

ARTICLE

Interacting ecological filters influence success and functional composition in restored plant communities over time

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Abstract

A trait-based community assembly framework has great potential to direct ecological restoration, but uncertainty over how traits and environmental factors interact to influence community composition over time limits the widespread application of this approach. In this study, we examined how the composition of seed mixes and environment (north- vs. south-facing slope aspect) influence functional composition and native plant cover over time in restored grassland and shrubland communities. Variation in native cover over 4 years was primarily driven by species mix, slope aspect, and a species mix by year interaction rather than an interaction between species mix and slope aspect as predicted. Although native cover was higher on wetter, north-facing slopes for most of the study, south-facing slopes achieved a similar cover (65%–70%) by year 4. While community-weighted mean (CWM) values generally became more resource conservative over time, we found shifts in particular traits across community types and habitats. For example, CWM for specific leaf area increased over time in grassland mixes. Belowground, CWM for root mass fraction increased while CWM for specific root length decreased across all seed mixes. Multivariate functional dispersion remained high in shrub-containing mixes throughout the study, which could enhance invasion resistance and recovery following disturbance. Functional diversity and species richness were initially higher in drier, south-facing slopes compared to north-facing slopes, but these metrics were similar across north- and south-facing slopes by the end of the 4-year study. Our finding that different combinations of traits were favored in south- and north-facing slopes and over time demonstrates that trait-based approaches can be used to identify good restoration candidate species and, ultimately, enhance native plant cover across community types and microhabitat. Changing the composition of planting mixes based on traits could be a useful strategy for restoration practitioners to match species to specific environmental conditions and may be more informative

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than using seed mixes based on growth form, as species within functional groups can vary tremendously in leaf and root traits.

KEYWORDS

California, community composition, functional traits, grassland, habitat filtering, photosynthesis, resource acquisition, resource conservation, root traits, shrubland, slope aspect

INTRODUCTION

As many plant communities experience mounting challenges associated with climate change, disturbance, and invasion, the need for an ecological framework to guide restoration efforts has never been greater. Community assembly theory holds great promise to enhance our understanding of differential species establishment and subsequent changes in community composition and function over time (Funk et al., 2008; Temperton et al., 2004), which are key concerns for restoration practitioners. A central tenet of assembly theory is that species traits interact with ecological filters, which are dispersal, abiotic, and biotic factors that sort species into a community (Weiher & Keddy, 1999). In the nearly two decades since a trait-based framework for restoration was proposed, functional traits have been increasingly used to direct ecological restoration (e.g., Carlucci et al., 2020; Hulvey & Aigner, 2014; Laughlin et al., 2018; Ostertag et al., 2015; Wainwright et al., 2018; Zirbel et al., 2017) but our understanding of how ecological filters interact to influence trait-based assembly and functional composition over time in restored communities is limited (Balazs et al., 2020; Funk, 2021).

Because ecological filters influence where species can occur based on their traits, traits can theoretically be used to overcome common restoration challenges associated with poor establishment and performance (Huang et al., 2016; Larson et al., 2015; Zirbel & Brudvig, 2020). A single restoration site may contain areas with varying soil depth, soil fertility, light environment, and water availability which can strongly influence species composition and diversity in restoration projects (Baer et al., 2020; Brudvig, 2011). Thus, species mixes could be modified within or across restoration sites to accommodate for variation in ecological filters. This might entail selecting a subset of species based on known distributions across environmental gradients (Kimball et al., 2017), or designing communities with a specific functional composition (Laughlin, 2014). For example, seed mixes could be constructed to achieve a community with mean trait values (community weighted mean, CWM) that optimize drought tolerance in dry sites (Laughlin et al., 2018) or

reduce light availability for invasive species (Schuster et al., 2018). Few experimental studies have addressed how species mixes with different functional trait compositions achieve restoration outcomes across diverse microhabitats (Kimball et al., 2016).

In addition to influencing plant performance, traits can also be used to achieve specific restoration outcomes. For example, managers may endeavor to restore or enhance wildlife habitat, erosion control, regulation of water flow, pollination, invasion resistance, or carbon sequestration (Bengtsson et al., 2019; Matzek et al., 2020; Schulte et al., 2017; Stanturf et al., 2014). Elucidating how functional traits and functional diversity metrics influence these desired community and ecosystem properties is an active area of research (Cadotte, 2017; Craven et al., 2018; van der Plas et al., 2020). As an example, functional trait composition could be used to restore communities that are resistant to invasion, which is a major impediment to restoration success in many systems (Wilsey, 2020). Results from studies that compare traits of co-occurring native and invasive species (e.g., Hulme & Bernard-Verdier, 2018; Lai et al., 2015; Matzek, 2012) suggest that restoration practitioners should favor native species with traits that promote high rates of resource acquisition, to better compete with fast-growing invasive species. Alternatively, a functionally diverse native community (high functional diversity or dispersion, FDis) may repel invaders by increasing the probability of including highly competitive species or through complementary resource use by multiple species (Fargione & Tilman, 2005). These trait-based approaches may lead managers away from seed mixes that represent historical community composition and, instead, toward a subset of native species that have desired traits for particular restoration outcomes (Hobbs et al., 2011). Studies have shown that functional metrics (e.g., CWM, FDis) are more predictable and less variable than community composition as restoration success metrics (Laughlin et al., 2017) and may be more practical in highly diverse systems (Brancalion & Holl, 2016).

Grasslands and shrublands, two common plant communities in Mediterranean-climate ecosystems, have experienced a substantial decline in spatial extent and function (e.g., native cover, habitat quality) over the past century due to land use change and urbanization

(Mooney & Zavaleta, 2016). While California grasslands contain a mix of annual and perennial forbs and grasses, coastal sage scrub contains drought-deciduous and evergreen woody shrubs and a diverse understory of grasses and forbs. The coastal mountains, where these two vegetation types occur, house a variety of habitats including exposed hilltops, flat meadows, and riparian areas. South-facing aspects tend to be warmer and drier than north-facing aspects and support different abundances of species (Ackerly et al., 2002; Kimball et al., 2017; Luong et al., 2019). In these communities, managers grapple with several impediments to restoration; namely, invasion by non-native annual forbs and grasses, and low establishment and persistence in dry microsites and during drought years (Kimball et al., 2015; Tamura et al., 2017). Thus, managers may consider tailoring seed mixes to address these different stressors. In the case of water limitation, managers may optimize for traits associated with stress tolerance or “resource conservation,” including species with longer-lived, robust tissues and lower rates of carbon assimilation and growth (Harrison & LaForgia, 2019; Laughlin et al., 2018). To enhance invasion resistance, managers may optimize functional diversity or trait values associated with “resource acquisition,” including species with less-robust structures that maximize resource uptake, carbon assimilation, and growth (Funk & Wolf, 2016; Hulme & Bernard-Verdier, 2018; Kunstler et al., 2016; Yannelli et al., 2020), although this may make communities more vulnerable to stress (Koziol et al., 2012). Ongoing restoration efforts in these California plant communities provide an excellent opportunity to explore how traits associated with different species mixes influence restoration outcomes across diverse microhabitats.

In this study, we conducted a large-scale (0.24 km²) restoration experiment using different species mixes based on growth form (e.g., forb, grass, shrub) for grassland and coastal sage scrub communities across two environments (north- and south-facing aspect). In the grassland plots, we used three species mixes (forb only, grass only, forb + grass) and in the coastal sage scrub plots we used four mixes (forb only, grass only, shrub only, forb + grass + shrub). We measured a suite of leaf and root traits on 19 species included in the restoration experiment as well as two commonly-used restoration outcomes (percent native cover and species richness) over 4 years. Our study addressed two questions. First, how do a biotic filter (species mix) and an abiotic filter (north versus south-facing aspect) interact to influence species cover, richness, and functional composition of the restored native plant community? On wetter, north-facing slopes, we expected that grassland mixes, dominated by resource-acquisitive annual and perennial forbs and grasses, would have higher

initial establishment success and cover. On drier, south-facing aspects, we expected to see higher cover in shrub-containing species mixes, which have traits aligned with resource conservation. Furthermore, we predicted that south-facing slopes would display less functional dispersion due to habitat filtering. Second, do these patterns hold over time? Plots were surveyed every year for 4 years after planting. We expected that CWM values would become more resource conservative over time in plots dominated by perennial species as older plants often show trait values aligned with resource conservation (e.g., Dayrell et al., 2018; Funk et al., 2021), which may be advantageous in this semi-arid system. While species mixes with resource acquisition strategies might initially have high cover, we expected higher cover in plots containing shrubs by the end of the 4-year experiment. We also expected that plots generated from more diverse species mixes would maintain high functional dispersion over time.

METHODS

Study site

Our study took place within the Loma Ridge Ecological Restoration Experiment (Kimball et al., 2015, 2017), which was established in 2009 by the Irvine Ranch Conservancy. The 0.24 km² (60-acre) restoration site is in a small watershed within the foothills of the Santa Ana Mountains in southern California, USA (33.7647° N 117.7382° W). Mean annual precipitation from the nearest long-term weather station (Tustin Irvine Ranch Station, OC Public Works no. 61), is 32.4 cm (July to June, 1897–2013). Rainfall for the 2010–2011, 2011–2012, 2012–2013, 2013–2014, 2014–2015, and 2015–2016 growing seasons (October to May) was 59.23, 21.74, 15.37, 12.39, 21.23, and 17.65 cm, respectively, with most years being drier than the historical average. The site experienced varying levels of cattle grazing from at least the mid-1800s until 2002. Fire is a natural disturbance in this system, with two fires occurring within the last 50 years (1967 and 2007). Prior to restoration, the area had ~99% cover of non-native species including annual grasses (primarily *Bromus diandrus*, *Brachypodium distachyon*, and *Avena fatua*) and forbs (almost all *Brassica nigra*).

Within the watershed, we established plots on one south-facing and one north-facing slope in a block design (Appendix S1). The south-facing slope included two grassland (GL) and two coastal sage scrub (CSS) blocks while the north-facing slope included three GL and three CSS blocks. While an ideal study design would have included multiple north- and south-facing slopes, our restored areas were large and encompassed a large range

of soil and radiation heterogeneity (Appendix S1). Within each GL or CSS block, strips containing our different species mixes (see below) were planted perpendicular to the slope. The number of strips that were initially planted in 2011 is not known but included several hundred strips. Grassland strips were 3 m wide and 10 m long and CSS strips were 2.1 m wide and 10 m long. CSS strips were separated by gaps of similar size (2.1×10 m). These gaps were cleared of weeds for 2 years (similar to the treatment plots described below) then left bare, with potential colonization of natives from the adjacent strips. Plots were sampled among these strips with an effort to capture the range of spatial variation at the site.

In 2009, the Irvine Ranch Conservancy initiated 2 years of weed control followed by seeding in the

2011–2012 growing season (Kimball et al., 2015). Strips were seeded with different mixes of native species based on their functional groups (Table 1). We used seven seed mixes, including four in the coastal sage scrub community (grasses, forbs, shrubs, and all combined), and three in the grassland community (grasses, forbs, and both combined). Target species and abundances within each seed mix were selected based on species composition in remnant patches of native vegetation at the site. An adaptive process, described in Kimball and Lulow (2019), was used to determine seeding rates needed to achieve desired abundances, which accounts for species differences in germination rate. Seeding rate (seed per square meter) varied across mix types in an additive fashion (i.e., mixes that combined groups had higher seed numbers per plot, Table 1). Seeds

TABLE 1 Species assignments and seeding rates in pure live seed (PLS) per square meter for different planting mixes used in the Loma Ridge restoration project.

Community	Seed mix	Species	Life form	PLS per square meter
Coastal sage scrub	Forb	<i>Deinandra fasciculata</i>	Biennial	171
		<i>Eschscholzia californica</i>	Biennial	147
		<i>Eucrypta chrysanthemifolia</i>	Annual	60
		<i>Malacothrix saxatilis</i>	Biennial	52
		<i>Phacelia cicutaria</i>	Annual	113
		<i>Salvia columbariae</i>	Annual	66
	Grass	<i>Elymus condensatus</i>	Perennial	125
		<i>Stipa pulchra</i>	Perennial	81
	Shrub	<i>Acmispon glaber</i>	Perennial	126
		<i>Artemisia californica</i>	Perennial	1375
		<i>Encelia californica</i>	Perennial	222
		<i>Eriogonum fasciculatum</i>	Perennial	370
		<i>Mirabilis californica</i>	Short-lived perennial	9
Grassland	Forb	<i>Salvia apiana</i>	Perennial	111
		<i>Acmispon strigosus</i>	Annual	196
		<i>Artemisia californica</i>	Perennial	330
		<i>Castilleja exserta</i>	Annual	360
		<i>Cirsium occidentale</i>	Short-lived perennial	17
		<i>Deinandra fasciculata</i>	Biennial	171
		<i>Grindelia camporum</i>	Annual	185
		<i>Isocoma menziesii</i>	Perennial	96
		<i>Lupinus microcarpus</i>	Annual	6
		<i>Lupinus succulentus</i>	Annual	12
		<i>Plantago erecta</i>	Annual	63
	Grass	<i>Stipa pulchra</i>	Perennial	327

Note: For the coastal sage scrub community, four seed mixes were used with varying initial species richness and seeding rate: forb (6 species, 609 seed m^{-2}), grass (2 species, 207 seed m^{-2}), shrub (6 species, 2213 seed m^{-2}), and all species (14 species, 3028 seed m^{-2}). For the grassland community, three seed mixes were used with varying initial species richness and seeding rate: forb (10 species, 1435 seed m^{-2}), grass (1 species, 327 seed m^{-2}), and all species (11 species, 1762 seed m^{-2}).

were added with a drill seeder in grassland plots and an imprint seeder in coastal sage scrub plots (Tamura et al., 2017). Each strip contained one mix type, and these were alternated within GL and CSS blocks (Appendix S1).

Following seeding, non-native species were controlled every 4 (high maintenance frequency), 6 (medium maintenance frequency), or 8 (low maintenance frequency) weeks by early-season hand pulling and late-season wicking with an herbicide. To compare the efficiency of selective herbicide applied over the canopy of all plants to that of spot weeding with broad-spectrum herbicide, half of the strips seeded with only grasses, forbs, or shrubs received a broad-spectrum, concentrated glyphosate (17%) applied as spot treatment with a weed wiper sponge applicator (The Red Weeder, Smucker Manufacturing, Inc.), and the other half received a selective herbicide. Broadleaf (Element 4 [triclopyr], 0.24 mL/m²) or grass-specific (Fusilade II [Fluazifop], 0.18 mL/m²) herbicide treatments were applied as a mist with a backpack sprayer to grass and shrub/forb-seeded plots, respectively.

In March 2013 and 2016, three soil moisture readings were taken at 10 cm in each plot with a handheld soil moisture probe (Hydrosense II, Campbell Scientific). All plots were gradually invaded to varying degrees by non-native forb species and these results will be reported in another paper.

Community composition measurements

We collected community composition data each May in four growing seasons: 2011–2012, 2012–2013, 2013–2014, and 2014–2015. For each species mix, we surveyed 2.1 × 10 m plots representing each combination of seed mix, herbicide method, and maintenance frequency (Appendix S1). Community composition was surveyed using a point intercept method as an estimate of species cover as described in Kimball et al. (2017). Due to the rectangular plot shape, we sampled four point-intercepts along a meter stick, centered horizontally across the plot, in six locations down the plot with 1 m separation (totaling 24 sample points). A “hit” was recorded if the plant was determined to be alive sometime that growing season. We recorded all native (including non-sown species) and non-native species, but our cover, richness, and functional composition metrics include only the sown native species. To account for the variation of slope and management treatment, there was a large sample size for each seed mix and aspect combination (Appendix S1).

Seedling density (seedlings per square meter) was measured in a subset of plots (630 of 4562) 4 to 6 weeks following seed addition to assess germination success across seed mix treatments. Despite a large range in seeding rate

(207 seed m⁻² in CSS grass to 3028 seed m⁻² in CSS all, Table 1), there were surprisingly few differences in the density of native seedlings that established in the 4 to 6 weeks post-seeding across species mixes (Appendix S2). We found no statistical difference in numbers of native seedlings among CSS mixes. The GL “all” species mix (seeded with grasses + forbs) had higher numbers of native seedlings than the CSS grass only and CSS shrub only mixes.

Trait measurements

Functional traits were measured on mature individuals at the Irvine Ranch Conservancy’s native seed farm (33°44′29.54″ N, 117°44′5.31″ W), located roughly 5 km away from the restoration site. At the farm, species are planted in monoculture rows, grown in well-tilled, homogenous soil, and irrigated as needed during establishment and dry periods to ensure survival. Over two growing seasons (2013–2014, 2014–2015), we collected data on 22 native species that were used in the West Loma Ecological Restoration Experiment (Table 1).

Area-based photosynthetic rate (A_{area}) and stomatal conductance (gs) measures were collected on five replicate plants per species with a LI-6400 portable photosynthesis system (LI-COR). Conditions in the chamber were 400 $\mu\text{L L}^{-1}$ CO₂, 1800 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$, relative humidity of 50%–65%, and block temperature of 25°C. Intrinsic water-use efficiency (WUE) was calculated as A/gs . Following physiology measures, leaves were harvested to determine specific leaf area (SLA, square centimeter per gram) and leaf N concentration. Leaves were scanned with a LI-3100 leaf area meter, dried at 65°C, and ground to pass a 40-mesh screen. Leaf N concentration was determined with a CHN elemental analyzer (Costech 4010 elemental combustion system). Seed mass was averaged over 20–30 seeds per species.

Root traits were collected on young seedlings grown in pots at Chapman University (Orange, CA), using seeds collected from the seed farm (i.e., same genetic material as physiology traits). Plants were grown in 2.42 L pots containing a 1:1:1 mixture of sand, perlite, and vermiculite and a nutrient solution designed to match the nutrient content typical for coastal sage scrub soils as described in Larson and Funk (2016). After 28 to 56 days, before plants became pot-bound, plants were harvested and separated into above and belowground components. Roots were carefully hand-washed and scanned on a dual-light flatbed scanner (Epson Perfection V700 Photo Scanner; Epson America Inc.) to determine total root length, average root diameter, and total root lengths within 0.1-mm-diameter classes (WinRHIZO; Regent Instruments Inc.). Roots and aboveground biomass were

dried at 60°C for at least 2 days and weighed. Root mass fraction (RMF) was calculated as the ratio of root mass to whole plant mass. Specific root length (SRL, meter per gram) was calculated as root length divided by root mass. Root tissue density (RTD; gram per cubic centimeter) was calculated as root mass divided by root volume.

Data analysis

We calculated CWM trait values and functional dispersion, FDis, for each seed mix and plot using the “FD” package in R (Laliberte et al., 2014). CWM trait values were calculated for each trait as the sum of species-level traits weighted by the species relative abundances. FDis was calculated as the mean distance of each species, weighted by relative abundances, to the centroid of all species in a plot for each trait (Laliberte & Legendre, 2010). Multivariate FDis was calculated as the mean distance of each species within multidimensional trait space to the weighted centroid of all species present in the plot. The 22 species we surveyed for trait data were the most dominant native species in the plots. We recorded an additional 30 species in the plots, but only 10 of these occurred in more than five plots (of 4562) and collectively these species averaged less than 0.1% cover across plots and years.

We used ANOVA to analyze average soil moisture values in each plot to understand how the abiotic environment changed with seed mix, slope aspect, and the interaction between the two factors in 2013 and 2016. In 2013, plots were measured once during the growing season. In 2016, plots were each measured twice during the growing season (February, March). Seed mix, aspect, and date were added as fixed effects in each model.

To partition the variance of trait CWM, trait FDis, multivariate FDis, and restoration outcomes (percent native cover, native species richness) by seed mix, slope aspect, herbicide treatment, and year, we constructed a multilevel Bayesian model for each response variable as follows:

$$R_i = \beta_0 + \beta_{\text{seed}[i]} + \beta_{\text{aspect}[i]} + \beta_{\text{herbicide}[i]} + \beta_{\text{year}[i]} \\ + \beta_{\text{seed} \times \text{aspect}[i]} + \beta_{\text{seed} \times \text{herbicide}[i]} + \beta_{\text{seed} \times \text{year}[i]} \\ + \beta_{\text{aspect} \times \text{herbicide}[i]} + \beta_{\text{aspect} \times \text{year}[i]} + \beta_{\text{herbicide} \times \text{year}[i]} \\ + \beta_{\text{seed} \times \text{aspect} \times \text{herbicide}[i]} + \beta_{\text{seed} \times \text{aspect} \times \text{year}[i]} \\ + \beta_{\text{seed} \times \text{herbicide} \times \text{year}[i]} + \beta_{\text{aspect} \times \text{herbicide} \times \text{year}[i]} \\ + \beta_{\text{seed} \times \text{aspect} \times \text{herbicide} \times \text{year}[i]} + \epsilon_i,$$

where i indexes each measurement, R is the response variable (CWM, FDis, restoration outcomes), β_0 is the intercept term, and the other β terms are group-level effects of seed mix, aspect, herbicide treatment, year, and all interactions. Response and predictor variables were z-scaled globally across plots. Given that scaling, we used the

default priors set by the “brms” package. Estimated standard deviation of effects as described in Qian and Shen (2007) are reported from this model (Appendix S3). Bayesian analyses were conducted using the “brms” package in R (Bürkner, 2017; Carpenter et al., 2017).

We created a visual summary of CWM, FDis, multivariate FDis, and restoration outcomes across different seed mixes and slope aspects over time by constructing a linear model with seed mix, slope aspect, herbicide treatment, year, and all interactions. The estimated marginal effects of seed mix, aspect, and year and their 95% confidence intervals (CIs) are reported from this model using the “ggeffects” R package (Lüdtke, 2018).

RESULTS

In 2013, soil moisture varied significantly across the growing season, but was not influenced by seed mix or aspect. A significant interaction between seed mix and date in 2013 reflected the fact that CSS plots were sampled over a larger number of days (16 days) than GL plots (8 days), and there was more variation in soil moisture across this time period due to rainfall. In 2016, soil moisture varied by seed mix and date, but there was also a significant interaction between aspect and date. In February 2016, when soil moisture was measured shortly after a rain event, north-facing aspects had higher soil moisture (17.8%) than south-facing aspects (15.3%; Appendix S4).

Selective versus broad-spectrum herbicide treatment explained some of the variation for several functional metrics (Appendix S3); however, there was large uncertainty associated with the herbicide main effect. We suspect that variation in the effectiveness of the different herbicides across seed mixes may have contributed to this uncertainty. Glyphosate was more effective than broadleaf-specific herbicide in the grass mixes, and marginally more effective than the grass-specific herbicide in the forb mixes (Appendix S2). Despite this, there were no significant herbicide by seed mix interaction terms (Appendix S3). We also observed no interactions between herbicide treatment and slope aspect or year.

Native species cover was generally higher in the CSS mixes and on north-facing slopes (Figure 1, Appendix S3). There was a strong interaction between year and seed mix reflecting an increase in native cover over time for the CSS shrub containing mix and small decreases in cover over time for several of the grass containing species mixes. While native cover was initially lower in the drier, south-facing slopes compared to wetter north-facing slopes, this increased over time (slope by time interaction, Figure 1, Appendix S3). Patterns of native cover cannot be linked to different seeding rates



FIGURE 1 Marginal effects plots of native cover (percentage), native species richness (number of species), and multivariate functional dispersion (FDis) for each species mix and aspect (north and south facing slopes) across the 4 years of the study. Dots on the left side of the diagram represent average FDis values and species richness of the initial seed mix. Bands are 95% CI. Seed mixes and slope aspects with non-overlapping bands are significantly different. CSS, coastal sage scrub; GL, grassland.

between seed mixes (Table 1) as the GL all seed mix had higher initial establishment (4–6 weeks) than the CSS grass only and CSS shrub only mixes (Appendix S2).

Seed mix was the strongest driver of trait CWM variation across plots and years (Figures 2 and 3, Appendix S3). Across plant communities, grassland seed mix treatments generally displayed more acquisitive leaf traits (A_{area}) than CSS communities. However, CWM values for root tissue density and root mass fraction were higher in grassland mixes relative to shrub-containing mixes (Figures 2 and 3) while specific root length was lower. By the end of the 4-year experiment, the shrub-containing plots had lower SLA and leaf N than other seed mixes. The grassland (GL all, GL forb, GL grass) and CSS grass plots generally had higher CWM seed mass than other CSS mixes, although this trait was variable within community types. Community traits became more resource conservative (lower A_{area} , SLA, specific root length, leaf N and higher

WUE, root diameter, root mass fraction) over time, but this was largely driven by the CSS seed mixes (seed mix by year interaction).

Across seed mixes, plots occurring on south-facing aspects had CWM values aligned with resource conservation (lower A_{area} , leaf N, SLA, specific root length; higher WUE, root diameter, root mass fraction, root tissue density; Figures 2 and 3). However, many of these patterns were stronger in later years of the experiment and in some communities as evidenced by sizable interaction effects among seed mix and year, or aspect and year (Appendix S3). In these cases, community-level traits were more conservative on drier, south-facing aspects for CSS mixes in year 4.

Species mix explained most of the variation in multivariate FDis with some variance explained by interactions between mix, year, and aspect (Appendix S3). Overall, we found higher functional dispersion in

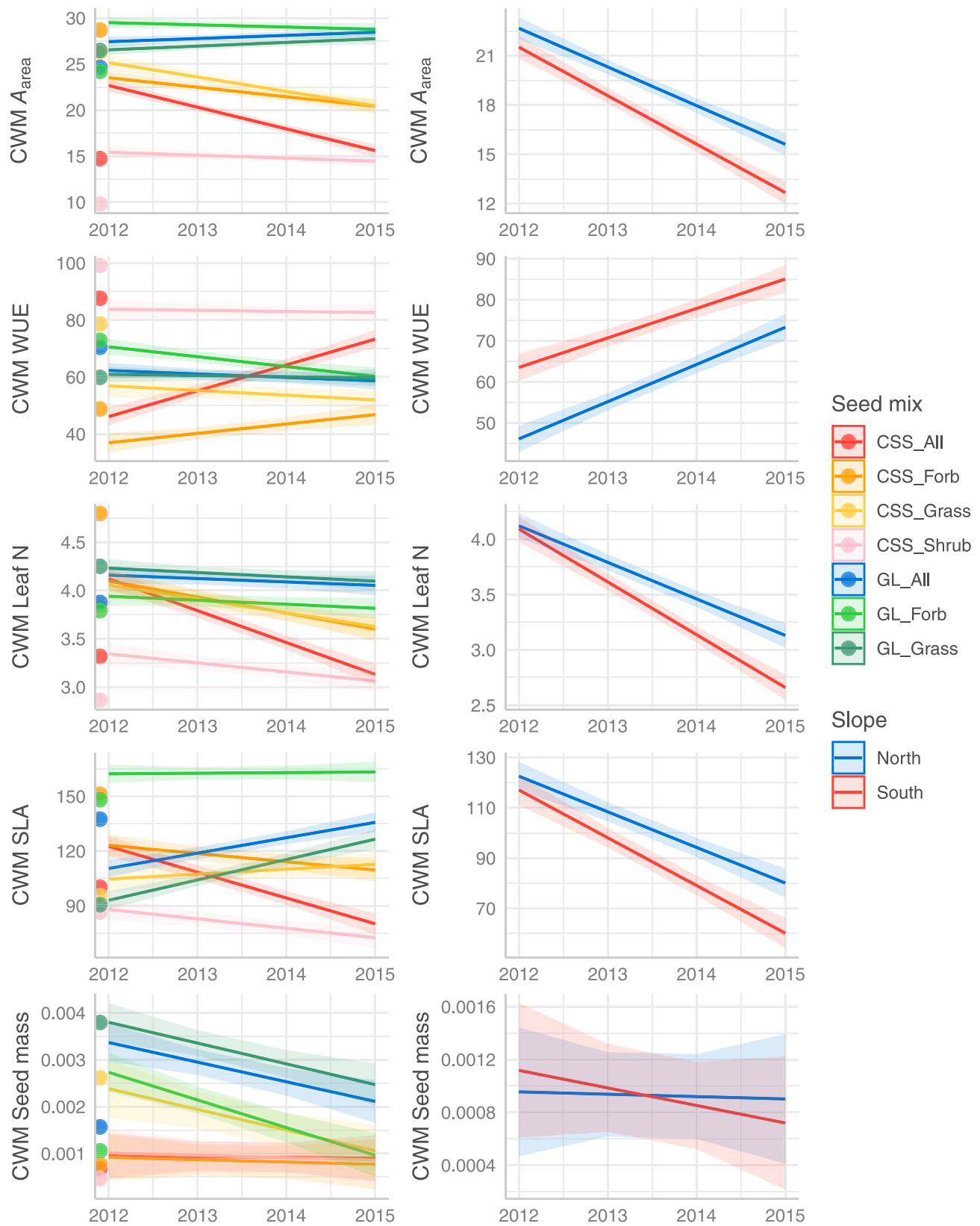


FIGURE 2 Marginal effects plots of community weighted means (CWM) for aboveground traits for each seed mix and aspect (north and south facing slopes) across the 4 years of the study. Dots on the left side of the diagram represent average CWM values of the initial seed mix. Bands are 95% CI. Seed mixes and slope aspects with non-overlapping bands are significantly different. Traits are A_{area} (area-based photosynthetic rate, micromole CO₂ per square meters per second), WUE (water-use efficiency, micromole CO₂ per mole H₂O), leaf nitrogen (percentage), SLA (specific leaf area, square centimeters per gram), seed mass (grams). CSS, coastal sage scrub; GL, grassland.

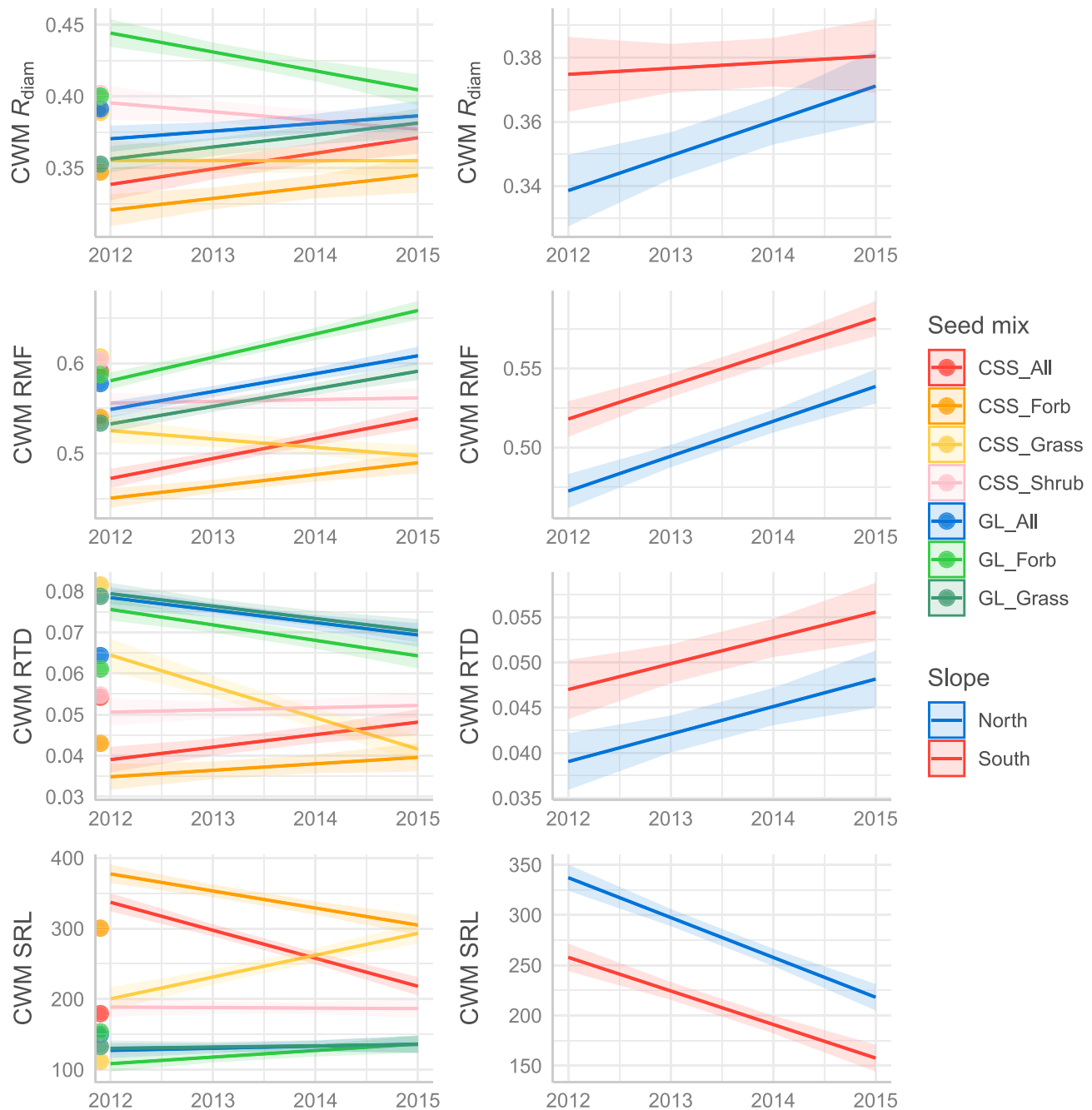


FIGURE 3 Marginal effects plots of community weighted means (CWM) for belowground traits for each seed mix and aspect (north and south facing slopes) across the 4 years of the study. Dots on the left side of the diagram represent average CWM values of the initial seed mix. Bands are 95% CI. Seed mixes and slope aspects with non-overlapping bands are significantly different. Traits are R_{diam} (root diameter, millimeters), RMF (root mass fraction, gram root per gram plant), RTD (root tissue density, grams per cubic centimeters), SRL (specific root length, meters per gram). CSS, coastal sage scrub; GL, grassland.

shrub-containing CSS mixes in most years and initially higher dispersion in drier, south-facing slopes compared to north-facing slopes (Figure 1). Multivariate functional dispersion was initially much larger in seed mixes containing forbs than those without forbs (grass and shrub only), but the shrub-containing communities had higher multivariate FDis by the end of the 4-year experiment.

Species mix, aspect, and year all explained some degree of variation in FDis of individual traits (Figures 4 and 5, Appendix S3). Functional dispersion for many traits was higher in the CSS mixes or all plots, and it remained high for shrub-containing mixes for several traits (A_{area} , WUE, leaf N, SLA, root diameter, specific root length) across the 4-year experiment (Figures 4 and 5). For many traits, the observed FDis was much lower (less than half) than that

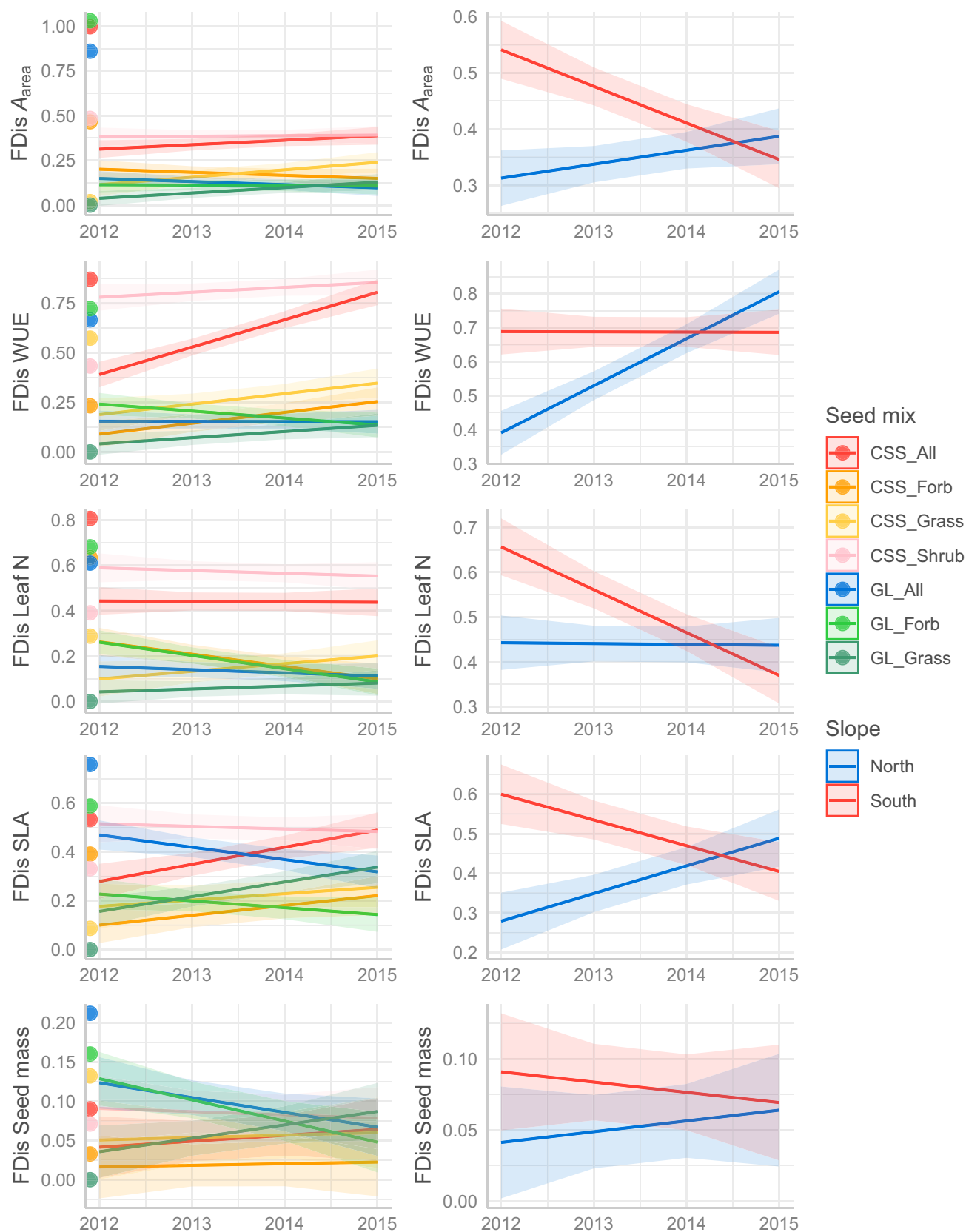


FIGURE 4 Marginal effects plots of functional dispersion (FDis) for aboveground traits for each seed mix and aspect (north and south facing slopes) across the 4 years of the study. Dots on the left side of the diagram represent average FDis values of the initial seed mix. Bands are 95% CI. Seed mixes and slope aspects with non-overlapping bands are significantly different. CSS, coastal sage scrub; GL, grassland; SLA, specific leaf area; WUE, water-use efficiency.

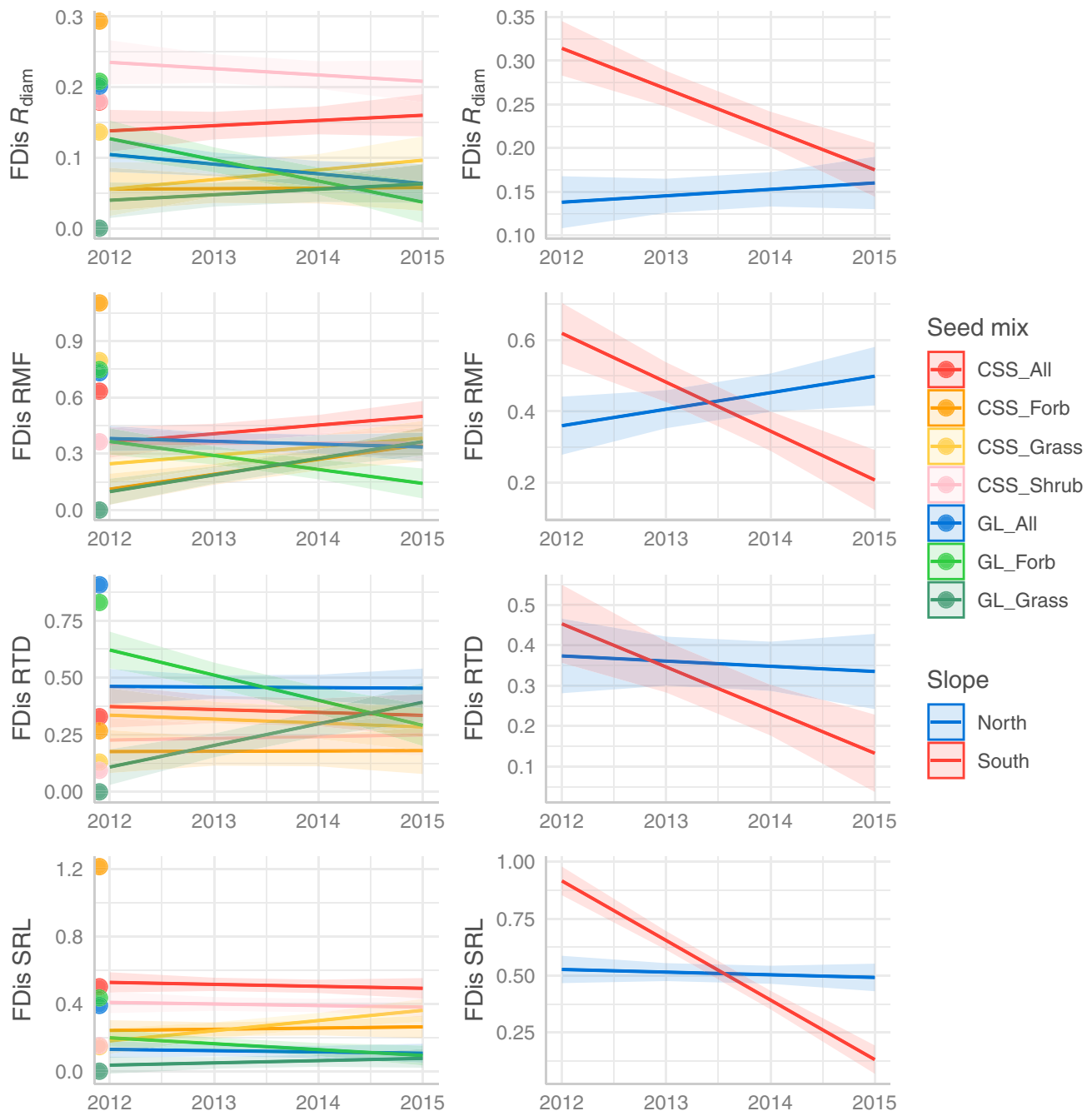


FIGURE 5 Marginal effects plots of functional dispersion (FDis) for belowground traits for each seed mix and aspect (north and south facing slopes) across the 4 years of the study. Dots on the left side of the diagram represent average FDis values of the initial seed mix. Bands are 95% CI. Seed mixes and slope aspects with non-overlapping bands are significantly different. CSS, coastal sage scrub; GL, grassland; RMF, root mass fraction; RTD, root tissue density; SRL, specific root length.

contained in the initial seed mix (e.g., A_{area} , root mass fraction). As with CWM seed mass, FDis seed mass was variable among seed mixes (Figure 4). A significant interaction between aspect and year was present for many traits, reflecting a decrease in FDis of many traits (A_{area} , leaf N, SLA, root diameter, root mass fraction, specific root length, root tissue density) in the south-facing aspects over time (Figures 4 and 5).

DISCUSSION

For many restoration projects, altering the planting palette may be one of the best ways to achieve desired outcomes as environmental characteristics (e.g., soil depth or quality, aspect, soil moisture) can be difficult or impossible to modify. Trait-based approaches, such as those used here, may help match species mix to environmental

conditions or desired outcomes and, thus, improve the predictability of restoration outcomes across different habitats and community types (Brudvig et al., 2017; Suding, 2011). Collectively, our results demonstrate that species mix (biotic filter) and slope aspect (abiotic filter) together influence the functional composition of restored communities and that functional metrics of restored communities can change over relatively short timeframes.

Traits and cover are driven by seed mix, aspect, and time since restoration

Our main prediction was that seed mixes dominated by species with resource-acquisitive trait values (e.g., grass and forb mixes) would have higher cover in moister north-facing slopes, while species mixes with resource-conservative trait values would fare better in drier south-facing slopes. This prediction was not supported; variation in native cover was primarily driven by seed mix, aspect, and a seed mix by year interaction rather than a seed mix by slope interaction. While native cover was indeed higher on north-facing slopes for most of the study, south-facing slopes exhibited a similar native cover (65%–70%) by year 4. Across years, native cover ultimately was highest in shrub-containing mixes. Many traits have been linked to early (i.e., 1–4 years) restoration success including colonization ability, competitive ability, and vegetative reproduction (e.g., Pywell et al., 2003) and restoration projects often include these types of species to quickly achieve restoration targets (Holl et al., 2022). However, we found no evidence that planting resource-acquisitive species is necessary to achieve high cover, and that cover can increase in stressful habitats over time.

Including 4 years of data allowed us to examine directional changes associated with community assembly processes, and our expectation that CWM values would become more resource conservative over time was partially supported. CWM values for several traits became more resource conservative (lower A_{area} , SLA, leaf N specific root length; higher WUE, root diameter, root mass fraction, root tissue density) but this was largely driven by changing values in CSS plots (all, forb, shrub). Two factors may explain this CWM trait shift. First, this could be evidence for a strengthening abiotic filter (low water availability) over time. Mean annual precipitation for all 4 years (21.74, 15.37, 12.39, and 21.23 cm) was below the historic average of 32.4 cm for this site and low water conditions may have benefited drought-resilient species with resource-conservative traits. Second, the CSS all and CSS shrub mixes contain long-lived shrubs and studies have demonstrated greater resource conservation in older

and larger plants (Dayrell et al., 2018; Funk et al., 2021; Mason et al., 2013). Changing functional metrics observed in our CSS communities suggests that the restoration of woody-dominated systems may be more dynamic than herbaceous communities.

The shifts in CWM values of particular traits over time provide insight into which species (based on their traits) would be good restoration candidates in this system. In this way, the trait-based approach provides more information than studies considering different seed mixes that are not informed by traits. One interesting pattern we observed for aboveground traits was high or increasing CWM SLA in grassland mixes but decreasing CWM SLA over time in CSS mixes. Thus, when restoring grassland systems, one might select species with “fast” leaf economic strategies, while this is less important in CSS mixes. Belowground, we found that CWM SRL was low or decreased over time in all seed mixes. Instead, CWM root mass fraction increased over time (except for shrub-containing mixes), suggesting that species that allocate preferentially to roots may perform better in these systems than ones with more acquisitive roots (high SRL). Community types displayed a lot of variation in seed mass, and seed mass was one of the few traits that did not show strong patterns over time or across south- and north-facing slopes. Others studies have found no association between environmental variables and seed mass (Bruehlheide et al., 2018), and Guerin et al. (2022) postulate that this may result from phylogenetic conservatism in seed size and the coexistence of species with very different seed sizes (Westoby et al., 2002).

Functional diversity

We predicted that plots generated from more diverse species mixes would maintain high functional dispersion over time; however, the patterns we observed were more nuanced. Multivariate functional dispersion remained high in shrub-containing mixes throughout the 4-year study, but was generally lower than expected for other mixes, particularly the GL all and both forb-containing mixes. High functional diversity in the shrub-containing CSS mixes was driven by several leaf (A_{area} , WUE, leaf N) and root traits (SRL, R_{diam}), suggesting that varying the identity of species in planting mixes can result in communities that diversify resource acquisition and use above and belowground. Because functional diversity may enhance invasion resistance (Byun et al., 2020; Hooper & Dukes, 2010; Kaul & Wilsey, 2020; Selmants et al., 2012) and recovery following disturbance or stress (Tilman & Downing, 1994; van Ruijven & Berendse, 2010), these results are encouraging for restoration of shrub-dominated systems. However, in diverse communities with

ample dispersal, such as grasslands, species mix may not be the principal driver of long-term community patterns following restoration. Trait convergence in restored grasslands has been found over time as available niches eventually get filled, while species composition stays the same or even diverges (Helsen et al., 2012).

We also expected that plots on south-facing aspects would show lower functional diversity due to habitat filtering. We found mixed support for this hypothesis; multivariate FDis and individual trait FDis metrics were generally lower for south-facing than north-facing aspects by the end of the 4-year experiment but started out (year 1) higher. Relatively high species richness on south-facing aspects in year one may be explained by differential establishment across mixes and aspects resulting from low rainfall during the experiment; all years of the experiment were drier (38%–65% of normal) than usual. These low precipitation levels may have favored relatively drought-tolerant CSS mixes on south-facing aspects, leading to greater establishment success and species richness. The relatively wetter, north-facing slopes may have experienced early dominance by a few species resulting in lower species richness and functional diversity. These results support findings that restoration success can vary across years and microhabitats, with planting year weather conditions (particularly precipitation) having long-term effects on community assembly (Werner et al., 2020) and community composition of restored sites (Groves et al., 2020; Stuble et al., 2017).

Implications for management

Altering the planting palette may be an effective way for restoration practitioners to match species to environmental conditions and improve the predictability of restoration outcomes across different habitats and community types. We found that different combinations of traits were favored in south- and north-facing slopes and that the trait values changed over time as the communities developed. This suggests that species identity, and trait-based models in particular (e.g., Laughlin et al., 2018), are credible tools that managers can use to direct ecological restoration across and within restoration sites. Species within functional groups (i.e., forbs, grasses) can vary tremendously in leaf and root traits (e.g., Freschet et al., 2017; Larson et al., 2016), suggesting that a trait-based approach is more informative than using seed mixes based on growth form.

While some studies have found that species composition can stabilize a few years following restoration (Henry et al., 2019; Stuble et al., 2017), our study demonstrates that functional composition can change across microhabitats

and over time, at least in our woody-dominated communities. For example, more stressful microhabitats, such as our south-facing slopes, may require more management due to lower initial cover (i.e., weeding) early in a restoration project, but planting species with resource conservative traits may lead to increased cover over time. Variable patterns across microhabitats and years suggest a targeted management approach for managers and also highlight the need for long-term monitoring of restoration projects. Collaborations between academics and practitioners could resolve some of the logistical and financial hurdles to collecting these important data (Funk et al., 2020).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Funk, 2023) are available in Zenodo: <https://doi.org/10.5281/zenodo.8023454>.

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REFERENCES

- Ackerly, D., C. Knight, S. Weiss, K. Barton, and K. Starmer. 2002. "Leaf Size, Specific Leaf Area and Microhabitat Distribution of Chaparral Woody Plants: Contrasting Patterns in Species Level and Community Level Analyses." *Oecologia* 130: 449–57.
- Baer, S. G., T. Adams, D. A. Scott, J. M. Blair, and S. L. Collins. 2020. "Soil Heterogeneity Increases Plant Diversity after 20 Years of Manipulation during Grassland Restoration." *Ecological Applications* 30: e02014.
- Balazs, K. R., A. T. Kramer, S. M. Munson, N. Talkington, S. Still, and B. J. Butterfield. 2020. "The Right Trait in the Right Place at the Right Time: Matching Traits to Environment Improves Restoration Outcomes." *Ecological Applications* 30: e02110.

- Bengtsson, J., J. M. Bullock, B. Egoh, C. Everson, T. Everson, T. O'Connor, P. J. O'Farrell, H. G. Smith, and R. Lindborg. 2019. "Grasslands—More Important for Ecosystem Services than you Might Think." *Ecosphere* 10: e02582.
- Brancalion, P. H. S., and K. D. Holl. 2016. "Functional Composition Trajectory: A Resolution to the Debate between Suganuma, Durigan, and Reid." *Restoration Ecology* 24: 1–3.
- Brudvig, L. A. 2011. "The Restoration of Biodiversity: Where Has Research Been and where Does it Need to Go?" *American Journal of Botany* 98: 549–58.
- Brudvig, L. A., R. S. Barak, J. T. Bauer, T. T. Caughlin, D. C. Laughlin, L. Larios, J. W. Matthews, K. L. Stuble, N. E. Turley, and C. R. Zirbel. 2017. "Interpreting Variation to Advance Predictive Restoration Science." *Journal of Applied Ecology* 54: 1018–27.
- Brulheide, H., J. Dengler, O. Purschke, J. Lenoir, B. Jiménez-Alfaro, S. M. Hennekens, Z. Botta-Dukát, et al. 2018. "Global Trait–Environment Relationships of Plant Communities." *Nature Ecology & Evolution* 2: 1906–17.
- Bürkner, P. C. 2017. "brms: An R Package for Bayesian Multilevel Models Using Stan." *Journal of Statistical Software* 80: 1–28.
- Byun, C., S. de Blois, and J. Brisson. 2020. "Restoring Functionally Diverse Communities Enhances Invasion Resistance in a Freshwater Wetland." *Journal of Ecology* 108: 2485–98.
- Cadotte, M. W. 2017. "Functional Traits Explain Ecosystem Function through Opposing Mechanisms." *Ecology Letters* 20: 989–96.
- Carlucci, M. B., P. H. S. Brancalion, R. R. Rodrigues, R. Loyola, and M. V. Cianciaruso. 2020. "Functional Traits and Ecosystem Services in Ecological Restoration." *Restoration Ecology* 28: 1372–83. <https://doi.org/10.1111/rec.13279>.
- Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. "Stan: A Probabilistic Programming Language." *Journal of Statistical Software* 76: 1–32.
- Craven, D., N. Eisenhauer, W. D. Pearse, Y. Hautier, F. Isbell, C. Roscher, M. Bahn, et al. 2018. "Multiple Facets of Biodiversity Drive the Diversity–Stability Relationship." *Nature Ecology & Evolution* 2: 1579–87.
- Dayrell, R. L. C., A. J. Arruda, S. Pierce, D. Negreiros, P. B. Meyer, H. Lambers, and F. A. O. Silveira. 2018. "Ontogenetic Shifts in Plant Ecological Strategies." *Functional Ecology* 32: 2730–41.
- Fargione, J. E., and D. Tilman. 2005. "Diversity Decreases Invasion Via both Sampling and Complementarity Effects." *Ecology Letters* 8: 604–11.
- Freschet, G. T., O. J. Valverde-Barrantes, C. M. Tucker, J. M. Craine, M. L. McCormack, C. Violle, F. Fort, et al. 2017. "Climate, Soil and Plant Functional Types as Drivers of Global Fine-Root Trait Variation." *Journal of Ecology* 105: 1182–96.
- Funk, J. L. 2021. "Revising the Trait-Based Filtering Framework to Include Interacting Filters: Lessons from Grassland Restoration." *Journal of Ecology* 109: 3466–72.
- Funk, J. L. 2023. "jlfunk/funk-et-al-2023-ecol-apps: Initial Release of Funk et al. (2023) Ecol Apps Data and Code (v1.0.0)." Zenodo. <https://doi.org/10.5281/zenodo.8023454>.
- Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. "Restoration through Reassembly: Plant Traits and Invasion Resistance." *Trends in Ecology and Evolution* 23: 695–703.
- Funk, J. L., J. E. Larson, and G. Vose. 2021. "Leaf Traits and Performance Vary with Plant Age and Water Availability in *Artemisia californica*." *Annals of Botany* 127: 495–503.
- Funk, J. L., I. M. Parker, V. Matzek, S. L. Flory, E. T. Aschehoug, C. M. D'Antonio, W. Dawson, D. M. Thomson, and J. Valliere. 2020. "Keys to Enhancing the Value of Invasion Ecology Research for Management." *Biological Invasions* 22: 2431–45.
- Funk, J. L., and A. A. Wolf. 2016. "Testing the Trait-Based Community Framework: Do Functional Traits Predict Competitive Outcomes?" *Ecology* 97: 2206–11.
- Groves, A. M., J. T. Bauer, and L. A. Brudvig. 2020. "Lasting Signature of Planting Year Weather on Restored Grasslands." *Scientific Reports* 10: 5953.
- Guerin, G. R., R. V. Gallagher, I. J. Wright, S. C. Andrew, D. S. Falster, E. Wenk, S. E. M. Munroe, A. J. Lowe, and B. Sparrow. 2022. "Environmental Associations of Abundance-Weighted Functional Traits in Australian Plant Communities." *Basic and Applied Ecology* 58: 98–109.
- Harrison, S., and M. LaForgia. 2019. "Seedling Traits Predict Drought-Induced Mortality Linked to Diversity Loss." *Proceedings of the National Academy of Sciences* 116: 5576–81.
- Helsen, K., M. Hermy, and O. Honnay. 2012. "Trait but Not Species Convergence during Plant Community Assembly in Restored Semi-Natural Grasslands." *Oikos* 121: 2121–30.
- Henry, H. A. L., S. D. Murphy, M. L. McFarlane, H. Barna, K. Dunning, A. Hood, and J. C. Crosthwaite. 2019. "Evaluating Outcomes of Restoration Ecology Projects on Limited Budgets: Assessment of Variation in Sampling Intensity and Sampling Frequency for Four Habitat Types." *Restoration Ecology* 27: 457–65.
- Hobbs, R. J., L. M. Hallett, P. R. Ehrlich, and H. A. Mooney. 2011. "Intervention Ecology: Applying Ecological Science in the Twenty-First Century." *Bioscience* 61: 442–50.
- Holl, K. D., J. C. Luong, and P. H. S. Brancalion. 2022. "Overcoming Biotic Homogenization in Ecological Restoration." *Trends in Ecology & Evolution* 37: 777–88.
- Hooper, D. U., and J. S. Dukes. 2010. "Functional Composition Controls Invasion Success in a California Serpentine Grassland." *Journal of Ecology* 98: 764–77.
- Huang, Z., S. Liu, K. J. Bradford, T. E. Huxman, and D. L. Venable. 2016. "The Contribution of Germination Functional Traits to Population Dynamics of a Desert Plant Community." *Ecology* 97: 250–61.
- Hulme, P. E., and M. Bernard-Verdier. 2018. "Comparing Traits of Native and Alien Plants: Can we Do Better?" *Functional Ecology* 32: 117–25.
- Hulvey, K. B., and P. A. Aigner. 2014. "Using Filter-Based Community Assembly Models to Improve Restoration Outcomes." *Journal of Applied Ecology* 51: 997–1005.
- Kaul, A. D., and B. J. Wilsey. 2020. "Exotic Species Drive Patterns of Plant Species Diversity in 93 Restored Tallgrass Prairies." *Ecological Applications* 31: e2252.
- Kimball, S., J. L. Funk, D. R. Sandquist, and J. R. Ehleringer. 2016. "Ecophysiological Considerations for Restoration." In *Foundations of Restoration Ecology*, 2nd ed., edited by M. A. Palmer, J. B. Zedler, and D. A. Falk. Washington, DC: Island Press.
- Kimball, S., M. Lulow, Q. Sorenson, K. Balazs, Y.-C. Fang, S. J. Davis, M. O'Connell, and T. E. Huxman. 2015. "Cost-Effective Ecological Restoration." *Restoration Ecology* 23: 800–10.
- Kimball, S., and M. E. Lulow. 2019. "Adaptive management in variable environments." *Plant Ecology* 220: 171–82.
- Kimball, S., M. E. Lulow, K. R. Balazs, and T. E. Huxman. 2017. "Predicting Drought Tolerance from Slope Aspect Preference

- in Restored Plant Communities." *Ecology and Evolution* 7: 3123–31.
- Kozioł, L., L. H. Rieseberg, N. Kane, and J. D. Bever. 2012. "Reduced Drought Tolerance during Domestication and the Evolution of Weediness Results from Tolerance-Growth Trade-Offs." *Evolution* 66: 3803–14.
- Kunstler, G., D. Falster, D. A. Coomes, F. Hui, R. M. Kooyman, D. C. Laughlin, L. Poorter, et al. 2016. "Plant Functional Traits Have Globally Consistent Effects on Competition." *Nature* 529: 204–7.
- Lai, H. R., M. M. Mayfield, J. M. Gay-des-combes, T. Spiegelberger, and J. M. Dwyer. 2015. "Distinct Invasion Strategies Operating within a Natural Annual Plant System." *Ecology Letters* 18: 336–46.
- Laliberte, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91: 299–305.
- Laliberte, E., P. Legendre, and B. Shipley. 2014. "FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology." R Package Version 1.0-12. <https://cran.r-project.org/web/packages/FD/>.
- Larson, J. E., and J. L. Funk. 2016. "Seedling Root Responses to Soil Moisture and the Identification of a Belowground Trait Spectrum across Three Growth Forms." *New Phytologist* 210: 827–38.
- Larson, J. E., R. L. Sheley, S. P. Hardegree, P. S. Doescher, and J. J. James. 2015. "Seed and Seedling Traits Affecting Critical Life Stage Transitions and Recruitment Outcomes in Dryland Grasses." *Journal of Applied Ecology* 52: 199–209.
- Larson, J. E., R. L. Sheley, S. P. Hardegree, P. S. Doescher, and J. J. James. 2016. "Do Key Dimensions of Seed and Seedling Functional Trait Variation Capture Variation in Recruitment Probability?" *Oecologia* 181: 39–53.
- Laughlin, D. C. 2014. "Applying Trait-Based Models to Achieve Functional Targets for Theory-Driven Ecological Restoration." *Ecology Letters* 17: 771–84.
- Laughlin, D. C., L. Chalmandrier, C. Joshi, M. Renton, J. M. Dwyer, and J. L. Funk. 2018. "Generating Species Assemblages for Restoration and Experimentation: A New Method that Can Simultaneously Converge on Average Trait Values and Maximize Functional Diversity." *Methods in Ecology and Evolution* 9: 1764–71.
- Laughlin, D. C., R. T. Strahan, M. M. Moore, P. Z. Fulé, D. W. Huffman, and W. W. Covington. 2017. "The Hierarchy of Predictability in Ecological Restoration: Are Vegetation Structure and Functional Diversity more Predictable than Community Composition?" *Journal of Applied Ecology* 54: 1058–69.
- Lüdecke, D. 2018. "ggeffects: Tidy Data Frames of Marginal Effects from Regression Models." *Journal of Open Source Software* 3: 772.
- Luong, J. C., M. P. Nolan, and L. C. Stratton. 2019. "The Importance of Pilot Studies and Understanding Microhabitat Requirements when Reintroducing Endemic Plants during Coastal Dune Restoration." *Journal of Coastal Conservation* 23: 553–62.
- Mason, C. M., S. E. McGaughey, and L. A. Donovan. 2013. "Ontogeny Strongly and Differentially Alters Leaf Economic and Other Key Traits in Three Diverse *Helianthus* Species." *Journal of Experimental Botany* 64: 4089–99.
- Matzek, V. 2012. "Trait Values, Not Trait Plasticity, Best Explain Invasive species' Performance in a Changing Environment." *PLoS One* 7: e48821. <https://doi.org/10.1371/journal.pone.0048821>.
- Matzek, V., D. Lewis, A. O'Geen, M. Lennox, S. D. Hogan, S. T. Feirer, V. Eviner, and K. W. Tate. 2020. "Increases in Soil and Woody Biomass Carbon Stocks as a Result of Rangeland Riparian Restoration." *Carbon Balance and Management* 15: 16.
- Mooney, H. A., and E. S. Zavaleta. 2016. *Ecosystems of California*. Oakland, CA: University of California Press.
- Ostertag, R., L. Warman, S. Cordell, and P. M. Vitousek. 2015. "Using Plant Functional Traits to Restore Hawaiian Rainforest." *Journal of Applied Ecology* 52: 805–9.
- Pywell, R. F., J. M. Bullock, D. B. Roy, L. Warman, K. J. Walker, and P. Rothery. 2003. "Plant Traits as Predictors of Performance in Ecological Restoration." *Journal of Applied Ecology* 40: 65–77.
- Qian, S. S., and Z. Shen. 2007. "Ecological Applications of Multilevel Analysis of Variance." *Ecology* 88: 2489–95.
- Schulte, L. A., J. Niemi, M. J. Helmers, M. Liebman, J. G. Arbuckle, D. E. James, R. K. Kolka, et al. 2017. "Prairie Strips Improve Biodiversity and the Delivery of Multiple Ecosystem Services from Corn–Soybean Croplands." *Proceedings of the National Academy of Sciences* 114: 11247–52.
- Schuster, M. J., P. D. Wragg, and P. B. Reich. 2018. "Using Revegetation to Suppress Invasive Plants in Grasslands and Forests." *Journal of Applied Ecology* 55: 2362–73.
- Selmants, P. C., E. S. Zavaleta, J. R. Pasari, and D. L. Hernandez. 2012. "Realistic Plant Species Losses Reduce Invasion Resistance in a California Serpentine Grassland." *Journal of Ecology* 100: 723–31.
- Stanturf, J. A., B. J. Palik, and R. K. Dumroese. 2014. "Contemporary Forest Restoration: A Review Emphasizing Function." *Forest Ecology and Management* 331: 292–323.
- Stuble, K. L., S. E. Fick, and T. P. Young. 2017. "Every Restoration is Unique: Testing Year Effects and Site Effects as Drivers of Initial Restoration Trajectories." *Journal of Applied Ecology* 54: 1051–7.
- Suding, K. N. 2011. "Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead." *Annual Review of Ecology, Evolution, and Systematics* 42: 465–87.
- Tamura, N., M. E. Lulow, C. A. Halsch, M. R. Major, K. R. Balazs, P. Austin, T. E. Huxman, and S. Kimball. 2017. "Effectiveness of Seed Sowing Techniques for Sloped Restoration Sites." *Restoration Ecology* 25: 942–52.
- Temperton, V. M., R. J. Hobbs, T. Nuttle, and S. Halle. 2004. *Assembly Rules and Restoration Ecology*. Washington, DC: Island Press.
- Tilman, D., and J. A. Downing. 1994. "Biodiversity and Stability in Grasslands." *Nature* 367: 363–5.
- van der Plas, F., T. Schröder-Georgi, A. Weigelt, K. Barry, S. Meyer, A. Alzate, R. L. Barnard, et al. 2020. "Plant Traits Alone Are Poor Predictors of Ecosystem Properties and Long-Term Ecosystem Functioning." *Nature Ecology & Evolution* 4: 1602–11.
- van Ruijven, J., and F. Berendse. 2010. "Diversity Enhances Community Recovery, but Not Resistance, after Drought." *Journal of Ecology* 98: 81–6.
- Wainwright, C. E., T. L. Staples, L. S. Charles, T. C. Flanagan, H. R. Lai, X. Loy, V. A. Reynolds, and M. M. Mayfield. 2018. "Links between Community Ecology Theory and Ecological Restoration Are on the Rise." *Journal of Applied Ecology* 55: 570–81.

- Weiher, E., and P. Keddy. 1999. "Assembly Rules as General Constraints on Community Composition." In *Ecological Assembly Rules: Perspectives, Advances, Retreats*, edited by E. Weiher and P. Keddy, 251–71. Cambridge: Cambridge University Press.
- Werner, C. M., K. L. Stuble, A. M. Groves, and T. P. Young. 2020. "Year Effects: Interannual Variation as a Driver of Community Assembly Dynamics." *Ecology* 101: e03104.
- Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. "Plant Ecological Strategies: Some Leading Dimensions of Variation between Species." *Annual Review of Ecology and Systematics* 33: 125–59.
- Wilsey, B. 2020. "Restoration in the Face of Changing Climate: Importance of Persistence, Priority Effects, and Species Diversity." *Restoration Ecology* 29: e13132. <https://doi.org/10.1111/rec.13132>.
- Yannelli, F. A., C. MacLaren, and J. Kollmann. 2020. "Moving Away from Limiting Similarity during Restoration: Timing of Arrival and Native Biomass Are Better Proxies of Invasion Suppression in Grassland Communities." *Frontiers in Ecology and Evolution* 8: 238.
- Zirbel, C. R., T. Bassett, E. Grman, and L. A. Brudvig. 2017. "Plant Functional Traits and Environmental Conditions Shape

- Community Assembly and Ecosystem Functioning during Restoration." *Journal of Applied Ecology* 54: 1070–9.
- Zirbel, C. R., and L. A. Brudvig. 2020. "Trait–Environment Interactions Affect Plant Establishment Success during Restoration." *Ecology* 101: e02971.

SUPPORTING INFORMATION

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

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