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Functional similarity and dissimilarity facilitate alien plant invasiveness along biotic and abiotic gradients in an arid protected area

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Abstract Two contradictory hypotheses have been put forth to forecast alien invasiveness: being either functionally similar, or dissimilar, to resident natives along environmental gradients. The 'try-harder' hypothesis predicts that alien plants will be functionally dissimilar to natives and should thus exhibit exaggerated trait values when compared to natives in respect to resource extraction or stress tolerance. In contrast, the 'join-the-locals' hypothesis, which is compatible with "environmental filtering", predicts functional similarities among alien and native species in richer, but not in resource-limited environments. Here, we propose a framework that links the successful alien plant strategy, i.e. being functionally similar or dissimilar to natives, to the harshness of the environment and the availability of resources. We tested these two hypotheses using a trait-environment dataset of 33 alien and 130 native plants in 96 sites covering a gradient of soil resources (organic matter, nitrogen, soil moisture) in Saint-Katherine, an arid protected area in Egypt. We estimated 18 interaction coefficients between three candidate traits (specific leaf area, above-ground biomass, height) of alien and native plants as well as soil resources using linear mixed-effects models. Additionally, we calculated the mean and the hierarchical functional distance among aliens and natives along soil gradients. Our results revealed that in extreme resource-limited environments, aliens and natives were functionally similar and had relatively equal trait values consistent with environmental filtering, thus supporting the 'join-the-locals' hypothesis. However, in environments richer in resources, aliens and natives were functionally dissimilar with aliens exhibiting more exploitative trait values (taller, higher SLA and biomass) than natives, providing support for the 'try-harder' hypothesis. While demonstrated in only one arid system, results suggest that linking soil resource availability with functional divergence and convergence among native and alien plants could be used as an informative strategy to predict alien invasiveness. Hence, future studies should investigate the functional response of alien and native plants in different environments against different resource gradients to test for the generality of the patterns we found.

Keywords Functional traits · Competition · Environmental filtering · Soil gradients

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Introduction

In recent decades, the comparative analysis of differences in the functional traits of alien and native plant species has expanded drastically in the context of plant invasion ecology (Pyšek and Richardson 2007; Tecco et al. 2010, 2013). Differences in the traits of native and alien plants have been proposed as a proxy to explain alien invasiveness in natural ecosystems (Funk et al. 2008; Leffler et al. 2014).This approach has often been used to examine trait variation across environmental gradients between alien and native plant species and investigate which traits facilitate aliens over resident natives to predict invasiveness (Funk and Vitousek 2007; Leishman et al. 2010; van Kleunen et al. 2010; Heberling and Fridley 2013). However, such an approach neglects the differences between alien and native species based on their functional relatedness and their functional responses along soil resource gradients.

How traits between alien and native plants vary with resource availability has been studied comparatively in high- versus low-resource conditions (Leishman and Thomson 2005; Funk and Vitousek 2007; González et al. 2010; Leishman et al. 2010). It has been proposed that aliens have the potential to outperform resident natives in nutrient-rich areas through the exploitation of resources unused by natives (Davis et al. 2000; Daehler 2003) and/or a reduction in herbivory/parasitism rates (Blumenthal 2005, 2006) or an evolution of high competitive abilities (Blossey and Notzold 1995). On the other hand, under limiting resource conditions, natives are predicted to outperform aliens due to the development of strategies that enable them to tolerate higher levels of stress through the extraction of limiting resources (however, for explanations of alien success in low-resource environments see Funk and Vitousek 2007; González et al. 2010).

Many hypotheses have been put forth to link alien invasiveness with being similar or dissimilar to natives, to the harshness of the environment, and the availability of resources. The 'try-harder' hypothesis, initially proposed by Crawley et al. (1996), states that successful aliens should be able to utilize local resources better than resident native species. According to this concept, aliens are functionally dissimilar from native species because they exhibit more conservative functional trait syndromes (e.g. low height values and small leaves, with low specific area) in extreme limiting resources environments (Leishman and Thomson 2005; Rejmánek et al. 2005; Burns 2006; Pyšek and Richardson 2007; Funk and Vitousek 2007) and more exploitative syndromes (e.g. high height values and large leaves, with high specific area) in resource-rich environments (Leishman et al. 2008; Tecco et al. 2010, 2013; Dyderski and Jagodziński 2019). This dissimilarity may arise as a consequence of competitive exclusion (MacDougall et al. 2009; Mayfield and Levine 2010; Li et al. 2015), which eliminates alien species that are too similar in their trait values (Macarthur and Levins 1967; Abrams 1983; Davies 2006). Under this hypothesis, an alien species' position in a competitive hierarchy is attributed to the differences in its functional trait values compared with resident natives. Within invaded communities, this concept has been suggested to explain invasion success due to the link between a species functional traits and competitive ability to acquire resources (Westoby et al. 2002; Gallien et al. 2017). For example, alien plants that grow taller (i.e. with a positive hierarchical value) than resident natives are usually expected to invade natural communities and outcompete resident natives (Conti et al. 2018).

In contrast, the 'join-the-locals' hypothesis proposes that a pattern of aliens co-occurring with functionally similar natives is expected due to the strong effect of environmental filtering (environmental conditions that select for species capable of surviving and reproducing in a given locale (Cadotte et al. 2018). This pattern has been attributed to the selection of alien species that are able to exploit similar resources and tolerate the same environmental stressors as natives and subsequently have similar traits (Funk et al. 2016). Eventually, alien species are presumed to occupy a portion of the functional space originally occupied by native species, leading to an increased functional similarity between both species' groups (Kembel and Hubbell 2006; Catford et al. 2009). Likewise, there is some support that alien and native species have similar trait values and share limited resources (Daehler 2001; Duncan and Williams 2002; Maitner et al. 2012; Allen et al. 2013; Park and Potter 2015).

This study aimed to (a) investigate whether alien and native plants are functionally similar or dissimilar in terms of three key traits (height, specific leaf area

SLA and biomass production) along a soil resource gradient and (b) determine which ecological process (environmental filtering/competitive exclusion) is driving the invasiveness of alien plant species along a soil resource gradient. We predicted that in environments with limited soil resources, alien and native plants would be functionally more similar (in terms of height, SLA and biomass), indicating similar competitive ability, due to the effect of environmental filtering ('join-the-locals' hypothesis). We also predicted that in resource-rich environments, alien plant species would be functionally dissimilar to natives and more competitive than resident natives due to competitive exclusion between functionally similar species, whereby the invading dissimilar alien species exploits resources unused by natives (Crawley et al.1996; Thuiller et al. 2010; 'try-harder' hypothesis).

Methods

Study area

This study was conducted in the Saint Katherine Protectorate (SKP), South Sinai, Egypt. SKP is located in the arid North African belt and is characterized by a Saharan-Mediterranean climate with extremely dry, hot summers and cold winters. Average rainfall is 57 mm a year, with average maximum temperatures of 35 °C and minimum temperatures of 5 °C (St Katherine Protectorate Management Unit, pers. comm.). The high mountains (1600–2460 m asl) surrounding the town of St Katherine receive higher levels of precipitation, of up to 100 mm per year (Ayyad et al. 2000). The area includes the highest peaks in Egypt and contains a unique assemblage of natural resources, notably high-altitude ecosystems with surprisingly diverse fauna and flora and with a significant proportion of endemic species. The diversity of both landforms and geologic structures of SKP leads to the differentiation of unique mountainous microhabitats (e.g. wadis, gardens, caves, inter-mountainous roads). SKP encompasses approximately 4350 km^2 of largely mountainous terrain in South Sinai, but the studied area was approximately 100–150 km^2 in size. Field surveys were carried out during spring and summer seasons from March to July 2018.

Stand and species data

A total of 110 stands of each 10 m^2 were arbitrarily placed throughout the locations of alien plant species to cover the entire range of the invaded plant communities within the study area. Only invaded locations with appreciable vegetation (e.g. presence of at least one alien / native plant individual) were selected as stands. Stand size was relatively small (10 m^2) due to the generally sparse vegetation cover under the arid conditions. For each stand, we recorded the coordinates and elevation using GPS. In total, 33 alien and 130 native plant species were recorded within the sampled stands, covering a gradient of soil resources. Of the 110 stands, 55 were principally distributed within resource-limited environments (dominated by rocky substrate with limiting soil resources) and 55 were distributed within comparably resource-rich environments, hereafter referred to as 'resource-rich' (moderately rocky sites with availability of soil resources). We excluded 14 stands in resource-rich environments where native plant species richness was almost zero, leaving a total of 96 sites.

Resource-rich environments were mostly dominated by woody alien plant species (e.g. small shrubs/sub-shrubs) with high cover percentage (70.16%) compared to woody native plant species (e.g. small shrubs/sub-shrubs, 30.81%). In contrast, resource-limited environments were dominated by herbaceous native species (cover 52.72%). All plants were identified to species and the number of alien and native individuals per stand was counted ("Appendix": Table 3).

Soil data

In each stand, soil moisture, soil nitrogen content and organic matter were measured. Soil moisture measurements were taken directly from the field in the early morning with a field hygrometer that measures the volumetric water content in soil. Soil samples (five samples per stand) were collected at random from each stand and air-dried to constant mass, then soil water extracts at 1:5 were prepared for the determination of soil nitrogen and organic matter content. The percentage of organic matter was calculated as the difference between total C and CaCO3% (Klute 1986). The total concentration of available nitrogen (mg/L) was calculated using standard methods as outlined in Allen et al. (1974) using a CHN analyser (EA1108, Carlo Erba Instruments).

Functional trait data

For alien plant species, we measured three key functional traits (plant height from the ground (cm), specific leaf area [SLA, (cm^2/g) and the above-ground biomass (kg)] directly from the field for each alien plant individual. These traits are thought to capture a large part of the ecologically significant differences among species (Westoby 1998) as well as influence resource acquisition and environmental tolerances (Weiher and Keddy 1995). SLA was calculated as the total leaf area (using IMAGEJ software 1.49 version) divided by leaf dry weight (e.g. Pérez-Harguindeguy et al. 2013). To obtain measurements for above-ground biomass of alien species, we collected leaves and stems destructively from the field, which were then dried in a drying oven (VWR International) at 50 °C for 3 days, then weighed using a Mettler Toledo ML Series Precision Balance (ML Analytical balance). For native plant species, plant height (cm), number of leaves, leaf area (cm^2) (drawn in the field then scanned using IMAGEJ software 1.49 version), number of flowers and fruits, were directly measured in the field. These non destructively measured traits were used as predictors to estimate the two destructive traits as response variables, SLA and biomass, through allometric equations (Basuki et al. 2009) as destruction of native biodiversity is strictly forbidden within SKP. We then constructed and validated a series of multivariate regression models using model selection criteria to select the best models of predicting native SLA and biomass within their protected range (see "Appendix": Table 3 and Figs 5, 6).

Estimation of the absolute mean functional distance (MFD)

To estimate the functional similarity and dissimilarity among aliens and natives, we measured the mean functional distance (MFD) as the mean weighted pairwise distance of each alien species to the native community (Gallien and Carboni 2017; Carboni et al. 2018). This distance measures the functional differences between aliens and the recipient native community based on the combination of height, SLA and the above-ground biomass. For each alien species, it was calculated using the 'dist' function in R (package '*stats*' version 3.5.2) as the 'Euclidean' distance of the alien species' traits to the mean of native species traits in each stand, weighted by their abundance.

Estimation of alien hierarchical distance

We calculated alien hierarchical distances as the differences in each key functional trait (height, SLA, biomass) between alien plants and the mean trait values of resident native plants within each stand. This hierarchical trait index is used as a proxy to test the relative competitive ability of alien species to native species (Kunstler et al. 2012; Gallien et al. 2017). For example, if the trait difference ($t_A - t_N$) between an alien species A (with trait value t_A) and a native species N (with trait value t_N) is positive, alien species A is expected to be more competitive than native species N. In this way, we constructed a competition trait hierarchy to test whether alien plants have higher competitive ability (positive hierarchical distances) or lower competitive ability (negative values) than natives or are equally competitive as natives (hierarchical value close to zero) for each trait (i.e. its hierarchical position on each trait gradient (Mayfield and Levine 2010; Kunstler et al. 2012; Gallien et al. 2015). This hierarchical index was calculated for each trait separately.

Multivariate modelling framework

We constructed a series of mixed-effect models, using species functional traits (height, SLA, biomass), MFD, and the hierarchical distances of height, SLA and biomass as response variables. Soil resource measures (organic matter, nitrogen, soil moisture) were included as explanatory variables, with analyses implemented using "*lme4*" (version 1.1-20; Bates et al. 2015). First, the fixed effects explaining functional traits were represented by two-way interactions between species identity (alien/native) and soil variables. Such interaction terms are designed to examine the influence of soil resources on alien and native trait values (e.g. Pollock et al. 2012). Positive species-soil interactions refer to higher values of a soil resource increase the species trait values and vice-versa. A benefit of this modelling approach is that we can visualize the extent of alien and native trait variation for a certain soil variable to unravel trait responses to soil resource gradients. Second, the fixed effects explaining MFD and the hierarchical distances were represented by the main effects of the three crossed continuous soil resources.

All response and explanatory variables were centred and standardized with respect to the overall mean and scaled by 1 SD (Schielzeth 2010). All explanatory variables included in the model (soil variables, traits and functional distance) were only weakly correlated with each other (Pearson correlations < 0.6), so that multicollinearity was not an issue.

In all models, we initially included site and stand identities as a random effect, but we found that the variance captured by site and stand identities was very low compared to the residuals. This might be attributed to including species identity in the fixed effects which turned out to be the main factor determining the variability in the studied trait values. Therefore, we simplified the model structure by removing site and stand identities from the random effect structure. Subsequently, we included a taxonomic nested classification (Family/Genus/Species) as a random effect that captured a considerable amount of variance, allowing slope and intercept parameters to account for shared evolutionary relationships among species (Table 1). Full models with all possible structures of the nested random effects and fixed effects were compared to test the potential explanatory power of the fully taxonomic structure of the nested random effect using Akaike's information criterion (AIC). We then tested whether such a structure of random effects effectively accounted for the phylogenetic non-independence among species by testing model residuals for evidence of phylogenetic signal (Revell 2010). For this test, we extracted model residuals and linked them to the corresponding species. Then, we tested for the strength of the phylogenetic signal of these residuals using the function 'phylosig' from 'phytools' (version 0.3-72, (Revell 2012; González-Suárez et al. 2015) and a phylomatic phylogeny including the studies species (aliens/natives). The 'phylosig' function computes the phylogenetic signal in a variable (in our case, model residuals) estimating Blomberg's K (Blomberg et al. 2003).

Finally, we constructed a series of models with all possible combinations of interactions. We calculated the explanatory ability of these models and ranked them by their AIC values (Johnson and Omland 2004). We also evaluated the predictive capacity of each model, by calculating the overall variance explained (conditional R^2, following (Nakagawa and Schielzeth 2013) using the package 'MuMIN' (version 1.43.6) (Barton 2016). The best models were filtered according to (1) lower values of AIC, (2) higher values of model probability Akaike's weights (AW) and (3) higher p values of Chi-square test ($p > 0.05$). We checked diagnostic plots (e.g. residuals versus fitted values and observed versus fitted values) for potential outliers and data trends. We plotted normalized residuals against fitted values to identify violation of homogeneity indicated by differences in spread. To overcome the large spread of fitted values, functional traits and MFD were log transformed in order to improve the normality of the error distribution (as determined by inspection of QQ plots), we also verified the normality using the Shapiro-Wilks test. All analyses were conducted in R v.3.3.1 (R Core Team 2018).

Results

Absolute trait differences among aliens and natives

Linear mixed effects model comparisons involving functional traits (height, SLA, biomass) as response variables revealed significant trait differences among alien and native plant species, indicating that these differences were mostly explained by availability of soil resources (Fig. 1 and Table 1). Alien plants had significantly higher SLA ($p < 0.001$, $R^2 = 0.89$), height ($p < 0.01$, $R^2 = 0.73$) and biomass ($p < 0.001$, $R^2 = 0.79$) than co-occurring native plants at high resource availability. In contrast, within resource-limited environments, we saw similar trait values in alien and native plants (Table 1 and Fig. 1). First, in high resource availability stands, alien plant species responded positively to increasing soil organic matter and nitrogen (Table 1), but negatively to high soil water content exhibiting high values of above-ground biomass, height and SLA (Fig. 1). Native plant species responded negatively to increases in soil moisture, nitrogen and organic matter and, on average, recorded lower values of above-ground biomass as well as SLA and height when compared to alien species (Table 1). Second, in resource-limited stands,

Table 1 Average and 95% confidence intervals (in square brackets) estimates from linear mixed effects models testing the response of alien and native plant species functional traits (Biomass, height and SLA) to soil resources (organic matter, nitrogen and soil moisture) including the taxonomic variance that was captured by the random effect

Fixed effects	Response variables						
	Biomass (kg)		Height (cm)		SLA (cm^2/g)		MFD
	Co-efficient CI [Upper, lower]		Co-efficient CI [Upper, lower]		Co-efficient CI [Upper, lower]		Co-efficient CI [Upper, lower]
	Alien	Native	Alien	Native	Alien	Native	
Soil moisture (%)	– 0.07	– 0.15 ***	0.01	– 0.06 *	0.00	– 0.13 ***	0.09*
	[– 0.15, 0.02]	[– 0.20, – 0.10]	[– 0.07, 0.09]	[– 0.11, – 0.01]	[– 0.05, 0.05]	[– 0.16, – 0.09]	[0.01, 0.16]
Nitrogen (mg/L)	0.10	– 0.53 ***	0.04	– 0.01	0.22 ***	– 0.18 ***	0.07 **
	[– 0.10, 0.30]	[– 0.65, – 0.41]	[– 0.05, 0.12]	[– 0.05, 0.03]	[0.17, 0.28]	[– 0.21, – 0.15]	[0.01, 0.14]
Organic matter (g/ml)	0.09	– 0.06 *	0.02	– 0.03	0.14 ***	– 0.09 ***	0.05*
	[– 0.01, 0.18]	[– 0.11, – 0.01]	[– 0.07, 0.11]	[– 0.08, 0.01]	[0.08, 0.20]	[– 0.12, – 0.06]	[– 0.02, 0.12]

Random effect	Variance/SD	Variance/SD	Variance/SD	Variance/SD
Species/genus/family	0	0.22/0.47	0.35/0.68	0
Genus/family	0.22/0.47	0.36/0.68	0	0.05151/0.2270
Family	0.81/0.98	0.14/0.37	0.74/0.86	0.12102/ 0.3479
Residuals	0.28/0.53	0.25/0.51	0.19/0.31	0.81219/0.9012
AIC	1556.66	1554.17	915.59	2206.75
BIC	1603.60	1605.79	967.18	2239.6
R^2 (conditional)/R2 (marginal)	0.79/0.14	0.74/0.044	0.89/0.041	0.3/0.037

Significant association test (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.)

aliens and natives tended to be more functionally similar. Both species groups exhibited more similar biomass, height and SLA values with low nitrogen content. However, native plants showed a slight increase in their above-ground biomass response to resource limitation (Fig. 1).

Absolute multi-trait functional distance along the soil resource gradient

Mixed model effects revealed a significant positive relationship between the availability of soil resources and the absolute mean functional distance (MFD) among aliens and natives in richer resource environments (Table 1 and Fig. 2). Such absolute distance increased significantly ($t = 2.695$, $p < 0.001$; $t = 2.495$, $p < 0.01$; $t = 1.660$, $p < 0.01$) with increasing availability of soil nitrogen, soil moisture and organic matter, respectively. Likewise, resource-limited environments had a significant negative effect on MFD among aliens and natives (Fig. 2) with more stressful conditions leading to a decline in the mean functional distance. This finding demonstrates that alien plants tend to co-exist with dissimilar native plants in richer resources environments but with more similar native plants under extreme limiting resources.

Alien hierarchical trait distance along the soil resource gradient

On average, there were significant positive relationships between alien hierarchical trait distances and soil resource availability (Table 2 and Fig. 3). Alien plants tended to have positive SLA and biomass hierarchical distances ($t = 1.471$, $p < 0.001$; $t = 1.416$, $p < 0.05$), which increased significantly with increasing soil

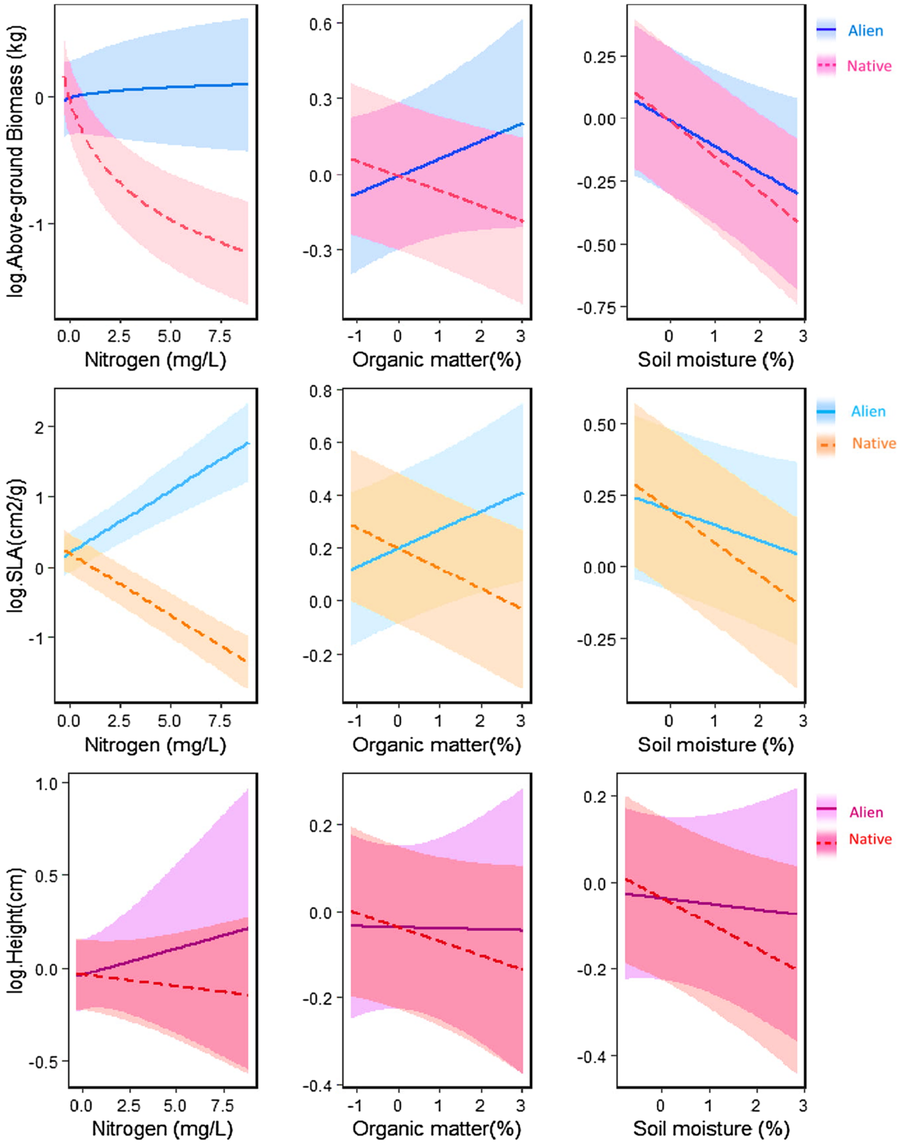

Fig. 1 Showing the trait differences (Above-ground biomass—specific leaf area (SLA)—height) among alien and native plant species in responding to soil resources (nitrogen, organic matter, soil moisture) availability in SKP.Continuous and dashed lines represent the average response of aliens and natives respectively expected by the model with 95% confidence intervals (shaded areas). All x-axes were scaled/y axes were logged and scaled

organic matter content respectively. In other words, alien species with high SLA, height and above-ground biomass values are more competitive than resident native plants particularly in richer organic carbon and nitrogen environments. However, we found a negative range of alien height hierarchical distance ($t = -1.213$, $p < 0.05$) in limited organic carbon environments. Likewise, alien biomass and SLA hierarchical distances were likely to be around zero in stands with limited soil moisture and nitrogen. These findings revealed that alien species had high functional trait values and tend to be dissimilar from natives in nutrient-rich environments, whilst alien plants tended to be functionally similar or had comparatively equal values of SLA, biomass and height, in such stressful or resource-limited stands (Table 2).

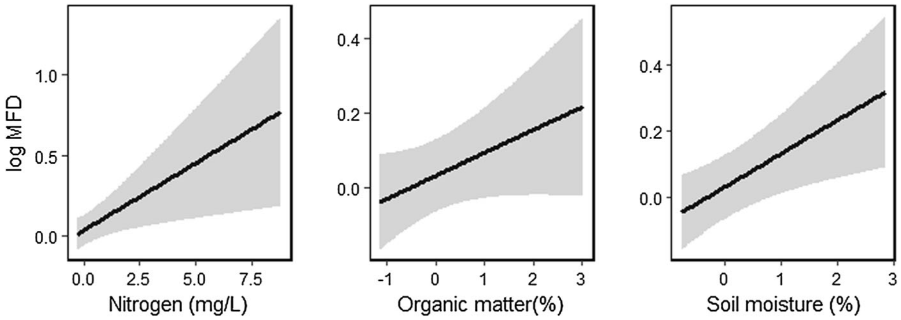

Fig. 2 The response of the mean functional distance (MFD) among aliens and natives to relation to soil resource (organic matter, nitrogen, soil moisture) availability expected by the model with 95% confidence intervals (shaded areas). All soil resources were scaled / MFD was logged and scaled

Table 2 Average and 95% confidence intervals (in square brackets) estimates from multivariate models testing the response of alien hierarchical distances for biomass, SLA and height to soil resource (organic matter, nitrogen, soil moisture) availability

Predictors	Response variables		
	Biomass (kg) Co-efficient CI [Upper, lower]	SLA (cm^2/g) Co-efficient CI [Upper, lower]	Height (cm) Co-efficient CI [Upper, lower]
Soil moisture (%)	− 0.01	0.01*	− 0.04
	[− 0.06, 0.04]	[− 0.01, 0.02]	[− 0.09, 0.01]
Nitrogen (mg/L)	− 0.01 *	0.01 ***	0.01
	[− 0.02, − 0.00]	[0.00, 0.01]	[− 0.01, 0.00]
Organic matter (g/ml)	0.15	0.08*	− 0.20
	[− 0.48, 0.18]	[− 0.03, 0.19]	[− 0.53, 0.13]
AIC	323.98	171.69	339.59
BIC	335.95	184.46	351.80
F-statistic	2.618	6.277	2.456

Significant association test (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.)

Discussion

Our study demonstrates that alien and native plant species are functionally similar in resource-limited environments, yet functionally dissimilar in comparably resource-rich environments within an arid ecosystem. The finding that alien species were dissimilar to natives and exhibited more acquisitive and competitive trait values (positive hierarchical distances values) than native species in the resource-rich environments partially supports the ‘try-harder’ hypothesis. However, under limited soil resources, alien and native plants revealed conservative and similar trait values, partially supporting the ‘join-the-locals’ hypothesis. Moreover, and in support of our expectations, mean functional distance among aliens and natives became greater with increasing resource availability (Fig. 4).

A possible explanation for the functional divergence among alien and native plants in more resource rich environments is likely a divergence in resource-use strategies caused by differentiation in resource acquisition. For example, it is frequently thought that a higher ability of nutrient acquisition will benefit the alien species and thus promote establishment success, subsequently enhancing their invasiveness (Davis et al. 2000; Dawson et al. 2012). To date, most comparative studies on such environments have found that native species tend to follow a slow-return strategy, while alien species follow a fast-return strategy (Leishman et al. 2008; Penuelas et al. 2010; Ordonez and Olff 2013). Thus, plant species with slow returns on resource investments (possessing lower trait values such as low specific leaf area) are supposed to have high construction costs and low photosynthetic rates. At the opposite extreme, plants with fast returns on resource investments, i.e. higher trait values such as

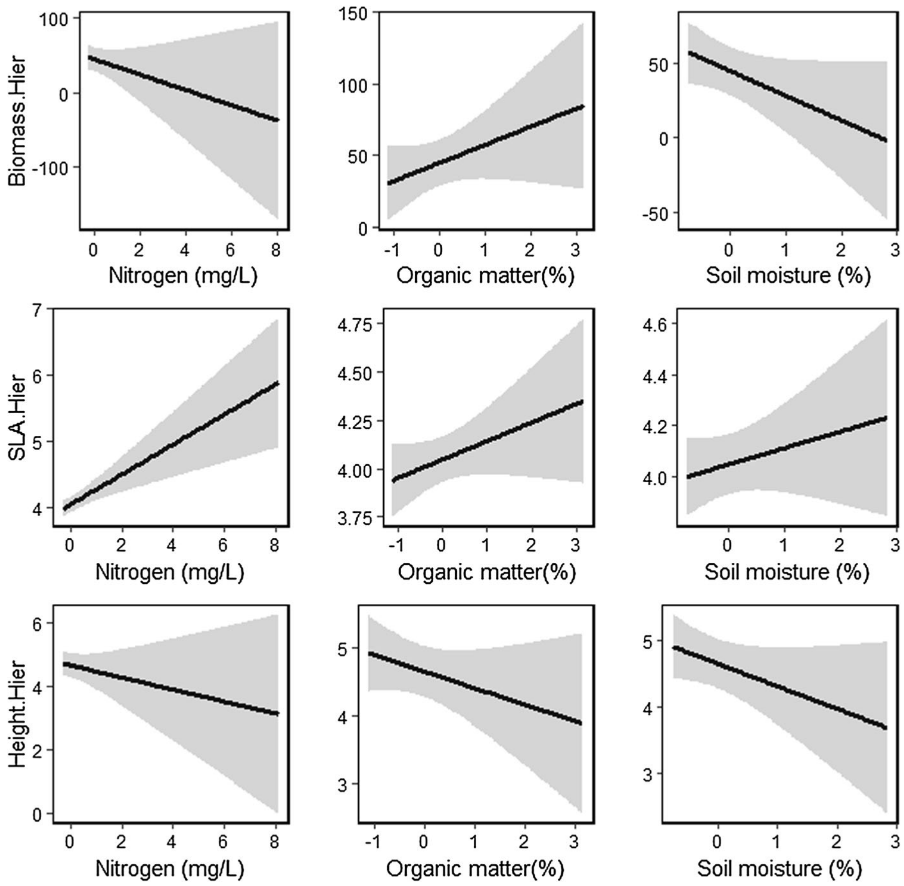

Fig. 3 The alien hierarchical distances for biomass, SLA and height in response to soil resources (organic matter, nitrogen, soil moisture) availability expected by the model with 95% confidence intervals. All soil variables were scaled

high specific leaf area, are supposed to have higher growth rates (Poorter and Evans 1998;Schieving and Poorter 1999).

Fast-growing alien species are presumably more successful at a global scale than slow-growing species (Grotkopp and Rejmánek 2007; Dawson et al. 2011). Specifically, fast-growing alien species tend to have a greater resource-capture ability (Wright et al. 2004; Rose et al. 2009), which might explain their invasion success. For example, Dawson et al. (2011), assessed the relationship between global invasiveness and the maximum relative growth rate of 105 plant species commonly occurring in the United Kingdom. They found that the maximum relative growth rate of alien species is positively associated with their global invasiveness. In accordance, our study added more evidence that alien plants with exploitative syndromes (tall, with high above-ground biomass and SLA values) were responding positively to soil resources. These functional attributes come up with an exploitative nutrient-use strategy that is expected to be associated with high resource availability (Laliberté et al. 2012; Dyderski and Jagodziński 2019). Hence, this strategy enables alien plants to capture a large proportion of light resources and conduct high rates of photosynthesis (Gaudet and Keddy 1988; Aerts 1999). This leads to greater assimilation of organic carbon and nitrogen compounds (Westoby 1998; Bullock et al. 2001; Grime 2006) and faster growth rates (Warren and Adams 2001; Onoda et al. 2004; Takashima et al. 2004; Feng et al. 2009). By contrast, native plants showed lower functional trait values (height, SLA and biomass) than aliens and responded negatively to soil resource availability. This is in line with conservative trait syndromes that seek resource conservation rather than acquisition (Lake and Leishman 2004).

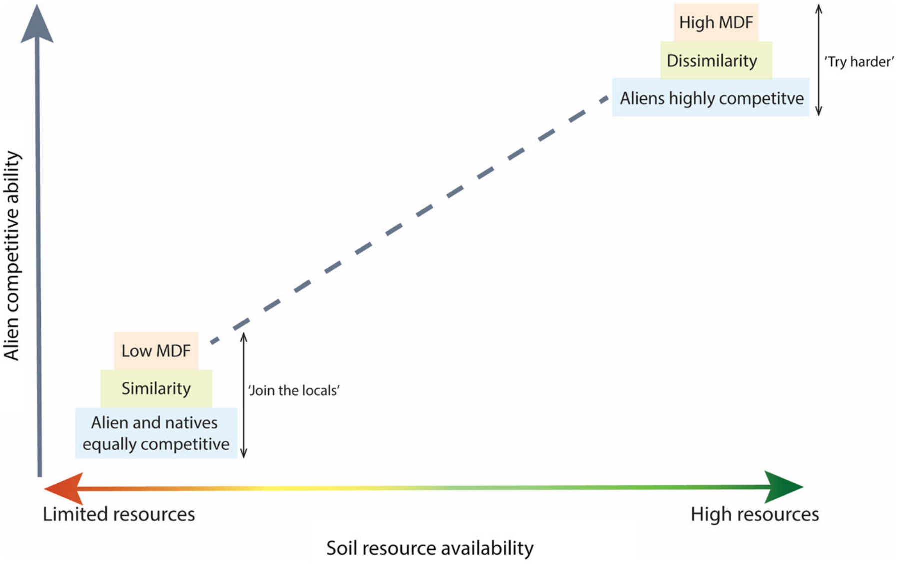

Fig. 4 Hypothetical functional similarity and dissimilarity between alien and native plants in response to soil resource gradients and alien competitive ability. Dashed line indicates the hypothesized responses of alien competitive ability and similarity between aliens and natives along gradients of resource availability

Functional dissimilarity among aliens and natives in resource-rich environments may also arise from the differences in the competitive abilities of both species groups (Cavender-Bares et al. 2004; Mayfield and Levine 2010; Kunstler et al. 2012). These differences were originally attributed to the superior competitive ability of alien plants to eliminate co-occurring resident native plants that have similar trait values and soil preferences. Therefore, if both species groups compete for different resources, and aliens outcompete resident natives, this should favour aliens that are functionally dissimilar from resident natives to become established (Duncan and Williams 2002; Richardson and Pyšek 2006). In this case, functional dissimilarity cannot be disentangled from competitive exclusion (Gallien et al. 2015).

Likewise, we found that alien and native plants were functionally similar in resource-limited environments and had similar trait values regarding their response to soil resources. Previous studies (e.g. Pyšek et al. 1995, 2005; Prinzing et al. 2002) have suggested that both species groups should be more similar under stressful conditions (van Kleunen et al. 2010; Jauni and Hyvönen 2012) and share analogous simultaneous responses to the limiting environmental resources. For example, Cadotte et al. (2018) suggested that in extreme environments, alien plant species are more likely to interact directly and compete for the same pool of limiting resources. Therefore, alien species should not be so different from natives since the maladaptation to harsh environmental conditions prevents them from becoming established (Thuiller et al. 2010).

There are two factors that have been suggested to explain functional similarity in such environments. First, environmental filtering selects species that can tolerate the extreme environmental conditions (Gallien et al. 2017; Cadotte et al. 2018). Second, competitive filtering, which is supposed to drive similarity among aliens and natives if both species groups compete for the same limiting resources (Mayfield and Levine 2010); only strong competitors with trait values similar to residents will be selected and are expected to survive (Gallien and Carboni 2017). However, we found that resident natives were less conservative species with moderately higher biomass and height values than aliens, indicating they might use a fast-return strategy for resource acquisition when harsh conditions prevail (Leishman et al. 2008; Penuelas et al. 2010; Ordonez and Olff 2013; but see Funk and Vitousek 2007; Dawson et al. 2011). Such a strategy might allow native species to be more tolerant to low-resource conditions and display trait values associated with slow growth, resource-use efficiency, high biomass, high tissue construction cost, and long-lived tissues (Chapin III 1980; Vitousek 1982; Craine 2009; Funk et al. 2013). This is in line with predictions of the resource-limitation theory, assuming that plants should allocate higher biomass to structures that help them to acquire more of the most limiting resources (Poorter and Nagel 2000).

Study constraints

We acknowledge some limitations associated with our study, necessitated by constraints working in the Saint Katherine Protectorate. First, our approach of arbitrarily selecting sampling plots may have led to some bias in the analysed community composition (Lepš and Hadincová 1992). For example, this approach may have caused a bias toward more resource-rich sites with higher species diversity. However, in contrast to a systematic random method for selecting plots, this approach meant that we ensured representation of the native and alien co-occurring plant communities (Holeksa and Wozniak 2005), necessary to our research aim. Second, given permit restrictions prohibiting the collection of native species, we were unable to obtain trait data requiring destructive methods. For future studies, we thus recommend designing a random sampling strategy for gathering a complete native plant species trait data set (destructive/non-destructive) outside their protected range within similar environmental conditions.

Conclusion

This study demonstrates that resource availability may explain the presence of contrasting strategies in alien plant species (more acquisitive and competitive/ more conservative) within one single arid ecosystem. The first group, the ‘acquisitive and competitive aliens/ dissimilar to natives’, are speculated to be more efficient and inhabit disturbed ecosystems with higher resource availability (Leishman et al. 2008, 2010). This is in part because these plants have strategies that correspond to the early successional, fast investment return strategy. They also experienced higher resource costs relative to natives. The other group, the ‘conservative aliens/similar to natives’, are expected to dominate resource-poor habitats, and have lower invasion success in highly human-modified environments. These plants are expected to follow strategies that place a higher premium on efficient use of resources (conservative strategies) at the expense of rapid growth (Aerts and Chapin III 1999). Thus, future studies should conduct similar studies in different environments to test the generality of our findings. It would further be interesting to test the roles of different nutrient-niches and the acquisition strategies of alien plants for other available nutrients in their introduced and native ranges that might be the foothold of their invasiveness.

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Authors’ Contribution RFE conceived the approach with substantial contributions from SB. IA and AK collected and compiled the datasets. RFE carried out the analyses with advice from RR. RFE wrote the first draft with substantial contributions of SB. AFP helped with the writing of the manuscript. All authors gave final approval for publication.

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Appendix: Estimation of native SLA and biomass data using allometric equations

Because there was no allowance of destructively measuring native biomass and SLA in SKP, we estimated the above-ground biomass and SLA of native plants using allometric equations (Basuki et al. 2009). First, we used four non-destructive traits directly measured in the field per native plant individual. These traits were plant height (cm), leaf area (cm^2) (drawn in the field then scanned using IMAGEJ), number of leaves and number of flowers and fruits. Second, we constructed series of multivariate regression models to calibrate a predictive model of aliens above-ground biomass and SLA as a function of their height (cm), number of leaves, flowers, fruits and leaf area (cm^2). Then, we validated the predictive power of this model through model selection criteria using Akaike Information Criterion (AIC) and Akaike Weights (AW) in addition to diagnostic regression plots (e.g. QQ plots) to infer the best regression models. Additionally, we found high correlation between the actual observed values of biomass and SLA and the predicted values from the best regression models. Based on this validation, the best fitted model was used to predict natives' biomass and SLA in each stand based on their empirical, field-measured trait values (see Table 3).

Initially, we considered using biomass and SLA data from global databases such as TRY or LEDA, because trait values were found for only 24 native species (out of 133). Likewise, database trait values of these native species that could also be measured non-destructively were much larger compared to the ones that were measured in the field. This difference might indicate the effects of the hyper arid conditions prevailing in Saint-Katherine. We also considered imputing missing values from less than 20% of the native species as extremely unreliable. Thus, we refrained from using trait values derived from databases and believe that the field - measured trait values (and their allometric derivatives) are more representative and relevant for this study.

Table 3 List of the 130 native and 33 alien plants with mean trait values and SD per species that were recorded in 96 stands

Species Status	Family	Scientific name	Number of individuals	Height (cm)		Biomass (kg)		SLA (cm2/g)	
				Mean	SD	Mean	SD	Mean	SD
Alien	Fabaceae	*Acacia_saligna*	34	463.88	268.28	75.55	64.41	42.42	12.12
Alien	Agavaceae	*Agave_americana*	7	131.66	51.07	2.66	0.57	3.67	0.08
Alien	Liliaceae	*Aloe_vera*	16	87	78.69	9	7.118	4.19	0.24
Alien	Amaranthaceae	*Amaranthus_caudatus*	45	38.33	14.84	0.33	0.33	48.49	10.88
Alien	Meliaceae	*Azadirachta_indica*	9	60	8.45	5	3.21	238.88	45.34
Alien	Chenopodiaceae	*Beta_vulgaris*	256	42.5	31.81	35	35.35	136.35	3.96
Alien	Theaceae	*Camellia_sinensis*	85	38.2	34.25	1.48	1.02	102.22	19.23
Alien	Casuarinaceae	*Casuarina_cunninghamiana*	3	700	424.26	80	56.56	52.92	4.11
Alien	Cactaceae	*Cereus_triangularis*	5	101	140.01	27	4.24		
Alien	Iridaceae	*Crocus_sativus*	46	10	5	0.05	0.045	133.82	172.79
Alien	Asteraceae	*Cynara_cardunculus*	1	60	0	4	0	32.66	0
Alien	Myrtaceae	*Eucalyptus_globulus*	55	1889.2	2864.2	144.7	147.8	39.73	12.73
Alien	Verbenaceae	*Lantana_camara*	3	123	34.21	5	0.62	67.5	3.76
Alien	Lamiaceae	*Mentha_longifolia*	420	71.7	35.26	4.25	3.73	231.16	66.12
Alien	Lamiaceae	*Mentha_spicata*	128	15.14	5.72	0.46	0.33	132.48	106.69
Alien	Aizoaceae	*Mesembryanthemum_acinaciforme*	10	10	3.56	25	5.42	297.42	38.42
Alien	Moringaceae	*Moringa_oleifera*	1	90	0	0.5	0	147.63	0
Alien	Scrophulariaceae	*Myoporum_laetum*	3	450	213.42	45	9.65		
Alien	Apocynaceae	*Nerium_oleander*	39	120.31	53.11	8.75	9.65	30.36	3.03
Alien	Solanaceae	*Nicotiana_rustica*	596	60	22.73	36.75	41.72	114.08	49.39
Alien	Cactaceae	*Opuntia_ficus.indica*	2	67.5	3.53	12	1.76	2.93	0.13
Alien	Lamiaceae	*Origanum_majorana*	31	27	13.94	0.97	0.78	126.34	28.51
Alien	Papaveraceae	*Papaver_somniferum*	12	61.16	25.65	0.24	0.21	73.43	3.1
Alien	Geraniaceae	*Pelargonium_peltatum*	4	67.5	74.24	1.5	0.7	40.24	4.77
Alien	Anacardiaceae	*Pistacia_lentiscus*	9	301.66	207.01	33.33	28.92	84.103	56.55
Alien	Lamiaceae	*Plectranthus_hadiensis*	200	60	0	80	20.37	140.88	76.21
Alien	Anacardiaceae	*Rhus_coriaria*	6	187.5	53.03	17.5	10.6	22.12	6.45
Alien	Rosaceae	*Rosa_gallica*	15	93.6	32.76	1.6	1.02	79.94	38.28
Alien	Lamiaceae	*Rosmarinus_officinalis*	271	83.44	56.98	23.15	33.79	39.62	21.53
Alien	Lamiaceae	*Salvia_fruticosa*	93	64.35	31.57	3.99	4.6	125.39	128.6
Alien	Simmondsiaceae	*Simmondsia_chinensis*	1	190	0	50	0	29	0
Alien	Cupressaceae	*Thuja_orientalis*	1	500	0	30	0	408.33	0

Table 3 continued

Species Status	Family	Scientific name	Number of individuals	Height (cm)		Biomass (kg)		SLA (cm2/g)	
				Mean	SD	Mean	SD	Mean	SD
Alien	Agavaceae	*Yucca_gloriosa*	9	172.5	48.55	9.66	10.67	145.29	20.47
Native	Asteraceae	*Achillea_fragrantissima*	91	53.13	27.77	1.62	0.44	23.12	78.15
Native	Fabaceae	*Alhagi_graecorum*	3	40	12.43	0.67	0	32.19	4.23
Native	Boraginaceae	*Alkanna_orientalis*	30	21.35	19.95	8.47	28.7	27.2	102.2
Native	Chenopodiaceae	*Anabasis_articulata*	15	34	10.35	1.58	0.26	2.598	0.52
Native	Primulaceae	*Anagallis_arvensis*	10	10	2.45	1.2	0.04	0.129	0
Native	Scrophulariaceae	*Anarrhinum_pubescens*	10	21	26.87	1.28	0.19	54.8	77
Native	Boraginaceae	*Anchusa_milleri*	20	7.25	2.217	1.28	0.11	0.772	0.973
Native	Asteraceae	*Artemisia_judaica*	93	80.95	31.8	1.9	0.39	4.985	6.578
Native	Poaceae	*Arundo_donax*	40	450	70.71	1.48	0.5	50.24	58.65
Native	Fabaceae	*Astragalus_spinosus*	2	266.5	330.2	2.19	0	5.797	6.26
Native	Fabaceae	*Astragalus_tribuloides*	16	2.667	0.816	1.15	0.49	10.93	15.33
Native	Asteraceae	*Atractylis_carduus*	1	4	0	1.42	0	7.222	0
Native	Poaceae	*Avena_barbata*	17	76.5	9.192	1.24	0.17	4.979	3.357
Native	Poaceae	*Avena_fatua*	10	130	70.46	1.55	0.06	1.371	0.03
Native	Lamiaceae	*Ballota_undulata*	7	35.2	18.66	1.64	0.22	2.182	1
Native	Acanthaceae	*Blepharis_attenuata*	1	7	0	1.53	0	1.101	0
Native	Poaceae	*Brachypodium_distachyon*	23	16.67	5.774	1.6	0.48	1.382	0.507
Native	Poaceae	*Bromus_pectinatus*	24	23.25	11.32	1.86	0.16	1.365	0.871
Native	Resedaceae	*Caylusea_hexagyna*	15	148.4	375.5	1.85	0.52	6.647	12.31
Native	Asteraceae	*Centaurea_scoparia*	10	35.75	19.81	1.98	0.35	7.637	11.17
Native	Asteraceae	*Centaurea_sinaica*	3	15	5.35	1.85	0.03	2.349	0.13
Native	Chenopodiaceae	*Chenopodium_album*	45	16.67	6.853	1.17	0.6	8.444	13.93
Native	Chenopodiaceae	*Chenopodium_murale*	8	15.5	0.707	0.54	0.4	17.2	24.1
Native	Asteraceae	*Chiliadenus_montanus*	13	22.5	2.887	1.52	0.73	44.34	48.59
Native	Cleomiaceae	*Cleome_arabica*	30	72	23.12	1.84	0.36	2.241	0.895
Native	Cleomiaceae	*Cleome_droserifolia*	3	14	6.42	1.59	0.02	1.203	0.01
Native	Lamiaceae	*Clinopodium_serpyllifolium*	1	80	0	1.92	0	3.418	0
Native	Fabaceae	*Colutea_istria*	5	216.7	11.55	1.53	0.36	6.044	0.606
Native	Asteraceae	*Conyza_aegyptiaca*	22	31	15.1	1.45	0.32	0.948	0.506
Native	Asteraceae	*Conyza_bonariensis*	4	37	4.243	1.02	0.29	0.965	0.137
Native	Cucurbitaceae	*Cucumis_prophetarum*	2	3	0.21	1.85	0.03	3.548	0.11
Native	Solanaceae	*Datura_ferox*	1	20	0	0.61	0	33.22	0
Native	Solanaceae	*Datura_stramonium*	1	20	0	0.8	0	0.842	0
Native	Poaceae	*Digitaria_sanguinalis*	10	60.5	7.778	1.48	0.87	1.664	0.198
Native	Brassicaceae	*Diplotaxis_acris*	39	41	23.12	1.46	0.32	2.478	1.724
Native	Brassicaceae	*Diplotaxis_harra*	10	17.5	10.61	1.12	0.03	0.408	0.087
Native	Asteraceae	*Echinops_glaberrimus*	2	150	45.32	1.47	0.11	2.732	0.36
Native	Asteraceae	*Echinops_spinosus*	5	41.5	46.36	2.1	0.51	16.36	23.26
Native	Geraniaceae	*Erodium_laciniatum*	4	3.233	0.252	1.42	0.31	1.185	1.582
Native	Brassicaceae	*Eruca_sativa*	4	25	10.21	1.14	0.02	0.976	0.01
Native	Euphorbaiceae	*Euphorbia_hirta*	5	4	1.22	1.01	0.03	0.875	0.01
Native	Euphorbaiceae	*Euphorbia_obovata*	3	10	4.65	1.44	0.02	0.373	0.02

Table 3 continued

Species Status	Family	Scientific name	Number of individuals	Height (cm)		Biomass (kg)		SLA (cm2/g)	
				Mean	SD	Mean	SD	Mean	SD
Native	Euphorbaiceae	*Euphorbia_peplus*	10	10	4.23	2	0.26	1.052	0.01
Native	Euphorbaiceae	*Euphorbia_retusa*	7	27.67	5.033	1.78	0.08	1.965	1.19
Native	Zygophyllaceae	*Fagonia_arabica*	34	16.65	10.2	8.57	28.7	2.16	1.538
Native	Zygophyllaceae	*Fagonia_bovie*	3	30	0	1.53	0.08	0.966	0.911
Native	Zygophyllaceae	*Fagonia_bruguieri*	1	10	0	2.93	0	36.56	0
Native	Zygophyllaceae	*Fagonia_mollis*	95	16.03	6.301	4.83	19.2	4.753	9.311
Native	Brassicaceae	*Farsetia_aegyptia*	2	35.5	3.536	2.13	0.75	26.14	34.39
Native	Moraceae	*Ficus_carica*	1	100	0	1.69	0	4.295	0
Native	Moraceae	*Ficus_palmata*	6	135	68.56	1.7	0.38	27.84	43.78
Native	Apiaceae	*Foeniculum_vulgare*	20	62.9	60.07	1.42	0.27	23.05	44.3
Native	Urticaceae	*Forsskaolea_tenacissima*	3	128	116	1.47	0.17	3.84	3.404
Native	Asteraceae	*Glebionis_coronaria*	2	17	4.23	1	0.01	0.707	0.01
Native	Chenopodiaceae	*Haloxylon_salicornicum*	5	50	12.24	1.96	0.02	3.374	1.41
Native	Boraginaceae	*Heliotropium_arbainense*	10	12.17	2.563	1.28	0.29	20	45.74
Native	Poaceae	*Hordeum_marinum*	107	11.45	3.616	1.51	0.61	7.646	14.82
Native	Solanaceae	*Hyoscyamus_boveanus*	2	24.5	2.121	1.5	0.5	2.441	0.45
Native	Solanaceae	*Hyoscyamus_pusillus*	1	7	0	1.66	0	123.4	0
Native	Asteraceae	*Iphiona_mucronata*	4	15.5	3.536	1.76	0.27	2.853	0.129
Native	Asteraceae	*Iphiona_scabra*	5	15	NA	1.92	NA	1.312	NA
Native	Juncaceae	*Juncus_bufonius*	5	63	NA	1.93	NA	2.238	NA
Native	Asteraceae	*Lactuca_serriola*	3	46	NA	1.46	NA	3.072	NA
Native	Lamiaceae	*Lamium_amplexicaule*	7	14	3.65	0.27	0.01	34.11	14.23
Native	Asteraceae	*Launaea_nudicaulis*	2	9	1.414	1.74	0.02	0.596	0.555
Native	Asteraceae	*Launaea_spinosa*	5	23.33	8.505	1.5	0.12	0.903	0.433
Native	Lamiaceae	*Lavandula_coronopifolia*	1	90	0	1.36	0	3.827	0
Native	Asteraceae	*Leysera_leyseroides*	4	14	0	1.75	0.08	1.911	1.212
Native	Plumbaginaceae	*Limonium_lobatum*	2	10	NA	1.47	NA	1.992	NA
Native	Plumbaginaceae	*Limonium_pruinosum*	7	21	3.606	1.39	0.33	1.793	0.419
Native	Plumbaginaceae	*Limonium_sinuatum*	2	35	10.23	1.17	0.01	3.441	2.52
Native	Fabaceae	*Lotononis_platycarpa*	1	2	0	1.1	0	1.628	0
Native	Solanaceae	*Lycium_shawii*	1	110	0	1.62	0	4.201	0
Native	Malvaceae	*Malva_neglecta*	39	6.308	2.323	1.16	0.57	16.1	31.37
Native	Malvaceae	*Malva_parviflora*	3	12	3.14	1.23	0.04	5.679	1.01
Native	Brassicaceae	*Matthiola_arabica*	17	27.67	14.11	14.9	39.4	2.632	1.14
Native	Brassicaceae	*Matthiola_longipetala*	37	45.38	12.74	1.75	0.59	43.77	117.7
Native	Brassicaceae	*Morettia_canescens*	3	3.25	0.354	1.79	0.27	4.842	1.655
Native	Solanaceae	*Nicotiana_glauca*	1	160	0	1.19	0	5.504	0
Native	Resedaceae	*Ochradenus_baccatus*	20	92.64	30.44	1.65	0.21	3.58	1.196
Native	Oleaceae	*Olea_europaea*	20	137.5	59.61	1.62	0.26	12.15	25.92
Native	Resedaceae	*Oligomeris_linifolia*	3	65	49.5	2.27	0.17	5.301	0.752
Native	Asteraceae	*Onopordum_ambiguum*	6	83.33	47.26	1.64	0.17	3.709	0.798
Native	Lamiaceae	*Origanum_syriacum*	214	21	17.18	1.81	0.8	52.22	60.96

Table 3 continued

Species Status	Family	Scientific name	Number of individuals	Height (cm)		Biomass (kg)		SLA (cm2/g)	
				Mean	SD	Mean	SD	Mean	SD
Native	Orobanchaceae	*Orobanche_palaestina*	3	30	4.54	0.25	0.01	32.86	6.47
Native	Oxalidaceae	*Oxalis_corniculata*	10	23	8.46	2.05	0.54	26.68	34.91
Native	Papaveraceae	*Papaver_decaisnei*	3	30	5.36	1.45	0.01	0.931	0.02
Native	Zygophyllaceae	*Peganum_harmala*	21	34.38	19.49	1.76	0.38	2.688	1.669
Native	Lamiaceae	*Phlomis_aurea*	3	132.5	17.68	1.74	0.01	5.061	1.449
Native	Poaceae	*Phragmites_australis*	10	134	45.21	1.63	0.03	107.9	35.32
Native	Plantagonaceae	*Plantago_sinaica*	9	14.67	4.041	1.57	0.11	0.754	0.322
Native	Portulacaceae	*Portulaca_oleracea*	13	20	5	1.17	0.17	0.955	0.697
Native	Asteraceae	*Pulicaria_incisa*	7	21.67	2.887	1.5	1.12	31.9	28.25
Native	Asteraceae	*Pulicaria_inuloides*	2	26.5	9.192	1.45	0.2	2.178	0.734
Native	Asteraceae	*Pulicaria_undulata*	15	41.5	8.347	1.25	0.76	107.2	210.7
Native	Tamaricaceae	*Reaumuria_alternifolia*	2	16.5	2.121	2.18	0.04	2.298	2.921
Native	Resedaceae	*Reseda_muricata*	9	17.75	4.031	1.6	0.21	1.196	1.257
Native	Resedaceae	*Reseda_pruinosa*	5	18.33	1.155	1.87	0.05	2.351	1.882
Native	Fabaceae	*Retama_raetam*	10	172.2	48.61	1.61	0.53	9.9	8.156
Native	Rosaceae	*Rosa_arabica*	1	80	0	1.27	0	2.015	0
Native	Lamiaceae	*Salvia_multicaulis*	14	15.5	9.983	1.66	0.27	1.933	0.79
Native	Asteraceae	*Seriphidium_herba.album*	39	33.8	19.09	1.67	0.49	11.77	30.2
Native	Brassicaceae	*Sisymbrium_erysimoides*	32	13.17	5.913	1.55	0.48	4.349	7.333
Native	Brassicaceae	*Sisymbrium_irio*	6	22.5	17.68	1.48	0.3	3.691	5.056
Native	Solanaceae	*Solanum_nigrum*	15	41.29	15.38	1.48	0.28	16.84	40.24
Native	Solanaceae	*Solanum_sinaicum*	3	58	2.828	1.45	0.2	2.373	0.281
Native	Solanaceae	*Solanum_villosum*	9	31	3.606	1.09	0.75	13.85	20.34
Native	Asteraceae	*Sonchus_asper*	3	7	0	0.9	0.6	11.89	18.72
Native	Asteraceae	*Sonchus_oleraceus*	35	8	4.32	1.12	0.51	22.36	44.88
Native	Poaceae	*Sorghum_virgatum*	12	78	7.071	1.46	0.33	1.93	1.285
Native	Lamiaceae	*Stachys_aegyptiaca*	17	32.6	5.727	1.48	0.27	1.599	0.846
Native	Poaceae	*Stipa_arabica*	3	23	0.01	1.67	0.04	3.443	0.03
Native	Poaceae	*Stipa_capensis*	10	23	5.67	1.14	0.02	1.008	0.01
Native	Poaceae	*Stipa_parviflora*	20	61.5	54.45	1.88	0.84	16.89	22.7
Native	Poaceae	*Stipagrostis_ciliata*	8	13	1.414	1.91	0.12	0.195	0.262
Native	Chenopodiaceae	*Suaeda_aegyptiaca*	4	34	9.34	1.46	6.25	2.003	0.02
Native	Poaceae	*Taeniatherum_caput.medusae*	8	30.5	23.84	1.66	0.72	10.32	15.85
Native	Tamaricaceae	*Tamarix_aphylla*	1	200	0	1.34	0	10.84	0
Native	Tamaricaceae	*Tamarix_nilotica*	4	203.8	26.89	1.85	0.21	9.057	1.725
Native	Asteraceae	*Tanacetum_sinaicum*	1	250	0	1.93	0	8.136	0
Native	Lamiaceae	*Teucrium_polium*	7	21.33	3.786	1.64	0.12	4.74	4.619
Native	Zygophyllaceae	*Tribulus_terrestris*	3	3	0.062	1.23	0.02	0.885	0.01
Native	Boraginaceae	*Trichodesma_africanum*	12	21	6.663	1.48	0.47	8.627	12.15
Native	Scrophulariaceae	*Verbascum_sinaiticum*	37	63.73	67.85	1.52	0.55	52.11	127.8
Native	Fabaceae	*Vicia_monantha*	5	10	2.43	1.95	0.02	1.381	0.01
Native	Solanaceae	*Withania_somnifera*	6	93.83	32.13	1.69	0.29	3.627	1.561

Table 3 continued

Species Status	Family	Scientific name	Number of individuals	Height (cm)		Biomass (kg)		SLA (cm2/g)	
				Mean	SD	Mean	SD	Mean	SD
Native	Brassicaceae	*Zilla_spinosa*	82	61.63	28.97	5.25	20	23.29	71.15
Native	Rhamnaceae	*Ziziphus_spina.christi*	6	95.6	41.79	1.41	0.39	7.751	10.46
Native	Zygophyllaceae	*Zygophyllum_coccineum*	1	23	0	1.86	0	2.846	0

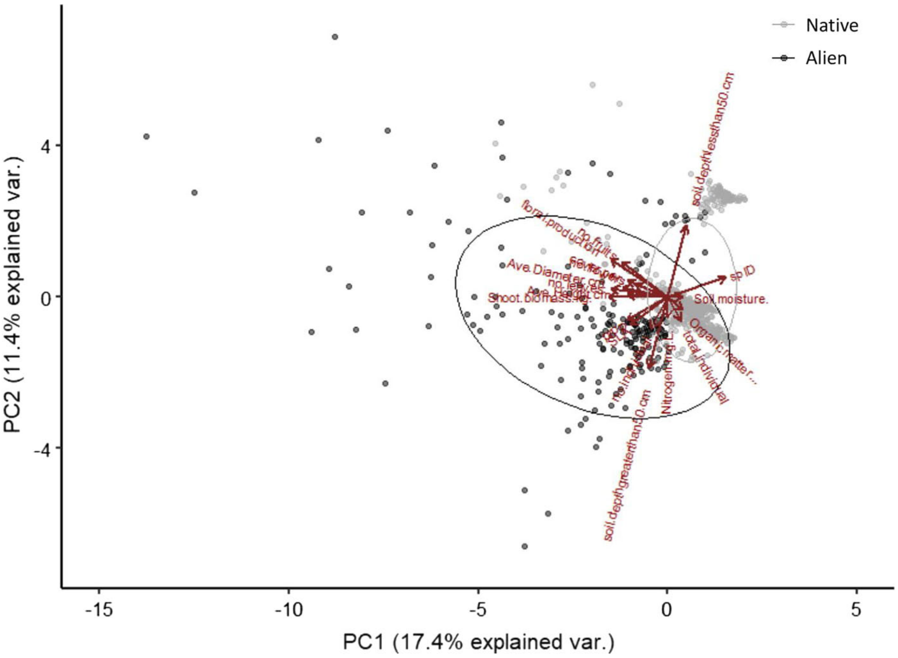

Fig. 5 PCA showing the contribution of the soil resources and functional traits of the two axes of the PCA in explaining the co-occurrence of aliens and natives that resulted in observed overlapped niche (similarity) and differential niche (dissimilarity)

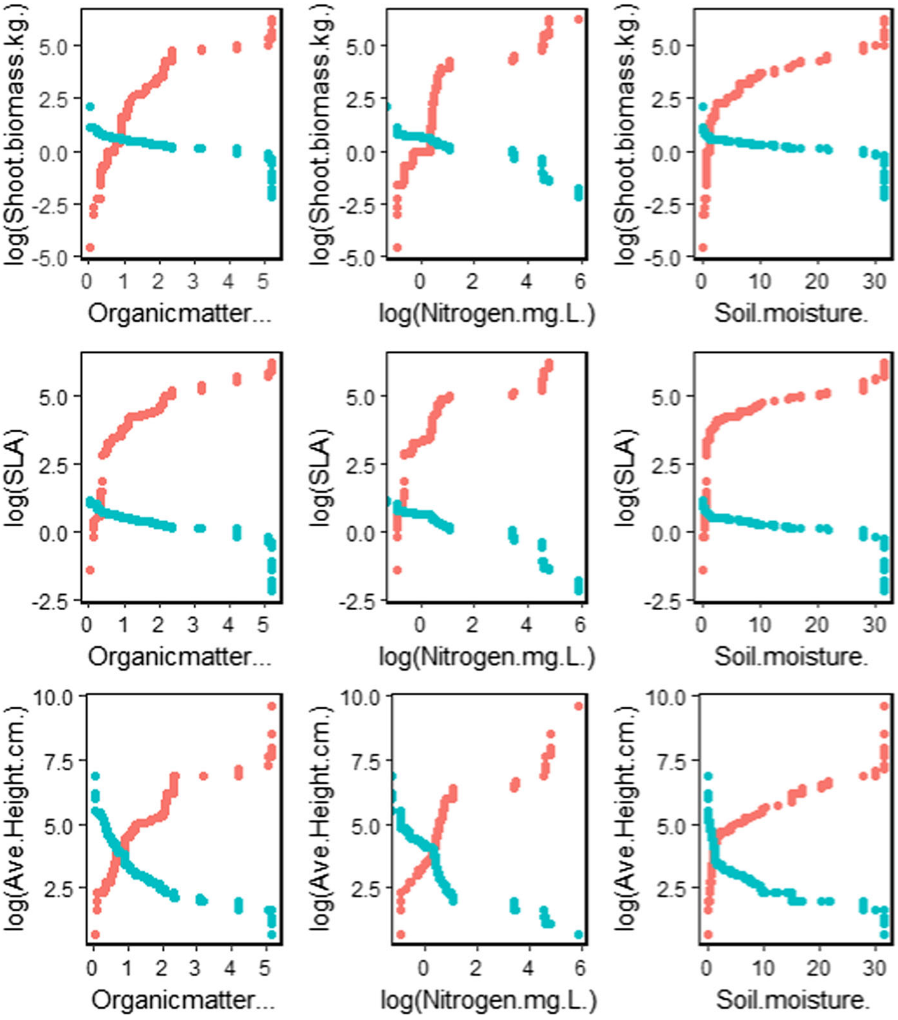

Fig. 6 Observed trait differences (Above-ground biomass-specific leaf area (SLA)—height) among alien (red dots) and native (blue dots) plant species in response to soil resources (nitrogen, organic matter, soil moisture) in SKP

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