

Grass trait-abundance relationships and the role of the functional composition of the neighboring community

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Abstract

Questions: Plant traits can predict a species' relative abundance and its influence on ecosystem processes. However, trait expression and the relative abundance of a species are also influenced by its abiotic and biotic environment. Here, we ask whether the relationship between plant traits and relative abundance is modified by abiotic (e.g., climate and topography) and biotic factors (e.g., community taxonomic and functional diversity) across Californian grasslands.

Location: San Francisco Bay Area

Methods: We measured specific leaf area (SLA; leaf area / dry mass) and plant height of 19 grass species (family: Poaceae) across 117 plots. We also quantified the relative abundance of each species as well as several biotic attributes of the neighboring grass community including total plant cover, species richness and evenness, community-weighted mean (CWM) traits, and functional diversity. Using multiple linear regression, we assessed whether abundance could be predicted from traits and the interactions between traits and both biotic and abiotic factors. We fit similar models predicting traits from relative abundance.

Results: Grass species had higher relative abundance in plots where they were taller and had higher SLA. They were also more abundant in communities with low functional richness (FRic) and high functional evenness (FEve), perhaps because of low resource use efficiency of their neighbors and a lack of dominant grasses. Neither abundance nor plant height were associated with abiotic variables, although SLA responded predictably to precipitation according to a bell-shaped curve. Grasses were taller where they were more abundant, but the impact of abundance on SLA depended on community FEve. Finally, we show strong evidence for community trait similarity, whereby an individual's trait expression was positively correlated with the traits of its grass neighbors.

Conclusions: Taken together, these results imply that traits are predictive of abundance and vice versa, and these relationships depend on biotic interactions more than climate.

Key words: plant functional traits, relative abundance, grasses, specific leaf area, plant height, functional diversity, community-weighted traits, climate, species interactions

Introduction

A major goal of ecological research is to understand where species occur and how abundant they are. Plant traits are key to understanding the environmental conditions under which species can exist (Diaz et al. 1998), and there is mounting evidence that traits can also predict the abundance of a species relative to co-occurring species (Reader 1998; Shipley et al. 2006; Cornwell and Ackerly, 2010; Laliberte et al. 2012). Understanding these trait-abundance relationships is critical for scaling from individuals to ecosystems, as the traits of more abundant species are likely to have the greatest impact on ecosystem processes (Grime 1998). However, much of this research has focused on whether plant traits can predict the abundance of a species (Shipley et al. 2006), and not the other way around. Substantial intraspecific trait variation exists across communities (Siefert et al. 2015), which may be explained by a species' relative abundance in that community. Moreover, both the traits expressed by a plant and its abundance at a particular location are functions of its biotic and abiotic environment. In this study, we therefore explore biotic and abiotic controls on abundance and trait expression, and the bi-directional relationship between them.

There are two major mechanisms by which the abundance of a species may predict its trait expression. The first is that a species' abundance can reflect, to some degree, the intensity of intraspecific competition in a plot, which is often stronger than interspecific competition (Adler et al. 2018) and can promote certain trait expressions. The effect competition has on trait expression depends on whether a species or individual tolerates or attempts to outcompete its competitor (Novoplansky 2009). In the case of intraspecific competition, evidence suggests species more often attempt to outcompete their neighbors (Bennett et al. 2016; Rehling et al. 2021). Compared to solitary individuals, for example, grasses growing in pots with a high density of conspecific individuals increased biomass allocation to roots, likely to outcompete neighboring individuals for belowground resources (Rehling et al. 2021). Among a diversity of grasses, legumes, and forbs, heightened intraspecific competition led to increased SLA, a trait associated with acquisitive resource use strategies (Bennett et al. 2016). And a recent meta-analysis suggests individuals growing in monospecific stands of higher density have higher SLA and specific stem length (Postma et al. 2021). Therefore, we expect high relative abundance should promote the expression of more competitive traits such as high SLA and taller growth.

The second major mechanism arises because of a shared response of abundance and trait expression to some environmental driver. In other words, spatial variation in a species' relative abundance may be predictive of trait variation across sites if abundance reflects the climatic suitability of a site. In this scenario, abundance would not directly influence trait values, yet the climate or other abiotic site characteristics that promote high abundance may also promote particular trait expressions. Relationships between abundance and the abiotic environment are often conceived as hump-shaped curves, where abundance is maximized in some optimal condition and declines away from that optimum (Van Couwenberghe et al. 2013). Functional traits, in turn, may show similar response curves if the trait is driven primarily by the degree of optimality of the environment, or could be more linear if the trait expression is directly driven by the environmental variable. In the latter case, we would not expect abundance to be predictive of trait expression. We know climate can partially explain spatial variation in the traits of a species (Sandel et al. 2021, Cardou et al. 2022), although there remains significant unexplained variation. And it is logical to assume that high relative abundance is indicative of greater climatic site suitability for growth/reproduction, although recent analyses disagree on whether this is empirically supported (Weber et al. 2017; Dallas and Hastings, 2018). Site suitability based on climate records alone does not account for the many biotic interactions that could influence species abundance. Furthermore, the impact these biotic interactions (e.g. herbivory, competition, fungal colonization) on relative abundance is context-dependent and can shift depending on temperature or other climatic variables (Lynn et al. 2019). Therefore, the effect of abundance on trait expression is likely dependent on both abiotic and biotic environmental conditions.

The potential for biotic interactions (at least plant-plant interactions) to influence traits and relative abundance can at least partially be summarized by the taxonomic and functional composition of the neighboring community. For example, forbs growing in higher richness treatments were taller and had larger leaves with higher SLA (Lipowsky et al. 2015). Evidence suggests that this response was due to biodiversity acting as a selective pressure on trait expression rather than trait plasticity driving the response (van Moorsel et al. 2018). Species-rich communities are also more likely to contain productive dominant species (e.g., selection effect, Huston 1997) that may limit the abundance and perhaps trait expression of other individuals. Similarly, communities with low species evenness often contain dominant species that, by

definition, have high relative abundance and outcompete their neighbors (Avolio et al. 2019). Community-weighted mean (CWM) plant traits (i.e., traits weighted by relative abundances) describe the trait composition of the entire community but mostly reflect dominant species, particularly in uneven communities. The CWM of a neighboring community may be predictive of a species/individual's trait expression if trait optima exist in certain environments (Dong et al. 2020), but may also say something about the competitive nature of the environment (e.g., high abundance of tall species with large leaves). Finally, functional diversity might influence a species relative abundance and trait expression if the size of the community functional niche space, and neighboring species' relative locations within that space, is indicative of potential functional trait overlap (Mason et al. 2005).

Here, we assessed whether the relative abundance of grass species influences the local expression of two traits, SLA and plant height, in California grassland communities. We tested the hypothesis that species are taller and have higher SLA where they are more abundant, but that this depends on climate and biotic interactions. Additionally, we assessed whether local trait values predict an individual's relative abundance (Cornwell and Ackerly, 2010). Specifically, we expected taller species with more acquisitive resource use strategies (e.g., high SLA) would be more abundant than co-occurring species. In our models, we included information about the biotic attributes of the community (e.g., taxonomic and functional diversity) as well as long-term and recent precipitation patterns because both abiotic and biotic factors are known to influence species abundance and trait expression (Novoplansky 2009; Weber et al. 2017; Lynn et al. 2019; Sandel et al. 2021). There is a need to make accurate predictions of the spatial variation in plant traits within species (Sandel et al. 2021), especially as traits such as height and SLA are incorporated into global vegetation models (Madani et al. 2018). This study may improve such models by increasing our understanding of trait-abundance relationships for grasses (family: Poaceae), an ecologically, economically, and culturally important plant family.

Methods

Data collection

We measured traits of grasses across several grassland communities in the San Francisco Bay Area, which is characterized by a Mediterranean climate with warm, dry summers and cool

wet winters. We measured SLA and plant height in late April through early June to capture the end of the growing season. These traits represent separate axes in the global spectrum of plant form and function, one related to size and the other to resource economics (Diaz et al. 2016; Sandel et al. 2016). Overall, we sampled 19 grass species from 117 plots across four growing seasons (2017-2019, and 2021) (Appendix S1). Most of these species are relatively abundant and widespread in California grasslands (Stromberg et al. 2007). Measurements were not repeated in each plot; rather, new plots were added in each year for a total of 117 plots across the four years of measurements. Measurements in 2020 were limited due to the COVID-19 pandemic.

Traits were measured on up to five arbitrarily selected individuals of each grass species present in a 5x5 meter plot. First, plant height was recorded as the distance from the ground to the base of the blade of the highest leaf (excluding flag leaves). Then, we collected the highest fully expanded, undamaged, green leaf and immediately photographed it against a white background with a reference scale bar. If necessary, a piece of plexiglass was used to hold the leaf flat during imaging. We then transported leaves back to the lab where they were oven-dried at 55-60 °C for at least 48 hours prior to measuring leaf dry mass. We estimated leaf area from images using ImageJ software and calculated SLA as leaf area divided by leaf dry mass. Trait measurements for a species were averaged across the plot.

Within each plot, we estimated the absolute abundance of each species present including non-grasses. Absolute abundance was estimated as binned values of aerial cover: 1% (present), 5%, 10%, and all multiples of 10 up to 100%. Note, total aerial plant cover can exceed 100% due to canopy layering. Relative abundance was then estimated as the absolute abundance divided by total plant cover in a plot. For each plot, we also estimated species richness as the total number of species present, and species evenness as the ratio of Shannon's diversity index and the natural logarithm of species richness (Pielou 1966). Finally, we calculated several indices of functional composition using the locally measured traits of the grass community. Plots were largely dominated by grasses (median relative abundance = 80%), so such measures are reflective of the larger plant community (Appendix S2). Specifically, we estimated community-weighted means (CWMs) for grass SLA and height (weighted by relative abundance), and three indices of functional diversity (Villéger et al. 2008; Laliberté et al. 2014): functional dispersion (FDis; the multivariate equivalent of mean absolute deviation in trait space), functional richness (FRic; the total volume of the 2-dimensional functional space occupied by the community), and functional

evenness (FEve; the regularity of spacing between species within multivariate trait space). We used the *dbFD* function in the *FD* package to estimate functional diversity indices in two-dimensional trait space (e.g. height and SLA combined) (Laliberté et al. 2014).

To describe recent and long-term precipitation patterns, we used PRISM climate data (PRISM Climate Group, 2021). For each sampling plot, we extracted the 30-year normal for precipitation and the monthly precipitation for the 12 months preceding sampling. We call these *P* and *P1*, respectively and from them computed *Pdev* as *P1-P*, which represents whether the year prior to sampling was relatively wet (positive values of *Pdev*) or dry (negative values of *Pdev*) at a site. Despite all measurements taking place within the San Francisco Bay Area, our sites covered a strong gradient of mean annual precipitation (588-1370 mm/year). Considering the strong topographic gradients present in this region, we also record the slope and aspect of each plot, obtained from the 10 m resolution digital elevation model from the National Elevation Dataset.

Data Analysis

To relativize across species, we determined the plot-level deviation in trait values (SLA or Height) from the species' mean trait value (deviation = (mean trait of a plot) - (mean trait averaged across plots)). Traits were averaged within plots before calculating the mean across plots. Positive values of trait deviation therefore indicate individuals in the plot were taller or had higher SLA relative to the species' average trait value. We then pooled data across species and ran multiple linear regression models predicting either SLA or Height deviation from a species' relative abundance and both abiotic and biotic plot characteristics. Species present in less than 3 plots were excluded (*n* = 19 total species included in the analysis). Relative abundance was used instead of absolute abundance to demonstrate the degree to which the species was dominant in a plot. We included all two-way interactions between relative abundance and each of the plot characteristics to determine whether the effect of relative abundance on traits was influenced by biotic and abiotic conditions. Abiotic predictor variables included *P*, *Pdev*, slope, and northness. Northness was estimated as the cosine of aspect, where positive values indicate more north-facing slopes. Biotic predictor variables included species richness and evenness, CWMs of SLA and Height, total plant cover, as well as all three indices of functional diversity (*FDis*, *FEve*, and

FRic). We also ran similar models with absolute abundance rather than relative abundance, although these models excluded total plant cover. Importantly, for each row in the dataset (plot $\times$ species combination; $n = 659$), we calculated plot-level CWMs (weighted by species relative abundance) and functional diversity excluding the focal species of the row (i.e., the species we were predicting trait deviation for). Therefore, CWMs and functional diversity indices represent the functional composition of the neighboring plant community. Given that FEve cannot be calculated on communities with less than three functionally distinct species, we removed 27 rows from the dataset prior to modeling due to missing values.

To determine whether traits predict relative abundance, we ran similar multiple linear regression models but with arcsin-transformed relative abundance as the response variable. Abiotic variables included climate, slope, and northness. Biotic variables included species richness and evenness as well as the functional diversity of the neighboring community (FDis, FRic, and FEve calculated the same as above). Finally, we included the trait deviation from local CWMs for both height and SLA as well as all two-way interactions between trait deviations and both biotic and abiotic plot characteristics. Similar models were run for absolute abundance which excluded total cover as a predictor variable.

We checked model assumptions using the *check_model()* function in the *performance* package (Lüdtke et al. 2021). When necessary, we log-transformed predictor variables to meet assumptions of normality and scaled all predictor variables to remove potential collinearities. We visualized the effects of significant predictor variables ($p < 0.05$) on response variables using partial residual plots produced with the *visreg* package (Breheny & Burchett 2017). All analyses were conducted in R Statistical Programming (version 4.1.3).

Process Model

To assess the robustness of our findings, we created a community process model to simulate the effects of plant traits, competition, and community composition on a species' relative abundance. The goal was to develop a model with known parameters affecting species abundances as a function of their functional traits and those of co-occurring species. We could then ask whether variation in these parameters could be detected using our empirical modeling approach described above.

The model begins with a set of S species randomly arrayed in a two-dimensional space. The species coordinates in this space were drawn within a unit circle using a polar coordinate system, with a random angle (with uniform probability across the interval $[0, 2\pi]$) and random radius (with uniform probability in the interval $[0, 1]$). Each starts the simulated growing season at low abundance and grows according to an adaptation of the discrete time Lotka-Volterra competition equations (modified to allow competition among multiple species):

$$N_{t+1} = N_t \left(1 + r \left(1 - \frac{N_t^*}{K} \right) \right)$$

Where N_t represents the population size of the species at time t , and r and K represent the population growth rate and carrying capacity. N_t^* represents the effective population size for the species, as follows:

$$N_t^* = N_t + \sum_{i=1}^S C_{i,t} P_i$$

Where $C_{i,t}$ is the abundance of the i^{th} of S competing species, and P_i represents the proximity to the focal species in the trait space. Thus, the effective population size is the species' own population size, plus contributions from each competing species, according to how functionally similar (proximate) these species were. Proximities were calculated according to a logistic transformation of a rescaled Euclidean distance (d) in the trait space:

$$P_i = \frac{e^{-5(d-0.5)}}{1 + e^{-5(d-0.5)}}$$

The rescaling was performed on the Euclidean distances, simply dividing each distance by a factor D . This has the result of simulating intense competition when D is large (i.e., many species are in close proximity to one another) or weak competition when D is small (i.e., most species interact only weakly with their neighbors).

For each simulation, we also defined an optimum X, Y position in the trait space. A species' carrying capacity was a function of its proximity to that optimum:

$$K = 100 + P_i A$$

Where A describes how advantageous it is to be near the optimum. The K values for all species in a simulation were then rescaled to a mean of 100.

After 100 time steps, we recorded each species' final abundance and considered its x and y coordinates to be its trait values. From this, we calculated $FDis$, $FRic$, and $FEve$ using the *FD* package. We also calculated a species deviation from the bivariate CWM (hereafter referred to as $FUniq$).

We repeated the simulation 10,000 times with random draws of: species richness (S , integers with uniform probability in $[3,10]$), the X,Y position of the trait optimum (within the unit circle), the optimum advantage (A , uniform probability in $[0,100]$), and the competitive radius (D , uniform probability in $[0,3]$).

Finally, we ran a multiple linear regression model predicting a species' abundance from each metric of functional diversity, species richness, total plant cover, and all two-way interactions between $FUniq$ and other predictor variables. This was done to match the empirical model as closely as possible. We included a new variable, Resource, to mimic precipitation. This was calculated from the competition scaling variable (D) as: $Resource = \sqrt{1/(1+D)}$.

Results

We found that intraspecific variation in SLA across 19 California grasses was linked to an individual's relative abundance, precipitation, and the functional composition of the local grass community. Our model explained 24% of variation in SLA deviation across plots and species (Table 1). We observed a positive relationship between SLA and community-weighted SLA whereby individuals tended to have higher SLA in plots where the local grass community (or at least the dominant species) also had high SLA (Figure 1). Notably, the focal species was excluded from estimates of CWM SLA, so these estimates represent traits of other neighboring grass species. Additionally, we observed a significant interaction between mean annual precipitation and the precipitation accumulated over the 12 months prior to trait measurements ($P \times P_{dev}$; Table 1). Specifically, in dry regions, individuals had higher SLA in wet years compared to their species' mean, but the opposite trend was observed in wet sites (Figure 2A). Finally, we observed a significant negative interaction between an individual's relative

abundance and the functional evenness of the neighboring community (Table 1). Individuals had higher SLA compared to their species mean where they were more abundant and the local community had low functional evenness. In contrast, abundant individuals had lower SLA in communities with high functional evenness (Figure 2B). We observed similar results for models including absolute abundance rather than relative abundance (Appendix S3), with the addition of absolute cover having a significantly negative main effect on SLA deviation.

Our model predicting height deviation from abiotic and biotic attributes of the sampling plot explained ~21% of trait variation (Table 1). We found that individuals were generally taller relative to their species' mean in plots where they had higher relative abundance (Figure 3A). Additionally, individuals were taller in plots with greater total plant cover (Figure 3B) and where/when the local grass community was taller (i.e., high community-weighted plant height excluding the focal species) (Figure 3C). Notably, none of the abiotic variables (e.g., climate or topography) influenced whether an individual was tall or short relative to its species mean. We observed similar results for the model including absolute abundance (Appendix S3), with the only change being an observed positive effect of neighboring community SLA on height expression.

We found that a species' traits, as well as the functional diversity of its neighboring grass community, influenced its relative abundance. Our model explained 16% of variation in relative abundance (Table 2). Individuals had the highest relative abundance where they had higher SLA and were taller compared to their neighboring grass community (Figure 4). The significant positive interaction term suggests relative abundance is maximized with a combination of tall stature and high SLA (Table 2). Additionally, species had higher relative abundance in plots where the local grass community had low functional richness but high functional evenness and total cover (Figure 5). Community functional richness is sensitive to gradients in species richness (Mason et al. 2013), so this could be indicative of a negative effect of species richness, which did vary across plots (Appendix S2); however, species richness was not a significant predictor of relative abundance (Table 2). Notably, none of the abiotic variables (e.g., climate or topography) influenced an individual's relative abundance in our model (Table 2). Results were generally similar for the model predicting absolute abundance from abiotic and biotic variables (Appendix S4). The major significant difference was an observed negative interaction between mean annual precipitation and recent precipitation ($P \times P_{dev}$; p -value = 0.032) suggesting absolute cover of

species increases in wet years, but this has a diminishing effect the wetter a site gets. Additionally, we observed a positive interaction between SLA and topographical slope, meaning the positive effect of SLA on absolute abundance is more pronounced on steeper slopes (Appendix S4).

Our process model largely supported our empirical results (Figure 6). A species' relative abundance in our simulated communities was strongly positively influenced by its trait deviation from the CWM trait. Abundance was also negatively correlated with FRic and positively correlated with FEve. The simulation model did have some differences from the empirical data. First, relative abundance was higher in plots with low species richness and low total cover, which was not the case in the empirical model. Additionally, FDis had a significant negative effect on relative abundance in simulated communities. We also found a positive effect of precipitation (i.e., resource availability) on relative abundance, although this specific variable was not included in our empirical dataset. Finally, we found that the positive effect of Funiq on abundance (i.e., trait deviation from CWM) depended on several other metrics of community composition. Specifically, we found a significant negative interaction between Funiq and FEve, species richness, and cover. This suggests being functionally different from the CWM has less of a positive influence on relative abundance in productive, species-rich communities with high functional evenness. On the other hand, we observed a significant positive interaction between Funiq and FDis, which indicates an even greater benefit of functional uniqueness on relative abundance when neighboring species are also functionally distinct.

Discussion

We measured trait-abundance relationships across 19 grass species in California to see how they might be modified by abiotic and biotic interactions. Our models support previous findings that SLA and height are predictive of a species' relative abundance (Cornwell and Ackerly, 2010). Furthermore, we found that species were more relatively abundant when growing in productive (i.e., high plant cover) communities with low functional richness, but high functional evenness. In addition, species were both taller and had higher SLA when growing in communities where their neighbors had similar traits, as inferred from community-weighted traits. Species were taller where they had higher relative abundance, but the influence of relative

abundance on SLA varied depending on the neighboring grass community's functional evenness. Climate was an important predictor of SLA variation, although biotic factors more strongly influenced the expression of both traits as well as species relative abundance. Taken together, these results imply that traits are predictive of relative abundance and vice versa, and these relationships depend on biotic interactions.

Precipitation is often not a strong predictor of SLA (Moles et al. 2014), yet we observed a hump-shaped relationship whereby grass SLA is maximized at intermediate precipitation and declines towards the extremes (Figure 2A). A positive effect of recent precipitation on SLA, as observed on the drier end of a species' range, likely represents a water conservation strategy whereby species reduce their evaporative surface area in drier conditions (Dwyer et al. 2014). On the wet end, however, the mechanism of declining SLA with increasing precipitation is unknown. The response was largely driven by changes in leaf tissue density rather than leaf thickness (Sandel and Griffin-Nolan *in review*), which might indicate a reduction in leaf air space and thus increased photosynthetic performance in wetter more competitive environments (Chazdon and Kaufmann 1993). Regardless of the mechanisms controlling SLA variation, these results suggest SLA-abundance relationships will likely depend on both long-term and recent annual precipitation.

Plant height was not correlated with long-term or recent precipitation, which supports previous findings of a weak effect of precipitation on both intra- and inter-specific variation in height (Siefert et al. 2015). A positive effect of precipitation on height might be expected given that taller plants are often more productive plants (Niklas and Enquist 2001) and grassland productivity is largely limited by precipitation (Churkina and Running 1998). However, grasses may invest more in horizontal growth and tiller density depending on their functional type (i.e., caespitose, rhizomatous and stoloniferous graminoids) which may complicate this relationship if stem density is more adaptive than vertical growth in certain environmental conditions (Hartnett and Fay 1998). Plant height was, however, associated with biotic variables in our models. Specifically, individuals were taller where they were more relatively abundant (Figure 3A). If relative abundance reflects the degree of intraspecific competition as we hypothesized, then this response may reflect a strategy of outcompeting other individuals of the same species via shading. However, a recent meta-analysis suggests a doubling of conspecific stand density has no significant effect on plant height (Postma et al. 2021). Alternatively, high relative abundance

may reflect greater site suitability (Weber et al. 2017) which should lead to taller growth relative to the species mean. Height was also positively associated with the total plant cover of a plot (Figure 3B), which can be viewed as a proxy for productivity, site suitability, and/or potential competition. In this case, we hypothesize that total cover is representative of site suitability and productivity, rather than competition, given its positive effect on height.

While height was positively influenced by relative abundance across all plots (i.e., significant main effect; Table 1), the effect of relative abundance on SLA depended on the functional evenness of neighboring communities (Figure 2B). Functional evenness describes the degree to which species are evenly distributed within the multivariate trait space. If we assume traits reflect resource use strategies, then communities with high FEve efficiently utilize the available resources in a plot (Mason et al. 2005). In such communities, we observed a negative effect of a species' relative abundance on SLA, which may reflect increased intraspecific competition selecting for resource conservative strategies in a community where neighbors efficiently utilize available resources. However, relative abundance had a positive effect on SLA when individuals were growing in low FEve communities. Such communities tend to have greater niche overlap, with only a few species dominating both community biomass and a certain region of the trait space (Ali et al. 2018). Therefore, high abundance may promote high SLA in these communities if such acquisitive traits help maintain dominance, although the link between traits and dominance is unclear (Avolio et al. 2019). Increased stand density and abundance of conspecific individuals generally leads to increased SLA in monocultures (Postma et al. 2021); however, our results highlight the importance of considering neighboring community functional diversity when assessing trait responses to conspecific stand density (i.e., abundance).

For both height and SLA, we observed a positive effect of CWM traits on an individual's trait expression (Figure 1 and Figure 3C), suggesting species have similar trait expression as their neighbors. This supports previous observations in herbaceous communities of plant trait convergence towards optimal expression under similar environmental conditions, particularly for productivity-related traits such as SLA (Grime 2006). It also suggests an optimal trait expression exists in a given environment and the benefits of this outweigh the potential benefits of niche differentiation (Weiher et al. 1998). Alternatively, plants may converge to similar heights as their neighbors, despite the competitive advantage gained by taller stature, as a mechanism to reduce

stress caused by wind (Nagashima and Hikosaka 2011), a likely mechanism in open windy grassland habitats.

Past research has confirmed that traits are predictive of a species' relative abundance. In a coastal California woodland, for example, taller plants and those with low SLA were the most abundant, likely due to their late successional growth strategy being optimal for an ecosystem that had not recently experienced large-scale disturbance (Cornwell and Ackerly, 2010). We observed slightly different results in California grasslands - taller plants and those with *high* SLA compared to neighboring grasses were the most abundant (Figure 4). This likely reflects the competitive advantage of having both high SLA and tall stature in a disturbance prone ecosystem. Tall individuals with high SLA are often more competitive and shade out neighboring plants (Westoby 1998). Importantly, we not only observed significant main effects of these traits, but also a significant interaction between these two traits (Figure 4). Height and SLA are often not correlated and represent separate axes in the global spectrum of plant form and function (Diaz et al. 2016). Therefore, species do not necessarily face a tradeoff between these two traits and can invest in both tall stature and high SLA to maximize relative abundance.

In addition to traits influencing abundance, functional richness and functional evenness of the neighboring community had contrasting effects on an individual's relative abundance (Figure 5A and B). Functional richness describes the overall size of the multivariate trait space in a community. Low FRic could imply available resources are not being utilized efficiently (Mason et al. 2005), although this metric does not account for unoccupied "holes" in the multivariate trait space (Legras et al. 2018). Thus, the negative effect of functional richness on relative abundance could indicate species are able to capitalize on the inefficient resource utilization of their neighbors in low FRic communities. The positive effect of FEve suggests that individuals can achieve particularly high abundance in communities where their neighbors are not overlapping in one region of the functional space. These two results could have implications for the management of invasive grasses in California and the restoration of communities with targeted functional diversity that supports high abundance of certain species but not others (Cadotte et al. 2011).

We also found species were more abundant in plots with high total plant cover, which can be viewed as a measure of plot productivity, but also a combined measure of potential inter- and

intraspecific competition. This positive, albeit weak, effect of total cover on relative abundance in our empirical models could be due to the target species' abundance contributing to total cover of that plot. We further tested these relationships using a community process model with much higher sample size and observed an overwhelmingly negative effect of total cover on a species' relative abundance. This suggests high total plant cover, and thus competition, should reduce a species' relative abundance in that plot, although this is likely context-dependent (Aschehoug et al. 2016). Importantly, this was the only major inconsistency between the observed significant effects in our empirical model and the directionality of those effects in the process model. In most respects, this model verified the efficacy of our statistical assessment in recovering known mechanistic processes.

Our empirical models do not perfectly describe the biotic attributes of the communities we studied; therefore, certain results should be viewed with caution. For example, our functional diversity metrics and CWMs exclude forbs and other non-grasses, which are interacting with focal species and may influence traits and abundance, especially if deep-rooted trees and shrubs facilitate shallow-rooted grasses through hydraulic lift (Priyadarshini et al. 2016). However, our plots were heavily dominated by grasses (Appendix S2) giving us high confidence that we represented the functional qualities of the local community. Additionally, our process model (which incorporates the abundances of 100% of species in the theoretical community) largely agreed with our empirical results (Figure 6). Moreover, grasses mainly interact with neighboring grasses, at least belowground, as forbs often occupy a different rooting space (Nippert and Knapp 2007). A final caveat of our analysis is that we assume species are responding similarly to climate and community composition (i.e., no random effect of species included in our models). This is perhaps a flawed assumption, but we opted to pool species together to avoid overfitting models.

The goal of this paper was to determine how abiotic and biotic factors influence trait-abundance relationships across grass species. Our empirical models suggest that traits do influence relative abundance, but that this is independent of climate. Indeed, climate had little to no influence on a species' relative abundance while indices of functional diversity did. The process model simulations suggested that functional aspects of the neighboring community do interact with an individual's traits to influence its abundance; thus, a higher sample size may reveal this pattern in natural ecosystems. We also considered how relative abundance influences

traits, which is less often discussed in trait-abundance literature. We found that relative abundance positively influences height, and has variable impacts on SLA depending on the functional evenness of the neighboring community. Moreover, we confirm previous findings that long-term and antecedent precipitation influence SLA, but not grass height, likely because grasses exhibit a range of vertical and horizontal stem growth strategies. Finally, we show strong support for community trait similarity, whereby an individual grass's trait expression was positively correlated with the traits of its grass neighbors. These results suggest trait-abundance relationships are more complex than previously thought and both biotic and abiotic factors should be considered in modeling trait variability.

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Author Contributions

BS led the data collection, RJG-N conducted the analysis, and both authors wrote the manuscript.

Data Availability

All original data and scripts to analyze them are available in the supplementary materials.

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602 **Supporting Information**

603 **Appendix S1.** List of sampled grass species with mean traits

604 **Appendix S2.** Plot community characteristics

605 **Appendix S3.** Model results predicting traits from absolute abundance

606 **Appendix S4.** Model results predicting absolute abundance from traits

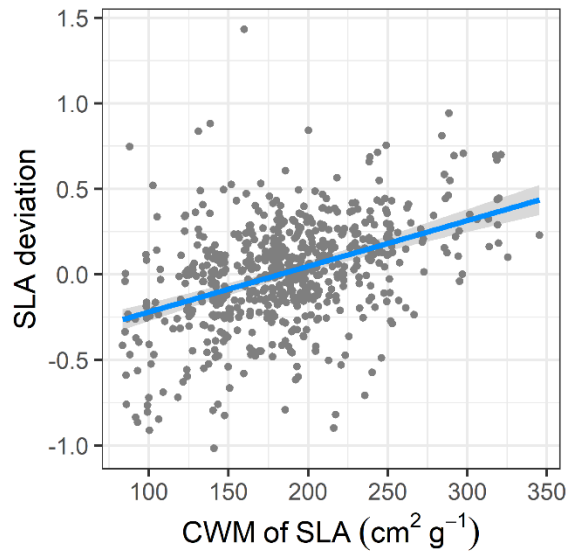
Table 1. ANOVA table showing results from two separate models predicting an individual plant's SLA and Height deviation (i.e., deviation from its species mean) from biotic and abiotic characteristics of the plot. Abundance refers to relative abundance

<i>Predictors</i>	SLA deviation				Height deviation			
	<i>Estimates</i>	<i>CI</i>	<i>T-value</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>T-value</i>	<i>p</i>
Intercept	0.013	-0.012 – 0.039	1.027	0.305	-0.003	-0.030 – 0.024	-0.212	0.832
abundance	-0.022	-0.047 – 0.002	-1.813	0.07	0.029	0.003 – 0.055	2.198	0.028
P	-0.053	-0.082 – -0.024	-3.563	<0.001	-0.009	-0.040 – 0.022	-0.585	0.559
Pdev	0.024	-0.010 – 0.057	1.372	0.17	0.004	-0.032 – 0.040	0.225	0.822
cover	-0.016	-0.047 – 0.015	-1.017	0.309	0.05	0.017 – 0.084	2.99	0.003
richness	-0.01	-0.047 – 0.026	-0.547	0.584	-0.028	-0.067 – 0.011	-1.405	0.161
evenness	-0.004	-0.033 – 0.024	-0.287	0.774	-0.001	-0.032 – 0.029	-0.093	0.926
CWM SLA	0.129	0.104 – 0.154	10.219	<0.001	0.022	-0.004 – 0.049	1.652	0.099
CWM Height	0.021	-0.005 – 0.048	1.566	0.118	0.126	0.098 – 0.155	8.629	<0.001
FDis	-0.017	-0.049 – 0.014	-1.093	0.275	-0.028	-0.062 – 0.005	-1.668	0.096
FRic	0.019	-0.015 – 0.053	1.116	0.265	0.028	-0.008 – 0.065	1.521	0.129
FEve	-0.005	-0.031 – 0.022	-0.351	0.726	0.017	-0.011 – 0.045	1.173	0.241
northness	0	-0.026 – 0.025	-0.016	0.987	0.015	-0.012 – 0.043	1.107	0.269
slope	0.004	-0.024 – 0.032	0.289	0.773	-0.026	-0.056 – 0.003	-1.746	0.081
abundance*P	0.022	-0.009 – 0.053	1.393	0.164	-0.006	-0.039 – 0.027	-0.361	0.718
abundance*Pdev	-0.013	-0.042 – 0.015	-0.913	0.361	-0.019	-0.050 – 0.011	-1.235	0.217
P*Pdev	-0.034	-0.064 – -0.003	-2.158	0.031	0.014	-0.019 – 0.047	0.852	0.394
abundance*cover	0.007	-0.025 – 0.038	0.428	0.669	-0.011	-0.045 – 0.022	-0.663	0.507
abundance*richness	-0.01	-0.045 – 0.025	-0.552	0.581	-0.006	-0.043 – 0.032	-0.305	0.76
abundance*evenness	-0.008	-0.037 – 0.021	-0.549	0.583	0	-0.030 – 0.031	0.021	0.983
abundance*SLA	-0.007	-0.031 – 0.017	-0.583	0.56	0.026	-0.000 – 0.051	1.954	0.051
abundance*Height	-0.004	-0.031 – 0.022	-0.309	0.758	0.016	-0.012 – 0.044	1.101	0.271
abundance*FDis	-0.011	-0.042 – 0.020	-0.724	0.469	-0.008	-0.041 – 0.025	-0.465	0.642
abundance*FRic	0.006	-0.027 – 0.040	0.367	0.713	0.011	-0.025 – 0.047	0.623	0.534
abundance*FEve	-0.033	-0.060 – -0.006	-2.371	0.018	-0.002	-0.031 – 0.027	-0.11	0.912
abundance*northness	0.025	-0.002 – 0.053	1.808	0.071	-0.019	-0.049 – 0.010	-1.292	0.197
abundance*slope	0.008	-0.019 – 0.036	0.594	0.553	0.005	-0.025 – 0.034	0.323	0.747
Observations	632				632			
R ² / R ² adjusted	0.243 / 0.211				0.208 / 0.174			

612 **Table 2.** ANOVA table showing results from a multiple linear regression model predicting an
613 individual grasses relative abundance from biotic and abiotic plot characteristics.

arcsin(Relative abundance)				
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>T-value</i>	<i>p</i>
Intercept	0.3187	0.2996 – 0.3379	32.6969	<0.001
P	-0.0063	-0.0279 – 0.0152	-0.5791	0.563
Pdev	-0.0069	-0.0313 – 0.0176	-0.5524	0.581
SLA deviation from CWM	0.0392	0.0207 – 0.0576	4.1734	<0.001
Height deviation from CWM	0.0491	0.0295 – 0.0687	4.9233	<0.001
northness	-0.011	-0.0292 – 0.0071	-1.1962	0.232
slope	0.0111	-0.0092 – 0.0314	1.0716	0.284
FDis	-0.0176	-0.0396 – 0.0045	-1.5642	0.118
FRic	-0.0314	-0.0557 – -0.0070	-2.5333	0.012
FEve	0.0196	0.0000 – 0.0391	1.9684	0.049
cover	0.0229	0.0008 – 0.0449	2.0378	0.042
richness	-0.013	-0.0380 – 0.0121	-1.0153	0.31
evenness	-0.0186	-0.0393 – 0.0021	-1.7655	0.078
P*Pdev	0.0052	-0.0171 – 0.0275	0.4579	0.647
P*SLA	0.0065	-0.0160 – 0.0291	0.5703	0.569
P*Height	0.0118	-0.0112 – 0.0348	1.004	0.316
Pdev*SLA	0.0008	-0.0195 – 0.0211	0.0761	0.939
Pdev*Height	-0.0045	-0.0275 – 0.0186	-0.3794	0.705
SLA*Height	0.027	0.0089 – 0.0452	2.9242	0.004
northness*SLA	0.0146	-0.0059 – 0.0350	1.3978	0.163
northness*Height	-0.0036	-0.0210 – 0.0138	-0.405	0.686
slope*SLA	0.021	-0.0004 – 0.0425	1.9276	0.054
slope*Height	0.0195	-0.0030 – 0.0420	1.6984	0.09
FDis*SLA	0.0027	-0.0217 – 0.0271	0.215	0.83
FDis*Height	0.0004	-0.0213 – 0.0222	0.0381	0.97
FRic*SLA	0.0002	-0.0252 – 0.0257	0.017	0.986
FRic*Height	0.0139	-0.0137 – 0.0415	0.988	0.324
FEve*SLA	-0.0127	-0.0333 – 0.0079	-1.2078	0.228
FEve*Height	0.0009	-0.0196 – 0.0215	0.0891	0.929
Cover*SLA	0.0124	-0.0105 – 0.0352	1.0636	0.288
Cover*Height	0.0207	-0.0003 – 0.0417	1.9324	0.054
Richness*SLA	-0.0111	-0.0387 – 0.0165	-0.7918	0.429
Richness*Height	-0.0234	-0.0505 – 0.0036	-1.7032	0.089
Evenness*SLA	-0.0102	-0.0335 – 0.0130	-0.8638	0.388
Evenness*Height	-0.0084	-0.0289 – 0.0121	-0.8079	0.419
Observations	632			
R ² / R ² adjusted	0.158 / 0.110			

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Figure 1. Partial residual plot showing the positive effect of community-weighted mean (CWM) specific leaf area (SLA) of the local community on SLA of the individual (presented as deviation from its species mean). Note, the CWM of the local community was calculated excluding the focal species. Individuals have higher SLA in plots where species in the local grass community also have higher SLA.

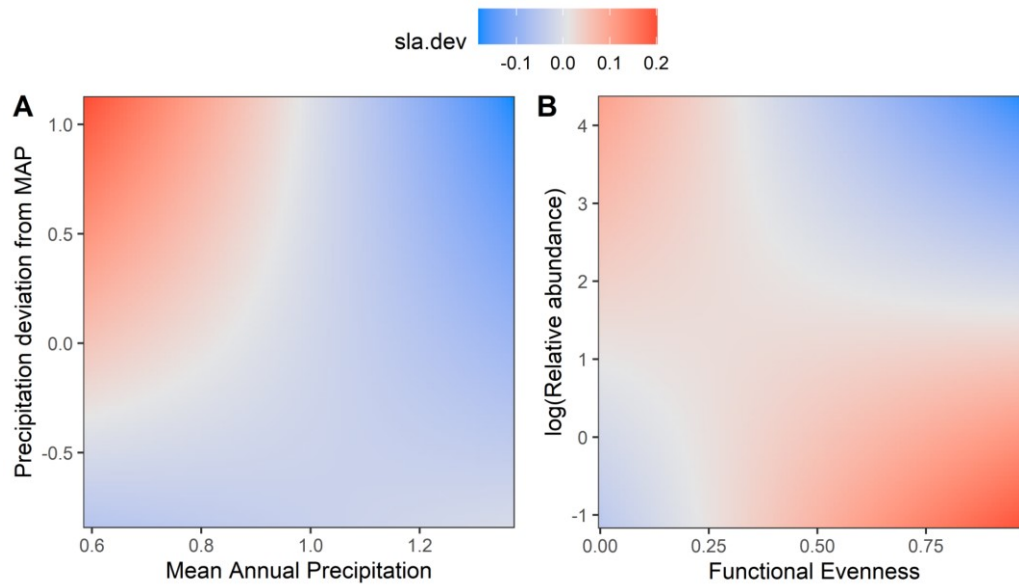


Figure 2. Partial residual plots showing **(A)** the interactive effect of mean annual precipitation (m/yr) and precipitation in the 12 months prior to sampling on SLA deviation, and **(B)** the interactive effect of functional evenness of the local grass community and the individual's local relative abundance on SLA deviation.

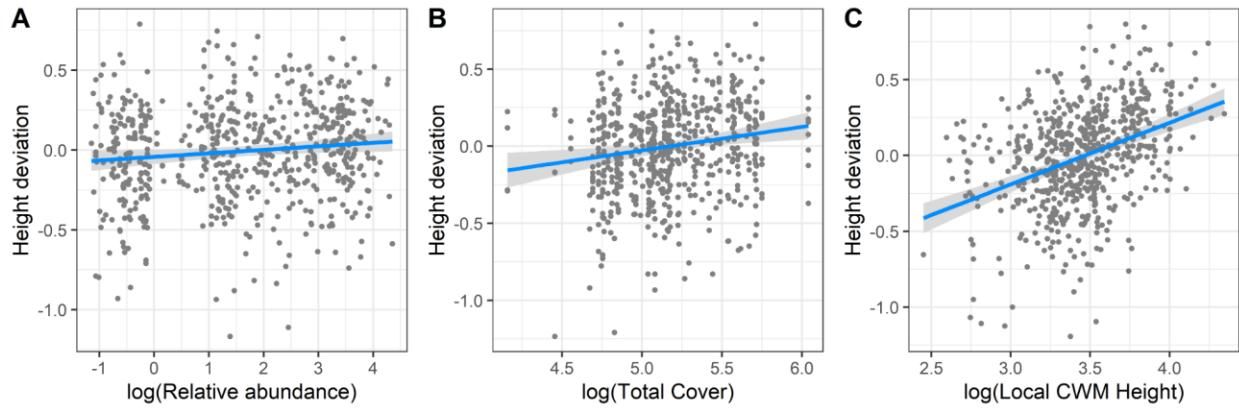


Figure 3. Partial residual plots showing the positive effects of **(A)** relative abundance, **(B)** total plant cover and **(C)** local community-weighted mean (CWM) height on height deviation. Note, the CWM of the local community was calculated excluding the focal species. Individuals are taller relative to their species' mean in plots where they are more abundant, plant cover is higher, and neighboring individuals are taller.

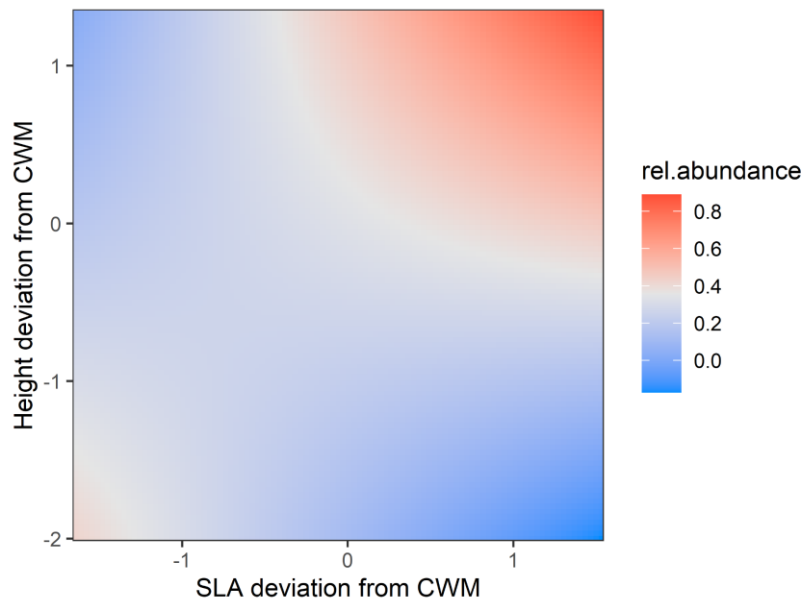


Figure 4. Partial residual plot showing the significant ($p = 0.003$) positive interactive effect of trait deviations from local community-weighted mean (CWM) traits on relative abundance. The significant main effects in Table 2 suggest species are more abundant in plots where they are taller or have higher SLA than their neighboring community. The interaction term suggests being higher in both traits is associated with still higher abundance

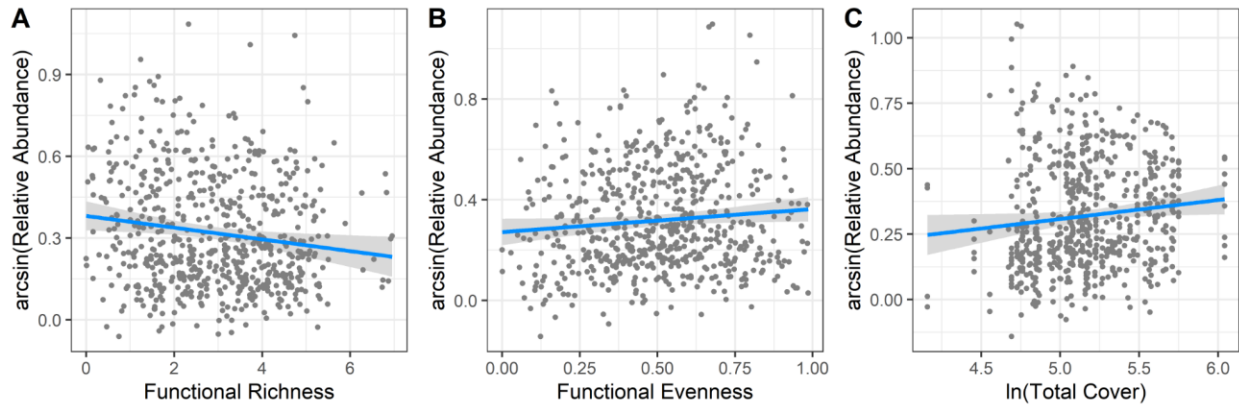


Figure 5. Partial residual plots showing the effect of community functional diversity on an individual's relative abundance. Individuals are more abundant in plots where the grass community is characterized by (A) low functional richness, (B) high functional richness and (C) high total plant cover. Note, all functional diversity indices were calculated for just the grass community excluding the focal grass species.

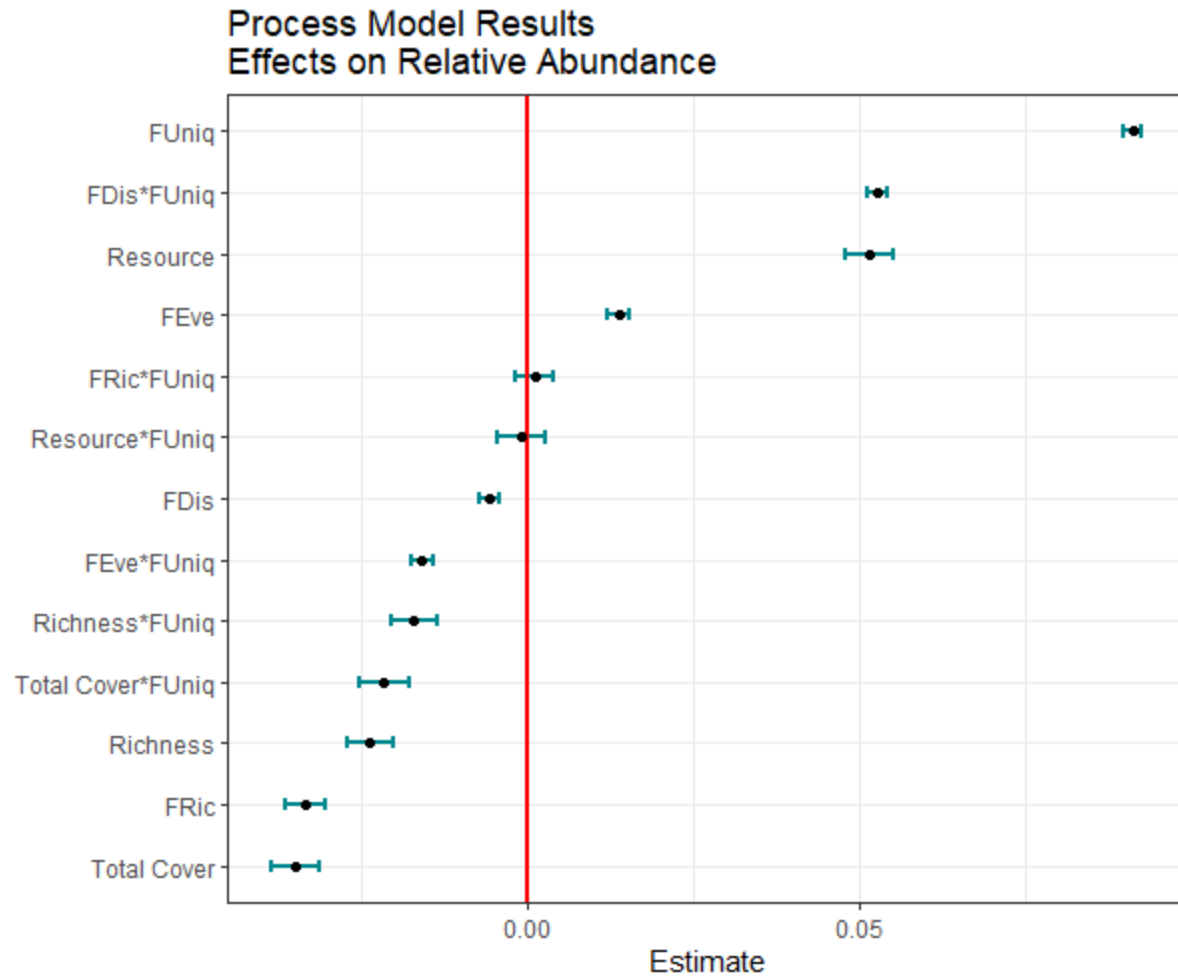


Figure 6. Results from the process model showing the estimated effects of community composition on species relative abundance. Shown are mean estimates with 95% confidence interval bands. Variables with statistically significant effects are those with confidence intervals that do not include zero (denoted with a vertical red line). Variables include FUniq: the difference between a species trait and the local CWM trait; Resource: an estimate of resource availability calculated from the competition radius in the model ($\text{resource} = \sqrt{1 / (1 + \text{'competition radius'})}$); FEve: functional evenness; FDis: functional dispersion; Richness = taxonomic (i.e. species) richness; Total Cover: total plant cover of the plot; and FRic: functional richness