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1   Running head: Functional traits and invasion

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3   **Plant functional traits of dominant native and invasive species in Mediterranean-climate**

4   **ecosystems**

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22   **Abstract**

23   The idea that dominant invasive plant species outperform neighboring native species through

24   higher rates of carbon assimilation and growth is supported by several analyses of global

25   datasets. However, theory suggests that native and invasive species occurring in low-resource

26   environments will be functionally similar, as environmental factors restrict the range of observed

27   physiological and morphological trait values. We measured resource-use traits in native and

28   invasive plant species across eight diverse vegetation communities distributed throughout the

29   five Mediterranean-climate regions, which are drought-prone and increasingly threatened by

30   human activities including the introduction of exotic species. Traits differed strongly across the

31   five regions. In regions with functional differences between native and invasive species groups,

32   invasive species displayed traits consistent with high resource acquisition; however, these

33   patterns were largely attributable to differences in life form. We found that species invading

34   Mediterranean-climate regions were more likely to be annual than perennial – three of the five

35   regions were dominated by native woody species and invasive annuals. These results suggest

36   that trait differences between native and invasive species are context dependent and will vary

37   across vegetation communities. Native and invasive species within annual and perennial groups

38   had similar patterns of carbon assimilation and resource-use, which contradicts the widespread

39   idea that invasive species optimize resource acquisition rather than resource conservation.

Introduction

40 One of the greatest challenges in conserving and restoring plant communities is identifying the

41 mechanisms by which invasive species outperform native species. Analyses of global datasets

42 suggest that invasive species generally display traits associated with high resource acquisition

43 (Leishman et al. 2007, van Kleunen et al. 2010) or broad physiological niches (Higgins and

44 Richardson 2014). However, most investigations of invasive species are conducted in high-

45 resource environments, which are characterized by an abundance of water, soil nutrients, light or

46 a combination of these factors. High-resource environments are thought to favor species with

47 high rates of resource acquisition while low-resource environments select for traits associated

48 with stress tolerance (Chapin 1980, Craine 2009). In low-resource environments (e.g., deserts,

49 ancient landscapes), plant productivity is severely limited by light, water, or soil nutrient

50 availability, and native plants often have adaptations allowing them to tolerate stress or enhance

51 extraction of the limiting resource (e.g., Cramer et al. 2014, Dallman 1998). Stress often limits

52 the range of trait values resulting in trait similarity between co-occurring species in low-resource

53 environments (e.g., habitat filtering; Weiher and Keddy 1999). Thus, theoretically, native and

54 invasive species in low-resource environments should display similar ranges of traits pertaining

55 to resource acquisition and use. Understanding these functional differences is critical to

56 designing management programs in invaded plant communities, especially where resources can

57 be manipulated (e.g., through fire, grazing, carbon amendments; Funk et al. 2008).

58

59 Plants native to drought-prone environments, one type of low-resource system, frequently

60 display one of two contrasting strategies: drought tolerance or drought avoidance (Ludlow 1989).

61 Mediterranean-climate ecosystems (MCEs), which are characterized by cool, wet winters and

63   hot, dry summers, provide examples of these two strategies. In response to summer water stress,

64   perennial species in MCEs have evolved traits associated with water conservation, including

65   high leaf mass per unit area (LMA), small evergreen leaves, and a large investment in below-

66   ground biomass (Schenk and Jackson 2002, Thompson 2005). In contrast, many MCEs

67   (California, Chile, Spain) also support a diversity of annual species, which complete their life

68   cycle during the cool, wet winter/spring season to avoid drought stress altogether (Franks 2011).

69   In contrast to perennial species, annual species often have traits associated with high resource

70   acquisition (e.g., low LMA, high growth rate; Garnier 1992) although there can be signficant

71   trait variability within life form groups (Ackerly 2004, Bermúdez and Retuerto 2014, Cramer et

72   al. 2014, Lambers et al. 2010).

73

74   Despite the summer drought, many invasive species thrive in MCEs (Arianoutsou et al. 2013),

75   though few studies have examined how their physiological strategies compare to those of native

76   species (e.g., Funk and Zachary 2010, Godoy et al. 2012). A recent review of invasion in low-

77   resource ecosystems found that invasive species in arid and semi-arid environments can display

78   resource conservation traits by investing more biomass in root systems and maintaining high

79   water-use efficiency (WUE) compared to native species (Funk 2013). While these trends begin

80   to identify traits associated with invasiveness in low-resource environments, the suite of

81   morphological and physiological traits associated with resource acquisition and use has yet to be

82   examined jointly at community- and global scales. Because MCEs are biodiversity hotspots and

83   are under increasing pressure from changing environmental conditions and human activity

84   (Ackerly et al. 2014, Sala et al. 2000), it is critical to advance our understanding of invasion

85 dynamics in these regions and the extent to which patterns are broadly generalizable (Fried et al.

86 2014, Gaertner et al. 2009, Martín-Forés et al. 2015, Vilà et al. 2008).

87

88 In this study, we measured 16 life-history, morphological, and physiological traits pertaining to

89 resource acquisition and use from native and invasive species occurring in eight vegetation

90 communities across the five MCE regions (Table 1). As fire history, soil nutrient availability

91 and grazing pressure differed across the eight sites, we expected substantial variation in trait

92 values. For example, ancient soils in South Africa and Australia are lower in soil phosphorus (P)

93 and, to a lesser extent, nitrogen (N) than other MCEs, and this should result in higher leaf

94 nutrient variation across sites (Stock and Verboom 2012). However, we predicted that drought

95 stress imposed by the hot, dry summers in MCEs would lead to trait similarity between native

96 and invasive species. This prediction diverges from the idea that invasive species display higher

97 resource acquisition than co-occurring natives, which is largely based on results from high-

98 resource environments. Because MCEs host drought-tolerant perennial species and annual

99 species that avoid summer drought, we examined resource traits across and within these two life

100 forms.

101

102 **Methods**

103 We selected eight moderately to heavily invaded MCE communities including grasslands,

104 shrublands, and woodlands (Table 1). Our sites had similar mean annual precipitation (330–834

105 mm), but varied greatly in soil nutrient availability, grazing frequency, and fire history (Table 1).

106 At each site, we collected functional trait data from five individuals of the most common

107 invasive (5–9 species per site) and native (7–47 species per site) species for a total of 39 invasive

108   and 129 native species (Appendix A, Table A1). Some species occurred in more than one

109   region. In our study "invasive" refers to non-native species that spread out of the area of

110   introduction, reaching high local abundance at each site (Colautti and MacIsaac 2004,

111   Richardson et al. 2000). Categorical data included nutrient acquisition strategy (NAS),

112   maximum rooting depth, and life form. Nutrient acquisition strategy was assigned using

113   information gathered from the literature (Appendix B). We grouped species into four NAS

114   categories: (1) facultative or obligate mycorrhizal, (2) nitrogen-fixing with or without

115   mycorrhizae, (3) specialized roots (i.e., cluster roots, fine roots and long root hairs, parasitic root

116   structures), and (4) none of the above (i.e., no specialized NAS, non-mycorrhizal plants). We

117   used three categories of root depth (0-30 cm, 30-100 cm, or greater than 100 cm). For annuals,

118   perennial forbs, and small-statured woody species, we excavated the entire root system and

119   measured maximum root depth. For large woody species, we assumed a root depth greater than

120   100 cm. We used the following six life form categories: petaloid monocot perennials, non-

121   petaloid monocot annuals, non-petaloid monocot perennials, annual forbs, perennial forbs, and

122   woody species. Petaloid monocots, or lilioids, is an informal, polyphyletic group of five

123   monocot orders with similar flower morphology (Angiosperm Phylogeny Group III 2009).

124

125   Plant height was measured between the base of the stem and the apical shoot or tallest leaf (i.e.,

126   grasses). Flowering stalks were excluded from height measurements. Seed mass was

127   determined using the Kew seed mass database (http://data.kew.org/sid). If a species was absent

128   from the database, we used the mean of all species within that genera. Specific root length

129   (SRL) was sampled for species with rooting depth less than 100 cm. Roots were either sub-

130   sampled from excavated root systems or taken from soil cores made at 10 cm depth immediately

131   adjacent (2-5 cm) to the stem. Root length was measured and roots were dried at 65 °C for 3

132   days and weighed to determine SRL (cm^2 g^{-1}).

133

134   Physiological and chemical traits were measured on fully expanded, recently mature leaves in the

135   middle of the spring growing season, prior to flowering. Photosynthetic and transpiration rates

136   were measured with a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE). All

137   measurements were conducted at saturating light levels (1600 μmol photon m^{-2} s^{-1}), 400 μL L^{-1}

138   CO_2, leaf temperature of 25 ^{o}C, and at relative humidity of 40-60%. When necessary,

139   photosynthetic rates were temperature-corrected using standard equations (von Caemmerer

140   2000). Water-use efficiency was calculated as the ratio of photosynthesis to transpiration.

141

142   After photosynthetic measures, leaves were collected, scanned to determine leaf area, dried at 65

143   °C for 3 days, and weighed to determine LMA. Ground leaves were analyzed for total plant N

144   with an elemental analyzer (Costech 4010 elemental combustion system, Valencia, CA).

145   Phosphorus content was determined colorimetrically using a discrete analyzer (SmartChem 200,

146   Unity Scientific, Brookfield, CT) following Kjeldahl digest. Photosynthetic rates and leaf

147   nutrient content were evaluated on an area and mass basis. Photosynthetic nitrogen-use

148   efficiency (PNUE) and phosphorus-use efficiency (PPUE) were calculated as the ratio of

149   photosynthesis to leaf N or P.

150

151   *Statistical analysis*

152   To examine differences in leaf-level traits between native and invasive plants across the five

153   MCE regions we used a mixed-model, nested ANOVA with region and origin (native or non-

154 native) as fixed factors and site (nested within region) and species (nested within origin) as

155 random factors. When there was a significant interaction between region and origin, we

156 conducted separate analyses within region, with origin as a fixed effect and site and species as

157 random effects. Because we lacked sufficient replication for SRL and seed mass for many

158 species, we used species means in our analysis and excluded 'species' from the model for these

159 two traits. Differences in trait values between native and invasive species were analyzed

160 separately for annual and perennial groups across regions with site and species as random

161 factors. Data were log transformed prior to analysis. All mixed models were fit with the `lme4`

162 package (version 1.7) and the `nloptr` package (version 1.0.4) using the R statistical computing

163 environment (version 3.2.0). In order to compute P-values we used the Satterthwaite correction

164 to approximate degrees of freedom, which are not well defined for a mixed-model.

165

166 To test whether native and invasive species differed in categorical variables, we conducted chi-

167 square tests on three-way contingency tables with the following log linear model: site + origin +

168 strategy + site × strategy + origin × site, where strategy is root depth, NAS, or life form. The null

169 hypothesis is that strategy is independent of origin, given site. All analyses were conducted

170 using the `loglm` function from the `MASS` package (version 7.3-40) in R.

171

172 **Results**

173 Across regions, many traits differed between native and invasive species (Appendix C, Table

174 C1). However, significant region by origin interactions (Appendix C, Table C1) suggested that

175 differences between species groups should be examined within regions. At the regional level,

176 invasive species had higher A_{mass} and lower LMA than native species in South Africa and

177   Western Australia (Fig. 1, Table 2). These patterns were evident within the coastal sage scrub

178   site in California as well (Fig. 1). With respect to leaf nutrient traits, invasive species had higher

179   N_{mass}, N_{area}, and PNUE than native species within the South Africa and Western Australia

180   regions (Table 2). Invasive species had higher P_{mass}, P_{area}, and PPUE in Western Australia,

181   which was largely driven by significant differences in the banksia woodland site (Fig. 1).

182

183   There were fewer differences between native and invasive species in non-leaf traits. Native

184   species were taller than invasive species in Western Australia (Table 2, Fig. 2). Seed mass was

185   higher for native species than invasive species in the coastal banksia woodland site (Western

186   Australia), but higher for invasive species in the serpentine grassland site (Table 2, Fig. 2).

187   Specific root length did not differ between native and invasive species within regions, but was

188   higher for invasive species at one site (Renosterveld, South Africa, Fig. 2). Root depth (Fig. 3,

189   $\chi^2 = 54.34$, $P < 0.0001$) was higher in native species relative to invasive species. Native and

190   invasive species were similar with respect to nutrient acquisition strategy ($\chi^2 = 27.49$, $P = 0.28$).

191

192   Invasive species were nearly twice as likely to be annual grasses and forbs compared to natives

193   (64% of invaders were annual compared to 38% of natives, Fig. 3, $\chi^2 = 116.63$, $P < 0.0001$).

194   When comparing native and invasive annual species exclusively, we found that invasive annuals

195   were taller with larger seeds and thinner roots (high SRL) – traits associated with greater

196   resource acquisition (Table 3). Despite these morphological differences, rates of resource

197   acquisition and use (e.g., photosynthetic rates, leaf nutrient content, resource-use efficiency)

198   were similar between native and invasive annual species (Table 3), which differs from the

199   pattern we observed in some regions when annuals and perennials were considered together.

200   Perennial native and invasive species only differed with respect to one trait. Invasive perennials

201   had higher leaf N content (N_{mass}) compared to native perennials (Table 3).

202

203   **Discussion**

204   Our results from a diverse range of drought-prone Mediterranean-climate ecosystems suggest

205   that the traits that make invasive species successful depend strongly on the invaded habitat.

206   Despite similar timing and magnitude of rainfall, our sites differed considerably in several

207   environmental factors such as soil nutrient availability, fire history, and grazing pressure. As a

208   consequence, traits differed more strongly across regions than between native and invasive

209   species. The regions with functional differences between native and invasive species (Chile,

210   South Africa, Western Australia) are dominated by woody (often evergreen) native species while

211   invasive species are almost exclusively annual (Appendix A, Table A1). The difference between

212   native and invasive species is particularly striking for the Western Australian ecosystems. In

213   contrast, the other three sites (Spain and California) were grasslands or shrublands where native

214   species are primarily herbs or drought-deciduous perennials. Drought-deciduous species often

215   have leaf characteristics that more closely resemble annual species than evergreen perennials

216   (e.g., Jacobsen et al. 2008). Thus, trait differences at the regional level may be explained by

217   differences in life form between native and invasive species groups.

218

219   Our finding that invasive species were more likely to be annual than native species contrasts with

220   results from Arianoutsou et al. (2013), who found that MCE invaders were more frequently

221   herbaceous perennials. This discrepancy may result from our narrowed focus on eight specific

222   communities as opposed to entire regions in Arianoutsou et al. (2013). Despite accounting for a

223   lower percentage of regional invaders, our findings may indicate that annuals achieve higher

224   abundances in the field compared to perennial species. Many annual and perennial herbs have

225   traits that facilitate invasiveness such as large seedbanks, increased propagule pressure, and

226   resilience to grazing. Additionally, annual invaders may succeed in MCEs through drought

227   avoidance. While our experiment was not designed to include a complete complement of life

228   forms within native and invasive species groups at each site (i.e., native and invasive annuals,

229   native and invasive perennials), to determine whether invasive annuals and perennials are

230   generally better than their native counterparts at acquiring resources, we analyzed functional

231   traits separately for these groups across regions. We found only one difference between native

232   and invasive perennial species, which suggests that invasive perennials are functionally similar

233   to natives in these drought-prone regions. Within annual species, we found that invasive species

234   had higher SRL, seed mass, and stature relative to native species. However, these morphological

235   advantages did not translate into greater carbon assimilation (A_{mass}, A_{area}) or resource-use

236   efficiency (WUE, PNUE, PPUE).

237

238   Why might morphological differences (e.g., height, SRL) between species groups not be

239   reflected in patterns of carbon assimilation? One reason is scale. Relationships between leaf-

240   and plant-level traits are often observed across diverse taxonomic and biogeographic ranges. For

241   example, the leaf economics spectrum, which shows strong correlations between key leaf-level

242   traits, was developed on a global scale encompassing a broad range of species and climates

243   (Reich et al. 1997). However, these key leaf-level traits do not necessarily correlate at smaller

244   scales, which is due in part to the low variation within some of these traits at the community

245   scale (e.g., grasslands dominated by annual species; Funk and Cornwell 2013).

246

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

248   environmental context. Great stature and low LMA facilitate light capture and have been

249   positively associated with competitive ability, but these traits may not confer higher rates of

250   carbon assimilation in drought-prone environments, where photosynthesis is more strongly

251   limited by carbon (e.g., stomatal closure in response to drought) than energy (e.g., light

252   limitation). Lastly, individual traits likely need to be interpreted in the context of other traits.

253   High SRL may facilitate rapid uptake of water and nutrients and, consequently, increase rates of

254   carbon assimilation. However, water and nutrient uptake will be influenced by a suite of traits

255   (e.g., root length density, root distribution, tissue density), not just SRL (Laughlin et al. 2010).

256   Thus, analyses of functional similarity among native and invasive species that rely exclusively

257   on a handful of traits, like LMA or height, may be misleading as the function of these traits can

258   be context-dependent.

259

260   Where there were differences between native and invasive species, either within sites or life form

261   groups, invasive species mostly displayed resource acquisition traits – low LMA, high

262   photosynthetic rate, and high leaf nutrient content – rather than traits associated with resource-

263   use efficiency. This finding supports recent work showing that invasive species tend to be

264   located at the "high-return" end of the leaf economics spectrum, which is characterized by high

265   rates of carbon assimilation and low investment in structure (Leishman et al. 2007, Ordoñez et al.

266   2010, Peñuelas et al. 2010). Notably, invasive species in the banksia woodland (Western

267   Australia) community displayed high resource acquisition (leaf N and P) and high resource

268   conservation (PNUE and PPUE). This result adds to growing evidence that some invasive

12

269 species succeed in low-resource ecosystems by employing both resource acquisition and

270 conservation strategies (Funk and Vitousek 2007, Matzek 2012, Oliveira et al. 2014).

271

272 Focusing on a broad range of traits pertaining to resource use, we found functional differences

273 between native and invasive species within MCE regions where species groups differed in life

274 form. Many invasive species in MCEs appear to succeed through drought avoidance associated

275 with an annual life form, but collectively they do not display superior resource acquisition traits

276 compared with native annual species. Our experiment focused on identifying traits of the most

277 abundant (i.e., successful) invasive species at a site, and was not designed to test how native and

278 invasive species differ within life form. Thus, additional studies are needed that survey traits

279 from a larger number of annual or perennial species within individual habitats. In light of our

280 context-dependent results across regions, we argue that attempts to identify the mechanisms of

281 invasiveness should be made within individual communities rather than at the global level

282 (Maron and Marler 2008, Moles et al. 2008). Finally, similar patterns of resource use among

283 native and invasive annual species may limit restoration approaches that aim to manipulate

284 resources to curtail the growth of invasive species, but our study ignored other key aspects of

285 resource use such as phenology and dormancy which may suggest alternative manipulations for

286 restoration (Funk et al. 2008).

287

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295

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411   Appendix A (Table A1). Information for species included in the study.

412   Appendix B. List of references for seed masses and for NAS data

413   Appendix C (Table C1). Results of mixed-model ANOVA for continuous traits across five

414   Mediterranean-climate regions.

415

416   **Author Contributions**

417   JLF and RJS conceived and designed the study. RJS, WDS and FV conducted field work and

418   contributed to writing. JLF was the primary writer.

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420   The authors declare no conflict of interest.

Table 1 - Site characteristics. 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).

Region	Site	Site code	Soil N (g/100g)	Soil total P (mg/kg)	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[1]	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

Table 2 – ANOVA for the effect of origin (native or invasive species) on continuous traits within each of the five Mediterranean regions. For F-values, numerator and denominator degrees of freedom are given in parentheses. Significant effects ($P < 0.05$) are in bold.

	California		Chile		South Africa		Spain		Western Australia	
	F	P	F	P	F	P	F	P	F	P
Leaf-level traits										
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 traits										
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**

Abbreviations: Area-based photosynthetic rate (A_{area}), mass-based photosynthetic rate (A_{mass}), water-use efficiency (WUE), leaf mass per area (LMA), mass-based leaf nitrogen content (N_{mass}), area-based leaf nitrogen content (N_{area}), photosynthetic nitrogen-use efficiency (PNUE), mass-based leaf phosphorus content (P_{mass}), area-based leaf phosphorus content (P_{area}), photosynthetic phosphorus-use efficiency (PPUE).

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 MCEs. 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.

	Annual species			Perennial species		
	Native	Invasive	Origin	Native	Invasive	Origin
Leaf-level traits						
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)	

23

Root, plant, and seed traits

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)

Figure Legend

Fig. 1. Leaf-level trait data for native and invasive species including area-based photosynthetic rate (a), mass-based photosynthetic rate (b), water-use efficiency (c), leaf mass per area (d), leaf N content (e), leaf P content (f), photosynthetic nitrogen-use efficiency (g), and photosynthetic phosphorus-use efficiency (h). Site codes are given in Table 1. Asterisks denote significant differences ($P < 0.05$) between native and invasive species within sites.

Fig. 2. Specific root length (a), plant height (b), and seed mass (c). Site codes are given in Table 1. Asterisks denote significant differences ($P < 0.05$) between native and invasive species within sites.

Fig. 3. The number of native and invasive species in six life form (a) and root depth (b) categories across eight sites from Mediterranean-climate ecosystems.
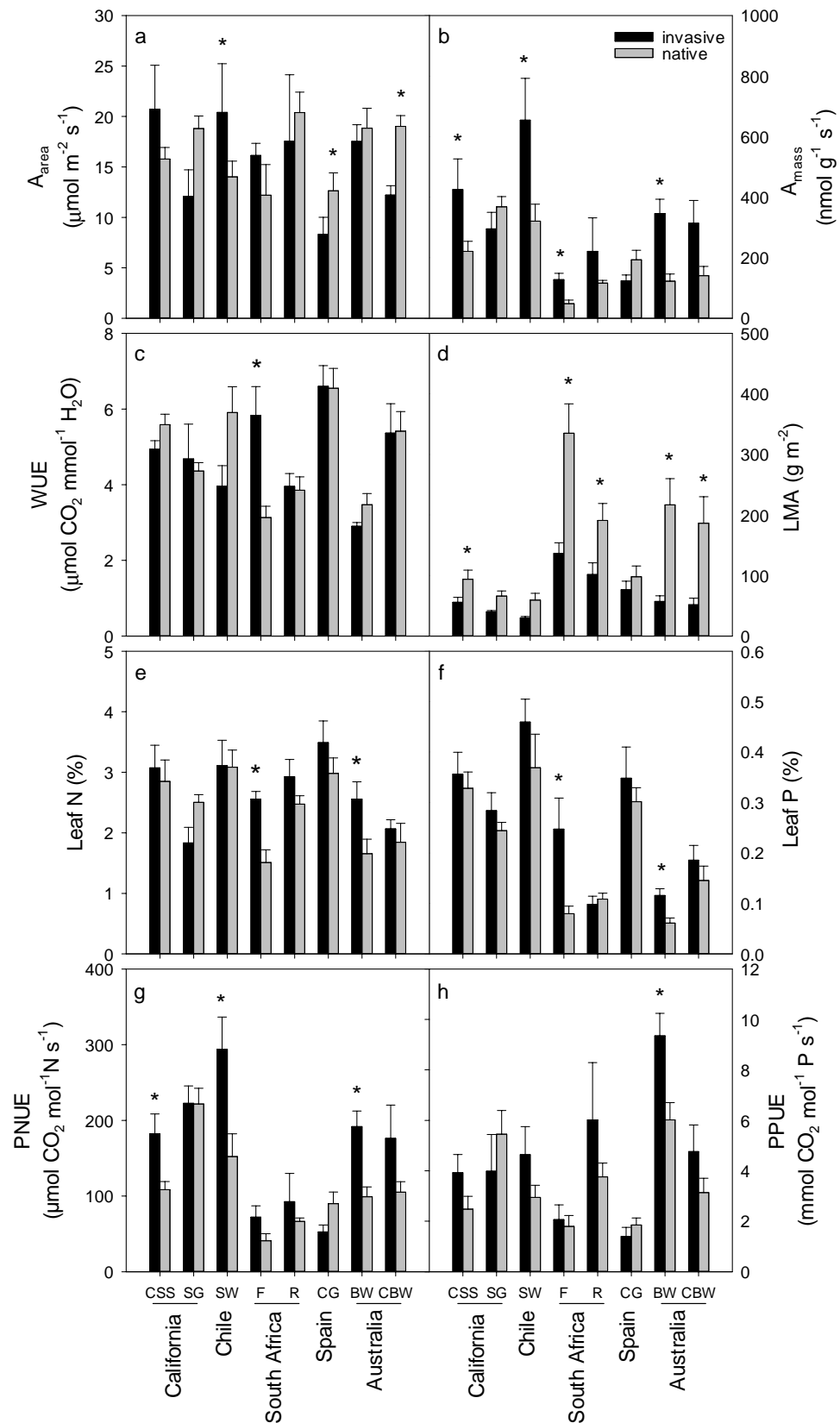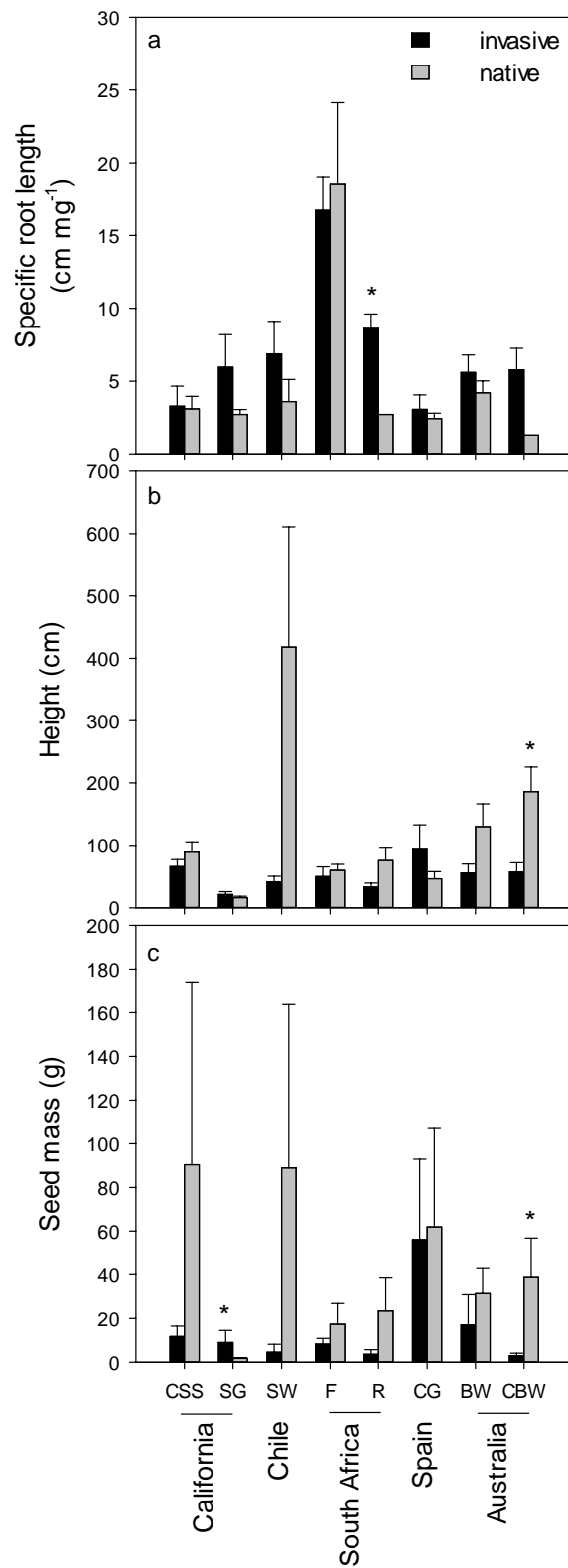
Figure 1

Figure 2

Figure 3