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RESEARCH ARTICLE

Home-range ecological dissimilarity and trait coordination promote the establishment of Mediterranean-origin plants in California

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Abstract

1. While ecological dissimilarity plays a critical role in biological invasions, it remains unclear whether ecological differences between alien species and co-occurring species in their native range persist after introduction.
2. Leveraging the unidirectional introduction of plant species native to the Mediterranean into California, we conducted a cross-continental study to examine whether Mediterranean-origin species are phylogenetically and functionally distinct from co-occurring species in their native range, and whether these differences are maintained relative to California native species after introduction.
3. Mediterranean-origin species introduced to California were phylogenetically and functionally distant from co-occurring native species in both native and introduced ranges. They also exhibited distinct patterns of trait coordination between stress tolerance-related traits (e.g., leaf dry matter content) and resource acquisition-related traits (e.g., leaf nitrogen concentration and specific root length), and a more acquisitive strategy across ranges.
4. *Synthesis*. These findings suggest that ecological dissimilarity and persistent trait coordination of species in their home range may contribute to their establishment after introduction, highlighting the value of native-range trait information for understanding invasion functional strategies in novel environments.

KEYWORDS
alien plants, biological invasions, cross-continental comparison, functional traits, Mediterranean-type ecosystems, phylogenetic distance, trait coordination

1 | INTRODUCTION

Biological invasion is widely considered a key driver of global environmental change (Crowl et al., 2008). Human-mediated dispersal of alien species frequently leads to a decline in biodiversity and changes in ecosystem processes (Pejchar & Mooney, 2009; Vilà et al., 2011). The success of alien species invasion is closely related to their intrinsic biological traits, the interactions with native species, and the environmental conditions of their introduced habitats (Carboni et al., 2016; Divíšek et al., 2018; Hejda et al., 2014). Thus, understanding the ecological differences between alien and native species, as well as the consistency of their trait relationships between native and introduced ranges, is critical to unravelling invasion mechanisms.

Alien species often outcompete native species by exhibiting distinct functional strategies, such as faster growth rates, enhanced resource-use efficiency, or greater stress tolerance (Carboni et al., 2016; Fridley et al., 2022; Funk & Vitousek, 2007; Gioria et al., 2023). The success of alien species is a dynamic process, driven by both pre-introduction sorting of advantageous traits and post-introduction rapid evolution (Bossdorf et al., 2005; Colautti & Barrett, 2013). Alien species may possess advantageous functional traits before arrival, and subsequent selection pressures and ecological interactions in the introduced range may further shape their performance and invasion success (Turner et al., 2015). However, focusing solely on the introduced range makes it difficult to disentangle whether observed trait advantages were inherent properties of the founding populations or products of post-introduction adaptation (van Kleunen et al., 2010). Thus, to determine whether alien and native species have different traits before introduction and whether these traits may confer preadaptation to invade new habitats, comparative work within the native and introduced ranges is important (Hierro et al., 2004).

The trait values of species in their native range may serve as a reasonable proxy for their trait values in the introduced range and support the use of trait-based prediction methods to assess the potential for the establishment of introduced plants (Galán Díaz et al., 2023; Pyšek et al., 2009; van Kleunen et al., 2011). For example, a common garden experiment demonstrated that the faster and more abundant emergence of South African Iridaceae in their native range compared with other non-naturalized species was associated with their naturalization elsewhere (van Kleunen & Johnson, 2007). Evidence suggests that species traits that contribute to high plant performance in their native range can facilitate invasiveness in the introduced range (Bucharova & Van Kleunen, 2009; Schlaepfer et al., 2010). Functional traits are often evolutionarily conserved, such that closely related species often share more similar traits than distantly related ones (Crisp et al., 2009; Losos, 2008). By contrast, if alien species are phylogenetically distant from native species, they are likely to exhibit distinct resource-use patterns and ecological strategies, thereby reducing interspecific competition and facilitating invasion success (Darwin's naturalization hypothesis; Darwin, 1859; Daehler, 2001; Strauss et al., 2006).

Functional trait trade-offs represent a key point for dissecting the mechanisms that make alien species successful (Funk & Vitousek, 2007; Garbowski et al., 2024). Although trait-based comparisons can identify whether alien species differ from native species in particular ecological characteristics, trait–trait relationships (trait coordination) provide additional insight into how species integrate multiple functional strategies related to resource acquisition, growth, and stress tolerance strategies (Osnas et al., 2013; Wright et al., 2004), thus providing mechanistic insight into how alien species achieve competitive advantages. Previous work proposed that native and alien plants share similar resource acquisition strategies, and invaders experience similar constraints between physiological investment and return as native species (Leishman et al., 2010; Mathakutha et al., 2019). However, other studies found that alien species exhibited growth strategies that enabled faster growth than native species or achieved greater returns on investment for a given leaf and root investment (Garbowski et al., 2024; Leishman et al., 2007). For example, a study in eastern North American forests showed that alien and native species differed in the relationships among leaf functional traits, suggesting contrasting patterns of trait coordination and resource allocation (Heberling & Fridley, 2013). These differences in trait strategy are likely attributable to preadaptation of alien plants in the native range (Heberling & Fridley, 2013). However, it remains unclear whether the differences in trait strategies between introduced species and co-occurring species in their introduced ranges correspond to those between analogous groups in the native range.

In recent centuries, herbaceous species native to the Mediterranean have been introduced to California on a large scale in a predominantly unidirectional way. Previous studies have examined the functional assembly of grassland plant communities along environmental gradients in both Spain and California (Galán Díaz et al., 2022), as well as the traits associated with the invasiveness of Mediterranean-origin species introduced to California, based on observations from their native range in Spain (Galán Díaz et al., 2023). However, whether Mediterranean-origin species differ from co-occurring native species in phylogenetic relatedness and functional trait composition across native and introduced ranges, and whether they exhibit distinct patterns of trait covariation, remain unclear. Here, we investigate how Mediterranean-origin grassland species differ from co-occurring native species in phylogenetic relatedness and functional traits across their native and introduced ranges, and compare the structure of trait relationships between the two groups across regions. Although our analyses are based on single observations and species trait patterns, they allow us to explore patterns of ecological differentiation associated with range expansion and establishment, rather than directly evaluating evolutionary shifts following introduction. Accordingly, we hypothesize that:

1. Mediterranean-origin species tend to be phylogenetically/functionally distant from California native species in their introduced range. They also differ from non-introduced Mediterranean species in their native range. Furthermore, Mediterranean-origin

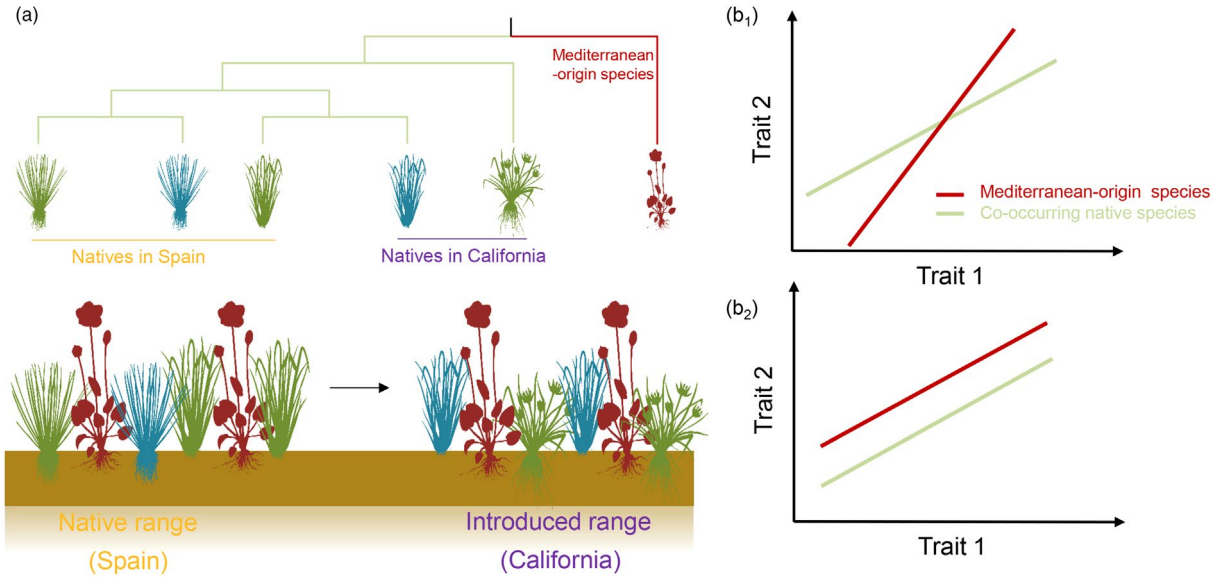

FIGURE 1 Schematic diagrams illustrate two key aspects: (a) the phylogenetic/functional relatedness between Mediterranean-origin and co-occurring native plants in both native and introduced ranges, where Mediterranean-origin plants are phylogenetically/functionally dissimilar to co-occurring native plants in both native and introduced ranges; and (b) the trait relationships in growth and stress tolerance between Mediterranean-origin and co-occurring native plants in their native and introduced ranges. Within panel (b), (b1) a significantly changed slope indicates that divergent patterns of trait covariation between Mediterranean-origin and co-occurring native species, whereas (b2) a consistent slope with a shifted intercept indicates that a consistent slope indicates higher overall trait levels. Red and green clades (or lines) represent Mediterranean-origin species introduced to California and co-occurring native species, respectively.

species exhibit greater phylogenetic and functional distances from California native species in the introduced range than from co-occurring native species in their native range (Figure 1a).

2. Across both native and introduced ranges, Mediterranean-origin species exhibit different patterns of trait covariation among traits related to resource acquisition and stress tolerance compared with co-occurring native species, as reflected by differences in the slopes and/or intercepts of trait–trait relationships (Figure 1b).

2 | METHODS

2.1 | Field survey

The plant species that we used were sourced from a cross-continental survey of four sites in Spain and four sites in California (Figure 2a). At each site, the composition and cover of the plant species were surveyed in 15 plots (0.50×0.50 m) located along a 1 km transect. The surveys in Europe and North America were conducted in 2018 and 2019, respectively. For full details on the field survey, see Galán Díaz et al. (2020) and Galán Díaz et al. (2022). Species were classified as 'Mediterranean-origin species' if they are native to Spain and documented as successfully established alien species in California. The status of the plant species was determined with reference to Valdés et al. (1987) and Calflora (2014). A total of 139 species have been documented in Spain, all native to the region. Among these Spanish native species, 73 have successfully established in California. A total of 96 species have been recorded in California, comprising 44 native species and 52 Mediterranean-origin species. Whether in their native range or introduced range, Mediterranean-origin plants are the dominant component of the community (Figure 2c). No specific permits were required for the fieldwork conducted in this study.

2.2 | Phylogenetic tree and functional traits

We generated a phylogeny for all 113 species in our dataset (Figure 2b) using the package 'V. PhyloMaker2' (Jin & Qian, 2022), with an updated and expanded version of the dated megaphylogeny 'GBOTB' as the backbone (Smith & Brown, 2018). All species in our dataset were resolved in the megaphylogeny (GBOTB.extended.TPL.tre).

At each site, species cover was summed across the 15 plots along the transect, and the species that account for 90% of the cumulative total cover were retained and we quantified eight functional traits that capture plant resource-use and acquisition strategies: specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), carbon isotopic composition ($\delta^{13}C$), specific root length (SRL), root dry matter content (RDMC), reproductive height (Height), and seed weight (SW). These selected above- and below-ground traits capture different aspects of plant resource-use strategies (Garnier et al., 2016). For each species × site combination, we sampled 10 flowering individuals and measured traits following the standardized protocols outlined in the handbook for measuring functional traits of plants (Pérez-Harguindeguy et al., 2013). In the final dataset,

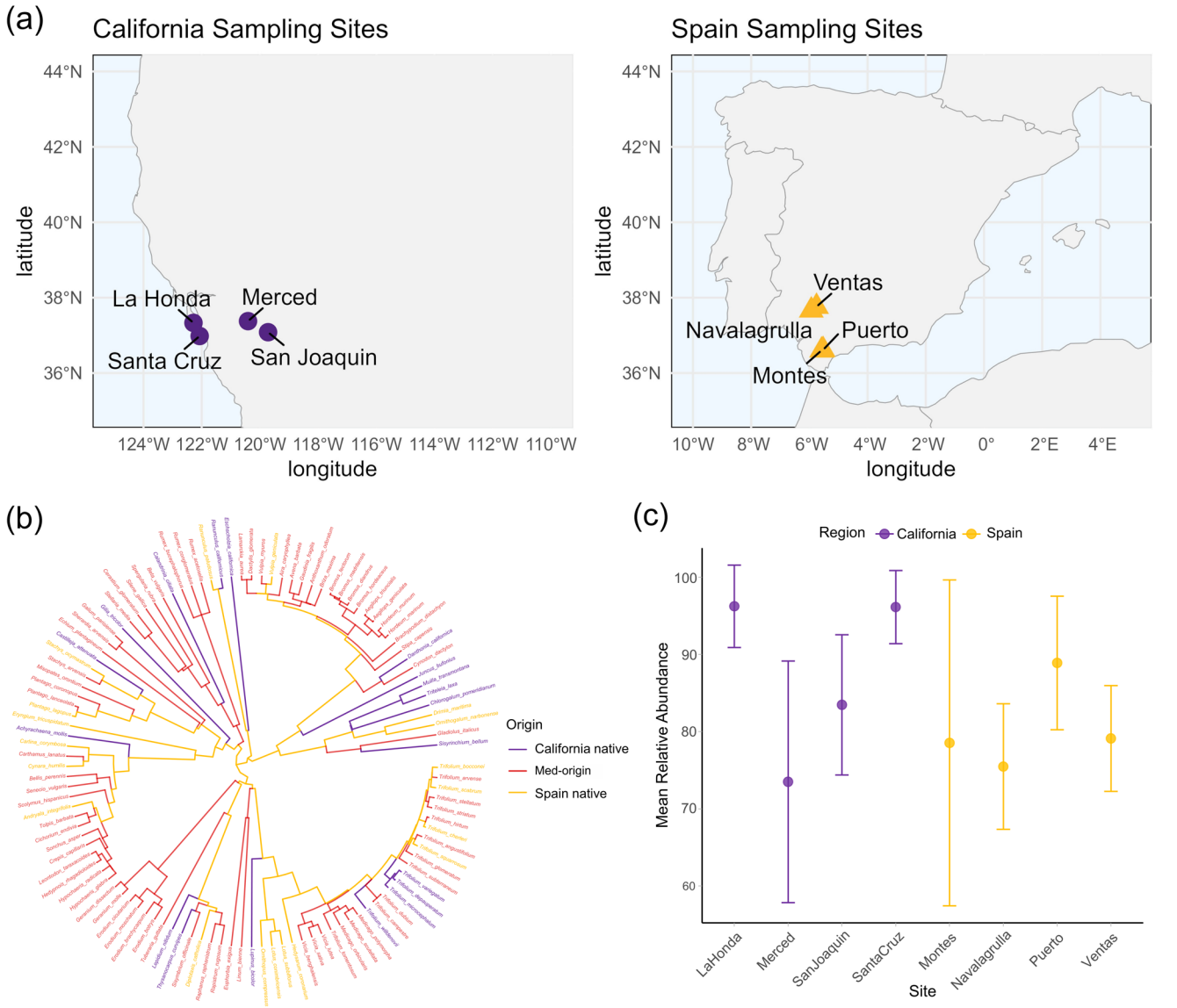

FIGURE 2 Geographical distribution of sampling sites from the cross-continental study in California and Spain (a), the phylogenetic tree of plant species included in the analysis (b), and the mean relative abundance of Mediterranean-origin species at each site in their native range (Spain) and introduced range (California) (c). Circles and error bars denote mean values and standard errors, respectively. Med-origin refers to Mediterranean-origin species.

5.47% of the trait records were missing due to insufficient material for reliable quantification. Missing values reduce statistical power and can bias inference. Thus, we applied a hierarchical imputation procedure. For species occurring at multiple sites, missing traits were replaced with the species mean across all sampled sites. For species restricted to a single site, missing values were substituted by the mean trait value of their genus or, when unavailable, their family (Divíšek et al., 2018).

To estimate the ecological differences between Mediterranean-origin species and co-occurring native plants in the native and introduced ranges, we excluded plots consisting exclusively of Mediterranean-origin species or lacking any Mediterranean-origin species. In total, 100 plots, comprising 113 plant species, were included in the final analysis.

2.3 | Statistical analysis

For each plot, we assessed the degree of phylogenetic and functional dissimilarity between Mediterranean-origin species and co-occurring native species. We computed abundance-weighted mean nearest taxon distance (MNPDw) and mean pairwise distance (MPDw) for phylogenetic metrics, along with their functional analogues (MNFDw and MFDw). Before calculating

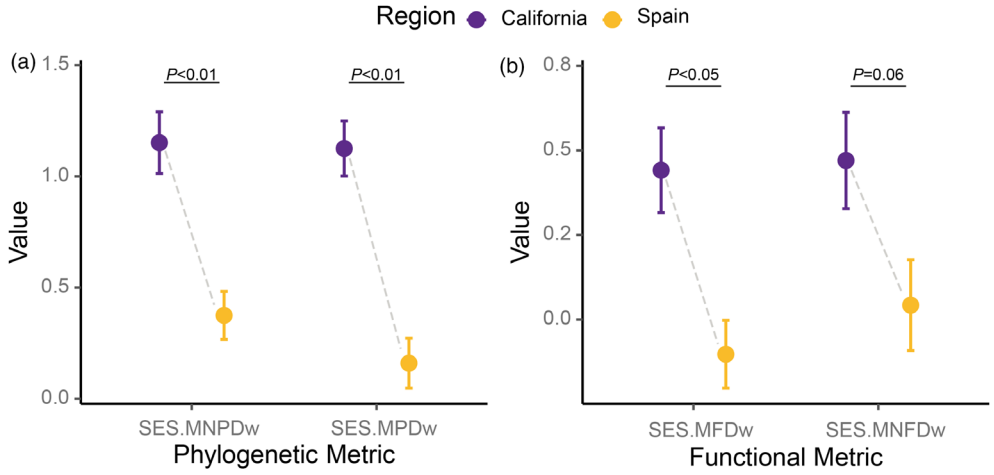

FIGURE 3 Comparison of phylogenetic (a) and functional (b) relationships between Mediterranean-origin and co-occurring native plants in the native range (Spain) and the introduced range (California). Error bars represent standardized errors. SES.MFDw, standardized effect size of abundance-weighted mean functional distance; SES.MNFDw, standardized effect size of abundance-weighted mean nearest functional distance; SES.MNPDw, standardized effect size of abundance-weighted mean nearest phylogenetic distance; SES.MPDw, Standardized effect size of abundance-weighted mean phylogenetic distance.

functional metrics, we $\log_{10}$-transformed all continuous trait values to homogenize variance and used absolute values of $\delta^{13}C$ for transformation because the original values were negative. To be concise, in the model expressions in the following (e.g., SLA-$\delta^{13}C$), $\delta^{13}C$ hereafter represents '$\log_{10}$-transformed absolute $\delta^{13}C$'. We used the Gower distance to quantify functional dissimilarity including MNFDw and MFDw (Laliberté & Legendre, 2010), because it standardizes all traits to a common scale, ensuring that traits measured on different units contribute equally to the overall distance.

To evaluate whether Mediterranean-origin species exhibited non-random phylogenetic or functional relationships with co-occurring native species, we employed a null model approach. We conducted 999 random simulations by keeping the co-occurring native species composition and the number of Mediterranean-origin species in a plot unchanged but randomly drawing the identities of the Mediterranean-origin species from the Mediterranean-origin species pool. The Mediterranean-origin species pool comprised all Mediterranean-origin species recorded in our study, and the null model maintained the native community structure while shuffling Mediterranean-origin species (Thuiller et al., 2010). For comparative purposes, we standardized all phylogenetic and functional metrics using standardized effect sizes (SES), calculated by subtracting the mean of the null distribution from the observed value and dividing the result by the standard deviation of the null distribution. This approach yields normalized Z scores, where SES >0 indicates phylogenetic or functional overdispersion (greater divergence than expected by chance), and SES <0 indicates clustering (greater similarity than expected by chance). To examine the phylogenetic and functional differences between Mediterranean-origin and co-occurring plants across the native and introduced ranges, we employed linear mixed models. In these models, the 'region' was included as a fixed effect, and the 'site' was included as a random effect. All analyses were performed using the R package 'lme4' (Bates et al., 2015).

We performed a standardized major-axis analysis (SMA) to explore the bivariate relationships between plant traits using species occurrence records combined with species-level trait values. All trait values were $\log_{10}$-transformed before the SMA analysis to achieve normality. To test the differences in SMA slopes between Mediterranean-origin species and co-occurring native species pools for each range, we used the 'sma' function in the R package 'smart' (Warton et al., 2012). Similar slopes and intercepts indicate that interspecific trait covariation patterns were consistent between the two species pools. In contrast, significant differences in the SMA slopes indicate that the relationship between traits differed between species pools, reflecting differences in the structure of interspecific trait covariation.

3 | RESULTS

3.1 | Phylogenetic and functional dissimilarity between Mediterranean-origin and co-occurring native species in native and introduced ranges

The SES values of MPDw (SES.MPDw) and MNPDw (SES.MNPDw) between Mediterranean-origin species introduced to California and co-occurring native plant species were greater than zero in both native and introduced ranges (Figure 3a), indicating that Mediterranean-origin plants tended to co-occur more with less phylogenetically related native species. Furthermore, in the introduced range, SES.MPDw and SES.MNPDw between Mediterranean-origin species and California co-occurring native plants were significantly greater than in the native range ($p < 0.01$; Figure 3a; Figures S2 and S3).

For the functional relationship, the SES value of MFDw (SES.MFDw) between Mediterranean-origin species and co-occurring native plant species was greater than zero in the introduced range but less than zero in the native range (Figure 3b; Figures S2 and S3). In contrast, the SES value of MNFDw (SES.MNFDw) between Mediterranean-origin and co-occurring native species was greater than zero in both ranges (Figure 3b; Figures S2 and S3), further supporting functional dissimilarity between Mediterranean-origin species and co-occurring native species, regardless of distribution ranges. Furthermore, SES.MNFDw in the introduced range was marginally higher than in the native range ($p = 0.06$; Figure 3b).

3.2 | Trait–trait relationships between Mediterranean-origin and co-occurring native species in the native and introduced ranges

In the introduced range, the SMA analysis revealed significant differences in the slopes of the SLA–LDMC, SLA–LNC, SLA–δ^{13}C, LDMC–LNC, LNC–δ^{13}C, LMDC–RDMC, and LDMC–SRL relationships between Mediterranean-origin species and co-occurring native species ($p < 0.001$; Figure 4a–e,h,i; Table S2). Specifically, LDMC increased faster as LNC, RDMC, and SRL increased in Mediterranean-origin species compared with co-occurring native species ($p < 0.001$; Figure 4d,h,i; Table S2). In contrast, California native species exhibited steeper slopes in the SLA–LDMC, SLA–δ^{13}C, and LNC–δ^{13}C relationships ($p < 0.001$; Figure 4a,c,e; Table S2).

Similarly, in the native range, the slopes of the relationships between LDMC and LNC, RDMC, and SRL were significantly steeper in Mediterranean-origin species compared with co-occurring native species ($p < 0.001$; Figure 5b,h,i; Table S3). Specifically, Mediterranean-origin species showed a greater increase in LDMC with increasing LNC and RDMC but with decreasing SRL compared with co-occurring native species. Consistent with the pattern observed in the introduced range, co-occurring native species maintained steeper slopes for the SLA–δ^{13}C and LNC–δ^{13}C relationships ($p < 0.001$; Figure 5c,e; Table S3), while the slopes of SLA–LNC, SLA–SRL, and SRL–RDMC did not differ significantly between groups ($p > 0.05$; Figure 5b,f,g; Table S3). Mediterranean-origin species tended to have higher SLA for a given LNC and higher SRL for a given RDMC than co-occurring native species (Figure 5b,g; Table S3).

4 | DISCUSSION

Our findings indicate that Mediterranean-origin species are phylogenetically and functionally distant from co-occurring species in both their native (Spain) and introduced ranges (California), with the strength of dissimilarity being lower in the native range. Additionally, in both native and introduced ranges, Mediterranean-origin species introduced to California exhibited steeper trait relationships associated with nutrient uptake and resource-use strategies, suggesting distinct patterns of trait covariation and stronger differentiation along the resource acquisition–conservation spectrum. These consistent patterns in Mediterranean-origin species across ranges suggest that similar patterns of functional trait coordination are expressed in both native and introduced environments, potentially reflecting ecological strategies that may facilitate establishment and contribute to persistence in the introduced range.

Our results are consistent with Darwin's naturalization hypothesis, suggesting that phylogenetic and functional differentiation may facilitate invasion through niche differentiation (Strauss et al., 2006). However, niche differentiation is unlikely to be the only mechanism underlying the successful establishment of Mediterranean-origin species in California. These species were intentionally introduced and subsequently spread within ecosystems profoundly modified by grazing, altered disturbance regimes, and land-use change, all of which likely increased invasion opportunities (HilleRisLambers et al., 2010). Consequently, observed phylogenetic and functional differentiation can reflect both ecological differences between alien and native species and historical and anthropogenic processes that shaped recipient communities (Schaefer et al., 2011). Consistent with our first hypothesis, this pattern was observed in both native and introduced ranges, though with stronger differences in the introduced range. This disparity in the magnitude of the effect might be related to a stronger competitive pressure of Mediterranean-origin species on recipient communities in California than in their local native range communities (Hejda et al., 2016; Taylor et al., 2016). In Mediterranean ecosystems, long-term species coexistence and species filtering have promoted adaptive mechanisms among native species (e.g., natural enemies and competitive interactions), mitigating the negative effects of dominant plants (MacDougall et al., 2018). In contrast, evolutionary and historical differences between European and North American ecosystems, such as differences in the intensity of species co-evolution and resistance to disturbances, may release European plants from natural constraints in North America (Hejda et al., 2016).

The invasion success of European grassland species has been facilitated by the adoption of European-style landscape management practices (di Castri, 1989; Lenzner et al., 2022; Seastedt & Pyšek, 2011). It has been hypothesized that Mediterranean species have evolved enhanced competitive ability, disturbance tolerance, and resource-use efficiency through prolonged exposure to environmental pressures in their native range, including frequent anthropogenic disturbances and complex interspecific competition (Hejcman et al., 2013; La Sorte & Pyšek, 2009). Conversely, California native species have not experienced such selective anthropogenic pressures and are therefore unable to effectively resist invasion by European Mediterranean species through their evolutionary adaptations (MacDougall et al., 2018; Seastedt & Pyšek, 2011).

In addition to potential evolutionary differences, contrasting habitat characteristics between native and introduced ranges may also contribute to this pattern. In general, California sites were characterized by stronger precipitation seasonality than the Spanish sites, reflected by lower annual precipitation and lower precipitation during the driest month, despite higher precipitation during the

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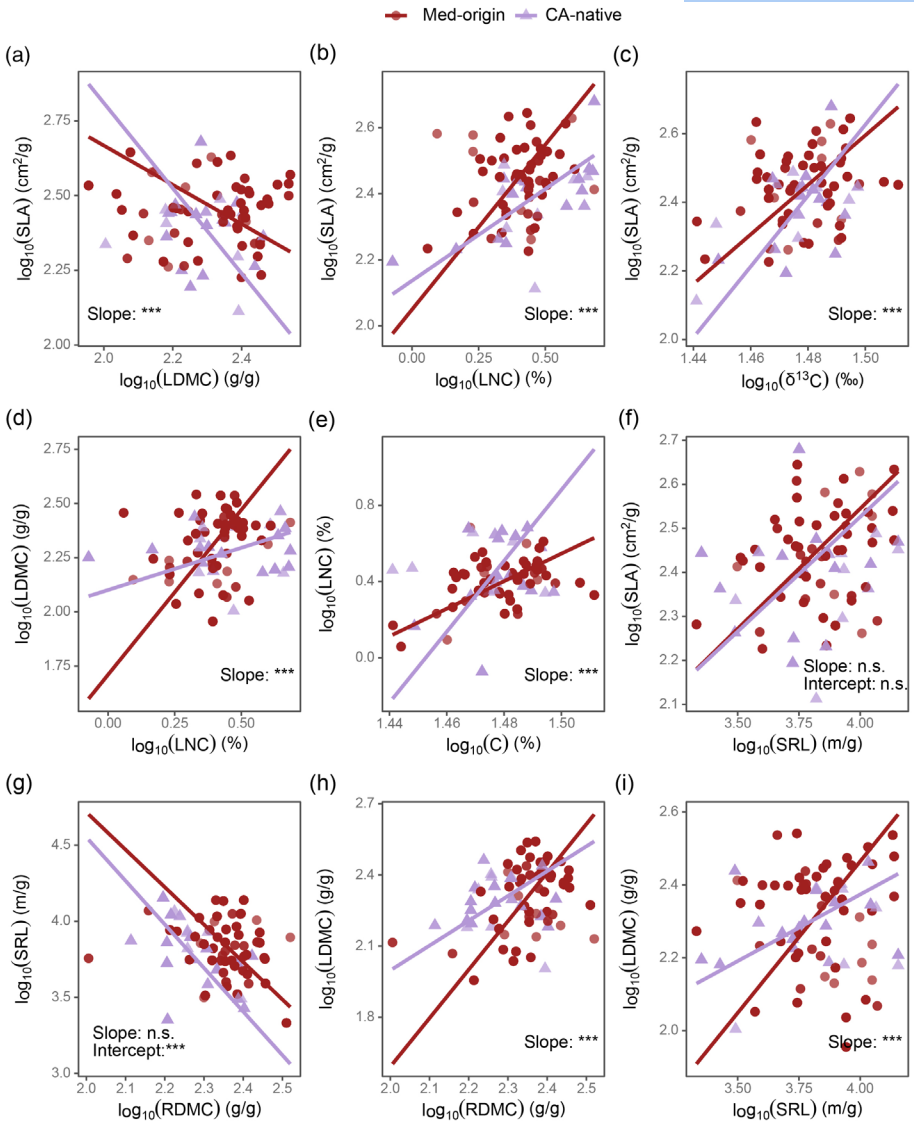

FIGURE 4 Trait–trait relationships between Mediterranean-origin species introduced to California and other co-occurring California native species in their introduced range (California). Panels (a–i) show the nine pairwise trait relationships, respectively. The red and purple lines represent standardized major-axis regressions of pairwise trait relationships of Mediterranean-origin and co-occurring native species, respectively. 'Slope' and/or 'Intercept' identify significant differences in the slopes or intercepts of pairwise traits between Mediterranean-origin and co-occurring native species. Changes in intercepts cannot be detected if the slopes differ significantly. LDMC, leaf dry matter content; LNC, leaf nitrogen content; R^2, adjusted R-squared; RDMC, root dry matter content; SLA, Specific leaf area; SRL, specific root length; $\delta^{13}C$, isotopic carbon fraction. n.s.: $p > 0.05$; $^{***}p < 0.001$. CA-native: Other co-occurring California native species; Med-origin: Mediterranean-origin species introduced to California.

wettest month (Figure S1), potentially favouring Mediterranean-origin annual species that complete their life cycle during the wet season and persist through summer drought as dormant seeds. Consequently, differences in life-history strategies and phenology, together with phylogenetic and functional differentiation, may have contributed to their successful establishment (Hejda et al., 2016). Furthermore, this pattern aligns with the long history of agricultural land use and disturbance in Mediterranean Europe (MacDougall et al., 2018), which may have favoured plant traits associated with disturbed environments in Spain. However, the successful establishment of Mediterranean-origin species in California was also likely facilitated by livestock introduction, pasture management, and other anthropogenic ecosystem changes that created comparable disturbance regimes (HilleRisLambers et al., 2010; Stahlheber & D'Antonio, 2013). Therefore, the greater phylogenetic distance between Mediterranean-origin and California native species may represent a consequence of altered community assembly under contrasting environmental conditions and disturbance histories.

Our results revealed consistent functional differentiation between species of Mediterranean origin and co-occurring native species in both their introduced and native ranges. However, this pattern was not detected using the mean functional distance (MFDw) in Spain. This difference likely arises because MFDw reflects the average functional dissimilarity between Mediterranean-origin species

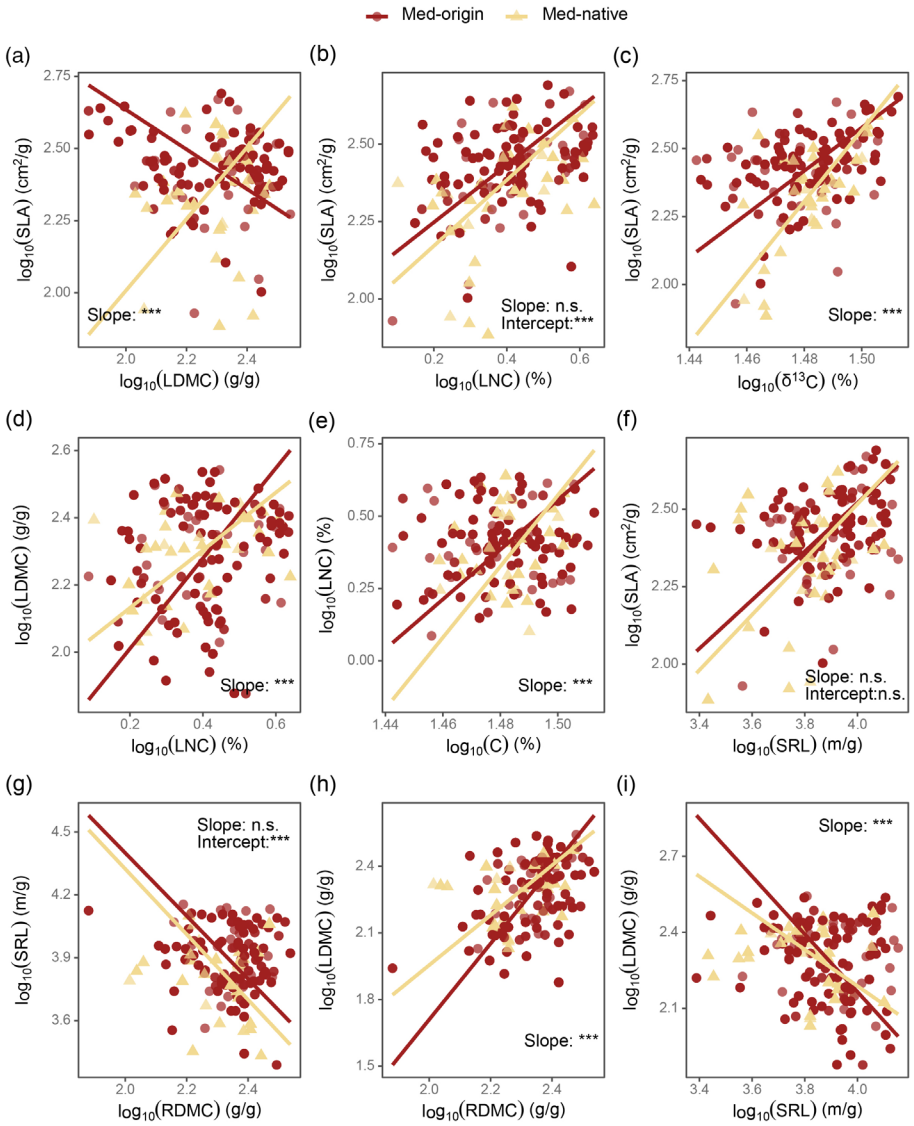

FIGURE 5 Trai–trait relationships between Mediterranean-origin species introduced to California and other co-occurring Mediterranean native plants in their native range (Spain). Panels (a–i) show the nine pairwise trait relationships, respectively. The red and yellow lines represent standardized major-axis regressions of pairwise trait relationships of Mediterranean-origin and co-occurring native species, respectively. 'Slope' and/or 'Intercept' identify significant differences in the slopes or intercepts of pairwise traits between Mediterranean-origin and co-occurring native species. Changes in intercepts cannot be detected if the slopes differ significantly. LDMC, leaf dry matter content; LNC, leaf nitrogen content; R^2, adjusted *R*-squared; RDMC, root dry matter content; SLA, Specific leaf area; SRL, specific root length; $\delta^{13}C$, isotopic carbon fraction. n.s.: $p > 0.05$; $^{***}p < 0.001$. Med-native: Other co-occurring Mediterranean native species; Med-origin: Mediterranean-origin species introduced to California.

and the entire native community, whereas MNFDw quantifies the functional distance to the most similar co-occurring competitors. Consequently, MNFDw provides a more sensitive measure of niche differentiation and potential competitive interactions (Schaefer et al., 2011; Thuiller et al., 2010). In addition, Blomberg's *K* and Pagel's λ values for several traits (e.g., LDMC, LNC, and SLA) suggest that evolutionary history exerts an influence on these traits (Table S1; Figure S4). However, the *K* values for the traits were significantly different from what would be expected in a BM model (Table S1), indicating that trait evolution likely deviates from neutrality and may be influenced by environmental selection (Le et al., 2024; Pellegrini et al., 2023). Therefore, in the context of our study, ecological selection pressures, such as seasonal drought and intense competition in the introduced range, exert a stronger influence on trait attributes than shared evolutionary history alone. This suggests that trait attributes within lineages were shaped by historical natural selection, which subsequently provided a selective advantage in novel environments, but remain highly responsive to the environment.

Changes in growth and tolerance investment are reflected in coordinated trait relationships (Pan et al., 2020; Wright et al., 2004). Mediterranean-origin species exhibited steeper SMA slopes for several trait relationships (e.g., LDMC–LNC, LDMC–RDMC, LDMC–SRL) than co-occurring native species. However, these differences were substantially weaker when analyses were

based on the mean values of the species trait, suggesting that both intraspecific variation and differences in species representation contributed to the stronger relationships observed in the species-pool analyses (Table S4). Therefore, these patterns should be interpreted as trait covariation among species pools rather than species-level trait relationships. One possible explanation is that long-term environmental filtering associated with Mediterranean ecosystems has contributed to the prevalence of species with particular combinations of acquisitive and conservative traits. Pronounced summer drought, seasonal resource limitation, and recurrent disturbances can favour coordinated investments in tissue construction and stress tolerance (Hodgson et al., 2011; Onoda et al., 2011). In this scenario, the distinct patterns of trait covariation observed among Mediterranean-origin species may reflect functional syndromes assembled through long-term environmental filtering. Alternatively, the steeper SMA slopes may arise because Mediterranean-origin species occupy a broader functional trait space or encompass a greater diversity of functional syndromes than co-occurring native species, rather than exhibiting stronger intrinsic trait coordination. The contrasting LDMC–SRL relationships between the native and introduced ranges may reflect the relatively weak phylogenetic conservatism of SRL (Figure S1), which may allow root morphological traits to respond more readily to environmental conditions and belowground biotic interactions. Collectively, these results suggest that historical environmental filtering, together with environmentally structured trait variation and species turnover, contributes to persistent differences in multidimensional trait covariation following introduction.

In contrast, Mediterranean-origin species and co-occurring native species exhibit similar slopes in the SLA–SRL and SRL–RDMC relationships across both ranges. However, the consistently higher intercepts observed in Mediterranean-origin species indicate a tendency for higher RDMC values at comparable SRL values relative to co-occurring native species, which aligns with our hypothesis. A higher RDMC is generally associated with roots characterized by thicker cell walls, greater lignification, or denser cortical tissues (Comas et al., 2012). This structural characteristic improves their resistance to root herbivory, pathogen infection, and desiccation during short-term drought events common to ecosystems in both the Mediterranean basin (native range) and California (introduced range) (Drenovsky et al., 2012; Nunez-Mir & McCary, 2024). This pattern likely reflects an intrinsic trait value favoured by selection during the evolutionary history of Mediterranean-origin species.

The slopes of the SLA–δ^{13}C and LNC–δ^{13}C relationships of co-occurring native species in the two regions were significantly higher than those of Mediterranean-origin species, which contradicts our hypothesis. Because high δ^{13}C values generally indicate greater intrinsic water-use efficiency (Prieto et al., 2018), suggesting that variation in leaf structure and nitrogen investment is more closely associated with water-use efficiency in co-occurring native species than in Mediterranean-origin species. One possible explanation is that co-occurring native species are predominantly perennial, whereas Mediterranean-origin species are largely annual. Annual species typically complete their life cycle during the wet season and avoid severe summer drought by escaping from drought, thus reducing selection for conservative water-use strategies and weakening the coordination between leaf functional traits and intrinsic water-use efficiency (Prieto et al., 2018; Ripullone et al., 2004). Although our analyses reveal consistent patterns of trait coordination across species pools, the ecological mechanisms underlying these patterns remain to be tested experimentally. Integrating trait covariation with manipulative experiments, demographic approaches, and broader biogeographic comparisons will help understand how evolutionary history, environmental filtering, and species interactions jointly shape invasion success.

5 | CONCLUSIONS

We conducted a cross-continental comparative analysis under Mediterranean climate to explore the phylogenetic and functional relationships between Mediterranean-origin species and co-occurring native species across both their native and introduced ranges. We further examined whether these species groups differed in trait coordination between growth-related and stress tolerance-related traits. Our findings reveal that Mediterranean-origin species are phylogenetically and functionally distant from co-occurring native species, and that these differences are consistently maintained across native and introduced ranges. Mediterranean-origin species also exhibited distinct trait coordination patterns between growth-related and stress tolerance-related traits, suggesting that characteristic functional relationships distinguishing Mediterranean-origin species from native species remain detectable after introduction. This study demonstrates that the trait coordination patterns observed in Mediterranean-origin species within their native range can persist in introduced environments. Our findings highlight the potential value of integrating native-range functional trait information to improve our understanding of alien species functional strategies under climate-matched conditions. Because the historical context of our study system is unique, it would be interesting to test whether these phylogenetic and functional patterns of invasion occur in other regions and habitat types.

AUTHOR CONTRIBUTIONS

Haichuan Le: Conceptualization, methodology, formal analysis, data curation, writing—original draft, writing—review and editing. Javier Galán Díaz: Conceptualization, investigation, data curation, writing—review and editing. Zongqiang Xie: Writing—review and editing. Enrique G. de la Riva: Writing—review and editing. Montserrat Vilà: Conceptualization, investigation, writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70436.

DATA AVAILABILITY STATEMENT

The code and data that support the findings of this study are available in Figshare at: https://doi.org/10.6084/m9.figshare.30111388 (Le et al., 2025).

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SUPPORTING INFORMATION

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

Figure S1. Comparison of environmental factors between Spain and California.

Figure S2. Density distributions of functional distance indices.

Figure S3. Mean values of phylogenetic and functional distances at each site.

Figure S4. Correlation relationships between phylogenetic and functional distances.

Table S1. Results of phylogenetic signal.

Table S2. Results of the standardized major-axis regression in California.

Table S3. Results of the standardized major-axis regression in Spain.

Table S4. Species-level mean standardized major-axis.

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