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PAPER



Evolutionary size changes in plants of the south-west Pacific

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ABSTRACT

Aim To investigate evolutionary changes in the size of leaves, stems and seeds of plants inhabiting isolated islands surrounding New Zealand.

Location Antipodes, Auckland, Campbell, Chatham, Kermadec, Three Kings and Poor Knights Islands.

Methods First, we compared the size of leaves and stems produced by 14 pairs of plant taxa between offshore islands and the New Zealand mainland, which were grown in a common garden to control for environmental effects. Similar comparisons of seed sizes were made between eight additional pairs of taxa. Second, we used herbarium specimens from 13 species pairs to investigate scaling relationships between leaf and stem sizes in an attempt to pinpoint which trait might be under selection. Third, we used herbarium specimens from 20 species to test whether changes in leaf size vary among islands located at different latitudes. Lastly, we compiled published records of plant heights to test whether insular species in the genus *Hebe* differed in size from their respective subgenera on the mainland.

Results Although some evidence of dwarfism was observed, most insular taxa were larger than their mainland relatives. Leaf sizes scaled positively with stem diameters, with island taxa consistently producing larger leaves for any given stem size than mainland species. Leaf sizes also increased similarly among islands located at different latitudes. Size changes in insular *Hebe* species were unrelated to the average size of the respective subgenera on the mainland.

Main conclusions Consistent evidence of gigantism was observed, suggesting that plants do not obey the island rule. Because our analyses were restricted to woody plants, results are also inconsistent with the ‘weeds-to-trees’ hypothesis. Disproportionate increases in leaf size relative to other plant traits suggest that selection may favour the evolution of larger leaves on islands, perhaps due to release from predation or increased intra-specific competition.

Keywords

Biogeography, dwarfism, gigantism, island, island rule, leaf, morphology, New Zealand, plant, seed.

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INTRODUCTION

There is a long history of interest in how plants evolve on isolated islands. The closest relatives of many tree species inhabiting isolated islands are small, herbaceous species, leading to speculation that island plants often follow a ‘weeds-to-trees’ evolutionary pathway (Carlquist, 1974). The weeds-to-trees pathway begins when isolated islands are colonized by weedy herbs, which often have elevated powers of dispersal relative to other types of plants. Due to the depauperate nature of islands, weeds evolve increased woodiness (i.e. arborescence) to exploit

the niche left open by the absence of trees, which often have reduced dispersal capacities compared to weeds. Phylogenetic work has confirmed that many plant species evolve increased woodiness after colonizing isolated islands (Böhle *et al.*, 1996; Panero *et al.*, 1999; Percy & Cronk, 2002; Lahaye *et al.*, 2005).

After dispersing to islands, plants might also be exposed to reduced levels of herbivory, as herbivore species that are common on the mainland often fail to reach isolated islands. This may allow for the evolution of larger leaves, given that small leaf sizes may deter large herbivores (Bond *et al.*, 2004). Once released from elevated levels of herbivory, selection may favour

large leaf sizes, which may be competitively advantageous in low-light environments (Williamson, 1983).

On the other hand, not all island plants show evidence of gigantism. Dwarfism has also been documented in plants inhabiting insular environments (Lloyd, 1981) and plants could fall under the domain of the island rule. The 'island rule' relates evolutionary changes in body size on isolated islands to the size of colonizing species (Van Valen, 1973). The island rule predicts that bigger animals evolve into dwarfs on islands and that smaller animals evolve into giants. The island rule has been the subject of intense empirical scrutiny and many studies have found support for it (Lomolino, 2005; Lomolino *et al.*, 2006; McNab, 2010). However, other studies indicate that evidence for the island rule is sensitive to how the data are analysed and to the types of animals under investigation (Meiri *et al.*, 2006, 2009; Welch, 2009).

Size is difficult to characterize with a single parameter and difficulties in characterizing body size are especially pronounced in plants. Plants are modular organisms that produce groups of organs (e.g. stems and leaves), which are coordinated physiologically but function somewhat autonomously. Corner (1949) was the first to recognize that different organs such as leaves, stems and flowers covary allometrically (see also Enquist *et al.*, 2007). Scaling relationships in plant traits make it possible to measure particular aspects of plant morphology, for example leaf size, from which inferences can often be made about other morphological attributes, such as stem and flower sizes (see Niklas, 1994).

Here, we investigate evolutionary size changes in plants inhabiting a series of islands that span over 20° in latitude in the south-west Pacific. First, we utilized plants growing in a large common garden to compare leaf, stem and seed sizes between island taxa and their 'mainland' relatives on New Zealand's North and South Islands. Second, using herbarium specimens, we assessed scaling relationships between leaf and stem sizes in an attempt to pinpoint which plant traits might be under selection on islands. Third, we used herbarium specimens to test whether size changes varied among islands situated at different latitudes. Lastly, we tested for insular size changes in the genus *Hebe*, which is a large genus of trees and shrubs that has radiated autochthonously in New Zealand and includes six species that are endemic to offshore islands. We used previously published records of maximum plant heights to test whether size changes in insular species of *Hebe* were linked to the phenotype of their mainland relatives.

MATERIALS AND METHODS

New Zealand is an isolated landmass in the south-west Pacific Ocean that comprises several main islands and numerous satellite islands (Fig. 1). The main islands (North, South and Stewart Islands) rifted away from Gondwana 80 million years ago and have changed in latitudinal position, size and elevation throughout their geological history (see Gibbs, 2006). At present, numerous satellite islands surround the main islands, the floras of which are derived from overwater dispersal from New Zealand. Although many of these islands were connected by land bridges during the Last Glacial Maximum, we focused on six island

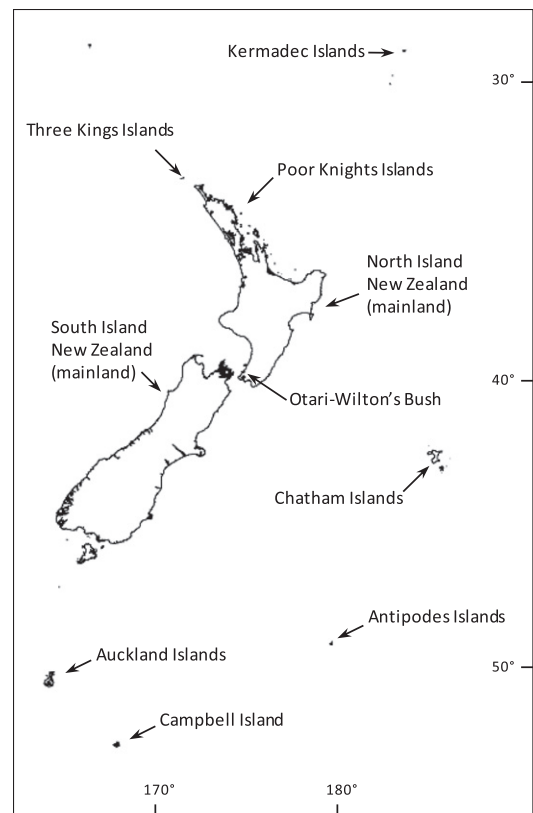


Figure 1 Map of study islands surrounding New Zealand.

groups that remained isolated from New Zealand in the Pleistocene and have long histories of geographic isolation (see Appendix S1).

Otari-Wilton's Bush (OWB, 41°14' S, 174°45' E) is located on the southern tip of the North Island of New Zealand. It consists of an extensive garden that is located immediately adjacent to approximately 70 hectares of undisturbed conifer-broadleaf forest (see Dawson, 1988). The garden contains many plant taxa that are native to the offshore islands described above, in addition to taxa that were sourced from other regions of the New Zealand mainland (i.e. the North and South Islands). Many taxa in the garden are long-lived trees that take decades to reach maturity. But because they were planted nearly a century ago, most were fully grown and all were reproductively mature. Consequently, many plants that are native to New Zealand's offshore islands grow immediately adjacent to related taxa from the New Zealand mainland, either in the garden or in the forest adjacent to the garden. This situation is ideal for investigating size changes in New Zealand plants because it literally is a 'common garden' and effectively controls for environmental effects on morphology. The climate in OWB is intermediate to the six offshore archipelagos used in this study, with a mean annual temperature of 13 °C and annual precipitation averaging 1250 mm.

Leaf, stem and seed size comparisons between islands and the mainland

To examine patterns of change in the morphology of plants on offshore islands, we compared the morphology of insular plants

Table 1 Source locations, average leaf area (cm²) and average stem diameter (cm) for 14 pairs of study species grown in standardized environmental conditions. All other plants were grown in a common garden in Otari-Wilton's Bush, Wellington, New Zealand. For each taxonomic pair, island taxa are listed first, followed by mainland taxa. Sources for mainland taxa refer to source locations for seeds. Numbers in parentheses refer to sample sizes; the number of individuals is followed by the number of leaves and stems, respectively. Nomenclature follows Allan (1961).

Species	Source	Leaf size	Stem size
1. <i>Alectryon excelsus</i> subs. <i>grandis</i>	Three Kings Islands	28.08 (1, 10)	1.84 (1, 20)
<i>Alectryon excelsus</i>	Wellington	20.77 (1, 7)	1.60 (1, 20)
2. <i>Apium prostratum</i>	Chatham Islands	6.73 (1, 20)	0.22 (1, 20)
<i>Apium prostratum</i>	Wellington	6.15 (1, 20)	0.25 (1, 20)
3. <i>Coprosma acerosa</i>	Chatham Islands	0.07 (1, 10)	0.82 (1, 20)
<i>Coprosma acerosa</i>	Canterbury, Wellington	0.06 (2, 20)	0.72 (2, 40)
4. <i>Coprosma macrocarpa</i>	Three Kings Islands	79.51 (3, 20)	2.80 (3, 60)
<i>Coprosma macrocarpa</i>	Surville Cliffs	12.41 (1, 10)	2.69 (1, 20)
5. <i>Coprosma propinqua</i> var. <i>martini</i>	Chatham Islands	0.50 (2, 20)	1.09 (2, 40)
<i>Coprosma propinqua</i>	Fjordland, Wellington, Canterbury	0.16 (3, 30)	0.91 (3, 60)
6. <i>Geniostoma rupestre</i>	Poor Knights Islands	23.13 (1, 10)	1.20 (1, 20)
<i>Geniostoma rupestre</i>	Wellington	17.49 (1, 10)	1.29 (1, 20)
7. <i>Macropiper melchoir</i>	Three Kings Islands	113.3 (1, 10)	n.a.
<i>Macropiper excelsum</i>	Wellington	49.68 (2, 20)	n.a.
8. <i>Melicope</i> aff. <i>ternata</i>	Three Kings Islands	14.15 (1, 10)	2.83 (1, 20)
<i>Melicope ternata</i>	Wellington	8.98 (1, 10)	0.83 (1, 20)
9. <i>Muehlenbeckia australis</i>	Chatham Islands*	1.47 (4, 20)	1.57 (4, 20)
<i>Muehlenbeckia australis</i>	Wellington*	0.46 (4, 20)	0.86 (4, 20)
10. <i>Myrsine divaricata</i>	Poor Knights Islands	1.36 (1, 10)	1.75 (1, 20)
<i>Myrsine divaricata</i>	Auckland, Southland, Stockton	0.87 (3, 30)	1.52 (3, 60)
11. <i>Myoporum laetum</i>	Three Kings Islands	30.68 (4, 40)	4.27 (4, 80)
<i>Myoporum laetum</i>	Wellington	12.69 (2, 20)	2.45 (2, 20)
12. <i>Pennantia baylissiana</i>	Three Kings Islands	160.72 (2, 20)	6.67 (2, 40)
<i>Pennantia corymbosa</i>	Wellington	9.56 (1, 10)	1.70 (1, 20)
13. <i>Plagianthus regius</i> var. <i>chathamica</i>	Chatham Islands	23.60 (4, 40)	1.69 (4, 80)
<i>Plagianthus regius</i>	Taranaki	13.92 (1, 10)	1.12 (1, 20)
14. <i>Streblus smithii</i>	Three Kings Islands	92.28 (1, 11)	4.11 (1, 11)
<i>Streblus banksii</i>	Wellington	8.18 (1, 11)	1.75 (1, 11)

*Denotes species grown in controlled glasshouse conditions.

with that of their closest relatives on the mainland. We evaluated three aspects of plant morphology: leaf, stem and seed sizes. Leaf and stem sizes were compared between all island taxa that were both cultivated in the garden at OWB and occurred in forest surrounding the garden (Table 1). We also investigated *Muehlenbeckia australis*, the seeds of which we collected by hand on Chatham Island and grew in a glasshouse alongside plants originating from seeds collected in OWB. The glasshouse was located 5 km south of OWB on the Victoria University of Wellington campus, which experiences similar temperatures to OWB. Glasshouse plants were watered to saturation daily and grown for a full calendar year.

Establishing the mainland relatives of island taxa that were undifferentiated taxonomically from the mainland was straightforward. Pairings between mainland species and insular varieties or subspecies were also straightforward. One taxonomic pair comprised an insular species of uncertain taxonomic status (*Melicope* aff. *ternata*) but which was clearly aligned with one particular mainland species (*Melicope ternata*). Three additional taxonomic pairs comprised different species which are closely

related florally and occasionally hybridize when grown together in cultivation, despite pronounced differences in vegetative morphology (e.g. *Pennantia baylissiana* and *Pennantia corymbosa*).

For each taxonomic pair, we collected 7–40 leaves and measured 11–80 stems from one to four plants from each taxon (see Table 1). The leaves and stems chosen for measurement were selected randomly from the total pool available on each plant and the number of individuals included in sampling was determined by their availability in the garden. Stem size was quantified with digital callipers as the diameter of the stem immediately adjacent to the point of petiole attachment, avoiding any swelling associated with the petiole. Leaf sizes were characterized by converting laminae (after removing the petiole) into digitized images using an HP Scanjet 5400c computer scanner. Images were imported into *Image-J* (Abramoff *et al.*, 2004) and their total area was obtained (cm²).

Insular tree species growing in OWB often produce seeds. Therefore, a similar species pool might have been used in island–mainland comparisons of seed sizes. However, the size and shape of seeds produced by insular taxa growing in the

Table 2 Average seed sizes (surface area, mm²) in eight plant taxa inhabiting both the Chatham Islands and the New Zealand mainland (Wellington). Numbers in parentheses refer to the number of individuals and seeds sampled, respectively. Three species have been designated a different status on the Chatham Islands (*Apium prostratum* var. *denticulata*, *Rhopalostylis* aff. *sapida*, *Coprosma propinqua* var. *martinii*).

Species	Island	Mainland
1. <i>Apium prostratum</i>	2.93 (5, 38)	4.05 (3, 30)
2. <i>Coprosma acerosa</i>	10.85 (2, 24)	3.26 (1, 30)
3. <i>Coprosma propinqua</i>	14.65 (3, 24)	11.75 (1, 30)
4. <i>Macropiper excelsum</i>	3.94 (3, 32)	3.59 (3, 30)
5. <i>Muehlenbeckia australis</i>	9.10 (3, 35)	6.98 (3, 30)
6. <i>Rhipogonum scandens</i>	69.55 (3, 23)	55.40 (5, 33)
7. <i>Rhopalostylis sapida</i>	175.93 (3, 24)	80.79 (3, 30)
8. <i>Tetragonia trigyna</i>	28.85 (2, 23)	14.25 (3, 30)

garden were sometimes anomalous. For example, the seeds of the insular form of *Coprosma macrocarpa* (Rubiaceae) regularly had a distinctive shrunken, withered appearance. Most insular taxa are represented by one or a small number of individuals in OWB, so out-crossing with mainland relatives may occur frequently. If insular taxa were self-incompatible or were reproductively isolated from their mainland relatives, the unusual appearance of seeds may result from genetic incompatibility between parent plants. Therefore, a different sampling protocol and species pool was used to investigate seed sizes.

Data on seed sizes were collected from species that could be collected by hand from Chatham Island in January 2008. Searches for seeds were made in Henga Forest Reserve (43°51.0' S 176°33.2' W), a 177-ha remnant forest patch on the central west coast of Chatham island, and Nikau Forest Reserve (43°45.7' S 176°34.8' W), a 19-ha forest patch near the northern coast of the island. Measurements were made on 23–38 seeds collected from two to five individuals of eight species on the Chatham Islands, and on 30–33 seed collected from one to five individuals from closely related taxa on the mainland (see Table 2). Seeds from mainland taxa were collected from either OWB or from Moa Point, which is located approximately 10 km south of OWB. For each individual, many fruits were collected haphazardly, from which a subset of approximately 30 was selected randomly. Seed size can be characterized in a variety of different ways (Cornelissen *et al.*, 2003). We used seed surface area (the product of the maximum length and width of each seed) because of its simplicity.

To test for size trends in plants on islands, we conducted reduced major axis regression between average values for island and mainland taxa. Average values of leaf, stem and seed sizes for island taxa were treated as dependent variables (*y*-axes), values for mainland taxa were treated as independent variables (*x*-axes) and separate analyses were conducted on each trait. We obtained slope and intercept parameters using reduced major axis regression (Bohonak & van der Linde 2004) instead of standard linear regression because both variables are subject to sampling and

measurement error (see Price & Phillimore, 2007). All data were natural logarithm-transformed prior to analyses to conform to assumptions.

Leaf and stem allometry

We used herbarium specimens to document scaling relationships between leaf and stem sizes and to establish whether they differ between islands and the mainland. For this analysis, we focused on species listed in Heenan *et al.* (2010), who identified the closest mainland relative of all species endemic to the Chatham Islands using molecular tools. We characterized leaf and stem sizes for all species listed in Heenan *et al.* (2010) that were also present in Te Papa Tongarewa, the National Museum of New Zealand ($n = 13$). In cases where a single unambiguous mainland ancestor could not be identified, and instead several possible mainland ancestors were identified, measurements were made on all putative mainland ancestors and averaged (see Table 3).

Herbarium policy prohibited destructive sampling, so exact measures of leaf size using computer scanners were impossible. Instead, we quantified leaf sizes by measuring leaf length (the linear distance between the leaf tip and the base of the petiole) and leaf width (the maximum distance perpendicular to the length measurement at the widest point of the leaf) on two randomly selected leaves from each specimen. Leaf area was then calculated as the product of leaf length and width. Stem diameters were measured 10 mm towards the base of the specimen from the point of petiole attachment for each randomly selected leaf. Measurements were averaged among leaves and stems within each specimen prior to analyses.

Species were often represented by a variable number of herbarium specimens. For those species that were represented by fewer than seven specimens, all specimens were analysed. However, most species were represented by more than seven specimens, from which seven were randomly selected for analyses. Therefore, a variable number of herbarium specimens were used to characterize each species (see Table 3).

To test whether leaf sizes scaled with stems sizes and to determine whether scaling relationships differed between islands and the mainland, we conducted an analysis of covariance (ANCOVA). Leaf sizes were treated as the dependent variable, stem sizes were included as the covariate and site (island versus mainland) was considered a fixed factor. We conducted the analysis using the general linear model procedure in SPSS (2002) on natural logarithm-transformed data following Engqvist (2005). In addition to this analysis, we also conducted reduced major axis regression to evaluate overarching evolutionary size trends using the same methods described previously.

Comparisons among islands

Herbarium specimens were also used to assess whether evolutionary size changes differed among islands. We identified 20 species that were represented by specimens that were collected on the New Zealand 'mainland' (North and South Islands) as well as

Table 3 Average leaf area (cm²) and average stem diameter (cm) of 13 plant taxa inhabiting both the Chatham Islands (listed first) and the New Zealand mainland (listed subsequently). Numbers in parentheses refer to the number of individuals and the numbers of leaves and stems sampled, respectively.

Species	Leaf size	Stem diameter
1. <i>Brachyglottis huntii</i>	142.47 (7, 14)	0.42 (7, 14)
<i>Brachyglottis stewartiae</i>	148.80 (7, 14)	0.38 (7, 14)
2. <i>Coprosma chathamica</i>	57.89 (7, 14)	0.15 (7, 14)
<i>Coprosma repens</i>	84.68 (7, 14)	0.26 (7, 14)
3. <i>Coprosma propinqua</i> var. <i>martini</i>	4.38 (7, 14)	0.12 (7, 14)
<i>Coprosma propinqua</i> var. <i>propinqua</i>	2.21 (7, 14)	0.15 (7, 14)
4. <i>Corokia macrocarpa</i>	82.78 (7, 14)	0.20 (7, 14)
<i>Corokia cotoneaster</i>	4.47 (7, 14)	0.12 (7, 14)
5. <i>Hebe barkeri</i>	61.96 (7, 14)	0.20 (7, 14)
<i>Hebe elliptica</i>	18.01 (7, 14)	0.18 (7, 14)
6. <i>Hebe chathamica</i>	11.72 (7, 14)	0.13 (7, 14)
<i>Hebe elliptica</i>	18.01 (7, 14)	0.18 (7, 14)
7. <i>Hebe diffenbachii</i>	100.56 (7, 14)	0.23 (7, 14)
<i>Hebe elliptica</i>	18.01 (7, 14)	0.18 (7, 14)
8. <i>Leptinella featherstonii</i>	24.04 (7, 14)	0.17 (7, 14)
<i>Leptinella serrulata</i>	2.83 (7, 14)	0.08 (7, 14)
9. <i>Linum monogynum</i> var. <i>chathamicum</i>	11.49 (4, 8)	0.19 (4, 8)
<i>Linum monogynum</i> var. <i>monogynum</i>	1.90 (7, 14)	0.09 (7, 14)
10. <i>Melicytus chathamicus</i>	131.68 (7, 14)	0.20 (7, 14)
<i>Melicytus</i> aff. <i>alpinus</i> 'Shannon'	1.76 (7, 14)	0.24 (7, 14)
<i>Melicytus</i> aff. <i>alpinus</i> 'Otago'	1.28 (7, 14)	0.25 (7, 14)
11. <i>Myoporum</i> aff. <i>laetum</i>	145.77 (7, 14)	0.25 (7, 14)
<i>Myoporum insulare</i>	230.54 (4, 8)	0.37 (4, 8)
<i>Myoporum laetum</i>	156.92 (7, 14)	0.28 (7, 14)
12. <i>Olearia traversiorum</i>	74.83 (7, 14)	0.22 (7, 14)
<i>Olearia virgata</i>	2.56 (7, 14)	0.10 (7, 14)
13. <i>Pseudopanax chathamica</i>	210.35 (7, 14)	0.32 (7, 14)
<i>Pseudopanax crassifolius</i>	204.77 (7, 14)	0.36 (7, 14)

offshore islands. Several of these species occurred on more than one island, leading to a total of 33 mainland–island comparisons. Measurements on herbarium specimens were identical to those described previously, except that leaf areas were measured on three randomly selected leaves on each individual specimen instead of two. A total of 1322 leaves were measured from a total of 434 individuals. An average of 24.92 leaves (± 0.92 SE, range 1–23 individuals) were measured from 8.19 individuals (± 2.80 SE, range 3–69 individuals) per species. Analyses were restricted to leaf area because previous analyses showed that size changes were most pronounced in leaves (see Results).

We conducted two statistical analyses with these data. First, we conducted reduced major axis regression to test for overarching size trends on islands, using the same methods described previously. Second, we used a linear mixed model to test whether differences in leaf size between islands and the mainland varied among island groups. The ratio between average values for islands and the mainland for each species was used as the dependent variable (values of the dependent variable that were greater

than one indicate gigantism, while values less than one represent dwarfism). Island group was considered a fixed factor with seven levels. To account for the independence problem generated by species occurring on more than one island, species identity was also included as a random factor.

Hebe heights

The genus *Hebe* encompasses a lineage of 93 woody plant species (mostly shrubs) whose centre of distribution is New Zealand. Bayly & Kellow (2006) recently completed an extensive taxonomic revision of the genus and Garnock-Jones *et al.* (2007) later subsumed the genus under the larger taxonomic heading *Veronica*. But for the purposes of this study, we will follow the nomenclature used by Bayly & Kellow (2006) to avoid confusion, because their volume provides a unified account of the distributional and morphological information required to test for insular size changes.

Most species of *Hebe* are confined to the New Zealand mainland, but six species are endemic to New Zealand's satellite islands. Species that are endemic to offshore islands dispersed from New Zealand's main island at some point in their evolutionary past and have subsequently become distinct species allopatrically (see Bayly & Kellow, 2006). Several other species occur on both the New Zealand mainland and on offshore islands. However, species that are distributed both in New Zealand and on offshore islands were removed from analysis to promote consistency between-species island–mainland comparisons.

To test for consistent size trends in insular species of *Hebe*, we obtained the maximum heights of all species that are exclusively distributed on offshore islands from Bayly & Kellow (2006), in addition to the heights of all mainland species in their respective subgenera. We conducted two-tailed, paired *t*-tests to test whether island species differed in height from subgeneric species on the mainland. To evaluate evolutionary size trends, we conducted reduced major axis regression to obtain slope and intercept parameters of the relationship between the height of island taxa (*y*-axis) and the average height of mainland taxa in the same subgenus (*x*-axis).

RESULTS

Leaf, stem and seed size comparisons between islands and the mainland

Leaf sizes were consistently larger in island taxa, regardless of the size of their mainland relatives (Table 1). Island leaf sizes scaled positively with mainland leaf sizes (Fig. 2a), with a slope (1.163) that was statistically indistinguishable from 1 (95% confidence interval = 0.865, 1.462). However, the intercept (0.761) was greater than zero (95% confidence interval = 0.086, 1.436), indicating a consistent trend towards gigantism.

Similarly, island stem sizes scaled positively with mainland stem sizes (Fig. 2b, Table 1), with a slope (1.264) that was statistically indistinguishable from 1 (95% confidence interval = 0.767, 1.760). However, the intercept (0.483) was greater than

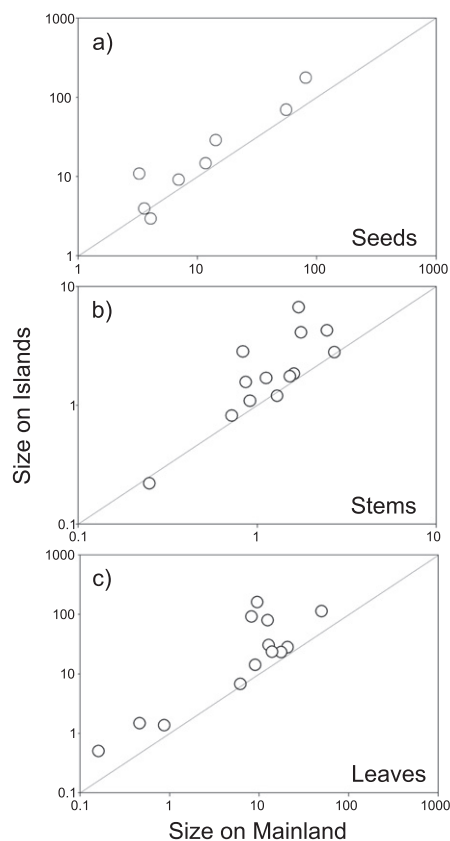


Figure 2 Relationships between seed (a, mm²), stem (b, cm) and leaf (c, cm²) sizes of woody plants inhabiting isolated islands in the south-west Pacific and their closest relatives on the New Zealand 'mainland'. Average values for islands are shown on the y-axis and average values for the mainland are shown on the x-axis. Each point is an average for a single species and both axes are logarithm transformed.

zero (95% confidence interval = 0.158, 0.808), indicating a consistent trend towards gigantism.

Different results were obtained for seed sizes. Island seed sizes scaled positively with mainland seed sizes (Fig. 2c, Table 2). However, the estimated slope parameter (1.132) did not differ statistically from 1 (95% confidence interval = 0.753, 1.510) and the estimated intercept parameter (0.078) did not differ statistically from zero (95% confidence interval = -0.935, 1.095).

Leaf and stem allometry

Scaling relationships between stem and leaf sizes suggest that morphological changes on islands are driven primarily by selection for large leaves (Fig. 3, Table 3). Leaf sizes scaled positively with stem sizes ($F_{1,23} = 43.306$, $P < 0.001$) and relationships between leaf and stem sizes had similar slopes on islands and the New Zealand mainland ($F_{1,22} = 0.036$, $P = 0.852$). However, the intercept of relationships between leaf and stem sizes on islands was larger than the intercept for the mainland ($F_{1,23} = 6.851$, $P = 0.015$), indicating that for any given stem size, island taxa consistently produced larger leaves.

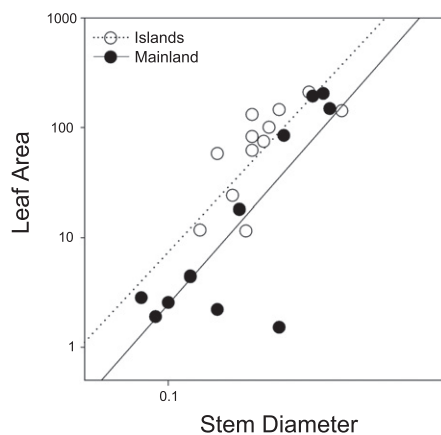


Figure 3 Relationship between leaf size (cm², y-axis) and stem diameter (cm, x-axis) in 13 pairs of sister species from the Chatham Islands (open symbols) and the New Zealand 'mainland' (closed symbols). Island species have a greater intercept than mainland species, indicating that for any given stem size, island species produce larger leaves than mainland species.

Reduced major axis regression analyses of herbarium data showed that the relationship between leaf sizes on islands and leaf sizes on the mainland had a slope (0.634) that was less than 1 (95% confidence interval = 0.349, 1.013), while the intercept (2.285) was greater than zero (95% confidence interval = 1.162, 3.409). Therefore, island taxa produced larger leaves consistently, but differences between island and mainland taxa declined with leaf sizes. The island-mainland stem size relationship had a slope (0.651) that was statistically indistinguishable from 1 (95% confidence interval = 0.280, 1.021) and an intercept (-0.487) that was statistically indistinguishable from zero (95% confidence interval = -1.140, 0.184).

Comparisons among islands

Reduced major axis regression showed evidence of gigantism, but in this instance only the slope parameter differed from isometry. Island leaf sizes scaled positively with mainland leaf sizes, with a slope (1.138) that was greater than 1 (95% confidence interval = 1.043, 1.232) and an intercept (-0.204) that was statistically indistinguishable from zero (95% confidence interval = -0.429, 0.022), indicating evidence for gigantism increased with leaf size. Increases in leaf size occurred similarly among islands (Fig. 4, Table 4). After controlling for the effects of species, the ratio between average leaf sizes on islands and the mainland did not differ among island groups ($F_{5,8} = 0.378$, $P = 0.851$).

Hebe heights

Insular species in the genus *Hebe* often grew to different sizes from their mainland relatives (Fig. 5). *Hebe benthamii*, which is endemic to the subantarctic Auckland and Campbell Islands, is the largest species in the subgenus *Connatae*. Statistically, its maximum height is larger than the average for mainland repre-

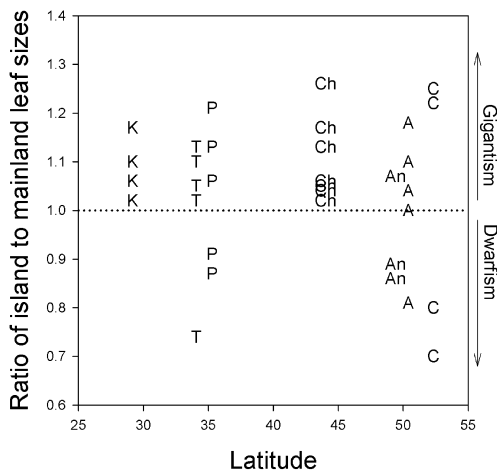


Figure 4 Size changes in plants distributed across seven islands groups in the south-west Pacific (K, Kermadec; T, Three Kings; P, Poor Knights; Ch, Chatham; An, Antipodes; A, Auckland; C, Campbell). The ratio between average leaf size on islands and average leaf size on the New Zealand mainland is plotted against island latitude for 33 island populations. Values above the dashed line represent gigantism, while values below the line represent dwarfism.

representatives of the subgenus ($T = -10.272$, $P < 0.001$). There are three insular species in the subgenus *Occlusae*, all of which are endemic to the Chatham Islands. *Hebe barkeri* and *Hebe chathamica* had the largest and smallest maximum height of the subgenus, respectively, and both were statistically different than the mainland representatives of the subgenus (*H. barkeri*: $T = -13.445$, $P < 0.001$; *H. chathamica*: $T = 12.153$, $P < 0.001$). The third insular species (*Hebe dieffenbachia*) was larger than mainland species of *Occlusae* ($T = -3.983$, $P = 0.001$). The maximum height of *Hebe insularis*, which is endemic to the Three Kings Islands, was smaller than the average maximum height of the small-leaved *Apertae* subgenus ($T = 4.179$, $P = 0.001$). The maximum height of *Hebe breviracemosa*, which is endemic to the Kermadec Islands, was statistically indistinguishable from mainland representatives of the large-leaved *Apertae* subgenus ($T = 0.147$, $P = 0.888$). The height of *Hebe* species that are endemic to offshore islands scaled weakly with the average height of mainland members of their respective subgenera ($r^2 = 0.036$, Fig. 5). The estimated slope parameter (0.784) was statistically indistinguishable from zero (95% confidence interval = $-0.284, 1.853$), indicating little support for the island rule.

DISCUSSION

Although some evidence for dwarfism was observed, most species showed evidence of gigantism. Size increases in stems and seeds were less pronounced than leaves, which consistently showed the largest increases in size. Among-island comparisons showed similar size increases in islands separated by more than 20° latitude. Three out of six insular species in the genus *Hebe* showed evidence of gigantism, two species were dwarfed and one species showed no size change.

Many processes have been hypothesized to promote evolutionary size changes on islands. Competition for limited resources might promote morphological changes in insular taxa (Blondel, 2000; Millien, 2004). Escape from mainland predators might also lead to insular size changes (Michaux *et al.*, 2002). Climatic differences (Clegg & Owens, 2002; Millien & Damuth, 2004), shifts in resource availability (Boyer & Jetz, 2010; McNab, 2010) and different rates of evolutionary change (Anderson & Handley, 2002; Millien, 2006) might also contribute to insular size changes.

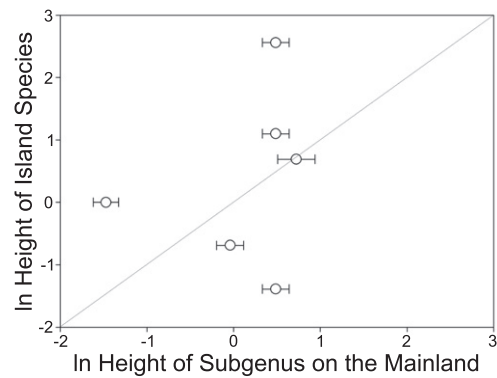
Leaf, stem and seed sizes can evolve in a coordinated fashion (Corner, 1949). So selection acting on just one trait could result in correlated evolution of other traits. Therefore, investigating allometric relationships between seed, stem and leaf sizes could help to identify the signature of selection (Niklas, 1994). Several lines of evidence suggest that the size changes identified here result from selection for larger leaves. First, larger insular leaf sizes were repeatedly observed, both in herbarium specimens and in plants growing in the common garden. Second, scaling relationships between leaf and stem sizes in herbarium specimens showed that for any given stem size, insular species consistently produce larger leaves. Therefore, insular gigantism may result from selection for larger leaves, with weaker correlated evolution in stems. Seed size relationships were based on only a small number of species pairs. Therefore, selection on seed sizes cannot be ruled out definitively and the conclusion that insular size changes results from selection for larger leaf sizes remains speculative.

Williamson (1983) discusses a potential evolutionary pathway towards gigantism that may be applicable here. Because islands usually house fewer species than comparable areas on the mainland, islands often support less diverse herbivore communities. For example, New Zealand housed several species of giant, flightless browsing birds prior to colonization by humans (e.g. Moa, *Struthioniformes*), which were always absent from the offshore island groups investigated here (see Tennyson, 2010). Small leaves can be a deterrent to large browsers (Bond *et al.*, 2004; Lee *et al.*, 2010), so island plants may be freed from selection towards small leaves in the absence of herbivores (Burns & Dawson, 2009; Fadzly *et al.*, 2009). Once released from elevated levels of herbivory, competition may favour the evolution of large leaves, given that increased leaf size can provide an advantage to plants experiencing strong competition for light (Schmitt & Wulff, 1993). Stem and seed sizes may in turn evolve larger sizes allometrically.

Previous research on size changes in insular plants has shown that herbaceous plants repeatedly evolve arborescence (i.e. woodiness), suggesting that gigantism is a common evolutionary pathway in plants. Using a phylogenetic approach, Böhle *et al.* (1996), Panero *et al.* (1999) and Percy & Cronk (2002) showed that arborescence has repeatedly evolved in different plant lineages inhabiting Macronesian islands in the North Atlantic. Results from this study support the generalization that gigantism is a more common evolutionary pathway than dwarfism, but they seem to be inconsistent with the mechanisms underpinning the weeds-to-trees evolutionary pathway. Not only were size changes strongest in leaves not stems, many study species were tall-stature trees on both islands and the mainland.

Table 4 Source locations, average leaf area (cm²) and sample sizes (the number of individuals followed by the number of leaves) for 20 study species found both on the New Zealand mainland and on offshore islands. Nomenclature follows Allan (1961).

Species	Source	Leaf size
1. <i>Ascarina lucida</i>	New Zealand	82.03 (19, 57)
	Kermadecs	118.40 (9, 27)
2. <i>Coprosma acerosa</i>	New Zealand	0.82 (20, 60)
	Chathams	1.20 (5, 15)
3. <i>C. ciliata</i>	New Zealand	2.98 (7, 21)
	Antipodes	1.15 (3, 9)
	Auckland	3.67 (3, 9)
	Campbell	1.90 (3, 9)
4. <i>C. cuneata</i>	New Zealand	1.74 (7, 21)
	Antipodes	0.97 (2, 6)
	Auckland	1.03 (5, 15)
	Campbell	1.41 (5, 15)
5. <i>C. foetidissima</i>	New Zealand	32.16 (20, 60)
	Auckland	53.90 (9, 27)
6. <i>C. petiolata</i>	New Zealand	49.59 (1, 3)
	Kermadecs	65.42 (6, 18)
7. <i>C. propinqua</i>	New Zealand	2.16 (17, 51)
	Chathams	4.92 (10, 30)
8. <i>C. perpusilla</i>	New Zealand	1.08 (17, 51)
	Antipodes	1.83 (2, 6)
	Auckland	1.58 (7, 21)
	Campbell	1.23 (7, 21)
9. <i>C. rugosa</i>	New Zealand	0.75 (5, 15)
	Antipodes	1.16 (9, 45)
10. <i>C. repens</i>	New Zealand	128.72 (14, 42)
	Poor Knights	75.23 (2, 6)
	Three Kings	174.50 (2, 6)
11. <i>C. rhamnoides</i>	New Zealand	4.68 (16, 48)
	Poor Knights	2.83 (1, 3)
	Three Kings	1.57 (1, 3)
12. <i>C. robusta</i>	New Zealand	176.70 (20, 60)
	Chathams	182.56 (2, 6)
13. <i>C. macrocarpa</i>	New Zealand	218.74 (10, 30)
	Poor Knights	350.32 (2, 6)
	Three Kings	562.67 (3, 9)
14. <i>Dodonia viscosa</i>	New Zealand	92.78 (23, 69)
	Chathams	119.98 (3, 9)
15. <i>Einadia triandra</i>	New Zealand	4.95 (13, 41)
	Chathams	5.66 (5, 15)
	Kermadecs	9.13 (2, 6)
16. <i>Hedicarya arborea</i>	New Zealand	194.60 (13, 41)
	Poor Knights	1026.32 (3, 9)
	Three Kings	400.38 (1, 3)
17. <i>Meliccytus ramiflorus</i>	New Zealand	282.55 (17, 51)
	Kermadecs	505.36 (4, 12)
	Poor Knights	684.41 (4, 12)
	Three Kings	272.62 (3, 9)
18. <i>Mysine australis</i>	New Zealand	66.79 (18, 54)
	Chathams	69.65 (2, 6)
19. <i>Pligianthus reguis</i>	New Zealand	86.86 (20, 60)
	Chathams	209.76 (7, 21)
20. <i>Raukaua simplex</i>	New Zealand	119.84 (20, 60)
	Auckland	116.56 (5, 15)

**Figure 5** Maximum height (m) of six *Hebe* species that are endemic to satellite islands offshore of New Zealand (*y*-axis) versus the average maximum plant height (\pm SE) for their respective subgenera on the mainland (*x*-axis).

Our results highlight a distinct difference in the methods used to investigate insular size changes in animals and plants. Studies of insular animals typically employ macroecological techniques to identify general trends in morphology among large numbers of species distributed across large geographic areas. On the other hand, studies of insular plants typically employ molecular tools to pinpoint evolutionary events in particular insular lineages that inhabit specific archipelagos. The present study is the first to use macroecological methods, which typify studies of insular animals, to investigate size changes in island plants. Further methodological cross-over in the future might lead to new insights concerning the evolutionary dynamics on islands, both in animals and plants.

Results were also inconsistent with the island rule, as support for gigantism was observed, regardless of the size of mainland taxa. Empirical support for the island rule in animals is equivocal. Evidence for the island rule has been found in a wide range of animal taxa (see Lomolino, 2005; Lomolino *et al.*, 2006; McNab, 2010, for recent reviews). However, other studies indicate that evidence for island rule is sensitive to how the data are analysed statistically and is also contingent on the type of animal lineage under investigation (Meiri *et al.*, 2006; 2008, 2009; Welch, 2009).

Macroecological analyses of size changes in insular animals have been conducted repeatedly for decades, and through time large datasets on animal body sizes have accumulated (see Lomolino *et al.*, 2006). As the first macroecological study of insular size changes in plants, the sample sizes presented here are comparatively small. Although the common garden helped to standardize environmental effects on leaf and stem morphology, many insular species were represented by only a small number of individuals. Greater numbers of individuals were often available as herbarium specimens. However, herbarium data are not free from environmental effects and some species were represented by three or fewer specimens. Consequently, our results are preliminary and definitive support for our conclusions requires additional data. Future work would also benefit from considering other archipelagos and perhaps changes in plant traits through ontogeny (e.g. Burns & Dawson, 2006, 2009; Fadzly *et al.*, 2009).

Two of the six species of *Hebe* that are endemic to isolated islands were smaller than their mainland ancestors, indicating that gigantism is not the only evolutionary pathway in island plants (see also Lloyd, 1981). However, these two species did not belong to subgenera comprising taller species. The evolution towards dwarfism also appears to be unrelated to island geography, because dwarfs occurred on both the Kermadec and Chatham Islands, which are separated by approximately 15° of latitude. The Chatham Islands are also home to two other *Hebe* species that showed evidence for gigantism. Therefore, the directionality of size changes does not appear to be associated with climatic conditions associated with differences in latitudinal positions of islands. Both species of dwarf *Hebe* inhabit scrubland (Bayly & Kellow, 2006), suggesting that the evolution of small plant size results from shifts in habitat preferences towards vegetation types with small vertical profiles. Alternatively, the observed size reductions might also be affected by plastic responses to limited resources in these habitats.

Morphological comparisons among island groups indicated that overall size changes were consistent among geographic locales. Given that the island groups were separated by more than 20° latitude and experience very different climates, it seems unlikely that evolutionary size changes are linked to local climatic conditions. Geographic similarity in size changes instead suggests that consistent trends towards gigantism are favoured by an evolutionary mechanism that is not contingent on local climates.

Overall results from this study show that investigations of the island rule can be expanded to include plants. In fact, plants may present several advantages for future work on insular size changes. Plants can be easily manipulated, which may provide a valuable opportunity to conduct experimental analyses of the mechanistic basis of island evolution. For example, future experiments could investigate the competitive potential of insular plants, or their susceptibility to mainland predators, in an effort to uncover why plants evolve large leaves on islands. Results from such experiments may even help determine whether size changes in insular plants and animals result from similar ecological and evolutionary mechanisms.

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SUPPORTING INFORMATION

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

Appendix S1 Physical geography of the seven island groups included in the study.

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