



ECOLOGICAL SOCIETY OF AMERICA

Ecology/Ecological Monographs/Ecological Applications

PREPRINT

This preprint is a PDF of a manuscript that has been accepted for publication in an ESA journal. It is the final version that was uploaded and approved by the author(s). While the paper has been through the usual rigorous peer review process of ESA journals, it has not been copy-edited, nor have the graphics and tables been modified for final publication. Also note that the paper may refer to online Appendices and/or Supplements that are not yet available. We have posted this preliminary version of the manuscript online in the interest of making the scientific findings available for distribution and citation as quickly as possible following acceptance. However, readers should be aware that the final, published version will look different from this version and may also have some differences in content.

The doi for this manuscript and the correct format for citing the paper are given at the top of the online (html) abstract.

Once the final published version of this paper is posted online, it will replace the preliminary version at the specified doi.

1 Running head: Functional traits and invasion

2

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

5

6 Jennifer L. Funk^{1*}, Rachel J. Standish^{2,3}, William D. Stock⁴ and Fernando Valladares^{5,6}

7

8 ¹ School of Earth and Environmental Sciences, Chapman University, Orange CA USA

9 ² School of Plant Biology, The University of Western Australia, Crawley, Western Australia

10 ³ School of Veterinary and Life Sciences, Murdoch University, Murdoch, Western Australia

11 ⁴ Centre for Ecosystem Management, Edith Cowan University, Joondalup, Western Australia,

12 6027

13 ⁵ Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

14 ⁶ Departamento de Ciencias, Universidad Rey Juan Carlos, Móstoles, Madrid, Spain

15

16 * Corresponding author: Jennifer Funk, Schmid College of Science and Technology, Chapman

17 University, 1 University Drive, Orange, CA 92866, USA. Phone: 1-714-744-7953. Email:

18 jlfunk@chapman.edu

19

20 **Keywords:** resource acquisition, resource-use efficiency, drought avoidance, stress tolerance,

21 functional traits, annual, perennial

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.

40 **Introduction**

41 One of the greatest challenges in conserving and restoring plant communities is identifying the
 42 mechanisms by which invasive species outperform native species. Analyses of global datasets
 43 suggest that invasive species generally display traits associated with high resource acquisition
 44 (Leishman et al. 2007, van Kleunen et al. 2010) or broad physiological niches (Higgins and
 45 Richardson 2014). However, most investigations of invasive species are conducted in high-
 46 resource environments, which are characterized by an abundance of water, soil nutrients, light or
 47 a combination of these factors. High-resource environments are thought to favor species with
 48 high rates of resource acquisition while low-resource environments select for traits associated
 49 with stress tolerance (Chapin 1980, Craine 2009). In low-resource environments (e.g., deserts,
 50 ancient landscapes), plant productivity is severely limited by light, water, or soil nutrient
 51 availability, and native plants often have adaptations allowing them to tolerate stress or enhance
 52 extraction of the limiting resource (e.g., Cramer et al. 2014, Dallman 1998). Stress often limits
 53 the range of trait values resulting in trait similarity between co-occurring species in low-resource
 54 environments (e.g., habitat filtering; Weiher and Keddy 1999). Thus, theoretically, native and
 55 invasive species in low-resource environments should display similar ranges of traits pertaining
 56 to resource acquisition and use. Understanding these functional differences is critical to
 57 designing management programs in invaded plant communities, especially where resources can
 58 be manipulated (e.g., through fire, grazing, carbon amendments; Funk et al. 2008).

59
 60 Plants native to drought-prone environments, one type of low-resource system, frequently
 61 display one of two contrasting strategies: drought tolerance or drought avoidance (Ludlow 1989).
 62 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 significant
 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 ($\text{cm}^2 \text{g}^{-1}$).

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 ($1600 \mu\text{mol photon m}^{-2} \text{s}^{-1}$), $400 \mu\text{L L}^{-1}$
 138 CO_2 , leaf temperature of 25 °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: $\text{site} + \text{origin} +$
 168 $\text{strategy} + \text{site} \times \text{strategy} + \text{origin} \times \text{site}$, 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

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

288 **Acknowledgements**

289 We thank F. Pérez, M. Vilà, C. Allen, T. Morald, M. Nguyen, A. Ortega, and K. Kariman for
 290 help in the lab and field, J. Larson for comments on the manuscript, and M. Macpherson for
 291 statistical advice. This work was supported by the National Science Foundation (grant OISE-

292 1132994) and a Jasper Ridge Restoration Fellowship from Stanford University to JLF. RJS was
 293 supported by the Australian Research Council Centre of Excellence for Environmental
 294 Decisions.

295

296 **Literature cited**

297 Ackerly, D. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit
 298 and disturbance. *Ecological Monographs* 74:25-44.

299 Ackerly, D. D., W. D. Stock, and J. A. Slingsby. 2014. Geography, climate, and biodiversity: the
 300 history and future of mediterranean-type ecosystems. Pages 361-376 in N. Allsopp, J. F.
 301 Colville, and G. A. Verboom, editors. *Fynbos: Ecology, Evolution, and Conservation of a*
 302 *Megadiverse Region*. Oxford University Press, Oxford, UK.

303 Angiosperm Phylogeny Group III. 2009. An update of the Angiosperm Phylogeny Group
 304 classification for the orders and families of flowering plants: APG III. *Botanical Journal*
 305 *of the Linnean Society* 161:105-121.

306 Arianoutsou, M., P. Delipetrou, M. Vilà, P. G. Dimitrakopoulos, L. Celesti-Grappow, G. Wardell-
 307 Johnson, L. Henderson, N. Fuentes, E. Ugarte-Mendes, and P. W. Rundel. 2013.
 308 Comparative patterns of plant invasions in the Mediterranean biome. *PLOS One*
 309 8:e79174 doi:79110.71371/journal.pone.0079174.

310 Bermúdez, R., and R. Retuerto. 2014. Together but different: co-occurring dune plant species
 311 differ in their water- and nitrogen-use strategies. *Oecologia* 174:651–663.

312 Chapin III, F. S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and*
 313 *Systematics* 11:233-260.

- 314 Colautti, R. I., and H. J. MacIsaac. 2004. A neutral terminology to define ‘invasive’ species.
 315 Diversity and Distributions 10:135–141.
- 316 Craine, J. M. 2009. Resource strategies of wild plants. Princeton University Press, Princeton, NJ.
- 317 Cramer, M. D., A. G. West, S. C. Power, R. Skelton, and W. D. Stock. 2014. Plant
 318 ecophysiological diversity. Pages 248-272 in N. Allsopp, J. F. Colville, and G. A.
 319 Verboom, editors. Fynbos: Ecology, Evolution, and Conservation of a Megadiverse
 320 Region. Oxford University Press, Oxford, UK.
- 321 Dallman, P. R. 1998. Plant Life in the World's Mediterranean Climates: California, Chile, South
 322 Africa, Australia, and the Mediterranean Basin. University of California Press, Berkeley.
- 323 Franks, S. J. 2011. Plasticity and evolution in drought avoidance and escape in the annual plant
 324 *Brassica rapa*. New Phytologist **190**:249–257.
- 325 Funk, J. L. 2013. The physiology of invasive plants in low-resource environments. Conservation
 326 Physiology **1**:doi:10.1093/conphys/cot1026.
- 327 Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through re-
 328 assembly: plant traits and invasion resistance. Trends in Ecology and Evolution **23**:695-
 329 703.
- 330 Funk, J. L., and W. K. Cornwell. 2013. Leaf traits within communities: context may affect the
 331 mapping of traits to function. Ecology **94**:1893-1897.
- 332 Funk, J. L., and P. M. Vitousek. 2007. Resource use efficiency and plant invasion in low-
 333 resource systems. Nature **446**:1079-1081.
- 334 Funk, J. L., and V. A. Zachary. 2010. Physiological responses to short-term water and light stress
 335 in native and invasive plant species in southern California. Biological Invasions 12:1685–
 336 1694.

- 337 Gaertner, M., A. Den Breeyen, C. Hui, and D. M. Richardson. 2009. Impacts of alien plant
 338 invasions on species richness in Mediterranean-type ecosystems: a meta-analysis.
 339 *Progress in Physical Geography* 33:319-338.
- 340 Garnier, E. 1992. Growth analysis of congeneric annual and perennial grass species. *Journal of*
 341 *Ecology* **80**:665-675.
- 342 Godoy, O., F. Valladares, and P. Castro-Díez. 2012. The relative importance for plant
 343 invasiveness of trait means, and their plasticity and integration in a multivariate
 344 framework. *New Phytologist* 195:912-922.
- 345 Higgins, S. I., and D. M. Richardson. 2014. Invasive plants have broader physiological niches.
 346 *Proceedings of the National Academy of Sciences* **111**:10610–10614.
- 347 Jacobsen, A. L., R. B. Pratt, S. D. Davis, and F. W. Ewers. 2008. Comparative community
 348 physiology: nonconvergence in water relations among three semi-arid shrub
 349 communities. *New Phytologist* **180**:100-113.
- 350 Lambers, H., M. C. Brundrett, J. A. Raven, and S. D. Hopper. 2010. Plant mineral nutrition in
 351 ancient landscapes: high plant species diversity on infertile soils is linked to functional
 352 diversity for nutritional strategies. *Plant and Soil* 334:11-31.
- 353 Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. Hull Sieg. 2010. A multi-trait test of the
 354 leaf-height-seed plant strategy scheme with 133 species from a pine forest flora.
 355 *Functional Ecology* **24**:493–501.
- 356 Leishman, M. R., T. Haslehurst, A. Ares, and Z. Baruch. 2007. Leaf trait relationships of native
 357 and invasive plants: community- and global-scale comparisons. *New Phytologist*
 358 **176**:635–643.

- 359 Ludlow, M. M. 1989. Strategies of response to water stress. Pages 269–281 in K. H. Kreeb, H.
 360 Richter, and T. M. Minckley, editors. Structural and functional responses to
 361 environmental stress. SPB Academic, The Hague, the Netherlands.
- 362 Maron, J. L., and M. Marler. 2008. Field-based competitive impacts between invaders and
 363 natives at varying resource supply. *Journal of Ecology* **96**:1187-1197.
- 364 Martín-Forés, I., L. Sanchez-Jardon, B. Acosta-Gallo, A. del Pozo, I. Castro, J. M. de Miguel, C.
 365 Ovalle, and M. A. Casado. 2015. From Spain to Chile: environmental filters and success
 366 of herbaceous species in Mediterranean-climate regions. *Biological Invasions* 17:1425-
 367 1438.
- 368 Matzek, V. 2012. Trait values, not trait plasticity, best explain invasive species' performance in a
 369 changing environment. *PLOS One* **7**:e48821.
- 370 Moles, A. T., M. A. M. Gruber, and S. P. Bonser. 2008. A new framework for predicting
 371 invasive plant species. *Journal of Ecology* **96**:13-17.
- 372 Oliveira, M. T., V. Matzek, C. D. Medeiros, R. Rivas, H. M. Falcao, and M. G. Santos. 2014.
 373 Stress tolerance and ecophysiological ability of an invader and a native species in a
 374 seasonally dry tropical forest. *PLOS One* **9**:e105514.
- 375 Ordoñez, A., I. J. Wright, and H. Olf. 2010. Functional differences between native and alien
 376 species: a global-scale comparison. *Functional Ecology* **24**:1353–1361.
- 377 Peñuelas, J., J. Sardans, J. Llusia, S. M. Owen, J. Carnicer, T. W. Giambelluca, E. L. Rezende,
 378 M. Waite, and U. Niinemets. 2010. Faster return on 'leaf economics' and different
 379 biogeochemical niche in invasive compared with native plant species. *Global Change*
 380 *Biology* **16**:2171-2185.

- 381 Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global
 382 convergence in plant functioning. *Proceedings of the National Academy of Sciences*
 383 **94**:13730-13734.
- 384 Richardson, D. M., P. Pysek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000.
 385 Naturalization and invasion of alien plants: concepts and definitions. *Diversity and*
 386 *Distributions* 6:93–107.
- 387 Sala, O. E., F. S. Chapin, 3rd, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-
 388 Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A.
 389 Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H.
 390 Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770-1774.
- 391 Schenk, H. J., and R. B. Jackson. 2002. The global biogeography of roots. *Ecological*
 392 *Monographs* **72**:311–328.
- 393 Stock, W. D., and G. A. Verboom. 2012. Phylogenetic ecology of foliar N and P concentrations
 394 and N:P ratios across mediterranean-type ecosystems. *Global Ecology and Biogeography*
 395 21:1147-1156.
- 396 Thompson, J. D. 2005. *Plant evolution in the Mediterranean*. Oxford University Press, Oxford,
 397 UK.
- 398 van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between
 399 invasive and non-invasive plant species. *Ecology Letters* 13:235-245.
- 400 Vilà, M., A. D. Siamantziouras, G. Brundu, I. Camarda, P. Lambdon, F. Médail, E. Moragues, C.
 401 M. Suehs, A. Traveset, A. Y. Troumbis, and P. E. Hulme. 2008. Widespread resistance of
 402 Mediterranean island ecosystems to the establishment of three alien species. *Diversity*
 403 *and Distributions* 14:839–851.

404 von Caemmerer, S. 2000. Biochemical models of leaf photosynthesis. Csiro Publishing,
 405 Collingwood, Australia.

406 Weiher, E., and P. Keddy. 1999. Assembly rules as general constraints on community
 407 composition. Pages 251-271 *in* E. Weiher and P. Keddy, editors. Ecological Assembly
 408 Rules: Perspectives, Advances, Retreats. Cambridge University Press, Cambridge.

409

410 **Ecological Archives**

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.

419

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	F	P	F	P	
<i>Leaf-level traits</i>															
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
<i>Leaf-level traits</i>						
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 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)

esa

preprint

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

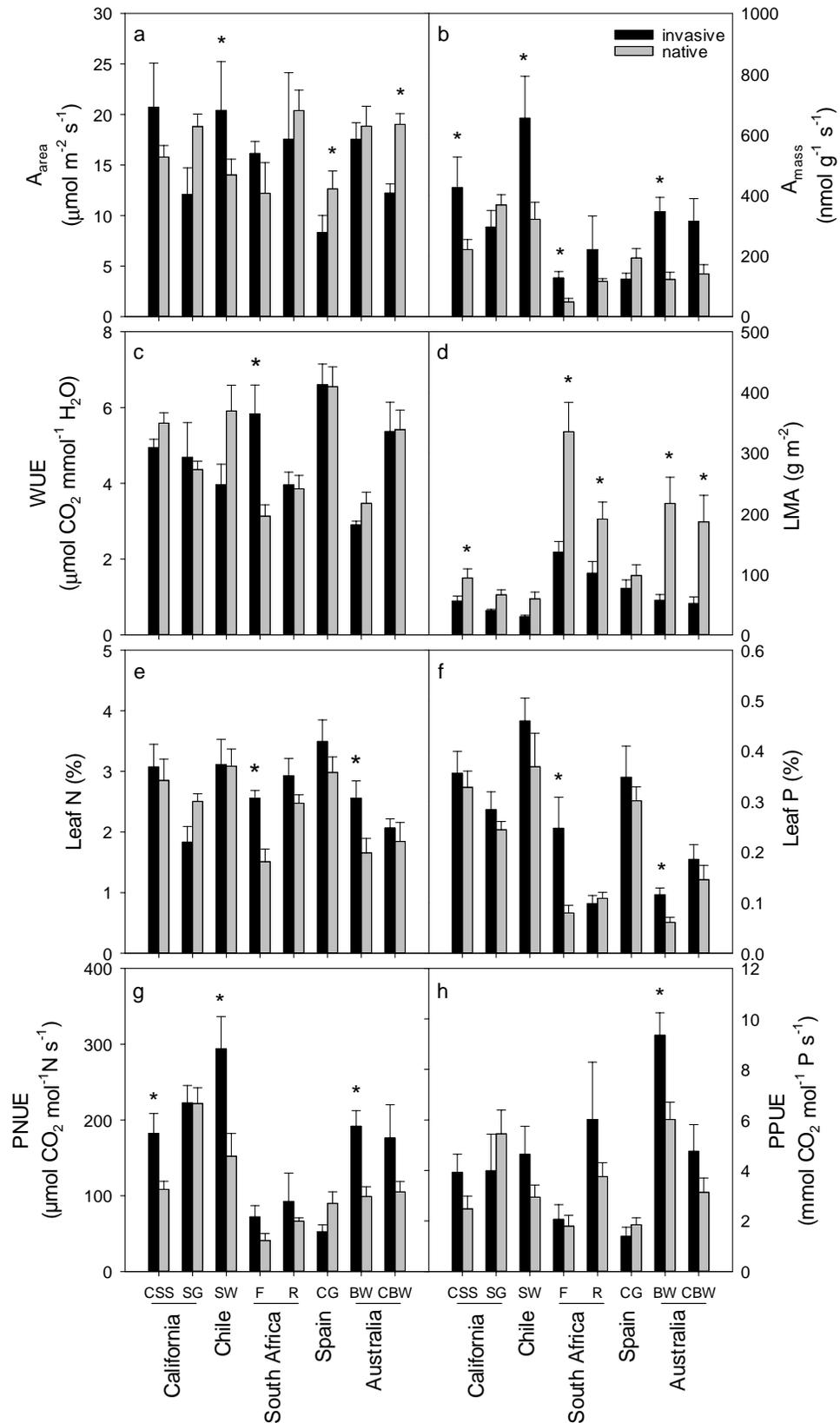


Figure 2

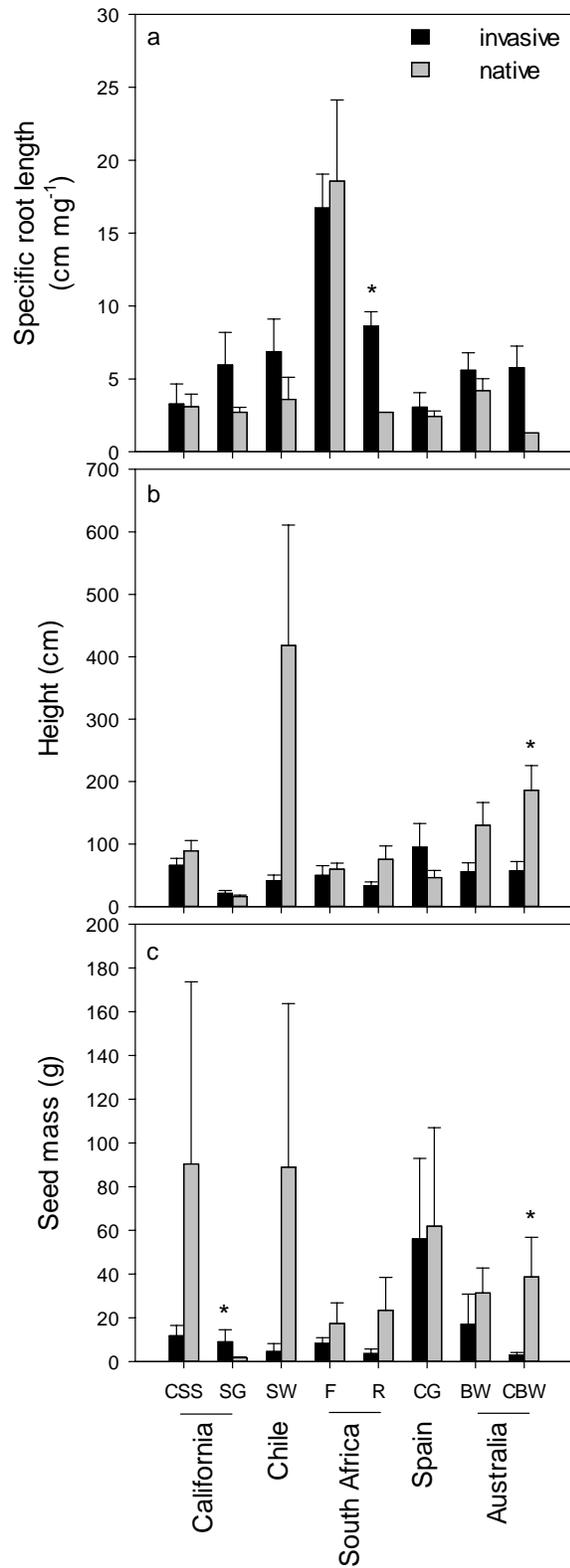


Figure 3

