Received: 2 May 2022 | Accepted: 13 October 2022

DOI: 10.1111/1365-2745.14027

Journal of Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Functional assembly of grassland plant species in native communities in Spain and recipient communities in California

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Funding information
"la Caixa" Foundation, Grant/Award Number: LCF/BQ/DI17/11620012; European Fund for Regional Development (FEDER, UE), Grant/Award Number: EXARBIN RTI2018-093504-B-I00; European Union's Horizon 2020 research and innovation programme / Marie Skłodowska-Curie grant agreement, Grant/Award Number: 713673; Ministerio de Ciencia e Innovación, Grant/Award Number: RTI2018-093504-B-I00

Handling Editor: Anne Kempel

Abstract

1. A major aim in invasion ecology is to understand the role of exotic species in plant communities. Whereas most studies have explored the traits of exotic species in the context of the introduced community, functional comparisons of entire assemblages of species in their native and introduced communities have rarely been analysed. Taking advantage of the unidirectional invasion of plant species of European origin (i.e. colonizers) into California, this study aims to investigate the relative importance of plant traits, environmental factors and invasion status in biological invasions.
2. We compared the functional structure (i.e. trait composition and diversity) along resource availability gradients in recipient and native Mediterranean grassland communities in California and Spain, respectively. Traits were related to resource use in above-ground and below-ground organs and reproductive strategy. We also investigated how niche differences vary along environmental gradients between coexisting colonizer and native species assemblages within communities.
3. There were clear differences in the functional structure of Mediterranean grassland communities between regions, which were associated with the resource availability gradient. Paradoxically, the most acquisitive communities occurred in resource-poor sites, highlighting that rapid acquisition and use of resources permit species to cope with environmental stress through stress avoidance. In Spain, colonizer species had greater specific leaf area than non-colonizers. Yet, differences between colonizer and non-colonizer species in Spain for other traits were mostly absent and did not change along the gradient. This might be a result of the greater native species richness as a consequence of the agricultural practices that have taken place in Europe for millennia and reflect that the entire species pool of grasslands is adapted to agricultural landscapes. In

comparison, in California, colonizer species were more acquisitive in their use of resources than natives under favourable conditions, but functionally converged in resource-limited sites.

4. *Synthesis*. These results underscore that the importance of niche differences between native and colonizer species as a community assembly mechanism is strongly subjected to the influence of habitat filtering. Trait comparisons are context dependent, and a correct interpretation of filtering processes in community assembly requires a regional perspective.

KEYWORDS
biological invasions, community assembly, functional diversity, functional traits, Mediterranean biome

1 | INTRODUCTION

A current challenge in the study of biological invasions is to understand the role of exotic species in community assembly to prevent them from threatening native species and changing the functional structure of the recipient communities (Gallien & Carboni, 2017; Hulme & Bernard-Verdier, 2018). To address this question, most studies have compared the functional differences between exotic species and native species in communities of the introduced range (Funk et al., 2017; Galán Díaz, de la Riva, Funk, & Vilà, 2021; Henn et al., 2019). These approaches are useful to suggest differences in the use of resources which might drive invasion success or impact. However, to disentangle differences between species identity and origin, we must compare the functional role of species in the structure of their native and introduced communities (Gallien & Carboni, 2017).

According to modern coexistence theory, both niche differences and average fitness differences can drive the persistence of exotic and native species within a community (Fried et al., 2019; MacDougall et al., 2009). Niche differences refer to the degree to which intraspecific exceeds interspecific competition, while average fitness differences refer to differences in the density-independent and density-dependent growth rates between the species (Godwin et al., 2020). Exploring trait differences between exotic and native plant species has been an approach to study mechanisms of species' coexistence more broadly. Exotic species may succeed by exploiting unused resources (Gallien et al., 2015), if they have different resource-use traits than native species (de la Riva et al., 2019). However, exotic species may also succeed by possessing traits similar to native species (Funk et al., 2016; Tecco et al., 2010). In this case, the absence of niche differences allows exotic species to displace native competitors by having higher population growth (higher average fitness) (Fried et al., 2019).

However, plant traits are modulated by environmental conditions. Several studies have studied trait variation in native and exotic species across environmental gradients (El-Barougy et al., 2020; Funk & Vitousek, 2007; Gross et al., 2013; Heberling & Fridley, 2016; Marini et al., 2012; Tecco et al., 2010). A classic expectation is that strong environmental stress limits the range of strategies that species can display, and therefore stress favours trait convergence through habitat filtering; as environmental stress decreases, trait divergence increases via niche differentiation because competitive interactions are stronger (Cornwell & Ackerly, 2009; Weiher & Keddy, 1995). For instance, it has been shown that functional differences in height and specific leaf area between native and exotic species increase with resource availability (Burns, 2006; El-Barougy et al., 2020; Henn et al., 2019), which points towards a greater competitive advantage of exotic species under favourable conditions and increasing overall trait diversity. Yet, we might expect deviations from this prediction. For instance, environments with high-resource availability might display habitat filtering and convergence for traits such as plant height or seed mass (Bernard-Verdier et al., 2012; Pakeman et al., 2011), if strong competitors have a disproportionately large effect on local resources (Grime, 2006). Also, plant species adapted to less favourable environments, such as dry habitats, may show contrasting resource uptake strategies due to opportunistic behaviour with respect to water and nutrient use efficiency (de la Riva et al., 2021; Querejeta et al., 2018). In fact, contrasting functional strategies have been shown to promote invasion of Mediterranean arid communities, where exotic species display contrasting life-history strategies and traits related to resource use (de la Riva et al., 2019; Galán Díaz, de la Riva, Funk, & Vilà, 2021).

Mediterranean grasslands are an excellent study system to compare differences in community assembly between introduced and native ranges. Over the last four centuries, there has been an overwhelmingly unidirectional movement of herbaceous species from Mediterranean Europe to other Mediterranean regions (Casado et al., 2018; Galán Díaz, de la Riva, Parker, et al., 2021). For example, in California, 672 out of the 975 herbaceous exotic plant species are from the Mediterranean Basin (Rejmanek & Randall, 1994). Here, we leverage this historical introduction of plants and take a multiple trait approach to assess community assembly mechanisms of exotic species in communities from their native and introduced ranges. We aim to elucidate the importance of traits, abiotic constraints and species origins (native/exotic) in explaining current patterns of community assembly. In grassland communities in California and Spain along parallel resource availability gradients, we measured eight functional traits for 159 species of 32 plant families to compare how abiotic constraints shape community functional structure (i.e. community-weighted means and functional diversity) of native and recipient communities. We use functional traits to explore niche differences between co-occurring exotic and native species. We expect that, in both ranges, changes in the functional structure of plant communities along the resource availability gradient will be mostly determined by trade-offs between acquisitive and conservative strategies (Bernard-Verdier et al., 2012; Gross et al., 2013). Also, because of the long, shared co-evolutionary history between plants and human agricultural practices in Europe (MacDougall et al., 2018), we expect grassland communities from Spain to be more diverse and the assemblage of colonizers from Spain to be more different from the native species assemblage in California than from co-occurring species in their native range and to have greater impacts on community structure in their introduced range.

2 | MATERIALS AND METHODS

2.1 | Grassland vegetation surveys

From March 2018 to May 2018, we sampled 60 vegetation plots across four sites in Spain; and from March 2019 to May 2019, we sampled 60 vegetation plots across four sites in California (Appendix S1). Sites were weekly monitored and sampled during the 2 weeks following flowering blooming peak, therefore on mature plants. Sites were located along a coast-inland transect in both regions. Mean annual precipitation across sites ranged from 596 to 796 mm in Spain to 375 to 794 mm in California. Because soil disturbance, fire and restoration treatments alter the ratio of native- and exotic species in Mediterranean grasslands (Stromberg & Griffin, 1996), we selected sites that, over the last 30 years, had been moderately grazed by wild and domestic ungulates and had not been burned, ploughed or planted. For each site, we estimated its aridity as in Trabucco and Zomer (2018). Aridity is expressed as a function of precipitation, temperature and evapo-transpiration and is negatively correlated with potential vegetative growth. Additionally, we quantified the average soil nutrient concentration in each site by collecting five cores of the top 20 cm of soil. Soil cores were separated at least 150 m along the 1 km vegetation transect. Samples were dried in the oven, then ground and sieved to 2 mm. Using the methods and equipment described in López et al. (2019), we estimated percentage total nitrogen (N) by Kjeldahl digestion, organic matter (OM) by the Walkley and Black method, and available phosphorus (P) by the Olsen method. Finally, we averaged the soil variables from the five samples within sites.

To encompass the local heterogeneity in plant species composition and diversity, in each site, we collected plant species composition and cover in 15 plots (0.50 × 0.50 m) located along a 1 km transect. Plots within a site were randomly located but at least 50 m apart. For each plot, species' cover was visually estimated by assigning a cover class: 1: 0–5%; 2: 5–10%; 3: 10–15%; up to 20: 95–100%. Then, we assigned to each observation (species × plot) the mean value of its class cover (class 1: 2.5%, class 2: 7.5%, etc.) and divided this value by the total sum cover of all species present in the plot to obtain the relative cover abundance.

We classified species as 'colonizers' if they were native to Spain and known to be successfully established as exotic species elsewhere (Galán Díaz, de la Riva, Parker, et al., 2021). In Spain, we found 139 species, all of them native to Spain (Valdés et al., 1987). In all, 79 were colonizers; 73 are established in California (Calflora., 2014; Galán Díaz, de la Riva, Parker, et al., 2021) and 6 more are established in other Mediterranean regions but were not introduced to California. These six species are expected to share similar traits and so were also considered colonizers (Arianoutsou et al., 2013). In California, we found 96 species in total, 44 natives and 52 exotics. All the exotics in California were native to the Mediterranean Basin and therefore referred as colonizers hereafter (Calflora., 2014).

2.2 | Functional traits measurements

At each site, we identified the species that contributed to 90% of cumulative cover of plots (ranging from 31 to 63 species per site; Appendix S1) and measured 8 plant traits for each species that are representative of the plant resource-use and acquisition strategies (Table 1). These are specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), isotopic carbon fraction ($\delta^{13}C$), specific root length (SRL), root dry matter content (RDMC), reproductive height (distance from the latest inflorescence to the ground) and seed mass. The chosen above-ground and below-ground traits reflect orthogonal axes of plant functioning related to resource acquisition, and reproductive potential (Garnier et al., 2016). For each combination of species × site, we collected 10 flowering individuals and then measured each trait following the protocols included in the handbook for standardized measurement of plant functional traits (Pérez-Harguindeguy et al., 2013; see Appendix S3).

In total, traits were measured in 117 species in Spain and 75 species in California, 248 species-site combinations in Spain and 120 species-site combinations in California. Some observations were missing from the final database (5.47% of the cells) due to the difficulty of collecting enough material to obtain reliable measurements. Missing data reduces sample size and introduces bias. Therefore, if the missing trait was available for the same species in other sites, we used the mean trait value for that species across sites; and if the missing trait belonged to a site-specific species, we used the mean trait value of that genus or family (Divíšek et al., 2018). In addition, we recorded whether the species were annual or perennial (hemicryptophytes).

TABLE 1 Traits measured in plant species from Spanish and California grasslands with indication of their related function

Trait	Abb.	Units	Related function
Specific Leaf Area	SLA	cm^2/g	Resource acquisition rate, photosynthetic rate, relative growth rate
Leaf Dry Matter Content	LDMC	mg/g	Leaf tissue density, resistance to physical hazards, stress tolerance
Leaf Nitrogen Content	LNC	%	Photosynthetic rate
Isotopic Carbon Fraction	$\delta^{13}C$	‰	Integrated water use efficiency
Specific Root Length	SRL	cm/mg	Resource acquisition rate and conservation, relative growth rate
Root Dry Matter Content	RDMC	mg/g	Root tissue density, resistance to physical hazards, drought resistance
Reproductive Height	Height	cm	Dispersal distance
Seed Mass		g	Seedling establishment

2.3 | Community functional indices

We compared the functional structure between plots from both regions, and between colonizer/non-colonizer and colonizer/native species assemblages in Spain and in California, respectively. Functional structure was estimated with two complementary metrics: community-weighted trait means (CWM) and mean functional dissimilarity (MFD). CWM is the average value of a trait across all the species present in the plot and weighted by their abundances (Garnier et al., 2004). CWM characterizes the most frequent trait values of a community and is based on the mass ratio hypothesis, which posits that the most frequent traits determine ecosystem processes (Garnier et al., 2004). MFD is a functional diversity index, unrelated to species richness (de Bello et al., 2016), calculated as the mean pairwise functional distance between all species in a community weighted by their abundances.

2.4 | Statistical analyses

2.4.1 | Resource availability gradient

To reduce the number of environmental variables and characterize the environmental gradient with a single composite variable, a principal component analysis (PCA) was performed with the variables soil nitrogen (N), soil phosphorus (P), soil OM and aridity. These environmental variables were largely correlated and all of them had high absolute loadings in the first principal component (71.2% of the total variation explained). PC1 indicated a clear gradient of increasing soil nutrient concentration and decreasing aridity from inland to coastal sites (Appendix S4). Therefore, in further analysis, we used the scores of PC1 as a proxy for resource availability.

2.4.2 | Functional structure of grassland communities in Spain and California

To estimate the functional structure of the studied grassland communities, we first performed a PCA with the CWM of the eight traits for all plots (the 60 plots from Spain and the 60 plots from California). For each region, we ran linear models for the functional composition of the communities with the first two principal components of the PCA with CWM of the eight traits as response variables and the score in the resource availability gradient as the predictor variable. In addition, we used a null model to detect the relative importance of niche differences and abiotic constraints in community assembly (Cornwell & Ackerly, 2009). For each plot, we recalculated MFD 499 times after shuffling species labels in the original plot × species abundance matrix and retained the mean across randomizations (de Bello et al., 2012). We included the entire regional pool of species in the randomizations because all species are known to occur across each region and maintained the observed species richness within plots to account for in carrying capacity across plots within a habitat (Loiola et al., 2018). If community assembly is determined by abiotic constraints, we might expect communities to be less functionally diverse than expected by chance, that is, the observed MFD would be less than MFD obtained from the randomizations (i.e. functional convergence). In contrast, an observed MFD equal to or greater than the randomization suggests, respectively, that community assembly is the result of random assembly or niche differences (i.e. functional divergence). To determine whether functional convergence is explained by resource availability, we ran a linear model with the syntax (observedMFD − nullMFD) ~ resource availability.

2.4.3 | Functional structure of colonizer species compared to native and non-colonizer assemblages

To assess the role of colonizer and non-colonizer species in the functional structure of the native communities in Spain, and colonizer and native species in the recipient communities in California, we investigated, for each region independently, changes in the functional composition (CWMs) and functional diversity (MFD) along the resource availability gradient for each species pool. For each region, we first fitted a linear model with the syntax MFD ~ origin (colonizer/non-colonizer) × resource availability to assess whether MFD depends on species origins and the resource availability of the site. Then, we followed the method proposed by Gross et al. (2013) to assess the effects of habitat filtering on niche differences in the assembly of colonizer and native (or non-colonizer) species along the resource availability gradient. We first assessed whether CWMs differ between colonizer and native (or non-colonizer) species, and whether they change along the resource availability gradient, by fitting a linear model with the syntax CWM ~ origin × resource availability for each trait and region. We then explored whether the observed trait differences reflect patterns of trait convergence or divergence. For each trait (*t*) and plot (*p*), we calculated the functional difference (FD) between colonizers and other species as follows:

$$\mathrm{FD}_{tp} = \frac{\left|\mathrm{CWMcolonizers}_{tp} - \mathrm{CWMnatives}_{tp}\right|}{\mathrm{CWMcolonizers}_{t} - \mathrm{CWMnatives}_{t}} \quad (1)$$

where the CWM difference between the two species pools is divided by the mean difference across plots within the region (see Gross et al., 2013). This analysis does not consider the role of colonizer and non-colonizer species in their communities but allows to identify overall functional divergence or convergence processes.

In addition, for each region, we compared the observed FD against null models to determine whether it differs from the random expectation. For this, we randomized species abundances within columns 99 times in the plot × species abundance matrix and, for each randomization, calculated FD between colonizers and others per trait and plot. This maintains species abundances within regions but allows changes in species richness within plots. Finally, for each plot, we compared the observed FD against the 95% confidence intervals of the null model to determine whether it reflects functional divergence (niche differences between colonizer and other species are greater than expected by chance) or functional convergence (niche differences between colonizer and other species are smaller than expected by chance). We ran a linear model with the syntax FD ~ resource availability to explore the relationship between the observed functional differences and the resource availability gradient. FD was log-transformed to meet assumptions of normality and homoscedasticity of residuals.

Finally, to interpret the observed patterns, we explored changes in the functional structure of colonizer and non-colonizer assemblages along the resource availability gradient considering their life-history traits (annual/perennial). We performed a linear regression on SLA-FD using resource availability, the ratio of annual colonizers and annual non-colonizers, and the ratio of perennial colonizers and perennial non-colonizers as predictors. All statistical analyses were performed with the software R v4.1.1 (R Core Team, 2021).

3 | RESULTS

3.1 | Functional structure of grassland communities in Spain and in California

The PCA of the CWM reflected that trait differences among plots are related to site differences. The first two principal components explained 65.31% of the total variance (Figure 1). Our results indicated a clear orthogonal segregation between regions. Spanish plots segregated significantly along PC1, which accounted for the covariation of $\mathrm{SRL}_{\mathrm{CWM}}$, $\delta^{13}\mathrm{C}_{\mathrm{CWM}}$ and Seed $\mathrm{mass}_{\mathrm{CWM}}$; while California plots segregated significantly along PC2, which represented a positive covariation of $\mathrm{Height}_{\mathrm{CWM}}$, $\mathrm{LDMC}_{\mathrm{CWM}}$ and $\mathrm{RDMC}_{\mathrm{CWM}}$.

In Spain, the resource availability gradient explained 68.94% of the community functional variance of PC1 ($F_{1,58} = 128.73$, $p < 0.001$; Figure 2a), and 22.93% of the variance of PC2 ($F_{1,58} = 17.26$, $p < 0.001$; Figure 2b). Communities in sites with less resources showed higher $\mathrm{SRL}_{\mathrm{CWM}}$ and $\mathrm{SLA}_{\mathrm{CWM}}$, whereas plots of wetter fertile sites had greater $\delta^{13}\mathrm{C}_{\mathrm{CWM}}$ and Seed $\mathrm{mass}_{\mathrm{CWM}}$. In California, whereas the resource availability gradient did not have a significant effect on PC1 ($F_{1,58} = 0.45$, $p = 0.50$; Figure 2c), we found a quadratic relationship between the resource availability gradient and PC2, explaining 73.48% of the variance, such that intermediate sites supported communities with more conservative strategies ($F_{1,58} = 78.97$, $p < 0.001$; Figure 2d).

In addition, MFD values mostly fell below the null expectation (Figure 3), which supports that niche differences among coexisting species are constrained by abiotic factors. Overall, in both regions, species that co-occurred in the same plot tended to be more functionally similar than expected by chance (48 out of 60 plots in California; 58 out of 60 in Spain). In Spain, there was a positive linear relationship between functional convergence and resource availability ($F_{1,58} = 5.70$, $p = 0.02$; Figure 3a). In California, there was also a strong positive linear relationship between functional convergence and resource availability ($F_{1,58} = 202.59$, $p < 0.001$; Figure 3b), with species from plots from resource-poor sites being more functionally different than expected by chance.

3.2 | Functional structure of species assemblages along the resource availability gradient

In both regions, the assemblage of colonizer species was on average functionally more diverse than that of the other coexisting species (Table 2; Spain: $\mathrm{colonizers}_{\mathrm{MFD}} = 3.07 \pm 0.07$, $\mathrm{non\text{-}colonizers}_{\mathrm{MFD}} = 2.49 \pm 0.09$; California: $\mathrm{colonizers}_{\mathrm{MFD}} = 2.91 \pm 0.09$, $\mathrm{natives}_{\mathrm{MFD}} = 2.19 \pm 0.09$). Also, the functional diversity of colonizer and other species did not change with resource availability.

There were significant differences in the response of the functional composition (CWMs) of colonizers and other species (native species in California, non-colonizer species in Spain) to resource availability between regions. Overall, we found that colonizer assemblages in Spain had greater $\mathrm{SLA}_{\mathrm{CWM}}$, $\delta^{13}\mathrm{C}_{\mathrm{CWM}}$ and $\mathrm{height}_{\mathrm{CWM}}$ than non-colonizer species (Table 2 and Figure 4a,c,g). Colonizer species in Spain consistently showed greater $\mathrm{SLA}_{\mathrm{CWM}}$ than non-colonizer species across sites. Whereas the functional difference in $\mathrm{SLA}_{\mathrm{CWM}}$ between colonizers and other species decreased significantly with resource availability (Figure 4b), functional differences for other traits did not change with resource availability (Figure 4d,f,h; Appendix S5).

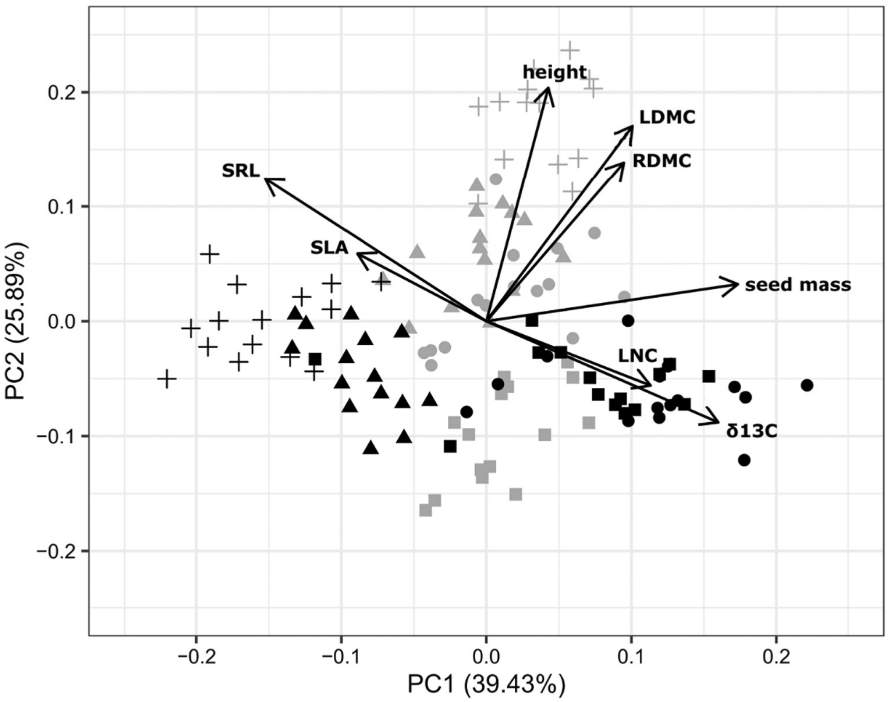

FIGURE 1 Principal component analysis of the community-weighted trait means (CWM) of Spanish and California grassland communities. Spain (black): + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes. California (grey): ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda. Sites in Spain are mostly differentiated along PC1, while sites in California are differentiated along PC2. Traits: specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), isotopic carbon fraction (δ^{13}C), specific root length (SRL), root dry matter content (RDMC), reproductive height and seed mass.

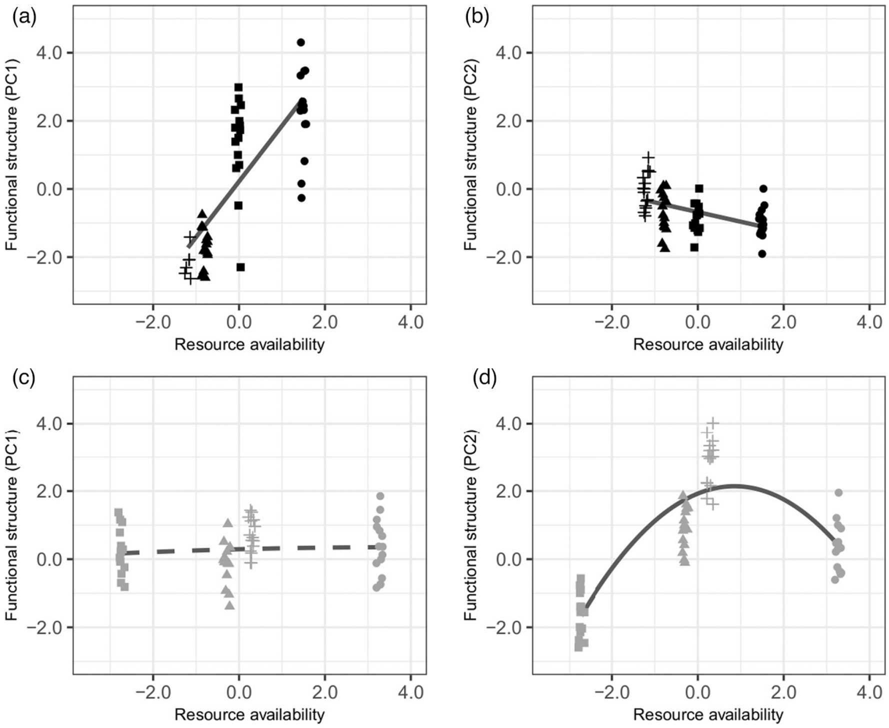

FIGURE 2 Changes in the functional structure of Spanish and California grassland communities along the resource availability gradient indicated by PC1 (a) and PC2 (b) in Spain and PC1 (c) and PC2 (d) in California. Spain (black): + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes. California (grey): ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda. Solid lines denote significant relationships (*p*-value <0.05).

In contrast, in California, we found significant differences between native and colonizer species for all traits except for $\text{height}_{\text{CWM}}$ (Table 2). Also, there were significant interactions between origin and resource availability for all traits. Colonizers increased SLA_{CWM} and RDMC_{CWM}, and decreased $\delta^{13}\text{C}_{\text{CWM}}$, along the resource availability gradient, whereas natives decreased in SLA_{CWM} and RDMC_{CWM} and increased $\delta^{13}\text{C}_{\text{CWM}}$ (Figure 5; Appendix S6). This resulted in increasing functional differences of their acquisitive (i.e. SLA and δ^{13}C) and resistance (RDMC) strategies with resource availability. The opposite pattern is observed for reproductive height, with functional convergence occurring in sites with more available resources.

In both regions, there were changes with resource availability in the relative proportions of native and colonizer annuals (see Appendix S7). In California, annual colonizers increased with greater resource availability and native species in high-resource environments were almost exclusively perennials, while in Spain, the

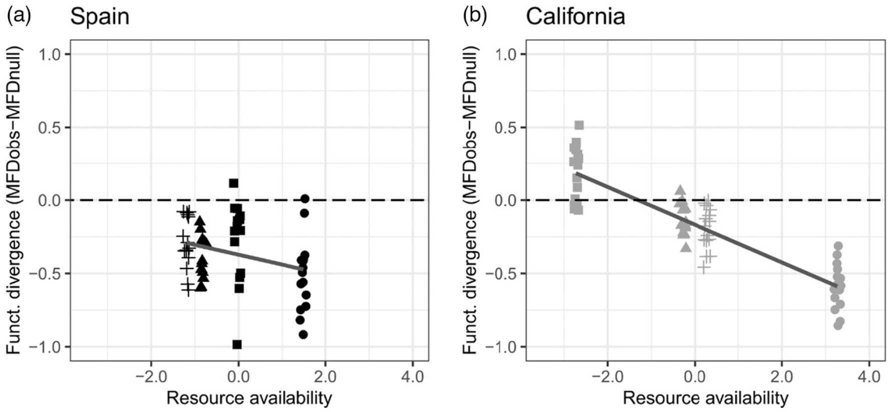

FIGURE 3 Functional assembly of grassland communities in (a) Spain and (b) California compared to the random expectation. An observed mean functional dissimilarity (MFD) less than the null MFD reflects functional convergence and suggests that the environment is constraining the potential range of niche differences; an observed MFD near the null MFD suggests random assembly; and an observed MFD greater than the null MFD suggests functional divergence. Spain (black): + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes. California (grey): ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda.

TABLE 2 Changes in the functional structure of Spanish and California grassland communities (community-weighted trait means [CWM] and mean functional dissimilarity [MFD]) in response to species origin and resource availability. For each trait and region, we ran a linear model with the following syntax: CWM ~ origin × resource availability. Asterisks denote significant terms: *p-value < 0.5, **p-value < 0.01, ***p-value < 0.001. See Table 1 for trait identity. Traits: specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), isotopic carbon fraction (δ^{13}C), specific root length (SRL), root dry matter content (RDMC), reproductive height and seed mass

Functional structure	Region	$F_{3,115}$	p	R^2	F_1 origin	F_1 resource availability	F_1 origin × resource availability
SLA_{CWM}	Spain	20.02	0.000	0.34	31.538***	24.669***	3.85
LDMC_{CWM}	Spain	7.35	0.000	0.16	8.723**	9.575**	3.78
SRL_{CWM}	Spain	46.50	0.000	0.54	0.08	135.724***	3.70
RDMC_{CWM}	Spain	1.15	0.000	0.02	0.03	3.44	0.00
$\delta^{13}\text{C}_{\text{CWM}}$	Spain	47.75	0.330	0.55	4.737*	132.215***	6.30*
LNC_{CWM}	Spain	30.86	0.000	0.44	5.793*	60.595***	26.20***
$\text{Height}_{\text{CWM}}$	Spain	9.49	0.000	0.19	12.527**	9.126**	6.83*
$\text{Seed mass}_{\text{CWM}}$	Spain	35.42	0.000	0.48	0.24	104.12***	1.91
MFD	Spain	19.16	0.000	0.34	54.79***	0.16	2.50
SLA_{CWM}	California	19.37	0.000	0.35	43.81***	0.00	14.32***
LDMC_{CWM}	California	20.38	0.000	0.36	36.555***	18.2***	6.41*
SRL_{CWM}	California	11.28	0.000	0.24	6.543*	16.115***	11.18**
RDMC_{CWM}	California	24.88	0.000	0.41	68.514***	0.43	5.71*
$\delta^{13}\text{C}_{\text{CWM}}$	California	12.68	0.000	0.26	24.741***	1.01	12.31**
LNC_{CWM}	California	16.50	0.000	0.31	37.115***	1.32	11.08**
$\text{Height}_{\text{CWM}}$	California	5.74	0.001	0.13	3.56	1.31	12.35**
$\text{Seed mass}_{\text{CWM}}$	California	7.51	0.000	0.17	10.753**	1.07	14.32***
MFD	California	21.26	0.000	0.40	59.53***	1.07	3.16

number of colonizer annual species declined with resource availability. This influenced the observed functional differences (see Appendix S8). For instance, this could explain why in California native species decreased in SLA_{CWM} with increasing resources, while SLA of colonizers increased. We found a significant interaction for SLA-FD between resource availability and the ratio of annual colonizers and annual non-colonizers in Spain ($F_{1,58} = 15.53$, $p < 0.001$) and California ($F_{1,58} = 10.11$, $p < 0.001$; Appendix S8).

4 | DISCUSSION

4.1 | Functional structure of grassland communities in Spain and in California

We found that the functional structure of the grassland communities along a resource availability gradient differed between the two regions. We identified two orthogonal axes of functional variation

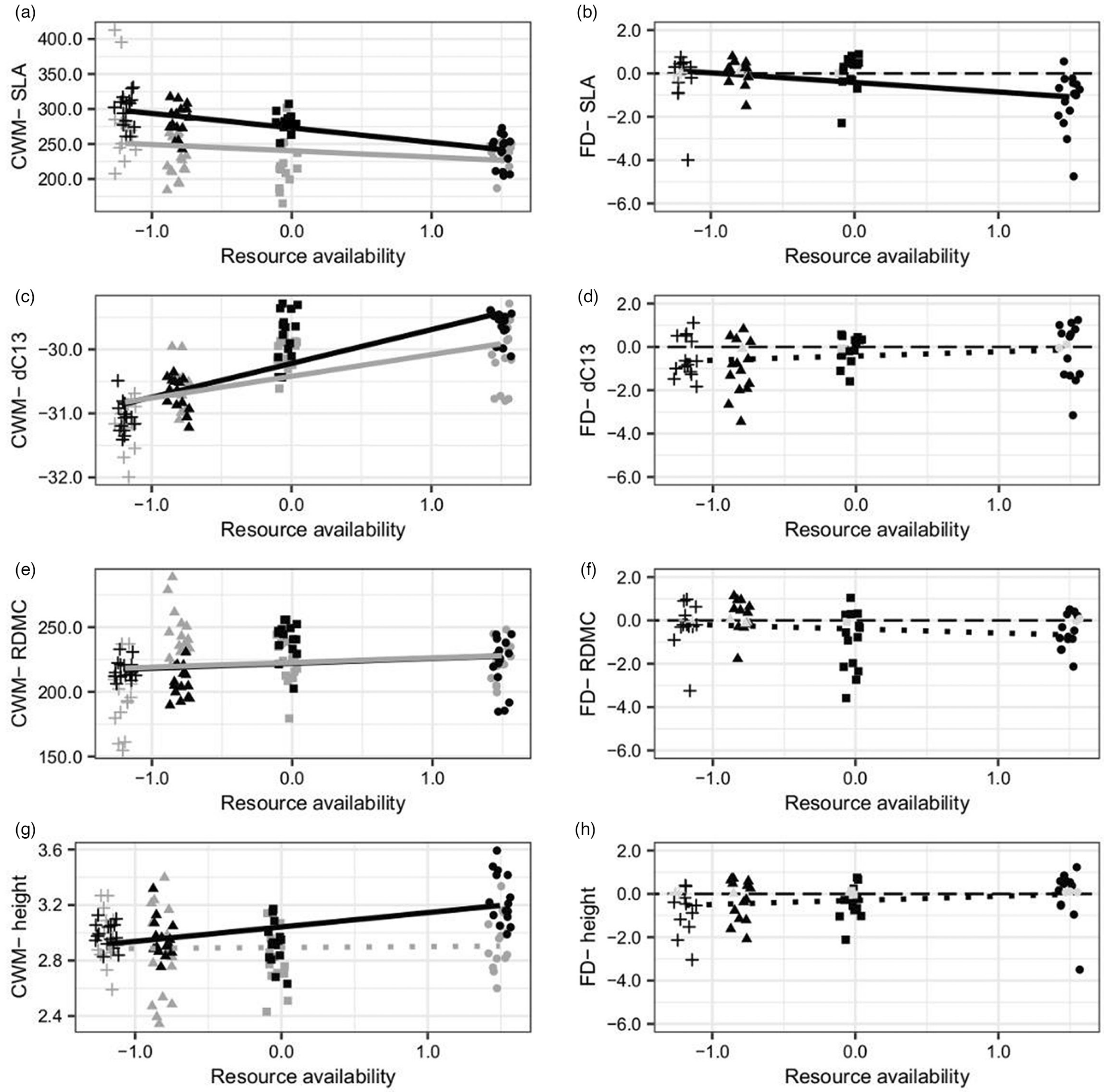

FIGURE 4 Relationship between resource availability and niche differences in Spain. Panels in the left show changes in community-weighted trait means (CWM) of colonizer (black) and non-colonizer (grey) species assemblages along the resource availability gradient. Panels in the right show functional differences (FD) between colonizer and non-colonizer species: Black dots over zero indicate functional divergence (niche differences greater than expected); black dots below zero indicate functional convergence (niche differences smaller than expected); grey dots indicate random assembly. (a) $\mathrm{SLA}_{\mathrm{CWM}}$, (b) SLA-FD, (c) $\delta^{13}\mathrm{C}_{\mathrm{CWM}}$, (d) δ^{13}C-FD, (e) $\mathrm{RDMC}_{\mathrm{CWM}}$, (f) RDMC-FD, (g) $\mathrm{height}_{\mathrm{CWM}}$, (h) height-FD. Solid lines indicate significant relationships ($p < 0.05$). Results of other traits can be found in Appendix S5. Sites: + Ventas, ▲ Navalagrulla, ■ Puerto, ● Montes. Traits: Specific leaf area (SLA), isotopic carbon fraction (δ^{13}C), root dry matter content (RDMC) and reproductive height.

related to the segregation of the study sites within each region: native sites in Spain segregated along the first axis mainly by the trade-offs in their resource uptake strategies (i.e. SRL, SLA and δ^{13}C) and seed mass; while recipient sites in California segregated along the second axis related to variation in reproductive height, LDMC and RDMC. In Spain, we observed that stress-tolerant traits were more common in the environments with more rainfall and nutrients, in contrast with the traditional expectations of the economic spectrum model (Reich, 2014; Wright et al., 2004). It is frequently assumed that high SLA and SRL facilitate rapid acquisition of resources and consequently faster growth rate, which is a common strategy in productive Mediterranean habitats (de la Riva

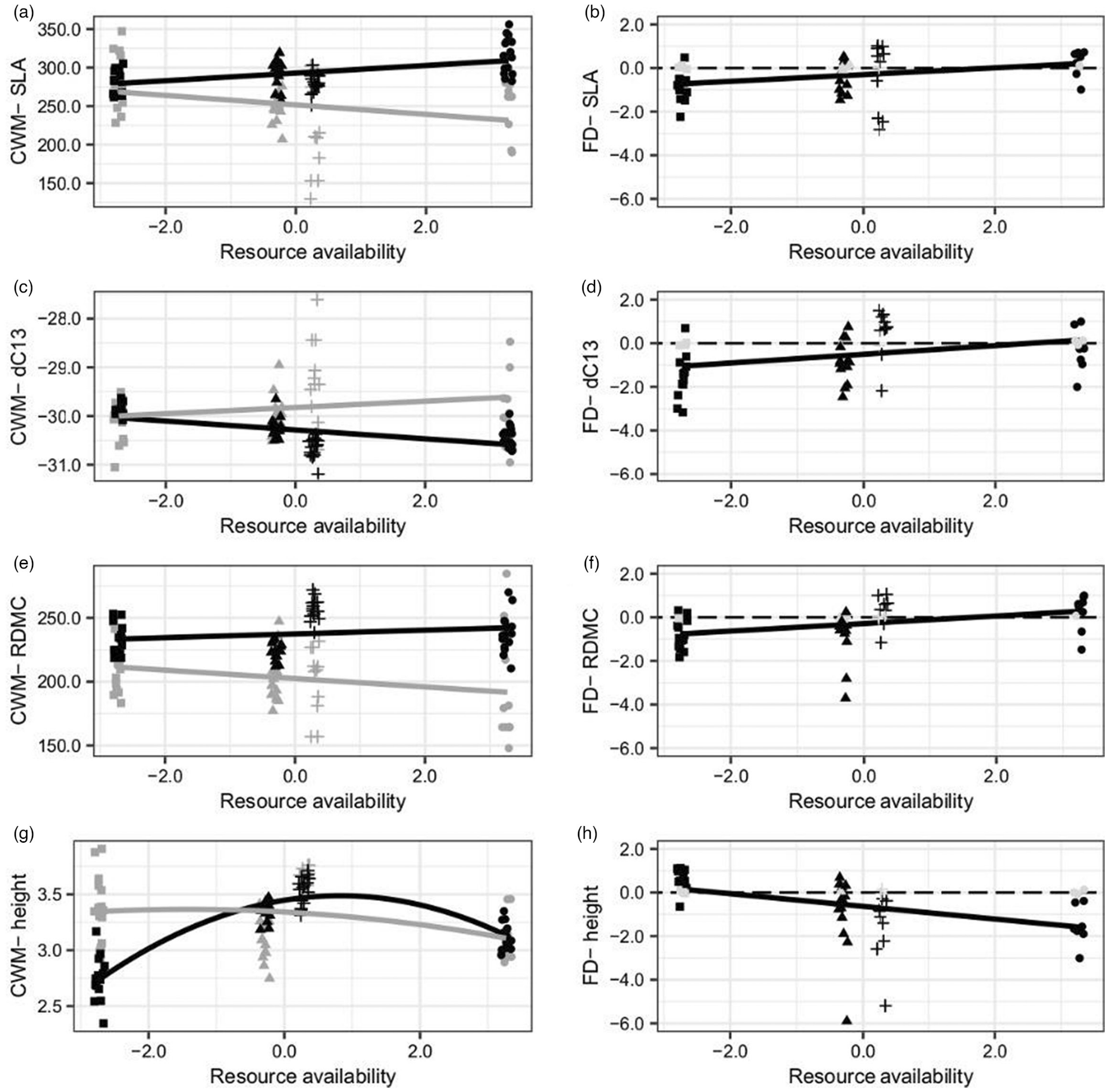

FIGURE 5 Relationship between resource availability and niche differences in California. Panels in the left show changes in community-weighted trait means (CWM) of colonizer (black) and native (grey) species assemblages along the resource availability gradient. Panels in the right show functional differences (FD) between colonizer and native species: Black dots over zero indicate functional divergence (niche differences greater than expected); black dots below zero indicate functional convergence (niche differences smaller than expected); grey dots indicate random assembly. (a) SLA_{CWM}, (b) SLA-FD, (c) $\delta^{13}C_{CWM}$, (d) δ^{13}C-FD, (e) $RDMC_{CWM}$, (f) RDMC-FD, (g) $height_{CWM}$, (h) height-FD. Solid lines indicate significant linear relationships ($p < 0.05$). Results of other traits can be found in Appendix S6. Sites: ■ San Joaquin, ▲ Merced, + Santa Cruz, ● La Honda. Traits: specific leaf area (SLA), isotopic carbon fraction (δ^{13}C), root dry matter content (RDMC) and reproductive height.

et al., 2018); while high δ^{13}C and seed mass have been interpreted as signs of a successful conservative strategy to cope with environmental stress such as summer drought (de la Riva et al., 2018; Prieto et al., 2018). In California, the community functional response to resource availability involved shifts in plant stature and tissue resistance, the dominant species being taller, with long-lived tissues (i.e. high LDMC and RDMC). This pattern also suggests that species from nutrient-rich sites opted for a conservative rather than an acquisitive strategy of resource use. Yet, the relationship was quadratic, which might reflect that the studied gradient was greater in California than in Spain, but also that idiosyncrasies of each site prevent the generalization of our findings.

This apparent paradox in our analysis can be explained by an underlying pattern in the life history of the dominant species. Particularly, the ratio of annual:perennial species decreased with resource availability in both regions. Perennial species in Mediterranean regions have been shown to be more dehydration tolerant than annuals (Volaire et al., 2009), thanks to their water use efficiency (higher δ^{13}C; Prieto et al., 2018) and higher seed mass, which may enhance seedling competition in resource-rich environments (Murray et al., 2005). This inversion of the economic spectrum has been previously observed in arid and semi-arid regions (Carvajal et al., 2019; de la Riva et al., 2021). Thus, herbaceous plants in Mediterranean regions can survive the summer drought by having a reduced metabolism (Volaire et al., 2009) or an annual life span, persisting in highly seasonal dry and low productive grasslands by maximizing nutrient capture and growth rate and showing an opportunistic behaviour of drought avoidance.

In both regions, the change in the functional trait composition across the environmental gradient indicates that habitat filtering constituted a main factor driving their functional structure (Spasojevic & Suding, 2012). Overall, coexisting species were more similar than expected by chance. This is what we expected to find, because trait convergence is common when comparing communities across large spatial scales (de Bello et al., 2012). This result supports that changes in resource availability frequently pair with changes in community traits related to carbon storage, nutrient cycling and litter decomposition, as well as anti-herbivore defence (Grime, 2006). In addition, community functional convergence increased with resource availability. Whereas functional convergence in the Spanish communities occurred along the entire gradient, communities in the site with less resources in California showed greater functional divergence than expected by chance. This may suggest that other processes could be important drivers of the assembly of this community (e.g. equalizing fitness and facilitation; Spasojevic & Suding, 2012). Although the relationship between resource availability and functional diversity is complex and context dependent (Bernard-Verdier et al., 2012; Carmona et al., 2012), the higher convergence across the resource gradient in California seems to be related with the increase in reproductive plant height. This pattern has been previously reported in other temperate and Mediterranean grasslands and might reveal that, as resource-availability increases, above-ground interspecific competition arises as an important mechanism of community assembly (Bernard-Verdier et al., 2012; Pakeman et al., 2011).

4.2 | Diversity and functional structure of species assemblages along the resource availability gradient

As hypothesized, we found that, in both regions, colonizer species assemblages were functionally more diverse than the other coexisting species. This adds to previous evidence that Spanish grassland communities hold greater species richness than California grasslands (Galán Díaz, de la Riva, Parker, et al., 2021; Leiva et al., 1997), and reflects that colonizer species might also dominate the trait space. Some authors suggest that ancient agricultural landscapes in Europe may have created human-mediated niches promoting high levels of biodiversity (Eriksson, 2013). When introduced to California grasslands, these species were pre-adapted to disturbed and managed habitats (MacDougall et al., 2018), and caused a rapid biodiversity decline by outcompeting the native plant communities (HilleRisLambers et al., 2010; Minnich, 2008).

Colonizer species assemblages showed on average higher values of SLA than other species in both regions. As colonizers were more diverse across sites in both regions, the observed difference in SLA suggests that faster acquisition and use of resources is a key mechanism for colonizers to thrive in grasslands (Sandel & Low, 2019). Whereas we did not find differences in other traits between colonizer species and other coexisting species in Spain, functional differences between colonizers and natives in California were evident for most traits. This supported our expectation that these colonizer species would have a greater impact on the structure of California communities than on the Spanish communities where they are native, and it points towards niche differences as an important mechanism of community assembly associated with invasion in these landscapes (Molinari & D'Antonio, 2014). As native species diversity in California has decreased over time (Minnich, 2008), we might expect the observed trait differences to confer a competitive advantage to exotic species over natives (MacDougall et al., 2009; Mayfield & Levine, 2010). This seems to be true in the context of other factors, such as grazing, where the traits of colonizer species have been shown to provide opportunities for colonizer species over natives (HilleRisLambers et al., 2010).

In Spain, functional differences between colonizer species and other coexisting species did not change along the resource availability gradient except for SLA, with colonizers being more acquisitive along the gradient but particularly in the low-resource end. In California, functional trait composition related to different aspects of plant strategies differed for natives and colonizers at both ends of the gradient (Galán Díaz, de la Riva, Funk, & Vilà, 2021; Hulme & Bernard-Verdier, 2018). Particularly, resource uptake strategies (i.e. SLA and δ^{13}C) tended to diverge with increasing resource availability. The increasing divergence in SLA and δ^{13}C with resource availability supports previous studies, which found that resource-use traits of native and exotic species diverged as resource-availability increased, with exotics being more acquisitive (Burns, 2006; El-Barougy et al., 2020; Gross et al., 2013; Henn et al., 2019). Thus, resource availability is a key driver of habitat filtering. In California, reproductive plant height converged at intermediate values with increasing resource availability. Differences between colonizer and native species for this trait were site dependent, obscuring the inference of mechanisms that might explain these results (Bernard-Verdier et al., 2012).

Differences in resource-use traits between native and colonizer species might indicate the importance of niche differences for the establishment success of exotic species, as well as the long-term coexistence of native and exotic species though niche complementarity

(MacDougall et al., 2009). Differences in life histories between the groups of species suggest that the temporal and spatial scope of a study influences the observed patterns of community assembly. As previously discussed, the proportion of annual species decreased with resource availability. Yet, whereas in Spain, this reflects a decrease in the richness of colonizer annuals, in California it reflects a strong decrease in the native annuals. In California, the two sites with greatest resource availability in our study are in the bioregion with the highest richness of exotic species (Dark, 2004). The great historical propagule pressure in that region probably combined synergistically with intense anthropogenic disturbance to promote exotic species establishment near California coastal areas (Rejmanek & Randall, 1994). In Spain, the decrease in annual colonizers with resource availability may reflect unaccounted-for differences in land-use over time on the selected sites. We suspect that the higher overall species richness in Spanish sites, along with the greater functional diversity of non-colonizers in these communities, buffers the effect of life-form on the analyses of this region.

5 | CONCLUSIONS

By comparing plant functional traits of invaders in recipient and native communities, we better understand the strategies plant communities adopt to cope with environmental constraints and disentangle the role of exotic species in community structure. While invasion history and mechanisms cannot be directly inferred from observed patterns, studying patterns of community assembly across environmental gradients allows for new insights on the relationship between trait differences and habitat filtering. Our results suggest that the establishment and subsequent spread of many exotic plants in Californian grasslands was not random but rather reflects the dominance and competitive advantage of these colonizer species in their region of origin in terms of relative cover and SLA. In addition, these colonizer species are more functionally distinct from native species in California than they are from non-colonizers in their region of origin. Their functional distinctness underlies the impact of these colonizer species on the functional structure of recipient communities and, presumably, on ecosystem function.

AUTHOR CONTRIBUTIONS

Javier Galán Díaz conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, writing – review and editing. Montserrat Vilà conceptualization, investigation, writing – review and editing. Ingrid M. Parker Investigation, Writing – review and editing. Enrique G. de la Riva conceptualization, methodology, formal analysis, investigation, writing – review and editing.

ACKNOWLEDGEMENTS

We thank M.J. Leiva, C. Dykstra, D. Ragel and R. Sutcliffe for fieldwork assistance; and J. Catford and two anonymous reviewers for their comments to a previous version of the manuscript. JGD and EGR are supported by a Margarita Salas and Maria Zambrano fellowships, respectively, funded by the Ministry of Universities and European Union-Next Generation Plan. JGD has received financial support through 'la Caixa' INPhINIT Fellowship Grant for Doctoral studies at Spanish Research Centers of Excellence (LCF/BQ/DI17/11620012) and from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No. 713673. This work was funded by the Spanish Ministry of Science and Innovation (MCI), the State Research Agency (AEI) and European Fund for Regional Development (FEDER, UE) grant EXARBIN (RTI2018-093504-B-I00). We did not need permission for fieldwork.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.14027.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.6wwpzgn2n (Galán Díaz et al., 2022).

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SUPPORTING INFORMATION

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

How to cite this article: Galán Díaz, J., Vilà, M., Parker, I. M., & de la Riva, E. G. (2022). Functional assembly of grassland plant species in native communities in Spain and recipient communities in California. *Journal of Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2745.14027