



Differences between introduced and native grassland species revealed by responses to prolonged drought

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Abstract Introduced species are a typical feature of modern plant communities and experience environmental challenges alongside native species, though introduced species are often hypothesized to be functionally distinct. Changes in the environment may reveal distinct responses to environmental change for native and introduced components of plant communities. We tested for differences in native and introduced plant community composition in California grasslands collected during a period of severe drought. Sampling was conducted across serpentine soils, which are resilient against colonization by introduced species and maintain diverse native species assemblages, and across heavily invaded non-serpentine soils. On native dominated serpentine soils, there was no relationship between climatic variables

and community composition over the survey period. On heavily invaded non-serpentine soils, compositional differences were significantly associated with precipitation. In particular, the native component of serpentine soils was only weakly correlated with current year precipitation and the native component of non-serpentine soils did not differ from null communities. In contrast, introduced species retained strong associations with precipitation on both soil types. We identified three introduced Eurasian grasses, *Bromus hordeaceus*, *Elymus caput-medusae*, and *Avena fatua*, as the greatest contributors to compositional change in non-serpentine communities. These analyses suggest that the majority of compositional change during this period of severe drought manifested within introduced species. Our results are consistent with a hypothesis that communities adapted to low-stress, high-competition plant conditions will experience substantial changes under drought, while communities adapted to high-stress, low-competition conditions exhibit greater resilience.

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Introduction

Introduced species are ubiquitous features of modern biological communities, in some cases representing major components of biomass and species

composition (Simberloff 1996; Bax et al. 2003; Powell et al. 2011; Vilà et al. 2011; Roy et al. 2016; Pyšek et al. 2020). They are also hypothesized to establish in part due to their functional uniqueness, though traits that characterize successful introductions have been difficult to identify or may be context dependent (Funk and Vitousek 2007; Ordonez et al. 2010; van Kleunen et al. 2010; Kaul and Wilsey 2023; Vivó-Pons et al. 2023; Zhu et al. 2024). Climate variability, climatic extremes, and stress can reveal interspecific differences, and may be useful for comparing native and introduced species (Urban et al. 2012; Boucek and Rehage 2014; Guisan et al. 2014; Fahey et al. 2018). Anthropogenic climate change specifically is expected to make habitats more stressful, shuffle biological communities due to climatically driven range shifts, and cause local extirpation of some native species (Jump and Penuelas 2005; Menzel et al. 2006; Parmesan 2006; Lurgi et al. 2012; Franklin et al. 2016; Antão et al. 2022). Research linking introduced species and climate change has rightfully focused on the question of whether climate change will make invasions worse (Liu et al. (2017)). However, there is also value in using climate change as a lens through which to compare native and introduced species and pinpoint important differences in their function, either as individual species or in aggregate.

In California, grassland ecosystems have been radically transformed through land use changes and subsequent invasion by introduced plants (Talbot et al. 1939; Murphy and Ehrlich 1989). Currently, introduced species dominate the cover and biomass of these communities, although species richness for native plants can be greater or equal to those of non-native species (Harrison et al. 2015a, b; Dudley et al. 2017). Within many California grasslands, intact native communities persist on isolated patches of serpentine soils which are distinct in their high heavy metal content, low water holding capacity, and lack of available nitrogen and phosphorus (Walker 1954; Kruckeberg 1984). Experimental work has demonstrated that the stressful nature of these soils contributes to their resilience against invasion (Huenneke et al. 1990; Harrison and Inouye 2002; Burge et al. 2016). Serpentine outcrops exist within a matrix of non-serpentine soil meaning that both plant communities are subjected to similar conditions, such as climate and propagule pressure from introduced plant species. Previous work in these systems has shown

that the plant communities found on the two soil types are distinct and respond differently to experimental manipulation of resources (Kruckberg 1954; Whittaker 1954; Brady et al. 2005). The close spatial proximity of serpentine and non-serpentine communities also makes them useful for comparing how different plant communities respond to similar environmental change.

Water is frequently a limiting resource in California plant communities, either by directly impacting plant fitness or by affecting the availability of soil nutrients, with consequences for competitive outcomes (Seabloom et al. 2003, Enloe et al. 2004, Dukes et al. 2005, Valliere et al. 2019, Luong et al. 2020). Additionally, water availability and precipitation can structure the species and trait composition of grassland communities generally (Craine et al. 2011; Tucker et al. 2011; Knapp et al. 2015). From 2006 to 2016 California experienced a decade long drought, culminating in some of the lowest annual and seasonal precipitation on record from 2012 through 2014 (Copeland et al. 2016; LaForgia et al. 2018). In more recent years, precipitation in this area has remained low and fires have become more frequent (Western Regional Climate Center 2023). These conditions have affected grassland plant communities by favoring traits that are expected to improve drought tolerance, particularly a lower specific leaf area (SLA) (Harrison et al. 2010, 2020; Hulshof et al. 2013; Eskelinen and Harrison 2015; LaForgia et al. 2018). Drought also has caused reductions in species richness on both soil types, which was caused primarily by the local loss of rare, high SLA species from sampling areas (Harrison et al. 2015a, b; Harrison et al. 2020). Thus, long-term drought also presents an opportunity to identify how native and introduced components of the community have responded differently to water stress, with implications for the future of these communities under climate change.

Here we test for divergent patterns in the composition of native and introduced plant communities found in California grasslands during a ten-year period that includes multiple consecutive years of drought. We leverage a long-term plant community dataset started and maintained by Harrison and colleagues in 2006 from across co-occurring serpentine and non-serpentine grasslands (Harrison et al. 2015a, b). Using plant cover data collected from 2006 to 2016, during a drought that began in 2003, we

compare compositional and functional change across both communities in a multivariate framework and evaluate the roles of native and introduced species in producing overall community change. To do this, we examine each community in whole and then as the native and introduced components separately, which allows us to describe the compositional change within each group independently of the other. We then identify the individual species most strongly associated with changes in whole community composition and we compare how well SLA predicts changes in abundance over the survey period for common and rare species, given previous work showing that drought promoted the loss of high SLA native species (Harrison et al. 2015a, b).

Expanding upon previous work showing community changes during this sampling period, we predict that (1) there will be greater compositional change in more heavily invaded non-serpentine plant communities than in serpentine communities, (2) compositional change in both communities will be correlated with precipitation, and (3) compositional change will be correlated with a decline in community weighted SLA. Finally, based on the findings of Harrison et al. (2015a), we predict that (4) abundant and rare species will possess different relationships with SLA and changes in abundance over the course of the survey period.

Methods

Study system

This study was conducted at the University of California McLaughlin Reserve, California, USA (Napa and Lake Co.). The region is characterized by a Mediterranean-type climate, with most annual rainfall occurring between the fall (October) and spring (April) seasons. Annual precipitation at the reserve has decreased from 2003 to 2016, culminating in years with some of the lowest rainfall on record (Harrison et al. 2015a, b; Copeland et al. 2016). Precipitation during this period was greatest in 2006, with ~610 mm of precipitation for the year, and lowest in 2012, with 166 mm. Herbaceous plant communities within the reserve occupy stressful serpentine rock-derived soils and relatively fertile non-serpentine soils. Serpentine soils are characterized by high levels

of heavy metals (Mg and Ni), low levels of N and Ca, and low water holding capacity compared to non-serpentine soils (Proctor and Woodell 1975; Marrs and Proctor 1976; Kruckeberg 2006). Non-serpentine grasslands in California have comparatively higher water holding capacity, more abundant N and Ca, and lower heavy metal content, in addition to being heavily invaded by non-native grasses and forbs that were primarily introduced from Eurasia (Jackson 1985; Mooney et al. 1986; Baker 1989). Serpentine soils are comparatively resilient against invasion (Huenneke et al. 1990; Going et al. 2009; Eskelinen and Harrison 2014) with low introduced species abundance.

Study design

Plant cover data used for this study were collected from 2006 to 2014 by Harrison et al. (2015a, b) and for 2015 and 2016 by Susan Harrison for the present study. Data were collected across 80 sites within the reserve (38 serpentine, 42 non-serpentine) spaced at least 50 m apart. Each site was surveyed along a 40 m transect with five permanent 1 m² plots established in 2000, but cover data used for this study were collected from 2006 onward. Species abundance was quantified with visual estimates of percent cover in each plot.

Measurements of specific leaf area (SLA; leaf area in mm² / leaf dry mass in g) for plants growing on serpentine or non-serpentine soils were collected by Harrison et al. (2015a, b) for 111 species using protocols from Cornelissen et al. (2003). This survey of SLA did not measure all plants on both soil types. For species lacking SLA measurements, we either calculated a mean SLA value from all observations available in the Botanical Information and Ecology Network (BIEN) database (71 species) or used SLA measurements from Stevens et al. (2015), which were collected across a mixture of serpentine and non-serpentine sites in California using similar methods to Harrison et al. (2015a, b) (serpentine: 11 species; non-serpentine: 12 species). The BIEN database is a global repository for plant trait information and is not available for the geographical region containing McLaughlin Reserve or specific to serpentine and non-serpentine communities. When SLA measurements at McLaughlin were only available for one soil type (serpentine: 20 species; non-serpentine: 11 species), we used that single value as the SLA estimate

for the species on both soil types (e.g. if SLA was only measured on serpentine soils, the same SLA value was used for analyses on serpentine and non-serpentine soils). In total there were 55 species for which no SLA value could be obtained using any of the methods described above and 186 species with estimates of SLA.

Community weighted SLA values were calculated for each plot as the sum of each species' SLA value multiplied by its proportion cover. Site level SLA values were then averaged over the 5 plots which composed each site. A Wilcoxon rank sum test was used to compare the distribution of SLA values for introduced and native species, with separate tests for serpentine and non-serpentine communities.

Climate data

Climate data were collected by the Western Regional Climate Center (2023) at Knoxville Creek, CA (38° 51' 43" 122° 25' 02"), roughly 8 km from McLaughlin Reserve. Measurements from this station are taken every 10 min and then provided as monthly averages. We collected variables from 2006 to 2016 that contributed to the climatic environment during the growing season for the herbaceous plant community including total winter precipitation (precipitation during other seasons was negligible), the mean and maximum annual temperature, the average winter, spring, and summer temperature, and the mean winter, spring, and summer daily total radiation. Annual averages were calculated from the beginning of December to the end of November, to better correspond to the growing seasons for plants in the community. Meteorological delineations for the seasons were used to calculate winter, spring, and summer averages.

We used principal components analysis (PCA), implemented with the *princomp* function in R, to identify the major axes of variation in climate and identify correlated variables. The PCA coordinates for individual years (e.g., 2006–2016) were extracted and used in downstream analyses to investigate correlations between climatic and vegetational change.

Changes in community composition

Significant change in community composition could require multiple years of accumulated change

to emerge. To identify this period of time, we used a permutation-based analysis of variance (PERMANOVA function from the *vegan* package) to compare the pairwise difference in species abundances from two different years to 999 pairs of randomly shuffled communities. This process was repeated for all pairwise year to year comparisons on serpentine and non-serpentine communities independently.

To test the predictions that compositional change will be correlated with precipitation, we averaged cover data for each site across all five plots for further analyses. Compositional differences between sites for 2006 to 2016 were evaluated with non-metric multidimensional scaling, hereafter 'NMDS' (Shepard 1962; Kruskal 1964b; Field et al. 1982) using Bray–Curtis distances with weighted average scores, implemented in the '*vegan*' package v2.5–4 in R (Dixon 2003). We conducted NMDS analyses separately for serpentine and non-serpentine communities. Ordinations were constrained to two dimensions for ease of visualization and use in downstream analyses.

The quality of an NMDS ordination is most often represented as its stress, the cumulative standardized differences between the original distance matrix and the matrix representing differences in ordination space, modeled via a stepwise, monotonically increasing function (Kruskal 1964a). Stress increases with the number of observations in the analysis, and may not be appropriate for evaluating the quality of NMDS ordinations of large datasets including hundreds of observations (Clarke 1993; Dexter et al. 2018), as we have in this study. To overcome this issue, we compared NMDS output to permutation-based ecological null communities as suggested by Dexter et al. (2018). Null communities were produced by randomly shuffling species observations to produce a novel distance matrix using the '*oecosimu*' function from the '*vegan*' package in R, with the '*swsh_swap*' permutation method (Dixon 2003). Stress values from the original dataset were then compared to the distribution of stresses for 99 null communities with a *z*-distribution. Significant results from this test indicate the presence of an underlying ecological pattern in the real data that does not exist in the null communities (Dexter et al. 2018). We performed these analyses separately for serpentine and non-serpentine communities.

For all NMDS plots which were significantly different from hypothetical null communities, we then

tested for correlations between climate and community weighted SLA with changes in community composition by fitting an explanatory vector with the function ‘*envfit*’ in the *vegan* package (Dixon 2003). We chose to consider precipitation independently of the climatic PCs, given past work associating precipitation specifically with community properties in California grasslands (Harrison et al. 2015a, b; Copeland et al. 2016). Additionally, we included both current and previous years precipitation (e.g. lagged precipitation), because studies of arid grasslands have shown this delayed effect of precipitation caused by changes fecundity of plants the previous year (Dudney et al. 2017). To avoid correlations between climate variables, we compared the effects of winter precipitation, lagged precipitation, and climatic principal components separately. This resulted in three models that were tested for each community: 1) weighted SLA and winter precipitation, 2) weighted SLA and lagged precipitation, and 3) weighted SLA and the first two climatic principal components.

A single ordination cannot differentiate between dynamics in the native and introduced species assemblages. Therefore, we split each community into its native and introduced components to test the prediction that changes in community composition will be different between native and introduced species. We then repeated all NMDS ordinations and *envfit* analyses on these four communities: serpentine native, serpentine introduced, non-serpentine native, and non-serpentine introduced.

After finding that the non-serpentine community exhibited significant compositional change and associations with explanatory variables, we attempted to identify which individual species most strongly contributed to these patterns. Individual species contributions to community change cannot be extracted from non-linear NMDS axes, so we used Gradient Boosted Models (GBM) to predict NMDS centroid values using a subset of the species abundance data. Generally, GBMs are a class of machine learning tool which produce a predictive model, in the form of decision trees, similar to random forest models. The predictive power of the decision tree is optimized through a secondary loss function describing the difference between predicted and observed values, which is then minimized by identifying the parameter values which minimize this function. We produced two GBMs which predicted either the first or second NMDS

axis values for the ten centroids grouping sites by year, with the species cover matrix as input. To test the predictive ability of GBM outputs, the dataset was randomly split into a training set (2/3 of observations per year) and testing set (1/3 of observations per year) prior to running the GBM. The ability of the GBM to accurately predict NMDS axis values with the testing data was calculated as the mean squared error, with better runs possessing lower error. We ran each GBM simulation 1000 times, because the optimization algorithm has the potential to identify local, rather than global, minima. To run the GBM we used function ‘*gbm*’ from the R package *gbm* v2.1.5 (Manion et al. 2024). Each model run included 4500 trees ($n.trees=4500$), with only one way interactions ($interaction.depth=1$), a minimum of three observations on terminal nodes ($n.minobsinnode=3$), and a learning rate of 0.1 ($shrinkage=0.1$). Parameters were optimized using the ‘*train*’ function from the ‘*caret*’ package (Kuhn 2008).

As a supplement to GBM analyses, we also performed a principal component analysis on the cumulative change in the abundances of native and introduced non-serpentine species over time, using the function ‘*prcomp*’ in R (R Core Team 2013). We extracted the top five species loadings for the first two PC axes and compared these with the GBM predictions.

SLA and cover differences across common and rare species

Functional distinctions between common and rare species could be lost with ordinations that abstractly consider communities as a singular unit for the purposes of comparison. Importantly, large changes in abundance of the most common species could disproportionately influence the relationship between changes in abundance and SLA at the community level. We therefore tested for a relationship between species rarity, changes in species specific percent cover, and SLA during the survey period.

To compare the changes in cover between common and rare species, we first binned the community into two abundance categories. Species with starting abundances above the 75th quartile were classified as common, and all remaining species were classified as rare. In total 44 species were classified as common (average cover at the start of the survey 0.27–14.8%)

and 127 were classified as rare on serpentine soils (average cover 0.0005–0.26%), while 39 species were classified as common (average cover 0.31–38.6%) and 116 classified as rare (average cover 0.0004–0.30%) on non-serpentine soils. SLA measurements were not available for four common species (9.1%) and 38 rare species (30%) on serpentine soils and were not available for six common species (15.4%) and 27 rare species (23.3%) on non-serpentine soils.

To quantify the rate of change in species specific cover in the non-serpentine community, we performed linear regressions with the percent cover as the response variable and the survey year as the explanatory variable, excluding years which the species was not observed (i.e., had a zero entry). Species observed only in a single year were excluded from this analysis. The slope of each of these regressions (hereafter population trajectory) was then used to compare the cover dynamics of rare and common species with SLA. We used phylogenetic generalized least squares analyses (PGLS; Symonds and Blomberg 2014) to separately test for correlations between the population trajectories as the response variable with rarity and SLA as explanatory variables. The influence of phylogenetic relatedness is calculated as λ , with values ranging from zero, no phylogenetic correlations, to a maximum value of 1, perfect phylogenetic correlation. To perform this analysis, we used a comprehensive phylogeny encompassing all land plants based on molecular data from Zanne et al. (2014). PGLS analyses were performed using the R package 'caper' v. 0.5.2 (Orme et al. 2013).

We found only weak effects of phylogeny on our analyses (see Results). We therefore performed regressions using ordinary least squares, because PGLS will not allow models with interaction terms. We used a generalized linear model with a Poisson error distribution to test for relationships between population trajectory as the response variable and SLA, rarity, and their interaction as fixed effects. Within this framework, a significant interaction between abundance category and SLA indicates that the relationship population trajectory and SLA depends on rarity. When graphing the relationship between population trajectories and SLA it appeared that a negative quadratic function might be a better fit than a linear function. After identifying *Bromus hordeaceus* as an outlier in these analyses using the studentized residuals analysis, we compared the fit of

linear and quadratic models without this species. All analyses were conducted in R v3.5.3 (R Core Team 2013).

Results

Changes in community composition between years

In both serpentine and non-serpentine habitats, we found significant differences in community composition across years (PERMANOVA: serpentine: $F=6.6$, $P<0.001$; non-serpentine: $F=30.8$, $P<0.001$), indicating that over the entire survey period and as drought continued to worsen, for one year or more, plant communities were compositionally distinct from other survey years. Moreover, the majority of all possible pairwise year-by-year comparisons of community composition were significantly different (non-serpentine: 44/55 comparisons; serpentine: 38/55 comparisons) (Fig. S1). Comparisons of community composition across consecutive years were significant for 70% of all tests on non-serpentine soil and 50% of all tests on serpentine soils.

Associations between composition, and climate, and traits

This study considered nine potentially correlated climatic variables. Eigenvalues for the first two PC axes of climatic variation explained 68.9% of the variation (Fig. S2A) and were used in subsequent analyses. The first PC axis, which explained 39.1% of total climatic variation, had a positive loading for winter precipitation and negative loadings for seasonal and mean average temperatures (Fig. S2B).

We found mixed support for the hypothesis that community composition would be correlated with climate and SLA in both non-serpentine and serpentine plant communities. Ordination of non-serpentine and serpentine communities yielded significantly lower stress than null communities (serpentine: stress=0.266, $z=-41.1$, $P<0.01$; non-serpentine: stress=0.24, $z=-66.6$, $P<0.01$; Fig. S3), indicating the presence of underlying ecological structure. On non-serpentine soils, vectors for site-level SLA, winter precipitation, lagged precipitation, and climatic PC1 were all significant when projected onto NMDS space (Table 1, Fig. 1B). The vectors for current year

Table 1 Vector fits of year, specific leaf area (SLA), and climatic variables in NMDS ordination space for McLaughlin grassland communities from 2006 to 2016. Values highlighted in bold indicate significance ($P < 0.05$)

Independent variable	Soil type	Community component	r^2	P -value
SLA	Serpentine	All	0.093	< 0.001
		Native	0.130	< 0.001
		Introduced	0.050	< 0.001
	Non-serpentine	All	0.015	0.031
		Introduced	0.074	< 0.001
Winter Precipitation	Serpentine	All	0.001	0.768
		Native	0.017	0.024
		Introduced	0.008	0.188
	Non-serpentine	All	0.034	< 0.001
		Introduced	0.041	< 0.001
Lagged Precipitation	Serpentine	All	0.001	0.759
		Native	0.006	0.340
		Introduced	0.017	0.045
	Non-serpentine	All	0.036	< 0.001
		Introduced	0.055	< 0.001
Climate PC1	Serpentine	All	0.002	0.569
		Native	0.011	0.104
		Introduced	0.004	0.463
	Non-serpentine	All	0.073	< 0.001
		Introduced	0.107	< 0.001
Climate PC2	Serpentine	All	0.009	0.172
		Native	0.003	0.486
		Introduced	0.040	< 0.001
	Non-serpentine	All	0.028	0.004
		Introduced	0.039	< 0.001

and lagged precipitation had similar fits to the data, but were nearly orthogonal in projection, suggesting that both factors are important for explaining different aspects of compositional change in this community (Fig. 1B). When we fit vectors onto serpentine NMDS space, SLA was significantly correlated with community structure while climate variables were not (Table 1, Fig. 1A).

Differences in the native and introduced components of the community

In serpentine communities, patterns of compositional change were different for native and introduced species, although both communities exhibited significant correlations between community structure and SLA (Table 1). Native species composition was significantly different from null communities (stress=0.25, $z = -47.8$, $P < 0.01$; Fig. S3). The relationship

between native composition and current year precipitation was significant, but the magnitude of the vector, and thus the r^2 value for this relationship were small, suggesting that the winter precipitation explains a small proportion of community differences through time (Fig. 1C). Ordination did not produce a significantly better fit than for null communities for introduced species on serpentine soil (stress=0.22, $z = -0.45$, $P = 0.43$; Fig. S3) and performing the ordination in three dimensions did not resolve this behavior. We chose to include this ordination in our interpretation because these results appear to be caused by the unusual structure of the species matrix. Although stress for this ordination was lower than most null communities, random permutation of the data yielded 15 out of 99 null communities with stress lower than that observed in the real data, including one run with stress very close to zero. The superior performance of some null communities could result

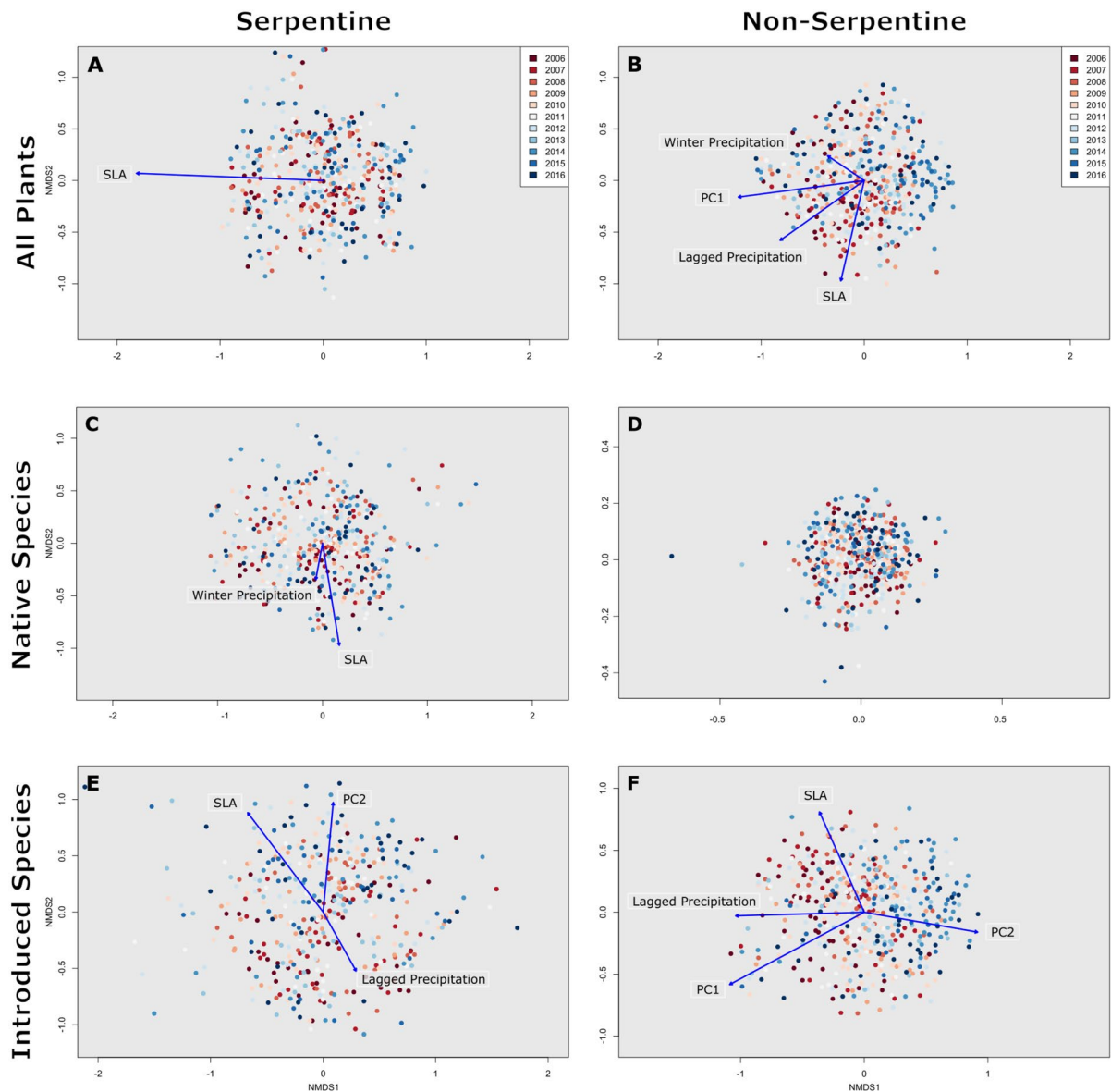


Fig. 1 Nonmetric multidimensional scaling (NMDS) ordinations in species space from 2006 to 2016. Individual sites (dots) are colored by year. Serpentine (A, C, E) and non-serpentine communities (B, D, F) exhibit different associations with aspects of climate. Plots are shown for the whole plant community (A, B), only native plants for each community (C, D), and only introduced species for each community (E, F). Significant vectors for annual winter precipitation, lagged precipitation, significant climatic PC axes, and com-

munity weighted specific leaf area are fitted for each plot (blue arrows). Significant vectors for annual winter precipitation, lagged precipitation, significant climatic PC axes, and community weighted specific leaf area are fitted for each plot (blue arrows). No vectors are shown for native plants on non-serpentine soils, which produced an NMDS ordination without convergence and also exhibited no difference from null communities

from the inability of the NMDS algorithm to successfully converge on a best fit NMDS ordination for the real community, which was observed in over half of

ordinations performed. This behavior appeared to be primarily the result of a small number of observations that had large Bray–Curtis distances with all

other observations, making them difficult to place in NMDS space. We therefore proceeded to test for correlations between community composition and explanatory variables. In contrast to native species, the introduced species composition was significantly correlated with lagged precipitation, rather than current year precipitation, and climatic PC2 (Fig. 1D). There was also apparent temporal structure to the NMDS, with communities from earlier in the survey clustered more towards the bottom of the Y-axis in NMDS space and more recent communities clustered at the top. This corresponded with the vector for climatic PC2, which aligned nearly parallel with the y-axis. Similarly, the vectors for SLA and lagged precipitation increased and decreased along the y-axis respectively. These relationships suggest that the composition of the introduced plants shifted towards species with higher SLA as lagged precipitation decreased, winter temperatures increased, and maximum temperatures decreased.

Ordination of native species on non-serpentine soils did not have significantly lower stress than null communities ($z=1.0$, $P=0.31$, Fig. S3), suggesting the lack of pattern in the NMDS ordination of these communities. Additionally, NMDS of the native community on non-serpentine soils never reached convergence after 999 configurations. We therefore did not investigate any correlations between climate, SLA, and year for this community within the NMDS framework.

Ordination for introduced species on non-serpentine soils performed significantly better than null communities ($z=-21.2$, $P<0.01$; Fig. S3). The

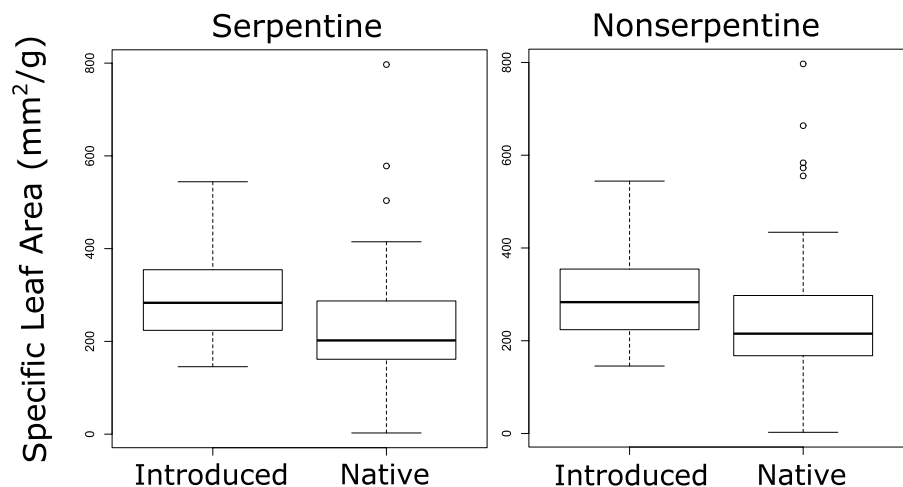
structure of this NMDS was similar to that for the whole non-serpentine community, with older communities clustered at low x-axis values and more recently sampled communities clustered at high x-axis values (Fig. 1F). Weighted SLA, lagged precipitation, and PC axes 1 and 2 were all significantly correlated with NMDS structure (Table 1, Fig. 1F). All three climatic variables aligned to the x-axis, with lagged precipitation and PC2 lying nearly parallel, suggesting that communities transformed through time as precipitation and maximum temperatures decreased. Surprisingly, the vector for SLA was largely orthogonal to the x-axis and the climatic vectors. Thus, although SLA was an important factor in explaining community dissimilarity, it did not correspond to structure associated with climate in NMDS space.

Traits of species contributing most to community change in non-serpentine communities

Overall, introduced species on both non-serpentine and serpentine soils had significantly greater SLA than native plants (non-serpentine: $W=4715$, $P<0.001$; serpentine: $W=4964$, $P<0.001$) (Fig. 2).

To identify the species most strongly contributing to patterns over time in the non-serpentine community, we used gradient boosted models to predict yearly movement along the first and second NMDS axes from a subset of species abundance data. GBM models consistently assigned the greatest predictive weight to a set of common introduced and invading species (Table S2). Along NMDS axis 1, the highest weighted species for all 1000 GBM

Fig. 2 The distribution of specific leaf area for introduced species is significantly greater than for native species ($P<0.001$) on both non-serpentine and serpentine soils. Error bars depict standard error



models was *Bromus hordeaceus*, followed by *Elymus caput-medusae*, and *Avena fatua* (Fig. 3a), all of which are annual Eurasian grasses common to invaded western landscapes. These three grasses were also the most important species for making accurate predictions along NMDS axis 2, but with

lower differences in weight among them (Fig. 3b). Native species were rarely ranked in the top five species for accurate predictions along either NMDS axis, with two native species identified as infrequent rank 4 and 5 predictors for NMDS axis 1 (*Clarkia purpurea* and *Dichelostemma capitatum*) and two

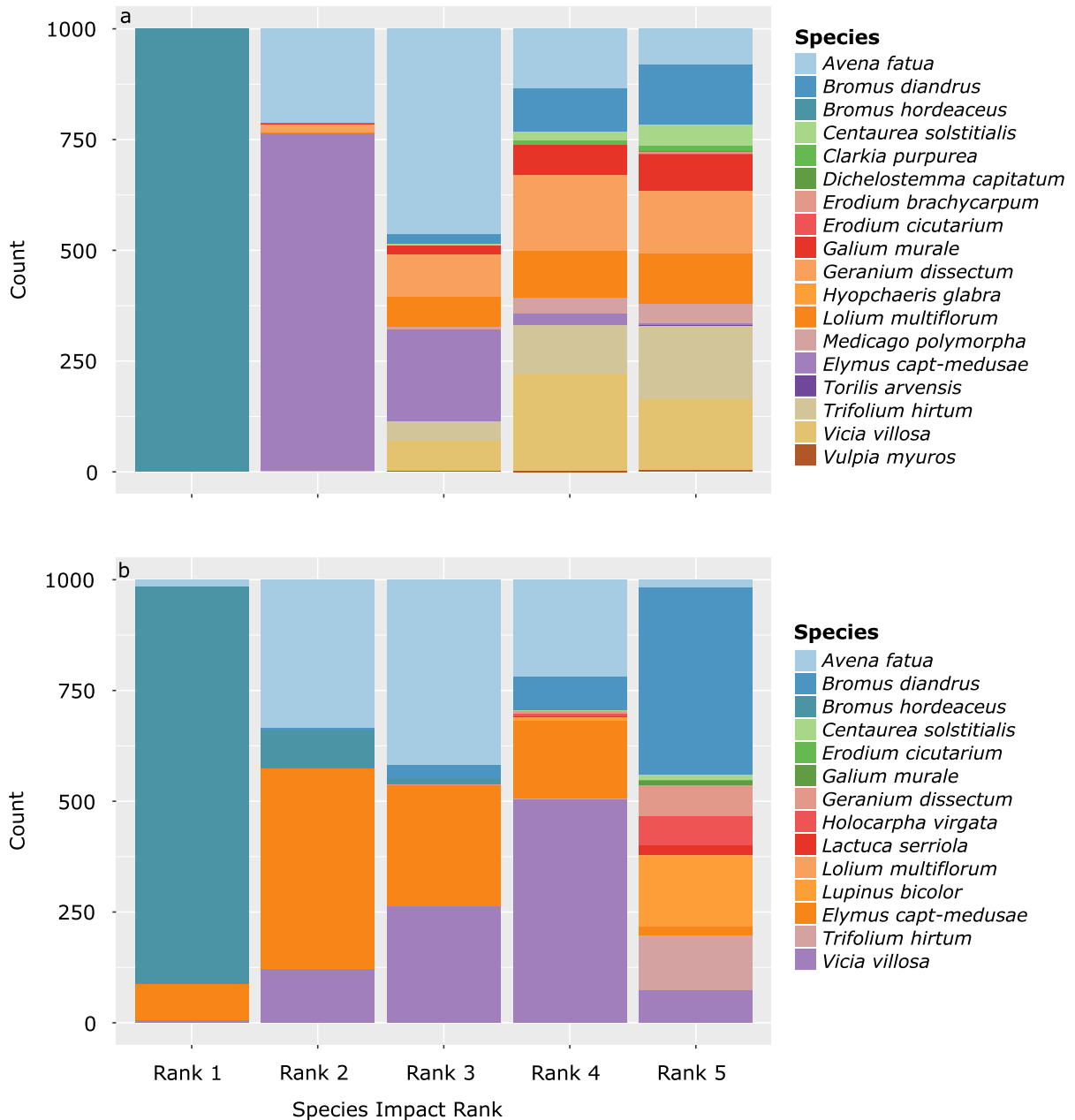


Fig. 3 Results from 1000 gradient boosted models which predict NMDS year centroids in Fig. 1B from individual non-serpentine site-level observations. Species are ranked by their

order of importance for producing accurate predictions. **a** predictions along NMDS axis 1; **b** predictions along NMDS axis 2

others for axis 2 (*Holocarpha virgata* and *Lupinus bicolor*).

We then compared our results from GBMs to a PCA ordination of the cumulative differences in species abundances over time. The set of five species with the greatest loading along the first and second PC axes did not include native species and were largest for the same three introduced grasses identified by GBM analysis: *B. hordeaceus*, *E. caput-medusae*, and *A. fatua* (Fig. S4).

Our community scale analyses, as well as those of past studies, have identified associations between reductions in SLA and community change. We therefore expected the three species identified by GBM and PCA would mirror these trends; they would have either high SLA and decrease in abundance or they would have low SLA and increase in abundance. The SLA for all three grasses was above the mean for plants in this community (*A. fatua*: 314 mm²/g; *B. hordeaceus*: 311 mm²/g; *E. caput-medusae*: 418 mm²/g; mean: 245 mm²/g; Fig. S6). Two of these species, *B. hordeaceus* and *E. caput-medusae*, decreased in abundance over the survey period, while *A. fatua* increased (Fig. S5).

Association between SLA, abundance, and changes in individual species cover

We found mixed support for the prediction that the abundance of individual species would be correlated with SLA. There was weak phylogenetic signal for rarity (serpentine: $\lambda=0$; non-serpentine: $\lambda=0$) and SLA (serpentine: $\lambda=0.098$; non-serpentine: $\lambda=0$), so all following tests were performed using ordinary least squares analyses. On serpentine soil the effects of starting abundance, SLA, and their interaction had significant relationships with population trajectories (Table S1). When the correlation between SLA and population trajectory was considered separately for common and rare species, we found a positive linear relationship between SLA and population trajectories for common species ($F_{1,3}=6.33$, $P=0.02$), but no significant effect for rare species ($F_{1,87}=1.83$, $P=0.14$) (Fig. 4A). Initially, a quadratic fit was not significantly different from a linear fit for this relationship in common species ($P=0.29$). We found significant support for *Bromus hordeaceus*, one of the species identified as most strongly predicting patterns of compositional change, as an outlier for

describing the relationship between SLA and population trajectories for linear and quadratic models (linear model: studentized residual = -4.7, Bonferroni corrected $P=0.002$; quadratic model: studentized residual = -11.5, Bonferroni corrected $P<0.001$). After removal of *B. hordeaceus*, the quadratic model performed significantly better than the linear model ($P=0.002$). Removal of *B. hordeaceus* also improved the fit of the quadratic model ($F_{2,36}=14.7$, $P<0.001$) (Fig. 5).

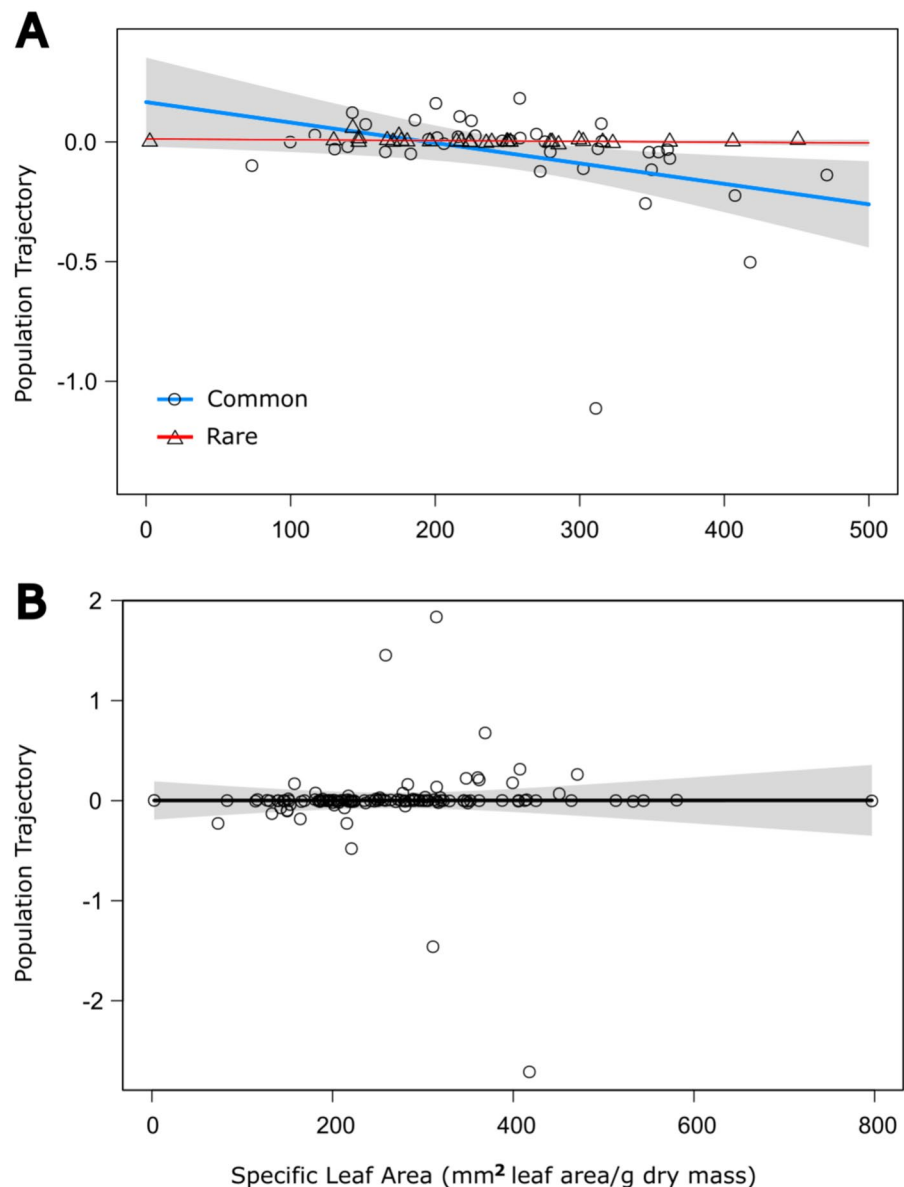
In non-serpentine communities, we did not find support for different relationships between population trajectory and SLA for common and rare species (Table S1). The original least squares linear model predicted a significant relationship between population trajectories and SLA, but the slope of the best fit line was shallow (Fig. 5B). When removing the non-significant interaction term or rarity from the linear model, the relationship between population trajectories and SLA became non-significant ($F_{2,120}=0.87$, adjusted $r^2=-0.002$, $P=0.42$ and $F_{1,121}=0.77$, adjusted $r^2=-0.002$, $P=0.38$ respectively). A quadratic fit did not improve this relationship ($F_{2,119}=0.40$, adjusted $r^2=-0.009$, $P=0.67$).

Discussion

By analyzing a long-term plant community dataset, we find that change in community composition during a period of unprecedented drought is primarily attributable to shifting abundances of introduced species. The composition of introduced species was most strongly correlated with the drought resistance trait SLA, lagged precipitation, and the first and second principal components of climatic variation. Corresponding patterns of directional change were not observed in the native component of these plant communities, despite a significant association between SLA and native community composition. Our results suggest the existence of functional differences between native and introduced species which may only be evident after multiple years of environmental stress.

Differences in drought tolerance between native and introduced species appeared to drive patterns of community structure during the survey. The years of this study had some of the lowest total annual rainfall on record in California (Copeland et al. 2016),

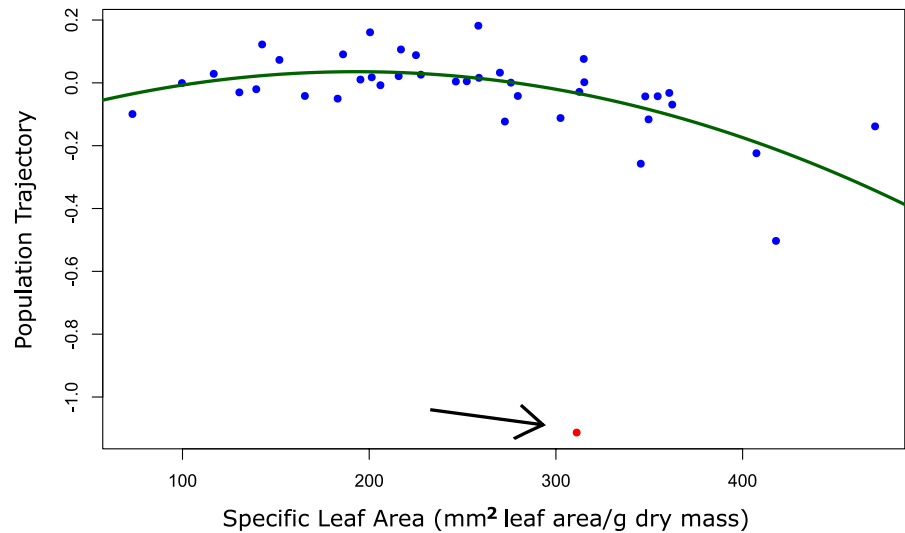
Fig. 4 The relationship between SLA and population trajectory, calculated as the slope extracted from linear regressions with the percent cover as the response variable and the survey year as the explanatory variable, during severe drought differs between abundant and rare species on serpentine soils (A), but not on non-serpentine soils (B). There is a significant, negative relationship between SLA and population trajectory for the most common species on serpentine soils, classified as those with abundance above the 75th quartile (blue line, circles) ($P=0.02$). There was no significant relationship between SLA and population trajectories for all remaining species in the community (red line, triangles) ($P=0.19$). There was a significant relationship between population trajectory and SLA for non-serpentine soils ($P=0.04$), but the slope was very close to zero over a large range of x-axis values (B)



which has been associated with reduced abundance of drought intolerant species and communities with lower weighted SLA (Harrison et al. 2015a, b; LaForgia et al. 2018). Across both soil types, introduced species collectively possessed greater SLA than native species, and in non-serpentine plant communities we observed a link between compositional change and precipitation, particularly for introduced species. Invading species appear to commonly have greater SLA when compared to native species in invaded communities, as this trait can

increase competitive ability by increasing growth and reproductive rates in the absence of drought stress (Ordóñez et al. 2010). The dominant, introduced grasses in this system are known to compete strongly for water, and water limitation affects their growth and fecundity (Suttle et al. 2007, Valliere et al. 2019), which can lead to lagged responses in introduced grass species when precipitation changes (Dudney et al. 2017). Indeed, lagged precipitation was the strongest climatic effect correlated with the composition of introduced species across both soil types. In

Fig. 5 The quadratic fit (green line) for the relationship between population trajectory and SLA for common species on serpentine soils at McLaughlin Reserve ($P < 0.001$). The model was fit was improved after removal of *Bromus hordeaceus* (arrow and red point), a significant outlier in this analysis



comparison, native communities appeared largely stable with regard to climatic variation (serpentine communities) or lacked apparent ecological structure (non-serpentine communities). Consistent with these results, an earlier version of this dataset spanning from 2000 to 2010 demonstrated lower variability in total species richness on more native dominated serpentine sites in response to annual precipitation (Fernandez-Goñi et al. 2012). Considered broadly, our work suggests that unlike native species, introduced species in these communities are more likely to possess drought intolerant phenotypes, increasing the effects of environmental stress and variation (Goergen and Daehler 2002, Diez et al. 2012, Wolkovich and Cleland 2014, Valliere et al. 2019, but see Funk and Vitousek 2007).

We identified the introduced grasses *A. fatua*, *B. hordeaceus*, and *E. caput-medusae* as the most influential species for describing community level change. *Avena fatua* quadrupled in abundance by the end of the survey (not including an outlier year in 2015 when its cover increased by an order of magnitude), while *B. hordeaceus*, and *E. caput-medusae* became less abundant. While we acknowledge the existence and importance of many drought tolerance traits in plants, we expected the species most strongly associated with directional change to increase or decrease based on their SLA in accordance with the consistent identification of SLA as a strong predictor of change in this community (Harrison et al. 2015a, b; Harrison et al. 2020). However, of the three grasses

most strongly associated with compositional change on non-serpentine soils, only the high SLA, *E. caput-medusae* matched the community wide pattern by decreasing in abundance over the course of the study. The other two grasses have almost identical SLA, close to the median for the non-serpentine plant community, but these species exhibited differing population trajectories. Additional traits are likely to be useful for more fully explaining the changes in species cover. Phenology traits, for example, can act as alternative mechanisms for coping with drought by ensuring growth and reproduction are completed before seasonal precipitation ends (Sherrard and Maherali 2006; Franks 2011) and the efficacy of specific drought tolerance strategies may also change with the competitive environment (Fotelli et al. 2001; Maestre et al. 2009; Luong and Loik 2022). Our results suggest that, although SLA may be useful for differentiating the responses of native and introduced species to environmental change, a multi-trait approach could be necessary to understand the specific mechanisms that underlie community wide patterns of change. As a composite economic trait, SLA encompasses multiple components of leaf morphology that might individually be useful for understanding plant drought responses. Leaf dry matter content, leaf thickness, osmotic potential and many other morphological and physiological traits, have also been observed to be significant predictors of plant drought resistance (Wilcox et al. 2020). Yet, our work also demonstrates that comparing changes in the composition of native

and introduced species can be a useful lens for understanding whole-community scale patterns.

Our analysis identified a weak relationship between serpentine native species composition and winter precipitation. In comparison, introduced species on serpentine soils had strong associations with both lagged precipitation and temperature (PC2). The apparent stability in the native component of this community could be explained by other environmental factors that contribute more strongly to community structure and thus mask any climatic effects. For example, the ‘harshness’ of serpentine soils can vary substantially over small spatial scales and can have greater effects than varied precipitation on plant community outcomes (Johnston and Proctor 1981; Wright et al. 2006; Eskelinen and Harrison 2014). Increasing water availability also does not significantly impact serpentine plant communities without additional nutrient supplementation, and the addition of both water and nitrogen decreases the abundance of low SLA species on these soils (Eskelinen and Harrison 2015). Studies conducted within an NMDS framework on infertile limestone soils in the UK also found that plant communities appear resilient to warming and drought due to a suite of traits which facilitate persistence in environments with scarce resources (Grime et al. 2000, 2008). Our results contribute to this small body of work suggesting that plant communities on stressful soils appear more stable, although not completely unaffected, by reductions in precipitation (Grime et al. 2000, Tielbörger et al. 2014; Harrison et al. 2015a, b). However, we note that there were indeed declines in species richness for both the native and introduced components of this community during the survey period. Although native species composition was stable within the framework of our results, we should not overlook other analyses detailing the vulnerability of rare species in this community.

We had initially predicted that changes in community composition would be primarily caused by a decrease in the abundance of native species, given the high variability in native forb cover and previous work finding that reductions in species richness stemmed from the loss of rare native forbs across soil types (Fernandez-Goñi et al. 2012; Harrison et al. 2015a, b). However, our analyses identified greater correspondence in community composition and climate for introduced species on serpentine soils and in more heavily invaded non-serpentine soils overall.

The paradox of species richness declines occurring in communities that appear stable could result from how each species is weighted in the calculations of Bray–Curtis distance. Calculations of species richness weigh each species equally, regardless of abundance. However, even though Bray–Curtis distances reduce the influence of common species by using rank order abundance, rare species will still have relatively small individual effects in highly diverse communities such as those considered here. On heavily invaded non-serpentine soils, introduced species comprise the majority of plant cover and biomass while native species often represent ~0.1% of plant cover and occur infrequently across sampling sites. The drop out of rare native species from these plots should therefore have small effects on our analyses of community composition while having large effects on species richness. An analysis of compositional differences will instead tend to reflect shifts in the most abundant species. Indeed, the species that were identified as most influential in structuring NMDS ordination of non-serpentine communities were some of the most abundant species across the ten years of surveys. The ability of multivariate analyses, such as those presented here, and analyses of species richness to detect distinct trends in community change occurring in different subsets of the community make them complementary approaches to understanding the full extent of community change.

The relationships between SLA, changes in cover, and rarity depended on soil type. However, there was not a relationship between SLA and population trajectories for rare species on either soil type. We are cautious in our interpretation of these results, because rare species are expected to naturally vary in whether they are observed in sampling plots. Stochastic changes in the abundance estimates of rare species cause relatively large changes in their recorded abundance from year to year (MacKenzie et al. 2005), and this behavior counteracts the ability to accurately model population trajectories for these species because of greater differences between observed and actual abundance. We therefore cannot confidently assert that SLA is not descriptive of population size changes for less common species in this community.

We observed that for common species on serpentine soils, those with the lowest and greatest SLA were more likely to decrease during the observation period. The shape of this relationship suggests the

presence of an optimum near the midpoint of the trait distribution of common species, while there was no relationship for rare species. Similarly, the population dynamics of Sonoran Desert annual plants was predicted by functional traits for only the most common species (Ge et al. 2019). Nevertheless, in California grasslands, population dynamics of some of the rarest species in the system are also associated with their trait values (Harrison et al. 2015a, b). Notably, we did not find this relationship in the non-serpentine community, which is dominated by introduced species.

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Trait differences between native and introduced species have been used to explain biological invasions dating back to Darwin with empirical support from experimental microcosm and greenhouse studies (Ordonez et al. 2010; Zavaleta and Hulvey 2004; Hulvey and Zavaleta 2012; Valliere et al. 2019; Kaul and Wilsey 2023), but with less consistent support from the field (Meiners 2007; Moles et al. 2012; van Kleunen et al. 2015). A decade of drought in California grasslands revealed functional differences between the communities of native and introduced species resulting from differences in their drought tolerances. Trade-offs in abundance among dominant introduced species and relative stability among common native species suggests that environmental stress favors certain functional types but not invading species as a whole. These patterns were only apparent in association with long term responses to environmental change, which may be essential for observing long-term differences between native and invader function. Comparisons of native and introduced species in other long-term datasets could similarly be useful, particularly when analyzed within the

context of environmental variation during the survey period. We argue that this is a valuable and complementary approach to studies that attempt to document environmental change, particularly in response to anthropogenic disturbances, and to studies that have attempted to identify differences between native and invasive species through pairwise species comparisons or meta-analyses (Funk and Vitousek 2007; van Kleunen et al. 2010; Vivó-Pons et al. 2023; Zhu et al. 2024).

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Author contributions J.B. and K.D. conceived of the study; J.B. and M.J. analyzed the data; J.B. wrote the manuscript; J.B. and K.D. revised and edited the manuscript. All authors have approved the final version of this manuscript.

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Data availability Plant community dataset is available from Susan Harrison at UC Davis upon request. Additional data used in this study is available through Figshare at https://figshare.com/projects/McLaughlin_Introduced_and_Native_Comparison/179787.

Code availability Code used in this study is available through Figshare at https://figshare.com/projects/McLaughlin_Introduced_and_Native_Comparison/179787.

Declarations

Competing interests The authors declare that they have no conflict of interest, financial or otherwise.

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