

Invasive species differ in key functional traits from native and non-invasive alien plant species

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Abstract:

Questions:

Invasive species establish either by possessing traits, or trait trade-offs similar to native species, suggesting pre-adaptation to local conditions; or by having a different suite of traits and trait trade-offs, which allow them to occupy unfilled niches. The trait differences between invasives and non-invasives can inform on which traits confer invasibility. Here, we ask: (a) are invasive species functionally different or similar to native species? (b) which traits of invasives differ from traits of non-invasive aliens and thus confer invasibility? and (c) do results from the sub-Antarctic region, where this study was conducted, differ from findings from other regions?

Location:

Sub-Antarctic Marion Island

Methods:

We measured 13 traits of all terrestrial native, invasive and non-invasive alien plant species. Using principal components analysis and phylogenetic generalized least-squares models, we tested for differences in traits between invasive (widespread alien species) and native species. Bivariate trait relationships between invasive and native species were compared using standardized major axis regressions to test for differences in trait trade-offs between the two groups. Second, using the same methods, we compared the traits of invasive species to non-invasive aliens (alien species that have not spread).

Results:

Between invasive and native species, most traits differed, suggesting that the success of invasive species is mediated by being functionally different to native species. Additionally, most bivariate trait relationships differed either in terms of their y-intercept or their position on the axes, highlighting that plants are positioned differently along a spectrum of shared trait trade-offs. Compared to non-invasive aliens, invasive species had lower plant height, smaller leaf area, lower frost tolerance, and higher specific leaf area, suggesting that these traits are associated with invasiveness. The findings for the sub-Antarctic corresponded to those of other regions, except lower plant height which provides a competitive advantage to invaders in the windy sub-Antarctic context.

Conclusion:

Our findings support the expectation that trait complexes of invasive species are predominantly different to those of coexisting native species, and that high resource acquisition and low defence investment are characteristic of invasive plant species.

Keywords: above-ground traits; below-ground traits; climate change; soil nutrients; trait differences; trait similarities

Abbreviations:

SLA – specific leaf area

SRL – specific root length

Running head: Plants that invade new environments are functionally different

1. Introduction

Globally, the problem of invasive species continues to worsen (Seebens et al., 2017). Identifying whether invasiveness is associated with specific traits is important for predicting which species may become invasive if introduced, and for managing established alien species (Pyšek & Richardson, 2007). These trait-based approaches to understanding invasion success rely on comparing the traits of invasive species to native, or to non-invasive alien species in a given environment, or within a taxon (van Kleunen, Weber, & Fischer, 2010).

A comparison of functional traits between invasive (widespread alien species) and native (species living within their natural range in the past or present) species provides an indication of how invasive species exploit niches and resources in new environments compared to the native community (Lambdon, Lloret, & Hulme, 2008), and thus how traits influence community assembly (Hulme & Bernard-Verdier, 2017). Two contrasting hypotheses about the traits that underlie invasive species' success have emerged from such comparisons: the 'phenotypic divergence' and 'phenotypic convergence' hypotheses (Ordonez et al., 2010). Phenotypic divergence stems from the concept of limiting similarity, proposing that successful invasive species possess traits different from native species, which facilitates invasion by enabling invaders to exploit empty niches (MacArthur & Levins, 1967; Ordonez, 2014; van Kleunen et al., 2010). Phenotypic convergence is based on the concept of habitat filtering (Cornwell, Schwilk, & Ackerly, 2006), where invasive species are pre-adapted to the introduced habitat. Strong environmental pressures limit the suite of species that can exist in an environment, resulting in trait similarity among native and invasive species (Ordonez, Wright, & Olf, 2010). Therefore, both hypotheses assume that the success of alien species is predicted from how invasive species compare functionally with co-occurring native species. Support exists for both the phenotypic divergence (Cleland, 2011; Gross, Borger, Duncan, & Hulme, 2013; Knapp & Kühn, 2012) and convergence (e.g., Drenovsky, Khasanova, & James, 2012; Lambdon et al., 2008; Leishman, Thomson, & Cooke, 2010) hypotheses. Furthermore, these two hypotheses are not necessarily mutually exclusive within a given community: some traits may display convergence and others divergence (e.g., Divíšek et al., 2018; Tecco et al., 2013).

A trait comparison between invasive and non-invasive alien species (aliens that have established in a particular area but have not become invasive) explores which traits predispose some alien species to become invasive (Hamilton et al., 2005), and is recommended as more effective than the invasive–native comparison for identifying traits associated with invasiveness (van Kleunen, Dawson, & Maurel, 2015). The outcome of this comparison is

pertinent for management applications, including formulating screening procedures (van Kleunen et al., 2010). The idea of the existence of a set of traits that confers invasiveness has been subject to some scepticism (Tecco, Díaz, Cabido, & Urcelay, 2010), with context-dependency in traits frequently reported as a major limitation to a broad application of this approach (Kueffer, Pyšek, & Richardson, 2013; Leffler, James, Monaco, & Sheley, 2014). Nonetheless, certain traits (e.g., increased height, use by humans, early and extended flowering, and high specific leaf area [SLA]), tested across a range of environmental and experimental conditions between invasive and non-invasive alien species, frequently emerge as being associated with invasiveness (Gallagher, Randall, & Leishman, 2014; Pyšek & Richardson, 2007).

Differences between groups of species can also be assessed in terms of trait trade-offs, which describe the functional compromises that plants make (Heberling & Fridley, 2013; Leishman, Haslehurst, Ares, & Baruch, 2007). Previous work found that different groups of plants (e.g., natives and invasives) exhibit the same general strategies: increases in one trait result in consistent decreases in another trait, suggesting convergent evolution in plant strategies (Reich, 2014; Wright et al., 2004). However, native and invasive species exhibit shifts along the same trade-off axis, with invasive species being positioned on the rapid growth end of the leaf economics spectrum (Leishman et al., 2007, 2010). Shifts along trade-off axes between native and invasive species could be considered a further indication of phenotypic divergence, while similarities would support convergence. Similarly, shifts along trade-off axes between invasive and non-invasive alien species would indicate which end of trade-off spectra sets invasive species apart from non-invasive aliens, and may thus explain the former's success.

Few studies have simultaneously compared traits between native, invasive and non-invasive alien species (although see van Kleunen et al., 2010). Given that alien species have to respond to the same biotic and abiotic filters as native species in their introduced range (for which information is often missing at regional or larger spatial scales), analyses at the local-community scale involving whole plant communities are recommended. This would allow for the assessment of the role traits play in assembly and could improve predictions of communities to plant invasions (Hulme and Bernard-Verdier, 2017; van Kleunen et al., 2015). Yet, such studies are rarely undertaken (Hulme and Bernard-Verdier, 2017; van Kleunen et al., 2015).

The remote sub-Antarctic islands offer a useful, and as yet unexplored, study system for examining the role of functional traits in plant invasions. Often, trait-based studies are confounded by extensive human influence on the environment, where it may become difficult to distinguish whether species are spreading because of the traits they possess or as a

consequence of human disturbance (Hamilton et al., 2005). In contrast to other terrestrial systems, the sub-Antarctic Islands have experienced little human disturbances (De Villiers et al., 2006). Nevertheless, biological invasions are one of the most pressing problems in the region (Frenot et al., 2005). The low diversity generally found in island systems (representing many potentially unfilled niches), renders islands more vulnerable to invasions than continental systems (Moser et al., 2018). As a result, determining which alien species are likely to both establish and spread on the sub-Antarctic islands is a key concern for the management of the region, but has been poorly explored to date (Greve, Mathakutha, Steyn, & Chown, 2017).

Here, we used sub-Antarctic Marion Island as a study system to test several key hypotheses. First, we tested the contrasting predictions of the ‘phenotypic divergence’ and ‘phenotypic convergence’ hypotheses by comparing traits and trait correlations of invasive and native species. The low diversity on Marion Island suggests it possesses unused niche opportunities that alien species could occupy, leading to phenotypic divergence. On the other hand, given the fairly harsh environmental conditions of the island, one may expect that certain traits are necessary to survive in that environment, leading to phenotypic convergence. Therefore, we had no a priori expectations that either limiting similarity or habitat filtering was the main driving force. Second, we compared the traits of invasive and non-invasive aliens to test if traits can distinguish invasive alien species from non-invasive aliens. We also sought further generality in how traits differ among the three groups of species by comparing, although not exhaustively, the findings from this study to those found elsewhere to obtain a better understanding of what traits might promote invasion. This study is one of very few to explore such differences for an entire flora of a mostly closed system and at a local scale (i.e., the scale at which plants interact with each other).

Our study also provides an alien risk assessment for Marion Island and can inform management considerations for the greater sub-Antarctic region across which many alien and invasive plant species are shared (Greve, Gremmen, Gaston, & Chown, 2005; Leihy, Duffy, & Chown, 2018).

2. Materials and methods

2.1. STUDY AREA

Sub-Antarctic Marion Island (46°54' S, 37°51' E) is the larger of the two islands in the Prince Edward Island group (Chown & Froneman, 2008). The sub-Antarctic islands, including Marion Island, are characterised by an aseasonal climate with cool, wet, windy and cloudy conditions (le Roux & McGeoch, 2008). Marion Island supports a tundra vegetation type (Smith &

Stenkamp, 2001). Due to its abiotically-extreme climate, isolation and relatively recent origin (c. 500 000 years old; McDougall, Verwoerd, & Chevallier, 2001), Marion Island is a species-poor system, harbouring only 22 native and 18 introduced vascular plant species, seven of which have become widespread across the island and are considered invasive (Gremmen & Smith, 2008). All extant alien plants on Marion Island have been introduced accidentally (Greve et al., 2017).

Mean annual rainfall on Marion Island has decreased by approximately 1,000 mm p.a., while the mean annual temperature has risen by 1°C, since the 1960s (le Roux & McGeoch, 2008). This amelioration of the climate is thought to especially benefit alien species (Frenot et al., 2005) and may increase the probability of successful establishment by introduced species (Frenot et al., 2005; Greve et al., 2017).

2.2. SPECIES SELECTION

Functional traits were measured on all extant terrestrial angiosperms (with the exception of one non-invasive alien that was first discovered in 2016) on Marion Island (Appendix S1). Species were classified as native, non-invasive alien or invasive based on Gremmen & Smith (2008). The presence of both non-invasive and invasive alien species on the island is a result of human introductions (Gremmen & Smith, 2008). Aliens that survive where they were first introduced, but have not spread, were classified as noninvasive aliens (Blackburn et al., 2011). In contrast, alien species that have spread a considerable distance from the initial point of introduction were considered invasive (Blackburn et al., 2011). The median residence time of both invasive and non-invasive alien species is 53 years, although mean residence time of invaders is higher than that of non-invasive aliens (Appendix S2). Therefore, we are fairly confident that our classification as invasive and noninvasive alien is reliable.

2.3. SAMPLING DESIGN

Field sampling was conducted on Marion Island in April and May 2015 and 2016. Plants were collected from different substrates and vegetation types, across altitudinal gradients and from different regions of the island (Appendices S3 and S4). Details of the sampling procedure, including the number of plants sampled for each trait by species, are given in Appendices S5 and S6. A trait value for each species was calculated by averaging data for a species' trait across all sampling localities (Appendix S7). Data for several traits were also compiled from published and unpublished literature sources (details below and in Appendices S8 and S9).

Table 1. Functional traits used to test differences between the native, non-invasive alien and invasive plant species of Marion Island.

Plant trait	Data type and attribute
Whole plant traits	
Life history	Nominal (1. Annual 2. Perennial 3. Annual and Perennial)
Growth form	Nominal (1. Graminoid 2. Herbaceous 3. Succulent 4. Semi-woody)
Plant height	Continuous (mm)
Leaf traits	
Leaf area	Continuous (mm ²)
Specific leaf area (SLA)	Continuous (mm ² mg ⁻¹)
Leaf toughness	Continuous (N)*
Electrolyte leakage	Continuous (μS g ⁻¹)
Leaf N and P concentration	Continuous (mg g ⁻¹)*
Leaf chlorophyll content	Continuous (mg m ⁻²)*
Below-ground traits	
Specific root length	Continuous (mg ⁻¹)*
Root diameter	Continuous (mm)*
Regenerative traits	
Dispersal mode	Nominal (1. Unassisted dispersal 2. External animal transport 3. Dispersal by water)

*Compared between native and invasive species only (i.e. excluding non-invasive alien species).

2.4. SELECTION OF TRAITS

Thirteen traits, including a combination of whole plant, leaf, belowground and regenerative traits (Table 1), were obtained for native and alien plant species on Marion Island. Each of these traits accounts for different plant properties and all were selected due to their association with community functioning and assembly processes (Appendix S10; Ordóñez, 2014). More importantly, the traits were selected based on their relevance in the sub-Antarctic environment (following van Kleunen et al., 2015). A description and measurement methods for each trait are provided in Appendix S10.

Life history, growth form, and dispersal mode data were available for all species (Appendix S7) and were selected as proxies for species' dispersal capabilities and establishment success (Pérez-Harguindeguy et al., 2013). Leaf area, leaf toughness, frost sensitivity (here measured as electrolyte leakage) and root diameter are conservative traits related to plant defence, slow growth, and resource conservation (Pérez-Harguindeguy et al., 2013). These traits were selected as proxies for species persistence and tolerance to the abiotically severe environments of Marion Island. Height, specific leaf area, leaf nitrogen (N) and phosphorus (P) concentration, leaf chlorophyll content, and specific root length (SRL) were selected as proxies for rapid resource acquisition and growth (Pérez-Harguindeguy et al., 2013). Such traits are useful for analysing how invasive species become successful relative to co-occurring natives and non-invasive aliens, as alien success is associated with how well invasive species exploit their new environment (van Kleunen et al., 2015).

The collection, measurement, and recording of traits mostly followed the guidelines of Pérez-Harguindeguy et al. (2013) (see Appendix S11). In all cases, sampling was conducted on reproductively mature, healthy individuals growing in unshaded habitats. In addition, most of the traits considered here have been previously used in studies comparing traits of alien and native species, facilitating the comparison between the findings from this study and those reported in the literature.

2.5. STATISTICAL ANALYSIS

To identify general trends in functional traits of invasive and native species, and to understand how these traits were related in a multivariate context, a principal components analysis (PCA) was performed using the `prcomp` function in R (Baayen, 2007). Traits collected from published studies (leaf N and P concentration, SRL and root diameter) were not included in the analysis due to too many missing values (Appendix S12). Separate t tests were performed to test for overall differences in the traits of invasive and native species along the two PCA axes. Another PCA was performed for invasive and non-invasive alien species for the traits that could be measured for all non-invasive aliens: height, leaf area, SLA and electrolyte leakage. This

analysis was run separately because fewer traits were available for this comparison. Continuous traits were log-transformed prior to ordination analyses.

We then tested whether individual traits differed between invasive and native, and between invasive and non-invasive alien species. For categorical data, Fisher's exact tests were performed for each trait (i.e., life history, growth form and dispersal mode). To compensate for the low sample size, this method uses simulated p-values based on 2000 Monte Carlo permutations (Hope, 1968).

For continuous traits, phylogenetic generalized least-squares models (PGLSs) were run using trait means per species (R package *caper*, Orme 2013). One model was run for each trait, with the trait value as response variable, and invasion status (invasive, native or non-invasive alien) as the predictor variable. Unlike standard statistical tests used in comparative studies, a PGLS takes the phylogenetic non-independence of species into consideration (Orme 2013). A phylogenetic tree of our study species (Appendix S13) was generated from Zanne et al. (2014) using the *ape* package in R (Paradis et al., 2012). Congeneric substitutes were used for species not available in Zanne et al. (2014). Variables were square-root transformed (SLA), log transformed (height, leaf area, leaf chlorophyll content and electrolyte leakage), or negative inversely transformed (leaf toughness, leaf N and P concentration, SRL, and root diameter) to meet the assumptions of PGLS models. To account for multiple comparisons in these PGLS analyses, we used the Benjamini–Hochberg procedure, which adjusts the significance level (p-value) to reduce the risk of a type I error in multiple comparisons (McDonald, 2014). PGLS analyses were conducted for a subset of traits (Appendix S14).

Because our data were not suited for running mixed models to take into consideration the influence of site-specific factors on trait variation (because some trait means were obtained from the literature, and there were large differences in sample sizes between species), PGLS analyses comparing invasive and native species were re-run using trait data only collected from plants collected from the low altitude nutrient-rich coastal zone (Appendix S15), which supports the highest abundance of invasive species (Hausmann, Rudolph, Kalwij, & McIntyre, 2013). This allowed us to test trait differences between invasive and native species while controlling for environmental variation that could have affected trait expression. These analyses could only be conducted for a subset of traits that were available for a sufficient number of species (Appendix S15). Most non-invasive aliens do not occur in the coastal zone; therefore, analyses were not repeated for the invasive vs non-invasive alien comparison.

Standardized major axis (SMA) regressions were implemented to test whether the plant groups [native, invasive and, for selected traits (see results), non-invasive alien species] differ in the nature of trait-correlations, i.e., the trade-offs exhibited between traits. Standardized

major axis regressions were run using the *smatr* package in R to describe the best-fit scaling relationship between pairs of traits on log–log axes using trait mean values per species (Warton, Wright, Falster, & Westoby, 2006). SMA regressions minimize residual variance in both x and y dimensions and thus estimate bivariate relationships with greater precision than major axis regressions or classical regression methods (Warton et al., 2006). The SMA analyses tested for differences in slope, for shifts in the y-intercept and for shifts in location on the x-axis of the best-fitting bivariate relationships between two traits of the three plant groups (Appendix S16).

All statistical analyses were performed in R version 3.3.1 (R Core Team, 2014).

3. Results

3.1. MULTIVARIATE ANALYSES

The first two axes of the PCA between native and invasive species explained 79% of the variation in the data set. PCA axis 1 (54% of variance explained, Figure 1a) separated invasive and native species ($t = -2.60$, $df = 19$, $p = 0.02$) (Figure 1b). Invasive species were negatively correlated with leaf toughness, and positively correlated with SLA and electrolyte leakage (Figure 1a), indicating a tendency towards acquisitive (tender and frost-sensitive leaves, with high SLA) traits in invasive species, while native species displayed conservative (tough, frost-tolerant leaves, with low SLA) plant trait syndromes. PCA axis 2 (25% of variance explained) was most strongly positively correlated with height and leaf area (Figure 1a), but did not separate out native and invasive species ($t = 1.81$, $df = 19$, $p = 0.09$) (Figure 1c). The first two axes of the PCA between invasive and non-invasive alien species cumulatively explained 86% of the variance but did not separate invasive species from non-invasive aliens: Axis 1 ($t = -0.59$, $df = 10$, $p = 0.58$), Axis 2 ($t = 1.70$, $df = 10$, $p = 0.13$) (Appendix S17). These analyses did not account for phylogenetic non-independence.

3.2. UNIVARIATE COMPARISONS

For whole-plant and regenerative traits, only life history differed between invasive and native species (Figure 2). Most invasive species displayed either the perennial or annual-and-perennial life history strategy while native species were predominantly perennial (Figure 2a). Invasive and native species did not show any significant differences in growth form, dispersal mode (Figure 2b, c) or height (Figure 3a).

Significant differences between invasive and native species were, however, found in all leaf traits (Figure 3b–h). Compared to native species, invasive species had significantly smaller leaves (also after removing *Pringlea antiscorbutica* as an outlier; not shown), higher SLA and

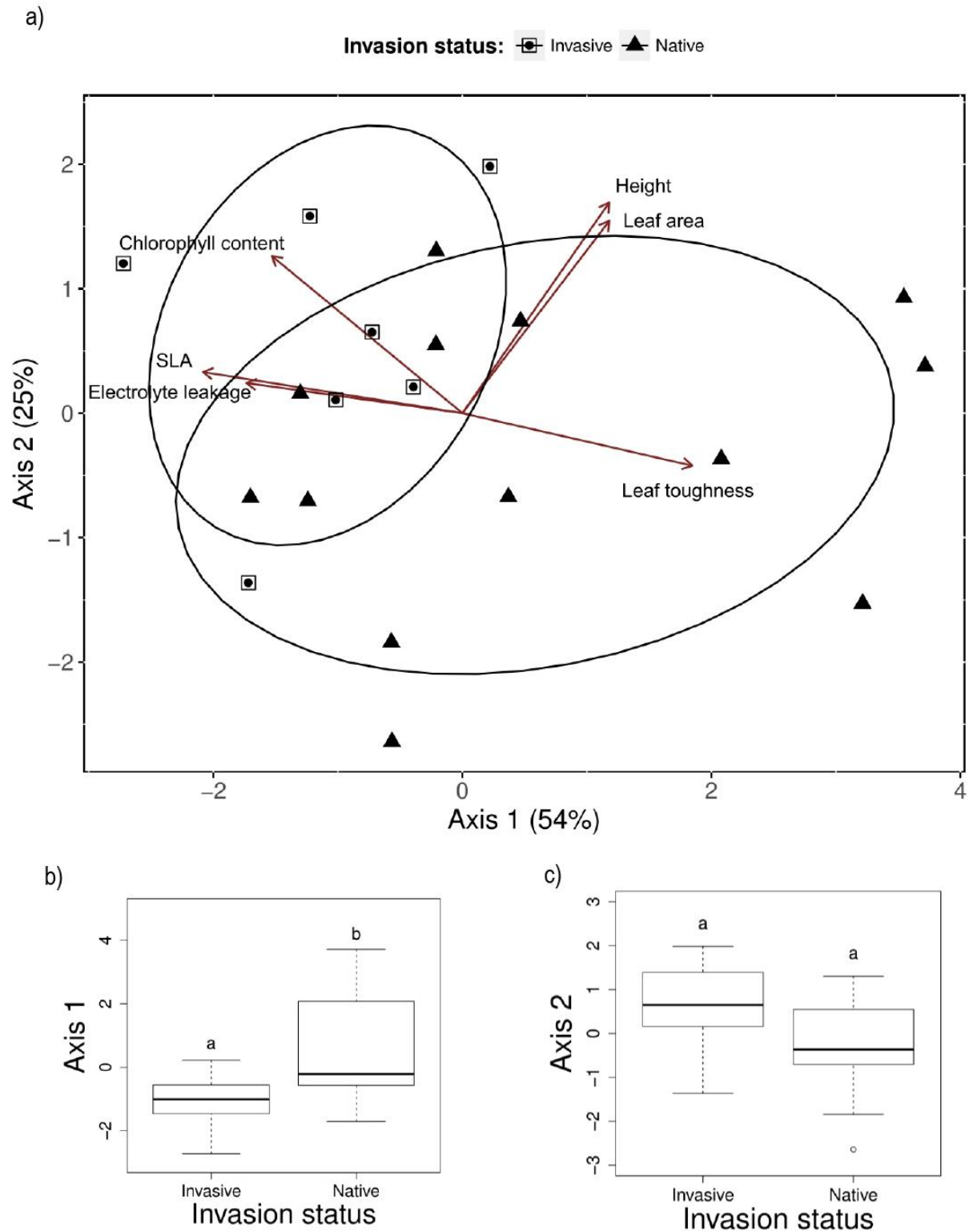


Figure 1. (a) Ordination of invasive ($n = 7$) and native ($n = 13$) species using principal components analysis (PCA) based on six variables (trait means): height, leaf area, specific leaf area (SLA), leaf chlorophyll content, electrolyte leakage (as an indicator of frost sensitivity), and leaf toughness. Ellipses are plotted to indicate the 95% confidence interval for each group. Axes 1 and 2 cumulatively explained 79% of the variance. (b, c) Results from two-tailed t tests depicting overall trait differences between invasive and native species along PCA axes 1 and 2, respectively. Different letters above the box plots indicate significant differences between groups

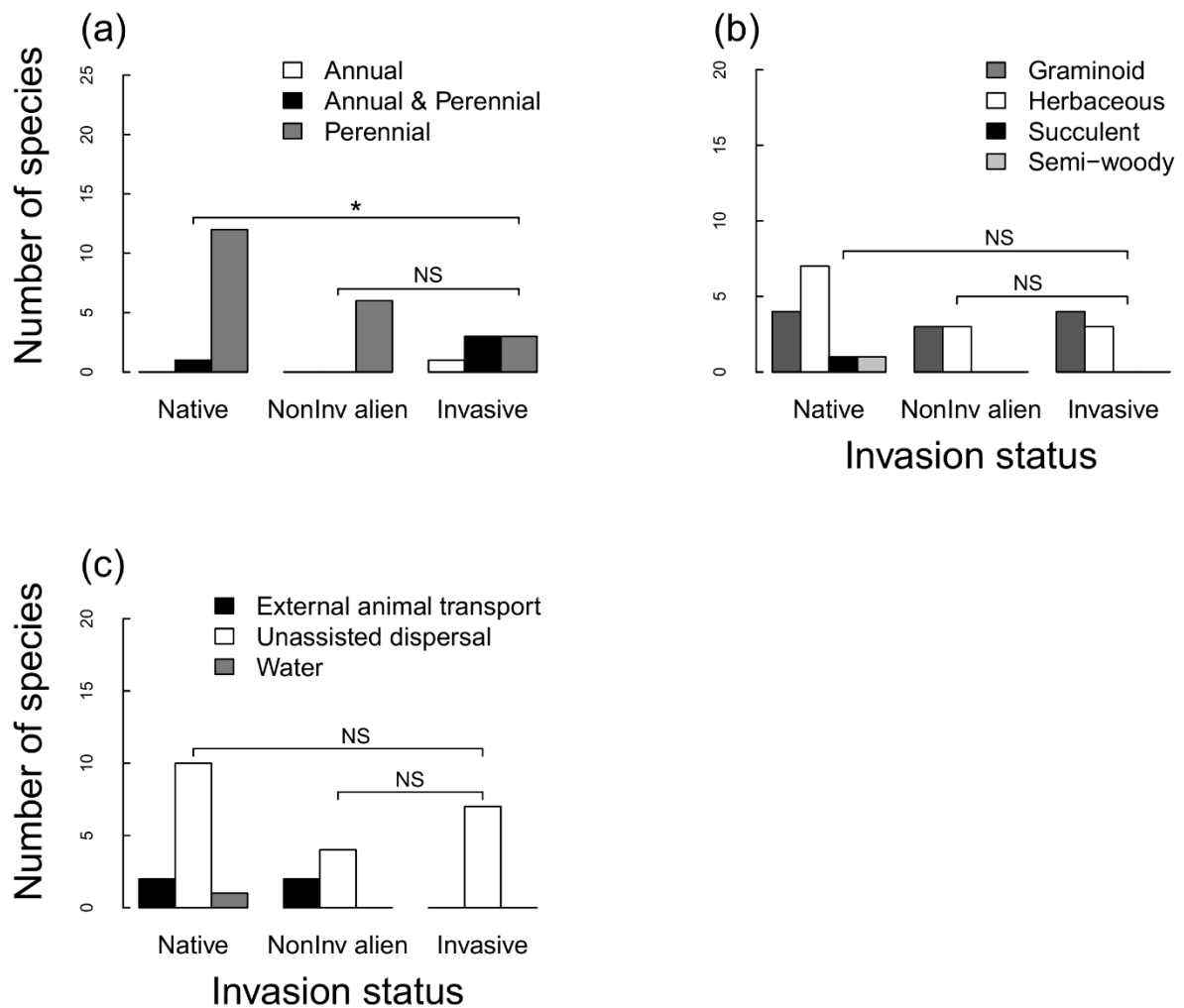


Figure 2. Number of species of native, non-invasive alien (NonInv alien) and invasive plant species on Marion Island displaying different modes of (a) life history, (b) growth form and (c) dispersal. The horizontal lines indicate the significance of pair-wise comparisons between invasive species and native and non-invasive alien species. * $P < 0.05$, NS, non-significant.

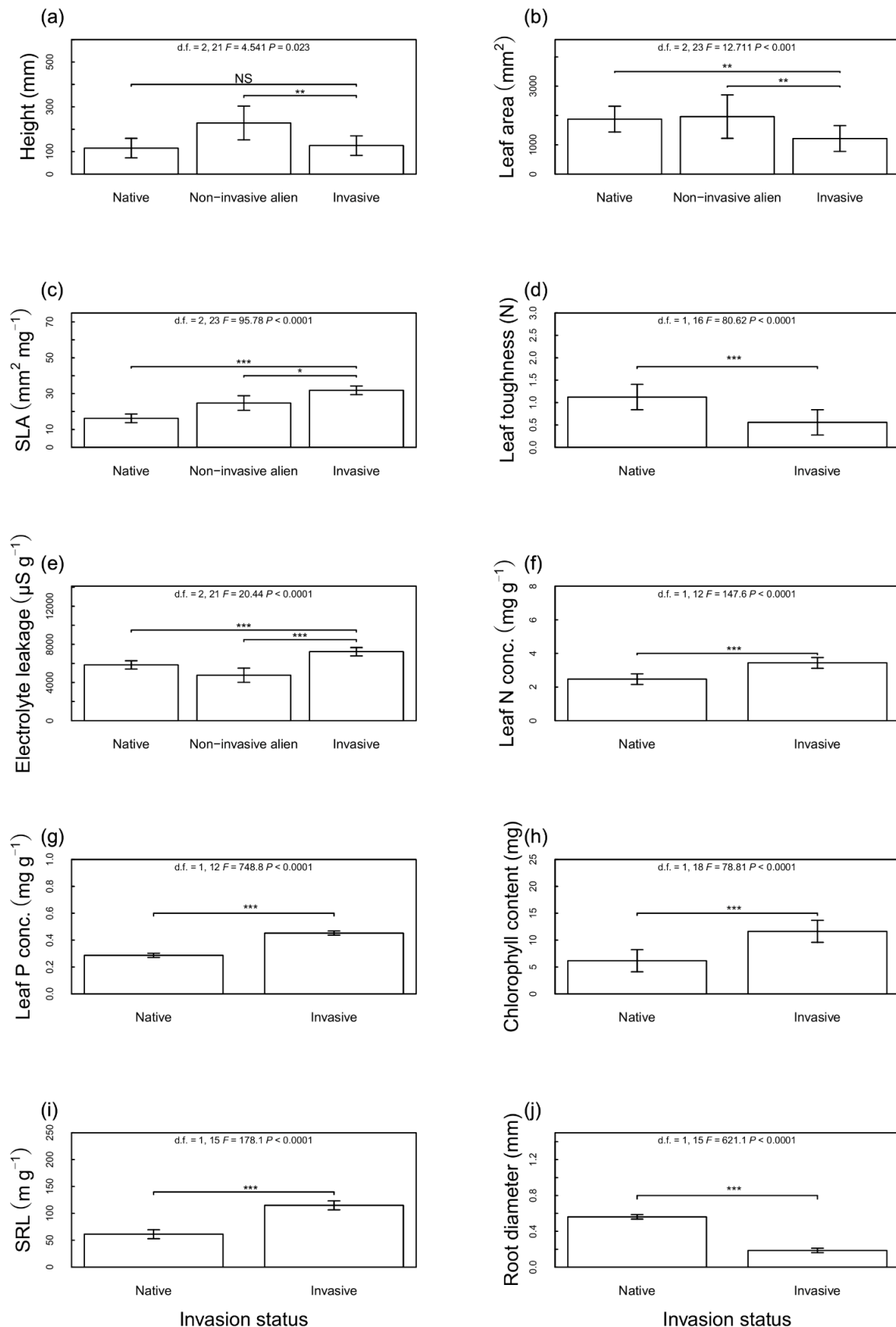


Figure 3. Bar graphs showing phylogenetically-corrected trait differences (\pm standard error) from phylogenetic generalized least-squares models between native, non-invasive alien and invasive plant species on Marion Island. (a) Height, (b) leaf area, (c) specific leaf area, (d) leaf toughness, (e) electrolyte leakage as an indicator of the inverse of frost sensitivity, (f) leaf nitrogen concentration, (g) leaf phosphorus concentration, (h) leaf chlorophyll content, (i) specific root length, (j) root diameter. The horizontal lines indicate the significance of pair-wise comparisons between invasive species and native and non-invasive alien species. F ratios (F), degrees of freedom (d.f.), and significant levels (* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$) are shown. Raw phylogenetically corrected trait values (y-axis) are plotted here for ease of interpretation, but statistics were conducted on transformed data to meet assumptions of phylogenetic generalized least-squares models.

lower leaf toughness (Figure 3c, d). Invasive species also displayed lower frost tolerance, i.e., higher electrolyte leakage, than native species (Figure 3e). The leaf physiological traits, namely leaf N and P concentration and chlorophyll content, were higher in invasive than native species (Figure 3f–h). Amongst the belowground traits, invasive species had a higher SRL and a lower root diameter than native species (Figure 3i, j).

When comparisons were conducted only for plants growing in low altitude nutrient-rich habitats, to control for intraspecific variation brought about by environmental variation, results for leaf area, SLA, leaf toughness and chlorophyll content were identical to results from analyses that considered all data, and plant height was significantly higher in invasive species than in native species (Appendix S18).

No differences in life history, growth form and dispersal mode were found between invasive and non-invasive alien species (Figure 2). However, non-invasive aliens were significantly taller than invasive species (Figure 3a), even after *Juncus effusus* (the tallest of the island's plants) was removed as an outlier (results not shown). Similar to the comparison between invasive and native species, invasive species had smaller leaves, higher SLA and lower frost tolerance than non-invasive alien species (Figure 3b, c, e).

3.3. BIVARIATE TRAIT RELATIONSHIPS

There were no differences in the slopes describing the bivariate relationships between traits for native, non-invasive alien or invasive species, although some trait pairs showed significant shifts in the y-intercept or the location of points along the x-axis (Appendix S19; Figure 4). Leaf area varied significantly only with SLA; the variables were negatively correlated. However, there were no differences in the nature of the bivariate relationship between leaf area and SLA for invasive, non-invasive alien and native species (Appendix S19). Specific leaf area was also positively related to electrolyte leakage and chlorophyll content, and inversely related to leaf toughness (Appendix S19, Figure 4a–c); SLA of invasives was higher than for natives (and for non-invasive aliens for electrolyte leakage) when the other trait was kept constant. Electrolyte leakage was furthermore positively related to chlorophyll content and negatively related to leaf toughness (Appendix S19, Figure 4d, e). When values of chlorophyll content and leaf toughness were kept constant, electrolyte leakage was higher for invasive than native species. Chlorophyll content and leaf toughness were negatively related (Figure 4f). When electrolyte leakage and leaf toughness were kept constant, chlorophyll content was higher for invasive than native species (Figure 4d). Specific root length and root diameter were negatively related; however, native and invasive species did not show shifts in the y-intercept or position for this bivariate relationship (Appendix S19).

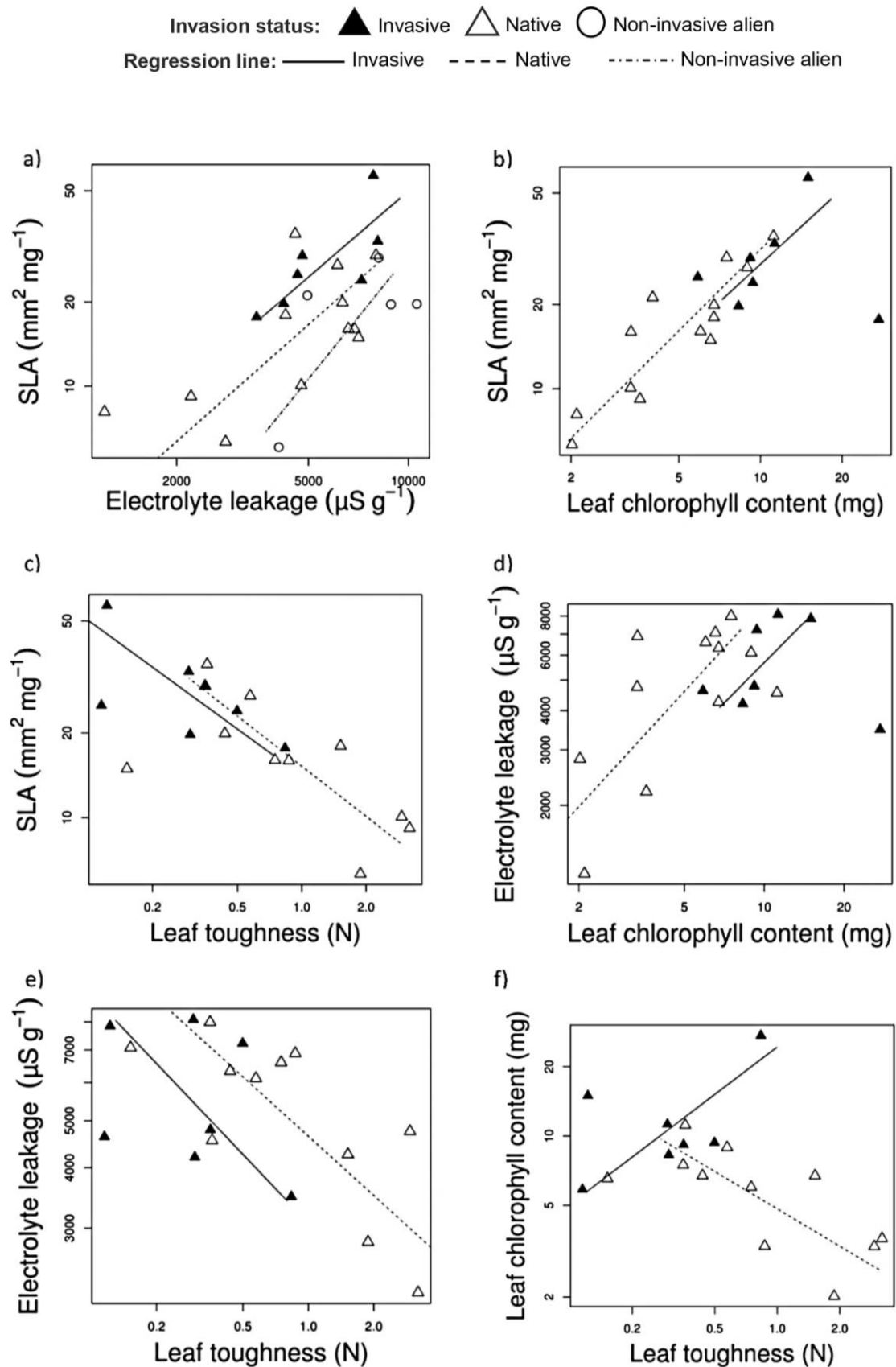


Figure 4. Significantly different standardized major axis regression relationships for leaf and below-ground traits between native, non-invasive alien and invasive vascular plant species of Marion Island. Points indicate trait mean values for each species. (a) Specific leaf area (SLA) vs electrolyte leakage (as an indicator of frost sensitivity); (b) SLA vs leaf chlorophyll content; (c) SLA vs leaf toughness; (d) electrolyte leakage vs leaf chlorophyll content; (e) electrolyte leakage vs leaf toughness; and (f) leaf chlorophyll content vs leaf toughness. Axes are log₁₀-scaled.

4. Discussion

This study shows that invasive species differ from native species in most traits, suggesting strong support for phenotypic divergence. Additionally, invasive species differ significantly from non-invasive alien species in several key traits. These traits may explain the success of invasives in the sub-Antarctic context (Figure 5).

4.1. INVASIVE VERSUS NATIVE TRAIT COMPARISON

Our results largely support the ‘phenotypic divergence’ hypothesis, indicating that functionally unique species are more likely to successfully invade new habitats, and that trait differences allow invasive species access to unused niche opportunities in the recipient ecosystem. This suggests that for most traits the spectrum of trait values expressed by native species does not represent the full spectrum of trait values that allow survival in an area. Support exists in the literature for both the ‘phenotypic divergence’ and ‘phenotypic convergence’ hypotheses, although, as here, the ‘phenotypic divergence’ hypothesis tends to be supported most commonly (e.g., Leishman et al., 2007, 2010; Ordonez et al., 2010; van Kleunen et al., 2010).

We found that invasive species possessed different trait complexes to native species (Figure 5a), whether phylogenetic non-independence was considered (PGLS), or not (PCA). PGLS showed stronger support for ‘phenotypic divergence’ than models that did not account for phylogenetic non-independence (results not shown). Therefore, had the PCA taken into consideration the effect of phylogeny on trait complexes, invasive and native species may have separated out even more clearly. Specific leaf area and electrolyte leakage most clearly separated native and invasive species; the high SLA of invasive species suggests an acquisitive syndrome of resource use (Díaz et al., 2004), while high electrolyte leakage indicates reduced tolerance to frost.

Differences observed in several traits between native and invasive species are consistent with findings from other environments (e.g., Daehler, 2003; Pyšek & Richardson, 2007; van Kleunen et al., 2010). For example, invasive species generally have higher SLA and SRL than native species, indicating the ability to rapidly capture resources (Grotkopp & Rejmánek, 2007), resulting in faster growth and root and leaf turnover rates (Eissenstat, Wells, Yanai, & Whitbeck, 2000; Grotkopp, Rejmánek, & Rost, 2002). Invasive species also tend to have higher leaf N and P concentrations and higher chlorophyll content than native species (Leishman et al., 2007, 2010), indicating improved leaf nutrient status and photosynthetic potential (Pérez-Harguindeguy et al., 2013). Thus, traits associated with faster growth and rapid resource acquisition appear to promote invasiveness (Gioria & Osborne, 2014).

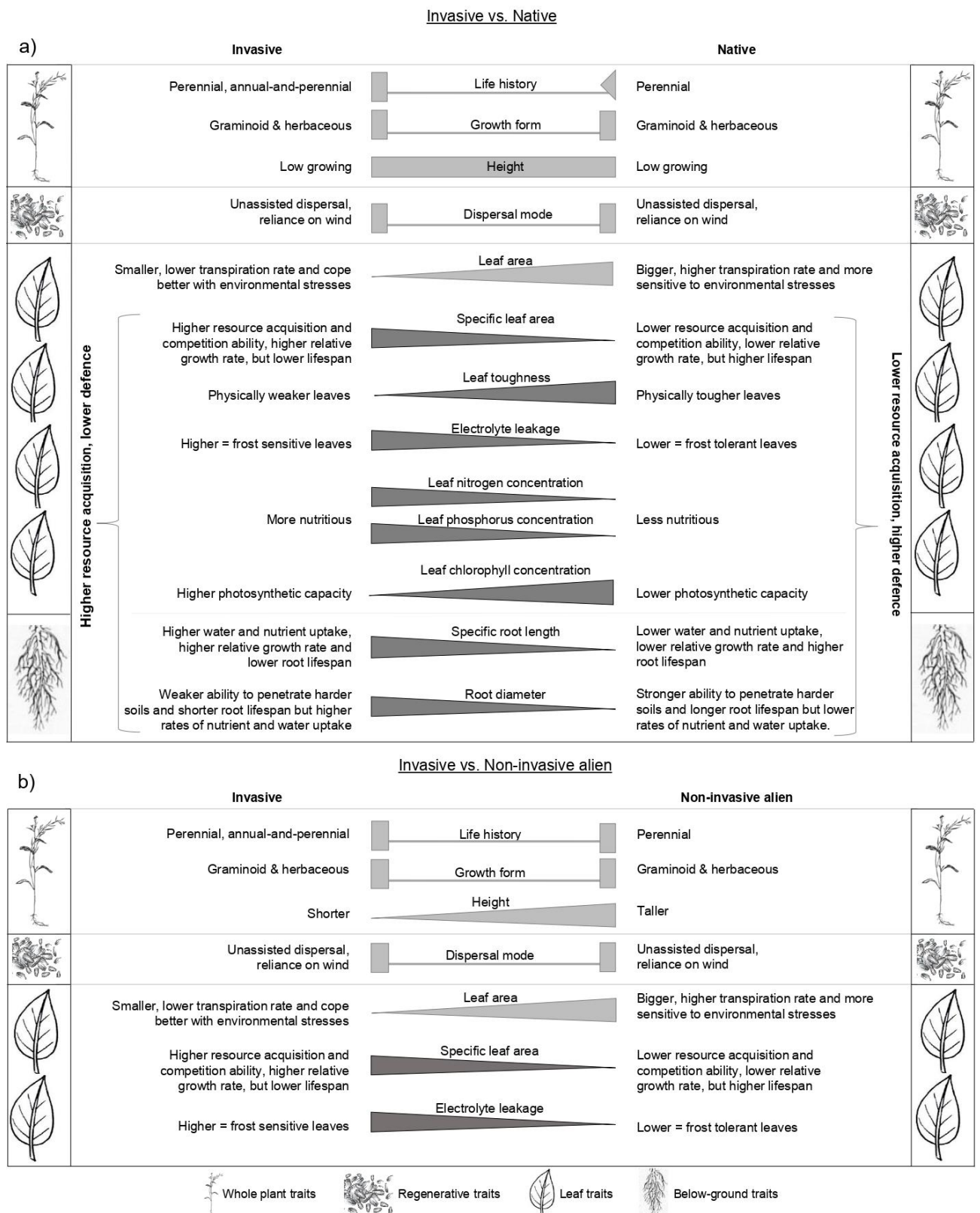


Figure 5. Schematic summary of functional trait differences found between (a) invasive and native, and (b) invasive and non-invasive alien vascular plant species on sub-Antarctic Marion Island. In the left and right columns, information is given about the trait characteristics of the respective groups. The central column informs about differences or similarities in traits between invasives and (a) natives or (b) non-invasive aliens. For categorical traits, two shapes are provided per trait-row; two different shapes indicate differences in traits, while two identical shapes represent no difference in trait characteristics. For continuous traits, a central bar is shown. Increasing width of the bar indicates an increase in trait size, while a rectangular bar width indicates no difference in trait characteristics. The colours of the bars indicate if the observed trait differences are in line with findings elsewhere: dark grey represents trait differences that agree with findings elsewhere, light grey represents trait differences that contradict (at least some) findings elsewhere. The comparisons to global functional patterns relied heavily on findings from reviews and meta-analyses (e.g., Daehler, 2003; Pyšek & Richardson, 2007; van Kleunen et al., 2010)

Generally, faster growth and resource acquisition trade off against abiotic stress tolerance (Herms & Mattson, 1992). Indeed, this appears to be true on Marion Island where invasive plants invested less in structural compounds and resource allocation associated with leaf defences: they exhibited lower leaf toughness and frost tolerance than native plants (in keeping with e.g., Daehler, 2003; see also Pammenter, Drennan, & Smith, 1986). In addition, the thicker roots of native species are more expensive (in terms of time, energy and resources) to construct and maintain, and are indicative of an ability to penetrate harder soils, to tolerate low soil moisture and of a longer life span (i.e., trading off resource acquisition for tolerance of abiotically stressful conditions; Pérez-Harguindeguy et al., 2013).

Our findings did not, however, agree with those of other studies from other regions in all instances (see Figure 5a for summary). For example, invasive species had smaller leaf area than natives, in contrast to Daehler (2003). Smaller leaf area can be an indication of a superior ability to deal with environmental stresses such as drought or heat, but can also be a by-product of a plant's anatomy (Pérez-Harguindeguy et al., 2013).

It could be argued that the differences between native and invasive species traits observed in this study are due to trait filtering of invasive species at the dispersal stage. However, several introduction pathways to the island exist, and there have been some intentional introductions to the island (Lee & Chown, 2009), enhancing the spectrum of traits arriving in the region. In addition, it is unlikely that dispersal traits constrained the variety of measured traits expressed by invasive species (since, for example, SLA and plant height vary independently of seed mass at broad spatial scales; Westoby, 1998). We are thus confident that differences in traits reported here are rather driven by trait filtering at the establishment and/or growth stage.

Only three of the thirteen traits assessed (growth form, height, and dispersal mode) did not differ between invasive and native species, lending only weak support to the 'phenotypic convergence' hypothesis (Figure 5a). For these traits, the sub-Antarctic environment appears to filter for typical tundra vegetation characteristics (e.g., low-growing graminoid and herbaceous plants with unassisted dispersal) (Gremmen & Smith, 2008). Therefore, invasive species may be pre-adapted to the local conditions with regards to these traits (which are likely related to tolerance of the extreme wind conditions; see Pammenter et al., 1986).

Results from the SMA indicate that there are no differences in the slope of any bivariate trait relationships when comparing native and invasive species, in agreement with similar studies (Heberling & Fridley, 2013; Leishman et al., 2007, 2010). Thus, plants, regardless of functional type or alien/invasive status, are constrained by the universal spectra of trade-offs (Leishman et al., 2007, 2010; Reich, 2014; Wright et al., 2004). However, several bivariate relationships between native and invasive species differed significantly by either showing shifts

on the y-axis or shifts along a common slope. Invasive species were generally shifted towards the rapid resource acquisition and low defence portion of the trait trade-off axis while native species were located on the opposite end of the axis, indicating further support for ‘phenotypic divergence’.

The broadly different strategies displayed by invasive and native species (Figure 5a) indicate that invasive species fill unoccupied niches, which are a distinct possibility on Marion Island because of the young geological age and isolation, and thus relatively low native species richness, of the island (Chown & Froneman, 2008; McDougall et al., 2001).

4.2. INVASIVE VERSUS NON-INVASIVE ALIEN TRAIT COMPARISON

We found differences between invasive and non-invasive alien plants in SLA, frost tolerance, leaf size, and plant height, suggesting that these traits predispose aliens to becoming invaders (Figure 5b; van Kleunen et al., 2010). A higher SLA and lower frost tolerance in invasive than in non-invasive alien species (Figure 5b) corroborate findings of other studies that invasives invest more in growth and resource acquisition at the expense of leaf defences (Gallagher et al., 2014; Grotkopp & Rejmánek, 2007; Ugoletti, Stout, & Jones, 2011). Leaf area and height were lower in invasives than in non-invasive aliens, contrary to findings elsewhere (e.g., Pyšek & Richardson, 2007; van Kleunen et al., 2010), suggesting that lower values of these traits are not indicative of species’ invasiveness for all ecosystems. Therefore, high SLA, low frost tolerance, low plant height and, possibly, small leaf area may be regarded as traits that confer invasiveness, with the latter two traits specifically conferring invasiveness in the windy sub-Antarctic context, but not always in other contexts. Results from the SMA indicate that invasive and non-invasive alien species are positioned on the same location along the spectrum of trait trade-offs.

4.3. IMPLICATIONS FOR CONSERVATION

The outcomes of this study have practical implications for the management of aliens in the greater sub-Antarctic region, because the sub-Antarctic islands share a similar climate and many alien and native species (Greve et al., 2005; Leihy et al., 2018). Where eradication efforts have to be prioritized across several recently introduced plant species, screening for the traits that distinguish contemporary invasives from non-invasive aliens (i.e., low height, small leaf area and high SLA at the expense of investment in structural compounds and frost tolerance) may improve the ability to predict potential invasiveness of alien species.

Our results also provide insight into what the invasion trajectory in the sub-Antarctic may look like in the future. The high leaf nutrient and acquisitive trait values of invasive species

suggest that invasives may grow especially well in nutrient-rich environments where they can outcompete native species (Hausmann et al., 2013). However, these results also suggest that many invasive species are unlikely to dominate in more nutrient-poor habitats, which is largely supported by observations (Gremmen, Chown, & Marshall, 1998).

Finally, invasions on sub-Antarctic islands are likely to intensify with climate change, particularly with the amelioration of temperatures (Frenot et al., 2005; le Roux & McGeoch, 2008). In our study, invasive plants are less well adapted to extreme cold than native species, but are more effective at resource acquisition, suggesting that a warmer environment will lead to increases in the performance of invasive species. This may also favour range expansions of invasive species to higher altitudes from which they are currently excluded because of low-temperature extremes (le Roux et al., 2013). Indeed, there is already evidence of range expansions of invasive species to higher altitudes since 1965 (Chown et al., 2013).

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Conflict of interest

We have no conflict of interest to declare.

Author Contributions

R.M. and M.G. conceived the idea; R.M., M.G. and P.C.I.R. designed methodology; M.G., R.M., C.S., I.J.B., A.L. and B.R. collected and assisted in processing the data; R.M. analysed the data with the assistance of M.G., P.C.I.R., B.H.D. and B.R.; R.M. led the writing with contributions from all authors. All authors gave final approval for publication.

Data availability statement

Most primary data have been submitted to the Tundra Trait Team Database (Bjorkman et al., 2018) and also stored in Supporting Information related to the present paper (Appendices).

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Supplementary information

Raw data, tables and figures of results from trait comparisons between native, invasive and non-invasive alien species of Marion Island

Appendix S1. A list of all vascular plants surveyed on Marion Island

Appendix S2. Residence time of alien vascular plants species on Marion Island

Appendix S3. Map of Marion Island and sampling localities

Appendix S4. Terrestrial habitats of Marion Island

Appendix S5. Sampling design

Appendix S6. Sampling data

Appendix S7. Trait data

Appendix S8. Literature sources

Appendix S9. Trait data from literature sources

Appendix S10. Descriptions of traits used

Appendix S11. Trait processing

Appendix S12. Multivariate analysis (principal component analysis)

Appendix S13. Phylogenetic tree of all study species

Appendix S14. Univariate analysis (phylogenetic generalized least-squares models)

Appendix S15. Trait data of vascular plant species common in the coastal areas of Marion Island

Appendix S16. Bivariate trait analysis (standardized major axis)

Appendix S17. Ordination of invasive and non-invasive vascular plant species

Appendix S18. Trait differences between native and invasive species common in the coastal areas of Marion Island

Appendix S19. Results of standardized major axis regression analysis for vascular plant species on Marion Island