

Intraspecific trait variation, functional turnover and trait differences among native and exotic grasses along a precipitation gradient

Brody Sandel  | Rebecca Low

Department of Biology, Santa Clara University, Santa Clara, California

Correspondence

Brody Sandel, Department of Biology, Santa Clara University, Santa Clara, CA.
Email: bsandel@scu.edu

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Abstract

Questions: California's grasslands are heavily invaded by exotic species. Counteracting these invasions depends on understanding the functional differences between native and exotic species and how these shift along environmental gradients. Focusing on grasses, we ask: (a) how native and exotic trait means and intraspecific trait variation (ITV) differ; (b) how the functional composition of grass assemblages shifts with precipitation; and (c) how species shift their functional strategies as precipitation changes.

Location: Marin County, California (USA).

Methods: In spring 2017, we censused grassland vegetation plots across eight reserves in Marin County that are arrayed along a precipitation gradient. At each plot, we measured traits of grasses, including height, leaf area and specific leaf area (SLA).

Results: We found modest differences in functional traits between native and exotic species. Exotic species had larger seeds and higher SLAs, indicating higher reproductive investments and a leaf strategy focused on obtaining rapid returns on investments with relatively short leaf life spans. Native and exotic species did not differ in the ITV for any of the measured traits. Variation in precipitation among sites drove strong turnover in the functional trait composition of grasses, as well as shifts within species. Wetter sites had shorter species with smaller leaf areas, smaller seeds and higher leaf N concentrations. There was also strong intraspecific SLA variation along the precipitation gradient; all species displayed lower SLA values as precipitation increased.

Conclusions: Consistent with previous results, native species had more conservative leaf strategies. Grasses that display these conservative strategies tend to be more abundant in dry climates, leading to increasing exotic abundance in wetter climates. However, each species shifted towards more conservative strategies as precipitation increased, suggesting that the factors that drive species turnover and ITV differ.

KEYWORDS

functional trait, grass, height, intraspecific trait variation, leaf area, N_{mass} , Poaceae, seed mass, specific leaf area

1 | INTRODUCTION

Understanding how exotic species differ from native species is crucial for understanding the ecosystem-level impacts of the replacement of native by exotic species and designing restoration treatments that can exert different effects on these species groups (Sandel, Corbin, & Krupa, 2011; Van Kleunen, Weber, & Fischer, 2010). Restoration efforts seek to shift the balance towards native species, often by attempting to leverage differences in ecological strategies of native and exotic species. Examples include soil nutrient reductions to favor less nitrogen-demanding species (Alpert & Maron, 2000) or mowing in early spring to reduce annual cover (Sandel et al., 2011). However, native and exotic species may often occupy very similar functional roles in the ecosystem, making it challenging to implement an intervention that promotes one over the other (Corbin & D'Antonio, 2010).

Plant functional traits are a powerful window into both the ecological strategies of plants and their impact on ecosystems (Lavorel & Garnier, 2002; Suding et al., 2008; Westoby & Wright, 2006). Functional traits are measures of an individual that influence its fitness (Violle et al., 2007), and can be used to describe the major axes of variation among species. One such classification of species is Westoby's (1998) leaf-height-seed (LHS) scheme, which describes species according to their specific leaf area (SLA), height and seed mass. SLA indicates a plant's position along the leaf economic spectrum (Wright et al., 2004), which ranges from long-lived, well-defended and expensive-to-produce leaves, to short-lived and inexpensive leaves that obtain rapid returns on the costs incurred in producing the leaf. Height indicates a species' investment in competition for light and correlates with a range of other important traits such as the leaf area ratio, longevity, whole-plant metabolic rate, and canopy size (Moles et al., 2009). Seed mass is an index of the degree of reproductive investment per offspring, and correlates with several traits related to life history and development, such as seedling growth rates, seedling drought tolerance and dispersal distance (Moles & Westoby, 2006; Moles et al., 2007; Nathan & Muller-Landau, 2000). In addition to these canonical traits, leaf nitrogen concentration is an important trait that relates to maximum photosynthetic rates and leaf area influences the gas exchange and heat transfer rates from a leaf by influencing the size of the boundary layer (Ackerly, Knight, Weiss, Barton, & Starmer, 2002; Wright et al., 2004).

A number of studies have attempted to identify general differences in ecological strategies between species that naturalize or become invasive in new regions and those that do not (Pyšek & Richardson, 2007). Compared to non-invasive species, there is a distinct set of functional traits often possessed by invasive plants. These include fast life cycles (e.g., short juvenile periods and short life spans, Rejmánek & Richardson, 1996; Cadotte, Murray, & Lovett-Doust, 2006), small wind-dispersed seeds (Cadotte et al., 2006; Rejmánek & Richardson, 1996), fast growth rates and high SLA (Gallagher, Randall, & Leishman, 2015; Grotkopp & Rejmánek, 2007; Pyšek & Richardson, 2007). Intriguingly, some invasive species also shift towards higher SLA in their invasive range compared to their native range (Leishman, Cooke, &

Richardson, 2014). In their invasive range, invasive plant species are typically taller and have higher SLA than co-occurring native species (Pyšek & Richardson, 2007). Considering only California grasses, exotic species are much more likely to be annuals, and are taller, heavier seeded and have higher SLA than native species (Sandel & Dangremond, 2012). The most consistent pattern to arise from this diverse body of work is that high SLA is associated with invasiveness.

Complementing these comparative studies, there is a suite of studies that examine changes in community-level functional trait composition along environmental gradients (e.g., Bjorkman et al., 2018; Šimová et al., 2018). Change in functional trait composition occur in part because species with disfavored traits in a particular environmental condition are likely to be absent or rare, and in part because species can shift their traits as environmental demands change (Lepš, de Bello, Šmilauer, & Doležal, 2011). Over long environmental gradients, such as those across continents, species turnover is likely to be the dominant factor influencing community-level shifts in functional trait composition (Albert et al., 2010). At smaller scales, intraspecific trait variation (ITV) may play an important role, though patterns of ITV are less well understood (Albert et al., 2010; Bolnick et al., 2011). ITV has two major components: variation in phenotypes resulting from different genotypes (adaptation) and variation in phenotypes within a genotype, due to environmental differences (plasticity; Lajoie & Vellend, 2018). Typically, common garden experiments are needed to separate these components. Here, we consider them together under the broad category of ITV. Most often, it is likely that environments that select for species with a particular trait state also select for individuals within a species with that trait state. That is, if warm environments tend to contain more tall species, a given species should usually be expected to grow taller in warm environments. It appears that this is typically the case (Ackerly & Cornwell, 2007; Derroire, Powers, Hulshof, Cárdenas Varela, & Healey, 2018; Kumordzi, Wardle, & Freschet, 2015; Lepš et al., 2011), though exceptions exist, such as the response of SLA to a mowing treatment (Lepš et al., 2011).

Understanding intraspecific shifts in functional traits along environmental gradients is important from both a basic and applied perspective (Violle et al., 2012). From a basic perspective, these shifts provide a useful test of hypotheses that link environmental factors to plant strategies. In particular, many hypotheses regarding community turnover make the same predictions for ITV, therefore predicting positive covariation between ITV and community mean traits. When negative covariation is found, the hypothesis in question may need to be revisited. From an applied perspective, variation in ITV among species may reflect different abilities to adapt or acclimate to novel conditions, which could prove important for making predictions under various types of environmental change (Albert et al., 2010; Moran, Hartig, & Bell, 2016).

In the context of ecosystems that contain a mix of long-resident native species and recently introduced exotic species, it is not clear how native and exotic species may differ in their ITV (Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006). One recent



meta-analysis has found higher ITV in invasive species (Davidson, Jennions, & Nicotra, 2011), while another did not (Palacio-López & Gianoli, 2011). Common garden experiments have found mixed results, with one comparison of invasive and non-invasive *Pinus* species finding differences in mean traits but not ITV (Matzek, 2012), and another finding higher trait variation in invasive species among five woody and grass species pairs (Funk, 2008). In wild populations growing along environmental gradients, one might expect that recently introduced exotic species have had relatively little time to adapt to local conditions, leading to little genetic differentiation among populations, and consequently less ITV.

Here, we focus on functional trait variation among native and exotic grasses in California. Exotic grasses are some of the most important invasive species in the state and have largely displaced a diverse suite of native grasses (D'Antonio, Malmstrom, Reynolds, & Gerlach, 2007). Despite some shared morphology, the grasses of California are functionally diverse, ranging from annuals to long-lived perennials, in height from about 8 cm to 8 m, and spanning about two orders of magnitude in seed mass (Sandel & Dangremond, 2012). We used a natural precipitation gradient across Marin County to assess community turnover and ITV among grasses. Within Marin, variation in precipitation and associated variation in water availability due to topographic position and soil types are major determinants of vegetation patterns (Howell, 1970). As is generally the case in California (D'Antonio et al., 2007), exotic grasses (such as *Avena barbata*, *Bromus diandrus*, and *Festuca perennis*) are the dominant species in grasslands throughout most of the county. This study aims to better understand how the variation in water availability drives turnover in grass species composition and shifts in functional traits of grasses, with particular attention to differences between native and exotic species. In particular, we ask three related questions:

1. How do native and exotic trait means and ITV differ?
2. How does the functional composition of grass assemblages change along a precipitation gradient?
3. How do species shift their functional strategies along the precipitation gradient?

2 | METHODS

2.1 | Taxon nomenclature

Taxon names follow the Jepson Herbarium eFlora, as of May 7, 2018 (<http://ucjeps.berkeley.edu/eflora>).

2.2 | Site selection

This study was conducted on land owned by Marin County Parks (California, USA), and designated as open space reserves. We had several goals in site selection. First, we identified sites with substantial cover of grassland, and among these selected eight sites that best spanned the rainfall gradient across Marin County. These sites (and their annual precipitation) were Old Saint Hilary's (690 mm/

year), Ring Mountain (825 mm/year), Mount Burdell (930 mm/year), Verissimo Hills (970 mm/year), Terra Linda/Sleepy Hollow Divide (1,000 mm/year), French Ranch (1,040 mm/year), Loma Alta (1,210 mm/year) and Lucas Valley (1,280 mm/year). In contrast to the strong precipitation gradient, these sites differ only slightly in mean annual temperature (all within 1.5°C; Appendices S1 and S2).

2.3 | Vegetation plots

Vegetation surveys were conducted from late April through early June 2017. We collected full species composition and trait data at five 5 m × 5 m vegetation plots within each site (see Appendices S1 and S2 for site-level summaries of vegetation and climate). Plots were randomly located within the portion of each site covered with grassland vegetation, though in some cases a plot had to be moved slightly or replaced with another location because the randomly generated location was inaccessible or not actually grassland. We identified all vascular plants in each plot and estimated percent cover for each species visually (to the nearest 10%). In addition, we surveyed a further 40 vegetation plots for species composition only.

2.4 | Trait measurements

When collecting trait measurements, we identified all grass species growing in or near the plot. We attempted to locate five individuals of each species, though this was sometimes not possible for uncommon species. From each individual, we measured the height to the highest leaf and collected one fully expanded leaf blade. The leaf blade was separated from the stem at the ligule, leaving behind the sheath. The leaf blade was then immediately photographed against a white background with a scale reference and stored individually in a coin envelope. They were returned to the lab, oven-dried at 55°C for at least 24 hr, then weighed. We used ImageJ (National Institutes of Health, Bethesda, Maryland, USA) to calculate the area of each leaf. From these measurements, we then calculated SLA, the ratio of the one-sided area of the leaf to its dry mass.

In addition, we used published and online sources to obtain leaf N concentrations (on a per-mass basis, expressed as a percentage), and seed mass. Seed mass data were available for all species from the Kew Gardens Seed Information Database (Royal Botanic Gardens Kew, 2018), while a literature review (described in Sandel, Monnet, & Vorontsova, 2016) found N_{mass} values for all but three species (*Briza minor*, *Danthonia californica* and *Hordeum marinum*).

Thus, for each species we considered five traits: SLA, height, leaf area (Area), leaf nitrogen content (N_{mass}) and seed mass (Seed). The first three were measured locally where each species occurred, while for the final two only species-level means are available.

2.5 | Environmental data

We extracted two measures of the local environment for each vegetation plot. The first was 30-year normal annual precipitation (AP),

extracted from PRISM data (provided as rasters with 800 m resolution, PRISM Climate Group, 2018). The second was the topographic aspect of the plot (NORTH, measured as the degree to which the slope was north-facing), which was derived from the National Elevation Dataset DEM (<http://ned.usgs.gov>), with a resolution of 1/9 arc-seconds, or approximately 3 m. We computed the topographic aspect (in degrees) using the R package *raster*, and computed the cosine of the aspect to obtain a measurement of northness, where a value of 1 indicates a perfectly north-facing slope, a value of -1 indicates a perfectly south-facing slope, and perfectly east- or west-facing slopes have a value of 0. Temperature is a potentially important driver of functional traits, but varied very little across the study sites, so we did not consider its effects here.

2.6 | Analysis

For each species, we computed the grand mean of each of its trait measurements, as well as the mean trait measurement of the (usually five) measurements of a species in each plot where it occurred (hereafter, species means [SM] and local measurements [LM], respectively). In addition, we computed the standard deviation of trait measurements for each species, as a measure of ITV. All trait values were log-transformed prior to analysis, to reduce the influence of extremely large measurements. We compared the SM and ITV values between native and exotic species using *t* tests.

For each vegetation plot and for each trait, we calculated community-weighted trait values (CWMs). This measure is the average value of a particular trait among all grass species in a plot, weighted by the relative abundance of the species. We calculated CWMs for quantitative traits using both SMs and LMs, and computed the proportion of grass species in each plot that were natives and the proportion perennial. We then related each of these plot level summaries of species composition to AP and NORTH in multiple linear regressions. The *p* values in these regressions can be biased by non-independence among the sampling points arising from the application of a species' mean trait value to each plot where it occurs (Peres-Neto, Dray, & ter Braak, 2017; Zelený, 2018), so we implemented null models to calculate corrected *p* values. In all cases, we compared the observed regression slopes to those from 1,000 randomizations to obtain a *p* value. For CWMs calculated from SMs, we used two null models. In null model 1, we randomly permuted the rows of the environment matrix. In null model 2, we permuted the rows of the environment matrix and the rows of the species-by-trait matrix, and recalculated the CWMs from this randomized trait matrix. This second null model is more conservative (Peres-Neto et al., 2017), but not applicable to LMs because there are no species mean trait values to permute (however, it is not clear that CWMs based on LMs suffer the same bias, as no species-level value is applied to all plots; Zelený, 2018). Thus, for CWMs based on LMs, we used only null model 1, and retain null model 1 for CWMs based on SMs for comparison.

Finally, we performed a trait gradient analysis (Ackerly & Cornwell, 2007). This analysis produces an additive decomposition of a species' trait value into beta and alpha components, in which the

beta represents the species' typical position along the trait gradient (e.g., is a species typically found in habitats that support low SLA species or high SLA species?), and the alpha component represents the species' trait value relative to the species with which it co-occurs (e.g., does the species typically have higher or lower SLA than the species it occurs with?). This is typically visualized in a two-dimensional space with CWMs based on LMs on the *x* axis, and LMs for individual species along the *y* axis. A species' mean position along these two axes indicates its beta and alpha components, respectively. In addition, one can examine ITV by fitting a regression line to the set of observations for one species. For this analysis, we had to remove two species that occurred in only one vegetation plot (*Aegilops triuncialis* and *Hordeum murinum*).

3 | RESULTS

In total, we collected trait measurements from 1,213 individuals across 22 species (eight native and 14 exotic). The most common species were *Avena barbata*, *Stipa pulchra* and *Brachypodium distachyon* (see Appendices S1 and S2 for full species list and trait means for each species).

Exotic grasses had higher SLA and seed mass than native grasses ($p < 0.03$), but did not differ significantly in leaf area, height or N_{mass} (Figure 1). While there was marked variation in ITV, native and exotic species as groups did not differ ($p > 0.5$).

Among all grass species and considering species means (SM), higher precipitation was associated with higher CWMs of SLA and N_{mass} , and lower CWMs of height and leaf area (Figure 2, Table 1). North-facing slopes had shorter species with smaller seeds and higher N_{mass} . Model R^2 values were moderate, ranging from 0.089 for Area to 0.365 for N_{mass} . CWMs based on local measurements (LM) were consistent with those for Height and Area, but not for SLA. For CWMs based on LMs, SLA decreased with increasing AP (Figure 2a).

These patterns displayed by the entire grass assemblages mask some differences between native and exotic species. For example,

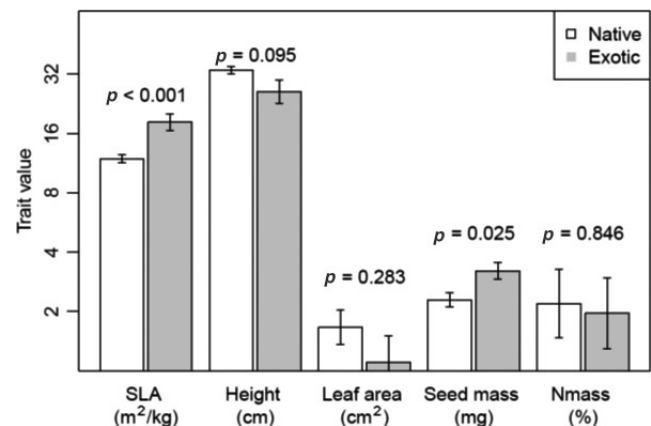


FIGURE 1 Functional trait differences between native ($n = 8$) and exotic species ($n = 14$). Error bars represent \pm one standard error about the mean. *p* values are from two-sampled *t* tests

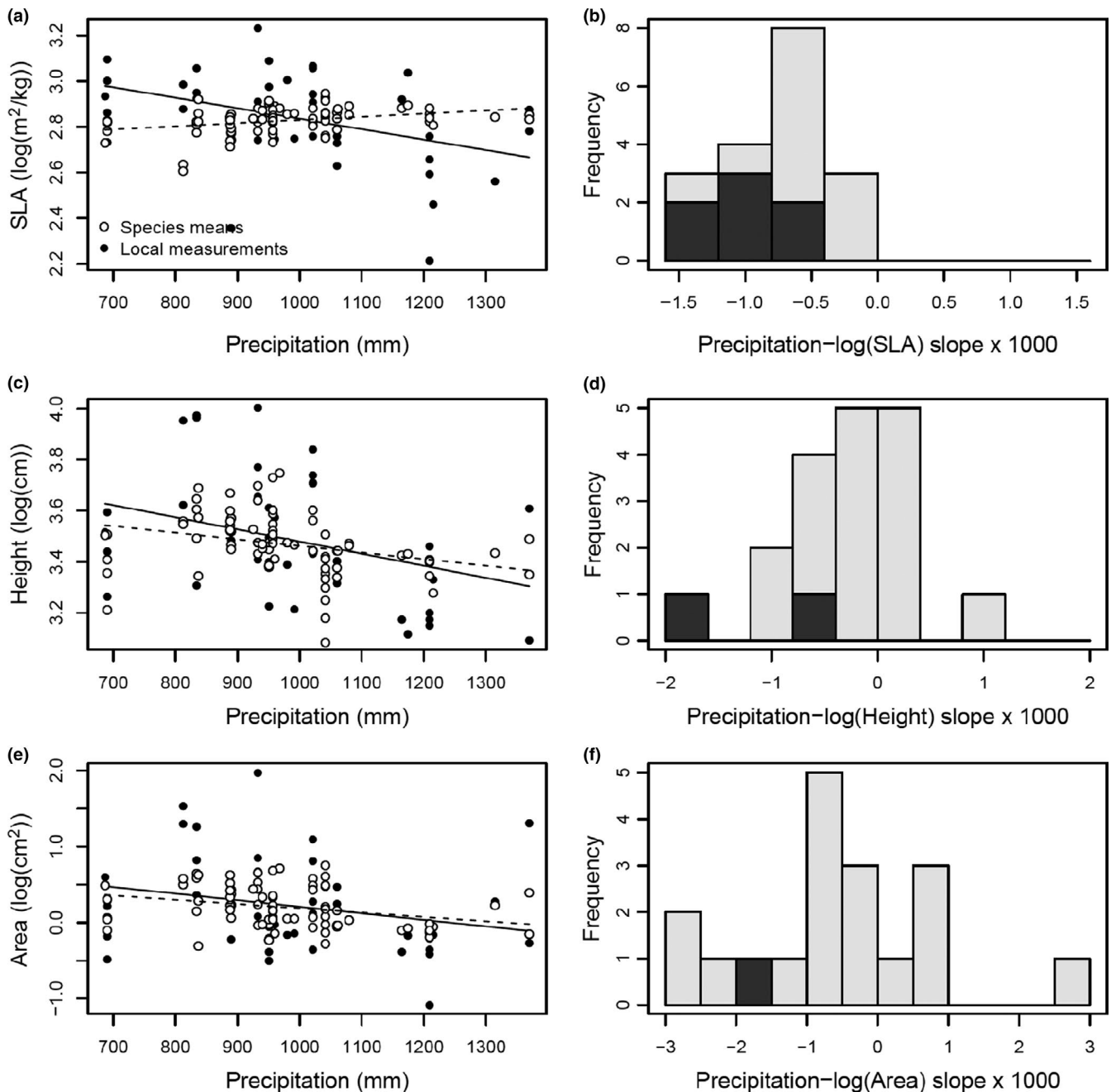


FIGURE 2 Relationships between trait values and precipitation. For each trait, the left panel (a, c, e) shows the relationship between precipitation and the community-weighted trait value for that trait, calculated either according to global species means, or trait values locally measured at that plot. The right panel (b, d, f) shows the distribution of intraspecific trait-precipitation relationships for each species. Dark gray indicates a significant trait-precipitation relationship for a species

there was a strong positive influence of north-facing aspects on native grass SLA, but not on exotic. Similarly, north-facing slopes tended to contain taller native grasses, but shorter exotic grasses (Table 1).

Seven of 18 species displayed significantly negative ($p < 0.05$) relationships between SLA LMs and AP, and all 18 were negative relationships (Figure 2b). The patterns for Height and Area were less clear, but still showed tendencies among species for shared intraspecific trait responses along the precipitation gradient.

Height decreased with precipitation for 12 of 18 species (significantly so for two of them, Figure 2d), while Area decreased with precipitation for 13 of 18 species (significantly so for one of them, Figure 2f).

The trait gradient analysis (Figure 3) replaces the environmental predictor variable (e.g., AP or NORTH) with one derived from the plant community, and thereby produces a synthetic measure of environmental gradients that incorporates both measured factors if relevant, and other unknown factors that drive changes in



	Species means			Local measurements		
	AP	North	R ²	AP	North	R ²
SLA						
All	0.330***	0.061	0.112	-0.411*	-0.01	0.167
Native	0.167	0.535***	0.282	-0.626***	-0.079	0.376
Exotic	0.137	0.074	0.024	-0.432**	0.015	0.19
Height						
All	-0.310*	-0.371***	0.231	-0.314	0.143	0.14
Native	-0.044	0.541***	0.278	-0.318	0.086	0.122
Exotic	-0.297*	-0.422***	0.264	-0.294	0.121	0.118
Area						
All	-0.290*	0.067	0.089	0.204	0.169	0.086
Native	0.141	0.478***	0.223	-0.326	-0.013	0.105
Exotic	-0.274*	0.02	0.076	-0.19	0.159	0.075
Seed						
All	-0.018	-0.357**	0.128			
Native	-0.374***	0.196	0.199			
Exotic	0.004	-0.366***	0.134			
N _{mass}						
All	0.214	0.567***	0.365			
Native	0.263*	0.47***	0.262			
Exotic	0.074	0.605***	0.371			
Perennial	-0.337**	0.095	0.123			
Native	-0.311**	0.041	0.099			

Notes: Mean traits were calculated from overall species means, or from traits measured at the vegetation plot itself.

p values are based on null model 1, but for species means the *p* value from null model 2 is shown after a comma if it differed (**p* < 0.05; ***p* < 0.01; ****p* < 0.001).

the functional trait composition of the community. There was remarkably strong coordination of species responses to these synthetic trait gradients. As community composition shifted towards larger-SLA species, all but one species (*Elymus multisetus*) likewise shifted towards higher SLA values. Similarly, only three species showed intraspecific leaf area variation that opposed the community-wide trend (*Elymus multisetus*, *Elymus glaucus* and *Vulpia myuros*). Height was less uniform, with six of 17 species showing responses opposite to the general community trend (four native grasses—*Elymus multisetus*, *Danthonia californica*, *Bromus carinatus* and *Elymus glaucus*—and two exotic grasses—*Bromus minor* and *Cynosurus echinatus*).

The trait gradient analysis revealed that there is little difference between native and exotic species regarding where along the trait gradient they are distributed. That is, exotic species were as likely to be characteristic of high-SLA assemblages as low-SLA assemblages. Rather, among species co-occurring in a plot, exotic grasses tended to have higher SLA and lower Height (*p* < 0.05) than native species (Figure 4). Thus, most differences between native and exotic traits were due to differences in their alpha component, not their beta components.

TABLE 1 Standardized regression coefficients for models relating community-weighted mean traits to annual precipitation (AP) and topographic aspect

The alpha-beta decomposition of SLA strongly separated native and exotic grasses (Figure 5). Two native species (*Elymus multisetus* and *Koeleria macrantha*) were confined to very low SLA sites (that is, had low beta SLA values). Two small exotic annuals (*Vulpia myuros* and *Aira caryophyllea*) occupied the middle of the SLA gradient. Many species shared the high end of the SLA gradient (high beta values), and were clearly separated along the alpha-SLA axis, with exotic grasses (both annual and perennial) having larger SLA values than the native species with which they co-occur (larger alpha values). The alpha-beta decomposition of leaf area and height were generally similar to one another. They demonstrated some separation of native and exotic species along the alpha axis, but with the two exotic *Avena* species (*Avena barbata* and *Avena fatua*) mixing with native species.

4 | DISCUSSION

Here, we sought out to: (a) assess trait differences between native and exotic grasses; (b) identify environmental drivers of functional turnover of grass assemblages; and (c) assess intraspecific functional trait shifts in response to environmental drivers.

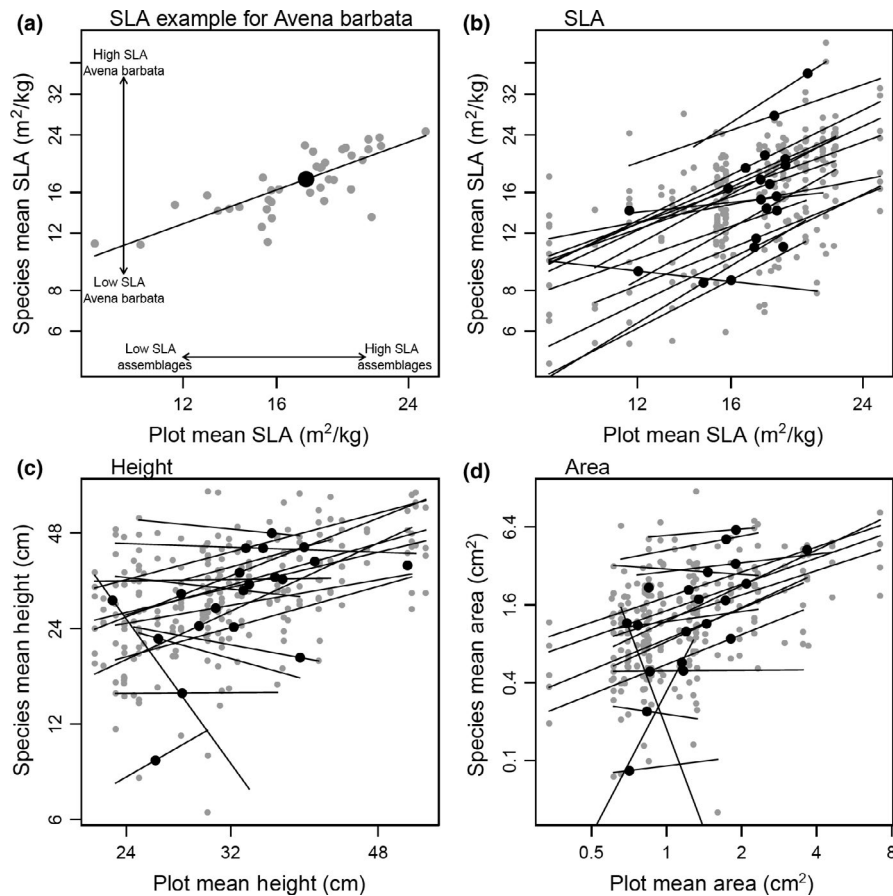


FIGURE 3 Trait gradient analysis for SLA (b), Height (c) and Area (d). Panel (a) illustrates the method with one example species (*Avena barbata*). Each gray circle indicates a species at a plot, arrayed along the x axis according to the community weighted trait value of that trait in the plot, and along the y axis according to the observed trait value of that species in that plot. Large black dots indicate species means. The horizontal position of these dots indicates whether the species tends to occur in high or low community-weighted trait value (CWM) communities, while the vertical position indicates whether it itself has high or low trait values. Each line shows the regression relationship for one species between the CWMs and its locally measured trait values

4.1 | Native and exotic species

All of the native grasses in this study are perennial species, while most of the exotic grasses are annuals. Despite this clear difference, quantitative trait distributions of native and exotic species were largely overlapping (Corbin & D'Antonio, 2010). Exotic species did have higher SLA than natives as a whole, as well as smaller seeds, and showed a tendency to be taller overall. A statewide analysis of native and exotic species found the same result for SLA and height, but found that exotic species tend to have larger seed masses (Sandel & Dangremond, 2012). However, relatively little variation in species mean trait values was explained by whether the species is native to California or not. Further, native and exotic grasses did not differ significantly in their ITV for any of the traits considered here, nor did they show different strengths of intraspecific responses to the trait gradients. Despite this, the decomposition of trait values into alpha and beta components did reveal groupings of species that were partly congruent with the native/exotic distinction.

While trait differences between native and exotic species were not dramatic, the most distinct trait was SLA. The fact that

exotic and invasive species have particularly high SLA has been repeatedly observed for a wide range of plant groups, suggesting that this trait is indeed useful in separating exotic from native

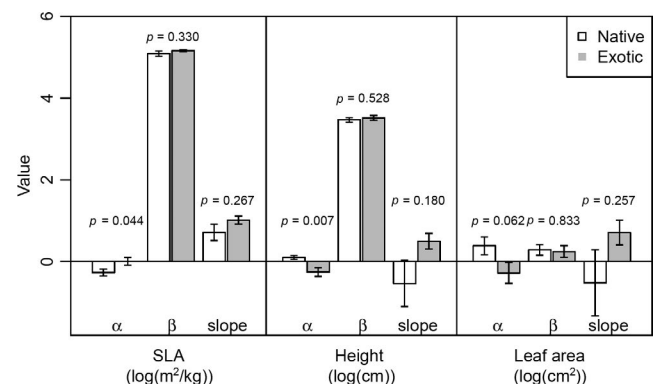


FIGURE 4 Components of the trait gradient analysis. For each trait, the average alpha and beta values for native ($n = 8$) and exotic species ($n = 12$) are plotted with standard error bars. The "slope" indicates the slope of the intraspecific trait variation line in the trait gradient analysis

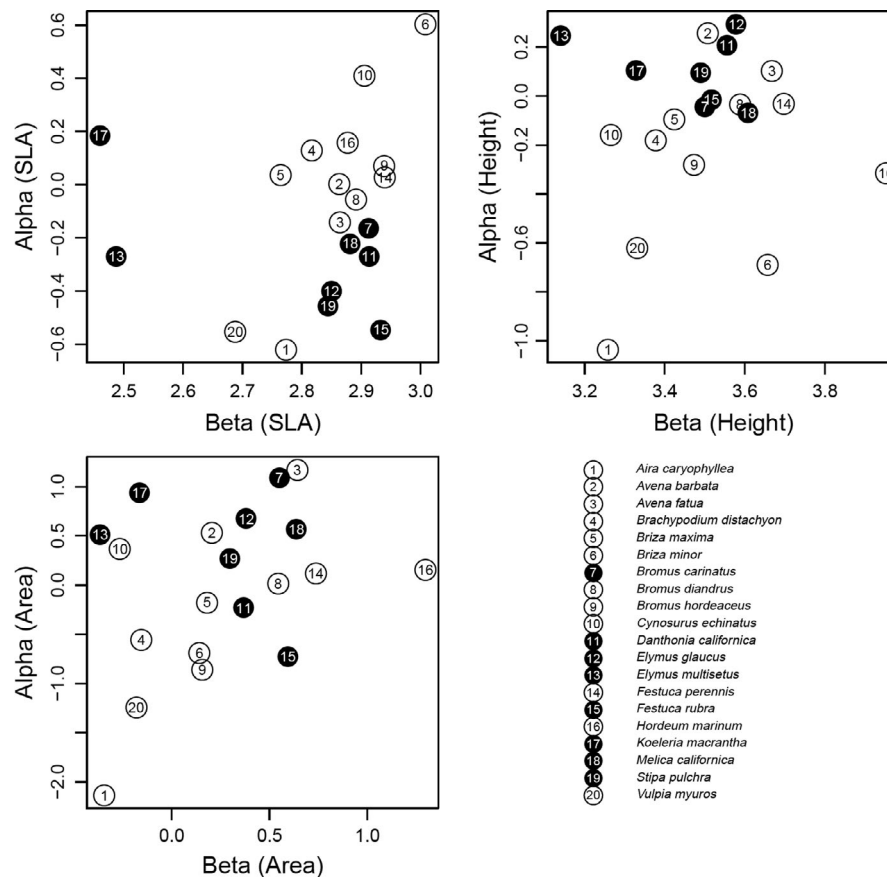


FIGURE 5 Positions of each grass species in the beta-alpha trait space identified by the trait gradient analysis. The number in each symbol codes the species name; native species are denoted with solid circles, and exotic species with open circles. The beta component of a species' trait value indicates its typical position along the trait gradient, while the alpha component indicates whether it tends to have higher (positive) or lower (negative) trait values than the species with which it co-occurs

species or invasive from non-invasive species (Gallagher et al., 2015; Grotkopp & Rejmánek, 2007; Leishman et al., 2014; Pyšek & Richardson, 2007).

4.2 | Environmental drivers of grass traits

Whenever AP and NORTH were both significant predictors of CWM, they shared a common direction of effect. This is consistent with the idea that the most important influence of aspect in these systems is via its influence on soil water balance, with north-facing slopes experiencing lower insolation and lower evaporative losses, and therefore behaving as if they received higher rainfall than a nearby south-facing slope (Moeslund et al., 2013). This gradient in water availability drove substantial turnover in the grass species composition, with drier sites containing taller species with larger seeds, larger leaves, lower SLA and lower leaf N concentration.

The overall larger size of grasses in dry sites might reflect a larger proportion of perennial species in these sites, though this pattern is at odds with that observed over a wider range of precipitations across the US and globally (Sandel et al., 2016). Globally, across low-to-medium precipitation values, grass assemblages tend

to become more perennial, taller and larger-leaved as precipitation increases (Sandel et al., 2016). This likely reflects the fact that all of the native grasses here are perennial and many of the exotic grasses are annual, and the exotic species have established more successfully in wetter sites, not necessarily reflecting a direct influence of life span on colonization success. Thus, the climatic selection that acts upon grass life span globally might not be reflected in California.

Wetter sites contained species with more acquisitive leaf strategies, including higher SLA and N_{mass} . This is consistent with other studies that have found that low SLA plants are generally more drought-tolerant (Ackerly, 2004; Jung et al., 2014; Wellstein et al., 2017). These shifts in leaf strategies differed somewhat from those observed at larger spatial extents for grasses. Here, we found that SLA and N_{mass} increased with increasing precipitation. Across California, the opposite patterns appear (Sandel & Dangremond, 2012), while the positive relationship between precipitation and grass SLA reappears when considering the continental United States (Sandel et al., 2016). In all cases, however, the relationship was fairly weak.

For Height and Area, it made little difference whether the CWM was calculated from species means (SM) or local measurements



(LM). This supports the bulk of previous results that have found that community turnover and ITV tend to positively covary (Ackerly & Cornwell, 2007; Derroire et al., 2018; Kumordzi et al., 2015; Lepš et al., 2011). However, this was not the case for SLA. Considering species means, higher precipitation supported grass assemblages with higher overall SLA. For example, moving from dry to wet sites, one will tend to see a lower abundance of low SLA species such as *Festuca rubra* and *Stipa pulchra* and more high SLA species such as *Cynosurus echinatus* and *Bromus minor*. This shift in community composition along the precipitation gradient tends to produce higher SLA values in higher precipitation sites. However, this trend is overturned when considering local measurements of SLA, because there was a remarkably consistent tendency for each species to display lower SLA values as precipitation increases. A similar result appeared in a study of SLA along an elevation gradient (Lajoie & Vellend, 2015). There, CWMs of SLA mainly decreased with increasing elevation, while ITV overall contributed to slightly higher SLA at higher elevations. On the other hand, a study of Australian annual plants found very little contribution of ITV to the precipitation–SLA relationship (Dwyer, Hobbs, & Mayfield, 2014).

This is somewhat paradoxical. Drier environments on one hand support species with more conservative leaf traits, while on the other hand supporting individuals within species with less conservative leaf traits. One possible explanation for this is that the covariance structure of plant traits is shifting along the environmental gradient. SLA is a central leaf trait that is correlated with many others (Poorter & Bongers, 2006), which are likely to vary in their variation in response to environmental selection. For example, in Costa Rican dry forests, ITV contributes more to spatial turnover of SLA than of other traits such as N_{mass} , suggesting that SLA is a more variable trait (Derroire et al., 2018). If one such trait that covaries with SLA is highly conserved within species, this could drive the turnover response. The ITV response, on the other hand, could be driven by a direct and opposite response of SLA itself to the precipitation gradient.

5 | CONCLUSION

Along the water availability gradient in Marin, there were clear shifts in grass assemblage composition. Large, perennial species with conservative leaf strategies gave way to smaller annual species with acquisitive leaf strategies as water availability increased. Intriguingly, while exotic species did differ from native species in some traits, these differences were expressed within, rather than between, communities. Thus, within a site the largest SLA species (for example) were consistently exotic species, but exotic species show no tendency to be distributed particularly on the high-SLA end of the trait gradient. This suggests that soil nutrient reductions, for example through reducing or mitigating atmospheric N deposition, is likely to favor native species, given their more conservative resource use strategies.

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DATA ACCESSIBILITY

Species and site summaries are available in the supporting information, and the full primary data can be downloaded from figshare.com (<https://doi.org/10.6084/m9.figshare.7904564>).

ORCID

Brody Sandel  <https://orcid.org/0000-0003-2162-6902>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Locations, climate and vegetation characteristics of the study sites

Appendix S2. Summary of grass species collections and trait measurements

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