npj | biodiversity

Article

https://doi.org/10.1038/s44185-025-00112-7

Living together in a context of plant invasion: the example of the plant communities at the Iles Kerguelen

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With invasions, functionally differing plant species meet. The traits of native and alien species should then be modified, affecting coexistence. We studied trait variation in four native and five alien plant species on the Iles Kerguelen along gradients of alien abundance. We measured traits related to competition and stress tolerance, and compared them along the gradients, their mean, variability, and range, at the species and the community levels, through univariate (analyses of variance) and multi-traits (hypervolume) approaches. Native and alien species occupied overlapping trait spaces, mostly because aliens are more variable than natives. Along the gradients, native and alien species showed similar mean strategies, with no variation in their trait range or variance. At the community level, a shift from convergence to divergence along the gradients was observed in most traits. Our results highlight that not only the response of aliens but also of native species should be studied under invasions.

The Southern Ocean islands host exceptional ecosystems facing biological invasions. Due to their geographic and climatic isolation, these ecosystems remained protected from human-mediated alien propagule introduction for a long time. However, recent human settlement has been accompanied by the introduction of alien plant species, some of which have become invasive[1,2]. Colonization by alien plant species is known as a major human-induced threat to biodiversity[3]. Understanding how the introduction of alien plant species may affect the dynamics of invaded plant communities is thus crucial, for the prediction of their fate and implementation of appropriate management policies[4–6].

When reaching a new region, alien plant species are likely to modify the biotic filtering process, *i.e.*, the existing interactions within plant communities[7,8], subsequently inducing intraspecific trait variation among native and alien species[5,9]. The traits of native and alien species have been compared in an increasing number of studies to understand why some alien species manage to become established outside of their native ranges[10]. However, little is known about how the traits of co-occurring native and alien species are modified by the new interaction context, although it could improve predictions of the outcome of their interactions, related to coexistence mechanisms, and the response of communities to plant invasions.

Based on trait comparison between native and alien species, two hypotheses can explain the success of alien species in novel habitats: phenotypic convergence and phenotypic divergence[11]. Phenotypic convergence implies that successfully established alien species have traits similar to those of native species, enabling them to cope with local abiotic constraints. Phenotypic divergence is based on the limiting similarity theory[12], which holds that alien species become invasive by possessing traits differing from those of native species (*i.e.*, empty niche occupancy). Results favoring the divergence hypothesis were found on the sub-Antarctic Marion Island[13], suggesting that alien species that manage to become established on the Southern Ocean islands have traits that are predominantly different from those of native species. As successfully established alien plants usually have higher performance-related trait values (rapid growth or acquisitive traits) than do native species[14,15], we expect alien species that became invasive on the Southern Ocean islands, to overall display more competitive phenotypes than natives.

Intraspecific trait variation in native and alien species related to their competitive responses[16,17] should depend on alien species abundances, as several studies have shown that the identity (*i.e.*, species) of the plants' neighbors influences trait responses to interaction[18–20]. On the one hand, this competitive response may involve variations in species trait means. Indeed, plants are known to increase their height and specific leaf area (SLA) under competitive interactions[19,21]. The leaf dry matter content (LDMC) and leaf area (LA), which are more sensitive to abiotic conditions than to biotic interactions[22], should still be influenced by the new interaction context due to trait relationships. Indeed, traits can be involved in trade-offs between

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plant functions[23,24] or be genetically related (pleiotropy, epistasis)[25]. On the other hand, species trait variance would also be affected by their competitive responses, especially in successful alien species that should be more plastic [phenotypic plasticity hypothesis[10,26,27]] compared to native species. Indeed, native species on Southern Ocean islands have long evolved in species-poor communities with stable abiotic conditions, ultimately decreasing the benefit of being plastic[25].

Intraspecific trait variation induced by the new context of interaction is expected to affect the community coexistence. In the early phases of invasions, native species can initially facilitate alien species, but can be negatively affected by their development later on, especially when alien species possess traits allowing them to outcompete their host[28,29]. In this case, species coexistence may be promoted by fitness equalizing and stabilizing niche differences[9,30]. Stabilizing niche differences arise from the divergence of trait values among community species, which allows them to coexist by occupying different niches [limiting similarity theory[12,31]], whereas fitness equalizing results from convergence toward trait values that minimize competitive differences among species by elimination of values that do not support competitive ability [e.g., greater height[31–33]]. According to the intraspecific trait variation expected, the coexistence mechanisms at play along a gradient of alien species abundance in the sub-Antarctic islands should differ according to community composition (abundance of dominant species). Stabilizing niche differences should be observed with functionally dissimilar native neighbors under low alien species abundance, as observed in alpine meadow under conditions similar to those of sub-Antarctic tundra[34]. A high abundance of competitive alien species (resulting in higher competition intensity) should result in a fitness equalizing mechanism.

In this study, we evaluated trait variations of different native and alien plant species, as a proxy of coexistence mechanisms[6,35], along a gradient of alien species abundance, on the Iles Kerguelen. Given the naturally cloudy conditions of the sub-Antarctic region, light is already a limiting factor for vascular plants, and we thus expect them to mostly compete for this resource. Such assessment of trait variations in both native and alien species is not common in this field, as emphasized by Gallien and Carboni[36], who called for the integration of native species into studies of invasions. Individuals of these plant species were sampled for the measurement of three leaf traits and height[37]. We performed univariate analyses to investigate intraspecific trait variation in response to new plant species interactions resulting from alien introductions, and multi-trait analyses based on the hypervolume method proposed by Blonder et al.[38,39] to determine the subsequent effects on coexistence mechanisms. We addressed the following hypotheses:

According to the phenotypic divergence hypothesis, alien species should exhibit different and more competitive trait values than native species.

Individual trait means should reflect stronger competitive ability at high alien species abundance. Intraspecific trait variation (mean and variance) should be lower for native than for alien species.

Trait divergence, indicating stabilizing niche differences, and trait convergence, indicating fitness equalizing, should be observed under low and high alien species abundance, respectively.

Results

Alien and native species showed significant differences in functional trait spaces

First, native (four species) and alien species (five species) were compared, all levels of alien species abundance combined, with the sampling areas (4 areas × 2 sites × 5 islands) set as a random variable. As expected, we found significant differences in trait means between native and alien species (Fig. 1 and Supplementary Table 1). Considering all native and all alien species, the two groups occupied overlapping functional trait spaces along the four trait axes considered, although native species were on the whole smaller, with smaller LAs and SLAs, and higher LDMC (Fig. 1). Height differences were species dependent, with three alien species (*Dactylis glomerata*, *Poa pratensis*, and *Taraxacum officinale*) being taller than native species, and the other two (*Cerastium fontanum* and *Taraxacum erythrospermum*) being smaller than the native species except for *Azorella selago* [Supplementary Table 1]. Relative to the alien species, the native species had smaller SLAs (except *Acaena magellanica*). LDMCs exhibited species-specific differences (see Supplementary Table 1 for more detailed comparisons of traits between species). As expected, the hypervolume of native species had a smaller size than that of alien species (*Z* test, $p < 0.001$; Fig. 2), reflecting a less variable growth strategy. These differences were related to higher variability in LA, height, and SLA in alien species compared to the native species (Fig. 1).

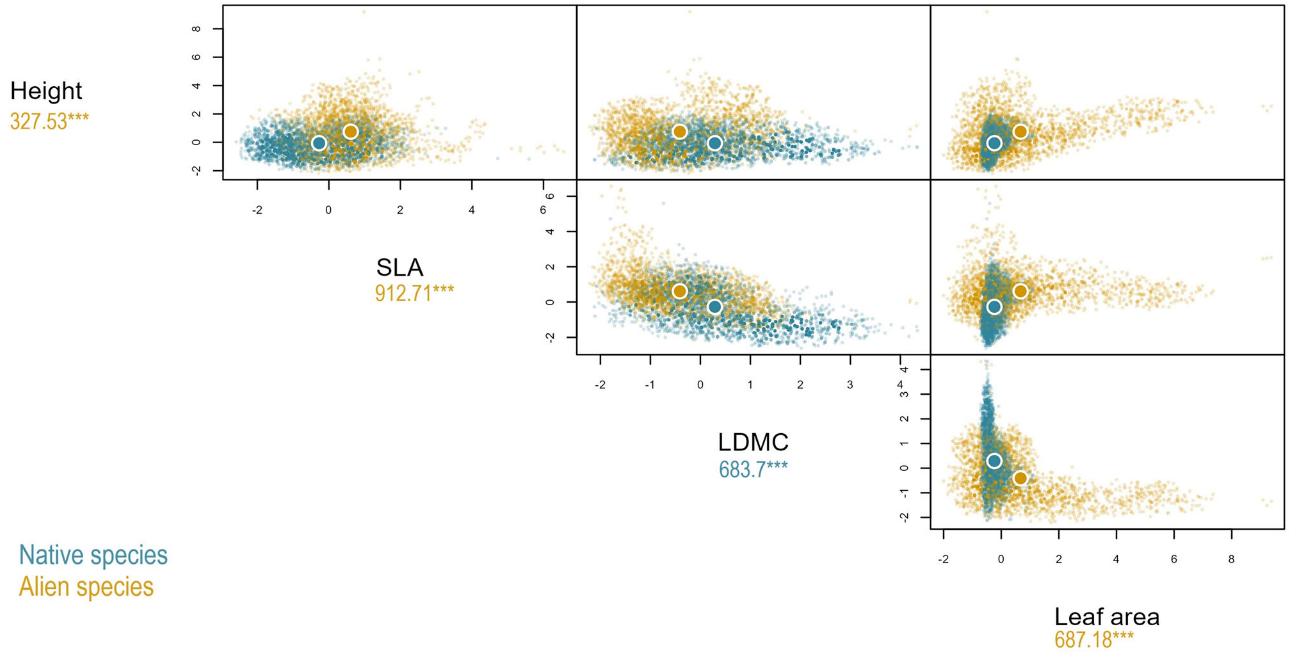

Fig. 1 | Native and alien species hypervolumes are shown as 2D projections for all combinations of trait axes: height, SLA, LDMC, and LA. Axes are standardized. Larger, colored dots are species centroids. In addition, for each trait, mean values were compared between native and alien species using a linear mixed effect model: t-value (blue, native > alien; orange, native < alien) are given with *p* values: $^{***}p < 0.001$; $^{**}p < 0.01$; “.”, $0.05 < p < 0.1$; no asterisk, $p \geq 0.1$.

Variations of alien species abundance induced changes in the mean but not in the range and the variance of traits for native and alien species

We here considered the effects of alien species abundance on the mean, range, and variance of traits in both the native and alien species.

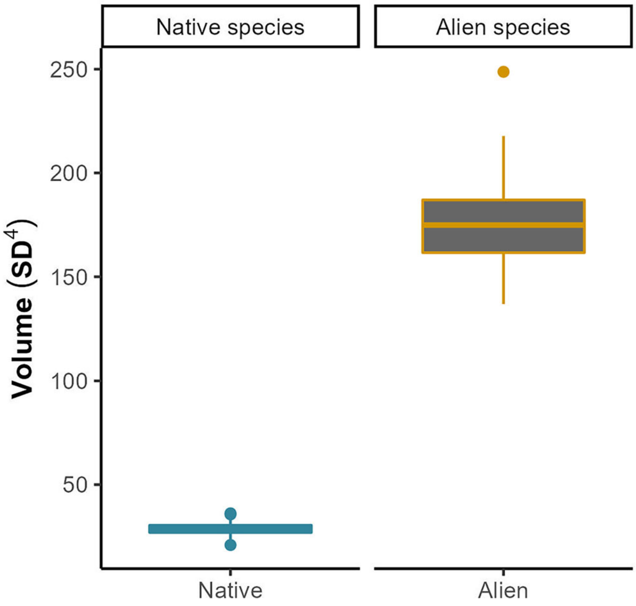

Fig. 2 | Distribution of hypervolume sizes (volume calculated based on the four traits examined) for native (blue) and alien (orange) species. SD standard deviation.

Contrary to our expectations, the overall trait mean variation along the gradient of alien species abundance was the same for alien and native species (Fig. 3). Native and alien species showed increases in the mean height, SLA, and LA, and a decrease in the mean LDMC, with few exceptions for each trait (Fig. 3). However, the threshold at which alien species abundance triggered the observed variations depended on the species. For example, among the less plastic species, *A. selago* showed increases in the mean height and LA (with no difference in the other two traits) when the alien species abundance reached 75–100%. Conversely, two traits of *A. magellanica* responded to 25–50% and 50–75% abundance. The trait range and variance did not differ significantly along the gradient of alien species abundance, regardless of the species, for both natives and aliens [Supplementary Table 2].

Trait divergence along the gradient of alien species abundance

Community Weighed Variance ESs close to zero were taken to indicate no link between species abundance and their trait values, whereas negative and positive values were interpreted as reflecting trait convergence and divergence, respectively (Fig. 4). Contrary to our expectation, CWV values showed increases in the height, LDMC, and LA with alien species abundance (Fig. 4), and a shift from trait convergence to divergence for height and LA along the gradient of alien species abundance. CWVs for the SLA peaked at 25–50% of abundance and then decreased, indicating a shift from trait divergence to random distribution and then to trait convergence, as expected.

Native and alien species strategies showed variation at the multi-trait scale

The hypervolume sizes of native species were smaller than those of alien species, regardless of alien species abundances (Fig. 5), reflecting a less

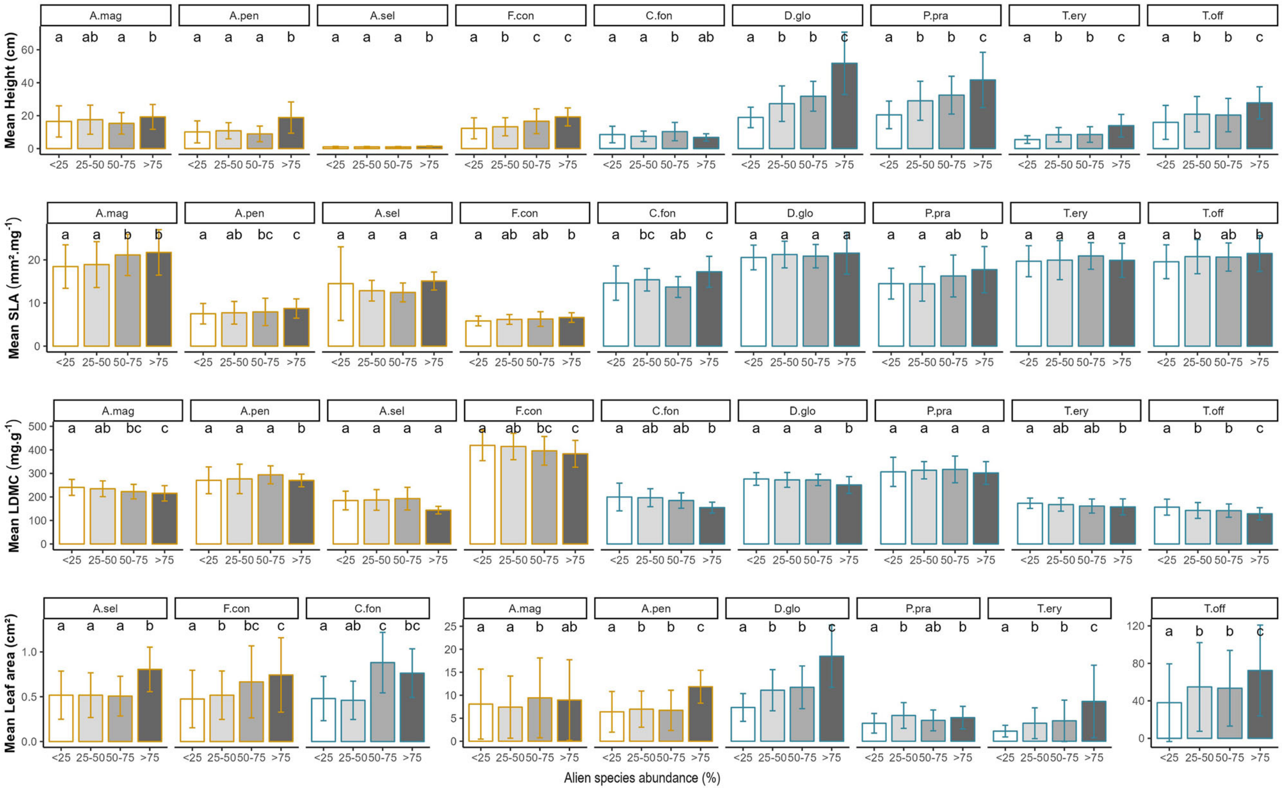

Fig. 3 | Studied species responses to alien species abundance. Mean (±SD) trait values of the nine studied species along the gradient of alien species abundance. Different letters above the bars indicate significant differences in trait means between levels of alien species abundance (linear mixed-effect models with *post-hoc* Tukey tests, $p < 0.05$). Native species (orange): A. mag *Acaena magellanica*, A. pen *Austroblechnum penna-marina*, A. sel *Azorella selago*, F. con *Festuca contracta*. Alien species (blue): C. fon *Cerastium fontanum*, D. glo *D. glomerata*, P. pra *P. pratensis*, T. ery *Taraxacum erythrospermum*, T. off *Taraxacum officinale*. For LA, three different scales are used to represent data for the different species.

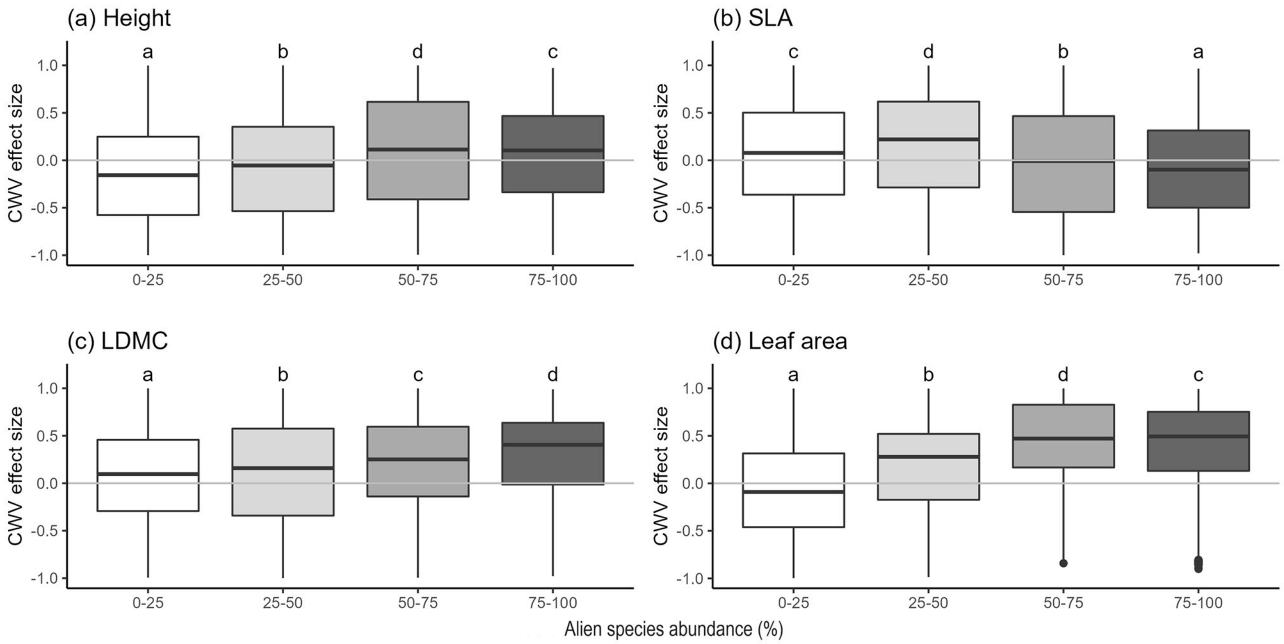

Fig. 4 | Community-weighted variance (CWV) of traits in individuals of all species at each level of alien species abundance. a Height; **b** SLA; **c** LDMC; **d** Leaf area. CWV effect sizes (ESs) were calculated by comparing observed CWVs to a null distribution obtained by randomly shuffling abundance among species in each community (Bernard-Verdier et al.[59]). Negative (positive) ESs represent less (more) CWV than expected, suggesting trait convergence (divergence). The solid horizontal gray lines indicate the null expectation (ES = 0). Different letters above the bars indicate significant differences between communities (Kruskal–Wallis and Dunn's *post-hoc* tests, $***p < 0.001$).

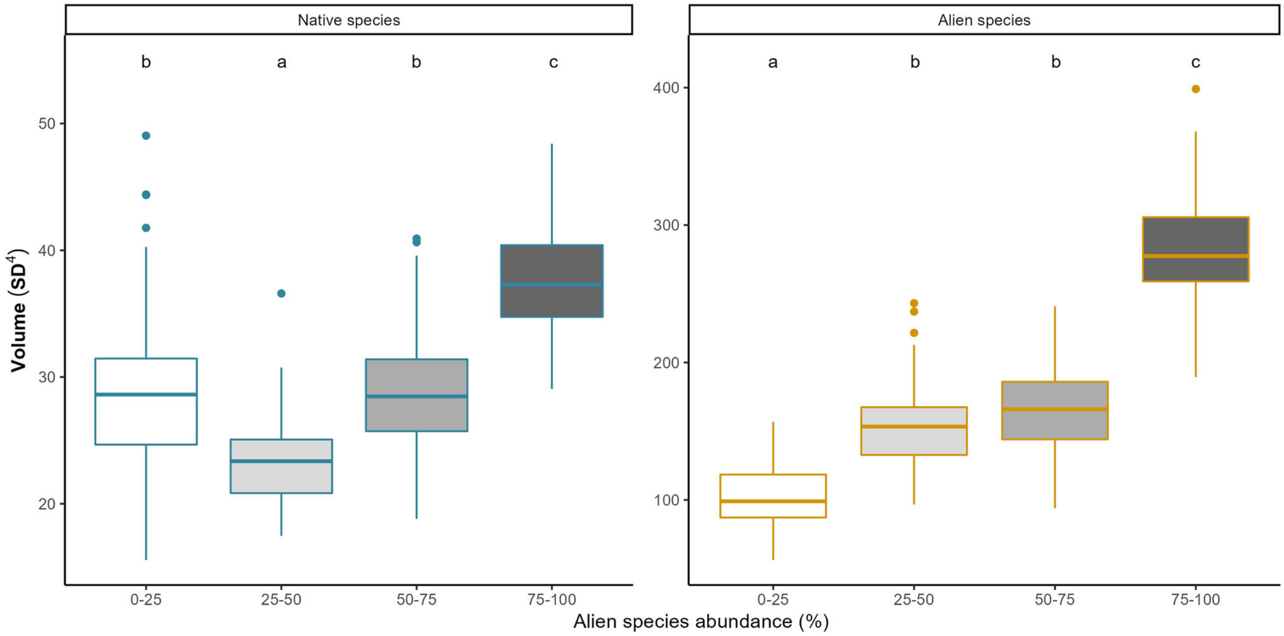

Fig. 5 | Distribution of hypervolume sizes (volume calculated based on the four traits examined) of all native (blue) and alien (orange) species along the gradient of alien species abundance. Volume indicates hypervolume size based on the four traits considered. Different letters above the bars indicate significant differences in volume between levels of alien species abundance (*Z* test, $p < 0.001$). SD standard deviation.

variable growth strategy in native than alien species. The gradient of alien species abundance significantly affected the native and alien species hypervolumes. Contrary to our expectation, the hypervolume size increased steadily along the gradient for alien species, and for native species from 25–50% to 75–100%. For native species, the sizes calculated at 0–25% and 50–75% of alien species abundance were equal to and greater than, respectively, that at 25–50%.

Discussion

We characterized the range of trait values expressed by native and alien species under the abiotic conditions of the Iles Kerguelen. According to the phenotypic divergence hypothesis, alien species were expected to display traits differing from those of native species[11,14,40]. Alien species were usually taller, with higher LA and SLA, and lower LDMC than native species. Regarding the leaf economic spectrum (LES), which reflects the trade-off between carbon gain and longevity[41,42], our findings in native species are consistent with a conservative strategy associated with a slow return on investment and long leaf lifespan, which has already been observed in cold environments[43]. Alien species exhibit a rather acquisitive strategy compared to native species, they are known to express globally[14]. However, these overall differences were not verified in all species, some alien species were smaller, with lower SLA and LA, and higher LDMC than some native species. Thus, successful alien species displayed intermediate characteristics between acquisitive and conservative strategies, as has already been reported for the sub-Antarctic region, given the environmental conditions[13]. Indeed, cold, wind, and humidity filter for trait values, allowing individual resistance.

The variability in overall strategies (size of hypervolumes) was greater in alien species than in native species, in relation to height, SLA, and LA, explaining that alien and native species have overlapping functional trait spaces. Species native to the Iles Kerguelen have evolved together in a stable environment over a lengthy period. Their genotypes may have been selected to express different low variable phenotypes, leading to the occupation of different narrow niches[25,43]. These stable long-term interactions may have made intraspecific trait variability less advantageous than the expression of a stable phenotype outside of other species' niches[44]. Successful alien species, in turn, are known to be quite plastic[26], which supports their invasiveness[45,46].

Along the gradient of increasing alien plant species abundance, individual traits were expected to converge toward values supporting competitive ability for alien species, and little phenotype variation for native species. We observed increases in height, SLA, and LA, and a decrease in the LDMC along the gradient of alien species abundance for alien species, but also more than expected for native species. These increases (especially that in height) occurred in spite of abiotic constraints, and more specifically of wind[13,47]. These results can be explained by our sampling design, which focused on sites that were sheltered. Under these conditions, plant height is not limited[48].

All traits (not only those related to competition) showed variation along the gradient of alien species abundance, illustrating the interconnectedness of traits. We observed trait displacement toward more competitive strategies, including for native species, which were expected to express low intraspecific trait variability. This strategy shift could have negative consequences for species, given the constraining climate of the sub-Antarctic islands, although climate change is altering abiotic conditions[2,49], reducing the necessity for plant species to invest in stress tolerance strategies, subsequently allowing them to invest more in their competitive ability.

We found no modification of the variance or range of trait values along the gradient of alien species abundance at the species level. Yet, the size of hypervolumes, reflecting the overall variability in strategy at the community level, increased both in native and alien species, ultimately indicating an increase in variability among, but not within, species. This is in line with the review by Renault et al.[50], who underlined that functional diversity can considerably vary during invasion from one situation to another.

Considering the harshness of environmental conditions, facilitation is likely to occur between alien and native species. Increasing alien cover could reduce stress (e.g., wind, temperature), creating more favorable microhabitats for both native and alien species, subsequently leading to higher height and SLA. These facilitative interactions would have particularly occurred between native and alien species in the early phases of invasions at the Iles Kerguelen[28,29]. Nevertheless, native species seemed negatively affected by the development of aliens later on[51], especially as these possess traits supporting their competitive abilities.

Under competitive interactions, we assumed that coexistence mechanisms would be affected by variations in trait values along the gradient of alien species abundance. Trait divergence, a proxy for stabilizing niche differences, and trait convergence, a proxy for fitness equalizing, were expected under low and high alien species abundance, respectively. However, the comparison of recorded CWV values with the null model revealed divergence in the height, LA, and LDMC at a higher abundance of alien species. Only the SLA showed convergence with high alien species abundance, as expected. Three processes that are probably non-mutually exclusive, can have led to the observed increase in height, LA, and LDMC CWV along the gradient of alien species abundance: the increase in the abundances of more functionally diverse species *i.e.*, aliens, the increase in the functional diversity (hypervolume size) of both native and alien species, and the increase in the functional distance between alien and native species. The first process is inherent to our sampling design, while the second and the third ones would actually result from (i) the simultaneous presence of two coexistence mechanisms involving different traits along the gradient of alien species abundance or (ii) ongoing competitive exclusion.

Traits related to persistence and the tolerance of environmental stress [*i.e.*, height, LA, and LDMC[22,52]]; shifted from convergence, probably related to a stringent abiotic filter, to divergence as the alien species abundance increased, reflecting stabilizing niche differences and supporting our first hypothesis (i). However, the SLA, associated with competition, shifted from divergence to convergence (and thus fitness equalizing) along the gradient with increasing alien species abundance. Different coexistence mechanisms at play in the same individuals have been described for traits in different categories [aerial *vs*. clonal[35]], but to our knowledge, not for traits within the same functional unit (*i.e.*, leaf), which could be explained by their associations with different functions.

Considering the variation in trait values, we propose an alternative hypothesis (ii) to explain our results, which is supported by long-term data showing the exclusion of native by alien species at different sites in the sub-Antarctic Kerguelen[51]. Increase in SLA, LA, and height, and decrease in LDMC are stronger along the tested gradient, in most alien species than in native species. The resulting increase in interspecific variability at the community level, along the gradient of alien species abundance, could have led us to misidentify stabilizing niche differences. Our observations may actually be related to ongoing competitive exclusion due to inefficient fitness equalizing. In the longer term, the least competitive (*i.e.*, native) species should be eliminated by species with the highest acquisitive trait values (i.e., alien), unless they manage to catch up on trait values. *A. magellanica* could perform well, as its height is close to that of the alien species, unlike *A. selago*, which is a cushion plant with limited height.

To validate one of these two hypotheses, the study sites would need to be resampled in a few years to determine whether native species have maintained their presence *via* the stabilizing niche differences and/or fitness equalizing mechanism, or have been excluded. In addition, this could be interesting to evaluate the relative importance of competitive *vs*. facilitative interactions in the coexistence of native and alien species.

To conclude, this work demonstrated the importance of the integration of native species into studies of invasion, as the species native to the Iles Kerguelen showed unexpected competition-induced trait variation in the presence of alien species that is likely to influence the outcomes of interaction[36]. This community approach, together with the context of multiple species invasion, also enabled the identification, of the coexistence mechanisms operating along a gradient of alien species abundance. Our findings have several implications for the invasion trajectories of alien species in the sub-Antarctic region. The trait variation of native species in the presence of alien species must be considered in the determination of the most appropriate management measures[44,53]. However, alien species exhibit trait values corresponding to a rather competitive strategy. They were thus unlikely to have dominated in the cold and windy original climate of the sub-Antarctic region, but they have already benefited from current climate changes[54].

Methods

Study site

This study was carried out on different islands of the sub-Antarctic Kerguelen archipelago (Southern Indian Ocean, 49° 25' S–69° 53' E) during the austral summer (December–early January) of 2019–2020. This archipelago began to grow ~40 Ma ago from volcanic activity, while basalt eruption essentially ceased at ~24 Ma[55]. The mean annual temperature on the Iles Kerguelen is about 4.6 °C, with low thermal amplitudes (± 6 °C) over the

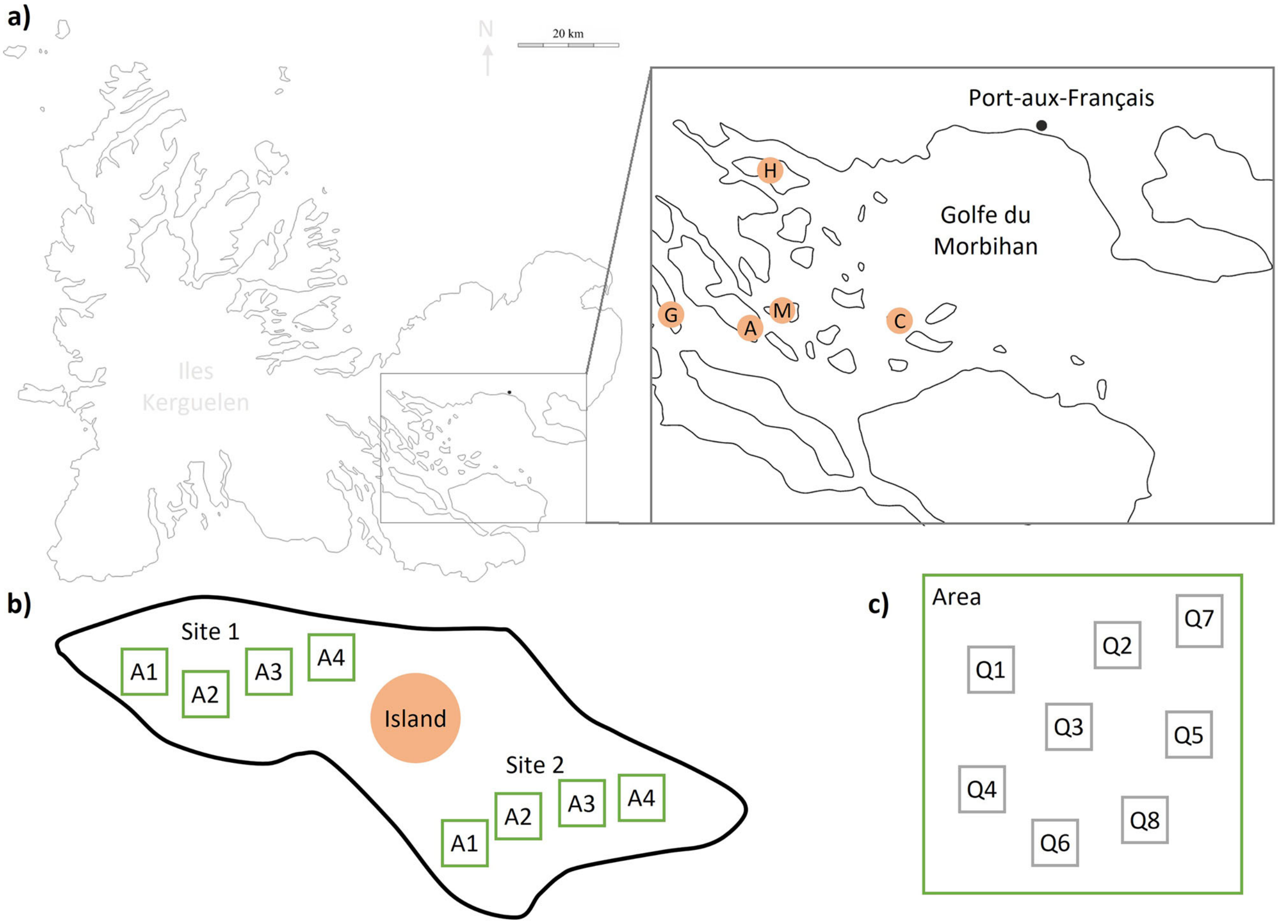

Fig. 6 | Description of the sampling design. **a** Sampled island within the Kerguelen archipelago. A Ile Australia, C Ile aux Cochons, G Ile Guillou, H Ile Haute, M Ile Mayes. The research station is located at Port-aux-Français. **b** Sampling design within each island: two sampled sites, each including four areas (1–4) with increasing abundance of alien plant species. **c** Eight quadrats are randomly positioned within each area to estimate plant species abundances.

year; precipitation is frequent, with an east–west gradient of 800–3200 mm[1]. In addition, they exhibit strong and regular winds (annual mean velocity of wind = 35 km·h^{-1}), occasionally reaching 200 km·h^{-1} [56,57]. The Kerguelen archipelago remained free of human disturbance until its discovery in 1772. Native vascular plant richness is exceptionally low, with only 29 species represented and a high rate of endemism. The isolation has been terminated with the recent human arrival, resulting in multiple alien species introductions, recorded since 1874 [*C. fontanum* and *P. pratensis*[1]]. Plant species were introduced through fodder and sowing for sheep farming, *i.e.*, through a large amount of seeds, likely limiting the genetic bottleneck of alien species. Alien species colonization on some islands in this archipelago is still in progress and can be studied over short distances (*i.e.*, under similar abiotic conditions).

Sampling design

Five islands in the Golfe du Morbihan (Iles Australia, Mayes, Guillou, Haute, and aux Cochons) were selected for plant sampling (Fig. 6a). On each island, we identified two sites that were divided into four 100-m^2 areas with increasing total abundance of alien species (0–25%, 25–50%, 50–75%, and 75–100% total cover), and decreasing total abundance of native species, creating a gradient (Fig. 6b). Depending on the island, the alien species that drives the increase in abundance varies [Supplementary Fig. 1]. As plant communities here are species-poor and locally homogeneous[1,57], the plant species composition characterized at a 100-m^2 spatial scale is a good proxy of the neighborhood composition of each sampled individual. The sampled sites were located at a distance from animal (seal, bird) colonies to prevent vegetation from trampling and massive nutrient addition. The areas within each site were <100 m from each other and at similar altitudes, slopes, and exposures, while nutrient conditions were assumed to be similar, to control the effects of abiotic filters. Abiotic conditions could vary between sites, within and between islands. In total, 40 100-m^2 areas were sampled *via* eight randomly positioned 1-m^2 quadrats each (Fig. 6c). The relative abundance (aerial cover) of all vascular species was recorded within each quadrat with 5% precision.

Trait measurement

Four traits were chosen to represent the trade-off between competitive ability (SLA, height) and stress tolerance (LDMC, LA)[37]. In each sampling area, ten mature, healthy, vegetative-stage individuals of each vascular species present were selected randomly for trait measurement. The four native and five alien plant species [Supplementary Fig. 2] that were occurring within all sampled sites, were then used for the species-level analyses (Table 1). The selected alien plant species were among the most invasive at the Iles Kerguelen[48,51].

We measured the maximum vegetative height in the field and collected a mature, sun-exposed, healthy leaf from each individual. The leaves were rehydrated for 12 h at 5 °C, weighed to determine the fresh mass (10^{-4} g precision), and scanned to determine the LA using WinFOLIA (Regent Instruments, Quebec, Canada). Then, they were dried in an oven at 65 °C for 48 h and weighed to determine the dry mass (10^{-5} g precision) for LDMC and SLA calculation[52]. As the SLA and LDMC are often correlated[22], redundancy among all traits was checked before analysis. As no significant correlation ($r > 0.7$) was observed[58], all four traits were retained in the analyses.

Table 1 | Sampled plant species

	Taxonomy		Life cycle	Growth form	
Native species					
A. magellanica Vahl, 1804	Rosaceae	Eudicotyledon	Perennial	Rhizomatous	
Austroblechnum penna-marina (Poir.) Gasper & V.A.O.Dittrich, 2016	Blechnaceae	Fern	Perennial	Rhizomatous	
A. selago Hook.f., 1847	Apiaceae	Eudicotyledon	Perennial	Cushion	
Festuca contracta Kirk, 1895	Poaceae	Monocotyledon	Perennial	Caespitose	
Alien species					*First record*
C. fontanum Baumg., 1816	Caryophyllaceae	Eudicotyledon	Biennial	Mat-forming	1874
D. glomerata L., 1753	Poaceae	Monocotyledon	Perennial	Caespitose	1977
P. pratensis L., 1753	Poaceae	Monocotyledon	Perennial	Rhizomatous	1874
T. erythrospermum Andrz. ex Besser, 1821	Asteraceae	Eudicotyledon	Perennial	Rosette	1953
T. officinale F.H.Wigg., 1780	Asteraceae	Eudicotyledon	Perennial	Rosette	1958

First records of alien species on the Iles Kerguelen are from ref. 1.

Data analyses

Univariate trait analyses at the species level. To assess whether native and alien species occupy similar trait spaces, we compared mean traits between each pair of native and alien species and between all native and alien species. We performed analyses of variance based on linear mixed-effects model procedures with the species serving as the explanatory variable (fixed effect), each trait (height, LA, SLA, and LDMC) serving as the response variable, and the sampling area/site/island serving as the random effect to account for the sampling design. Data were log-transformed before analyses when necessary.

The same procedure was used to examine trait variation along the gradient of alien species abundance in each species. The four levels of alien species abundance served as the explanatory variable (discrete variable). For each species, we built models with either the mean, variance, or range of each of the four traits serving as response variables and the site/island serving as the random effect (*i.e.*, 12 models in total per species). When a significant effect of the tested factor was found, we applied the *post-hoc* Tukey test to assess pairwise differences between levels of alien species abundance.

Univariate trait analyses at the community level. We assessed whether the distribution values of the trait along the gradient of alien species abundance differed from random (*i.e.*, reflected convergence or divergence) within communities, as a proxy of the coexistence mechanisms. For each trait, we used a null model based on the community-weighted variance (CWV) in trait values. This model was built according to Bernard-Verdier et al.[59] and considered traits and species abundance [Supplementary Fig. 1]. The null hypothesis was that species abundance would be distributed randomly with respect to trait values. Species abundance in eight quadrats per sampling area and trait values from 10 individuals distributed randomly throughout the area were assessed, with a bootstrap procedure used to match quadrats and individuals. One hundred times per quadrat, one individual per species present was selected randomly and associated with the quadrat. The observed CWV for each quadrat was then calculated[59]:

$$CWV = \sum\nolimits_{i=1}^{S} p_i \times \left(t_i - \left(\sum\nolimits_{i=1}^{S} p_i \times t_i\right)\right)^2$$

where S represents the species, t_i is the trait value of the individual of species i associated with the quadrat, and p_i is its relative abundance. Then, randomization was performed in which the list of species observed in each quadrat remained unchanged, and abundance values were shuffled among species[59]. This procedure severed relationships between trait values and species abundance while maintaining the species richness, creating a null community with no trait convergence or divergence. For each trait and quadrat, the observed CWV was compared with the CWV distribution of 999 runs of the null model. An effect size (ES) corresponding to the quantile of the null distribution to which the observed value belonged was calculated according to Bernard-Verdier et al.[59], and rescaled to the range of −1 to 1. ESs close to zero were taken to indicate species abundance that was distributed randomly with respect to trait values, and negative and positive values were interpreted as reflecting trait convergence and divergence, respectively. The ESs were submitted to the nonparametric Kruskal–Wallis rank-sum test to identify differences between levels of species abundance along the gradient, given the non-normal shape of their null distributions. When a significant level effect was found, we applied Dunn's *post-hoc* test with Bonferroni correction to assess pairwise differences between levels.

Multi-trait analyses at the community level

As changes in coexistence mechanisms must involve simultaneous variation in multiple linked traits, we built hypervolumes using multidimensional kernel density estimation[38] to account for all traits simultaneously at the community level. We computed one hypervolume with four dimensions (traits) for each species group (native and alien) and level of alien species abundance (*i.e.*, eight hypervolumes). As the abiotic conditions within each gradient of alien species abundance were similar, we assumed that observed hypervolume variations between levels of abundance were due to biotic interaction. Individual trait values were centered and scaled using means and standard deviations (SDs) for all areas and species groups simultaneously, to obtain comparable units for the axes[38]. For the centered and reduced data, hypervolumes are reported in units of SDs to the power of the number of trait dimensions used. A kernel based on the Silverman estimator and a density threshold of 5% were used[38].

To characterize the variation along the gradient of alien species abundance in each community, hypervolume sizes (volumes) were compared between levels of alien species abundance. These sizes are considered the range of values observed along each trait axis, *i.e.*, the variability of all traits forming the hypervolume, simultaneously. As they are related to the numbers of individuals used to calculate the hypervolumes[38], bootstrap techniques were used to simulate 100 hypervolumes per level of abundance with the same number of individuals[20]. Sampling with replacement was performed, with the setting of the number of draws to the case (level of abundance) with the fewest individuals sampled (*i.e.*, 180). Then, sizes were compared between levels of alien species abundance using Z tests, and p values were adjusted with Bonferroni correction for multiple comparisons. Hypervolumes were constructed using the 'hypervolume' package[38].

Hypervolume mean sizes were also compared between native and alien species. To build native and alien species hypervolumes, the same bootstrap techniques were used (100 hypervolumes were built per species group), with 500 individuals drawn for this case (from all areas, sites, and islands combined), and their mean sizes were compared using the Z test.

All analyses were performed using R ver. 4.1.2 (<www.r-project.org>).

Data availability

Data associated with the study is archived in Figshare (https://doi.org/10.6084/m9.figshare.30364114).

Received: 12 December 2024; Accepted: 23 September 2025;

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Acknowledgements

This research was supported by the French Polar Institute [projects 1322-SUBANTECO and 136-SEELIFE SUBANTECO], by the BiodivERsA ‘ASICS’ [ANR-20-EBI5-0004, BiodivClim call 2019-2020] project, and the long-term research network on biodiversity in Antarctic and sub-Antarctic ecosystems (Zone Atelier InEE-CNRS Antarctique et Terres Australes). The authors wish to thank François Massol and Hugo Saiz for their valuable advice on data analyses and Jennifer Piehl for her detailed revision of the manuscript, which greatly improved its grammatical structure.

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Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s44185-025-00112-7.

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