Functional differences between native and alien species: a global-scale comparison

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Summary

1. A prevalent question in the study of plant invasions has been whether or not invasions can be explained on the basis of traits. Despite many attempts, a synthetic view of multi-trait differences between alien and native species is not yet available.

2. We compiled a database of three ecologically important traits (specific leaf area, typical maximum canopy height, individual seed mass) for 4473 species sampled over 95 communities (3784 species measured in their native range, 689 species in their introduced range, 207 in both ranges).

3. Considering each trait separately, co-occurring native and alien species significantly differed in their traits. These differences, although modest, were expressed in a combined 15% higher specific leaf area, 16% lower canopy height and 26% smaller seeds.

4. Using three novel multi-trait metrics of functional diversity, aliens showed significantly smaller trait ranges, larger divergences and a consistent differentiation from the median trait combination of co-occurring natives.

5. We conclude that the simultaneous evaluation of multiple traits is an important novel direction in understanding invasion success. Our results support the phenotypic divergence hypothesis that predicts functional trait differences contribute to the success of alien species.

Key-words: alien/native plants, functional diversity, invasive biology, plant height, plant introductions, seed size, SLA, traits

Introduction

The introduction of alien plant species ranks high among major global biodiversity threats. As a result, the ability to predict which species are likely to be successful invaders and have large impacts when introduced has become a priority for conservation efforts. Although many studies have quantified the extent to which native and alien species differ in their main characteristic traits, attempts to draw generalizations across these studies have met limited success (Daehler 2003; Pysek & Richardson 2007).

In essence, two alternative approaches have been used to characterize the traits of a typical successful introduced species: (i) to compare pairs of native and alien congeners, confamilials, and otherwise taxonomically and/or phylogenetically related species, irrespective of the communities in which these occur (D'Antonio 1998; Grotkopp, Rejmanek & Rost 2002; Mcdowell 2002; Gerlach & Rice 2003; Burns & Winn 2006; Funk & Vitousek 2007; Van Kleunen, Weber & Fischer

2010); or (ii) multi-species approaches based on comparisons of whole floras (Thompson, Hodgson & Rich 1995; Crawley, Harvey & Purvis 1996; Lake & Leishman 2004; Hamilton *et al.* 2005; Lambdon, Lloret & Hulme 2008). Both approaches aim to identify recurring trait differences between the two groups. Although most efforts have used the first alternative (i.e. pair-wise comparisons), the best progress to date towards a general screening system of possible invasive plants has been achieved by pooling evidence from both approaches (Rejmanek & Richardson 1996; Grotkopp, Rejmanek & Rost 2002; Richardson & Rejmanek 2004; Rejmanek *et al.* 2005; Pysek & Richardson 2007).

From these comparisons, two alternative hypotheses have emerged as explanations to the success of alien species. First, several authors have argued that greater phenotypic difference to natives increases the probability of success of an alien (Naeem *et al.* 2000; Dukes 2001; Lake & Leishman 2004; Hamilton *et al.* 2005; Pokorny *et al.* 2005; Lambdon, Lloret & Hulme 2008; Van Kleunen, Weber & Fischer 2010). This idea, 'phenotypic divergence', is based on the concept of limiting similarity (Hutchinson 1959; MacArthur & Levins 1967a;

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Abrams 1983) and proposes that an introduced species will be more successful in a community that lacks species that are ecologically similar to it.

Alternatively, others have argued that the opposite tendency is true. That is, the more similar the traits of an alien are to those of the native community, the more likely it is to succeed in the introduced range – as the better it will be adapted to the local conditions (Smith & Knapp 2001; Prieur-Richard *et al.* 2002; Daehler 2003). This idea, 'phenotypic convergence', is based on the concept of habitat filtering mechanisms (e.g. due to dispersal, stress and competition), which can be thought as reducing the range of successful strategies observed among coexisting species (Keddy 1992; Weiher, Clarke & Keddy 1998). In theory, both of these mechanisms could operate simultaneously in a given community, influencing one or more traits simultaneously. Both mechanisms share the idea that the success of an alien species relies on how its traits match with those of co-occurring native species.

To date, most work considering this problem has focused on combinations of the presence/absence of certain traits (Bradshaw *et al.* 2008; Lambdon, Lloret & Hulme 2008), while quantitative traits are typically considered one at a time (Hamilton, Holzapfel & Mahall 1999; Lake & Leishman 2004; Funk & Vitousek 2007; Van Kleunen, Weber & Fischer 2010; but see Leishman *et al.* 2007). This is perhaps surprising since it is certain that species generally diverge along more than one niche axis at a time (e.g. resource partitioning, tolerance to abiotic stress and interactions with herbivores and pathogens) affecting multiple quantitative traits simultaneously. Consequently, we here suggest that a multidimensional approach to quantitative traits might be valuable for inferring the relative importance of differences in attributes between aliens and co-occurring native species.

Presumably, trait differentiation among natives and aliens can arise through various mechanisms. For example, if aliens manage to escape some of the costs faced by natives then, enabled via new trait combinations, they might exploit novel regions of the local niche space. One example is aliens that are not recognized as food by the resident herbivores, and therefore require less investment in chemical or physical defences, allowing a great allocation to vegetative growth or reproduction (Keane & Crawley 2002).

The first aim of this study is to compare native and alien plant species in terms of three key traits (specific leaf area – SLA; average individual seed weight – SWT; typical maximum height of adults – H_{max}), each representing an essentially independent axis of ecological strategy, or niche dimension (Westoby *et al.* 2002). Second, we aim to establish whether native and alien species differ in their position within the multidimensional trait space generated by the three traits under consideration. Third, we assess whether the trait composition of co-occurring native and alien species supports either the idea of phenotypic convergence (and thus of habitat filtering and common constraints) or the idea of phenotypic divergence (and thus of limiting similarity and empty niches).

Materials and methods

SELECTION OF TRAITS

Each of the three traits (SLA, H_{max} and SWT) represents an approximately independent axis (or spectrum) of ecological strategic variation. These spectra are themselves underpinned by various tradeoffs such that a wide range of trait values is typically seen, even among co-occurring species (Westoby *et al.* 2002; Westoby & Wright 2006).

Specific leaf area (leaf area per dry mass; SLA) indexes a species' position along a multi-trait spectrum describing the dry mass and nutrient economics of carbon gain – the 'leaf economics spectrum' (Westoby *et al.* 2002; Wright *et al.* 2004). This spectrum runs from species with high SLA, leaf N and P concentrations, fast maximum photosynthetic and dark respiration rates, and short leaf lifespan, to species with the opposite suite of traits. Typically, species towards the high-SLA end of the spectrum are relatively fast growing and good light competitors, but tend also to be highly palatable to herbivores. Herbs, grasses and deciduous trees tend towards the high-SLA end of this spectrum, and evergreen shrubs and trees towards the low SLA end, but there is wide overlap between growth forms.

Individual seed weight (SWT) indexes a species' position along the trait-strategy dimension emerging from the trade-off between the number of seeds, and the size of those seeds, that can be generated for a given reproductive effort (Westoby *et al.* 2002; Moles *et al.* 2004; Moles & Westoby 2006). This resembles the classic axis of r-K strategies (MacArthur & Wilson 1967b), where producing many small seeds generally improves dispersal distances (in the case of wind dispersal) and promotes longevity in the seed bank. Thus, small-seededness may be beneficial in disturbed habitats where random juvenile mortality due to disturbance is high. That said, seedlings of smaller-seeded species tend to be outcompeted by those of larger-seeded species, under a variety of environmental conditions (Westoby *et al.* 2002).

Typical maximum height (H_{max}) of adult plants indexes a species' position along a height-strategy spectrum that includes the time-trajectory and pace of height growth, as well as H_{max} itself (Weiher *et al.* 1999; Westoby *et al.* 2002; Falster & Westoby 2003). H_{max} represents the outcome between benefits associated with greater light interception of taller plants, and the higher costs of growing tall, such as greater investment in stem tissue, higher maintenance respiration costs of stem tissue, and greater risk of breakage. As a result of these trade-offs, species with a wide range of maximum heights often co-occur at a site, e.g. in forest with gap-phase dynamics.

DATABASE COMPILATION

A database of SLA, SWT and H_{max} data for native and alien species was compiled from both published and unpublished sources. Papers and databases were located through electronic searches using relevant keywords, examination of the references in these citations, and direct communication with data owners. A dataset was considered suitable if it included measurements for at least two of the traits of interest, for at least four co-occurring species (whether native, alien or both). Only measurements made under natural conditions were used (greenhouse studies were discarded), so that for each dataset a location (e.g. latitude and longitude), biome, eco-region, habitat and environmental conditions could reasonably be assigned. Further details of the data compilation process are given as Supporting Information (Appendix S1).

Each dataset was assigned to a particular plant 'community' by placing a 25 × 25 km grid over a distribution map of all sampled locations, and grouping together all the locations within each grid cell.

This spatial aggregation scale was selected for three reasons: (i) It is large enough to capture processes occurring at landscape, regional and biogeographical scales, but small enough to show signals from meta-communities and local inter-specific interactions (Blackburn & Gaston 2002); (ii) Environmental aspects for each grid cell can be generally considered homogeneous (e.g. climates, overall soil type, vegetation physiognomy), despite some clearly being heterogeneous (e.g. small scale disturbance); (iii) It is the area of preference for storing, evaluating and reporting information on the distribution of native and alien species (Larsen *et al.* 2009).

Species traits were summarized within each community by calculating the geometric mean of all measurements of a particular trait across all studies within the same grid. We used this approach as it allowed us to compile a dataset in which a pool of native and aliens are known to co-occur under broadly similar landscape and environmental conditions. The influence of choice of grouping scale was evaluated (Appendix S1 and Fig. S1) and no major evidence of a size effect was found. For each of these plant communities we followed the Richardson *et al.* (2000b) definition of alien species. That is, alien plants were defined as those whose presence at a site is presumed due to intentional or accidental introduction as a result of human activity.

The resulting database contains 4473 species sampled over 95 communities (3784 species measured in their native range, 689 species in their introduced range, 207 in both ranges). The database covers 66 eco-regions, all continents and all major biomes of the world. The species-list includes taxa from 219 plant families, representing a range of growth forms and lineages: 3717 dicots, 514 monocots, 76 Gymnosperms, 130 ferns and Fern Allies, and 37 undetermined species. A summary of the database is presented as supporting information (Appendix S2).

INDIVIDUAL TRAIT COMPARISONS

Linear mixed models were used to test whether native and alien species differed significantly in individual traits (SLA, SWT and H_{max}), while simultaneously taking into account the influence of taxonomic relationships and whether a given species in a given community was considered as either native or alien. In these analyses the species status (native/alien) was treated as a fixed factor, while community identity and species identity (nested within community) were treated as random factors. The use of community as a random factor allowed us to compare native and alien communities broadly co-occurring under the same general landscape and environmental conditions. Additionally, the use of species identity (within communities) as a random factor controlled for the possible relatedness of native and alien species. Contrasts based on taxonomic similarity (i.e. congeneric/confamilial contrasts) are not presented since neither genus nor family showed a significant influence as random factors (Appendix S1 and Table S2). Each of the three focal traits (SLA, SWT, H_{max}) showed a strongly right-skewed distribution (ca. lognormal as shown in Fig. S2) and thus all traits were log_{10}-transformed for all analyses.

MULTIDIMENSIONAL TRAIT COMPARISONS

Two analytical approaches were used to detect differences in the trait combinations of native and alien species. First, a discriminant analysis (Legendre & Legendre 1998) was implemented to determine which traits best differentiated between native and alien species. With this analysis our aim was not to determine which of the traits differed more relative to others, but rather to establish if the evaluated traits (SLA, H_{max}, SWT) could be used to discriminate between native and alien species in a multivariate space. Computationally, discriminant analysis is similar to a multiple regression, but with group membership instead of a continuous variable chosen as the response variable to be predicted from a set of covariates. Classification accuracy and its significance was quantified using both the correct classification rate (CCR) and the area under the receiver-operator curve (AUC) (Hanley & McNeil 1982; Swets 1988).

Second, the trait composition of native and alien species was compared using a convex hull approach. The convex hull is the minimum convex geometry that includes all the considered observations (Preparata & Shamos 1985) and has been recently proposed as a method to represent the volume of functional space used by a community (Cornwell, Schwilk & Ackerly 2006; Villeger, Mason & Mouillot 2008). This approach, in conjunction with re-sampling techniques, allowed representing, measuring and comparing the trait variation of native and alien species in multiple dimensions, using a distribution-independent approach (Cornwell, Schwilk & Ackerly 2006). To avoid problems with differences in the measurement domains of each of our traits, convex hull were calculated from standardized (mean = 0, and SD = 1) log_{10}-transformed traits. The mean trait separation between native and alien species-groups within multidimensional trait space was quantified in terms of the Euclidean distance between the group centroids. Hull centroids are themselves calculated as the mean values in each dimension using the outermost hull vertices. Additionally, we used two indices of functional diversity related to convex hulls: 'functional richness' (i.e. convex hull volume) and 'functional divergence' (i.e. the spread of native and alien traits in relation to the community-mean trait combination; Villeger, Mason & Mouillot (2008).

A null model approach (Gotelli & Graves 1996) was used to determine if the observed differences between native and aliens were different from those expected by chance alone. The use of this approach allows the comparison of functional diversity values among species pools with different species richness and regional spaces (Mason *et al.* 2007; Villeger, Mason & Mouillot 2008). Null-communities were generated using a random assembly process drawing from the overall pool of native species with the same number of species in each draw, while maintaining the proportion of each growth form constant. The process was repeated 1000 times, each time determining the functional richness, divergence and mean trait separation. Differences between the null and observed species pools were tested using a two-tailed Wilcoxon signed-ranks test (Sokal & Rohlf 1995). All analyses where done using R 2.10 (R Development Core Team, 2009).

Results

INDIVIDUAL TRAIT COMPARISONS

Linear mixed-model comparisons involving the individual traits indicated that alien species have, on average across all species and growth forms, 15% higher SLA ($t = -5.54$, $P < 0.001$), 16% lower H_{max} ($t = 2.99$, $P = 0.003$), and 26% smaller SWT ($t = 2.44$, $P = 0.015$) than co-occurring native species. By implication we found that aliens tend to produce more seeds per unit reproductive effort (smaller SWT), have faster growth rates (at least as seedlings; via high SLA), and take a shorter time to reach reproductive age (lower H_{max}). These differences – although modest – were significant for all three traits (Table 1) even after controlling for

Table 1. Comparison of mean trait values of alien and native species, considering all species, and species grouped by growth form. Comparisons were made using linear mixed models; t and P values from these analyses are given in the right-hand column (significance levels indicated as *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, NS, nonsignificant). Trait abbreviations: SLA, specific leaf area (cm^2 g^{-1}); H_{max}, maximum Canopy height (m) and SWT, seed weight (mg). All traits were log$_{10}$ transformed before these analyses. Additional information includes standard errors (SE) of trait means, the number of 25×25 km^2 communities involved in each comparison ('no. of sites'), and the number of species in each group ('no. of species')

Trait [no. of sites]	Alien mean (SE) [no. of species]	Native mean (SE) [no. of species]	Linear mixed model
All			
SLA	133·3 (1·06)	115·1 (1·04)	$t = -5.51$***
[138]	[788]	[3164]	
H_{max}	3·3 (1·14)	3·9 (1·11)	$t = 3.71$***
[190]	[647]	[3562]	
SWT	5·6 (1·19)	7·6 (1·18)	$t = 2.8$**
[190]	[491]	[2319]	
Graminoids			
SLA	155·7 (1·08)	116·4 (1·09)	$t = -2.52$*
[22]	[39]	[206]	
H_{max}	0·6 (1·12)	0·6 (1·14)	$t = -1.18$ NS
[31]	[42]	[295]	
SWT	0·4 (1·38)	0·7 (1·26)	$t = 2.01$*
[24]	[31]	[198]	
Herbs & forbs			
SLA	172·2 (1·09)	130·5 (1·07)	$t = -3.99$***
[57]	[166]	[610]	
H_{max}	0·3 (1·13)	0·3 (1·09)	$t = -1.75$ NS
[64]	[172]	[652]	
SWT	0·7 (1·17)	0·9 (1·17)	$t = 0.51$ NS
[61]	[155]	[510]	
Shrubs			
SLA	125·3 (1·1)	114·2 (1·08)	$t = 1.36$ NS
[36]	[269]	[386]	
H_{max}	1·5 (1·12)	1·5 (1·1)	$t = -1.73$ NS
[49]	[106]	[265]	
SWT	1·7 (1·41)	1·4 (1·4)	$t = -0.85$ NS
[44]	[67]	[198]	
Trees			
SLA	107·8 (1·09)	101·8 (1·06)	$t = -1.82$ NS
[76]	[238]	[1088]	
H_{max}	17·4 (1·08)	15·5 (1·07)	$t = 0.49$ NS
[109]	[224]	[1503]	
SWT	31·7 (1·21)	50·8 (1·18)	$t = 1.55$ NS
[107]	[176]	[889]	
Vines			
SLA	260 (1·19)	243·6 (1·12)	$t = -1.43$ NS
[11]	[24]	[74]	
H_{max}	3·3 (1·46)	3·2 (1·38)	$t = 0.57$ NS
[11]	[25]	[57]	
SWT	39·2 (1·39)	22·4 (1·55)	$t = -0.24$ NS
[12]	[21]	[74]	

growth form as a random effect (as described in Appendix S1 and Table S1). Trait-differences between native and alien species were smaller for the woody species group (shrubs and trees) than for non-woody species (grasses and herbs/forbs), with trait differences ranging from 1·5 to 5% for woody species, and between 3 to 100% for non-woody species.

Trait comparisons were also made within each growth form (Table 1) since we expected patterning of trait values according to growth form and aliens and natives differed in growth form representations. Alien species had higher SLA than natives within grasses and herbs (just as across all species), whereas no difference was seen within trees, shrubs or vines. For seed weight the group differences were deemed nonsignificant in all growth forms except grasses, with this difference in the same direction as for all species together (smaller seeds in aliens). A nonsignificant group difference in H_{max} was seen for all growth forms, with shifts in the opposite direction to that is seen in the all-species comparison for trees. In summary, alien and native species showed relatively few trait differences for individual growth form comparisons. Still, there was only one case where the difference found was incongruent with that seen in the all-species comparison.

MULTIDIMENSIONAL TRAIT COMPARISONS

The discriminant function analysis for all species pooled showed that all three traits contributed to the best-fit discrimination function (Table 2). However, the effect of SLA was by far the largest of the three, and that of H_{max} was only marginally significant (SLA: $F_{(1,1955)} = 72.99$, $P < 0.001$; SWT: $F_{(1,1955)} = 7.52$, $P = 0.006$; H_{max}: $F_{(1,1955)} = 3.21$, $P = 0.073$). A model based only on SLA and SWT had a better than random predictive ability, as both the AUC (0·67) and the correct classification rate (85·5% of correct predictions) showed (where AUC and CCR values between 0 to 0·50 and 0% to 50% respectively represent predictions no better than random or random guessing).

Comparisons within each growth form resulted in broadly similar predictive ability: correct classification rates were all above 75%, and AUC all above 65%. Nonetheless, examination of the discriminant function coefficients shows differences in the relative discrimination power of traits between woody and non-woody species (Table 2), also pointing to a broad difference in the strategies of successful aliens in relation to life history. Specifically, for non-woody species (i.e. herbs & forbs and graminoids) SLA and H_{max} (and also SWT in the case of graminoids) allowed a significant discrimination between groups. In the case of woody species (i.e. shrubs and trees) and vines, SLA was the only variable that allowed a correct classification between groups.

Although the tests involving convex hulls involved all three traits, for ease of presentation in Fig. 1 we show the component set of convex hulls in 2-dimensional cross-sections. Trait separation measurements showed significant multivariate differentiation between the native and alien species pools (Table 3). That is, distances between native and alien centroids were larger than expected from comparisons involving randomly assembled native communities. This trend was consistent for comparisons made within growth forms ($P < 0.001$ in all cases), with herbs & forbs being the most divergent group and shrubs the most convergent (Fig. 1). In general, shrubs showed the smallest differences between groups (distributions appear to be centred similarly in both

Table 2. Summary of discriminant analyses used to determine which traits best differentiated between native and alien species in multivariate trait-space, considering all species, and species grouped by growth form. Summary statistics shown are (from left to right) standardized classification coefficients (for Native and Alien species), results from significance tests for the discrimination ability of each trait, number of species involved in each comparison, and classification proficiency statistics that describe the discrimination potential of multiple trait combinations (CCR, correct classification rate and AUC, area under a receiver operator curve). CCR and AUC values were used as a significance test of the overall discriminant power of Native vs. Alien status, based on the three traits. Trait abbreviations and significance levels follow Table 1

Group	Trait	Classification function coefficients Native	Alien	Trait significance test	Number of species Native	Alien	CCR	AUC
All	SLA	24·0	25·8	$F_{(1,1955)} = 72.99$, ***	13032	1544	84·5%	0·67
	H_{max}	1·8	2·0	$F_{(1,1955)} = 3.21$, NS				
	SWT	1·0	0·9	$F_{(1,1955)} = 7.52$, **				
Graminoids	SLA	27·1	28·5	$F_{(1,577)} = 14.69$, ***	893	153	80·8%	0·75
	H_{max}	−3·1	−1·7	$F_{(1,577)} = 25.24$, ***				
	SWT	1·6	1·4	$F_{(1,577)} = 0.83$, NS				
Herbs & forbs	SLA	29·0	31·8	$F_{(1,257)} = 25.68$, ***	2059	394	76·7%	0·69
	H_{max}	−0·4	0·6	$F_{(1,257)} = 5.54$, *				
	SWT	−0·4	−0·8	$F_{(1,257)} = 4.23$, *				
Shrubs	SLA	26·1	27·9	$F_{(1,369)} = 9.21$, **	2518	354	88·3%	0·68
	H_{max}	0·5	1·1	$F_{(1,369)} = 1.91$, NS				
	SWT	1·0	1·2	$F_{(1,369)} = 0.55$, NS				
Trees	SLA	21·8	23·1	$F_{(1,697)} = 9.23$, **	6604	544	89·4%	0·61
	H_{max}	4·6	4·6	$F_{(1,697)} = 0.001$, NS				
	SWT	1·0	0·9	$F_{(1,697)} = 1.71$, NS				
Vines	SLA	31·3	34·0	$F_{(1,55)} = 5.23$, *	395	54	76·4%	0·70
	H_{max}	1·6	1·7	$F_{(1,55)} = 0.08$, NS				
	SWT	5·8	6·1	$F_{(1,55)} = 0.18$, NS				

groups); alien vines present a higher SLA; alien herbs & forbs possess a higher H_{max}; introduced trees differentiate from native species with both higher SLA and H_{max}; and alien graminoids have both a high SLA and a low SWT in comparison to native species.

Relative to the native species pool alien species showed a significant reduction in the occupied multivariate range (56% smaller functional richness), and convex hulls clustered towards the edge of the native species trait distributions. Using a two-tailed non-parametric test, the distribution of native and alien species functional richness was significantly different than expected from comparing two null communities (Wilcoxon-P and Observed Vs. Expected ratios in Table 3). The same results and significance levels were found for comparisons within growth forms.

Functional divergence measurements indicated that native and alien species differed in their average location in multivariate trait space (Table 3). On average, alien species were located 5% further away from the overall community-mean position (centroid) than were native species. Within-growth form comparisons (Table 3) also showed significant divergences between alien and native species in this regard. This suggests that aliens are located towards the edge of the natives' trait distributions for most of the compared growth forms.

Discussion

We found that alien species as a group differ in their trait composition from co-occurring natives, for three key traits,

each representing an approximately independent axis of trait/strategy variation. Additionally we found that alien species had the tendency to occupy regions clustered towards the edge of at least one evaluated dimension, when compared to natives. Therefore, alien species could be considered as a biased subsample of species with regard to the evaluated traits, such that they tend to represent greater SLA, lower maximum height and smaller seed size. These results are in line with two possible (related) mechanisms determining the success of alien species: (i) the idea of limiting similarity, e.g. invasive species are less likely to establish in communities that are dominated by species with similar traits (Hutchinson 1959; MacArthur & Levins 1967a; Abrams 1983; Van Kleunen, Weber & Fischer 2010); and (ii) Darwin's naturalization hypothesis, e.g. invading species are less likely to establish in communities with congenerics (Daehler 2001; Duncan & Williams 2002; Strauss, 2006; Diez *et al.* 2008). This means that, when compared at a community scale, the more dissimilar (functionally and/or phylogenetically) an alien species is to the native species community pool, the greater its chances are that it will be successful when introduced. We emphasize that, although the summarized patterns of differentiation seem rather small, whether the analyses were univariate or multivariate it is very difficult to predict how big a trait difference should be in order to make an ecological difference (e.g. in competition), as hardly any data on this are available in the literature. In fact, the classic principle of competitive exclusion (Gause 1934) can be interpreted such that very small
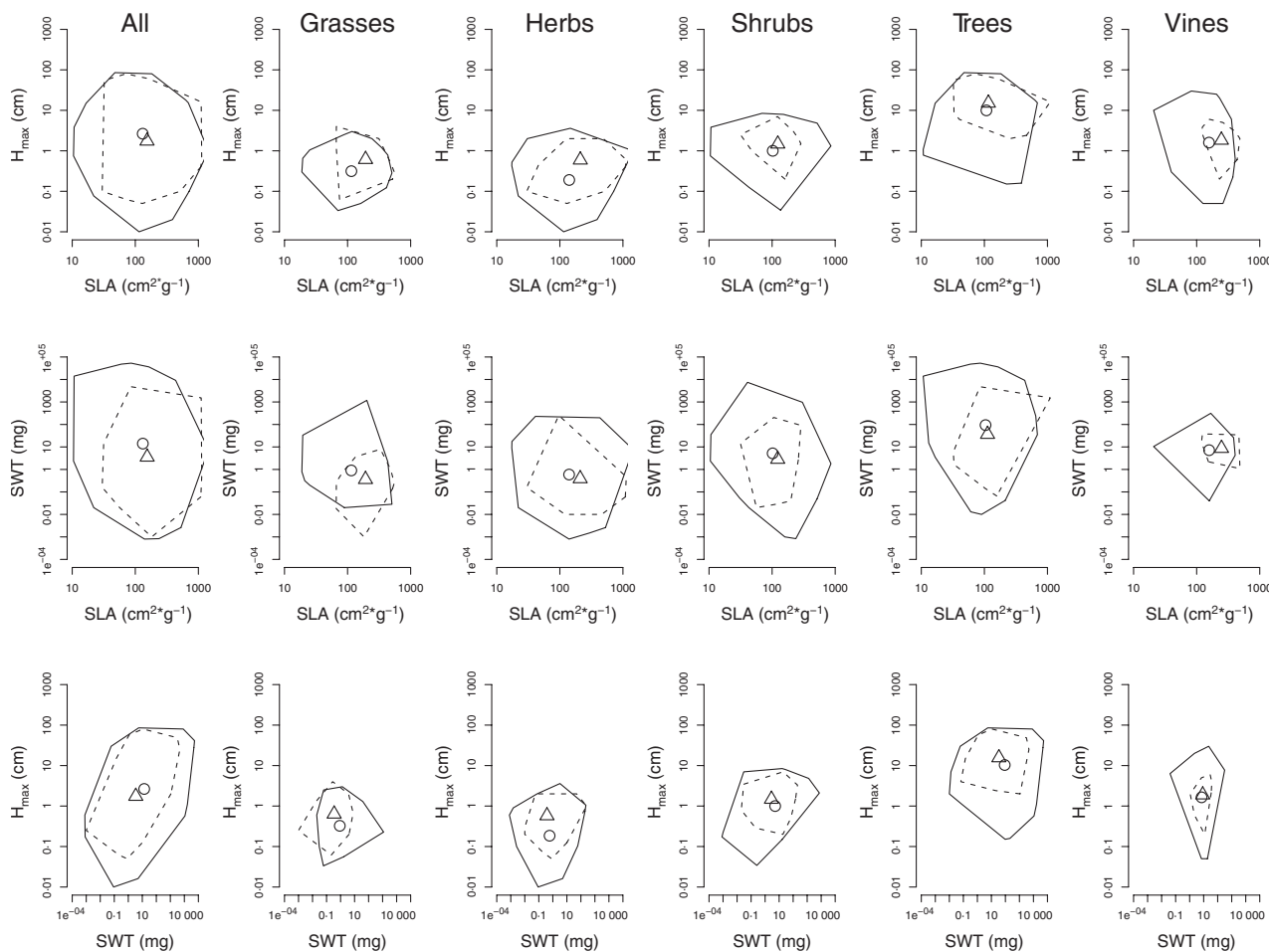
Fig. 1. Minimum convex hull projections of native and alien species, showing the differences between these species-groups in the multidimensional trait space that they occupy, two traits at a time. Traits: specific leaf area (SLA, $cm^2\ g^{-1}$); maximum canopy height (H_{max}, m) and individual seed size (SWT, mg). The polygons represent 2-dimensional cross-sections of the convex hull volumes for each of the evaluated planes. Traits and axes were log_{10} transformed for analysis and representation. Measurements of functional richness represent the volume of each convex hull; trait divergence corresponds to the distance between centres of gravity (centroids); functional divergence corresponds to relative distance of alien and native species' centroids from the community mean trait combination.

Table 3. Descriptive attributes of multi-trait convex hulls describing native and alien species, considering all species, and species grouped by growth form. Functional richness, divergence and mean trait separation are measured as unit-less values standardized by the mean and standard deviation. Differences in Functional Richness are presented as the percentage reduction in the occupied multivariate range, comparing alien to native species. Differences in Functional Divergence are presented as the percentage difference in distance from the overall community-mean position (centroid), of alien compared to native species. A null model approach was used to test for significant differences between Native and Alien species in the various convex hull attributes (H_0: differences are significantly less than would be expected from comparing two randomly-assembled communities). Results from two-tailed Wilcoxon signed-ranks test are also presented. Significance levels are marked as in Table 1

Pair	Native (N)	Alien (N)	Functional richness Differences (%)	Wilcoxon P	% trials Obs. > Exp.	Functional divergence Differences (%)	Wilcoxon P	% trials Obs. > Exp.	Trait similarity Wilcoxon P	% trials Obs. > Exp.
All	1651	305	−55·8	***	1000/1000	5·0	***	572/1000	***	933/1000
Graminoids	197	60	−64·2	***	938/1000	4·0	***	982/1000	***	881/1000
Herbs & forbs	464	113	−63·4	***	998/1000	1·1	***	708/1000	***	886/1000
Shrubs	326	43	−79·8	***	1000/1000	4·1	***	981/1000	NS	545/1000
Trees	623	75	−71·8	***	1000/1000	−1·0	***	308/1000	***	776/1000
Vines	41	14	−88·1	***	943/1000	14·2	***	1000/1000	***	298/1000

but consistent trait differentiation among species competing for a single resource will always lead to full competitive displacement.

The view that phenotypic divergence between native and alien species predisposes a particular introduced species to success has also been addressed using alternative approaches

based on (i) history (i.e. the invasive-elsewhere principle; (Rejmanek 1999; Muth & Pigliucci 2006); (ii) taxonomy (i.e. Darwin's naturalization hypothesis; (Vivanco *et al.* 2004; Mack 2003; Strauss, 2006, Fargione, Brown & Tilman 2003); and (iii) disturbance data (i.e. invasion of human-disturbed areas; (Leishman & Thomson 2005; Funk & Vitousek 2007). These efforts have come as a response to the problems of measuring the niche relationships between natives and aliens, and of identifying a series of species' or habitat characteristics that could predict invasiveness. In agreement with our own study, results from studies using these approaches have generally suggested that whether an alien species could be successful in establishing depends on how its traits compare to those of native species in the introduced community.

It is interesting to view these findings in relation to the evidence of aliens having lower rates of herbivory, seed predation and pathogen attack when compared to co-occurring natives (Mitchell *et al.* 2006; Callaway & Aschehoug 2000; Richardson *et al.* 2000a, Keane & Crawley 2002). Consequently, one might expect alien species to be able to reallocate resources from defence to growth and/or to reproduction (Blossey & Notzold 1995; Crawley, Harvey & Purvis 1996; Van Kleunen, Weber & Fischer 2010). Higher growth rates may be possible, via higher SLA or higher leaf mass per g plant, while increased total seed production may be possible, via lower individual seed mass (Westoby *et al.* 2002; Westoby & Wright 2006).

Could functional relatedness and the idea of limiting similarity then provide a framework to determine possible problematic species and threats to native communities? With some caution, we suggest yes – because such measures reflect the dynamics and diverse interactions among co-occurring species, and hence capture the constraints imposed by physiological limitations, habitat filtering and limiting similarity. In particular, the use of multidimensional metrics of functional diversity may allow discrimination between mechanisms causing trait convergence (i.e. habitat filtering) from those driving trait divergence (i.e. limiting similarity). Here, comparison of all multidimensional metrics showed a significant differentiation between native and alien species, suggesting that the presence of multiple closely functional equivalent species in the native pool (i.e. species with similar trait combinations) could be a factor limiting the success of introduced species.

The idea of functional dissimilarity between native and aliens has been tested previously using various approaches, most of which compare a single attribute between pairs of species pairs based on their taxonomic relatedness (e.g. between pairs of congeneric or confamilial species). Overall, these studies show mixed results (Daehler 2003; Pysek & Richardson 2007). By contrast, the results from our present study indicate a significant differentiation between groups based on a multi-site, multi-species, multi-trait comparison, which can be attributed to larger and additive differences when multiple traits are compared simultaneously and/or the role of phenotypic plasticity or evolutionary changes in alien species attributes they have been introduced; but the identifi-

cation of the actual mechanism remains to be determined. Evidence for this was the significant differences between multidimensional trait-space centroids (trait divergences) and ranges (functional richness and divergence measurements).

Two aspects of our study warrant further comment. First, our comparisons between native and alien species evaluate post-established population interactions only, hence mechanisms causing either an establishment failure, or trait evolution, post-introduction, cannot be tested. Second, traits in this study are assumed to be independent (that is how they were selected), with each representing an approximately independent ecological strategy dimension (Westoby *et al.* 2002). We believe, as Leishman *et al.* (2007), Leishman, Thomson & Cooke (2010) showed, that comparisons of traits within each ecological strategy-dimension would not show fundamentally different strategies for native and alien species; rather we believe that aliens will differentiate from natives by having trait combinations towards the extreme of a given trait-strategy dimension. This difference may result from (for example) a shift in the allocation of resources from defence to growth/reproduction, made possible by release from natural enemies and/or a increased availability of resources (Blumenthal 2006). Alternatively, trait-shifts may be associated with an enhanced ability to take advantage of disturbance. These hypotheses remain to be evaluated at the spatial scale of this study, as the spatial scale used to define our 'communities' was too coarse and did not capture small scale inter-specific interactions nor the effect of disturbance to which disturbance-adapted aliens can specialize.

As this and other studies have addressed (Thompson, Hodgson & Rich 1995; Crawley, Harvey & Purvis 1996; Williamson & Fitter 1996; Lake & Leishman 2004; Ricciardi & Atkinson 2004; Leishman & Thomson 2005; Strauss, Webb & Salamin, 2006), a key element to understand the success of alien species in their alien range is considering the relatedness (functional or phylogenetic) between the alien and natives community. We have demonstrated that alien species have a combination of traits that significantly differs from those of the native community where they are introduced, suggesting support for the classic 'empty niches' idea to explain invasions. Understanding the mechanisms generating these patterns might then help to develop a trait-based framework for predicting the successes/failure of aliens to establish and maintain successful populations when introduced to a novel region. And finally, this approach could then be used to address three fundamental questions in invasive biology: which species are likely to become invasive; which habitats or communities are susceptible to invasion; and how can we manage invasions once they have occurred?

In conclusion, determining successful introductions will require the evaluation of three community attributes: the level of functional similarity between natives and aliens, as this study has done; the degree of phylogenetic relatedness between these groups; and the disturbance regime of the target community. This work focused on one of this dimensions

and determined the importance of functional differentiation as a mechanism associated with alien success. Our results, coupled with other recent findings in 'functional trait ecology' (Fargione, Brown & Tilman 2003; Ricciardi & Atkinson 2004; Rejmanek *et al.* 2005; Strauss, Webb and Salamin 2006) highlight the need to take special consideration of those newly introduced aliens for which the target native community has no close functional similar species.

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Supporting Information

Additional Supporting information may be found in the online version of this article.

Appendix S1. Description of the protocol used to build the trait database.

Appendix S2. Native and alien species data and data sources.

Fig. S1. Relationships between the mean difference in traits of co-occurring alien and native species (*y*-axis) and size of the grouping scale (*x*-axis).

Fig. S2. Model residuals histograms from lineal mixed effect models using $\log_{10}$ transformed traits.

Table S1. Variance components from a linear mixed model comparing the differences in SLA H_{max} and SWT between native and alien species.

Table S2. Variance components from a linear mixed model evaluating the differences in SLA, H_{max} and SWT between native and alien species. The model included the full taxonomic identity structure (i.e. family/genus/species).

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