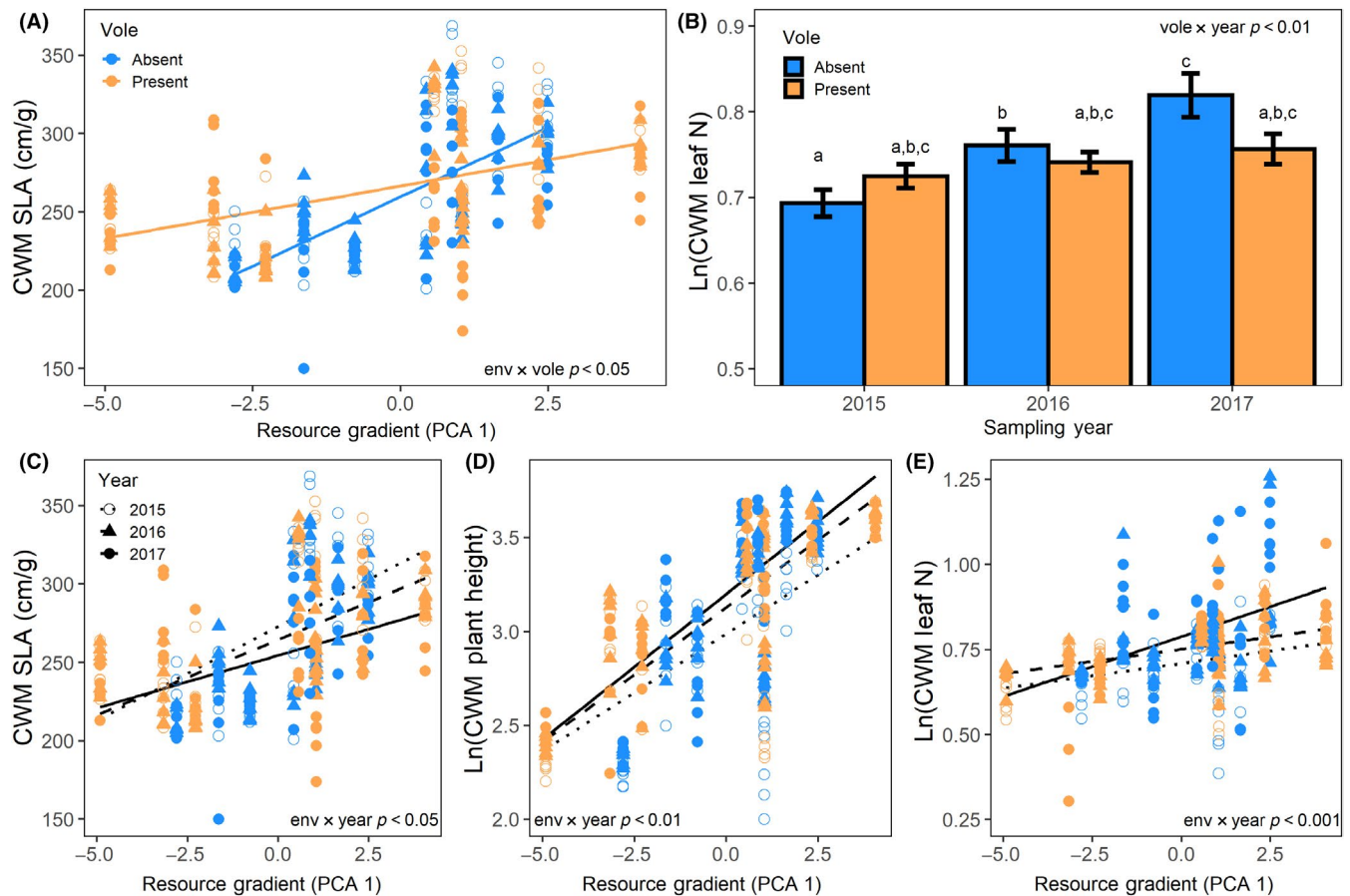


FIGURE 3 Single trait functional strategies illustrating vole (A, B) and year (C–E) effects for grassland plots along a resource gradient that indicates low above-ground productivity with low soil nitrogen (N) at the low end and high above-ground productivity and soil N at the other. Lines and letters indicate significant relationships and differences, at $p < 0.05$, respectively. Orange and Blue symbols represent the presence and absence of voles respectively; years are represented by different shapes (2015-○, 2016-▲, 2017-●)

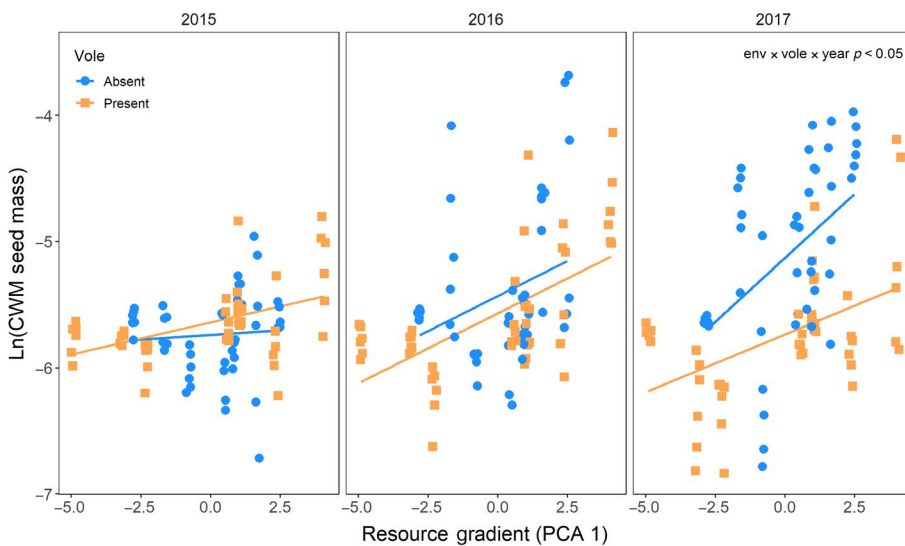


FIGURE 4 Trends of community seed mass along a resource gradient over 3 years. More negative PCA1 values indicate low above-ground productivity with low soil nitrogen (N) while higher PCA values indicate high above-ground productivity and soil N. Orange and blue symbols and lines represent the presence and absence of voles, respectively. Lines indicate significant relationships, at $p < 0.05$, respectively

CWM plant height increased along the environmental gradient regardless of the presence of voles (Table 1B; $\text{env} \times \text{vole } p = 0.29$). Vole effects on CWM leaf N were observed most strongly in the absence of voles such that average CWM leaf N increased from 2015 to 2017 (Figure 3B; Table 1B). CWM leaf N was similar across

years when voles were present (Figure 3B; Table 1B). This increasing relationship between CWMs SLA, height, and plant leaf N and the environment varied over time (Figure 3C–E), with communities being taller and having more plant N at the high-resource end of the gradient in the wettest year (Figure 3D,E, solid black lines,

Table 1B). CWM seed mass patterns along the resource gradient differed over time, and these differences were driven by vole exclusion treatments (Figure 4; Table 1B; $\text{env} \times \text{vole} \times \text{year}$, $p < 0.05$). Over the 3 years, CWM seed mass increased similarly along the resource gradient in the presence of voles (i.e. no difference between slopes of orange lines among years, Figure 4). However, when voles were excluded, the trait–environment relationship shifted from an almost neutral relationship in 2015 to a positive relationship in both 2016 and 2017, with the slope being greatest in 2017 (Figure 4, solid blue lines). This trait–environment relationship for CWM seed mass only differed between the vole treatments in 2017.

Within a given year, functional richness did not differ in the presence or absence of voles, but functional richness did tend to decrease over the course of the study (Figure 5A). In the absence of voles, functional richness decreased from 2015 to 2016 but was

similar in 2016 and 2017, while in the presence of voles, functional richness was similar in 2015 and 2016 but significantly decreased in 2017 (Figure 5A; Table 1D; $\text{vole} \times \text{year}$, $p < 0.05$; Tukey, post-hoc $p < 0.05$). We observed that functional richness increased along the resource gradient in 2016 and 2017 (Figure 5B; Table 1D; Table S2D; $\text{env} \times \text{year}$, $p < 0.001$) but was not impacted by the presence of voles ($\text{env} \times \text{vole}$, $p = 0.59$). Multivariate functional diversity patterns along the resource gradient differed over time, and these differences were driven by vole exclusion treatments (Figure 5C; Table 1D; Table S2D; $\text{env} \times \text{vole} \times \text{year}$, $p = 0.09$). Functional diversity increased along the resource gradient in all years, and in 2015 and 2016 the pattern was similar in the presence or absence of voles. In 2017, the increase in functional diversity was greater in the absence than presence of voles (Figure 5C, comparison between blue and orange dashed lines in 2017 panel).

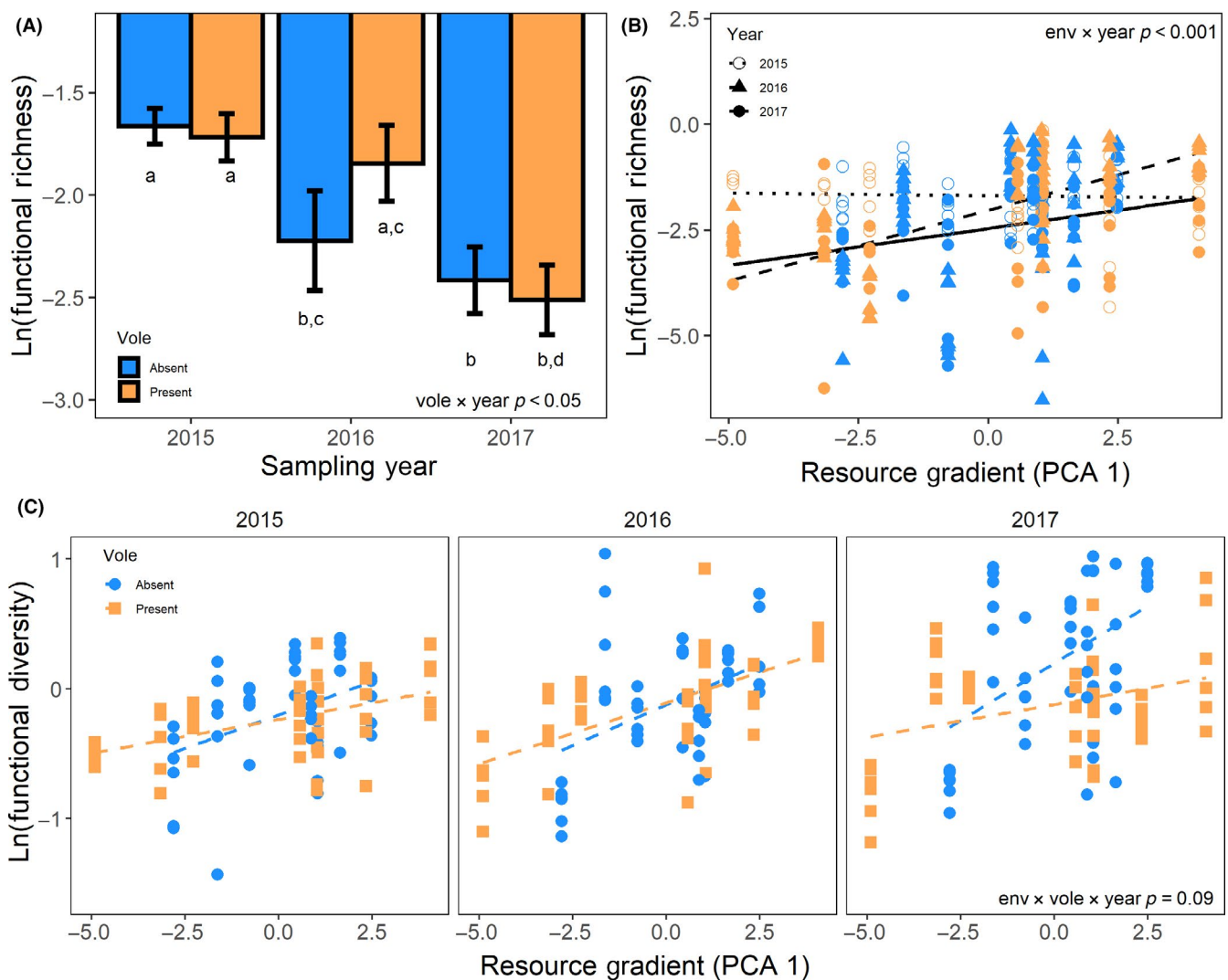


FIGURE 5 Functional richness (A, B) and diversity (C) patterns over time in the presence or absence of voles (orange and blue, respectively) and along a resource gradient (i.e. from lower to higher productivity/resource sites). Functional richness decreased in the absence of voles between 2015 and 2016 and in the presence of voles between 2016 and 2017 (A), and functional richness increased along the gradient in 2016 and 2017 but not in 2015 (B). Functional diversity (estimated as functional dispersion) increased along the resource gradient in all years, but vole effects were only visible in 2017 (C). Solid lines indicate significant relationships at $p < 0.05$ and dashed lines indicate marginal significance at $p < 0.10$. Years are represented by different shapes in b (2015–○, 2016–▲, 2017–●)

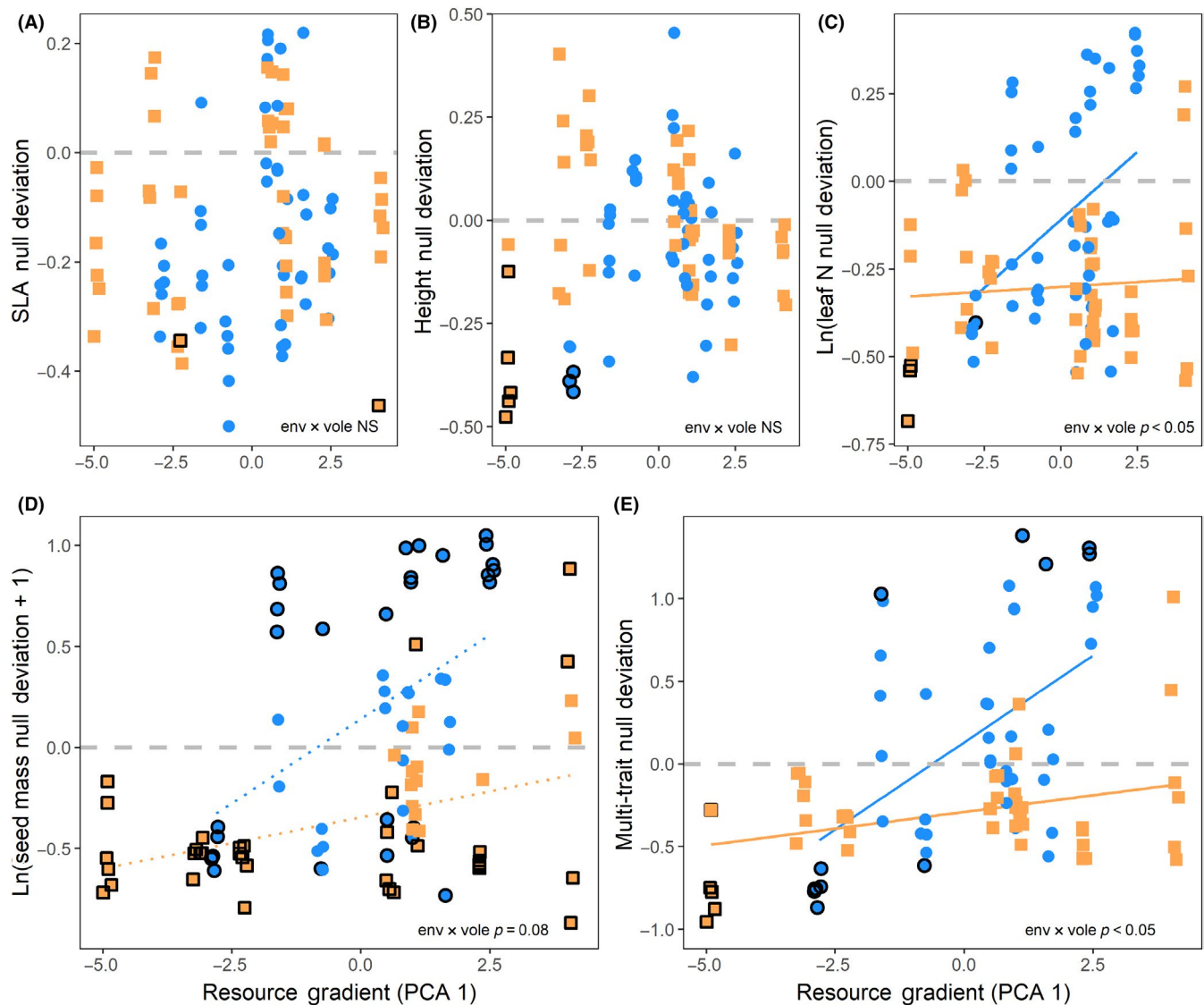


FIGURE 6 Null deviations of functional diversity metrics for grassland plots in the presence of voles (orange, squares) and absence of voles (blue, circles) along a resource gradient (i.e. from lower to higher productivity/resource sites) within 2017. Solid lines indicate significant relationships $p < 0.05$, and dashed lines indicate marginal significance at $p < 0.10$. Black outlined symbols indicate plots where observed species' traits were significantly different from null. Positive outlined symbols indicate that trait functional diversity was significantly overdispersed; if negative, trait functional diversity was significantly underdispersed. Horizontal line at 0 indicates neutral trait dispersion patterns

Based on the 2017 null modelling, the within trait diversity for SLA and height functional strategies did not vary predictably along the environmental gradient (SLA env $p = 0.50$; height env $p = 0.28$) nor did they change in the presence of voles (SLA vole, $p = 0.47$; height vole $p = 0.69$; Figure 6A,B; Table S3). The diversity in total leaf N increased along the resource gradient only in the absence of voles (Figure 6C; Table S3; env \times vole $p = 0.04$). For SLA, Height and leaf N functional diversity, few plots exhibited trait convergence or divergence and dispersion patterns were not affected by vole treatments (Fisher's exact test SLA, $p = 0.49$; Height, $p = 0.71$, leaf N, $p = 0.62$). Seed mass functional diversity tended to increase with higher resources and more strongly in the absence of voles (Figure 6D; Table S3; env \times vole $p = 0.08$). Moreover, a large number of plots exhibited significant trait dispersion patterns, with plots more often overdispersed (positive values) in the absence of voles

and underdispersed (negative values) with voles present ($\chi^2 = 18.95$, $df = 2$ $p < 0.001$). Altogether the seed mass and leaf N individual trait dynamics resulted in multi-trait functional diversity increasing with resource availability and more strongly in the absence than presence of voles (Figure 6E; Table S3; env \times vole $p = 0.04$). The number of plots that exhibited significant dispersion were affected by vole treatments such that overdispersion was observed more than expected in the absence of voles (Fisher's exact test, $p = 0.056$).

4 | DISCUSSION

Overall, we found that vole impacts on plant trait composition and trait diversity were driven primarily by effects on two key plant traits related to herbivore vulnerability (i.e. leaf N and seed size). Within

our system, resources drove the dominant functional trait strategy selecting for a resource acquisitive trait strategy with species that had greater SLA, were taller, and had greater leaf N and seed mass at high-resource sites. Vole foraging affected this pattern for SLA, where SLA increased more strongly in the absence of voles than in the presence, supporting our first hypothesis (Figure 3A). Vole foraging decreased CWM leaf N over the course of the study yet independent of resource availability (Figure 3B), but foraging effects on CWM seed mass were dependent on the environmental condition, year and voles (Figure 4). Contrary to our predictions, the effects of vole foraging did not mirror those of large grazers. Whereas large grazers often increase plant diversity by suppressing competitively dominant species (Hillebrand et al., 2007), voles tended to reduce plant community functional diversity. By the end of the study, functional diversity was greater at high-resource sites when voles were absent than present (Figures 5C and 6E), likely as a result of an increase in diversity of leaf N and seed size traits over time (leaf N Figure 6C; seed mass Figure 6D). These results suggest that vole herbivory can interact with environmental filtering to determine functional trait diversity within California's annual grasslands.

Preferential consumption of the competitive dominant species in high-resource areas versus palatable species in low-resource areas are predicted to have opposing effects on plant diversity, whereby consumers are thought to increase diversity at high-resource sites but decrease diversity at low-resource sites (Borer et al., 2014; Hillebrand et al., 2007). Voles exerted a similar top-down effect on taxonomic richness with richness decreasing more strongly in the absence of voles at high resources, but this effect was not present in every year (i.e. no effect in 2015; only present in 2016, 2017, Figure 2A). Unlike what often occurs with larger herbivores (Hillebrand et al., 2007), we did not find that voles decreased richness at sites with lower-resource availability (Figure 2B). This likely occurred due to reduced vole activity at these sites (Figure 1). The decreased use of these habitats is suggestive of these areas being more marginal habitats for voles, which may act to lessen the effects of vole herbivory at these low-resource availability sites.

The opposing effects of herbivory and resources on plant community structure are predicted to occur because traits that allow a species to do well in high-resource environments may also affect a species' vulnerability to herbivory by generalist consumers (Evju et al., 2009). Therefore, herbivory is predicted to have a significant effect on the dominant trait strategies in plant communities. Yet, we observed that the environmental gradient universally influenced the dominant trait strategy for all of our focal traits (Figures 3 and 4). CWMs SLA, height, leaf N and seed mass all increased at higher resource sites, suggesting that these traits may be part of a broader syndrome of functional traits that are indicative of a species' ability to acquire resources (Grime, 1977; Reich, 2014). In our study, we were only able to account for the intra- and interspecific variation in traits along the soil resource gradient not within the vole treatments. It would be interesting to similarly understand how traits such as plant height plastically change in response to herbivory, but we were unable to measure this.

Vole herbivory only influenced the CWM of a subset of functional traits measured (leaf N and seed mass). Leaf N increased in

the absence of voles over the course of the study (Figure 3B), and seed mass increased along the resource gradient more strongly in the absence than presence of voles in 2017 (Figure 4). Moreover, these traits differ from the traits influenced by larger grazers (Diaz et al., 2007; Eskelinen et al., 2012), although similar to what other small mammal studies have observed (Maron et al., 2012, 2014). Indeed, the traits that responded to our small mammal manipulation loaded on separate trait axes from those that were responsive to only resources (Figure S2). These herbivory-related traits coincide with the nutritional and dietary needs of voles, who require high protein grass shoots to maintain growth and reproduction during their breeding season (Batzli, 1986) and rely primarily on seeds during the dry summers (Batzli & Pitelka, 1970, 1971).

By the final year of the study, we observed higher multivariate functional trait diversity at high-resource sites, in the absence of voles (Figure 5B). Thus, while the number of species decreased at high-resource sites, there was greater diversity in functional traits within that community in the absence of voles. This trend was primarily driven by the strong effects of voles on seed mass and leaf nitrogen. We observed that diversity in seed mass and leaf N traits increased at high-resource sites in the absence of voles (Figure 6C,D). Moreover, more plots exhibit significant trait overdispersion for seed mass in the absence of voles than expected by chance, while more plots exhibit underdispersion in the presence of voles (Figure 6D, black outlined circles compared to outlined squares). Together, these results suggest that in the absence of voles, there was greater niche differentiation of seed mass at higher-resource sites, while in the presence of voles there was greater convergence in seed mass. This was likely the result of greater recruitment of additional large seeded species when voles were excluded. This result is counter to previous work demonstrating that herbivory decreases dominant species to promote increased plant taxonomic evenness at higher-resource sites (Hillebrand, 2003; Hillebrand et al., 2007), as we observed a trend of higher functional diversity in high-resource sites but when voles were absent. Future studies in our system are needed to disentangle whether the observed trend is exclusively due to vole herbivory or due to other changes in the ecosystem such as litter accumulation shifting the dominant successful strategy, as has been observed in other studies (Eskelinen et al., 2012). However, previous research has demonstrated that voles can reduce about 70% of the seed rain of preferred species (Batzli & Pitelka, 1970) and may therefore greatly impact seed trait composition and diversity. These results further suggest that to disentangle the multiple effects of community assembly processes and to prevent overestimating a single process, studies need to assess multiple attributes of traits (i.e. individual trait diversity and CWM vs. multivariate trait diversity) that better capture the multiple axes on which biotic processes may act.

California grasslands are very dynamic because annual plant composition and biomass are quite sensitive to annual variation in precipitation (Dudney et al., 2017; Hallett et al., 2014; Pitt & Heady, 1978). This was evident in the strong year-to-year variation we found. For example, the increase in plant SLA and height along the environmental

gradient was strongest in the wettest rainfall year. Our study also coincided with the end of the worst multi-year drought California had experienced (Griffin & Anchukaitis, 2014), which had large-scale impacts on plant and animal communities across the state (Copeland et al., 2016; Prugh et al., 2018). We observed lagged impacts of this drought and the likely recovery in vole populations, as manifest by increasing vole runway abundance (Figure 1). Voles are very sensitive to changing precipitation patterns due to precipitation impacts on plant productivity (Batzli & Pitelka, 1970; Cockburn & Lidicker, 1983).

Taken together, our results provide evidence that small mammals do indeed impact the trait composition and trait diversity within this grassland system and that predictions developed based for larger herbivores may not readily translate to smaller generalist consumers. Furthermore, this work suggests that studies that infer community assembly processes from trait patterns need to account for the presence of small mammal consumers, as overlooking them may result in overestimating the impacts of competitive interactions in high-resource environments.

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AUTHORS' CONTRIBUTIONS

L.L. and J.L.M. designed the experiment; L.L. collected and analysed the data; L.L. led the writing. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.6086/D18Q3X> (Larios & Maron, 2020).

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