Biol Invasions (2020) 22:2699–2712
https://doi.org/10.1007/s10530-020-02290-w

ORIGINAL PAPER

Functional traits indicate faster resource acquisition for alien herbs than native shrubs in an urban Mediterranean shrubland

Samantha D. Díaz de León Guerrero · Georgina González-Rebeles Guerrero · Teresa M. Ibarra-Montes · Anaid Rodríguez Bastarrachea · Ramiro Santos Cobos · Stephen H. Bullock · Lawren Sack · Rodrigo Méndez-Alonzo

Received: 13 August 2019 / Accepted: 16 May 2020 / Published online: 23 May 2020

Abstract In urban Mediterranean ecosystems, invasive alien plants should have characteristics that enable faster resource acquisition and utilization than native species. We tested this hypothesis by comparing stem and leaf functional traits from five abundant native woody shrubs and five of the most abundant alien species within an urban coastal scrub community in Ensenada, Baja California, México. Twelve anatomical and ecophysiological traits were studied: light-saturated CO_2 assimilation rate, stomatal conductance, stem and leaf water potentials during transpiration, % stem allocation to bark, xylem and pith, stem xylem vessel diameter and density, leaf size, and % allocation to spongy and palisade mesophyll. Alien species varied more in these traits, and their trait combinations reflected less investment in long-lived tissues; they had higher CO_2 assimilation and stomatal conductance rates, higher values of leaf and stem water potential, and higher allocation to pith, larger stem xylem vessels, and larger leaf areas. In contrast, native woody shrub species were relatively convergent in leaf and stem traits reflecting more conservative resource use. Within disturbed urban environments, alien species may outcompete the native stress-

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-020-02290-w) contains supplementary material, which is available to authorized users.

S. D. Díaz de León Guerrero · T. M. Ibarra-Montes · A. Rodríguez Bastarrachea · R. Santos Cobos
Posgrado en Ciencias de la Vida, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, B.C., Mexico
e-mail: dsamantha@cicese.edu.mx

T. M. Ibarra-Montes
e-mail: ibarrateresa@cicese.edu.mx

A. Rodríguez Bastarrachea
e-mail: anaidr@cicese.edu.mx

R. Santos Cobos
e-mail: rsantos@cicese.edu.mx

G. González-Rebeles Guerrero
Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Ciudad De México, CDMX, Mexico
e-mail: georgina_bio12@ciencias.unam.mx

S. H. Bullock · R. Méndez-Alonzo (✉)
Departamento de Biología de la Conservación, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, B.C., Mexico
e-mail: mendezal@cicese.mx

S. H. Bullock
e-mail: sbullock@cicese.mx

tolerant species through rapid resource acquisition, enhanced by a broader set of functional trait combinations across species.

Keywords Carbon assimilation · Functional traits association · Leaf water potentials · Urban environments

Introduction

Invasive alien plant species are a threat to biodiversity and human welfare, costing over 500,000 million US dollars per year in restoration and control efforts globally (Paini et al. 2016). Invasive plants are generally alien or exotic species with high potential to spread and colonize untended areas, often due to a combination of traits that differ from those of native species that evolved in the local climate and soil (Rejmánek and Richardson 1996; Richardson et al. 2000; Sax et al. 2007; van Kleunen et al. 2010; Leishman et al. 2014). Annual invasive plant species may benefit from adaptations that maximize rates of resource acquisition, enabling them to increase their population density faster than perennial native species due to traits that permit greater resource use efficiency (Everard et al. 2010). Within urban ecosystems, in particular, high water and nutrient availability associated with irrigation and fertilization may promote advantages for invasive species (McDowell 2002; Funk and Vitousek 2007). In Mediterranean ecosystems, invasive species may be pre-adapted to maximize rates of resource acquisition during wet seasons, and additionally to exploit water sources unavailable to native species during dry seasons, enabling them to increase their population density faster than perennial native species (Caplan and Yeakley 2010; Everard et al. 2010). However, previous studies of plant invasion ecology have found mixed evidence for differences in functional traits between native and invasive species (e.g., Ehrenfeld 2010; van Kleunen et al. 2010; Funk and Zachary 2010; Godoy et al. 2011; Drenovsky et al. 2012; Leffler et al. 2014; Heberling and Fridley 2013; Hulme and Bernard-Verdier 2018). Within urban Mediterranean ecosystems, it is critical to understand if there are consistent patterns of traits that could favor invasion by alien species, such as ecophysiological trends in resource exploitation (Gaertner et al. 2017).

Eco-physiological traits such as photosynthetic rates, operating water potentials, and investment in xylem are directly involved in functions critical to sustaining growth, survival, and reproduction (Westoby et al. 2002; Wright et al. 2004; Reich 2014; Díaz et al. 2016; Brodribb 2017). Therefore, a comparison of eco-physiological trait profiles may reveal differences in abilities to cope with conditions and resources between plants with different growth forms and between alien-invasive and native species (Lodge 1993; Cleland et al. 2011; Kleine et al. 2017). For example, alien species in greenhouse or field conditions may have higher relative growth rates, higher photosynthetic rates, and leaves of lower dry mass content (with thicker palisade tissue and higher stomatal density) in comparison to native perennial shrubs (García-Serrano et al. 2005), woody vines (Osunkoya et al. 2014), or combinations of growth-forms (Funk et al. 2016). In contrast, other studies report no apparent differences between invasive and native species in hydraulic traits, such as vessel size and density in shrubs and trees (Smith et al. 2013), or in response to water and light stress in both herbaceous and woody species (Funk and Zachary 2010). Thus, additional research is needed to clarify the importance of the traits that may distinguish alien-invasive and native species, particularly within urban Mediterranean ecosystems, as well as the environmental or evolutionary conditions which promote species differences.

Within Mediterranean-type ecosystems (MTEs), alien species are often, but not always, herbaceous species, differing in life-form from the dominant native vegetation of woody perennials (Funk et al. 2016). According to their annual or herbaceous life-form, alien species from MTEs display traits corresponding to a “fast-revenue” in the leaf economics spectrum (Westoby et al. 2002), including high leaf carbon assimilation rates, fast growth, low specific leaf area, and high nitrogen and phosphorous use per unit carbon, in comparison to native woody species (Ordonez and Olff 2012; Funk et al. 2016). Other

L. Sack
Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA
e-mail: lawrensack@ucla.edu

meta-analyses suggest that alien flora may also have higher variability in structure and function than native flora. This difference may be due to higher phenotypic plasticity in alien species, allowing them to colonize a broader range of conditions (Caplan and Yeakley 2006; Ordonez et al. 2010; Leffler et al. 2014; Ordonez 2014). Intra-generic comparisons of multiple physiological traits have demonstrated that there are differences between alien and native species' traits in MTEs. For example, in the species complex *Rubus fruticosus*, a pervasive invader in MTEs, *R. armeniacus* has higher carbon assimilation rates and stomatal conductance, higher leaf and stem water potentials, and higher relative growth rate, than congeneric native species (McDowell 2002; Caplan and Yeakley 2010, 2013). Quantifying species' abilities to capture carbon and to modulate their water relations provides a framework to understand the success of invasive species in Mediterranean ecosystems around the world.

Urban ecosystems with remnant and ruderal plants offer the opportunity to clarify differences between invasive and native species in traits related to resource acquisition. When urbanization modifies the landscape, each altered patch presents opportunities for invasion by both local and immigrant species, potentially differing in evolutionary and life histories as well as anatomical and physiological traits (Seabloom et al. 2006; Strauss et al. 2006; Didham et al. 2007). For example, the California Floristic Province (CFP) probably has the highest proportion of invasive plant species of any region in the world (Eagle et al. 2007; van Kleunen et al. 2015; Early et al. 2016; Turbelin et al. 2017). This abundance is attributed to landscape transformation by human activities, which has impacted soil structure, water availability, and the amount of open space, particularly in locations close to the coast (Seabloom et al. 2006; Brusati et al. 2014). Within the coastal CFP, chaparral and coastal scrub communities are a showcase of contrasting native and invasive plant species. In the lists of invasive species reported by the California Invasive Species Advisory Committee (CISAC), 62% are herbaceous, 22% are graminoids, and 16% are woody species (California Invasive species advisory committee (CISAC) 2010). It is unclear how these species can outcompete native perennial plants of the CFP, which are characterized by high resistance to drought and mechanical stress, and by low rates of resource use (Jacobsen et al. 2008; Méndez-Alonzo et al. 2013). In contrast, invasive species have higher mass-based photosynthetic rates and lower leaf mass per area (LMA) than native species within the CFP (Funk et al. 2016). The surplus availability of water and nutrients in the highly-modified landscape of urban California may promote some invasions, but it is unclear how aliens can colonize areas with scarcer resources. Thus, more extensive characterization of differences in trait states between invasive and native species is needed to test for potential contrasts in water use efficiency, carbon assimilation, and drought tolerance.

Multivariate comparisons of anatomical and physiological traits related to water and carbon acquisition between alien and native plant species offer a way to test the hypothesis that invasive "fast" species have traits associated with a low resource investment and rapid resource acquisition, such as profligate water use and rapid carbon assimilation, relative to "slow" native species with longer tissue life spans (Reich 2014; Díaz et al. 2016) (Table 1). Moreover, quantifying the magnitude of trait covariation across species may indicate if alien species have higher functional variability than native species. Due to a combination of evolutionary and ecological pressures, traits within a species should tend to either vary in concert, serving to increase fitness within specific environmental conditions, or to evolve independently, allowing for acclimation to a broad set of environments (Klingenberg 2014; Messier et al. 2017). Alien species, having broader distributions, would be expected to display higher variability in the coordination of traits.

To understand how functional traits of invasive species differentiate from those of native species, particularly in relation with water use and carbon assimilation, we studied ten species (Table 2) near the arid southern end of the CFP for twelve traits (Table 3). We also calculated ordination metrics using principal component analysis and phenotypic integration indices for each species, which indicate the degree of covariation within a set of traits. Clarifying trait variation between native and invasive species will provide bases for resource managers to better identify species with the potential to be invasive in southern CFP as well as others sites with similar climatic and soil characteristics (Goodwin et al. 1999; van Kleunen et al. 2010; Lee et al. 2017).

Table 1 Hypotheses for structural and functional variation between alien and native species, and predictions for specific traits

Hypotheses	Traits involved	Rationale	References
Alien species have traits associated with a rapid carbon assimilation rate	Photosynthetic rate and stomatal conductance	Alien species would present larger rates of leaf carbon assimilation and higher rates of water use than native species	Baruch and Goldstein (1999), Durand and Goldstein (2001), Funk and Vitousek (2007), Cavaleri and Sack (2010), van Kleunen et al. (2010), Funk (2013), Lee et al. (2017) Martínez and Fridley (2018)
Alien species have traits associated with profligate water use	Vessel diameter and vessel density Stem and leaf water potential	Alien species would possess larger vessels per unit of stem diameter than native plants, allowing higher values of stem hydraulic conductivity. Alien species would operate at higher stem and leaf water potentials than native species	Funk and Zachary (2010), Funk (2013), Smith et al. (2013), Hulme and Bernard-Verdier (2018)
Alien species have structural traits associated with a higher capacity to acquire light and CO_2	Proportion of spongy and palisade mesophyll. Leaf area	Alien species would possess leaves of greater area, with larger proportions of spongy mesophyll and reduced proportions of palisade mesophyll, thus allowing for fast gas exchange	Grotkopp et al. (2002), Gallagher et al. (2015), Leishman et al. (2014)
Alien species have lower density, reflecting lower investment in carbon expensive tissues	Proportion of bark, xylem and pith in cross-sectional stem samples	Alien species would allocate relatively more volume to pith, and native species to xylem, as xylem is a slow-growing secondary tissue and pith is fast growing tissue composed of large-vacuolated cells	Evert (2006), Smith et al. (2013), González-Muñoz et al. (2014)

Table 2 Study species, family, common names (English/Spanish), growth form, native versus invasive status, geographical origin, and ecological impact category according to the California Invasive Plant Council (https://www.cal-ipc.org/plants/inventory/ accessed on Nov. 22, 2018) of the species employed in this study

Species	Family	Common names	Growth form	Treatment	Origin	Ecological impact
Adenostoma fasciculatum	Rosaceae	Chamise/Chamizo	W	Native	CFP	
Artemisia californica	Asteraceae	Sagebrush/Artemisa	W	Native	CFP	
Eriogonum fasciculatum	Polygonaceae	Buckwheat/Flor de Borrego	W	Native	CFP	
Rhus integrifolia	Anacardiaceae	Lemonade Sumac/Saladito	W	Native	CFP	
Simmondsia chinensis	Simmondsiaceae	Goatnut/Jojoba	W	Native	CFP	
Chrysanthemum (Glebionis) coronarium	Asteraceae	Crown daisy/Margarita	H	Alien	Mediterranean	Limited
Datura wrightii	Solanaceae	Jimsonweed/Toloache	H	Alien	Central México	Watch
Malva neglecta	Malvaceae	Mallow/Malva enana	H	Alien	Mediterranean	Not assessed
Nicotiana glauca	Solanaceae	Tree tobacco/Tabaquillo	W	Alien	Argentina	Moderate
Salsola (Kali) tragus	Amaranthaceae	Russian thistle, tumbleweed/Cardo, rodadora	H	Alien	Europe	Limited

CFP California floristic province. Growth form: W woody, H herbaceous

Table 3 Traits quantified in this study, abbreviations, and comparison of leaf and stem traits using Bayesian t-tests for five native versus five alien plant species within an urban Mediterranean coastal scrub in Ensenada, México

Trait	Abrv	Units	Native species				Alien species				t-test
			Mean	SE	Min	Max	Mean	SE	Min	Max	BF_{10}
Photosynthetic rate	A_{sat}	µmol m^2s^{-1}	3.2	0.4	0.08	13.6	10.5	1.6	1.5	22	$> 10^8$
Stomatal conductance	g_s	mmol m^2s^{-1}	0.17	0.01	0.02	0.6	0.40	0.1	0	1.59	109
Stem water potential	Ψ_{stem}	MPa	− 2.1	0.2	− 2.9	− 0.6	− 1.4	0.2	− 2.0	− 0.8	7.3
Leaf water potential	Ψ_{leaf}	MPa	− 2.6	0.2	− 3.6	− 1.6	− 1.9	0.2	− 2.6	− 1.2	9.8
Vessel diameter	VD	µm	34.0	13.8	6.5	126	51.5	10.2	1.8	201	2.4
Vessel density	VDen	Vessels μm^{-2}	2.73	1.55	0.02	19	0.54	0.22	0.01	2.7	13
Proportion of bark	%Bark	%	42.1	5.2	15.5	70.5	27.1	3.9	9.3	74	$> 10^3$
Proportion of xylem	%Xyl	%	50.0	5.9	19.5	81.2	31.1	3.9	10.1	66.3	$> 10^5$
Proportion of pith	%Pith	%	7.9	2.0	0.05	22.0	41.1	6.0	1.0	88	$> 10^{16}$
Leaf area	LA	cm^2	2.6	1.5	0.02	15	42.5	14.1	0.17	296	222
Proportion of spongy mesophyll	%SM	%	42.9	3.6	19.1	82.6	36.4	2.2	18	59.2	3.6
Proportion of palisade mesophyll	%PM	%	39.1	3.2	11.5	62.6	43.9	3.4	11	67.2	1.0

BF_{10} inverse Bayesian factor. Higher BF_{10} values correspond to higher probability of occurrence of the alternative hypothesis. Abrv abbreviation

Materials and methods

Study site

This study was performed in patches of remnant native and ruderal vegetation on the campus of the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), in the city of Ensenada, Baja California, México (31°52′11″N, 116°40′05″W), which is less than 1 km from the coastline. For 2008–2017, mean annual temperature was 17.5 °C and mean annual precipitation was 212 mm, with rain mostly falling during winter. For the study year (2017), the mean temperature was 17.7 °C and total precipitation was 160 mm (data from the meteorological station at CICESE). Four sites were selected that were no more than 400 m from each other (Figure S1). The remnant vegetation at CICESE is mainly Diegan Coastal Sage Scrub (Westman 1983), an association with substantial endemism and threatened by changes in land-use and climate (Riemann and Ezcurra 2005; Riordan and Rundel 2014). A previous vegetation survey of the area found 33 native plant species and nine alien species (*unpublished*, Committee for Ecological and Sustainable Development, CICESE). The ecological impact of the alien species was described according to the classification of the California Invasive Plant Council (https://www.cal-ipc.org/). Five native species and five invasive species (Table 2) were selected from the species pool; these had wide phylogenetic variation across the Angiosperm phylogeny (Figure S2). We selected highly abundant species, but excluded CAM and C_4 grass species. For each species, three individuals were selected (n = 30 plants) for quantification of twelve leaf and stem functional traits (Table 3). All measurements were performed late in the rainy season, from 6 March to 4 April, 2017.

Physiological traits

Rates of light-saturated photosynthesis (A_{sat}) and stomatal conductance (g_s) were measured on three leaves from three individuals per species using a portable photosynthesis system with a transparent leaf chamber (LI-6400XT, LI-COR Biosciences, Lincoln, NE, USA). Measurements were made from 1100 to 1400 h on sunny days, and the temperature and relative humidity adjacent to the leaf were quantified with a thermo-hygrometer (Traceable humidity pen, Thomas Scientific, Swedesboro, NJ, USA). Average photosynthetically active radiation (PAR) inside the chamber was 1716 ± 280 μmol m^{-2} s^{-1} (mean ± SD), average leaf temperature was 26 ± 2 °C, average relative humidity was 39.5 ± 4.4%, and reference CO_2 was set at 380 μmol mol^{-1}.

Stem and leaf midday water potentials (Ψ_{stem} and Ψ_{leaf}, respectively) were quantified with a pressure chamber (Model 1505D, PMS Instrument Company, Albany, OR, USA) using the average values of two branches from the same plants to quantify gas exchange and anatomical traits. A_{sat}, g_s, Ψ_{stem}, and Ψ_{leaf} measurements were made on four sunny days between 1300 and 1400 h (1–4 April 2017). The remaining measurements were performed on 6–10 March 2017, which correspond to the late rainy season in our study site. Samples varied widely in their number of leaves because some species contained over one hundred leaves per terminal stem, such as *Artemisia fasciculatum* and *Eriogonum fasciculatum*, while others had fewer than ten leaves per stem, such as *Nicotiana glauca*. Ψ_{leaf} was determined from transpiring leaves, including petioles, whereas Ψ_{stem} was measured using branches that had been enclosed with moist paper in opaque, self-sealing bags (Whirl–Pak, Nasco Inc. Fort Atkinson WI, USA) 15 min before leaf excision (Melcher et al. 1998).

Structural traits

For three plants from each of the ten focal species, stem samples were hand-sectioned in the transverse plane 10, 20 and 30 cm from the apex. After cutting, samples were immediately examined in a stereomicroscope at 2-5X (Nikon SMZ-745T, Tokyo, Japan; Infinity 1 microscope camera; Lumenera Corporation, Ottawa, ON, Canada) to quantify the major and minor diameters at the limit of each tissue; image analysis was performed using ImageJ software (Ferreira and Rasband 2012). The areas occupied by each tissue were calculated as ellipses, subtracting the areas of the xylem and pith to obtain the bark fraction (%Bark) and of pith (%Pith) to obtain the xylem fraction (%Xyl). Vessel diameter (*VD*) and density (*VDen*) were determined in each sectioned sample of xylem, using an optical microscope at 10-40 × (Nikon Eclipse E200; Infinity Analyze 6.4 software; Lumenera Corporation, 2006).

For the same shoot samples used for analyzing stem tissue, samples of the largest, smallest, and mid-sized leaves were taken to calculate the proportions of the palisade and spongy mesophyll tissue. Leaf samples were first hand-sectioned transversely, then the thickness of the palisade and spongy mesophyll (%PM and %SM, respectively) was measured using an optical microscope at 10× and analyzed using ImageJ (Schneider et al. 2012). Leaf area (*LA*) was quantified using the Android app Easy Leaf Area Free (Easlon and Bloom 2014).

Statistical analyses

Before statistical analyses, replicate samples from each individual were averaged, as were data from the three individuals per species. Comparisons of traits between invasive and native species were performed using Bayesian *t*-tests, and patterns of covariation among traits were explored using Bayesian correlation analyses. Hierarchical one-way ANOVA was used to identify differences in traits between categories and species nested in categories (invasive vs. native), and a Pearson correlation matrix was employed to identify relationships among traits (at the species level), using R 3.6.2 (R Core Team 2017). For Bayesian analysis, the ratio of the likelihood of the alternative hypothesis to that of the null hypothesis, termed the Inverse Bayes Factor (BF_{10}, Jarosz and Wiley 2014), was employed as the goodness of fit parameter. A BF_{10} between 3 and 10 is often considered positive evidence for the alternative hypothesis, a BF_{10} between 20 and 150 is considered strong evidence for the alternative hypothesis, and a BF_{10} above 150 represents powerful evidence (Jarosz and Wiley 2014). Although Bayesian analysis does not provide a minimum threshold on which to draw conclusions like the *P* value-based significance cutoffs in frequentist analyses, we highlight findings that are supported with $BF_{10} \geq 5$. Bayesian statistics were performed in JASP 0.8.1.0 (Love et al. 2019). To summarize the patterns of trait covariation and to visualize the distinctions between alien and native species, we performed principal component analysis (PCA) in R.3.6.2 (R Core Team 2017). Further, we quantified the degree of integration indices corrected by sample size (PINTc) using the package PHENIX in R. Phenotypic integration indices quantify the integration of a dataset as the magnitude of the sum of Eigenvalues normalized by the number of species-trait combinations, thus acting as a measure of the tendency of traits to vary in convert within species (Wagner 1984; Torices and Muñoz-Pajares 2015).

Results

The twelve traits showed strong variation across species and most traits differed between alien and native species (Tables 3, Fig. 1). Physiological traits differed between alien and native species, as alien species had traits reflecting higher water use and higher tissue water content during transpiration. Photosynthesis, i.e., light-saturated carbon assimilation rate per leaf area, A_{sat}, was three-fold higher in alien species than native species (mean ± SE: 10.5 ± 1.6 vs. 3.2 ± 0.4 μmol m^{-2} s^{-1} BF_{10} $> 10^8$; Table 3) and stomatal conductance, g_s, was more than two-fold higher (0.40 ± 0.1 vs. 0.17 ± 0.01 mmol m^{-2} s^{-1}, $BF_{10} = 109$; Table 3). Alien species had, on average, less negative values of Ψ_{stem} (− 1.4 ± 0.2 vs. − 2.1 ± 0.2 MPa, $BF_{10} = 7.3$) and Ψ_{leaf} (− 1.9 ± 0.2 vs. − 2.6 ± 0.2 MPa, $BF_{10} = 9.8$; Table 3).

Structural traits also differed between alien and native species. The relative percentages of stem xylem (%Xyl), pith (%Pith) and bark (%Bark) differed strongly between alien and native species. Alien species had a higher proportion of pith (41.1 ± 3.8% vs. 7.9 ± 0.6%, $BF_{10} > 10^{16}$) and lower proportions of xylem (31.2 ± 2.9% vs. 50.0 ± 4.4%, $BF_{10} > 10^5$)

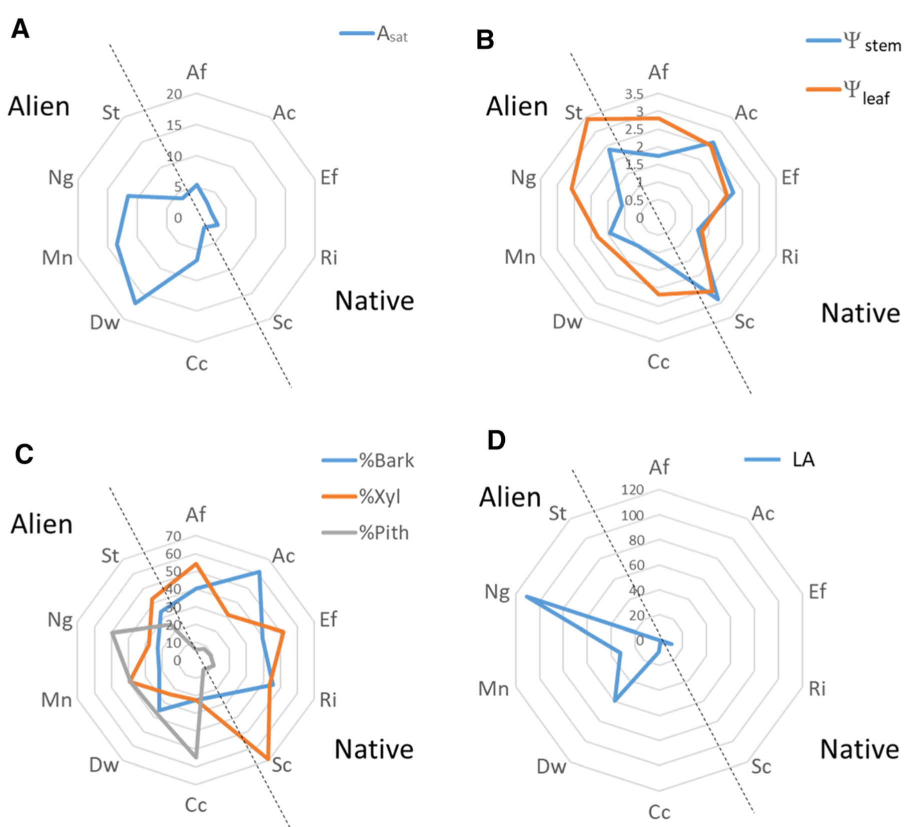

Fig. 1 Comparison of the mean values of traits reflecting the carbon assimilation (**A**, A_{sat}, in μmol m^{-2} s^{-1} of CO_2) the water potential of leaves and stems (**B**, Ψ_{stem} and Ψ_{leaf}, in MPa), the anatomy of stems (**C**, percentages of pith, xylem and bark from 1 cm diameter stem sections), and leaf area (**D**, LA in cm^2) in five common native (inner circle) and five common alien (outer circles) species from Ensenada, Baja California, México. Native species: Af *Adenostoma fasciculatum*, Ac *Artemisia californica*, Ef *Eriogonum fasciculatum*, Ri *Rhus integrifolia*, Sc *Simmondsia chinensis*; Alien species: Cc *Chrysanthemum* (*Glebionis*) *coronarium*, Dw *Datura wrightii*, Mn *Malva neglecta*, Ng *Nicotiana glauca*, St *Salsola* (*Kali*) *tragus*

and bark (27.1 ± 2.1% vs. 42.1 ± 4.2%, $BF_{10} > 10^3$). Alien species had a lower vessel density (*VDen*, 0.5 ± 0.22 vs. 2.7 ± 15 vessels μm^{-2}, BF_{10} = 13), which was correlated with higher vessel diameters (Fig. 2A; $R = -0.38$, BF_{10} = 108), although vessel diameter did not differ between alien and native species (51.5 ± 9.1 vs 34.0 ± 7.8 µm, BF_{10} = 2.4; Table 3).

Alien species had greater leaf area than native species on average (42.5 ± 14.1 vs. 2.6 ± 1.5 cm^2, BF_{10} = 222), but aliens and natives were statistically similar in the proportion of palisade mesophyll (%PM; 43.9 ± 3.4 vs. 39.1 ± 3.2%, BF_{10} = 1.0) and spongy mesophyll tissues (%SM; 36.4 ± 2.2 vs. 42.9 ± 3.6%, BF_{10} = 3.6; Table 3). Across all species, tissue proportions, in particular %Xyl and %Pith, were associated with physiological traits. Leaf areas,

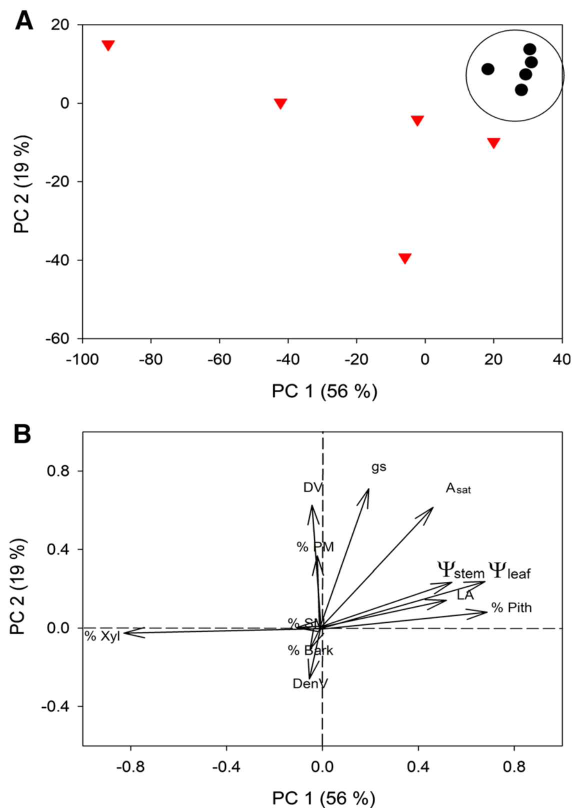

Fig. 2 Principal Component Analysis summarizing the correlations of 12 traits within five native (black circles) and five alien (red triangles) species co-occurring within the city of Ensenada, Baja California, México. **A** PCA scores diagram showing morphological and physiological variability in 12 traits across native and alien species. **B** PCA loadings diagram showing the patterns of trait covariation across species

assimilation rates, and leaf and stem water potentials were negatively associated with %Xyl and positively associated with %Pith (Table 4). Vessel diameter and vessel density were associated with leaf and stem structural traits (Table 4).

We summarized the patterns of trait covariation using PCA. The proportions of variance explained by the first and second components were 56% and 19%, respectively (Eigenvalues 2.4 and 1.3). The ordination analysis using PCA scores showed that the native species were clustered in a small and separate fraction of the possible trait space in comparison to alien species, which showed substantial variability (Fig. 2A). The PCA loadings showed that most traits were closely related to each other. %Xyl had a strong loading correlation only with Component 1, while vessel diameter and density and the proportion of %PM loadings correlated only to Component 2. Ψ_{leaf}, Ψ_{stem}, and leaf area had similar ordination values, with moderate loading correlations to the first component and the second, but were separated from g_s. Photosynthesis showed a similar loading than g_s with both first and second components (Fig. 2B).

Native and alien species did not differ in phenotypic integration indices (PINTc; $t = -0.62$, BF_{10} = 0.50). Mean ± SE PINTc for native species was 2.01 ± 0.39 versus 2.28 ± 0.89 for alien species. Alien species had higher variability in phenotypic integration, with a PINTc coefficient of variation of 38.9% versus 19.3% for native species. *Salsola tragus* was the species with the lowest PINTc (1.16 ± 0.14, 12% integration among traits), and *Nicotiana glauca* was the species with the highest PINTc (3.09 ± 0.28, 32% integration among traits; Table S1).

Discussion

Differences in traits between alien and native species

Alien and native species differed in most of the twelve functional traits quantified in this study. In particular, alien species showed higher photosynthetic rates (A_{sat}), stomatal conductance (g_s), and water potentials during transpiration, in concordance with a previous report for chaparral and coastal Mediterranean-type ecosystems (Funk et al. 2016). Within our study area, aliens were mainly herbaceous species that dominate

Table 4 Correlation matrix among leaf and stem physiological and anatomical traits for five natives and five alien species within an urban Mediterranean coastal scrub in Ensenada, México

Traits	A_{sat}	g_s	Ψ_{stem}	Ψ_{leaf}	%Bark	%Xyl	%Pith	VD	VDen	LA	%SM	%PM
A_{sat}	–	0.70	0.59	0.52	−0.27	−0.43	0.52	0.37	−0.23	0.49	0.01	0.28
g_s		–	0.15	0.09	−0.16	−0.25	0.33	0.40	−0.19	0.25	−0.09	0.25
Ψ_{stem}			–	0.72	−0.26	−0.48	0.57	0.02	0.2	0.38	0.12	0.21
Ψ_{leaf}				–	−0.01	−0.63	0.52	0.07	0.20	0.38	0.13	0.05
%Bark					–	−0.19	−0.56	−0.27	0.21	−0.35	0.12	−0.39
%Xyl						–	−0.67	−0.01	0.09	−0.38	0.11	0.01
%Pith							–	0.20	−0.22	0.55	−0.18	0.28
VD								–	−0.38	0.25	−0.12	0.39
VDen									–	−0.13	0.12	−0.12
LA										–	0.02	0.14
%SM											–	0.38
%PM												–

In bold, associations with $BF_{10} \geq 5$

the disturbed urban landscapes after the rainy season. Among alien species, the highest A_{sat} was found for *C. coronarium* (17.9 μmol m^{-2} s^{-1} CO_2), followed by *N. glauca* (12.5 μmol m^{-2} s^{-1} CO_2), the only woody alien species. The lowest A_{sat} for alien species was found for *D. wrightii* (1.9 μmol m^{-2} s^{-1} CO_2). Notably, despite *N. glauca* being a woody species, it had among the highest trait values of the alien species. This set of traits may help explain the highly invasive status of this species, which has colonized most of South and Central America, as well as the Mediterranean Basin, from its native range in North Argentina (González et al. 2012).

Plant hydraulic traits also showed marked differences between alien and native species. For example, native plants had higher vessel density and narrower vessel diameters. According to global surveys, lower vessel diameter confers lower hydraulic conductance and a lower risk of xylem cavitation (Hacke et al. 2001, 2017; Olson et al. 2018). Consistent with greater tolerance of dehydration, native species showed more negative water potentials during the late rainy season, highlighting their ability as perennials to cope with summer drought, which most invasive species would avoid with their annual life cycle. Further, variation in stem and leaf water potentials was particularly marked across native species, ranging from − 1.16 MPa in *Rhus integrifolia*, the species with the least negative values of stem water potential, to − 2.85 MPa in *Simmondsia chinensis*, the native species with the most negative stem water potential values. *R. integrifolia*, like its close relative *Malosma laurina*, is known for its deep roots, obtaining reliable sources of water through the year, and thus reducing the need to construct highly resistant xylem (Venturas et al. 2016). Also, native species from our study site had low values for g_s and carbon assimilation, equivalent in magnitude to other perennial shrubs of MTEs in California and Chile (Mooney and Dunn 1970). The low but sustained g_s values of native species allows carbon uptake throughout a more significant portion of the year without compromising the hydraulic integrity of the transpiration stream, though it comes at the cost of lower A_{sat} (Mooney and Dunn 1970).

The difference in water status between aliens and natives at our site contrasted with that shown in a global analysis, in which alien species operated with lower values of Ψ_{stem} than native plants in the community they invaded (Cavaleri and Sack 2010). Within the urban environment of Ensenada, México, the alien species had lower drought tolerance on average than native species. These aliens were able to establish a different hydraulic niche by occupying patches where vegetation was denuded and therefore had higher water availability due to leaks and abundant surface providing runoff (Lodge 1993). Further studies should test the differences between predawn and midday Ψ_{stem} throughout the year or the lifetime of alien species, and their association with soil water potential, to elucidate the acclimation to different hydraulic niches by species from different provenances.

In addition to photosynthetic rates, the traits that varied most strongly between alien herbs and native shrubs were the proportions of tissues in stem-cross sections, with alien herbs having a significantly higher percentage of pith and bark than native shrubs, which had a higher proportion of xylem. The higher pith proportion could be related to longer internodes, which could help avoid self-shading (Olson et al. 2009) and make possible faster and cheaper height growth to overtop competitors in the short season and life cycle. Moreover, higher pith proportions may act as storage for sugars to promote fast growth or mitigate daily embolism (Zwieniecki and Holbrook 2009). Thus, the quantification of tissue proportions may confer information relating to a suite of functional traits and enable rapid assessment of water use strategies across a broad set of species. The variation in tissue proportions may indicate that alien herbs have a lower tissue density and higher relative water content, two traits that are indicative of hydraulic function. Specifically, a low stem density has been associated with isohydric regulation of plant water status (i.e., plants maintain relatively constant Ψ_{stem} via stomatal regulation during soil dehydration) while a high stem density is associated with anisohydric regulation (i.e., plants decline in Ψ_{stem} as soil dehydrates) (Fu et al. 2019). Because water stress is probably the main constraint for the establishment of plant species within Mediterranean-type ecosystems, species may have diverged into fast-growing species, which take advantage of the periods in which resources are widely available, and slow-growing species, in which low rates of resource uptake are sustained through-out most of the year. In this study, alien herbs are an extreme example of fast-growing species whereas native drought-tolerant shrub species are examples of slow-growing species adapted to slow rates of photosynthesis and resource accumulation (Reich 2014; Meinzer et al. 2016). The achievement of fast and slow strategies and isohydric and anisohydric behavior implies coordination among several traits; the multivariate analysis offers a way to explore how species converge in drought-prone ecosystems.

Characterization of trait covariation by ordination analysis

The twelve studied traits showed strong trait covariation. By examining patterns of covariation using Principal Component Analysis, we simplified the variety of possible morpho-physiological states to a two-dimensional space wherein the distinction of strategies is readily visualized. Alien species are mainly herbaceous species that maximize productivity during the rainy season, shedding their leaves or dying at the onset of the dry season. In agreement with Grime (1977) and Reich (2014), we found that alien herb species had functional trait values denoting a tendency towards rapid resource acquisition. The alien species, lacking investment in long-lived tissues, occupied disturbed sites and were less restricted in their morphology and physiology. In contrast, native species were relatively convergent in the PCA-identified strategies, denoting functional redundancy across species. Mediterranean environments promote high values of cavitation resistance, given the extreme seasonality and low precipitation (Maherali et al. 2004; Jacobsen et al. 2008; Choat et al. 2012). Within the flora of the CFP, other modes of persistence are present, such as succulent species (Cactaceae, Crassulaceae and Euphorbiaceae), though uncommonly dominant (Westman 1981), with functional traits that may deviate from the slow-fast scheme proposed by Reich (2014).

Given the identity of species in our native and alien communities, it was difficult to disentangle the effect of life-form from provenance (four of five alien species were herbaceous versus five woody perennials from the native species pool). This same situation has been found in other analyses, including those in Mediterranean-type ecosystems (Funk et al. 2016); these systems have a higher prevalence of herbaceous species in the alien flora than in the native flora. A comparative study of native herbaceous species is therefore needed. The group of alien species was highly variable when summarizing functional and physiological traits, as indicated by our PCA (Fig. 2). That diversity may have derived from a more extensive set of environmental pressures during their evolution in other regions or may relate to life-history traits in each case. Notably, phenotypic integration indices of functional traits of native (18.2%) and alien (21%) species were similar and also comparable in magnitude to the integration of flowers (average of 21%) across broader sets of species (Ordano et al. 2008), supporting the idea that suites of functional traits have consistent covariation to allow the functioning of individuals (Murren 2012). If alien species modify their structure and function when released from selective pressures, it would be expected that they should achieve higher trait variability across sets of environmental conditions. High phenotypic variability may have therefore allowed alien herbaceous species to colonize a variety of environments in MTEs and elsewhere.

Acknowledgements SDDLG, GGRG, TMIM, ARB, and RSC acknowledge scholarships from the Consejo Nacional de Ciencia y Tecnología, México (CONACYT). RMA was supported by FONSEC CONACYT-INEGI 278755, PN-2015-01-251, and CICESE 681-117.This study was supported by the Posgrado de Ciencias de la Vida, CICESE. The orthomosaic map of the study area was generously provided by A. Hinojosa. We appreciate the comments of two anonymous reviewers on a previous version of this manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia 121:183–192. https://doi.org/10.1007/s004420050920

Brodribb TJ (2017) Progressing from 'functional' to mechanistic traits. New Phytol 215:9–11. https://doi.org/10.1111/nph.14620

Brusati ED, Johnson DW, Di Tomaso JM (2014) Predicting invasive plants in California. Calif Agric 68:89–95. https://doi.org/10.3733/ca.v068n03p89

California Invasive species advisory committee (CISAC) (2010) The California invasive species list http://www.iscc.ca.gov/cisac.html

Caplan JS, Yeakley JA (2006) *Rubus armeniacus* (Himalayan blackberry) occurrence and growth in relation to soil and light conditions in western Oregon. Northwest Sci 80:9–17

Caplan JS, Yeakley JA (2010) Water relations advantages for invasive *Rubus armeniacus* over two native ruderal congeners. Plant Ecol 210:169–179. https://doi.org/10.1007/s11258-010-9747-4

Caplan JS, Yeakley JA (2013) Functional morphology underlies performance differences among invasive and non-invasive ruderal *Rubus* species. Oecologia 173:363–374. https://doi.org/10.1007/s00442-013-2639-2

Cavaleri MA, Sack L (2010) Comparative water use of native and invasive plants at multiple scales: a global meta-analysis. Ecology 91:2705–2715. https://doi.org/10.1890/09-0582.1

Choat B, Jansen S, Brodribb TJ et al (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–755. https://doi.org/10.1038/nature11688

Cleland EE, Clark CM, Collins SL et al (2011) Patterns of trait convergence and divergence among native and exotic species in herbaceous plant. J Ecol 99:1327–1338. https://doi.org/10.1111/j.1365-2745.2011.01860.x

Díaz S, Kattge J, Cornelissen JHC et al (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489–496. https://doi.org/10.1016/j.tree.2007.07.001

Drenovsky RE, Grewell BJ, D' Antonio CM et al (2012) A functional trait perspective on plant invasion. Ann Bot 110:141–153. https://doi.org/10.1093/aob/mcs100

Durand LZ, Goldstein G (2001) Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126:345–354

Eagle AJ, Eiswerth ME, Johnson WS, Shoenig SE, van Kooten GC (2007) Costs and losses imposed on California Ranchers by Yellow Starthistle. Rangeland Ecol Manage 60:369–377. https://doi.org/10.2111/1551-5028(2007)60%5b369:CALIOC%5d2.0.CO;2

Early R, Bradley BA, Dukes JS et al (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. Nat Commun 7:12485. https://doi.org/10.1038/ncomms12485

Easlon HM, Bloom AJ (2014) Easy leaf area: automated digital image analysis for rapid and accurate measurement of leaf area. Appl Plant Sci 2:1400033. https://doi.org/10.3732/apps.1400033

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650

Everard K, Seabloom EW, Harpole WS, de Mazancourt C (2010) Plant water use affects competition for nitrogen: Why drought favors invasive species in California. Am Nat 175:85–97. https://doi.org/10.1086/648557

Evert RF (2006) Esau's plant anatomy: meristems, cells, and tissues of the plant body: their structure, function, and development. Wiley. https://doi.org/10.1002/0470047380

Ferreira T, Rasband WS (2012) ImageJ User Guide—IJ 1.46. U.S. National Institutes of Health, Bethesda

Fu X, Meinzer FC, Woodruff DR, Liu YY, Smith DD, McCulloh KA, Howard AR (2019) Coordination and trade-offs between leaf and stem hydraulic traits and stomatal regulation along a spectrum of isohydry to anisohydry. Plant Cell Environ 42:2245–2258

Funk JL (2013) The physiology of invasive plants in low-resource environments. Conserv Physiol. https://doi.org/10.1093/conphys/cot026

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081. https://doi.org/10.1038/nature05719

Funk JL, Zachary VA (2010) Physiological responses to short-term water and light stress in native and invasive plant species in southern California. Biol Invasions 12:1685–1694. https://doi.org/10.1007/s10530-009-9581-6

Funk JL, Standish RJ, Stock WD, Valladares F (2016) Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. Ecology 97:75–83. https://doi.org/10.1890/15-0974.1

Gaertner M, Wilson JR, Cadotte MW, MacIvor JS, Zenni RD, Richardson DM (2017) Non-native species in urban environments: patterns, processes, impacts and challenges. Biol Invasions 19:3461–3469. https://doi.org/10.1007/s10530-017-1598-7

Gallagher RV, Randall RP, Leishman MR (2015) Trait differences between naturalized and invasive plant species independent of residence time and phylogeny. Conserv Biol 29:360–369. https://doi.org/10.1111/cobi.12399

García-Serrano H, Escarré J, Garnier É, Sans FX (2005) A comparative growth analysis between alien invader and native *Senecio* species with distinct distribution ranges. EcoScience 12:35–43. https://doi.org/10.2980/i1195-6860-12-1-35.1

Godoy O, de Lemos-Filho JP, Valladares F (2011) Invasive species can handle higher leaf temperature under water stress than Mediterranean natives. Environ Exp Bot 71:207–214. https://doi.org/10.1016/j.envexpbot.2010.12.001

González A, Tezara W, Rengifo E, Herrera A (2012) Ecophysiological responses to drought and salinity in the cosmopolitan invader *Nicotiana glauca*. Braz J Plant Physiol 24:213–222

González-Muñoz N, Linares JC, Castro-Díez P, Sass-Klaassen U (2014) Predicting climate change impacts on native and invasive tree species using radial growth and twenty-first century climate scenarios. Eur J For Res 133:1073–1086. https://doi.org/10.1007/s10342-014-0823-5

Goodwin BJ, McAllister AJ, Fahrig L (1999) Predicting invasiveness of plant species based on biological information. Conserv Biol 13:422–426. https://doi.org/10.1046/j.1523-1739.1999.013002422.x

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194. https://doi.org/10.1086/283244

Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. Am Nat 159:396–419. https://doi.org/10.1086/338995

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126:457–461

Hacke UG, Spicer R, Schreiber SG, Plavcová L (2017) An ecophysiological and developmental perspective on variation in vessel diameter. Plant Cell Environ 40:831–845

Heberling JM, Fridley JD (2013) Resource-use strategies of native and invasive plants in Eastern North American forests. New Phytol 200:523–533. https://doi.org/10.1111/nph.12388

Hulme PE, Bernard-Verdier M (2018) Comparing traits of native and alien plants: Can we do better? Funct Ecol 32:117–125. https://doi.org/10.1111/1365-2435.12982

Jacobsen AL, Pratt RB, Davis SD, Ewers FW (2008) Comparative community physiology: non-convergence in water relations among three semi-arid shrub communities. New Phytol 180:100–113. https://doi.org/10.1111/j.1469-8137.2008.02554.x

Jarosz AF, Wiley J (2014) What are the odds? A practical guide to computing and reporting Bayes Factors. J Probl Solving 7:2–9. https://doi.org/10.7771/1932-6246.1167

Kleine S, Weissinger L, Müller C (2017) Impact of drought on plant populations of native and invasive origins. Oecologia 183:9–20. https://doi.org/10.1007/s00442-016-3706-2

Klingenberg CP (2014) Studying morphological integration and modularity at multiple levels: concepts and analysis. Philos Trans R Soc B 369:20130249. https://doi.org/10.1098/rstb.2013.0249

Lee MR, Bernhardt ES, Bodegom PM et al (2017) Invasive species' leaf traits and dissimilarity from natives shape their impact on nitrogen cycling: a meta-analysis. New Phytol 213:128–139. https://doi.org/10.1111/nph.14115

Leffler AJ, James JJ, Monaco TA, Sheley RL (2014) A new perspective on trait differences between native and invasive exotic plants. Ecology 95:298–305. https://doi.org/10.1890/13-0102.1

Leishman MR, Cooke J, Richardson DM (2014) Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants. J Ecol 102:1451–1461. https://doi.org/10.1111/1365-2745.12318

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol 8:133–137. https://doi.org/10.1016/0169-5347(93)90025-K

Love J, Selker R, Marsman M et al (2019) JASP: graphical statistical software for common statistical designs. J Stat Soft. https://doi.org/10.18637/jss.v088.i02

Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85:2184–2199. https://doi.org/10.1890/02-0538

Martínez KA, Fridley JD (2018) Acclimation of leaf traits in seasonal light environments: are non-native species more plastic? J Ecol 106:2019–2030. https://doi.org/10.1111/1365-2745.12952

McDowell SC (2002) Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). Am J Bot 89:1431–1438. https://doi.org/10.3732/ajb.89.9.1431

Meinzer FC, Woodruff DR, Marias DE, Smith DD, McCulloh KA, Howard AR, Magedman AL (2016) Mapping 'hydroscapes' along the iso-to anisohydric continuum of stomatal regulation of plant water status. Ecol Lett 19:1343–1352

Melcher PJ, Meinzer FC, Yount DE, Goldstein G, Zimmermann U (1998) Comparative measurements of xylem pressure in transpiring and non-transpiring leaves by means of the pressure chamber and the xylem pressure probe. J Exp Bot 49:1757–1760. https://doi.org/10.1093/jxb/49.327.1757

Méndez-Alonzo R, Ewers FW, Sack L (2013) Ecological variation in leaf biomechanics and its scaling with tissue structure across three Mediterranean-climate plant communities. Funct Ecol 27:544–554. https://doi.org/10.1111/1365-2435.12059

Messier J, Lechowicz MJ, McGill BJ, Violle C, Enquist BJ (2017) Interspecific integration of trait dimensions at local scales: the plant phenotype as an integrated network. J Ecol 105:1775–1790. https://doi.org/10.1111/1365-2745.12755

Mooney HA, Dunn EL (1970) Photosynthetic systems of Mediterranean-climate shrubs and trees of California and Chile. Am Nat 104:447–453. https://doi.org/10.1086/282679

Murren CJ (2012) The integrated phenotype. Integr Comp Biol 52:64–76

Olson ME, Aguirre-Hernandez R, Rosell JA (2009) Universal foliage-stem scaling across environments and species in dicot trees: plasticity, biomechanics and Corner's rules. Ecol Lett 12:210–219. https://doi.org/10.1111/j.1461-0248.2008.01275.x

Olson ME, Soriano D, Rosell JA et al (2018) Plant height and hydraulic vulnerability to drought and cold. Proc Natl Acad Sci USA 115:7551–7556. https://doi.org/10.1073/pnas.1721728115

Ordano M, Fornoni J, Boege K, Domínguez CA (2008) The adaptive value of phenotypic floral integration. New Phytol 179:1183–1192

Ordonez A (2014) Functional and phylogenetic similarity of alien plants to co-occurring natives. Ecology 95:191–1202. https://doi.org/10.1890/13-1002.1

Ordonez A, Olff H (2012) Do alien plant species profit more from high resource supply than natives? A trait-based analysis. Glob Ecol Biogeogr 22:648–658. https://doi.org/10.1111/geb.12019

Ordonez A, Wright IJ, Olff H (2010) Functional differences between native and alien species: a global-scale comparison. Funct Ecol 24:1353–1361. https://doi.org/10.1111/j.1365-2435.2010.01739.x

Osunkoya OO, Boyne R, Scharaschkin T (2014) Coordination and plasticity in leaf anatomical traits of invasive and native vine species. Am J Bot 101:1423–1436. https://doi.org/10.3732/ajb.1400125

Paini DR, Sheppard AW, Cook DC, De Barro PJ, Worner SP, Thomas MB (2016) Global threat to agriculture from invasive species. Proc Natl Acad Sci USA 113:7575–7579. https://doi.org/10.1073/pnas.1602205113

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. J Ecol 102:275–301. https://doi.org/10.1111/1365-2745.12211

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661. https://doi.org/10.2307/2265768

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta D, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Riemann H, Ezcurra E (2005) Plant endemism and natural protected areas in the peninsula of Baja California, Mexico. Biol Conserv 122:141–150. https://doi.org/10.1016/j.biocon.2004.07.008

Riordan EC, Rundel PW (2014) Land use compounds habitat losses under projected climate change in a threatened California ecosystem. PLoS ONE 9:e86487. https://doi.org/10.1371/journal.pone.0086487

Sax DF, Stachowicz JJ, Brown JH et al (2007) Ecological and evolutionary insights from species invasions. Trends Ecol Evol 22:465–471. https://doi.org/10.1016/j.tree.2007.06.009

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. https://doi.org/10.1038/nmeth.2089

Seabloom EW, Williams JW, Slayback D, Stoms DM, Viers JH, Dobson AP (2006) Human impacts, plant invasion, and imperiled plant species in California. Ecol Appl 16:1338–1350. https://doi.org/10.1890/1051-0761(2006)016%5b1338:HIPIAI%5d2.0.CO;2

Smith MS, Fridley JD, Yin J, Bauerle TL (2013) Contrasting xylem vessel constraints on hydraulic conductivity between native and non-native woody understory species. Front Plant Sci 4:486. https://doi.org/10.3389/fpls.2013.00486

Strauss SY, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. Proc Natl Acad Sci USA 103:5841–5845. https://doi.org/10.1073/pnas.0508073103

R Core Team (2017). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Torices R, Muñoz-Pajares AJ (2015) PHENIX: an R package to estimate a size-controlled phenotypic integration index. Appl Plant Sci 3:1400104

Turbelin AJ, Malamud BD, Francis RA (2017) Mapping the global state of invasive alien species: patterns of invasion and policy responses. Glob Ecol Biogeogr 26:78–92. https://doi.org/10.1111/geb.12517

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

van Kleunen M, Dawson W, Essl F et al (2015) Global exchange and accumulation of non-native plants. Nature 525:100–103. https://doi.org/10.1038/nature14910

Venturas MD, MacKinnon ED, Dario HL, Jacobsen AL, Pratt RB, Davis SD (2016) Chaparral shrub hydraulic traits, size, and life history types relate to species mortality during California's historic drought of 2014. PLoS ONE 11:e0159145. https://doi.org/10.1371/journal.pone.0159145

Wagner GP (1984) On the eigenvalues distribution of genetic and phenotypic dispersion matrices: evidence for a non-random organization of quantitative character variation. J Math Biol 21:77–95. https://doi.org/10.1007/BF00275224

Westman WE (1981) Diversity relations and succession in Californian coastal sage scrub. Ecology 62:170–184. https://doi.org/10.2307/1936680

Westman WE (1983) Xeric mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. Vegetation 52:3–19. https://doi.org/10.1007/BF00040012

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Annu Rev Ecol Evol Syst 33:125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827. https://doi.org/10.1038/nature02403

Zwieniecki MA, Holbrook NM (2009) Confronting Maxwell's demon: biophysics of xylem embolism repair. Trends Plant Sci 14:530–534. https://doi.org/10.1016/j.tplants.2009.07.002