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RESEARCH ARTICLE

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Leaf traits and phylogeny explain plant survival and community dynamics in response to extreme drought in a restored coastal grassland

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Abstract

1. Climate change will increase uncertainty in restoration outcomes due to greater water stress and other abiotic filters that limit plant survival. Drought-related plant functional traits can help species withstand filters in a semi-arid environment. Our objective was to provide guidance for selecting species to improve restoration success in a changing climate.
2. We planted 12 native species in ambient rainfall and under 60% rain-out shelters in an invaded coastal grassland in central California. We measured survival and size annually for 4 years and quantified plant community and trait composition in the third and fourth years. We measured growth rate, specific leaf area (SLA), leaf C:N, leaf lobedness and leaf $\delta^{13}C$ of all planted species and dominant extant species, and evaluated the effect of treatments, traits and phylogenetics on mortality risk using Cox proportional hazards.
3. Native perennial species cover was greater, whereas thatch depth and per cent cover of shrubs and non-native annual grasses were lower, on drought plots. Drought plots had lower community-weighted leaf C:N and higher leaf lobedness.
4. Planted species with resource conservative traits, such as higher leaf lobedness and lower growth rate, had lower mortality risk. Increased plasticity of morphological traits (SLA and lobedness) was associated with decreased mortality risk, whereas increased plasticity of physiological traits (leaf C:N and $\delta^{13}C$) and risk was positively correlated. Trait plasticity explained a greater degree of plant mortality risk compared to absolute trait values.
5. Plants that were more phylogenetically related to the surrounding plant community had lower mortality risk. Traits of planted species that were important for determining plant mortality in this coastal grassland may be conserved, which was supported by a phylogenetic signal (Blomberg's $K = 0.380$, Pagel's $\lambda = 0.830$) in leaf C:N.
6. *Synthesis and applications*. Our results suggest that leaf traits and phylogenetics could serve as plant selection criteria for reducing plant mortality risk during drought, thereby improving restoration outcomes. Because some traits have a phylogenetic signal that explains drought survival, restoration practitioners could

expand the use of trait-based selection for closely related species when restoring other arid- and semi-arid ecosystems.

KEYWORDS
Cox proportional hazard, environmental filter, leaf C:N, leaf lobedness, leaf $\delta^{13}C$, phylogenetic signal, relative distance plasticity index (rdpi), trait plasticity

1 | INTRODUCTION

Ecological restoration is expensive and funding is often limited (Holl & Howarth, 2000), so new approaches are needed to improve restoration success. Restoration currently suffers from unpredictable outcomes (Suding, 2011) and climate change will likely increase restoration variability (Harris et al., 2006), as models forecast that precipitation will become more temporally and spatially variable (Swain et al., 2018). One reason for uncertain restoration outcomes is a focus on taxonomic composition without consideration of how species respond to changing environments (Funk et al., 2008). Incorporating community metrics that directly respond to environmental conditions when selecting species may decrease some of the uncertainty faced by restoration practitioners (Carmona et al., 2016; Verdu et al., 2012).

Precipitation timing and magnitude in California and many parts of the world will likely vary more within and across years in the future (Swain et al., 2018). This variability will result in more rainfall being lost as run-off during large rain pulses and less infiltration to replenish soil-water (Loik et al., 2004). This will cause longer time periods between rainfall events during the wet season, contribute to increasing climatic water deficit and enhance plant drought stress (Loik et al., 2004). Therefore, it may help to draw from trait-based coexistence and community assembly theory that focus on methods for matching plant traits to changing environmental conditions to maximize restoration efficacy (Adler et al., 2013; Funk et al., 2008; Verdu et al., 2012). Because plant traits exhibit plasticity which causes traits to change in response to environmental conditions (Valladares et al., 2006), understanding how a range of traits adjust can help identify key traits that drive plant survival, community composition and restoration outcomes (Griffin-Nolan et al., 2018).

Plants must pass through a series of abiotic and biotic environmental filters in order to establish at a new site and persist (Funk et al., 2008). Abiotic filters can select for multiple and overlapping traits among species (Verdú et al., 2003). Abiotic filters may become more selective in a changing climate, driving communities towards trait convergence in order to survive the enhanced filters. By contrast, biotic filters tend to cause traits to diverge (Funk et al., 2008). For example, competition may cause traits to adjust resource acquisition strategies or to escape shared natural enemies and facilitate niche-based coexistence (Chesson, 2018).

Phylogenetics can improve understanding of competitive dynamics and aid with species selection for restoration (Hipp et al., 2015; Tucker et al., 2017). For example, species that are less phylogenetically related are more likely to coexist because they are less likely to share pests, diseases or similar vulnerabilities (Gilbert et al., 2012; Parker et al., 2015). Phylogenetic niche conservatism predicts that closely related species that have recently diverged in a particular climate tend to have a greater number of similar traits (trait convergence) than expected under Brownian evolution (Losos, 2008). If traits are conserved in plant communities (Kraft et al., 2008; Webb et al., 2002), this could help in identifying candidate species for restoration. For example, when species with certain traits are unavailable for restoration efforts, related species with similar traits could be used instead (Verdu et al., 2012).

California coastal prairies are a rare type of grassland that receive winter rainfall and summer water input from coastal fog (Baguskas et al., 2018). These grasslands are dominated by perennial bunchgrasses and annual forbs. Coastal prairies are one of the most diverse grassland types in North America but are threatened by land development, over-grazing and non-native species invasions (Ford & Hayes, 2007). Because restoration is mandated for disturbed coastal prairies under the California Coastal Act of 1976, identifying strategies that reduce planting mortality and improve native cover is crucial for achieving restoration goals.

We tested the role that leaf traits play in structuring plant communities and how mortality risk of planted native seedlings is affected by traits and phylogenetic relationships. We used a field drought experiment at a coastal grassland in Santa Cruz, California, USA to measure survival and growth of native species over a 4-year span. We quantified trait values for surviving individuals of the planted seedlings and for the 11 dominant extant species (2 native and 9 non-native) in years 3 and 4. We hypothesized that native species would have greater cover than non-natives in drought plots due to adaptations to low rainfall conditions that frequently occur in this Mediterranean climate region. We predicted that native plants that survived through the fourth year would have functional traits associated with drought tolerance (e.g. low SLA, high C:N, low N and high $\delta^{13}C$ (a proxy for water-use efficiency, WUE); Nobel, 2009). We also hypothesized that surviving individuals would be less phylogenetically related to nearby plants. Last, we anticipated that plant communities (composed of native and non-native species) would shift towards species with drought-adapted traits on drought plots compared to ambient rainfall treatments.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study was conducted at the University of California Younger Lagoon Reserve (YLR) in Santa Cruz, California (36.951918°N, 122.063116°W). The site is a highly degraded coastal prairie located on the first marine terrace adjacent to the Pacific Ocean. The area was historically utilized for cattle grazing between the 1820s and the 1920s, for row crop agriculture (using tillage) between the 1920s and the 1980s, and entered the UC Natural Reserve System in 1986. The site is dominated by non-native annual grasses and forbs, and is part of ongoing habitat restoration efforts (Holl et al., 2014).

The climate is Mediterranean with wet, cool (but not freezing) winters and hot, dry summers. This region receives water input 30%–40% of summer days from coastal fog (Baguskas et al., 2018). During the study period (2016–2019), the site experienced mean annual precipitation near the 100-year average with some interannual variability (796 mm, CV = 0.259; Figure 1), and was emerging from a major drought (Swain et al., 2018). Meteorological data were measured on the roof of a building <500 m from the field site (Campbell Scientific UT-30).

2.2 | Experimental design

2.2.1 | Drought treatment

We constructed drought (rain-out) shelters in August 2015 using the standardized protocol of the International Drought Experiment (IDE; Knapp et al., 2015). The structures exclude 60% of incoming rainfall to simulate a 1-in-100-year drought, based on 100 years of rainfall records for this area. Each shelter is 4 × 4 m and built with polycarbonate troughs, metal electrical conduit and wooden support frames. Shelters produce minimal impacts on microclimate and photosynthesis of well-watered potted plants (used as phytometers; Loik et al., 2019). We trenched and lined all drought plots with 6-mil plastic, 50-cm deep, to reduce lateral water flow and root growth. We included a 0.5-m buffer around each edge of the research plots allowing for a 3 × 3 m central research area. Five plots each were assigned to drought (60% rainfall exclusion) and ambient rainfall treatments. The reduction in soil moisture caused by drought plots was confirmed with two soil volumetric water sensors (METER Environmental GS1 VWC, Pullman, Washington, USA) placed in each plot type (Figure S1).

2.2.2 | Restoration plantings

We selected plant species (Table 1) from a list of those that likely occurred historically at Younger Lagoon Reserve. Seeds were collected in 2015 from local reference sites (<40 km from the field site) and were grown in the UCSC Jean H. Langenheim Greenhouses. Plots were mowed prior to planting to remove all standing biomass and then planted in January 2016. The 12 species were randomly assigned to standard planting positions on a grid for each plot. Non-native plants were removed from the all plots once early (January 2016) and once late in the growing season (April 2016) of the first year of the experiment, but not thereafter. Non-natives were removed by hand from wooden planks suspended above the plots to minimize soil compaction.

2.3 | Monitoring protocol

2.3.1 | Plant community composition

We assessed plant community composition in April of years 3 and 4. We randomly selected and permanently marked six locations within 0.25 × 1 m quadrats and estimated cover of all species to the nearest 5% for cover values >10%, and to the nearest 1% for cover values ≤10%. We estimated absolute cover at the ground level and at multiple leaf canopy heights to ensure all species were represented, so total cover may exceed 100%.

2.3.2 | Native seedling survival and biometrics

We quantified survival and growth-form-specific biometrics in April of years 1–4, and recorded survival using a right-censored method

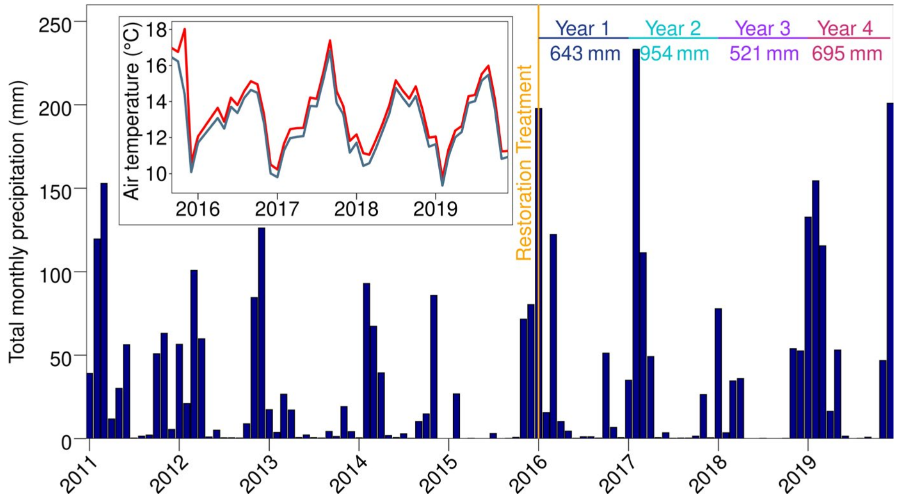

FIGURE 1 Monthly precipitation totals at the site from 2009 to 2019. Ticks on the *x*-axis correspond to January of each year. Precipitation totals on the top right of the figure are for the hydrologic year. Inset shows average monthly air temperature. Red = maximum temperature; Blue = minimum temperature

TABLE 1 Functional groups and sample sizes of the California native species planted in this experiment. Total per plot indicates the number of replicates of each species planted per plot

Scientific name	Family	Functional group	Total per plot
Achillea millefolium L.	Asteraceae	Perennial rhizomatous forb	8
Artemisia californica Less.	Asteraceae	Shrub	8
Bromus carinatus Hook. & Am.	Poaceae	Perennial bunchgrass	7
Diplacus aurantiacus Curtis	Phrymaceae	Shrub	8
Eschscholzia californica Cham.	Papaveraceae	Perennial rosette forb	7
Ericameria ericoides (Less.) Nutt.	Asteraceae	Shrub	8
Hosackia gracilis (Fabaceae) Benth.	Fabaceae	Annual N-fixer	4
Lupinus nanus (Fabaceae) Benth.	Fabaceae	Annual N-fixer	7
Lupinus variicolor (Fabaceae) Steud.	Fabaceae	Perennial N-fixer	7
Sidalcea malviflora (DC.) A. Gray	Malvaceae	Perennial rhizomatous forb	3
Sisyrinchium bellum S. Watson	Iridaceae	Perennial rosette forb	7
Stipa pulchra Hitchc.	Poaceae	Perennial bunchgrass	7

TABLE 2 Family and functional group of extant plants on which trait measurements were measured

Scientific name	Family	Functional group
Avena barbata Pott ex Link	Poaceae	Non-native annual grass
Baccharis glutinosa Pers.	Asteraceae	Native rhizomatous forb
Bromus hordeaceus L.	Poaceae	Non-native annual grass
Carduus pycnocephalus L.	Asteraceae	Non-native annual forb
Erigeron canadensis L.	Asteraceae	Native annual forb
Festuca bromoides L.	Poaceae	Non-native annual grass
Festuca perennis (L.) Columbus & J.P. Sm.	Poaceae	Non-native annual grass
Geranium dissectum L.	Geraniaceae	Non-native annual forb
Medicago polymorpha L.	Fabaceae	Non-native annual N-fixer
Raphanus sativus L.	Brassicaceae	Non-native annual forb
Sonchus asper (L.) Hill	Asteraceae	Non-native annual forb

(Harrington & Fleming, 1982). We grouped species by growth forms (Table 1): for bunchgrasses and rosette forbs we measured basal circumference; for woody or semi-woody shrubs and N-fixing forbs we measured stem diameter; for rhizomatous forbs we measured spreading distance. Growth-form-specific measurements were used to calculate growth rates between each sampling period (where i is the time step prior to j), then averaged across the entirety of the project (Equation 1).

$$\text{Growth Rate} = \left\{ \frac{\text{size}_j - \text{size}_i}{\text{time}_j - \text{time}_i} \right\}. \tag{1}$$

2.3.3 | Functional traits

We quantified the functional traits for surviving planted native species (Table 1) and for the 11 most abundant extant species (Table 2) in years 3 and 4. These accounted for 22 of 41 species and 70%–90% of overall cover in the plots. We collected leaves from each surviving planted individual (ranging from three to seven individuals per species). For dominant extant species we collected leaves from four individuals from each plot. *Hosackia gracilis* has no trait data because it had zero survivors after year 1 and relevant trait data were not available on the TRY Plant Trait Database.

Leaves from herbaceous basal species were removed distally from the centre; leaves from shrubs and herbaceous cauline species were taken distally two to three levels of leaves from the apical meristem. Leaves were refrigerated and scanned within 72 hr using an Epson photo scanner at 400 dpi. Leaves with overlapping leaflets were dissected to allow accurate measurements of area and perimeter. We collected two leaves from each plant to account for variability.

We selected drought-related traits (specific leaf area, leaf C:N ratios, δ^{13}C, leaf lobedness and growth rate) based on the trait literature, and measured them using standardized protocols (Cadotte et al., 2015; Pérez-Harguindeguy et al., 2016). Low SLA in plants can be related to drought resistance and is generally correlated with high investments in structural leaf defences and increased leaf life span (Pérez-Harguindeguy et al., 2016). Leaf area and perimeter were measured using ImageJ. Specific leaf area (SLA) was measured as the ratio of fresh leaf area by oven-dried mass. Increased leaf lobedness decreases the boundary layer by decreasing the effective length that wind travels at the leaf surface, which facilitates leaf cooling by conduction/convection instead of transpiration (Nobel, 2009). Leaf lobedness was calculated using

Equation 2, where the feret diameter is the largest leaf diameter if it was a circle, which is calculated by dividing the leaf perimeter by π (Cadotte et al., 2015).

$$\text{Leaf Lobedness} = \frac{\text{perimeter}}{\text{area}} \times \text{feret diameter}. \tag{2}$$

C:N ratios in leaves can predict survival during drought, as increased C:N is associated with greater energy investment in individual leaf development, higher leaf longevity (Nobel, 2009) and lower palatability (Loiola et al., 2012). Leaf δ^{13}C is highly correlated with intrinsic water-use efficiency (WUE; Nobel, 2009). Leaf elemental C:N and δ^{13}C content were quantified using mass spectrometry (ThermoFinnigan Delta Plus XP) after Dumas combustion (Carlo Erba 1108 Elemental Analyzer) at the UCSC Stable Isotope Laboratory.

Trait plasticity can enhance drought tolerance by allowing for rapid changes in certain traits within an individual's life span to match changing environments. We quantified plasticity for the traits described above with the relative distance plasticity index (rdpi; Equation 3; Valladares et al., 2006) for planted species that had more than 1 year of trait data (8 of 12 species). We were interested in the magnitude, and not direction of trait variability, so we used absolute values for rdpi. The rdpi ranges from zero (no plasticity) to one (maximum relative plasticity).

$$\text{Relative Distance Plasticity Index} = \frac{\text{mean}\,(\text{drought traits}) - \text{mean}\,(\text{control traits})}{\text{mean}\,(\text{control traits})}. \tag{3}$$

2.3.4 | Phylogenetic relationships

A dated phylogenetic tree containing all 41 species present at the site was created using PHYLOCOM BLADG (Figure S2; Webb et al., 2008). To determine relationships between the planted species, we used ages from Parker et al. (2015), who sequenced and aged California taxa at species and genus levels, and added them to the super tree R2G2_20140601. We calculated phylogenetic signal based on Blomberg's *K* (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999), using the PICANTE and APE packages in R (Kembel et al., 2010; Paradis et al., 2017). Phylogenetic signal was tested only for traits collected for both planted and extant species.

2.4 | Analyses

All analyses were conducted in R (v3.6.1; R Core Team, 2020). We quantified Pearson's correlation between traits with the CORRPLOT (Wei et al., 2017) and HMISC packages (Harrell, 2020). When traits were highly collinear (Variance Inflation Factor >3), we selected the more ecologically relevant trait based on the literature to use for analysis (Figure S3). In order to compare traits and phylogenetic distances (PD) at different scales of magnitude, we used a z-standardization for hazard models (Zhu et al., 2016). Traits from planted species (Table 1) were used for all analyses and traits from extant species (Table 2) were incorporated into community composition and phylogenetic signal analyses, but not hazard models.

2.4.1 | Plant community composition

We calculated Bray–Curtis dissimilarity indices and used non-metric dimensional scaling (NMDS) ordination to compare compositional differences between drought and ambient rainfall plots using the VEGAN package (Oksanen et al., 2018). Plant functional groups were determined using the Jepson eFlora (Jepson eFlora, 2020). We used a permutational analysis of variance (PERMANOVA) to test whether leaf traits and functional groups were associated with plant communities from different treatments (Laughlin et al., 2012). Community abundance-weighted trait values were calculated as the cross-product of species trait and species cover matrices (Laughlin et al., 2012). We used canonical correspondence analysis to determine the variance that could be explained by leaf traits and functional groups (Oksanen et al., 2018). We combined data collected in 2018 and 2019 because prior results from annual California grasslands were not necessarily auto-correlated between years (Zhu et al., 2016).

2.4.2 | Survival analysis

We used the SURVIVAL package in R to compare Kaplan–Meier survival estimates across treatments (Kaplan & Meier, 2013; Kassambara et al., 2020; Therneau, 2018). This nonparametric approach compares empirical estimates using log-rank tests against the null hypothesis that survival of all groups is equal (Harrington & Fleming, 1982). After examining empirical species survival at an individual level, we pooled all species to model Cox proportional hazard risk at a community level and compared risk for drought and ambient rainfall plots. Hazard risk (hereafter referred to as plant mortality risk) indicates the likelihood that a planted seedling will experience mortality. Trait values for this analysis were averaged for each planted species in a plot. The mortality risk associated with trait plasticity was modelled separately from trait values because only one rdpi value can be calculated per species. We analysed mortality for drought-only and ambient rainfall-only plantings separately since we hypothesized that drought-related traits would respond differentially across treatments.

2.4.3 | Phylogenetic analyses

We calculated the cumulative phylogenetic distance metrics at quantile zero (PD_0) and 50 (PD_{50}) to describe the distribution of evolutionary relationships within a community of species, and their relationships to plant survival and growth (Parker et al., 2015; Verdu et al., 2012). Phylogenetic distance at quantile zero (PD_0) represents the nearest neighbour distance. PD_{50} is a common measure of the median phylogenetic distance and often represents the maximum distance between groups of related genera or families (taxonomic scale depends on scale of phylogeny). Phylogenetic distances were abundance weighted with community plant cover.

3 | RESULTS

3.1 | Community composition and plant cover

Plant community composition differed in drought and ambient rainfall plots in both 2018 and 2019, and a significant amount of the variation was explained by abundance-weighted community trait values ($k = 3$, stress = 0.138; Figure 2). Leaf C:N (PERMANOVA; $R^2 = 0.20$, $p = 0.008$), and leaf lobedness ($R^2 = 0.12$, $p = 0.002$) explained the most variance in community composition. Leaf $\delta^{13}C$ (a measure of water-use efficiency (WUE)) and SLA were not significantly related to plant community composition. Canonical correspondence analysis (CCA) showed that abundance-weighted traits explained 48.2% of the variation in community composition between drought and ambient rainfall treatments.

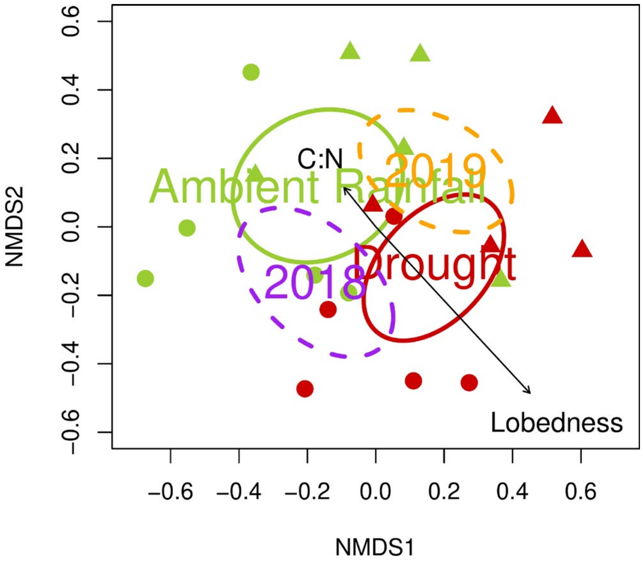

FIGURE 2 Non-metric multidimensional scaling ordination of plant community composition. Each point represents a plot (red = drought, green = ambient rainfall) monitored in 2018 (circle) or 2019 (triangle). Separation of ellipses indicates distinctive community composition between groups. Arrows represent CCA of the traits that explain variance between communities. The arrow direction indicates the highest values of a particular trait

Plant functional groups explained 68.8% of variation in plant community composition. Even though plant communities were dissimilar between 2018 and 2019 (Figure 2), we found that native rhizomatous forbs (PERMANOVA; $R^2 = 0.26$, $p \le 0.001$) and native perennial grasses ($R^2 = 0.07$, $p = 0.002$) had greater cover on drought plots compared to ambient rainfall plots. Ambient rainfall plots had greater cover of non-native annual grasses ($R^2 = 0.16$, $p \le 0.001$), non-native N-fixers ($R^2 = 0.08$, $p \le 0.001$) and shrubs (primarily *Baccharis pilularis*, $R^2 = 0.13$, $p \le 0.001$). Annual forbs did not vary between treatments.

Drought plots had higher native species cover, but lower non-native species cover and litter depth (Figure 3).

3.1.1 | Plant survival

Three planted native species (*Lupinus nanus*, *Ericameria ericoides* and *Sidalcea malviflora*) had higher survivorship on drought plots, while four others (*Eschscholzia californica*, *Hosackia gracilis*, *Sisyrinchium bellum* and *Stipa pulchra*) had higher survivorship in the ambient rainfall treatments in years 1 and 2 (Table S1). In year 3, planted natives had lower community-level mortality risk on drought plots ($p = 0.007$). The only species that had significantly higher survivorship on drought plots was *S. malviflora*, whereas *E. californica* showed the opposite trend. By year 4, community-level mortality risk for natives did not differ between treatments, and survivorship was similar for all species except *S. malviflora* (Figure 4; Table S1).

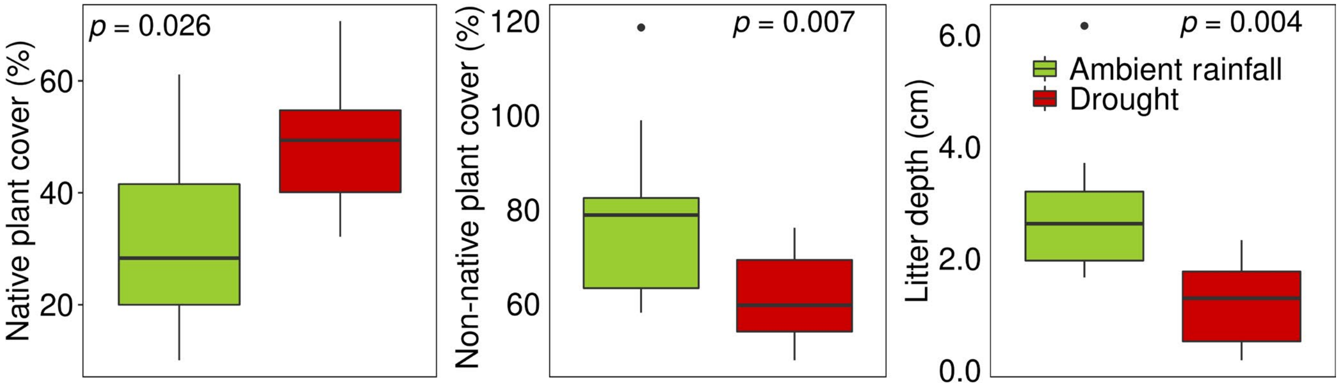

FIGURE 3 Native and non-native plant cover, and litter depth for 2018 and 2019 data combined. Boxes represent the interquartile range; the inner horizontal line represents the median. Lines extending out of the box represent the upper and lower quartiles. Points represent outliers

3.1.2 | Functional traits

Functional traits and phylogenetics explained a significant portion of the variation in mortality risk at a community-level in both years 3 and 4, when all species were pooled ($p_{global} \leq 0.001$, concordance = 0.710). The traits that explain mortality risk differed for plants on drought compared to ambient rainfall plots (Figure 5). For both treatments, increased growth rates were correlated with elevated plant mortality, whereas higher leaf lobedness was related to lowered mortality risk. Leaf $\delta^{13}C$ (WUE) was correlated with decreased plant mortality risk on drought ($p = 0.006$), but not ambient rainfall plots ($p = 0.290$). Increased leaf C:N was associated with a 25% reduction in mortality risk for native plantings in the ambient rainfall treatment only ($p \leq 0.001$).

Increased trait plasticity of leaf C:N and $\delta^{13}C$ was associated with increased mortality risk, whereas plasticity in SLA and lobedness was associated with decreased mortality risk ($p_{global} \leq 0.001$, concordance = 0.680; Figure 6). Variability in $\delta^{13}C$ and lobedness was negatively correlated (Pearson's $R = -0.64$, $p = 0.026$), as was the variability in SLA and growth rate (Pearson's $R = -0.61$, $p = 0.045$; Table 3).

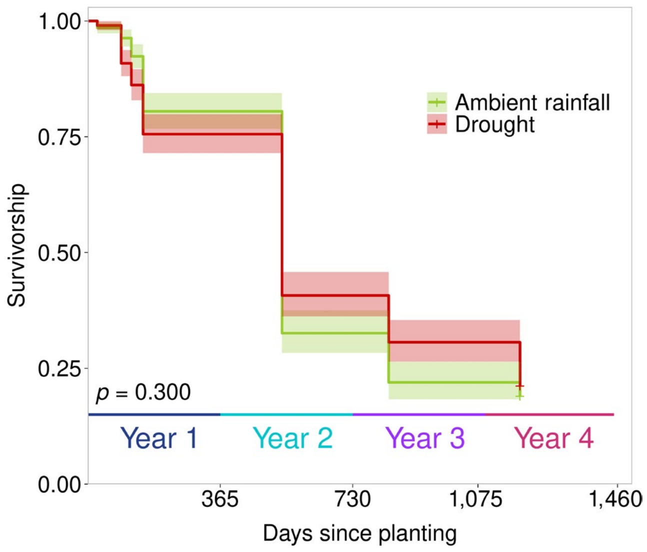

FIGURE 4 Kaplan–Meier survival estimates for all native species combined. Solid lines = average survivorship. Shaded areas = 95% confidence interval

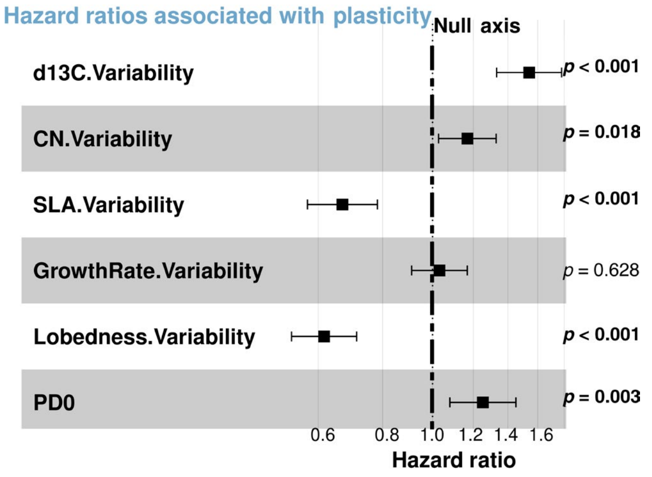

FIGURE 6 Cox proportional hazard models for native species relating mortality risk associated with relative distance plasticity index of leaf traits (Equation 3). PD_0 informs how trait rdpi may be related to phylogeny

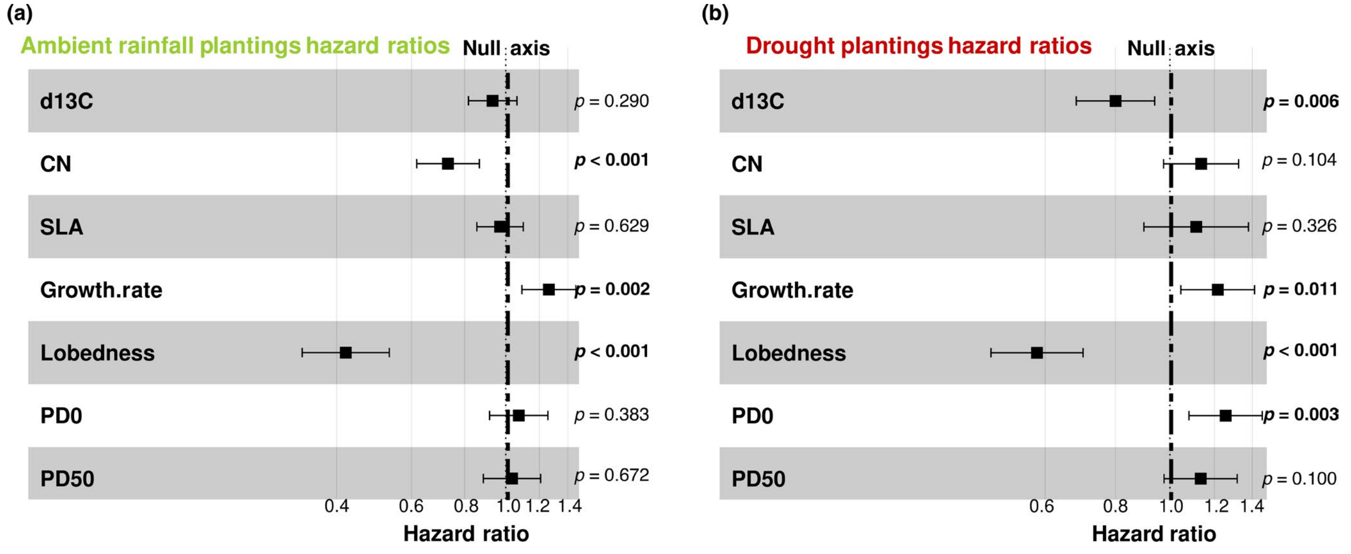

FIGURE 5 Cox proportional hazard models for native species cumulative to year 4 (2016–2019) on (a) ambient rainfall plots and (b) drought plots. Hazard ratio is a multiplier for mortality risk. Factors are significant when the confidence interval does not cross the null axis. The mortality risk decreases to the left and increases to the right of the null axis

TABLE 3 Relative distance plasticity index (rdpi) in relation to drought for species with traits collected in 2018 and 2019. Values range from 0 (no plasticity) to 1 (maximum relative plasticity)

Species	$\delta^{13}C$	C:N	Growth rate	Lobedness	SLA
Achillea millefolium	0.002	0.161	0.186	0.596	0.010
Artemisia californica	0.026	0.226	0.237	0.242	0.008
Bromus carinatus	0.014	0.020	0.346	0.119	0.056
Eschscholzia californica	0.027	0.007	0.026	0.169	0.395
Diplacus aurantiacus	0.039	0.080	0.002	0.020	0.105
Sisyrinchium bellum	0.015	0.255	0.122	0.254	0.194
Sidalcea malviflora	0.040	0.240	0.146	0.066	0.012
Stipa pulchra	0.006	0.067	0.070	0.122	0.078

TABLE 4 Blomberg's *K* and Pagel's λ; Values range from 0 (no phylogenetic signal) to 1 (high phylogenetic signal)

Functional trait	Blomberg's *K*	Pagel's λ
Specific leaf area	0.100	<0.001
Leaf lobedness	0.150	<0.001
$\delta^{13}C$	0.120	<0.001
Leaf C:N	0.380	0.830

3.1.3 | Phylogenetics

Although phylogenetics did not explain mortality risk of plants on ambient rainfall plots (Figure 5), plants that were less related to their nearest neighbour (higher PD_0) had higher mortality risk on drought plots ($p = 0.003$). Blomberg's *K* and Pagel's λ both indicated that leaf C:N is phylogenetically conserved or convergent, at least among these species (Table 4). Because increased relatedness at PD_0 was related to decreased mortality in drought plots, but PD_{50} had no effect on mortality, leaf C:N is likely convergent, not conserved.

4 | DISCUSSION

Several planted species had greater survivorship on drought compared to ambient rainfall plots in year 2 after experiencing their first dry season, a trend that persisted into year 3, but survival differences across treatments were minimal by year 4. Our results showing lower mortality risk of planted species (Table S1) and lower cover of non-native species (Figure 3) on drought compared to ambient rainfall plots before year 4, suggest that at early life stages planted native species could have been experiencing competitive release from non-native species. Native California grassland species are negatively affected by non-native species competition, particularly in the first year or two of growth (Buisson et al., 2006), and non-native species may respond more negatively to drought compared to natives (Valliere et al., 2019), which could have reduced non-native competition. Differences in survival across treatments may have faded by the fourth year as planted species increased in size, both above- and below-ground, and were better able to compete with non-native species (Corbin & D'Antonio, 2004; Seabloom et al., 2003). Furthermore, the area had recently experienced a major drought (2011–2014) at the start of the study, which may have resulted in lower propagule pressure from non-native annual grasses early in the experiment (Copeland et al., 2016). Annual grass cover and litter are often positively related, so lower litter depth in drought plots in years 3 and 4 suggests lower productivity of non-native annual grasses in prior years.

Although survivorship of planted individuals on drought and ambient rainfall plots was similar for nearly all species by the fourth growing season (Figure 4), overall species composition (i.e. cover of planted and unplanted species) still differed substantially (Figure 2). This difference was largely explained by the lower cover of unplanted, non-native annual grasses in drought plots, as noted above. In addition, native perennial grasses and rhizomatous forbs had greater cover in drought plots. These functional groups typically invest substantial resources below-ground that enable them to better withstand variable rainfall conditions (Kooyers, 2015).

Leaf lobedness, which explained a substantial amount of variation in both mortality of planted species and community cover, is not included within the 'trait handbook' (Pérez-Harguindeguy et al., 2016). Yet leaf shape and lobedness determine the contribution of boundary layer thickness to leaf energy balance, and affects plant water use in transpiration (Nobel, 2009). Unlike leaf WUE (via $\delta^{13}C$) and C:N, which are more expensive to measure, lobedness helped explain variance in plant cover and mortality risk regardless of treatment. Measuring lobedness does not require specialized equipment but can be labour intensive because dissection is needed for compound leaves that are divided into many fine leaflets, such as for *Achillea millefolium* and *E. californica*. We recommend that lobedness be further evaluated as a criterion for restoration plant selection in other abiotically driven ecosystems.

Across species in these communities, increased plasticity of measured physiological traits that we measured (i.e. C:N and WUE) were associated with increased mortality, yet decreased mortality was associated with more plastic morphological traits (i.e. leaf lobedness and SLA). Notably, SLA, which is commonly associated with drought tolerance, was not a significant driver of mortality risk, but *variability* in SLA reduced plant mortality risk on drought plots (Figure 6). In other words, the ability to adjust investment into individual leaves was key for survival of the planted native seedlings. Morphological traits last for a leaf lifetime and can provide important fitness value, thus plasticity in these traits can allow plants to better survive constantly changing environmental conditions (Valladares et al., 2006). Increased plasticity of physiological traits could be related to mortality risk because changes in physiological processes may occur faster than morphological changes, which could enhance plant stress. For example, a rapid decrease in WUE without a change in SLA could lead to increased plant water stress (Haworth et al., 2013). For some traits (e.g. C:N), increased plasticity may not provide adaptive survival value for resource conservative species. In this regard, we found a negative correlation between lobedness and WUE (Figure S3), which could indicate trade-offs between morphological and physiological traits in relation to drought.

Increased relatedness of planted species with neighbours was associated with lower mortality risk on drought, but not ambient rainfall plots. This could indicate that there are key traits related to drought survival that are convergent across native and non-native plants in this semi-arid coastal grassland. Our results are consistent with studies in other semi-arid grasslands (Loiola et al., 2012) and more general observations (Gilbert & Parker, 2016) that show water-use efficiency is often not phylogenetically conserved. Leaf C:N and WUE showed parallel trends with PD_0 in hazard models, but phylogenetic signal analysis found that only leaf C:N appeared to be phylogenetically convergent. This may make it possible to assume a similar range of C:N values for closely related taxa used for restoration in semi-arid grasslands (Verdu et al., 2012). Although we found no signal in any other trait we tested (Table 4), Larson et al. (2020) reported that SLA had a weak phylogenetic signal for native annual California coastal sage scrub seedlings. Even with strong a phylogenetic signal, however, low phylogenetic diversity in a particular plant community may make phylogeny less instructive for restoration planning (Funk & Wolf, 2016).

Our findings, along with studies from other ecosystems such as arid shrublands (Ackerly, 2004), tropical forests (Kraft et al., 2008) and other grasslands (Loiola et al., 2012), suggest that quantifying functional traits can help improve understanding species-specific survival and growth with increasingly variable climatic conditions. Trait plasticity can sometimes be more important than absolute trait values for survival and growth (Carmona et al., 2016). Therefore, restoration practitioners could select plants with traits suitable for particular climate scenarios or extant plant communities. In our case, this would likely include species with low above-ground growth rates and small leaf boundary layers (via leaf lobedness), like *A. millefolium* or *S. pulchra*. Moreover, phylogenetics has informed restoration practices by suggesting which species are most likely to survive surrounding competitors in tropical rainforests (Kraft et al., 2008), midwestern grasslands (Barak et al., 2017) and chaparral (Verdú et al., 2003). Similarly, our result that closely related species are more likely to survive in drought suggests that planting species from drought tolerant families can lead to higher plant establishment. We recognize that quantifying functional traits and phylogenetics is expensive, technically complex and labour intensive. Nonetheless, such information is becoming increasingly accessible through online databases such as TRY-TRAIT (Kattge et al., 2020), and could be helpful for selecting species for ecological restoration in a changing climate.

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AUTHORS' CONTRIBUTIONS

M.E.L. and K.D.H. conceived the experimental design; J.C.L., M.E.L. and K.D.H. conceived the research ideas; J.C.L. collected and analysed the data; J.C.L. led the writing of the manuscript with editorial contributions from M.E.L. and K.D.H. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Plant trait data were deposited in the TRY-TRAIT database. Data presented in this manuscript are all available on Pangaea Earth and Environmental Sciences Data Publisher https://doi.org/10.1594/PANGAEA.922919 (Luong et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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