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META-ANALYSIS



Do alien plant species profit more from high resource supply than natives? A trait-based analysis

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ABSTRACT

Aim Previous studies comparing conditions of high- versus low-resource environments have pointed at differences in key traits that would allow aliens to perform better than natives under high-resource conditions. We generalize and test the robustness of this idea by exploring how trait differentiation between aliens and natives changes along continuous resource gradients.

Location Global.

Methods We constructed a database of three leaf traits (specific leaf area, SLA; photosynthetic capacity, A_{mass}; leaf nitrogen content, N_{mass}) that are important for carbon capturing strategies in plants. The database includes 2448 native and 961 alien species over 88 locations world-wide. Using rank correlations and mixed-effect linear models, we assessed the relations between plant traits and climatic, edaphic and human disturbance gradients. Then we determined how the differences in traits between natives and aliens changed along the same gradients.

Results Across all environments, aliens were found to have higher SLA, N_{mass} and A_{mass} than natives. These differences were observed both globally and when controlling for co-occurrence. Also, higher average trait values were found in higher resource supply environments. However, trait differences between natives and aliens remained constant along the evaluated environmental and disturbance gradients. When compared in a multidimensional trait space defined by the leaf economics spectrum, co-occurring aliens and natives showed no between-group differences and no relation with any of the evaluated gradients.

Main conclusions We suggest that although increased resource availability is positively related to higher carbon capture strategies (determined via higher plant leaf trait values), these benefits remain the same for aliens and natives. Therefore, we conclude that high-resource environments do not specifically cause aliens to outperform natives with respect to carbon capture, or at least not more than in other environments.

Keywords
Alien, alien plants, foliar nitrogen, functional traits, invasions, leaf economics spectrum, native, photosynthetic capacity, plant ecological strategies, specific leaf area.

INTRODUCTION

Only a small fraction of all introduced organisms become invasive (Richardson & Pyšek, 2006), making the understanding of 'why' and 'how' some introduced plants and animals become successful invaders vital for the maintenance of biodiversity in native communities and ecosystem functioning (Srivastava & Vellend, 2005). To reach this goal, two different methodological approaches have been used: (1) a species-focused approach, aiming to determine which characteristics/traits make a given specie invasive, and (2) a site-based approach, focused on determining which factors make a given location/community susceptible to invasions.

Results from the species-based approach (mainly based on comparisons of co-occurring aliens and natives) have provided some generalizations on the attributes of successful aliens.

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Specifically, some of the analyses comparing regional and global species pools of natives and aliens have found that aliens have faster growth rates, higher leaf nutrient contents, higher specific leaf areas, shorter life cycles, devote more resources to reproduction and produce more seeds that are better dispersed and germinate faster (Grotkopp *et al.*, 2002; Leishman *et al.*, 2007, 2010; Pyšek & Richardson, 2007; Ordonez *et al.*, 2010; van Kleunen *et al.*, 2010). Additionally, different sets of traits have been shown to confer advantages to aliens in disturbed areas (e.g. traits promoting high reproduction rates and rapid spread) and mesic conditions (e.g. fast growth and resource acquisition) and high fertility (e.g. investment in traits important for light competition, reduced investment in defences). Together this illustrates how multiple traits contribute to the success of alien plants, and that the significance of individual or multiple traits is context dependent (Thompson *et al.*, 1995; Richardson & Pyšek, 2006; Moles *et al.*, 2008).

In the case of site-based approaches, the susceptibility of a community to accept new members has been explained based on the biotic (e.g. effects of herbivores or pathogens) and abiotic conditions (e.g. effects of pH or nutrient availability) of the introduced area. For example, in a global meta-analysis González *et al.* (2010) in terrestrial and aquatic ecosystems, the performance of invasive species (measured as growth and production rates) was generally higher than that of natives under low- and high-nutrient conditions. Also, analyses of Leishman *et al.* (2007, 2010) of traits associated with the carbon capture strategies of plants showed how the traits of invasive and native plants are a reflection of the environmental conditions of the sites where they occur (mainly disturbance regime and resource availability).

The most promising approach in connecting traits of aliens to the susceptibility of a community to them is the use of site-based comparisons of key traits along large-scale environmental and disturbance gradients. However, only a handful of studies have aimed to link these species-based and location/community-based approaches, most of them focusing on recently available distribution, trait and environmental information.

The choice of the right plant traits is crucial in the investigation of the differences between natives and aliens, particularly when evaluating performance differences. We expect that specific leaf area, leaf nutrient concentrations and the maximum rate of photosynthesis are attributes suitable for this, due to their central role in the carbon fixation strategies of plants, thus representing a major axis of variation in plant ecological strategies and plant performance (carbon assimilation or photosynthetic nitrogen use efficiency). Additionally, the success of aliens is often attributed to their capacity for fast growth, particularly when resources are abundant (e.g. due to higher carbon capture rates in high-nutrient sites), and these traits are highly correlated to plant maximum growth rates (Poorter *et al.*, 1990; Poorter & Bongers, 2006). Therefore, comparing carbon-capture-related traits between aliens and natives under high- and low-resource environments can help to understand the mechanisms of invasions.

How trait differences between aliens and natives vary along large-scale resource availability gradients is a subject that has been rarely studied (although for works comparing high- versus low-resource conditions see Leishman & Thomson, 2005, Funk & Vitousek, 2007, González *et al.*, 2010, and Leishman *et al.*, 2010). The few studies evaluating this relation suggest that, specifically under high-nutrient conditions, aliens have the potential to outperform natives if there is an increase in unutilized resources (Davis *et al.*, 2000; Daehler, 2003) and/or a reduction in herbivory/parasitism rates (Blumenthal, 2005, 2006; Blumenthal *et al.*, 2009). Alternatively, under low-resource conditions aliens have been generally seen as not particularly favoured, as natives and the environment keep them better 'under control', despite their plasticity (however, for explanations of alien success in low-resource environments see Funk & Vitousek, 2007, and González *et al.*, 2010).

The aim of this paper is to explore if key trait differences (that is, fixed species differences in traits associated with carbon capture strategies) exist between co-occurring aliens and natives and to see how these differences change in direction and magnitude along continuous resource availability gradients. For this, we compiled a global database of continuous plant traits associated with the 'leaf economics spectrum' (the balance in carbon gains and losses of leaves defining the carbon economics of a plant; Wright *et al.*, 2004) and linked to information on climate, soil nutrient availability and the human disturbance regime at each site.

METHODS

Database compilation and selection of traits

We focused on three traits: specific leaf area, photosynthetic capacity and leaf nitrogen content (as described in Table 1). Together, they describe a species' position along the 'leaf economics spectrum' (Wright *et al.*, 2004). Specific leaf area (SLA; $cm^2\ g^{-1}$) reflects the area that a plant produces per unit of leaf dry-mass. Photosynthetic capacity (A_{mass}; $nmol\ g^{-1}\ s^{-1}$) is a measurement of a plant's potential photosynthetic assimilation rate per unit leaf mass. Leaf nitrogen content (N_{mass}; $g\ g^{-1}$ or %) is a measurement of the resource investment in the photosynthetic machinery and possible losses due to herbivory. Together these traits covary along a spectrum that runs from opportunistic, fast-growing species susceptible to herbivory that are characterized by high SLA, leaf N concentrations, maximum photosynthetic, dark respiration rates and short leaf life span, to species with the opposite suite of traits that are more conservative, slower growing and better able to cope with herbivory and desiccation.

The data sets used for this paper were selected using literature searches and direct communication with authors of specific papers. We searched the ISI Web of Science using both individual, and all combinations of the following keywords: 'plant traits', 'SLA', 'leaf nitrogen', 'maximum photosynthetic rate', 'LMA', 'leaf size', 'leaf nutrients', 'leaf economics', 'resource use efficiency', 'plant traits', 'LHS', 'plant physiology', 'weed', 'weeds', 'naturalized', 'invasive', 'exotic', 'noxious', 'introduced', 'alien', 'foreign', 'non-native'.

Table 1 Description of the variables used in this study.

	Variable (abbreviation)	Definition	Units
Traits	Specific leaf area (SLA)	Reflects the leaf area that a plant produces per unit of leaf dry mass. It is positively related to plant relative growth rates, leaf carbon assimilation rates and energy supply defining a key axis of the leaf economics spectrum	$cm^2\ g^{-1}$
	Photosynthetic capacity (A_{mass})	Measurement of a plant potential photosynthetic assimilation rates (that is the rate leaves are able to fix carbon during photosynthesis) per unit leaf mass	$nmol\ g^{-1}\ s^{-1}$
	Leaf nitrogen content (N_{mass})	Measurement of the resource investment in the photosynthetic machinery, and possible losses due to herbivory. It is a common proxy for the type of nutrient limitation	$g\ g^{-1}$ or %
	Multi-trait (Multi)	Position along the multivariate 'leaf economics spectrum'. It is a measurement of the trade-offs between the investments of nutrients and dry mass in leaves and the rate of return in terms of carbon acquisition	Unit less
	Human impact (HII)	Measurement of anthropogenic disturbance in each of the sampled locations	%
Climate	Total annual precipitation (AnnPre)	Total amount of precipitation fallen in a location or area, over a 1-year period	$mm\ year^{-1}$
	Mean annual temperature (AnnTmp)	Average temperature for a year period, in a given location or area	°C
	Potential annual evapotranspiration (EvptYr)	Total amount of evaporation that would occur if a sufficient water source were available. The rate expresses the amount of water lost from a cropped surface in units of water depth	$mm\ year^{-1}$
	Daily irradiance (DayIrr)	Measure of how much solar power (insolation) reaches a particular location or area	$Wh\ m^{-2}$
	Temperature seasonality (TmpSeas)	Variability in the mean monthly temperature in a given location or area, across a 1-year period	SD × 100
	Precipitation seasonality (PreSeas)	Variability in the total amount of precipitation fallen in a given location or area, across a 1-year period	CV
Soils	Available water capacity (TAWC)	Amount of water that a soil can store that is available for use by plants	$cm \times m^{-1}$
	pH measured in water (PHAQ)	Measure of the acidity or basicity of the soil	pH units
	Total nitrogen (TOTN)	Total nitrogen content in the soil available as ammonium or nitrate	$g \times kg^{-1}$
	Carbon:nitrogen ratio (CNRT)	Proportion of carbon in relation to the amount of available nitrogen	C/N
	Effective cation exchange capacity (ECEC)	Total amount of exchangeable (available) cations, (i.e. sodium, potassium, calcium and magnesium), bases and aluminium	$cmol_c\ kg^{-1}$
	Bulk density (BULK)	Measurement of the mineral make up of soil and the degree of compaction	$kg\ dm^{-3}$
	Total organic carbon content (TOTC)	Total carbon content in the soil	$g\ kg^{-1}$
	Cation exchange capacity (CECS)	Maximum quantity of total cations, of any class, that a soil is capable of holding. It provides a measure of fertility, nutrient retention capacity and the capacity to protect groundwater from cation contamination	$cmol_c\ kg^{-1}$

Plant status was defined following the alien–naturalized–invasive continuum defined by Richardson *et al.* (2000). Herein, alien species are considered to be intentionally or accidentally introduced as a result of human activity. Aliens therefore, include both naturalized (aliens that sustain viable populations without direct intervention by humans) and invasive plants (the subset of all naturalized species that produce large numbers of reproductively viable offspring at considerable distances from parent plants). For each location/study, plant status (native or aliens) was established using national, regional and global databases of introduced species. An alternative approach would be to compare traits between species with invasive (either alien or native) and non-invasive (either alien or native) behaviour in communities. With scarce data on long-term community dynamics world-wide, this would only leave the selection of species on the basis of traits as an option. But this would of course introduce a circularity of argument if invasive and non-invasive species were then compared for traits.

Only site-based environmental data were used so that a gradient of resources and disturbances with information on climatic, edaphic and human disturbance conditions could be reasonably attached to each locality. This resulted in a dataset with 2448 native and 961 alien species with information on one or more of the selected traits across 88 locations around the world. It encompasses most climates, soil characteristics and human disturbance regimes. A summary of the database is included as Supporting Information (Appendix S1).

Trait differentiation between native and alien species

Native and alien species were compared using two alternative approaches: (1) linear (generalized least squares and mixed effects) models using the plant traits as the response variable and site properties as predictors, and (2) site-based comparisons where the native–alien contrast is captured in log-response ratios

and absolute differentiation levels. In the case of log-response ratio contrast, observations were weighted using the alien–native comparison variance (as done in flexible meta-analytic procedures; Nakagawa *et al.*, 2007). Using these two approaches we determined: (1) differences in individual traits between plant types, (2) the effects of environmental conditions on each group of traits, and (3) how the differences between aliens and natives changes along the same environmental gradient.

In both approaches, linear mixed models were used to test how the differences between native and aliens changed across sampled sites. Implemented linear and mixed effects models used species status (native or alien) as a fixed factor, and in the case of mixed effects models sampled locations were used as random effects (using a random slope and intercepts). Models were compared using a log-likelihood ratio test to determine the significance of the random components. Regressions and test were implemented using the *nlme* package (Pinheiro *et al.*, 2009) in R version 2.12.

The second set of comparisons (site-based comparisons) was used in two ways: first to measure the absolute (i.e. are aliens different from natives) and second the directional differences (i.e. are trait values of aliens higher than those of natives) between co-occurring alien and native species across all sampled locations as a response variable. The absolute magnitude of differentiation between alien and natives was determined using the absolute differences in traits between co-occurring alien and natives, i.e. Abs[log(alien/native)]. Directional differences between plants groups were measured using Hedges *et al.*'s (1999) log response ratios, calculated as log(alien/native), a tool often used in meta-analyses. Both of these measurements express the proportionality of the changes across the sampled locations, and together allow the separation of the direction and magnitude of the net differentiation between natives and aliens, while eliminating or reducing the bias and variation associated with individual studies. To test the significance of mean effect sizes, we used an inverse variance weighted flexible meta-analytic procedure (Nakagawa *et al.*, 2007) using species identity as a grouping random factor.

Association with the environmental conditions

We used three different groups of variables (as described in Table 1) to characterize the environmental-disturbance conditions on each of the sampled locations: climatic factors, edaphic factors and human influence. The climate at each site was captured by: total annual precipitation (mm $year^{-1}$), mean annual temperature (°C), mean potential annual evapotranspiration (mm $year^{-1}$), daily irradiance (Wh m^{-2}), temperature seasonality (standard deviation of monthly temperature for a year in °C [SD] × 100) and precipitation seasonality (yearly precipitation coefficient of variation [CV]). These were used to characterize the environmental conditions that potentially limit the resource acquisition rates via photosynthesis. All temperature and precipitation measures were derived from the 5-arcmin WorldCLIM database (Hijmans *et al.*, 2005; http://www.worldclim.org), the mean annual potential evapotranspiration was obtained from the 5-arcmin UN FAO global agro-ecological assessment study (Hoogeveen, 2009; http://www.fao.org/geonetwork/srv/en/main.home?uuid=750d56ca-f92a-405e-8bbc-302221d55917) and daily irradiance was estimated using ArcGIS, on the basis of longitude/latitude position, and the 5-arcmin resolution digital elevation model used to construct the WorldClim database.

Site edaphic characteristics were described by the available water holding capacity (cm m^{-1}), pH in a water extract (pH units), total soil nitrogen (g kg^{-1}), soil carbon nitrogen ratio (C/N), effective soil cation exchange capacity or total exchangeable bases ($cmol_c$ kg^{-1}), soil bulk density (kg dm^{-3}) and total soil organic carbon content (g kg^{-1}). These soil characteristics were used to represent the nutrient pools, quality of the organic matter available for plants on a site and indices for availability nutrients to plants (Heal *et al.*, 1997). All soil parameters were obtained from the 5-arcmin ISRIC-WISE derived soil map of the world (Batjes, 2004; http://www.isric.org), which is based on extensive field sampling.

Last, we used the human impact index (%) as a measurement of anthropogenic disturbance in each of the sampled locations. This index is a regionally consistent way to represent land transformation, due to human activity (e.g. population density, land transformation, accessibility and electrical power infrastructure) on a global scale. It expresses the continuum of human influence (ranging from 0% in natural areas to 100% for completely transformed habitats) stretched across the land surface. The impact index was obtained from a rasterized map in 1-km resolution (Sanderson *et al.*, 2002; http://sedac.ciesin.columbia.edu/wildareas) and rescaled to 5 arcmin for use in this study.

The association between all available plant traits of natives and aliens and climatic, edaphic and human disturbance measurements were quantified using two statistical methods: Spearman rank correlations and linear mixed models. Spearman rank correlations allowed us to determine nonparametric correlations between traits and site descriptors, while mixed models allowed us to test for interactions between site conditions and native–alien differences, which is not possible with nonparametric methods.

In the linear mixed models, we used environmental and disturbance metrics as fixed effects, while sampled sites were included as a random factor, to account for the non-independence of trait observations at a site. As all traits were approximately log-normally distributed (right-skewed), a $\log_{10}$ transformation was used to improve normality and homogeneity of variances. We also built regression models that included a full factorial combination of plant status (i.e. native or alien) and each environmental variable, to test for the dependence of native–alien differences on environmental conditions. For this, we tested for the significance of the interaction between native/alien status and environmental variables (homogeneity in the relation with the environment) and of the native/alien status (differences in native and alien mean trait across the gradient).

To determine if the association between traits and climatic, edaphic or human disturbance changed between aliens and native species, relative and absolute trait differences of co-occurring alien and native species were regressed against each

of the evaluated edaphic and human impact variables. For this, we used a mixed effect modelling framework that incorporated a grouping factor (sites) and weighted the alien–native differences using the inverse variance of the corresponding comparisons.

Multivariate trait-space: ranking species along the 'leaf economics spectrum'

To determine possible changes between aliens and natives in the coordination among analysed traits (as discussed in Ordonez *et al.*, 2010), the association between all trait pair-wise contrasts was evaluated using standardized major axis (SMA) regressions (also known as reduced major axis slopes; Sokal & Rohlf, 1995). This method is preferred to classical linear regressions as both the variables on the *x*- and *y*-axes are subject to biological variability. The bivariate relationships of aliens and natives (that is SMA slopes) were tested for significant differences between groups. In those cases where a common slope was detected, differences between SMA regressions intercepts were compared. Last, in those cases where no differences in slopes or intercepts were found, we tested for shifts between plant types (the alien–native trait difference) along the common fitted slope. As for regression analysis all traits were $\log_{10}$ transformed for analysis. SMA regressions and tests were implemented using the SMATR package in R (Warton & Ormerod, 2007).

To summarize the multivariate variation in SLA, A_{mass} and N_{mass} of aliens and natives, a principal components analysis (PCA) was used to explore if the multi-dimensional trait variation could be reduced down to one main 'plant strategy' axis. The main axis (i.e. PCA-1) in this case was indeed found to represent the multivariate 'leaf economics spectrum' (Wright *et al.*, 2004) and captured the trade-offs between the investments in nutrients and dry mass in leaves and the rate of return in terms of carbon acquisition. By measuring the strength of association between PCA-1 species scores (as an additional multivariate trait) and climatic, edaphic and human disturbance variables for alien or native species, we tested for trait shifts along the resource acquisition axis along the evaluated environmental and disturbance gradients.

Similar to the procedure used for individual traits, the relation between the alien or native individual species PCA-1 scores (our multivariate trait) and environmental/disturbance parameters were evaluated using Spearman rank correlations and mixed effect models. Also, using the relation between alien–native relative and absolute multivariate trait differences (that is differences in PCA-1 scores between both groups) and climatic edaphic and human disturbance variables, we evaluated if the associations between native and alien plants changes along environmental and disturbance gradients.

RESULTS

Environment-independent trait differentiation between native and alien species

For comparisons involving all sampled individuals, aliens showed significantly higher SLA [2.1 (1.2–3.1)%], A_{mass} [4.7 (1.7–7.6)%] and N_{mass} [15.6 (10.3–20.9)%]. In the case of site-controlled comparisons, differences were also significant [i.e. SLA 2.4 (1.3–3.5)%; A_{mass} 4.8 (1.1–8.4)%; N_{mass} 13.4 (6.7–20.1)%] but had broader 95% CI than for site-uncontrolled contrasts. Log-likelihood ratio comparisons of models controlling for site differences, versus those that do not, showed a significant effect of the between-sites differences in size and direction of the alien–native dissimilarity (log-likelihood model comparisons $P < 0.001$ for all the evaluated traits). As the factor site was found to have a significant and strong effect on the traits of plant species, the results presented hereafter refer to site-based alien–native contrasts only.

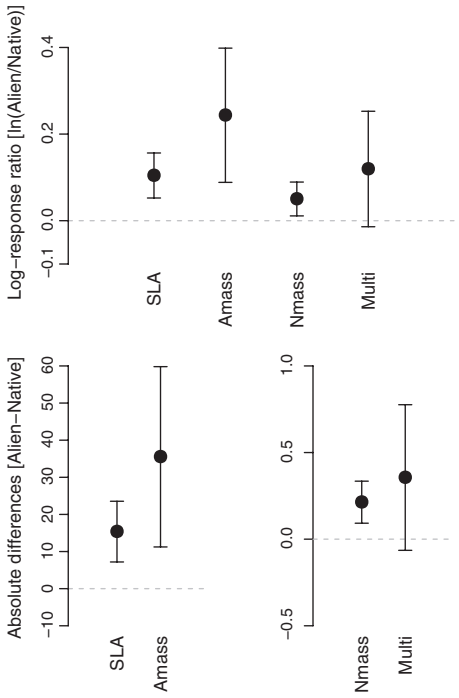


Figure 1 Differences between alien and native plants specific leaf area (SLA), foliar nitrogen per mass basis (N_{mass}), maximum photosynthetic rate per mass basis (A_{mass}) and the position in the multi-trait 'leaf economics spectrum' (Multi) between alien and native plants. Points mark the mean between-group differentiation and whiskers above and below the point indicate the 95% confidence intervals. Number of contrasted communities: 72 SLA; 22 A_{mass}; 59 N_{mass} and 17 for Multi.

Traits of co-occurring aliens and natives on a site were significantly different (log-response ratio and absolute dissimilarity, Fig. 1). Aliens had significantly higher SLA ($t_{(58)} = 3.9$, $P < 0.001$), A_{mass} ($t_{(20)} = 3.1$, $P = 0.006$) and N_{mass} ($t_{(49)} = 1.76$, $P = 0.015$) than their co-occurring natives (log-response ratios in Fig. 1). Growth form-controlled contrasts (i.e. separate for woody and non-woody species) yielded different results (Fig. 2). Using log-response ratios, only SLA and N_{mass} of non-woody species were significantly higher in alien plants when compared with natives (Fig. 2). Non-woody species thus seem to drive the patterns found across all growth forms. Contrasts based on absolute differences revealed no significant differences in evalu-

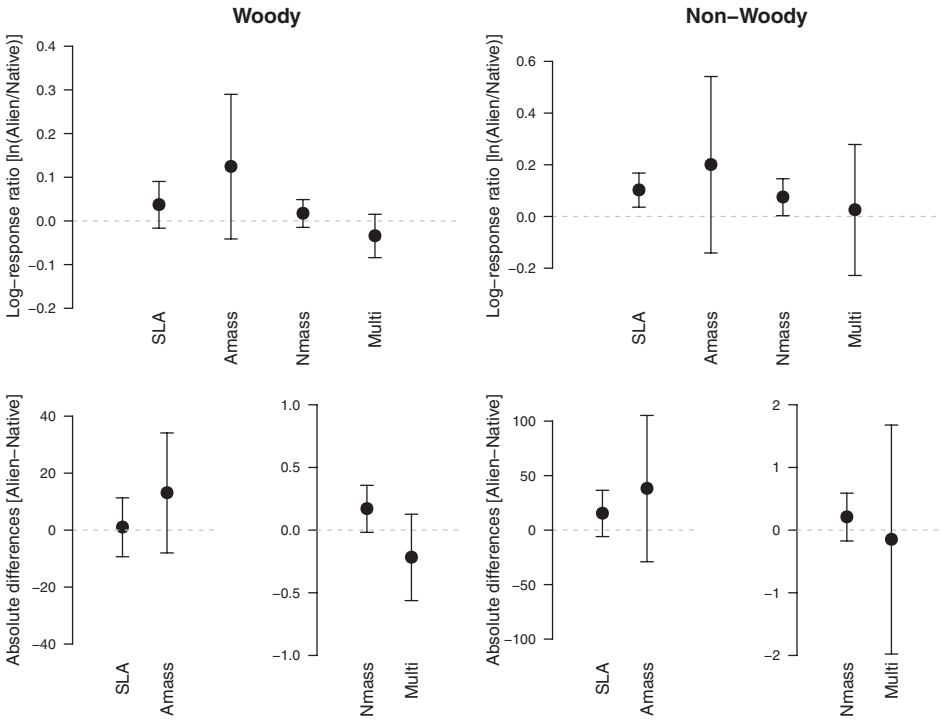


Figure 2 Plots for the alien–native differences in specific leaf area (SLA), foliar nitrogen per mass basis (N_{mass}), maximum photosynthetic rate per mass basis (A_{mass}) and the position in the multi-trait 'leaf economics spectrum' (Multi) of the two main plant growth forms (Woody, shrubs and trees; Non-Woody, graminoids and herbs/forbs). Number of contrasted communities: 47 woody and 40 non-woody SLA; 17 woody and 7 non-woody A_{mass}; 41 woody and 25 non-woody N_{mass}; and 12 woody and 5 non-woody for Multi. Woody species alien–native comparisons of SLA: $t_{(42)} = 1.351$ $P = 0.184$, A_{mass}; $t_{(15)} = 1.471$ $P = 0.162$, N_{mass}; $t_{(35)} = 1.049$ $P = 0.302$; and Multi: $t_{(11)} = -1.361$ $P = 0.201$. Non-Woody species alien–native comparisons of SLA: $t_{(30)} = 3.026$ $P = 0.005$; A_{mass}; $t_{(7)} = 1.149$ $P = 0.288$; N_{mass}; $t_{(20)} = 2.043$ $P = 0.054$; Multi: $t_{(5)} = 0.194$ $P = 0.854$.

ated traits between co-occurring aliens and natives, neither for woody nor for non-woody growth forms.

Association of traits and environmental parameters

For natives and aliens, both Spearman rank correlation coefficients (Table 2) and linear mixed model regressions (Table 3, Appendix S2) indicated a significant correlation of traits with most of the evaluated climatic and edaphic variables. However, the relation between traits and environmental disturbance factors was homogeneous (had common slopes) between native and alien plants, as indicated by a non-significant interaction between native/alien status and environmental variables for almost all our comparisons (Appendix S3).

For trait differences (absolute and log-response ratios, so controlling for site differences) between alien and native plants, we found no significant correlation with climatic, edaphic or human disturbance factors (Spearman rank correlations $P > 0.05$ in almost all cases; Appendix S3). This was confirmed by linear mixed model regression analyses (Appendix S3). Trends from Spearman correlations and mixed models, for both trait and alien–native trait differences versus environment relations, were consistent for analyses for each growth form.

Differentiation in multivariate trait space

Principal components analysis was used to reduce the multivariate variation in SLA, N_{mass} and A_{mass} down to one main axis of trait variation (i.e. PCA-1). This axis explained 68% of the total multi-trait variability among sampled species; additionally, it was positively correlated to SLA, A_{mass} and N_{mass}. Therefore, the score of species on this PCA-1 axis can be seen as their position along the 'leaf economics spectrum'.

Comparison of leaf trait relationships among plant types (Fig. 3) showed that SMA slopes did not vary significantly between alien and native species ($P \geq 0.05$ for all pair-wise comparisons). After fitting a common slope, there were no significant differences in *y*-intercepts between groups. However, significant shifts along a common SMA regression were detected between alien and native species, indicating how shifts in one trait cause shifts in all associated traits (Fig. 3). Separate comparisons for each plant growth form indicated that slopes do not vary significantly nor were differences between *y*-intercepts significant for either woody or non-woody species, so there was no difference between aliens and natives in their position along the leaf economics spectrum (Appendix S4).

Table 2 Correlations between alien and native leaf traits (log_{10} transformed) and site climatic, edaphic or human disturbance factors. Association between variables was determined using Spearman rank correlations (ρ). Number of species used is also indicated. Significant associations (association test $P < 0.05$) are marked in bold. Variables abbreviations as defined in Table 1.

	SLA [N_{Nat} = 1858] [N_{Ali} = 1125]		A_{mass} [N_{Nat} = 308] [N_{Ali} = 154]		N_{mass} [N_{Nat} = 1228] [N_{Ali} = 571]		Multi [N_{Nat} = 250] [N_{Ali} = 103]	
Predictor	Native ρ	Alien ρ	Native ρ	Alien ρ	Native ρ	Alien ρ	Native ρ	Alien ρ
HII	0.030	**−0.347**	−0.106	−0.077	0.036	−0.021	**0.328**	**0.195**
AnnPre	**0.232**	**0.116**	−0.096	−0.005	**−0.181**	**−0.121**	**−0.126**	0.036
AnnTmp	**−0.200**	**−0.275**	**−0.169**	0.104	**−0.279**	**−0.198**	0.040	−0.144
EvptYr	0.025	**0.210**	**−0.197**	−0.102	**−0.191**	**−0.096**	0.112	0.168
DayIrr	**−0.074**	**−0.216**	0.101	0.013	−0.012	0.063	−0.020	0.033
TmpSeas	**−0.059**	**−0.196**	0.053	−0.025	0.010	**0.111**	0.008	0.054
PreSeas	**0.064**	**0.334**	**0.135**	−0.090	**0.245**	**0.087**	0.085	**0.241**
TAWC	**−0.210**	**−0.416**	**0.129**	0.087	**−0.12**	−0.070	0.046	−0.019
PHAQ	**0.047**	**−0.018**	**0.130**	0.003	**0.211**	**0.122**	−0.080	−0.108
TOTN	**−0.193**	0.030	**0.300**	**0.177**	0.034	−0.016	**−0.283**	**−0.419**
CNRT	**0.222**	**0.061**	**0.131**	**−0.16**	**0.105**	**0.188**	−0.064	0.082
ECEC	**0.174**	**−0.120**	−0.074	0.018	**−0.189**	0.046	0.012	0.115
BULK	**−0.095**	**−0.206**	0.084	0.120	**0.174**	**0.120**	0.005	**−0.239**
TOTC	**−0.141**	−0.023	**−0.349**	−0.076	**−0.160**	**−0.173**	**0.137**	0.022
CECS	**0.193**	**−0.157**	**0.130**	−0.088	**0.061**	**0.184**	−0.082	0.075

N_{Nat}, number of native species; N_{Ali}, number of alien species; SLA, specific leaf area.

Aliens tended to express trait combinations that positioned them at the fast returns end of the leaf economics spectrum (higher PCA-1-values), while natives were positioned at the opposite side of the spectrum (positive log-response ratios as shown in Fig. 1, multi-trait contrast). This trend was also observed for associations within specific growth forms. Absolute and log-response ratio comparisons showed that differences between alien and native species in position along the leaf economics spectrum (i.e. the scores along PCA-1) were marginally significantly different for all-species contrast (Multi comparisons in Fig. 1), but non-significant for within growth form contrasts (Multi comparisons in Fig. 2).

Additionally, the position of a species along the leaf economics spectrum (their PCA-1 score) was not correlated to either environmental or disturbance conditions (Table 1). Linear mixed model regression analyses also did not indicate any significant relations between traits and climatic, edaphic or human disturbance variables (Table 2 and Appendix S3). This pattern was also observed when the analyses were done for woody and non-woody species separately (R^2 values ranged between 0.4 to 0.6 with $P > 0.05$ in all cases). Together, these results provide evidence to the idea of a constant difference in carbon acquisition strategy between natives and aliens across different environmental conditions.

DISCUSSION

We report that alien species as a group differ from natives in both individual traits and their positioning along the 'leaf economics spectrum'. This, together with the significant variability in trait differentiation between sites (as illustrated by the significant random intercepts of linear mixed models), highlights the importance of the particular ecological-abiotic background a species faces once introduced. Consequently, introduction success is not only dependent of area of origin, but also on introduced aliens having a suite of traits that enable them to use the new habitat (Thompson & Davis, 2011).

The non-woody species group mainly drove the average trait differences between natives and aliens in our study. This suggests that other plant traits than those related to leaf economics might better explain the invasiveness of woody species. Potential candidates are differences in wood and stem properties (Kooyman & Westoby, 2009), certain reproductive traits or traits related to sensitivity to, or impact on, fire regimes (e.g. Brooks *et al.*, 2004; Pierson *et al.*, 2011).

Although individual or multivariate traits varied with both climatic and edaphic factors in a similar way to that reported on other works (e.g. Wright *et al.*, 2005; Ordoñez *et al.*, 2009), we also show how these associations did not change between native and alien plants (neither absolute nor directional trait differences in uni- and multivariate trait spaces show significant associations with the evaluated climatic, edaphic and disturbance gradients). The similarity between alien and natives along the evaluated gradients suggest that trait–environment associations converge across different groups of plants, possibly due to the unavoidable restrictions imposed by physical, physiological and evolutionary factors.

Based on our results, we conclude that successful aliens are generally characterized by a higher resource uptake (as shown by their positioning at the fast returns end of the leaf economics spectrum), faster growth rates (Grotkopp *et al.*, 2002) and a higher reproductive output (Mason *et al.*, 2008; Ordonez *et al.*,

Table 3 Linear mixed effect model regressions coefficients (intercept α and slope β) of native/alien leaf traits (log_{10} transformed) and site climatic, edaphic or human disturbance factors. Significance of the associations (regression slopes β) marked with bold characters (slope significance test $P < 0.05$). Variables abbreviations as defined in Table 1.

	SLA				A_{mass}				N_{mass}				Multi			
	Native (N_{Nat} = 1858)		Alien (N_{Ali} = 1125)		Native (N_{Nat} = 308)		Alien (N_{Ali} = 154)		Native (N_{Nat} = 1228)		Alien (N_{Ali} = 571)		Native (N_{Nat} = 250)		Alien (N_{Ali} = 103)	
Predictor	α	β	α	β	α	β	α	β	α	β	α	β	α	β	α	β
HII	**2.05**	-3.6×10^{-4}	**2.27**	$\mathbf{-4.1 \times 10^{-3}}$	**2.11**	-1.0×10^{-3}	**2.21**	-1.2×10^{-3}	**0.26**	$\mathbf{8.7 \times 10^{-4}}$	**0.35**	1.6×10^{-4}	**−0.72**	**0.03**	−0.79	0.02
AnnPre	**1.98**	$\mathbf{6.4 \times 10^{-5}}$	**2.05**	4.0×10^{-5}	**2.18**	-8.9×10^{-5}	**2.14**	3.1×10^{-5}	**0.36**	$\mathbf{-5.7 \times 10^{-5}}$	**0.41**	$\mathbf{-5.9 \times 10^{-5}}$	0.22	-1.6×10^{-4}	−0.04	-5.4×10^{-5}
AnnTmp	**2.14**	$\mathbf{-6.3 \times 10^{-4}}$	**2.22**	$\mathbf{-1.1 \times 10^{-3}}$	**2.19**	-7.3×10^{-4}	**2.11**	4.2×10^{-4}	**0.38**	$\mathbf{-5.7 \times 10^{-4}}$	**0.43**	$\mathbf{-6.4 \times 10^{-4}}$	−0.10	1.2×10^{-3}	0.22	-2.3×10^{-3}
EvptYr	**2.02**	$\mathbf{4.4 \times 10^{-5}}$	**2.04**	9.7×10^{-5}	**2.24**	-2.5×10^{-4}	**2.23**	-1.2×10^{-4}	**0.37**	$\mathbf{-1.2 \times 10^{-4}}$	**0.43**	$\mathbf{-1.5 \times 10^{-4}}$	−0.38	$\mathbf{7.3 \times 10^{-4}}$	−0.74	1.1×10^{-3}
DayIrr	**1.88**	2.8×10^{-5}	**2.85**	$\mathbf{-1.4 \times 10^{-4}}$	0.39	3.0×10^{-4}	**1.77**	7.0×10^{-5}	0.10	$\mathbf{3.3 \times 10^{-5}}$	0.21	2.5×10^{-5}	**6.55**	$\mathbf{-1.1 \times 10^{-3}}$	3.51	-6.3×10^{-4}
TmpSeas	**2.00**	$\mathbf{7.8 \times 10^{-6}}$	**1.95**	$\mathbf{2.8 \times 10^{-5}}$	**2.04**	8.3×10^{-6}	**2.25**	-1.6×10^{-5}	**0.23**	$\mathbf{1.2 \times 10^{-5}}$	**0.33**	4.3×10^{-6}	−0.07	2.1×10^{-5}	**−0.82**	$\mathbf{1.2 \times 10^{-4}}$
PreSeas	**2.11**	$\mathbf{-1.4 \times 10^{-3}}$	**2.28**	$\mathbf{-3.5 \times 10^{-3}}$	**1.97**	$\mathbf{2.4 \times 10^{-3}}$	**2.13**	1.0×10^{-3}	**0.33**	$\mathbf{-6.3 \times 10^{-4}}$	**0.38**	$\mathbf{-6.9 \times 10^{-4}}$	−0.14	4.1×10^{-3}	−0.08	-9.3×10^{-5}
TAWC	**2.05**	-9.9×10^{-4}	**2.23**	**−0.01**	**1.93**	0.01	**2.23**	−0.01	**0.14**	**0.01**	**0.24**	**0.01**	0.22	−0.01	−0.55	0.04
PHAQ	**2.32**	**−0.04**	**2.06**	3.5×10^{-3}	**1.53**	**0.09**	**1.65**	**0.08**	**0.32**	-4.6×10^{-3}	**0.45**	**−0.01**	**2.08**	**−0.31**	**4.05**	**−0.61**
TOTN	**1.95**	**0.09**	**2.12**	−0.02	**1.95**	0.13	**2.32**	−0.15	**0.25**	**0.03**	**0.25**	**0.08**	0.25	−0.17	−0.17	0.07
CNRT	**1.70**	**0.03**	**2.66**	**−0.05**	**2.16**	−0.01	**2.17**	-2.9×10^{-4}	**0.62**	**−0.03**	**0.22**	0.01	−0.37	0.04	−1.22	0.11
ECEC	**2.09**	$\mathbf{-3.1 \times 10^{-3}}$	**2.19**	**−0.01**	**2.07**	8.5×10^{-4}	**2.04**	0.01	**0.27**	$\mathbf{1.4 \times 10^{-3}}$	**0.34**	9.0×10^{-4}	−0.21	0.02	**0.89**	**−0.06**
BULK	**2.35**	**−0.22**	**1.97**	0.09	**4.41**	**−1.72**	**2.38**	−0.16	**0.66**	**−0.28**	**0.74**	**−0.29**	−2.85	2.17	1.87	−1.44
TOTC	**1.98**	**0.01**	**2.20**	**−0.01**	**1.99**	0.01	**2.24**	−0.01	**0.27**	1.6×10^{-3}	**0.27**	**0.01**	0.06	-1.8×10^{-4}	−0.16	0.01
CECS	**2.06**	-1.2×10^{-3}	**2.24**	**−0.01**	**2.04**	3.6×10^{-3}	**2.09**	4.8×10^{-3}	**0.25**	$\mathbf{3.3 \times 10^{-3}}$	**0.27**	**0.01**	−0.15	0.02	**1.12**	**−0.09**

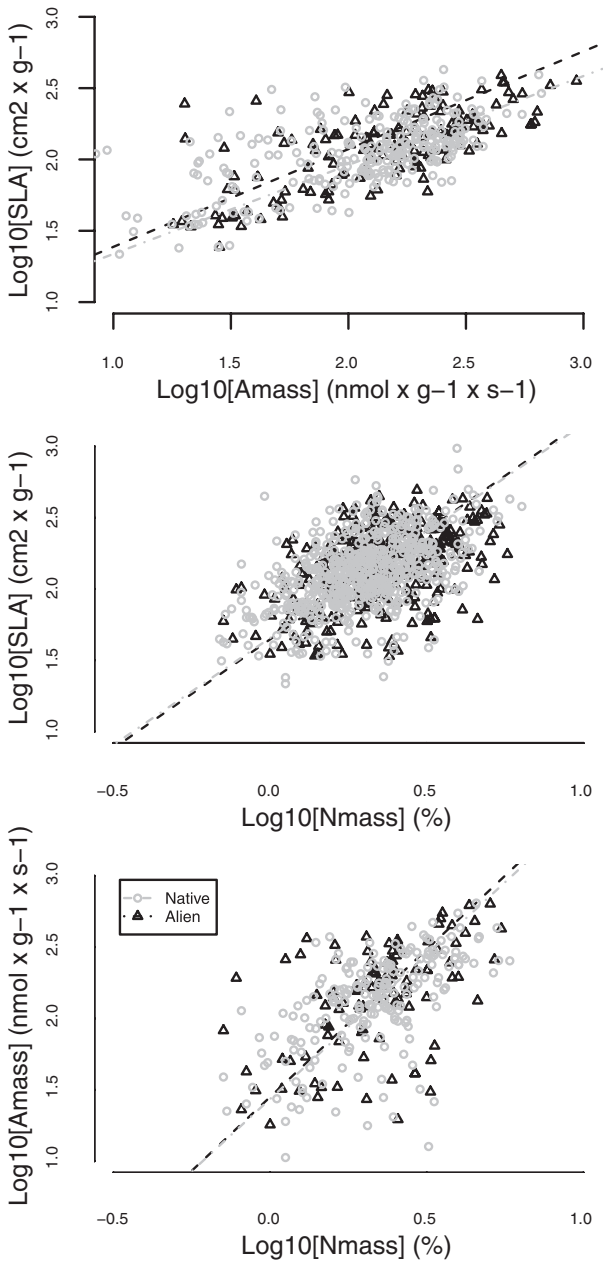


Figure 3 Standardized major axis (SMA) regression relationships between specific leaf area (SLA), foliar nitrogen (N_{mass}) and photosynthetic capacity (A_{mass}). Grey circles and grey-dashed line represent aliens; black triangles and black-dashed line represent native species. Axes are $\log_{10}$ scaled so that relations represent proportional changes in traits. Pearson correlation coefficients for evaluated relations are: SLA–N_{mass} = 0.623; SLA–A_{mass} = 0.467; N_{mass}–A_{mass} = 0.566). For all pairwise comparisons, trait relation slopes (SLA–N_{mass} P = 0.181; SLA–A_{mass} P = 0.703; N_{mass}–A_{mass} P = 0.818) and elevations (SLA–N_{mass} P = 0. 544; SLA–A_{mass} P = 0.535; N_{mass}–A_{mass} P = 0.719) were homogeneous between alien and native species. This indicates that alien and natives are positioned along the same leaf economics axis. However, the positioning along slope was different between alien and native species (aliens at the fast end and natives at the slow end of the spectrum; SLA–N_{mass} P = 0.025; SLA–A_{mass} P < 0.001; N_{mass}–A_{mass} P = 0.572).

2010). However, the level of differentiation in these traits from natives was found to be similar across both low- and high-resource and disturbance regimes. These two factors would imply that the spread of alien plants into new habitats is independent of the geography of origin or arrival, highlighting how aliens need to have a typical suite of traits that enable them to exploit the conditions of the area they are introduced.

Several previous studies have addressed changes in alien species colonization success, as a function of alien–native performance differences across environmental, resource availability, disturbance and release of enemies' gradients (Leishman *et al.*, 2007, 2010; González *et al.*, 2010). Although we find no changes across the evaluated gradient, it is difficult to determine what level of trait differentiation can cause ecological differentiation between two sites, especially since the competitive exclusion principle (Gause, 1934) can be interpreted such that small but consistent trait differentiation between two species can lead to large ecological differences (e.g. in resource uptake or loss rates; Tilman, 1982). Additionally, how the observed differences translate to environmental and disturbance gradients is still unknown, as hardly any data on this subject are available in the literature.

Our multi-trait analysis also shows that native and alien species both share the same carbon assimilation strategies (i.e. they are constrained within the same leaf economic spectrum) but express different leaf trait combinations (in both absolute and relative terms). These differences between groups are in line with other regional and global works comparing native and aliens leaf traits (e.g. Gulías *et al.*, 2003; Leishman & Thomson, 2005; Funk & Vitousek, 2007; González *et al.*, 2010; Ordonez *et al.*, 2010; Penuelas *et al.*, 2010; van Kleunen *et al.*, 2010) and the association between them (e.g. Leishman *et al.*, 2007; Leishman *et al.*, 2010; Penuelas *et al.*, 2010). The reported positional differences support the idea that, regardless of site conditions, aliens have a higher growth capacity, carbon use efficiency and photosynthetic nitrogen use efficiency than their native counterparts.

The similarity of the differences between alien and native species in both individual traits, and the position along the leaf economics spectrum, along the evaluated gradient of climatic, edaphic and human impacts; supports those hypotheses where alien organisms are considered to outperform natives in both low- and high-resource/disturbance environments (Funk & Vitousek, 2007; Leishman *et al.*, 2007, 2010; González *et al.*, 2010). This is in line with Leishman *et al.* (2007, 2010), suggesting that successful alien species have the same resource use efficiency as co-occurring natives, and only local conditions (such as ecological interactions and disturbance regimes) will determine the level of differentiation between groups. Furthermore, based on our results, we suggest that alien species are successful not only because they have different resource acquisition strategies or lower nutrient requirements. Rather, we consider that, as suggested by Thompson & Davis (2011) and Leishman *et al.* (2010), the success of any given alien is also determined by it having a suite of traits that enable it to exploit the new environment, providing a competitive advantage over co-occurring natives. This can be due to higher specific leaf areas, shorter life cycles, investment of more resources in reproduction, producing

more seeds that are better dispersed and germinate faster, and/or better coping with the biotic–abiotic disturbances with which it is confronted.

CONCLUSION

In this paper we have shown that aliens have significantly different leaf traits than co-occurring natives. Nonetheless, these differences are not translated into different carbon capture strategies (that is different leaf trait associations); both groups instead fall along the same axis of variation that describes the 'leaf economics spectrum' of plants. We have shown that although individual traits change in a predictable way with environmental conditions, trait differences (in uni- and multi-trait spaces) show no relation with climate, soil or human disturbance. We suggest that although increased resource availability could benefit alien plants via changes in performance related traits (i.e. a movement to the fast return end of the leaf economics spectrum), these benefits are the same for both aliens and natives. In other words, differences between aliens and natives in traits do not reflect the resource availability conditions on a site. This discards the hypothesis that high-resource environments specifically allow aliens to outperform natives due to differences in key traits: their differences matter under all conditions.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Summary of leaf traits from species included in this study.

Appendix S2 Correlations between leaf traits (for natives, aliens and differences between them) and climatic, edaphic and human disturbance parameters.

Appendix S3 Association between absolute and directional differences on individual traits and selected environmental factors.

Appendix S4 Standardized major axis (SMA) regression relationships between leaf traits for alien and native species for woody and non-woody species.

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