

Endemic species have highly integrated phenotypes, environmental distributions and phenotype–environment relationships

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ABSTRACT

Aim Why are some species geographically restricted? Ecological explanations suggest that endemic species may have restricted distributions because limited phenotypic variability results in narrow niches. However, studying variability of traits independently may not fully explain the interactions within and between complex phenotypes and environments. Here, we hypothesize that endemic species are restricted to a narrow range of habitats due to strong phenotypic integration (i.e. strong correlations among traits), strong environmental integration (i.e. strong correlations among the environments occupied) and strong correlations among trait–environment combinations.

Location The Kerguelen Islands, sub-Antarctic.

Methods We measured flowering phenology, multiple morphological characters, and species distribution along three abiotic environmental gradients (elevation, soil moisture and soil salinity) in 14 plant species whose distributions range from strictly endemic to cosmopolitan.

Results We found that for individual species, trait means and variances were independent of endemism, but that endemics occupied higher and less variable microhabitats. However, phenotypic integration, environmental integration along the three gradients, and the strength of trait–environment correlations all increased with the level of species endemism.

Main conclusions Higher levels of integration within and between phenotypes and environments are associated with more restricted geographical ranges in the species studied. In endemic species phenotypic integration may explain range contraction during the taxon cycle and reduce the ability to adapt to novel microhabitats formed as a result of environmental change.

Keywords

Abiotic environmental gradients, endemism level, functional biogeography, island biogeography, Kerguelen Islands, life-history traits, multi-species comparison, phenotypic integration, range size, sub-Antarctic.

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INTRODUCTION

Endemic species are restricted to specific, sometimes very small, geographical regions (Kruckeberg & Rabinowitz, 1985). The causes of such limited distributions have been debated for nearly two centuries (e.g. de Candolle, 1855; Stebbins, 1980; Lavergne *et al.*, 2004). Presumably, the narrow ecological and phenotypic range of a species may result in a progressive range contraction and finally lead to ende-

mism (i.e. palaeoendemism of Stebbins & Major, 1965; taxon cycles of Wilson, 1959, 1961; reviewed in Ricklefs, 2011). Alternatively, long-term *in situ* evolution within an isolated and confined area such as a remote oceanic island may lead to the appearance of new species that are endemic and which often display phenotypic adaptations to the local ecological conditions [i.e. neoendemism as described in Kruckeberg & Rabinowitz (1985) and Kraft *et al.* (2010); anagenesis of Stuessy *et al.* (2006)]. In each of these two cases, it has been

argued that endemic species are restricted to a narrow range of habitats because their phenotypes are less variable than those of widespread species (e.g. Sultan, 2001). However, it is not clear that phenotypic variability alone explains the complex nature of phenotypic responses to environmental variation (Richards *et al.*, 2005). As environment drives variability in multiple phenotypic traits (Schlichting, 1986), understanding why species have restricted distributions requires that we also examine covariation between traits (Callahan & Waller, 2000).

Phenotypic integration describes covariance in phenotypic traits that may have a shared functional, developmental or genetic basis (Pigliucci & Preston, 2004). Strong phenotypic integration means that only a subset of possible trait combinations will exist within a species – even in cases where one or more of the traits displays considerable variation (Schlichting, 1989a). Phenotypic integration may therefore limit how a species can respond to environmental variation, as traits must respond in correlated ways to change (Schlichting, 1989b). If so, being restricted to a narrow range of habitats may be due to high levels of phenotypic integration (Callahan & Waller, 2000). Alternatively, the challenge of variation in one or more environmental variable(s) may lead to the evolution of generalist strategies in which traits may vary independently. Thus widespread distributions may be associated with limited trait covariation and lower levels of phenotypic integration (Callahan & Waller, 2000).

Phenotypic integration may be influenced by both ecology and evolutionary history (Murren *et al.*, 2002). Integration levels may be increased by natural selection that improves adaptation to the external environment and/or maintains the coherence of developmental systems (Pigliucci, 2003). Alternatively, phenotypic integration may constrain phenotypic evolution because developmental and functional processes will change in a coordinated manner across the phylogeny (Fink & Zelditch, 1996; Kolbe *et al.*, 2011). Functional, developmental or genetic links between traits within a species will effectively limit its evolutionary trajectory (Pigliucci & Preston, 2004). Strong phenotypic integration may therefore contribute to endemism by driving habitat specialization (e.g. Prinzing *et al.*, 2001).

Some studies have suggested that endemic species have narrower niches than widespread species (e.g. Sultan, 2001; Kagiampaki *et al.*, 2011). However, endemic and widespread species have rarely been compared in this context (but see Richards *et al.*, 2005). Also, ecological distributions are commonly estimated using the variability associated with a single environmental variable (e.g. Richards *et al.*, 2005). However, covariation along multiple environmental axes may be more informative. We define environmental integration as the degree of correlation between abiotic variables in the habitats occupied by a species. We suggest that strong environmental integration may restrict species to certain subsets of the combinations of abiotic conditions. This may lead to the restriction of a species' ecological distribution and has often been observed within specialist species (Levins, 1968;

Ricklefs, 2011). Strong environmental integration may therefore also contribute to endemism by promoting habitat specialization.

Plant phenotypes are related to environmental variation (e.g. Murray *et al.*, 2003). Assuming that endemic species show higher levels of phenotypic and environmental integration, we would also expect phenotypes and environments to be strongly integrated for these species; that is, trait values will be strongly correlated with those of the abiotic variables. Strong correlations between traits and environments – strong phenotype–environment integration – suggest a tight relationship between the organism and the environment. Strong phenotype–environment integration may therefore act to restrict species to specific combinations of environmental variables and may lead to endemism if these combinations are themselves geographically restricted.

Traits are often compared between endemic and widespread congeners (e.g. Brown *et al.*, 2003). In such cases observed patterns may be lineage-specific (Murren *et al.*, 2002) and some authors have suggested that species from various lineages should be compared in order to account for phylogenetic effects (Gitzendanner & Soltis, 2000; Lavergne *et al.*, 2004). Moreover, such comparisons are often performed using only narrowly endemic and widely distributed species (e.g. Lavergne *et al.*, 2004). A more powerful approach to study the links between geographical restriction and trait or environmental variation is to compare species across the spectrum of distributional types. However, because differences in regional histories can strongly influence patterns of endemism (Cowling *et al.*, 1994) such comparative studies need to be made on a single regional flora (Lavergne *et al.*, 2004). Oceanic islands are especially rich in endemic species (Kruckeberg & Rabinowitz, 1985) and so make good systems for such studies. In this context, the sub-Antarctic Kerguelen Islands are of particular interest because they host species that differ in taxonomic position and geographical distribution, but that co-exist along strong abiotic gradients. The Kerguelen flora consists of 97 phanerogam species with 29 autochthonous and 68 introduced species (Frenot *et al.*, 2001; see also Hennion *et al.*, 2006a).

In this study we evaluate phenotypic integration and environmental integration as factors contributing to endemism using 14 plant species from the Kerguelen Islands. Although our sample is relatively small it includes representatives of three major angiosperm lineages (Poales, Ranunculales, core eudicots) and species with geographical distributions ranging from strictly endemic to widespread. We measured environmental and phenotypic characteristics for each species along gradients of elevation, moisture and salinity. We hypothesize that (1) correlations among traits, (2) correlations among abiotic variables in the occupied habitats, and (3) correlations between traits and environments increase with the endemism level of a plant species (Fig. 1). We also examined the relationships between endemism and phenotypic variability, mean trait values, environmental variation and mean environmental distributions.

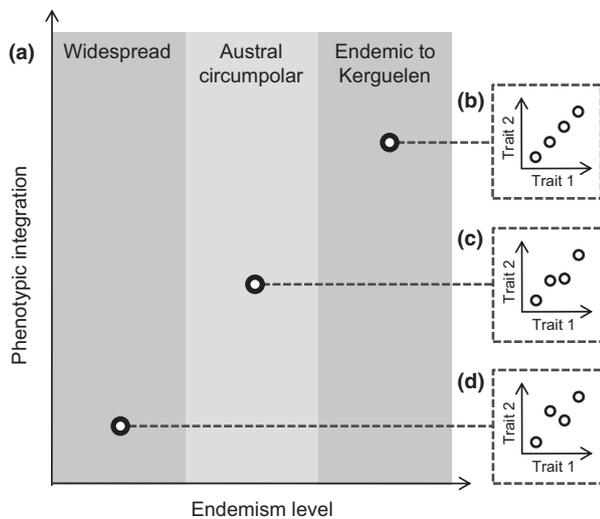


Figure 1 Schematic representation of our expectation that phenotypic integration will increase with endemism level. In this example the distributions of three hypothetical species are widespread, austral circumpolar and endemic to the Kerguelen Islands. Phenotypic integration is represented as the correlation between two traits (Trait 1 and Trait 2). In panel (a), each point represents one species. In panels (b), (c) and (d), each point represents an individual of the corresponding species. Traits are correlated within all three species, but the extent to which traits are correlated differs between species, with integration being much stronger for the Kerguelen endemic than the widespread species. We have the same expectations for environmental integration (i.e. correlations among the positions of conspecific individuals along different abiotic gradients) and phenotype–environment integration (i.e. correlations among traits and environments across the individuals of a given species).

MATERIALS AND METHODS

Study sites

The sub-Antarctic zone extends from 46° to 55° S and includes the Kerguelen Islands (49°20'00" S, 69°20'00" E) in the southern Indian Ocean (Bergstrom & Chown, 1999) (Fig. 2). We worked at four sites in the east of this island group between December 2008 and March 2009. The three coastal sites (Île Australia, Île Guillou and Isthme-Bas) have strong salinity and moisture gradients while the inland site (Val Studer) provided a strong elevational gradient (Hennion *et al.*, 2006a). Here we have used elevation as a proxy for a range of microclimatic and edaphic stressors (e.g. temperature, soil nutrient content, soil acidity) known to strongly influence plant distributions (Huntley, 1971; Anic *et al.*, 2010). In each site, we established three to nine sampling units each consisting of three sampling points (except one sampling unit of two points in Val Studer) between which we maximized differences in salinity, moisture or elevation. We replicated each type of sampling unit (salinity, moisture or elevation) under different exposures, topographic relief, etc. in order to minimize their possible effects. Over the four sites a

total of 22 sampling units and 65 sampling points were established that cover the largest possible range of salinity, moisture and elevation within the Kerguelen Islands (Table 1, Fig. 2).

Study species and endemism level

From the 97 flowering plant species that occur on the Kerguelen Islands (Frenot *et al.*, 2001) we selected 14 for our study based on three prerequisites. First, we identified plant species with different geographical distributions. We obtained geographical distributions for species from the literature and assigned each to one of seven endemism levels (see Appendix S1 in Supporting Information): (1) widespread, a worldwide distribution; (2) austral, a distribution including the sub-Antarctic region and South America; (3) sub-Antarctic; (4) endemic to the southern Indian Ocean floristic province plus Macquarie Island; (5) endemic to the southern Indian Ocean floristic province; (6) endemic to the Kerguelen and Heard & MacDonald Islands; or (7) endemic to the Kerguelen Islands. We also explored alternative assignment strategies (with three, four and five categories). However, these all resulted in the same general conclusions and we report only results based on seven categories. Four of the five widespread species (endemism category 1) were introduced within the last 200 years (Frenot *et al.*, 2001). The remaining 10 selected species were autochthonous and are assumed to have long histories in the region (Van der Putten *et al.*, 2010; Bartish *et al.*, 2012).

The second prerequisite concerned ecological characteristics. Specifically, that each of the studied species had at least one large population at the study site and species co-existed at one or more of our sampling points. The number of species sampled at each point ranged from one to eleven (with an average of five). The third prerequisite was to select both highly endemic and widespread species across a range of taxonomic positions in order to ensure that any observed patterns were independent from the position of species in a particular lineage. Species nomenclature follows Van der Putten *et al.* (2010) and higher-level relationships the APGIII (Bremer *et al.*, 2009). The selected species were distributed across seven families and three major flowering plant lineages: Poales (Poaceae), Ranunculales (Ranunculaceae), and core eudicots (Caryophyllaceae, Portulacaceae, Rosaceae, Brassicaceae and Asteraceae) (Appendix S1).

Phenotypic measurements

At each sampling point, we selected five individuals from each of the species present. Sampling was limited due to the sparse vegetation in some sites (i.e. < 10 individuals m⁻² at high elevation or high salinity sites; M. Hermant, pers. obs.). We chose robust and well-established plants. Herbivore pressure by introduced mammals was either nil (Île Australia, Île Guillou) or low (rabbits and reindeer occur at Isthme-Bas and Val Studer; Chapuis *et al.*, 1994) and at the latter sites we excluded plants obviously affected by herbivory. At each sampling point we selected plants exposed to typical environ-

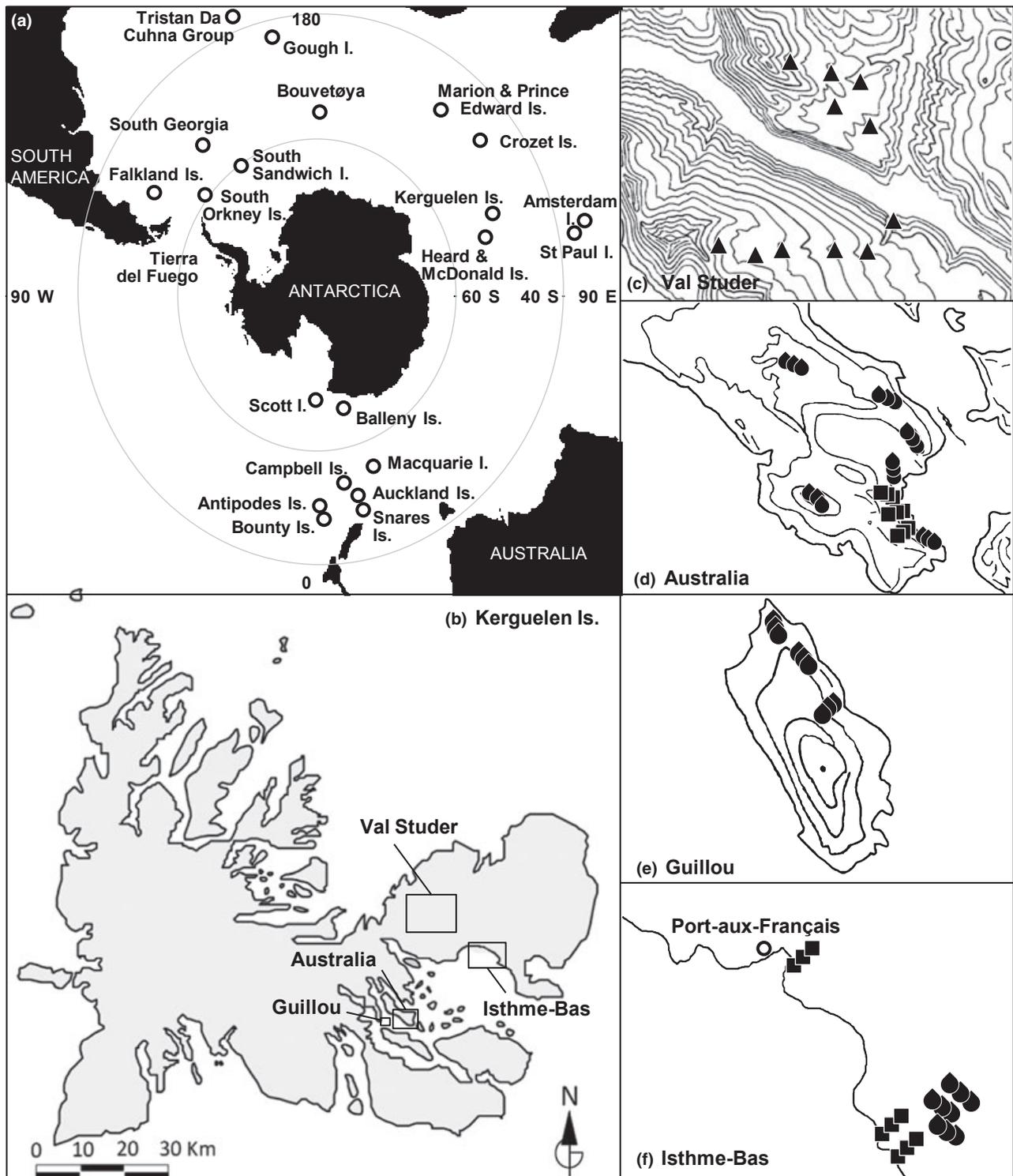


Figure 2 (a) Map of the main landmasses and islands in the Southern Hemisphere. (b) Location of the four sampling sites (Val Studer, Île Australia, Île Guillou and Isthme-Bas) on the Kerguelen Islands. Panels (c), (d), (e) and (f) show the distribution of the sampling points at the four study sites (see Table 1). We represent sampling units (each of two or three points) using different symbols (i.e. salinity (■), moisture (●) and elevation (▲)).

mental conditions (e.g. excluding individuals protected from wind by a rock).

For each individual, we measured plant height, plant diameter and the length of the largest leaf as indicators of

plant size. We adapted measurements of plant height and plant diameter to the growth form of each species (Appendix S2) and did not measure leaf length for *Lyallia kerguelensis* as it has small, coriaceous and densely imbricated leaves that

Table 1 Descriptive statistics of the three measured abiotic variables across 65 sampling points in the Kerguelen Islands.

	<i>n</i>	Mean	Minimum	Maximum	Standard deviation
Elevation (m)	65	85.52	0.00	569.00	141.30
Moisture (%)	65	53.07	9.99	94.57	24.03
Conductivity (µS/cm)	65	349.80	25.06	1585.40	350.15

n, sample size.

are not informative with respect to plant size. We recorded a fourth trait, the most advanced flowering stage, as an indicator of the plant reproductive stage (Appendix S3). These four traits are expected to be correlated within species and informative with regard to whole-plant organization. However, they are also expected to have different variances and for species to vary in their degree of integration (Fig. 1).

Environmental sampling

We measured elevation, soil moisture and soil conductivity at each sampling point (Table 1). These measurements were made at the same time as plant trait measurements. We determined elevation with a GPS (eTrex H GARMIN, resolution < 10 m). Close to the measured plants we collected five samples each of 40 mL from the uppermost 5 cm of the soil (except where the soil was thinner than 5 cm). To determine water content half of each soil sample was dried at 60 °C to constant weight. The remainder was mixed with a known volume of distilled water (15–40 mL) to obtain a supernatant. After mixing and sedimentation we determined pore water conductivity using a conductivity meter (CONSORT K810, resolution 0.1 µS cm⁻¹). We then calculated mean water content and conductivity for each sampling point. Inevitably these measures represent a snapshot of the edaphic conditions and therefore may not fully represent seasonal variation. However, we stress that the buffering effect of the ocean means that these islands are known to be among the least seasonal in the world (Convey, 1996) and that relative positions of sites along gradients are stable throughout the year. Any seasonal shifts in absolute values will have little impact on our analyses as measurements were made in a stratified fashion with the entire range of variation being sampled simultaneously at a given site.

Data analyses

Mean phenotype and phenotypic variability

For each species at each sampling point we calculated mean values of each of the traits. We also calculated mean trait values based on all sampling points in order to characterize the mean phenotype of each species within the study area. To quantify the phenotypic variability of each species we calculated coefficients of variation (CV = standard deviation/

mean) for each trait. The CV was used rather than standard deviations because the latter increased with mean values. We tested the relationships between endemism level of species and both means and CVs using Spearman rank correlation analyses. This nonparametric method was used for all our statistical tests because trait values are not normally distributed and sample sizes differed between species (Table 2), both increasing the potential bias due to outliers. We applied a Bonferroni correction to account for multiple comparisons.

Environmental means and variability

To characterize the mean position of each species along each of the three environmental gradients, we calculated mean values of elevation, conductivity and moisture based on all the sampling points where the species occurred. To quantify the environmental variability of each species we calculated CVs for elevation and salinity and the standard deviation for moisture (as this was independent of its mean). As above, we tested the relationship between endemism level and the mean and variability of species using Spearman rank correlation analyses. We applied a Bonferroni correction to account for multiple comparisons.

Phenotypic and environmental integration

There is no generally accepted method for analysing multiple trait correlations. In the current study, we quantified the level of phenotypic integration (i.e. the overall magnitude of correlations among traits) using two different approaches. First, we quantified the overall level of integration across all traits using a principal components analysis (PCA) and calculated the variance of the eigenvalues (as in Waitt & Levin, 1993; Gotsch *et al.*, 2010); the higher variance of eigenvalues indicating higher phenotypic integration. Second, we estimated for each species the total level of integration (i.e. the average correlation among pairs of traits) (García-Verdugo *et al.*, 2009). We calculated effect sizes for each pairwise comparison using the Fisher *z*-transformed Pearson correlation coefficient ('*Zr*'; Rosenthal, 1984). This coefficient was calculated from the absolute values of the correlation coefficients ('*r*' values) and reflects the strength of the relationship between traits. We also calculated the mean *Zr* values for each species, whereby higher mean *Zr* values suggest higher levels of phenotypic integration. We tested the relationships of both variance of eigenvalues and mean *Zr* values to endemism level of species using Spearman rank correlation analyses. These two approaches were also used to quantify the environmental integration of each species within the study area.

Integration between phenotype and environment

For each species we first examined the relationship between phenotype and the abiotic environment using a linear regression of a composite phenotypic variable (coordinates of local

Table 2 Sample size (n = number of sampling points occupied), mean phenotype (mean values of the four traits), phenotypic variability (coefficients of variation, CVs, of the four traits), mean position along the three environmental gradients (mean values of the three environmental variables), and variation along the three environmental gradients (CVs of elevation and salinity and standard deviation of moisture) for each of the 14 plant species studied in the Kerguelen Islands. The Spearman rank correlation coefficients (r_s) between these variables and the endemism level of species are given (n = 14, except for length of the largest leaf where n = 13, as it was not measured for *Lyalia kerguelensis*).

Species	Endemism level	n	Plant height (cm)		Plant diameter (cm)		Length of the largest leaf (cm)		Flowering stage		Elevation (m)		Moisture (%)		Salinity ($\mu\text{S}/\text{cm}$)	
			Mean	Variability	Mean	Variability	Mean	Variability	Mean	Variability	Mean	Variability	Mean	Variability	Mean	Variability
<i>Acaena magellanica</i> Vahl	2	50	17.71	28.51	11.96	25.79	6.77	33.77	2.78	74.52	32.80	227.60	59.79	21.28	487.55	127.28
<i>Colobanthus kerguelensis</i> Hook.f.	5	10	1.72	47.04	2.79	85.31	1.00	108.68	1.44	64.08	373.60	36.11	38.55	18.70	43.23	41.61
<i>Deschampsia antarctica</i> É.Desv.	3	16	5.98	30.08	9.94	48.10	6.12	39.06	1.60	46.77	145.75	132.47	67.54	23.70	787.03	127.80
<i>Festuca contracta</i> T.Kirk	3	30	17.15	44.59	16.89	32.44	17.56	42.88	3.06	37.15	60.73	181.86	53.38	21.76	382.17	193.25
<i>Lyalia kerguelensis</i> Hook.f.	7	9	6.06	44.10	12.79	42.60	–	–	2.11	80.12	132.22	9.87	23.28	9.82	122.33	52.71
<i>Montia fontana</i> L.	1	15	2.99	46.47	2.96	70.40	1.39	105.59	2.29	62.18	10.07	217.23	70.79	15.34	881.15	107.35
<i>Poa annua</i> L.	1	30	5.10	65.72	8.93	35.51	5.45	67.39	4.70	35.41	45.97	217.56	54.17	23.27	586.58	132.49
<i>Poa cookii</i> (Hook.f.) Hook.f.	4	8	11.48	33.36	17.42	53.98	12.01	32.89	1.28	144.24	236.50	109.14	77.04	11.12	1162.03	136.95
<i>Poa kerguelensis</i> (Hook.f.) Steud.	6	13	4.11	32.45	7.81	25.59	3.26	29.16	2.69	59.94	299.92	61.90	35.03	20.05	73.60	78.70
<i>Pringlea antiscorbutica</i> R.Br. ex Hook.f.	5	19	14.61	67.52	22.32	56.54	12.15	66.02	2.86	91.63	186.00	110.79	45.89	18.22	466.10	212.65
<i>Ranunculus bitermatus</i> Smith	3	18	3.12	62.36	4.32	41.17	3.41	48.90	1.16	121.45	168.11	112.46	65.58	24.98	235.97	89.54
<i>Sagina procumbens</i> L.	1	15	1.58	47.86	5.20	29.12	0.91	23.19	1.61	64.32	15.40	147.83	55.07	17.92	793.13	127.04
<i>Senecio vulgaris</i> L.	1	14	15.82	43.31	8.42	65.72	2.73	40.58	5.13	40.05	7.14	71.36	46.70	13.93	672.54	145.50
<i>Taraxacum erythrospermum</i> Andrzej. ex Besser	1	28	11.60	63.43	18.77	37.61	14.03	52.78	3.88	61.63	31.14	181.87	52.73	17.33	354.13	204.61
Relationship to endemism (r_s)	–	–	0.00 ^{ns}	–0.23 ^{ns}	0.16 ^{ns}	0.06 ^{ns}	0.16 ^{ns}	–0.09 ^{ns}	–0.43 ^{ns}	0.41 ^{ns}	0.85 ^{***}	–0.73 [*]	–0.47 ^{ns}	–0.05 ^{ns}	–0.56 ^{ns}	–0.37 ^{ns}

^{ns} $P > 0.05$, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$, after Bonferroni correction.

populations on PC1 of the four trait variables) and a composite environmental variable (coordinates on PC1 of the three abiotic variables). As above, we calculated the effect size of this linear regression as a Fisher coefficient Z_r from the corresponding r values. Because species may possess fundamentally different morphological and physiological characteristics in response to different environmental gradients, we also examined the univariate relationships between traits and abiotic variables for each species. Plant traits were regressed against environmental variables using simple linear regressions (we confirmed the absence of nonlinear relationships). We again calculated the effect sizes using a Fisher coefficient Z_r . Thus for each species, we obtained 12 effect sizes. Finally, we tested relationships between the endemism level of species and (1) the effect sizes from the regression of trait coordinates and environmental coordinates, and (2) the mean of effect sizes using Spearman rank correlation analyses. All analyses were performed with the statistical software STATISTICA 9.1 (Statsoft Inc., Tulsa, OK, USA, 2010).

RESULTS

Phenotypic and environmental mean values and variabilities

Relationships between endemism level and the means and variabilities of traits and environmental values are given in Table 2. We found that neither mean values nor CVs of plant traits correlate with endemism levels. Similarly, we found no significant relationship with moisture or salinity gradients. However, means and variabilities of abiotic variables along the elevational gradient do vary significantly with species endemism level. Endemics occupy higher elevation and less variable positions along this gradient.

Phenotypic integration

The variance of eigenvalues from the phenotype PCA significantly increased with species endemism (Spearman rank correlation, $n = 14$; $r_s = 0.78$; $P = 0.001$). Species with the greatest integration were *Pringlea antiscorbutica* (eigenvalue variance of 3.09) and *Lyallia kerguelensis* (2.02), which belong to endemism categories 6 and 7, respectively. The species with the least integration were *Montia fontana* (0.77) and *Sagina procumbens* (0.49), which are both widespread (endemism category 1). Only one strongly endemic species exhibited low phenotypic integration, *Poa kerguelensis* (1.37). The mean effect sizes from pairwise comparisons of traits also suggested that integration increases with species endemism level (Fig. 3a).

Environmental integration

The variance of eigenvalues from the environmental PCA also significantly increased with species endemism level (Spearman rank correlation, $n = 14$; $r_s = 0.55$; $P = 0.03$).

The level of environmental integration across the species in the five highest endemism levels (categories 3–7) was highly variable (eigenvalue variance = 0.33–1.25) but less so for more widespread species (categories 1–2) (0.21–0.82). Analysis of mean effect sizes from pairwise comparisons of environmental variables also supported this result (Fig. 3b). Note that exclusion of an outlier (*Deschampsia antarctica*, $Z_r = 1.22$) does not alter the overall result (Spearman rank correlation: $n = 13$; $r_s = 0.72$; $P = 0.005$).

Phenotype–environment integration

Effect sizes from regression of trait PC1 coordinates on environmental PC1 coordinates significantly increased with species endemism level (Spearman rank correlation, $n = 14$; $r_s = 0.64$; $P = 0.01$). The highest effect sizes were found for *Poa kerguelensis* (1.22) and *Lyallia kerguelensis* (0.77) and the lowest for the more widely distributed *Poa annua* (0.06) and *Ranunculus biternatus* (0.03). Analyses based on individual traits also indicate that species means increase significantly with endemism level (Fig. 3c).

DISCUSSION

This study combines geographical distribution information with field measurements of phenotype and environmental variables for 14 plant species growing in the sub-Antarctic Kerguelen Islands. With the exception of elevation we found that trait means and variabilities are independent of species endemism levels. This is not consistent with the hypothesis that endemic species are specialized to narrow habitats due to less variable phenotypes (e.g. Sultan, 2001). However, it does fit with the idea that phenotypic variability does not fully describe the phenotypic responses of species to environmental variation (Richards *et al.*, 2005). Our study provides the first evidence for increases in phenotypic integration, environmental integration and phenotype–environment integration with species endemism levels. Our data suggest that species with higher endemism levels may only exhibit certain combinations of phenotypic traits and be limited to particular combinations of environmental conditions. Ultimately, high phenotypic and environmental integration may result in strong trait–environment correlations. These patterns were consistent across taxonomic groups and the represented life-history modes (e.g. growth form, reproduction and dispersal).

We found that the more endemic species grow at higher mean elevations and exhibit less elevational variation. In the Kerguelen Islands this corresponds to harsher abiotic conditions (see Le Roux & McGeoch, 2010, for analogous data from Marion Island). These harsh abiotic conditions may constrain endemic species to certain trait combinations (Schlichting, 1989a; Gianoli & Palacio-López, 2009; see Hermant *et al.*, 2012, on clade-level variation) even if each of the traits vary markedly. This interpretation provides a new perspective on the well-established hypothesis that endemic species

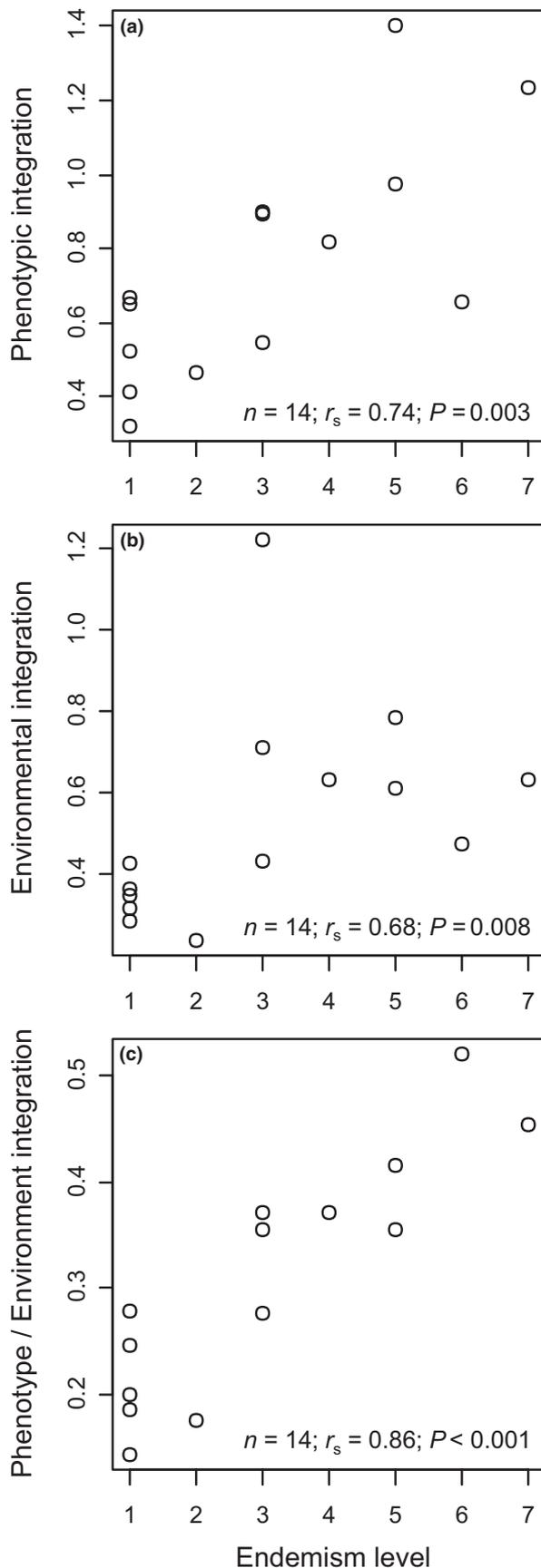


Figure 3 Relationships between the level of plant species endemism in the Kerguelen Islands and (a) phenotypic, (b) environmental, and (c) phenotype–environment integration. Phenotypic integration is given as the mean effect size (i.e. the Fisher z -transformed Pearson correlation coefficient, Z_r) from pairwise comparisons of the traits measured for each species. Environmental integration is given as the mean effect size from pairwise comparisons of environmental variables measured at the sites where a species is present. Phenotype–environment integration is the mean effect size from simple linear regressions between traits and environmental variables. The endemism level of species was determined according to their geographical distribution (see Materials and Methods).

are specialists to particular ecological conditions (Stebbins, 1980). Endemics may perform very well in their own habitats, in terms of survival and reproduction, but be unable to occupy others (Caley & Munday, 2003). Conversely, widespread species may cope with a wider range of habitats but their performance will be weaker in most habitats (Sultan *et al.*, 1998; Richards *et al.*, 2005). There is some evidence for such trade-offs in the autochthonous sub-Antarctic flora. All but one of the species endemic to the South Indian Ocean Province have regular and relatively high viable seed production as well as sharing rapid seed development and early ripening, a phenology considered opportunistic and adaptive to a harsh climate (Hennion *et al.*, 2006b). The exception is *Lyallia kerguelensis*. In contrast, some non-endemic members of the autochthonous flora have limited seed fertility (Hennion *et al.*, 2006b). One approach to testing whether stronger phenotypic integration results from specialization of endemic species to high-elevation habitats would be to cultivate these species in a common, low-elevation environment and examine whether integration weakens after several generations (e.g. Gianoli, 2004).

We found that endemics are characterized by both phenotypic and environmental integration and that these are themselves correlated. This suggests that integration may be self-reinforcing and could eventually lead to plants specializing on particular combinations of traits and environments. Evolutionary trajectories that lead to increasing specialization have previously been discussed (i.e. ‘generalist-to-specialist’ or ‘specialization as a dead end’ hypothesis; Colles *et al.*, 2009), but supporting evidence is mixed (see Colles *et al.*, 2009, for a review). In particular, the underlying mechanisms have prompted considerable debate (see Fry, 2003, for a review). The process suggested above, where integration generates further integration, represents an additional mechanism and might function entirely via the interconnectedness of phenotype and niche. The underlying mechanism may be the existence of genetic covariances (Pigliucci & Schlichting, 1998) that limit independent trait responses to environmental changes, thereby maintaining and, indeed, increasing levels of phenotypic integration. Phenotypic integration may result in more efficient adaptation because natural selection would

operate on trait sets rather than on several individual traits. Increasing integration would be most successful when local environmental conditions are stable (Sandel *et al.*, 2011); in the sub-Antarctic islands such stability is promoted by the buffering impact of the surrounding ocean (Convey, 1996). Our hypothesized mechanism should be reversible. We see no reason that disintegration or reduced integration should not promote further disintegration. Such disintegration might be triggered, for instance, by a shift in geographical extent that exposes a species to novel combinations of environmental factors (Jackson & Overpeck, 2000). Species that currently have wide geographical distributions may have experienced multiple perturbation events and therefore be less specialized.

The conclusion raised from our described case that integration may be a self-reinforcing process that may lead to adaptation in climatically stable insular environments is consistent with a scenario of novel endemic species originating from long-term *in situ* evolution within islands [i.e. neoendemism as described in Kruckeberg & Rabinowitz (1985) and Kraft *et al.* (2010); anagenesis of Stuessy *et al.* (2006)]. However, this conclusion is also consistent with the alternative hypothesis of endemism resulting from progressive restriction of species ranges through time (i.e. palaeoendemism of Stebbins & Major, 1965). Increased knowledge of the relationships and colonization histories of sub-Antarctic plant species would be required to be able to putatively assign one or the other scenario to the origin of each of the species. However, the hypothesis of palaeoendemism is somewhat supported, with evidence for the long-term (million year time-scales) survival of the flora and particular species in the region. Large-scale analyses of present-day vegetation, combined with all glaciological, geological and palaeobotanical observations available for the sub-Antarctic islands, suggest survival of at least part of the autochthonous sub-Antarctic flowering plant flora in local refugia during the last ice age (Van der Putten *et al.*, 2010), a scenario that was supported for terrestrial arthropods in the Antarctic continent (Mortimer *et al.*, 2011; Allegrucci *et al.*, 2012). Moreover, the dates of phylogenetic divergences in several plant groups support this scenario (Wagstaff & Hennion, 2007; Wagstaff *et al.*, 2011; Bartish *et al.*, 2012).

Otherwise, our results are consistent with and may even help explain 'taxon cycles' (Wilson, 1959, 1961; Ricklefs, 2011), the repeated expansion and contraction of species ranges that have been associated with shifts in ecological distribution and adaptations to changing ecological conditions (Ricklefs & Bermingham, 2002). Ricklefs & Cox (1972) suggest that range contractions during such taxon cycles are due to co-evolution with antagonists together with competition from newly arrived colonists. Our results suggest another, non-exclusive, explanation. Specifically, that species arriving in relatively stable and buffered island climates show increasing, self-reinforcing phenotypic and environmental integration, resulting in range contractions. To test this hypothesis further data on the phylogenies and histories of colonization and habitat shifts of sub-Antarctic species and their

continental relatives are required (Mosyakin *et al.*, 2007; Bartish *et al.*, 2012).

Although our study provides evidence for endemism being associated with strong phenotypic, environmental and phenotype-environment integrations, several potential issues remain. First, our species sample is relatively small and this may limit our ability to generalize. However, this is somewhat offset by the broad taxonomic range and distributional types of the included species. Second, we recognize that our analyses are based on realized niches and that endemic species, like any other, may have fundamental niches that potentially allow them to persist in a wider range of environments. It is nearly impossible to identify the fundamental niche of a species. However, if fundamental and realized niche sizes are correlated then our findings would still hold. The absence of correlations between variability of traits or environmental characteristics (except elevation) and endemism does not rule out such a link between fundamental and realized niches. That sub-Antarctic species generally occupy highly similar habitats throughout their geographical range (Huntley, 1971; Smith, 1984) certainly tends to support the suggestion that the fundamental and realized niches may be closely related in these species. Third, the limited number of traits and individuals measured may limit our ability to estimate levels of integration. In both cases the issue is that outliers could have biased our estimates of means and variability. Indeed, this might explain the relatively low estimate of phenotypic integration for *Poa kerguelensis*. However, because the variability of individual traits is not related to endemism (Table 2) it appears that estimates of integration for endemic species were not influenced by extreme variability in a single trait. In addition, integration still significantly increased with endemism level when sample size was included as a covariable in multiple linear regressions (results not shown). In these analyses, sample size was not significantly related to integration or endemism level. Finally, our approach did not consider the possibility that plants have distinct functional units and that integration may vary between them (Pigliucci & Schlichting, 1998). In this case we have used traits that are integrative at the whole-plant level. We have provided a first estimation of the phenotypic integration and in order to better understand the relationship between integration and endemism further studies are required to explore how patterns of phenotypic integration in different subsets of traits vary among species and environments (e.g. Kolbe *et al.*, 2011).

The fact that endemic species have higher levels of phenotypic integration and are restricted to certain combinations of environmental conditions may have important implications given climate change trends in the sub-Antarctic (Bergstrom & Chown, 1999; Frenot *et al.*, 2006). High sensitivity to desiccating conditions has already been reported for several endemic species and implies a limited ability to cope with certain environmental changes (Chapuis *et al.*, 2004; Hummel *et al.*, 2004). Moreover, a recent study has shown that a relatively short period of rapid warming has led to large changes in the distribution of species and community

organization on Marion Island. This suggests that autochthonous communities may be particularly sensitive to climate change (Le Roux & McGeoch, 2008). Our analyses suggest that the sensitivity of endemics may be linked to the disappearance of the small sets of environmental combinations that they can occupy. If so, this presents a major challenge to their survival. Weak integration in cosmopolitan species may allow them to occupy a wide range of habitats and thus contribute to invasion success (Stohlgren *et al.*, 2011). Such insights may help in the prediction of vegetation changes in the sub-Antarctic, as well as the conservation of these floras, given the rapid climatic change in this region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Phylogenetic relationships, geographical distributions and the corresponding endemism levels of the 14 plant species studied in the Kerguelen Islands.

Appendix S2 Measurements of plant height and plant diameter appropriately to the growth form of each plant species.

Appendix S3 Flowering stages of the 14 plant species studied in the Kerguelen Islands.

BIOSKETCH

Marie Hermant is a post-doctoral researcher interested in evolutionary ecology. She is currently focusing on the ecological causes and implications of trait variability and covariability in plant species and clades.

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Author contributions: M.H. and F.H. conceived the ideas with assistance from A.P.; M.H. collected the data; M.H. analysed the data with the assistance of A.P.; M.H., F.H. and A.P. led the writing; and P.V. and P.C. provided input that aided in the development of ideas, methods and the writing.

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