Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems

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Abstract. The idea that dominant invasive plant species outperform neighboring native species through higher rates of carbon assimilation and growth is supported by several analyses of global data sets. However, theory suggests that native and invasive species occurring in low-resource environments will be functionally similar, as environmental factors restrict the range of observed physiological and morphological trait values. We measured resource-use traits in native and invasive plant species across eight diverse vegetation communities distributed throughout the five mediterranean-climate regions, which are drought prone and increasingly threatened by human activities, including the introduction of exotic species. Traits differed strongly across the five regions. In regions with functional differences between native and invasive species groups, invasive species displayed traits consistent with high resource acquisition; however, these patterns were largely attributable to differences in life form. We found that species invading mediterranean-climate regions were more likely to be annual than perennial: three of the five regions were dominated by native woody species and invasive annuals. These results suggest that trait differences between native and invasive species are context dependent and will vary across vegetation communities. Native and invasive species within annual and perennial groups had similar patterns of carbon assimilation and resource use, which contradicts the widespread idea that invasive species optimize resource acquisition rather than resource conservation.

Key words: annual; drought avoidance; functional traits; perennial; resource acquisition; resource-use efficiency; stress tolerance.

INTRODUCTION

One of the greatest challenges in conserving and restoring plant communities is identifying the mechanisms by which invasive species outperform native species. Analyses of global data sets suggest that invasive species generally display traits associated with high resource acquisition (Leishman et al. 2007, van Kleunen et al. 2010) or broad physiological niches (Higgins and Richardson 2014). However, most investigations of invasive species are conducted in high-resource environments, which are characterized by an abundance of water, soil nutrients, light, or a combination of these factors. High-resource environments are thought to favor species with high rates of resource acquisition while low-resource environments select for traits associated with stress tolerance (Chapin 1980, Craine 2009). In low-resource environments (e.g., deserts, ancient landscapes), plant productivity is severely

limited by light, water, or soil nutrient availability, and native plants often have adaptations allowing them to tolerate stress or enhance extraction of the limiting resource (e.g., Dallman 1998, Cramer et al. 2014). Stress often limits the range of trait values resulting in trait similarity between co-occurring species in low-resource environments (e.g., habitat filtering; Weiher and Keddy 1999). Thus, theoretically, native and invasive species in low-resource environments should display similar ranges of traits pertaining to resource acquisition and use. Understanding these functional differences is critical to designing management programs in invaded plant communities, especially where resources can be manipulated (e.g., through fire, grazing, carbon amendments; Funk et al. 2008).

Plants native to drought-prone environments, one type of low-resource system, frequently display one of two contrasting strategies: drought tolerance or drought avoidance (Ludlow 1989). Mediterranean-climate ecosystems (MCEs), which are characterized by cool, wet winters and hot, dry summers, provide examples of these two strategies. In response to summer water stress, perennial species in MCEs have

evolved traits associated with water conservation, including high leaf mass per unit area (LMA), small evergreen leaves, and a large investment in belowground biomass (Schenk and Jackson 2002, Thompson 2005). In contrast, many MCEs (California, Chile, Spain) also support a diversity of annual species, which complete their life cycle during the cool, wet winter/spring season to avoid drought stress altogether (Franks 2011). In contrast to perennial species, annual species often have traits associated with high resource acquisition (e.g., low LMA, high growth rate; Garnier 1992) although there can be significant trait variability within life form groups (Ackerly 2004, Lambers et al. 2010, Bermúdez and Retuerto 2014, Cramer et al. 2014).

Despite the summer drought, many invasive species thrive in MCEs (Arianoutsou et al. 2013), though few studies have examined how their physiological strategies compare to those of native species (e.g., Funk and Zachary 2010, Godoy et al. 2012). A recent review of invasion in low-resource ecosystems found that invasive species in arid and semiarid environments can display resource conservation traits by investing more biomass in root systems and maintaining high water-use efficiency (WUE) compared to native species (Funk 2013). While these trends begin to identify traits associated with invasiveness in low-resource environments, the suite of morphological and physiological traits associated with resource acquisition and use has yet to be examined jointly at community and global scales. Because MCEs are biodiversity hotspots and are under increasing pressure from changing environmental conditions and human activity (Sala et al. 2000, Ackerly et al. 2014), it is critical to advance our

understanding of invasion dynamics in these regions and the extent to which patterns are broadly generalizable (Vilà et al. 2008, Gaertner et al. 2009, Fried et al. 2014, Martín-Forés et al. 2015).

In this study, we measured 16 life-history, morphological, and physiological traits pertaining to resource acquisition and use from native and invasive species occurring in eight vegetation communities across the five MCE regions (Table 1). As fire history, soil nutrient availability, and grazing pressure differed across the eight sites, we expected substantial variation in trait values. For example, ancient soils in South Africa and Australia are lower in soil phosphorus (P) and, to a lesser extent, nitrogen (N) than other MCEs, and this should result in high leaf nutrient variation across sites (Stock and Verboom 2012). However, we predicted that drought stress imposed by the hot, dry summers in MCEs would lead to trait similarity between native and invasive species. This prediction diverges from the idea that invasive species display higher resource acquisition than co-occurring natives, which is largely based on results from high-resource environments. Because MCEs host drought-tolerant perennial species and annual species that avoid summer drought, we examined resource traits across and within these two life forms.

Methods

We selected eight moderately to heavily invaded MCE communities including grasslands, shrublands, and woodlands (Table 1). Our sites had similar mean annual precipitation (330–834 mm), but varied greatly in soil

Table 1. Site characteristics.

Region and site	Site code	Soil N (g N/100 g soil)	Soil total P (mg P/kg soil)	Soil pH	MAP (mm)	Grazing	Fire (yr)
California							
Coastal sage scrub	CSS	0.19	628.3	6.58	330	Low	3
Serpentine grassland	SG	0.23	30	6.69	760	Low	>50
Chile							
Sclerophyll woodland	SW	0.09	1001	7.15	360	None	>100
South Africa							
Fynbos	F	0.03	31.0	4.81	522	None	10
Renosterveld	R	0.29	304.0	5.75	515	None	>50
Spain							
Coastal grassland	CG	0.05	117.8	7.96	550	High	>50
Western Australia							
Banksia woodland	BW	0.05	47.7	5.38	834	Low	>20
Coastal banksia woodland	CBW	0.06	150.9	5.74	734	None	>30

Notes: Mean annual precipitation is abbreviated as MAP. Fire denotes the number of years since the last fire. Soil P values for SG are from Reference 1 and SW are from a nearby site (Pudahuel, http://ssldata.nrcs.usda.gov).

nutrient availability, grazing frequency, and fire history (Table 1). At each site, we collected functional trait data from five individuals of the most common invasive (5–9 species per site) and native (7–47 species per site) species for a total of 39 invasive and 129 native species (Appendix S1: Table S1). Some species occurred in more than one region. In our study, "invasive" refers to nonnative species that spread out of the area of introduction, reaching high local abundance at each site (Richardson et al. 2000, Colautti and MacIsaac 2004). Categorical data included nutrient acquisition strategy (NAS), maximum rooting depth, and life form. Nutrient acquisition strategy was assigned using information gathered from the literature (Appendix S2). We grouped species into four NAS categories: (1) facultative or obligate mycorrhizal, (2) nitrogen-fixing with or without mycorrhizae, (3) specialized roots (i.e., cluster roots, fine roots and long root hairs, parasitic root structures), and (4) none of the above (i.e., no specialized NAS, non-mycorrhizal plants). We used three categories of root depth (0–30 cm, 30–100 cm, or >100 cm). For annuals, perennial forbs, and small-statured woody species, we excavated the entire root system and measured maximum root depth. For large woody species, we assumed a root depth greater than 100 cm. We used the following six life form categories: petaloid monocot perennials, non-petaloid monocot annuals, non-petaloid monocot perennials, annual forbs, perennial forbs, and woody species. Petaloid monocots, or lilioids, is an informal, polyphyletic group of five monocot orders with similar flower morphology (Angiosperm Phylogeny Group III 2009).

Plant height was measured between the base of the stem and the apical shoot or tallest leaf (i.e., grasses). Flowering stalks were excluded from height measurements. Seed mass was determined using the Kew seed mass database (*available online*).[8] If a species was absent from the database, we used the mean of all species within that genera. Specific root length (SRL) was sampled for species with rooting depth less than 100 cm. Roots were either subsampled from excavated root systems or taken from soil cores made at 10 cm depth immediately adjacent (2–5 cm) to the stem. Root length was measured and roots were dried at 65°C for 3 d and weighed to determine SRL (cm^2·g^{-1}).

Physiological and chemical traits were measured on fully expanded, recently mature leaves in the middle of the spring growing season, prior to flowering. Photosynthetic and transpiration rates were measured with a LI-6400 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA). All measurements were conducted at saturating light levels (1600 µmol photons·m^{-2}·s^{-1}), 400 µL·L^{-1} CO$_2$, leaf temperature of 25°C, and at relative humidity of 40–60%. When necessary, photosynthetic rates were temperature-corrected using standard equations (von Caemmerer 2000).

Water-use efficiency was calculated as the ratio of photosynthesis to transpiration.

After photosynthetic measures, leaves were collected, scanned to determine leaf area, dried at 65°C for 3 d, and weighed to determine LMA. Ground leaves were analyzed for total plant N with an elemental analyzer (Costech 4010 elemental combustion system; Costech, Valencia, California, USA). Phosphorus content was determined colorimetrically using a discrete analyzer (SmartChem 200; Unity Scientific, Brookfield, Connecticut, USA) following Kjeldahl digest. Photosynthetic rates and leaf nutrient content were evaluated on an area and mass basis. Photosynthetic nitrogen-use efficiency (PNUE) and phosphorus-use efficiency (PPUE) were calculated as the ratio of photosynthesis to leaf N or P.

Statistical analysis

To examine differences in leaf-level traits between native and invasive plants across the five MCE regions, we used a mixed-model, nested ANOVA with region and origin (native or nonnative) as fixed factors and site (nested within region) and species (nested within origin) as random factors. When there was a significant interaction between region and origin, we conducted separate analyses within region, with origin as a fixed effect and site and species as random effects. Because we lacked sufficient replication for SRL and seed mass for many species, we used species means in our analysis and excluded "species" from the model for these two traits. Differences in trait values between native and invasive species were analyzed separately for annual and perennial groups across regions with site and species as random factors. Data were log-transformed prior to analysis. All mixed models were fit with the lme4 package (version 1.7; Bates et al. 2015) and the nloptr package (version 1.0.4, *available online*)[9] using the R statistical computing environment (version 3.2.0; R Development Core Team 2015). In order to compute *P* values, we used the Satterthwaite correction to approximate degrees of freedom, which are not well defined for a mixed model.

To test whether native and invasive species differed in categorical variables, we conducted chi-square tests on three-way contingency tables with the following log-linear model: site + origin + strategy + site × strategy + origin × site, where strategy is root depth, NAS, or life form. The null hypothesis is that strategy is independent of origin, given site. All analyses were conducted using the loglm function from the MASS package (version 7.3-40; Venables and Ripley 2002) in R.

Results

Across regions, many traits differed between native and invasive species (Appendix S3: Table S3). However, significant region by origin interactions (Table S3)
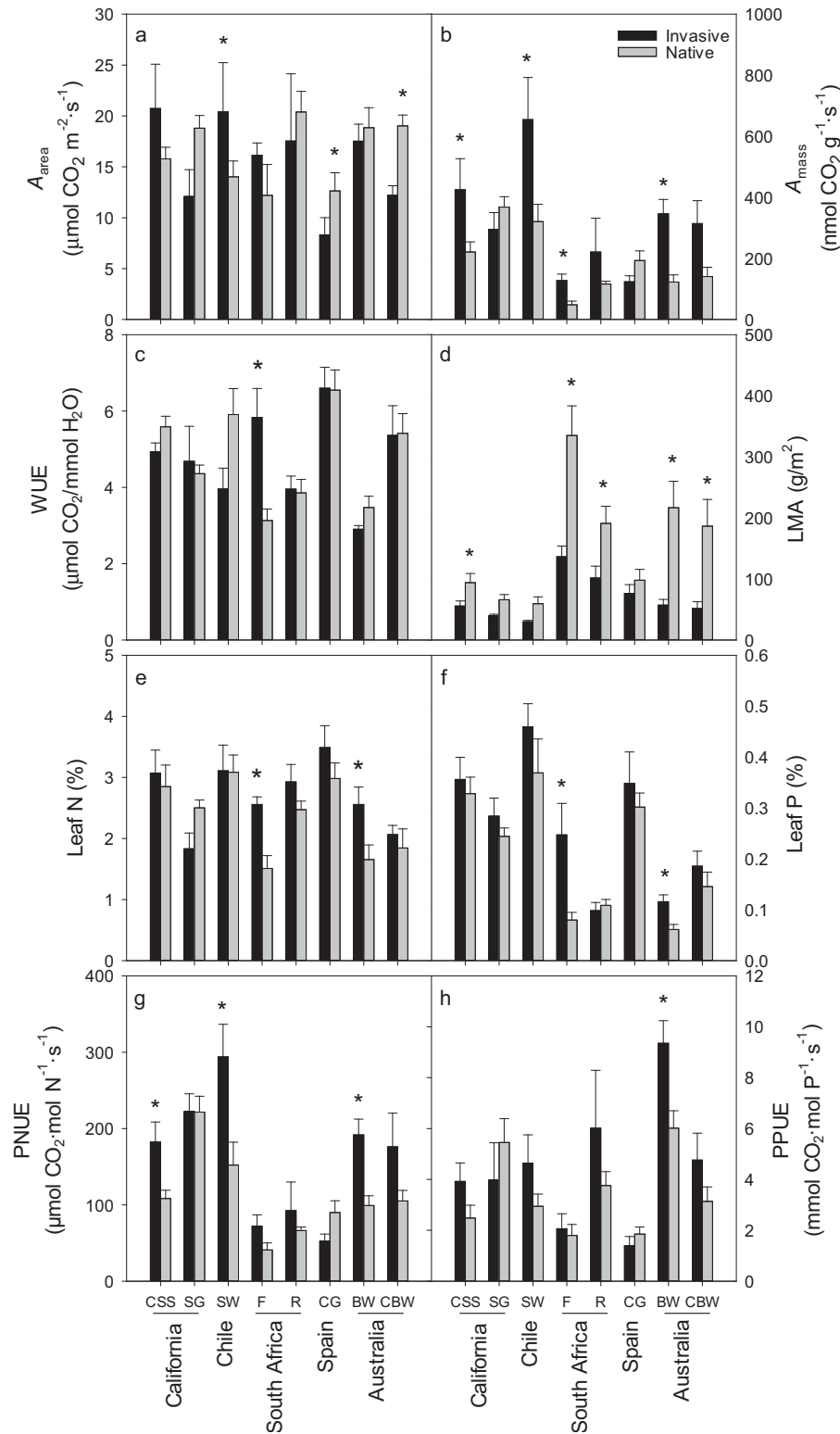
FIG. 1. Leaf-level trait data for native and invasive species including (a) area-based photosynthetic rate (A_{area}), (b) mass-based photosynthetic rate (A_{mass}), (C) water-use efficiency (WUE), (d) leaf mass per area (LMA), (e) leaf N content, (f) leaf P content, (g) photosynthetic nitrogen-use efficiency (PNUE), and (h) photosynthetic phosphorus-use efficiency (PPUE). Site codes are given in Table 1. Asterisks denote significant differences ($P < 0.05$) between native and invasive species within sites. Error bars show SE.

suggested that differences between species groups should be examined within regions. At the regional level, invasive species had higher mass-based photosynthetic rate (A_{mass}) and lower LMA than native species in South Africa and Western Australia (Fig. 1, Table 2). These patterns were evident within the coastal sage scrub site in California as well (Fig. 1). With respect to leaf nutrient traits, invasive species had higher mass-based leaf nitrogen content (N_{mass}), area-based leaf nitrogen content (N_{area}), and PNUE than native species within the South Africa and Western Australia regions (Table 2). Invasive species had higher mass-based leaf phosphorus content (P_{mass}), area-based leaf phosphorus content (P_{area}), and PPUE in Western Australia, which was largely driven by significant differences in the banksia woodland site (Fig. 1).

There were fewer differences between native and invasive species in non-leaf traits. Native species were taller than invasive species in Western Australia (Table 2, Fig. 2). Seed mass was higher for native species than invasive species in the coastal banksia woodland site (Western Australia), but higher for invasive species in the serpentine grassland site (Table 2, Fig. 2). Specific root length did not differ between native and invasive species within regions, but was higher for invasive species at one site (Renosterveld, South Africa; Fig. 2). Root depth (Fig. 3, $\chi^2 = 54.34$, $P < 0.0001$) was higher in native species relative to invasive species. Native and invasive species were similar with respect to nutrient acquisition strategy ($\chi^2 = 27.49$, $P = 0.28$).

Invasive species were nearly twice as likely to be annual grasses and forbs compared to natives (64% of invaders were annual compared to 38% of natives, Fig. 3, $\chi^2 = 116.63$, $P < 0.0001$). When comparing native and invasive annual species exclusively, we found that invasive annuals were taller with larger seeds and thinner roots (high SRL), traits associated with greater resource acquisition (Table 3). Despite these morphological differences, rates of resource acquisition and use (e.g., photosynthetic rates, leaf nutrient content, resource-use efficiency) were similar between native and invasive annual species (Table 3), which differs from the pattern we observed in some regions when annuals and perennials were considered together. Perennial native and invasive species only differed with respect to one trait. Invasive perennials had higher leaf N content (N_{mass}) compared to native perennials (Table 3).

DISCUSSION

Our results from a diverse range of drought-prone mediterranean-climate ecosystems suggest that the traits that make invasive species successful depend strongly on the invaded habitat. Despite similar timing

TABLE 2. ANOVA results for the effect of origin (native or invasive species) on continuous traits within each of the five mediterranean-climate regions.

Traits	California		Chile		South Africa		Spain		Western Australia	
	F	P	F	P	F	P	F	P	F	P
Leaf-level										
A_{area}	0.48 (1,56)	0.49	5.74 (1,17)	**0.03**	0.34 (1,27)	0.56	1.47 (1,28)	0.24	2.40 (1,21)	0.14
A_{mass}	0.53 (1,69)	0.47	8.67 (1,17)	**0.009**	7.34 (1,28)	**0.01**	0.15 (1,28)	0.70	13.55 (1,21)	**0.001**
WUE	0.00 (1,73)	0.95	2.61 (1,17)	0.12	4.27 (1,27)	0.05	0.13 (1,28)	0.72	1.95 (1,20)	0.18
LMA	3.20 (1,72)	0.08	3.16 (1,17)	0.09	12.04 (1,28)	**0.002**	0.70 (1,28)	0.41	31.32 (1,22)	**<0.0001**
N_{mass}	0.22 (1,75)	0.64	0.10 (1,17)	0.76	5.49 (1,28)	**0.03**	1.69 (1,28)	0.20	6.49 (1,22)	**0.02**
N_{area}	3.18 (1,73)	0.08	1.87 (1,17)	0.19	4.74 (1,28)	**0.04**	0.00 (1,28)	0.98	28.55 (1,22)	**<0.0001**
PNUE	1.98 (1,72)	0.16	9.51 (1,17)	**0.007**	5.71 (1,27)	**0.02**	0.95 (1,28)	0.34	11.27 (1,21)	**0.003**
P_{mass}	2.14 (1,53)	0.15	3.05 (1,17)	0.10	1.98 (1,28)	0.17	0.18 (1,28)	0.67	8.90 (1,22)	**0.007**
P_{area}	0.07 (1,53)	0.79	0.02 (1,17)	0.89	1.53 (1,27)	0.23	0.33 (1,28)	0.57	19.87 (1,22)	**0.0002**
PPUE	0.02 (1,53)	0.88	4.05 (1,17)	0.06	4.06 (1,27)	0.05	0.57 (1,28)	0.46	9.05 (1,21)	**0.007**
Root, plant, and seed										
SRL	0.87 (1,67)	0.36	0.06 (1,8)	0.81	1.33 (1,10)	0.28	0.00 (1,20)	0.98	1.44 (1,17)	0.25
Height	1.70 (1,75)	0.20	2.40 (1,17)	0.14	0.64 (1,28)	0.43	1.79 (1,28)	0.19	6.89 (1,21)	**0.02**
Seed mass	5.18 (1,73)	**0.03**	0.28 (1,12)	0.61	0.06 (1,28)	0.81	0.01 (1,28)	0.92	9.67 (1,27)	**0.004**

Notes: For F values, numerator and denominator degrees of freedom are given in parentheses. Significant effects ($P < 0.05$) are in boldface type. Abbreviations are A_{area}, area-based photosynthetic rate; A_{mass}, mass-based photosynthetic rate; WUE, water-use efficiency; LMA, leaf mass per area; N_{mass}, mass-based leaf nitrogen content; N_{area}, area-based leaf nitrogen content; PNUE, photosynthetic nitrogen-use efficiency; P_{mass}, mass-based leaf phosphorus content; P_{area}, area-based leaf phosphorus content; PPUE, photosynthetic phosphorus-use efficiency.
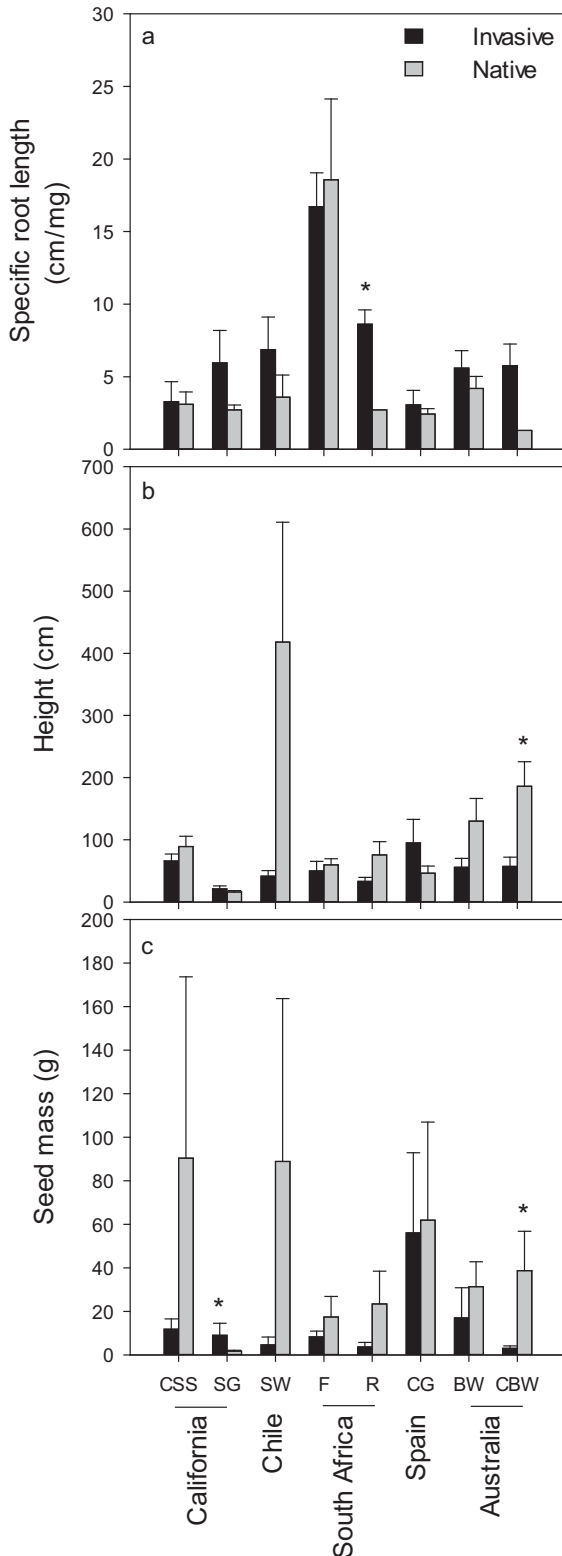
Fig. 2. (a) Specific root length, (b) plant height, and (c) seed mass. Site codes are given in Table 1. Asterisks denote significant differences ($P < 0.05$) between native and invasive species within sites. Error bars show SE.

and magnitude of rainfall, our sites differed considerably in several environmental factors such as soil nutrient availability, fire history, and grazing pressure. As a consequence, traits differed more strongly across regions than between native and invasive species. The regions with functional differences between native and invasive species (Chile, South Africa, Western Australia) are dominated by woody (often evergreen) native species while invasive species are almost exclusively annual (Appendix S1: Table S11). The difference between native and invasive species is particularly striking for the Western Australian ecosystems. In contrast, the other three sites (Spain and California) were grasslands or shrublands where native species are primarily herbs or drought-deciduous perennials. Drought-deciduous species often have leaf characteristics that more closely resemble annual species than evergreen perennials (e.g., Jacobsen et al. 2008). Thus, trait differences at the regional level may be explained by differences in life form between native and invasive species groups.

Our finding that invasive species were more likely to be annual than native species contrasts with results from Arianoutsou et al. (2013), who found that MCE invaders were more frequently herbaceous perennials. This discrepancy may result from our narrowed focus on eight specific communities as opposed to entire regions in Arianoutsou et al. (2013). Despite accounting for a lower percentage of regional invaders, our findings may indicate that annuals achieve higher abundances in the field compared to perennial species. Many annual and perennial herbs have traits that facilitate invasiveness such as large seedbanks, increased propagule pressure, and resilience to grazing. Additionally, annual invaders may succeed in MCEs through drought avoidance. While our experiment was not designed to include a complete complement of life forms within native and invasive species groups at each site (i.e., native and invasive annuals, native and invasive perennials), to determine whether invasive annuals and perennials are generally better than their native counterparts at acquiring resources, we analyzed functional traits separately for these groups across regions. We found only one difference between native and invasive perennial species, which suggests that invasive perennials are functionally similar to natives in these drought-prone regions. Within annual species, we found that invasive species had higher SRL, seed mass, and stature relative to native species. However, these morphological advantages did not translate into greater carbon assimilation (A_{mass}, A_{area}) or resource-use efficiency (WUE, PNUE, PPUE).

Why might morphological differences (e.g., height, SRL) between species groups not be reflected in patterns of carbon assimilation? One reason is scale. Relationships between leaf- and plant-level traits are often observed across diverse taxonomic and
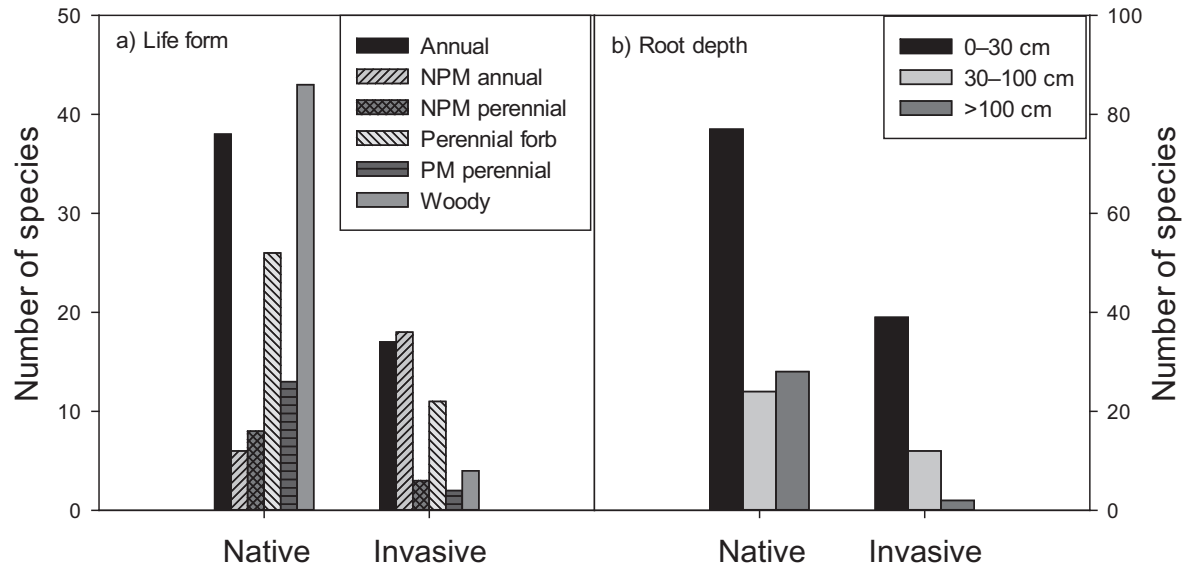
FIG. 3. The number of native and invasive species in (a) six life form and (b) three root depth categories across eight sites from Mediterranean-climate ecosystems.

biogeographic ranges. For example, the leaf economics spectrum, which shows strong correlations between key leaf-level traits, was developed on a global scale encompassing a broad range of species and climates (Reich et al. 1997). However, these key leaf-level traits do not necessarily correlate at smaller scales, which

is due in part to the low variation within some of these traits at the community scale (e.g., grasslands dominated by annual species; Funk and Cornwell 2013).

A second reason for the decoupling between morphological and physiological traits is environmental

TABLE 3. Trait values for native ($n = 44$) and invasive ($n = 35$) annual and native ($n = 90$) and invasive ($n = 20$) perennial species, pooled across eight sites within the five mediterranean-climate ecosystems.

Traits	Annual species			Perennial species		
	Native	Invasive	Origin	Native	Invasive	Origin
Leaf-level						
A_{area}	18.5 (1.4)	16.7 (1.6)		15.7 (0.8)	14.1 (2.2)	
A_{mass}	352 (27)	363 (39)		190 (20)	249 (70)	
WUE	4.8 (0.3)	4.5 (0.3)		4.8 (0.2)	5.4 (0.5)	
LMA	62.0 (7.3)	59.3 (6.2)		153 (14)	78.1 (10.1)	
N_{mass}	2.7 (0.1)	2.7 (0.1)		2.4 (0.1)	2.9 (0.3)	*
N_{area}	1.8 (0.3)	1.6 (0.2)		2.9 (0.2)	2.1 (0.3)	
PNUE	200 (16)	192 (17)		110 (11)	110 (22)	
P_{mass}	0.30 (0.02)	0.28 (0.03)		0.20 (0.02)	0.25 (0.04)	
P_{area}	217 (53)	152 (21)		212 (15)	163 (25)	
PPUE	3.9 (0.5)	5.0 (0.6)		3.4 (0.4)	3.8 (0.8)	
Root, plant, and seed						
SRL	3.0 (0.5)	6.8 (0.9)	**	4.1 (0.8)	4.5 (1.1)	
Height	16.5 (2.8)	42.1 (5.3)	*	126 (29)	81.9 (17.3)	
Seed mass	3.8 (1.6)	9.7 (3.6)	*	50.8 (19.4)	30.4 (17.9)	

Values in parentheses are SE. Asterisks denote a significant difference between native and invasive species within each group ($*P < 0.05$, $**P < 0.01$). Trait abbreviations as in Table 2.

context. Great stature and low LMA facilitate light capture and have been positively associated with competitive ability, but these traits may not confer higher rates of carbon assimilation in drought-prone environments, where photosynthesis is more strongly limited by carbon (e.g., stomatal closure in response to drought) than energy (e.g., light limitation). Lastly, individual traits likely need to be interpreted in the context of other traits. High SRL may facilitate rapid uptake of water and nutrients and, consequently, increase rates of carbon assimilation. However, water and nutrient uptake will be influenced by a suite of traits (e.g., root length density, root distribution, tissue density), not just SRL (Laughlin et al. 2010). Thus, analyses of functional similarity among native and invasive species that rely exclusively on a handful of traits, like LMA or height, may be misleading as the function of these traits can be context dependent.

Where there were differences between native and invasive species, either within sites or life form groups, invasive species mostly displayed resource acquisition traits—low LMA, high photosynthetic rate, and high leaf nutrient content—rather than traits associated with resource-use efficiency. This finding supports recent work showing that invasive species tend to be located at the "high-return" end of the leaf economics spectrum, which is characterized by high rates of carbon assimilation and low investment in structure (Leishman et al. 2007, Ordoñez et al. 2010, Peñuelas et al. 2010). Notably, invasive species in the banksia woodland (Western Australia) community displayed high resource acquisition (leaf N and P) and high resource conservation (PNUE and PPUE). This result adds to growing evidence that some invasive species succeed in low-resource ecosystems by employing both resource acquisition and conservation strategies (Funk and Vitousek 2007, Matzek 2012, Oliveira et al. 2014).

Focusing on a broad range of traits pertaining to resource use, we found functional differences between native and invasive species within MCE regions where species groups differed in life form. Many invasive species in MCEs appear to succeed through drought avoidance associated with an annual life form, but collectively they do not display superior resource acquisition traits compared with native annual species. Our experiment focused on identifying traits of the most abundant (i.e., successful) invasive species at a site, and was not designed to test how native and invasive species differ within life form. Thus, additional studies are needed that survey traits from a larger number of annual or perennial species within individual habitats. In light of our context-dependent results across regions, we argue that attempts to identify the mechanisms of invasiveness should be made within individual communities rather than at the global level (Maron and Marler 2008, Moles et al. 2008). Finally, similar patterns of resource use among native and invasive species may limit restoration approaches that aim to manipulate resources to curtail the growth of invasive species, but our study ignored other key aspects of resource use such as phenology and dormancy which may suggest alternative manipulations for restoration (Funk et al. 2008).

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