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Global resource acquisition patterns of invasive and native plant species do not hold at the regional scale in Mediterranean type ecosystems

Jennifer L. Funk · Monica A. Nguyen · Rachel J. Standish · William D. Stock · Fernando Valladares

Abstract Invasive species may outperform native species by acquiring more resources or by efficiently using limited resources. Studies comparing leaf traits as a metric of carbon capture strategies in native and invasive species have come to different conclusions. Some studies suggest that invasive species are better at acquiring resources, but that native and invasive species use resources similarly. Other studies have found that native and invasive species differ in resource use efficiency, which implies different biochemical or physiological mechanisms of carbon capture. To resolve this debate, we examined relationships among four leaf traits (photosynthetic rate, specific leaf area, foliar nitrogen, foliar phosphorus) in co-occurring native and invasive species from eight plant communities across five Mediterranean-climate ecosystems. We performed standardized major axis regression for all trait combinations within and across sites, testing for slope homogeneity and shifts in elevation (y-intercept) or along a common slope between species groups. Across the global dataset, native and invasive species had similar carbon capture strategies (i.e., similar slopes), with invasive species occupying a position of greater resource acquisition. However, these patterns did not hold when regions were analyzed individually. Regional differences may be driven by differences in life form between native and invasive species, and variation in soil resource availability among regions. Our context-dependent results reveal not only that management of invasive species will differ across regions but also that global comparisons of invasive and native species can be misleading.

J. L. Funk (✉) · M. A. Nguyen
Schmid College of Science and Technology, Chapman University, 1 University Drive, Orange, CA 92866, USA
e-mail: jlfunk@chapman.edu

R. J. Standish
School of Veterinary and Life Sciences, Murdoch University, Murdoch, WA, Australia

W. D. Stock
Centre for Ecosystem Management, Edith Cowan University, Joondalup, WA 6027, Australia

F. Valladares
Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

F. Valladares
Departamento de Ciencias, Universidad Rey Juan Carlos, Móstoles, Madrid, Spain

Introduction

Many invasive species outperform native species through faster rates of carbon capture and growth

(Grotkopp et al. 2002; Leishman et al. 2007; Pysek and Richardson 2007). In the last decade, a debate has emerged about how invasive species achieve higher rates of carbon capture: are they more effective at acquiring resources or are they more efficient in using them (e.g., Funk and Vitousek 2007; Heberling and Fridley 2016; Leishman et al. 2007, 2010)? Identifying the mechanisms that promote higher carbon capture in invasive species will help inform control and restoration strategies. For example, returning resource levels to pre-disturbance conditions should curtail the growth of invasive species if they succeed through higher resource acquisition, but may have no effect if invasive species efficiently use those resources (Funk et al. 2008).

Plants optimize resource capture through specialization (e.g., cluster roots, rhizobial partners), differential allocation of biomass to above- and belowground organs, and physiological and morphological characteristics of individual organs. Trade-offs in the allocation to structure and photosynthetic function at the leaf level are characterized by the leaf economics spectrum (LES), which shows that relationships exist among several leaf traits across biomes and life forms (Reich et al. 1997; Wright et al. 2004). For example, leaf photosynthetic rate (A_{mass}) scales positively with leaf nitrogen concentration (N_{mass}) reflecting the role of N-rich proteins in light harvesting and carbon assimilation (Fig. 1; Evans 1989; Field and Mooney 1986). Species with high resource acquisition generally have a "fast return" on their structural investment and are positioned at the upper end of this relationship. However, a species with high resource use efficiency may achieve high carbon assimilation with a lower amount of N through long-lived evergreen leaves and efficient N recycling. Thus, the nature of trait relationships (e.g., slope, elevation) can be used to assess differences in carbon capture strategies between native and invasive species groups (see Fig. 1). Species groups with similar carbon capture strategies should share a common (i.e., homogenous) slope, indicating similar trade-offs or constraints with respect to how resources are acquired or used (Fig. 1a). Groups may or may not display a shift along that slope. In contrast, species groups with different carbon capture strategies should have different slopes (Fig. 1b) or homogenous slopes with a significant shift in elevation between species groups (Fig. 1c). These distinctions are important because

they suggest different mechanisms of competition between native and invasive species. Invasive species that are positioned further along the "fast return" end of trait relationships likely exhibit morphological or physiological differences enabling higher resource acquisition (e.g., belowground traits). In contrast, invasive species with high photosynthetic nitrogen use efficiency (PNUE) may divert N away from structure and defense and towards compounds associated with light harvesting and carbon fixation reactions of photosynthesis (Feng et al. 2009; Funk et al. 2013).

Studies of leaf-level relationships have found similar and distinct carbon capture strategies among native and invasive species groups. Discrepancies across studies may arise because of differences in spatial scale and context. While strong LES relationships have been found in regional and global datasets that encompass a wide range of leaf form and function (Leishman et al. 2007, 2010; Ordonez and Olff 2012; Penuelas et al. 2010), these trade-offs may not be exhibited in all species or plant systems (Funk and Cornwell 2013; Mason et al. 2016; Wright and Sutton-Grier 2012). In particular, systems with relatively low interspecific trait variation (e.g., systems dominated by deciduous species) may fail to show strong LES relationships, making comparisons of carbon capture based on these relationships difficult to interpret.

Discrepancies among studies may also arise because of regional differences in resource availability. Studies conducted in low-resource systems often find different carbon capture strategies among native and invasive species owing to higher resource use efficiency in invasive species (Funk 2013; Funk and Vitousek 2007; Heberling and Fridley 2013, 2016; Matzek 2011; Oliveira et al. 2014). Because high resource use efficiency may only be meaningful in resource-limited environments, and most studies of invasive species occur in resource-rich environments (e.g., Davis et al. 2000; Gross et al. 2005; Huenneke et al. 1990; Stohlgren et al. 2006), it is possible that this tendency underlies discrepancies among studies.

In this study, we test the paradigm that invasive and native species have similar carbon capture strategies by examining relationships among four leaf traits (A_{mass}, specific leaf area [SLA], N_{mass}, and foliar phosphorus concentration [P_{mass}]) from a large dataset of native and invasive species in eight sites across the five Mediterranean climate ecosystems (Funk et al. 2016). While climate is relatively constant across the
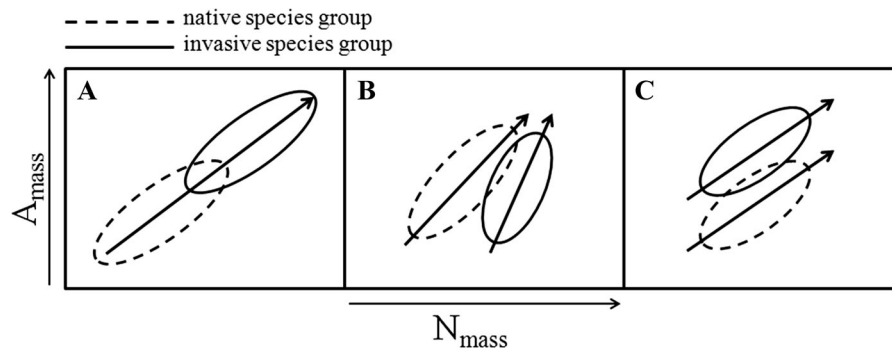
Fig. 1 Potential differences in the relationship between leaf nitrogen concentration (N_{mass}) and mass-based photosynthetic rate (A_{mass}) for native and invasive species groups following standardized major axis regression. *Ellipses* depict the scatter of data points within a species group. The *two lines* may exhibit: **a** a shift along a common slope (different resource acquisition), **b** different slopes (i.e., different resource acquisition or use efficiency), or **c** a shift in elevation while maintaining a common slope (different resource use efficiency). In our example, invasive species exhibit higher N_{mass} and A_{mass} than native species (**a**), which indicates similar strategy tradeoffs. In contrast, species groups with different carbon capture strategies should have different slopes (**b**) or homogenous slopes with a significant shift in elevation between species groups (**c**). Either of these variations could indicate that groups differ in resource use efficiency. For example, if invasive species have a steeper slope (**b**) or higher y-intercept (**c**) in the N_{mass}–A_{mass} relationship than natives, this relationship indicates they can achieve higher photosynthetic rates for the same amount of acquired N (i.e., greater photosynthetic nitrogen use efficiency; PNUE). Note that the example in **b** can take several forms (e.g., slopes can intersect at high or low N_{mass}), leading to different functional interpretations

eight sites, soil nutrient content and disturbance (grazing and fire) varied. We expected to find similar carbon capture strategies among native and invasive species in the global dataset, which includes a large range of leaf types and resource availabilities. In contrast, at the level of individual communities, we expected that differences would be context-dependent owing to differences in resource availability and the extent of trait variation. Because many studies report relationship ratios (e.g., PNUE and A_{area} [area-based photosynthetic rate, which is equivalent to A_{mass}/ SLA]) rather than a comprehensive analysis of trait relationships (e.g., Funk and Vitousek 2007; Heberling and Fridley 2016; Matzek 2011), we also compared these traits across native and invasive species groups to determine how conclusions are influenced by these two analytical approaches.

Methods

We selected eight moderately to heavily invaded communities across the five Mediterranean climate regions, including coastal sage scrub (Irvine, California), serpentine grassland (Portola, California), sclerophyllous woodland (Santiago, Chile), coastal grassland (Bolonia, Spain), acid-sands fynbos (Pella,

South Africa), Renosterveld (Tygerberg, South Africa), banksia woodland (Perth, Australia) and coastal banksia woodland (Perth, Australia). Communities differed in soil N, soil P, and extent of grazing (Table 1). As described in Funk et al. (2016), we collected functional trait data from five individuals of the most common invasive (5–9 species per site) and native (7–47 species per site) plant species at each site. An invasive species was defined as a non-native species that had spread from the area of introduction, reaching high local abundance at each site (Colautti and MacIsaac 2004; Richardson et al. 2000).

Physiological measurements began in the middle of the spring growing season before the onset of flowering. Ambient air temperature at the time of measurement was similar across all eight sites, from 24.6 °C in serpentine grassland (California) to 27.1 °C in Renosterveld (South Africa). Photosynthetic rates were measured on healthy, fully developed leaves with a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE), maintaining chamber conditions with light levels at 1600 μmol photon/m^2/s, CO_2 at 400 μL/L, leaf temperature at 25 °C, and relative humidity at 40–60 %. Photosynthetic rates were temperature-corrected when necessary using standard equations (von Caemmerer 2000). Leaves were collected following gas exchange measurements. To

Table 1 Soil N and P values for eight sites within a Mediterranean climate region (after Funk et al. 2016)

Mediterranean climate region	Community	Site	Soil N (g/100 g)	Soil total P (mg/kg)	Grazing
Western Australia	Banksia woodland (BW)	Perth, Australia	0.05	47.7	Low
	Coastal banksia woodland (CBW)	Perth, Australia	0.06	150.9	None
California	Coastal sage scrub (CSS)	Irvine, California	0.19	628.3	Low
	Serpentine grassland (SG)	Portola, California	0.23	30	Low
Chile	Sclerophyllous woodland (SW)	Santiago, Chile	0.09	1001	None
South Africa	Acid-sands fynbos (F)	Pella, South Africa	0.03	31	None
	Renosterveld (R)	Tygerberg, South Africa	0.29	304	None
Spain	Coastal grassland (CG)	Bolonia, Spain	0.05	117.8	High

determine SLA, leaves were scanned to measure total area, dried for 3 days at 65 °C, and weighed. Dried leaves were then ground and analyzed for total plant N content using an elemental analyzer (Costech 4010 elemental combustion system, Valencia, CA). Colorimetric analysis following Kjeldahl digest was performed to determine total P content using a discrete analyzer (SmartChem 200, Unity Scientific, Brookfield, CT). Photosynthetic nitrogen and phosphorus use efficiency (PPUE) were calculated as A_{mass} divided by N_{mass} and P_{mass}, respectively.

Statistical analyses

We assessed how five traits related to relationship ratios differed between native and invasive species groups: A_{area} (A_{mass}/SLA), N_{area} (N_{mass}/SLA), P_{area} (P_{mass}/SLA), PNUE (A_{mass}/N_{mass}), and PPUE (A_{mass}/P_{mass}). To examine differences in leaf-level traits between native and invasive plants across the five regions, we used a mixed-model, nested ANOVA with region and origin (native or nonnative) as fixed factors and site (nested within region) and species (nested within origin) as random factors. Because there were significant interactions between region and origin for all traits, we conducted separate analyses within region, with origin as a fixed effect and site and species as random effects. Data were log-transformed prior to analysis. Mixed models were fit with the lme4 package (version 1.7) and the nloptr package (version 1.0.4) using R (version 3.2.0, R Core Development Team 2015). To compute P values, we used the Satterthwaite correction to approximate degrees of freedom, which are not well-defined for mixed models.

To compare bivariate trait relationships between native and invasive species, we performed standardized major axis (SMA) regression for each possible combination of traits (A_{mass}, N_{mass}, P_{mass}, and SLA) within each region and across regions using species means. Standardized major axis regression determines the best fit line for a scatter of bivariate data in order to provide a summary of the relationship between the variables, rather than to use one variable to predict the other (Warton et al. 2006). The data for each group (native or invasive) were log_{10}-transformed and individually fitted with an SMA slope. The slopes of the scaling relationships were tested for homogeneity, and those found to have a common slope were then tested for shifts in elevation and shifts along the slope (Fig. 1) using the WALD test. All analyses were performed using SMATR software (version 2.0, Falster 2006), with significance level set at $\alpha = 0.05$. All bivariate graphs were created using the smatr package (version 3.4-3) in R.

Results

Functional trait differences based on origin

Traits varied across regions (except P_{area}) and origin (except PPUE); however, significant interactions between region and origin for all traits required that effects of origin be evaluated within each region (Table S1). In California and Spain, there was no effect of origin on any of the trait values measured, while in Western Australia all but one trait (A_{area}) showed a significant effect of origin (Table S2). In Chile and South Africa, results were mixed: A_{area} and

PNUE differed between native and invasive species in Chile while SLA, N_{area}, and PNUE differed in South Africa (Table S2). Where significant differences were detected, invasive species had higher trait values except for N_{area} and P_{area}, which were higher for native species.

Global leaf trait relationships

When data were pooled across the five regions, slopes for all leaf trait relationships were similar between native and invasive species (slope homogeneity, Table 2). Only one trait pair (SLA–P_{mass}) displayed a significant shift in elevation between groups ($P = 0.048$, Table 2). All relationships exhibited a shift along a common slope, with native species generally displaying wider trait distributions relative to invasive species, and invasive species occupying regions of higher trait values than native species (Table 2; Fig. 2).

Regional leaf trait relationships

Trait relationships varied across regions. Shifts along slope were prevalent in data from South Africa and Western Australia (Table 3; Figs. S3, S5). For Chile, patterns were mixed: there were two shifts along slope (SLA–A_{mass}, P_{mass}–A_{mass}), but species groups had different slopes for two trait relationships (SLA–

N_{mass}, N_{mass}–P_{mass}), and there was one shift in elevation (N_{mass}–A_{mass}; Fig. S2). No shifts in elevation or along a common slope were observed for data collected in California and Spain (Table 2; Figs. S1, S4); instead, we observed different slopes for SLA–N_{mass} (California), SLA–P_{mass} (California), and P_{mass}–A_{mass} (Spain). In many cases where significant differences in slope between native and invasive species groups were detected, the trait relationships were weak in one or both species groups ($r^2 < 0.10$, Figs. S1–S5).

Trait relationships can be analysed using two methodological approaches: SMA regression (e.g., N_{mass}–A_{mass}) and relationships ratios (e.g., PNUE). Theoretically, results from these approaches should be similar. Where SMA analysis reports a shift in elevation or a difference in slope homogeneity between two species groups, we should also observe a significant difference in relationship ratio. At the regional level, these two approaches were in agreement only 68 % of the time (Table S3).

Discussion

Our survey of eight vegetation communities across the five Mediterranean climate ecosystems demonstrated that differences in carbon capture strategies among native and invasive species groups were context-dependent. At the global level, we found that invasive

Table 2 Results of standardized major axis (SMA) regression analysis for all trait combinations of specific leaf area (SLA), mass-based photosynthetic rate (A_{mass}), leaf nitrogen concentration (N_{mass}), and leaf phosphorus concentration (P_{mass}) across all Mediterranean regions

Trait pair	Origin	n	r^2	P	Slope	Intercept	SH (P)	SIE (P)	SACS (P)
SLA–A_{mass}	Invasive	45	0.469	**<0.001**	1.525	−1.0482	0.142	0.093	**0.001**
	Native	129	0.711	**<0.001**	1.26	−0.3795			
SLA–N_{mass}	Invasive	46	0.009	0.539	0.6666	−1.0731	0.272	0.289	**<0.001**
	Native	129	0.248	**<0.001**	0.5542	−0.7869			
SLA–P_{mass}	Invasive	45	0.221	**0.001**	1.2127	−3.360	0.058	**0.048**	**<0.001**
	Native	110	0.424	**<0.001**	0.8998	−2.570			
N_{mass}–A_{mass}	Invasive	45	0.066	0.088	2.314	1.385	0.925	0.916	**0.002**
	Native	129	0.333	**<0.001**	2.274	1.410			
P_{mass}–A_{mass}	Invasive	44	0.101	**0.035**	1.271	3.192	0.689	0.372	**0.002**
	Native	110	0.373	**<0.001**	1.360	3.182			
N_{mass}–P_{mass}	Invasive	45	0.089	**0.046**	1.885	−1.455	0.389	0.711	**0.005**
	Native	110	0.449	**<0.001**	1.640	−1.331			

P values are reported for slope homogeneity (SH), shift in elevation (SIE), and shift along a common slope (SACS). Values in bold represent significant results ($P \leq 0.05$)
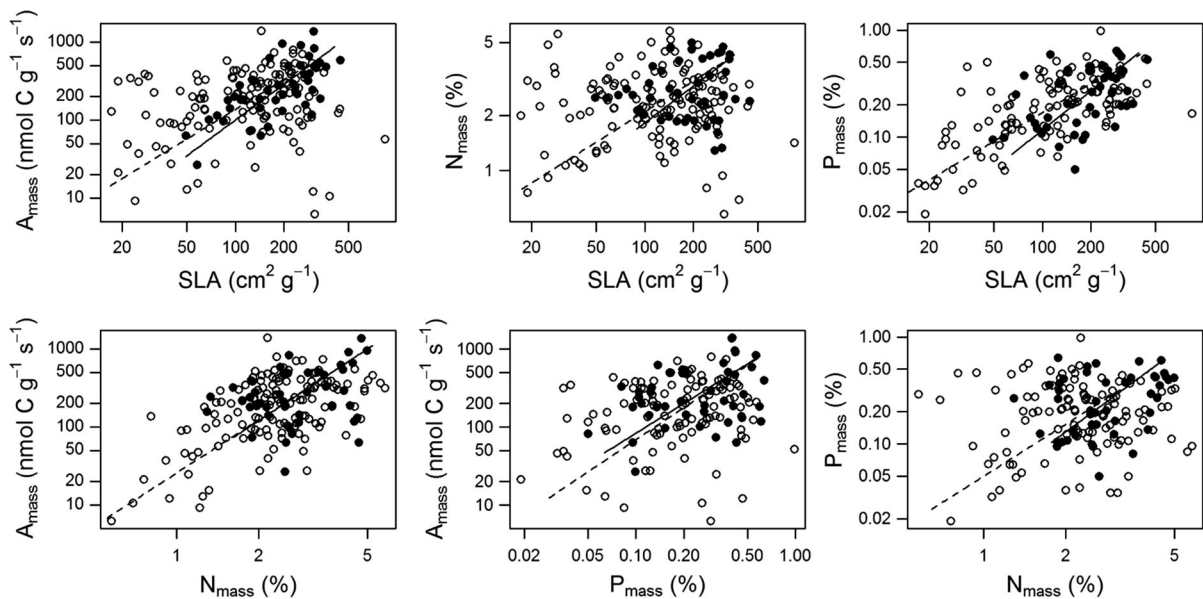
Fig. 2 Standardized major axis regressions for all possible combinations of traits (A_{mass}, N_{mass}, P_{mass}, and SLA) for the combined Mediterranean data set. *Filled circles* and *solid lines* represent invasive species; *open circles* and *dashed lines* represent native species. Axes are $\log_{10}$ scaled. R^2 and P values are given in Table 2

species were located on the fast return end of the LES relative to natives (i.e., there was a significant shift along slope), which supports the view that native and invasive species have similar carbon capture strategies and that invasive species are better at acquiring resources (Leishman et al. 2007, 2010; Ordonez and Olff 2012; Penuelas et al. 2010). However, when evaluated at the regional scale, the patterns were more nuanced. Western Australia was the only region where native and invasive species displayed homogenous slopes for all trait relationships. As we discuss below, differences across scales and regions may be attributable to variation in life form between native and invasive species groups, and variation in soil resource availability across regions.

Contrary to patterns observed at the global level, we did not see a universal shift along a common slope across all regions or for all trait relationships. A likely explanation for the regional pattern is that shifts along a common slope only occurred in regions with differences in life form between species groups. Funk et al. (2016) found that invasive species in these Mediterranean climate regions were more likely to be annual rather than perennial. Because annual species tend to be on the fast return end of the LES (Garnier 1992), regions where native and invasive species

groups differ in life form might show a shift along a common slope. In contrast to California and Spain, which included both native and invasive annual species, sites in Chile, South Africa, and Western Australia had few native annuals resulting in a comparison of native woody species and invasive annual species (see Funk et al. 2016 for complete species list). Thus, shifts along a common slope, with invasive species occupying the fast return end of the LES, may have been driven by life form rather than invasive status in these three regions.

While we observed some differences in slope homogeneity across regions, these results must be interpreted with caution as several groups had weak ($r^2 < 0.10$) and/or statistically insignificant relationships (Figs. S1–S5). Specifically, for the seven cases where slopes were found to differ, only one case had significant relationships for both native and invasive species (N_{mass}–A_{mass}, South Africa). Weak trait relationships may have occurred for two reasons: low sample size and low trait variation. For some regions, only one site was sampled (Chile, Spain) or there was significant species overlap between sites (South Africa, Western Australia) resulting in low sample size for these species-level trait relationships ($n = 6–10$ species). For example, the SMA analysis

Table 3 Results of standardized major axis (SMA) regression analysis for all trait combinations of specific leaf area (SLA), mass-based photosynthetic rate (A_{mass}), leaf nitrogen concentration (N_{mass}), and leaf phosphorus concentration (P_{mass}) for five Mediterranean-climate regions

Trait pair	California			Chile			South Africa			Spain			Western Australia		
	SH	SIE	SACS	SH	SIE	SACS	SH	SIE	SACS	SH	SIE	SACS	SH	SIE	SACS
SLA–A_{mass}	0.079	0.533	0.108	0.212	0.236	**0.002**	0.896	0.205	**0.001**	0.145	0.103	0.779	0.275	**0.02**	**<0.001**
SLA–N_{mass}	**0.017**			**0.041**			0.11	0.328	**<0.001**	0.731	0.694	0.257	0.887	**0.009**	**<0.001**
SLA–P_{mass}	**0.005**		0.616	0.457	0.864	**0.012**	0.276	0.526	**<0.001**	0.339	0.665	0.533	0.558	**0.014**	**<0.001**
N_{mass}–A_{mass}	0.294	0.391	0.99	0.254	**0.006**	0.055	**0.05**	0.914	0.006	0.346	0.11	0.614	0.628	0.101	**<0.001**
P_{mass}–A_{mass}	0.518	0.146	0.405	0.595	0.382	**0.001**	0.358			**0.043**			0.654	**0.033**	**0.001**
N_{mass}–P_{mass}	0.846	0.476		**0.011**			**0.023**			0.177	0.426	0.423	0.726	0.986	**0.003**

P values are reported for slope homogeneity (SH), shift in elevation (SIE), and shift along a common slope (SACS). Values in bold represent significant results ($P \leq 0.05$). Trait combinations with significant values for slope homogeneity (i.e., with different slopes) were not tested for shifts in elevation or along slope

reported different slopes between native and invasive species groups for N_{mass}–A_{mass} and N_{mass}–P_{mass} in South Africa, but a careful inspection of these relationships revealed high variation (and insignificant correlations) within the invasive species groups (n = 8 species), yielding a pattern that more closely resembles a shift along a common slope with invasive species at the fast return end of the LES (Fig. S3). Low trait variation may also diminish the strength of trait relationships (Funk and Cornwell 2013), but the range of trait values in the two regions with abundant herbaceous species (California and Spain) was similar to other regions.

We observed several shifts in elevation across regions; however, due to weak relationships within some species groups, the only robust differences in elevation occurred in Western Australia (Fig. S5). In this region, lower intercepts for native species in the A_{mass}–N_{mass} (not statistically significant, but see Fig. S5) and A_{mass}–P_{mass} relationships indicates lower PNUE and PPUE, respectively. However, native species also had higher N_{area} and P_{area}, which could reflect differential allocation of N and P to enhance photosynthetic function and growth in the face of water limitation. For example, high N_{area} has been observed for species in arid and semi-arid systems as greater allocation to N-rich photosynthetic enzymes can increase water use efficiency (Mooney et al. 1978; Wright et al. 2005; Wright and Westoby 2002). These observations support the widespread pattern that PNUE and WUE are negatively correlated (e.g., Field et al. 1983). However, lower resource use efficiency in native species may also signal a greater investment in structural tissue at the expense of photosynthetic function and growth. High PNUE and PPUE in invasive species observed here is consistent with the idea that invasive species can use resources efficiently in resource-poor environments (reviewed in Funk 2013), but may simply reflect differences in life form between native (i.e., woody perennials) and invasive (i.e., annual) species groups.

The strong influence of resource availability and disturbance (e.g., N deposition, grazing) on leaf trait relationships (e.g., Adamidis et al. 2014; Ochoa-Hueso et al. 2011; Wright et al. 2005) may also explain discrepancies among studies of carbon capture strategies in native and invasive species. For example, Leishman et al. (2010) found that species from disturbed sites, regardless of origin, were positioned

on the fast return end of LES relationships compared with species from undisturbed sites with lower resource availability. Thus, sites with higher soil nutrient availability or disturbance may attract exotic species with faster return rates leading to a shift along a common slope. While our sites varied in grazing status and resource availability (Table 1), differences in carbon capture strategy (e.g., shift along a common slope) did not correspond to resource availability. For example, shifts along slope were strong in Western Australia but absent in Spain, even though both sites had nutrient-impoverished soils. Differences in life form among native and invasive species within regions likely counfounded our ability to decipher the role of resource availability on carbon capture strategy.

Lastly, different methodological approaches for analyzing leaf trait relationships may contribute to discordance among study results (SMA analysis versus relationship ratios). Native and invasive species with different relationship ratios (e.g., PNUE) should also have different slopes or elevations of scaling relationships (e.g., N_{mass}–A_{mass}) rather than a shift along a common slope; however, this is not always the case. At the regional level, SMA analysis and relationship ratio comparisons aligned only 68 % of the time (Table S3). For example, PNUE was higher in invasive than native species in Western Australia; this is apparent from the bivariate plot (Fig. S5). However, the SMA analysis reported a significant shift along a common N_{mass}–A_{mass} slope, with invasive species at the fast return end of the spectrum. It is possible such differences are the result of outlying values, which though not strong enough to drastically alter the slopes, could have led to a difference in the relationship ratios. While relationship ratios integrate functional strategies across an entire distribution of traits and are easier to present than scaling relationships, they do not always predict specific trends in leaf trait relationships. For example, different slopes can arise through several mechanisms (Fig. 1b) and this information is not apparent from relationship ratios. Thus, we recommend using both approaches to interpret data.

In conclusion, at the global level, native and invasive species displayed shifts along a common slope and, thus, similar carbon capture strategies with invasive species occupying the fast return end of trait relationships. At the regional level, patterns were varied: species groups did not always share a common slope and invasive species were not always positioned on the fast return end of trait relationships. This result supports the idea that invasive species dynamics can be context-dependent (Daehler 2003; Leffler et al. 2014; Matzek 2011; Thompson et al. 1995) and that management of invasive species may differ across communities. If invasive species are consistently on the fast return end of the LES (as in South Africa and Western Australia), ecologists can predict species most at risk of becoming invasive when introduced to a new environment. Furthermore, if native and invasive species differ in the timing or magnitude of resource acquisition and use, lowering resource availability or reinstating natural disturbance regimes may facilitate the restoration of native plant species (e.g., Funk and McDaniel 2010; Steers et al. 2011). Alternatively, where native and invasive species share strategies (as in California and Spain), we may identify native species that can compete with invasive species in restored communities (Funk et al. 2008).

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