MACROEVOLUTIONARY CHANGES OF PLANTS ON ISLANDS

BY

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General abstract

Insularity is known to produce predictable evolutionary changes in plants. For example, herbaceous plants often evolve woodiness and seeds tend to have reduced dispersal capabilities on islands. However, our understanding of how other plant traits may evolve on islands is lacking. Furthermore, plants are modular organisms and by investigating evolutionary changes in specific plant traits we may better understand macroevolutionary processes on islands.

In this thesis, I investigate evolutionary changes in a range of plant traits on islands. First, I tested for evolutionary changes in seed size on islands (Chapter 2). Island plants consistently produced larger seeds than mainland relatives. Furthermore, this result was consistent regardless of differences in dispersal mode, growth form and evolutionary history. Selection may favour increased seed size to reduce dispersal distances. Additionally, selection may favour larger seeds due to the competitive advantage conferred to developing seedlings.

Many animal taxa exhibit increased sexual size dimorphism (SSD) on islands, as predicted by the niche variation hypothesis. However, patterns of SSD among dioecious plants on islands are unknown. In Chapter 3 I tested for differences in SSD of dioecious plants that colonized four island groups from New Zealand (mainland). The degree of SSD did not vary predictable between island and mainland plants, contrary to predictions of the niche variation hypothesis. However, SSD was consistently female biased on the mainland and results suggest selection is acting to increase the size of both sexes on islands.

Evolutionary changes in island plants may be a response to herbivory by unique large browsers. For example, the divaricate growth form is common in the New Zealand flora and may have deterred browsing moa. In Chapter 4 I tested for differences in traits associated with the divaricate growth form between plants from mainland New Zealand and Chatham Island.

Results suggest that an absence of moa on Chatham Island has relaxed selection for traits associated with the divaricate growth form.

An emerging body of research suggests aposematism (warning signals to herbivores) may be common in plants. However, previous investigations have not appreciated the fact that the perspective of terrestrial herbivores changes as plants grown vertically. Furthermore, ontogenetic changes in the capacity of plants to defend themselves may influence the reliability of warning signals. In Chapter 5 I tested for ontogenetic changes in two potentially aposematic signals produced by *Pseudopanax crassifolius*. Aposematism on upper leaf surfaces peaked early in ontogeny, providing a dishonest signal of defense. Conversely, signaling on the underside of leaves peaked later in ontogeny and scaled positively with structural defenses.

The results of this thesis suggest selection is acting on specific plant traits on islands. Evolutionary pathways, such as the evolution of woodiness, may be better explained by considering selection acting on other plant traits. For example, selection acting on seed size may facilitate evolutionary size changes evident at later life-history stages. A lack of consensus exists regarding the role of insular herbivores in the evolution of island plants. The results of Chapters 4 and 5 suggest herbivory has played an important role in the evolution of novel morphology of island plants. Considering trait specific changes of plants on islands may further our understanding of prominent evolutionary pathways by pinpointing the action of selection.

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Media articles

Island gigantism, Natural History Magazine, Volume 122, number 6

Island life makes plant seeds bigger, ABC Science Online, 21 May 2014.

Island life promotes evolution of larger seeds, Science News, 26 May 2014

Bigger is better for island seeds, Today's Science, August 2014

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Chapter 1 - General introduction

Insularity often results in repeated evolutionary pathways. For example, island animals often evolve to become giants or dwarfs when compared to mainland relatives (Van Valen, 1973a; Case, 1978; Lomolino, 2005; Meiri *et al.*, 2006; Meiri *et al.*, 2008). Insular size changes are not restricted to animals. Many island trees are descended from small, herbaceous mainland plants (Carlquist, 1974). The evolution of 'woodiness' (arborescence) on islands was first noted by Darwin (1859) and modern phylogenetic approaches have confirmed its occurrence in a variety of plant lineages and island systems (Bohle *et al.*, 1996; Panero *et al.*, 1999; Percy & Cronk, 2002). However, our understanding of the processes responsible for many trends exhibited by insular plants is incomplete. For example, a lack of consenus exists regarding the selective pressures responsible for the evolution of woodiness on islands (Darwin, 1859; Wallace, 1880; Carlquist, 1974; Bohle *et al.*, 1996; Givnish, 1998). Furthermore, previous investigations have not appreciated the modularity of plant structure when investigated evolutionary changes in island plants (but see Burns *et al.*, 2012). Thus, our understanding of how plants evolve on islands is incomplete.

Unexplored size changes

A reduction in the dispersal ability of seeds is common on islands (Carlquist, 1974; Cody & Overton, 1996). Selection may favour reduced dispersibility to decrease propagule mortality due to seeds landing in the ocean (Darwin, 1859; Carlquist, 1974). Furthermore, the small size of islands may result in suitable habitat zones being smaller and favour dispersal of seeds within the limits of suitable conditions (Carlquist, 1974). Structural changes of seeds consistent with reduced dispersal ability have been documented in wind dispersed (Carlquist, 1974; Cody & Overton, 1996), fleshy-fruited, and ectozoochorous (dispersed on the outside of animals) species (Carlquist, 1974). Reduced dispersal ability of seeds has been detected in as few as five generations after island colonization, suggesting strong selection pressures (Cody & Overton, 1996).

Selection may favour increased seed sizes on islands to reduce dispersal distances (see Greene & Johnson, 1993). Additionally, it may

improve rates of establishment and confer a competitive advantage to developing seedlings (Leishman *et al.*, 1995; Lord *et al.*, 1995; Moles & Westoby, 2004). Seed size also covaries with many other plant traits (Corner, 1949; Westoby *et al.*, 1996). Therefore, selection acting on seed size may facilitate evolutionary changes in other plant traits. However, our understanding of how seed sizes may evolve on islands is lacking.

It is estimated that only 6-7% of angiosperm species worldwide are dioecious (separate male and female individuals; Renner & Ricklefs, 1995). However, many island floras are characterized by having relatively large proportions of dioecious plant taxa. For example, 14.7% of species in the native Hawaiian flora (Sakai *et al.*, 1995) and 13% of species in New Zealand are dioecious (Godley, 1979). Sexual Size Dimorphism (SSD) is common in dioecious plants (Bond & Midgley, 1988; Obeso, 2002; Kavanagh *et al.*, 2011; Barrett & Hough, 2013) and the niche variation hypothesis predicts the degree of SSD to increase on islands (Van Valen, 1965; Ebenman & Nilsson, 1982; Meiri *et al.*, 2005). Insular populations face fewer competing species and increasing SSD (and consequently, morphological variability within a population) may facilitate occupation of available niche space (as advocated to explain size changes of insular animals, Grant, 1965; Lomolino, 2005). Additionally, SSD may increase in response to elevated levels of intraspecific competition (Rothstein, 1973; Shine, 1989). Many animals conform to the prediction of increased SSD on islands (Ebenman & Nilsson, 1982; Dayan & Simberloff, 1998; Simberloff *et al.*, 2000; Pearson *et al.*, 2002). However, insular patterns of SSD in plants have yet to be investigated.

Insular herbivory

Large mammalian herbivores are uncommon on islands due to being poor over-water dispersers (Whittaker & Fernandez-Palacios 2007). However, large browsing birds are often dominant components of insular herbivore communities (Olson & James, 1982; Atkinson & Greenwood, 1989a; Livezey, 1993; Givnish *et al.*, 1994; Bond & Silander, 2007). Herbivory pressure often selects for unique changes in plant morphology (e.g. thorns and spines -

Cooper & Owensmith, 1986) and the unusual herbivore communities on islands may play an important role in the evolution of insular flora. For example, heteroblasty (ontogenetic changes in leaf morphology) is common to many unrelated plants in New Zealand and may be an adaptation to deter extinct browsing birds (Moa – Aves: Dinornithiformes; Greenwood & Atkinson, 1977). The divaricate growth form (small, widely spaced leaves, narrow stems and high branching angles) is another common feature of the New Zealand flora (Greenwood & Atkinson, 1977). Plants sharing similar traits are also common in Madagascar (Bond & Silander, 2007). This unique growth form may also be an adaptation to deter herbivory by extinct browsing birds (Greenwood & Atkinson, 1977; Bond *et al*., 2004; Bond & Silander, 2007). Alternatively, both heteroblasty and the divaricate growth form may be adaptations to environmental conditions (McGlone & Webb, 1981; Day, 1998).

The isolation of islands often results in depauperate herbivore communities (Carlquist, 1974; Whittaker & Fernández-Palacios, 2007). Therefore, a reduction in herbivory pressure may be common on islands and lead to predictable evolutionary changes in plants. For example, antiherbivore defenses may be under strong selection on the mainland, however selection for these traits may be relaxed after island colonization. Chemical defenses are often absent or less effective in island plants when compared to mainland relatives (Bowen & VanVuren, 1997; Vourc'h *et al*., 2001). Plant-ant mutualisms that deter insect herbivores are often lost after island colonization (Janzen, 1973; Rickson, 1977). Furthermore, structural defenses such as prickles or thorns are often greatly reduced in island plants (Bowen & VanVuren, 1997; Burns, 2014). The floras of the offshore islands surrounding mainland New Zealand (North and South Islands) are derived primarily from taxa that have dispersed overwater from the main islands (Wardle, 1991). Furthermore, moa were absent from many of these offshore islands (see Greenwood & Atkinson, 1977). Therefore, a reduction in herbivory pressure may have relaxed selection for anti-herbivory traits that had evolved on the New Zealand mainland. This offers a unique opportunity to test anti-herbivore

hypotheses for the evolution of unique morphology, such as the divaricate growth form.

Recent research suggests some plants produce aposematic (warning) signals (Lev-Yadun, 2001; Lev-Yadun & Ne'eman, 2004; Lev-Yadun & Gould, 2007; Fadzly *et al.*, 2009; Cooney *et al.*, 2012). Furthermore, Fadzly *et al.* (2009) suggest that aposematism may occur in response to extinct avian browsers. Aposematic signals tend to be reliable advertisements of defense (Summers & Clough, 2001; Lev-Yadun, 2003; Bezzerides *et al.*, 2007; Cooney *et al.*, 2012). However, dishonesty is common in animal signaling systems and rates of dishonesty often decline through ontogeny (Saetre & Slagsvold, 1996; Bee *et al.*, 2000; Whiting *et al.*, 2009; Hawkins *et al.*, 2012; Valkonen *et al.*, 2014). *Pseudopanax crassifolius* displays are remarkable series of morphological transitions as it develops (Gould, 1993). Seedlings are camouflaged against background leaf-litter, saplings produce leaves with marginal teeth and associated aposematic spots, and adult leaves lack structural defenses (Gould, 1993; Fadzly *et al.*, 2009). The reliability of aposematic signals may vary through ontogeny in response to changes in defense and herbivory pressure. However, signal reliability through ontogeny in plants has not been investigated.

Thesis overview

In this thesis, I investigated evolutionary patterns in a variety of plant traits on islands. I used an island-mainland comparison approach, where insular taxa were compared to sister taxa on the mainland. Specifically, data were collected from plants on the main islands of New Zealand (North and South Island – 'mainland') and offshore islands surrounding the New Zealand mainland. I also tested for novel patterns of aposematic signaling by a species endemic to the New Zealand mainland, where moa were once a dominant component of the fauna. Each chapter of this thesis was written as a stand-alone manuscript for publication. Therefore, there may be some repetition in the information presented in the introduction and method sections of some chapters.

In chapter 2, I tested for differences in seed size between related island and mainland plants. Seed size data were collected in the field and augmented with published seed descriptions to produce a comprehensive dataset of 40 island-mainland taxonomic parings. First, I tested for overarching changes in seed size on islands. Secondly, I tested for any effects of evolutionary history, growth form, and dispersal mode on the island-mainland seed size relationship.

In chapter 3, I investigated patterns of sexual size dimorphism (SSD) in dioecious plants from four island groups surrounding New Zealand. Leaf and stem sizes were quantified on herbarium specimens of 28 dioecious taxa allowing for 14 island-mainland taxonomic comparisons. First, I tested for an increase in the degree of SSD, as predicted under the niche variation hypothesis. I then developed a novel analytical technique to test for differences in the direction (which sex is larger) of SSD between related island and mainland plants. Lastly I tested for sex specific size changes of plants on islands.

In chapter 4, I tested for differences in traits associated with the divaricate growth form between plants from Chatham Island and the New Zealand mainland. The divaricate growth form is suggested to be an adaptation to deter herbivory by extinct avian browsers (moa). However, moa never reached Chatham Island. Therefore, I predicted Chatham Island plants to have lost morphological adaptations that may have deterred moa herbivory.

In chapter 5, I investigated patterns of aposematic signaling in *P. crassifolius*. First, I develop predictions based upon the changing perspective of terrestrial herbivores as plants grow vertically. Second, I used an avian vision model to whether variation in the colour of abaxial (lower) leaf surfaces may be aposematic. Third, I tested the following predictions: aposematic signals on upper leaf surfaces will peak early in ontogeny, when structural defenses are poorly developed, providing a dishonest signal. Conversely, aposematism on the underside of leaves will peak later in ontogeny and be reliable.

In chapter 6, I synthesized my findings. Overall, this thesis furthers our understanding of insular evolution by examining trait specific changes of plants

on islands. Furthermore, results benefit our understanding of insular size changes and highlight the role herbivores play in the evolution of island plants

Chapter 2 - The repeated evolution of large seeds on islands

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Abstract

Several plant traits are known to evolve in predictable ways on islands. For example, herbaceous species often evolve to become woody and species frequently evolve larger leaves, regardless of growth form. However, our understanding of how seed sizes might evolve on islands lags far behind other plant traits. Here, I conduct the first test for macroevolutionary patterns of seed size on islands. I tested for differences in seed size between 40 island-mainland taxonomic pairings from four island groups surrounding New Zealand. Seed size data were collected in the field and then augmented by published seed descriptions to produce a more comprehensive dataset. Seed sizes of insular plants were consistently larger than mainland relatives, even after accounting for differences in growth form, dispersal mode and evolutionary history. Selection may favour seed size increases on islands to reduce dispersibility, as long-distance dispersal may result in propagule mortality at sea. Alternatively, larger seeds tend to generate larger seedlings, which are more likely to establish and outcompete neighbours. My results indicate there is a general tendency for the evolution of large seeds on islands, but the mechanisms responsible for this evolutionary pathway have yet to be fully resolved.

Introduction

Seed size varies greatly among plant species, from tiny wind-dispersed orchid seeds to the massive double coconut (*Lodoicea maldivica*) (Harper *et al.*, 1970), and has important consequences for reproductive success (Leishman *et al.*, 1995; Lord *et al.*, 1995; Moles & Westoby, 2004). Seedling survival is directly influenced by seed size (Leishman & Westoby, 1994; Moles & Westoby, 2004) and many functional traits covary with the size of seeds. These traits include dispersal mode, growth form, specific leaf area, and seed number (Corner, 1949; Westoby *et al.*, 1996). Many of these other traits evolve predictably on islands (e.g. growth form and leaf area - Carlquist, 1974; Burns *et al.*, 2012), however detailed quantitative investigations of how seed size is affected by insularity are lacking.

A reduction in the dispersal ability of seeds is a common evolutionary pathway for plants on islands (Carlquist, 1974; Cody & Overton, 1996). For example, wind-dispersed members of the family Asteraceae typically display a reduction in pappus size relative to achene size on islands (Carlquist, 1974; Cody & Overton, 1996). Animal-dispersed taxa (such as *Bidens*), which produce structures that promote ectozoochory, illustrate a similar pattern, with a reduction in the size of hooks and awns relative to achene size (Carlquist, 1974). Furthermore, fleshy-fruited members of the family Araliaceae tend to produce larger fruits and seeds on islands (Carlquist, 1974). The evolution of reduced dispersibility has also been detected in as few as five generations, suggesting strong selection pressures (Cody & Overton, 1996).

One explanation for potential changes in seed size on islands is that the small size and isolation of islands may select against dispersal to reduce propagule mortality at sea (Darwin, 1859; Carlquist, 1974). Selection acting to increase seed size may reduce wind dispersal distances in anemochorous species (Greene & Johnson, 1993). The same may be true for fleshy-fruited plants, although tests for directional changes in seed size of fleshy-fruited species have yet to be conducted.

Selection may favour larger seed size on islands for reasons other than dispersal ability. For example, most islands house fewer species than

comparable communities on the mainland. Therefore, a germinating seedling on an island is more likely to be adjacent to a conspecific, leading to greater levels of intraspecific competition (Grant, 1965; Case, 1978). Larger seeds are more competitive than small seeds, all else being equal (Leishman & Westoby, 1994; Leishman *et al.*, 1995; Moles & Westoby, 2004). Therefore, higher levels of intraspecific competition on islands may also select for increases in seed size.

Here, I conduct the first macroevolutionary test for increased seed size on islands. By collecting specimens in the field and using published seed descriptions I compiled a diverse dataset, consisting of 40 island-mainland taxonomic pairings from four island systems surrounding mainland New Zealand. To test for overarching changes in seed size on islands, I first compared seed sizes on islands to seed sizes on the mainland using reduced major axis regression. Secondly, I used a mixed-effects modelling approach to test for effects of evolutionary history, growth form, and dispersal mode on the island-mainland seed size relationship.

Methods

New Zealand has a long history of geological isolation. It separated from Gondwana 80 million years ago and has been isolated in the southwest Pacific since. The three main islands (North, South and Stewart Islands) are encircled by numerous smaller islands (Gibbs, 2006), the flora of which consists mainly of taxa that have dispersed overwater from New Zealand. Although many of these islands were once connected by land bridges, I focused on four island groups that remained isolated from the main islands during the Pleistocene (Kermadec, Three Kings, Chatham and Sub Antarctic Islands - see Wallis & Trewick, 2009). In particular I focused on the Chatham group (176°W, 44°S), situated 850 km east of the main islands (see figure 2.1).

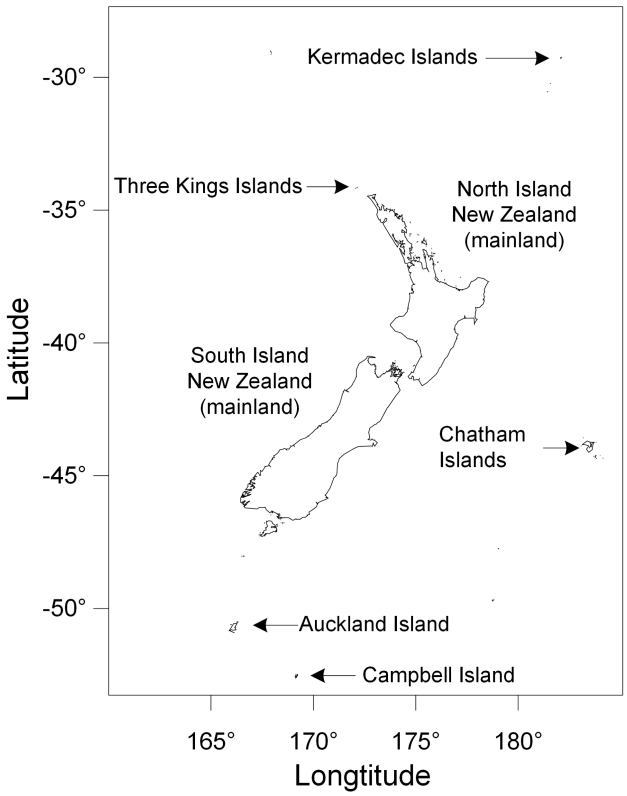

Figure 2.1 Map of study islands surrounding New Zealand

To maximise the number of species in the dataset, the Chatham Islands were visited twice, at different times of year. This allowed the inclusion of species with different fruiting phenologies. Seed sizes were measured on Chatham Island taxa in January 2008 (Burns *et al.*, 2012) and March 2012. Searches were made in Henga Scenic Reserve (43°51.0′ S 176°33.2′W), Nikau Forest Reserve (43°45.7′ S 176°34.8′W), and Rangaika Scenic Reserve (44° 3' 37.0182"S 176° 26' 6.0792"W). Mainland samples were collected from Otari Wilton's Bush (41°14′ S, 174°45′ E), Moa Point (41°20′ S, 174°49′ E), and Nelson Lakes National Park (41°48′ S, 172° 50′ E). Fruits were randomly selected from each individual, collecting five or more from at least five individuals (following Cornelissen *et al.*, 2003). This was not always achievable; therefore a variable number of seeds were used to characterize seed size (see Table 2.1). Seed size was estimated as the product of seed length (length of the longest axis) x seed width (maximum distance perpendicular to the length measurement at the widest point of the seed).

To allow for the greatest number of island-mainland comparisons possible, I supplemented field data (25 taxa) with seed measurements contained in *Seeds of New Zealand gymnosperms and dicotyledons* ('seed atlas' from here after; Webb & Simpson, 2001). Seed descriptions in the seed atlas result from the examination of at least 10 seeds from each of 10 collections of fruiting material for each species. I obtained the median value from seed dimension ranges when compiling data from within the seed atlas. To justify the use of seed atlas data and to promote accuracy, I ran Ordinary Least Squares (OLS) regression of field measures against data from the seed atlas. Measurements for two *Hebe* species were not contained in the seed atlas and seed sizes were obtained from *An Illustrated Guide to New Zealand Hebes* (Bayly & Kellow, 2006). In many cases (42 taxa) the literature only provided length dimensions for seed size. I therefore ran OLS regression of area (length x width, as described above) against length, for the 36 taxa where both length and width parameters were available. Regression parameters were then used to estimate area for those taxa where only a length dimension was available. ANOVA of observed versus predicted values was carried out to test

the robustness of seed area predictions. Variables were log transformed prior to analysis.

Determining mainland relatives for insular species was simple when taxa were undifferentiated (see Table 2.1). For Chatham Island endemics, the recent molecular analysis by Heenan *et al*. (2010) was utilised where possible. In this study DNA sequence data was used to identify the closest relatives for 35 taxa endemic to the Chatham Islands. For taxa from other island systems, phylogenetic analyses were used where available (Winkworth *et al.*, 2002; Glenny, 2004; Wagstaff *et al.*, 2006; Perrie & Shepherd, 2009; Wagstaff *et al.*, 2011; Himmelreich *et al.*, 2012). When multiple mainland taxa were identified as being equally related to an island endemic, the average seed size of the mainland taxa was used (*Myrsine chathamica* - see Stockler, 2001; *Leptinella plumosa* and *L. lanata* - see Himmelreich *et al.*, 2012). Where taxa were differentiated at species but not genus level the mainland taxon chosen is the most likely relative based on morphological similarities (e.g. *Macropiper melchior* and *M. excelsum*; *Coprosma acutifolia* and *C. tenuifola* - see Dawson & Lucas, 2011). In other cases insular taxa were a variety or subspecies of well-known mainland species.

To test for differences in seed size among island and mainland taxa a variety of statistical methods could be used. Regressing mean values for insular taxa against mainland taxa is one option. The slope and intercept parameters providing information on the relationship (slope > 1 and intercept > 0 = island taxa with larger seeds; slope < 1 and intercept < 0 = mainland seed size larger). However, the use of OLS regression minimizes the sum of squared variation in the Y (in this case, island) direction and is not appropriate when measurement error in X and Y variables is likely. To avoid these confounding sources of bias, I ran Reduced Major Axis (RMA) regression. RMA was used to obtain slope and intercept parameters along with 95% confidence intervals.

Phylogenetic relatedness between island-mainland taxonomic pairs creates a lack of independence in the dataset. To overcome this, I ran a mixed effects model treating seed size as the dependent variable, location (island or mainland) as a fixed factor, and 'species-pair' (island-mainland taxonomic

pairing) as a random factor. Many of the taxonomic pairings are separated at species level, potentially indicating more evolutionary divergence than conspecific pairings. I therefore included a second random effect of nested taxonomy (with two levels: undifferentiated at species level, or differentiated at species level) in the model structure. Seed dispersal mode and plant growth form were included as fixed factors to test for effects they may have on the island-mainland seed size relationship.

The majority of taxa in the dataset were either wind dispersed or fleshy-fruited plants. I therefore defined dispersal modes as either 'dry-fruited' (wind, water, ballistic/wind) or 'fleshy-fruited'. Only two island-mainland taxonomic pairings were vines, I therefore removed these taxa from the growth form analysis. I am specifically interested in whether dispersal mode or growth form influences seed size differences between 'locations' (island or mainland). Therefore, the two-way interactions between location and these two factors were maintained in the model structure. I calculated the ratio of island seed size to mainland seed size to visualise whether seeds tended to be larger on islands for each level of dispersal mode and growth form. Ratios greater than one indicate a tendency for larger island seeds (see Fig 2.4). Kruskal-Wallis tests were then used to compare ratios between dispersal modes and growth forms. Robust tests for the effect of island system were not possible due to uneven sample sizes between islands.

All analyses were conducted in the R environment for statistical computing (R-Development-Core-Team, 2011). RMA analyses were conducted with the SMATR package (Warton *et al.*, 2012a), and the CAR package (Fox & Weisberg, 2011) was used to carry out a likelihood ratio test for the mixed effects model. Seed size data were logarithm transformed to conform to normality assumptions.

Table 2.1 Average seed area for insular species and mainland relatives (mm^2). Numbers in parentheses refer to the number of individuals and seeds sampled, respectively. Italicised letters in parentheses indicates data acquired from published sources (a - Webb & Simpson, 2001;; h - Bayly & Kellow, 2006). † Indicates cases where seed area was estimated from length measurements (see methods).

Insular taxa	Seed size (mm^2)	Growth form	Dispersal mode	Mainland taxa	Seed size (mm^2)
Olearia chathamica	19.94 (5, 25)†	tree	wind	*Pleurophyllum criniferum*	14.56 (*a*)†
Olearia traversiorum	3.26 (6, 30)†	tree	wind	*Olearia virgata*	1.27 (*a*)†
Ripogonum scandens	71.78 (7, 48)	vine	fleshy fruit	*Ripogonum scandens*	55.40 (3, 22)
Myrsine chathamica	39.30 (7, 67)	shrub	fleshy fruit	*Myrsine argentea*	8.7 (*a*)
				Myrsine divaricata	8.1(*a*)
Corokia macrocarpa	40.44 (8, 66)	shrub	fleshy fruit	*Corokia cotoneaster*	18.01 (3, 16)
Leptecophylla robusta	18.63 (6, 49)	shrub	fleshy fruit	*Leptecophylla juniperina*	5.93 (6, 46)
Coprosma propinqua var. martinii	13.93 (8, 84)	shrub	fleshy fruit	*Coprosma propinqua var. propinqua*	11.75 (1, 30)
Melicytus chathamicus	20.43 (7, 118)	shrub	fleshy fruit	*Melicytus aff. alpinus*	9.04 (2, 12)
Coprosma acerosa	9.87 (5, 58)	shrub	fleshy fruit	*Coprosma acerosa*	3.26 (1, 30)
Macropiper excelsum	3.94 (3, 32)	shrub	fleshy fruit	*Macropiper excelsum*	3.59 (3, 30)
Apium prostratum subsp. denticulatum	2.93 (5, 38)	herb	water	*Apium prostratum subsp. prostratum*	4.05 (3, 30)
Rhopalostylis aff. sapida	175.83 (3, 24)	tree	fleshy fruit	*Rhopalostylis sapida*	80.79 (3, 30)
Muehlenbeckia australis	9.10 (3, 35)	vine	fleshy fruit	*Muehlenbeckia australis*	6.98 (3, 30)
Tetragonia implexicoma	28.85 (2, 24)	herb	fleshy fruit	*Tetragonia implexicoma*	14.26 (3, 30)
Coprosma chathamica	38.76 (*a*)	tree	fleshy fruit	*Coprosma repens*	21.61 *(a)*
Hebe dieffenbachii	1.17 *(a)*†	shrub	wind	*Hebe elliptica*	1.83 *(a)*†
Pseudopanax chathamicus	19.92 *(a)*†	tree	fleshy fruit	*Pseudopanax crassifolius*	6.74 *(a)*†
Pseudopanax kermadecensis	12.03 *(a)*†	tree	fleshy fruit	*Pseudopanax arboreus*	11.14 *(a)*†
Alectryon excelsus subsp. grandis	55.4 *(a)*†	tree	fleshy fruit	*Alectryon excelsus*	45.52 *(a)*†
Streblus smithii	43.52 *(a)*†	tree	fleshy fruit	*Streblus banksii*	26.96 *(a)*†
Myoporum kermadecense	31.57 *(a)*†	tree	fleshy fruit	*Myoporum laetum*	35.52 *(a)*†
Metrosideros kermadecensis	11.44 *(a)*†	tree	wind	*Metrosideros excelsa*	12.95 *(a)*†
Macropiper melchior	5.23 *(a)*†	shrub	fleshy fruit	*Macropiper excelsum*	4.42 *(a)*†
Ascarina lucida var. lanceolata	1.6 *(a)*†	tree	fleshy fruit	*Ascarina lucida var. lucida*	2.35 *(a)*†
Coprosma acutifolia	15.93 *(a)*	shrub	fleshy fruit	*Coprosma tenuifolia*	17.39 *(a)*
Stilbocarpa polaris	4.27 *(a)*†	herb	fleshy fruit	*Stilbocarpa lyalii*	5.03 *(a)*†
Olearia lyallii	38.63 *(a)*†	shrub	wind	*Olearia colensoi*	21.88 *(a)*†
Myosotis capitata	2.87 *(a)*	herb	wind	*Myosotis australis*	1.44 *(a)*
Gentianella cerina	0.51 *(a)*†	herb	wind	*Gentianella saxosa*	0.89 *(a)*†
Leptinella plumosa	3.57 *(a)*†	herb	wind	*Leptinella nana*	0.73 *(a)*†
				Leptinella minor	1.07 *(a)*†
				Leptinella filiformis	0.73 *(a)*†
Leptinella lanata	3.4 *(a)*†	herb	wind	*Leptinella nana*	0.73 *(a)*†
				Leptinella minor	1.07 *(a)*†
				Leptinella filiformis	0.73 *(a)*†
Abrotanella rosulata	2.08 *(a)*†	herb	wind	*Abrotanella rostrata*	4.27 *(a)*†
Abrotanella spathulata	2.78 *(a)*†	herb	wind	*Abrotanella rostrata*	4.27 *(a)*†
Pennantia baylisiana	43.52 *(a)*†	tree	fleshy fruit	*Pennantia corymbosa*	23.93 *(a)*†
Embergeria grandifolia	17.32 *(a)*†	herb	wind	*Kirkianella novae-zelandiae*	12.64 *(a)*†
Hebe chathamica	1.54 *(h)*	shrub	wind	*Hebe elliptica*	1.74 *(a)*
Hebe barkeri	1.86 *(h)*	tree	wind	*Hebe elliptica*	1.74 *(a)*
Leptinella featherstonii	1.27 *(a)*†	herb	wind	*Leptinella serrulata*	1.48 *(a)*†
Geranium traversii	5.23 *(a)*†	herb	wind	*Geranium brevicaule*	3.08 *(a)*†
Brachyglottis huntii	5.23 *(a)*†	tree	wind	*Brachyglottis stewartiae*	7.92 *(a)*†

Results

Field measurements scaled positively with those contained in the seed atlas (OLS regression: $R^2 = 0.912$; $p < 0.001$). Slope and intercept parameters were not significantly different from one and zero respectively (Slope: 0.971, 95% confidence interval = 0.811-1.131, $p = 0.698$; Intercept: -0.054, 95% confidence interval = -0.373-0.266, $p = 0.721$), indicating that published seed sizes accurately reflect field measurements. OLS regression showed seed lengths scaled strongly with seed surface area ($R^2 = 0.928$; $p < 0.001$, see figure 2.2). Seed area estimates calculated using the regression equation did not differ significantly from observed values ($F_{1, 70} = 0.086$, $p = 0.770$), indicating that estimates accurately reflected real seed sizes.

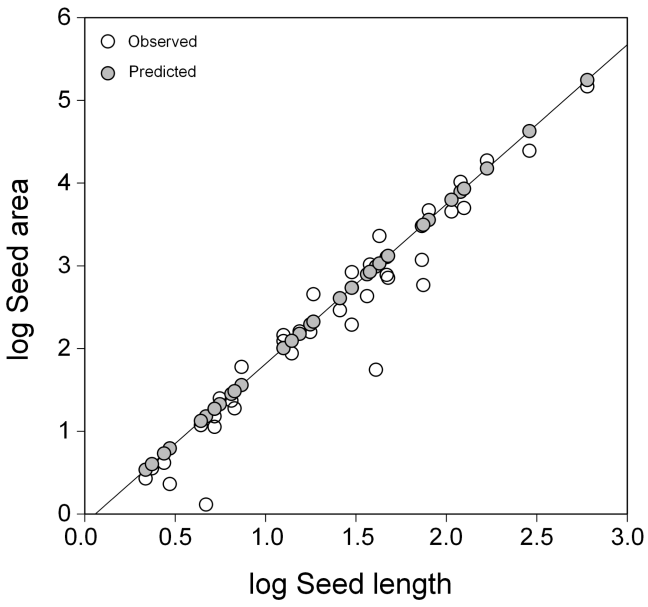

Figure 2.2 Relationship between seed length (mm) and seed surface area (length and width, mm^2) for 36 taxa. Solid line is the result of OLS regression analysis. Open circles are observed values; closed circles are predicted values (based on regression parameters). Data are natural logarithm transformed.

Island seed sizes scaled positively with mainland seed sizes (RMA analysis: $R^2 = 0.854$, $p < 0.001$, see figure 2.3). However, the island-mainland seed size relationship had a slope greater than one (1.18; 95% confidence interval = 1.041 – 1.338) and an intercept marginally less than zero (-0.021; 95% confidence interval = -0.166 – 0.123). This indicates a tendency for insular taxa to produce larger seeds than mainland relatives, particularly at the larger end of the seed size spectrum.

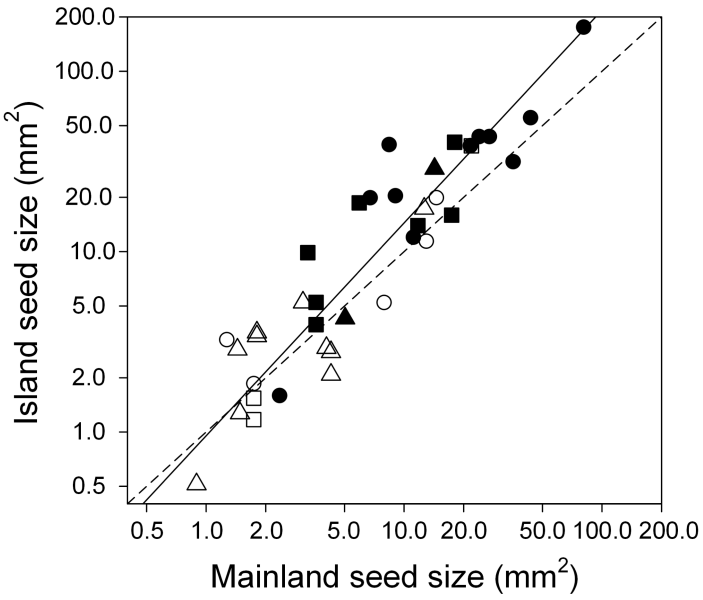

Figure 2.3 Relationship between island and mainland seed size. Each point represents a taxonomic pairing between an insular taxon and its corresponding mainland relative. Circles represent trees, squares are shrubs, and triangles are herbs. Closed symbols indicate fleshy-fruited taxa and open symbols dry-fruited. The dashed line represents isometry and the solid line is the result of RMA regression (y = 1.180x -0.021). Both axes are logarithm transformed.

The likelihood ratio test from the mixed effects model showed no significant effect of plant growth form on the island to mainland seed size relationship (χ^2 = 7.32, d.f = 4, p = 0.120). However, there was a significant effect of dispersal mode (χ^2 = 14.328, d.f = 2, p <0.001). Seed sizes did differ significantly by location (island or mainland) (χ^2 = 12.562, d.f. = 1, p < 0.001), consistent with results of the RMA analysis, and all dispersal modes and growth forms displayed a tendency for larger seed sizes on islands (see figure 2.4 a & b).

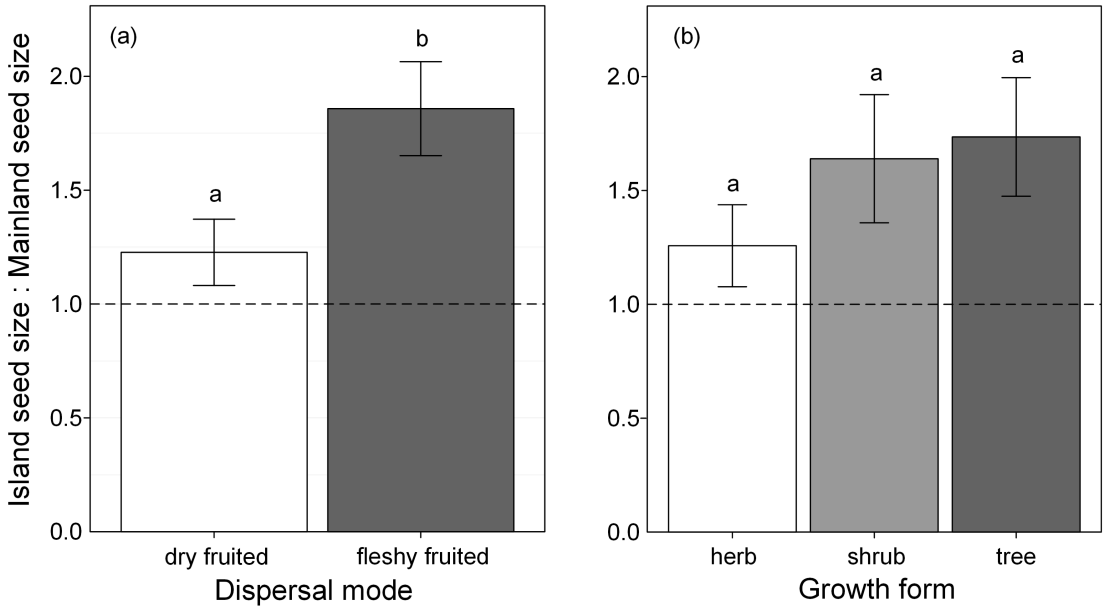

Figure 2.4 Average island seed size to mainland seed size (mm^2) ratio by (a) dispersal mode and (b) growth form. The dashed horizontal line represents equal island and mainland seed size (ratio = 1; ratio > 1 indicates larger seeds on islands, ratio < 1 indicates larger mainland seeds). Error bars are standard error. Letters indicate whether average island to mainland seed size ratios are different between dispersal modes and growth forms (Kruskal-Wallis test: (a) $\chi^2 = 5.61$, d.f = 1, $p = 0.018$; (b) $\chi^2 = 2.28$, d.f = 2, $p = 0.321$).

Discussion

Seeds of insular taxa were consistently larger than those of their mainland relatives. Furthermore, this result was consistent regardless of dispersal mode and growth form. Increasing seed size reduces dispersibility in anemochorous species, as large seeds are likely to disperse over shorter distances than small seeds (Harper *et al.*, 1970; Augspurger, 1986; Greene & Johnson, 1993; Benkman, 1995; Cody & Overton, 1996). In the case of fleshy-fruited plants, this is the first time an increase in seed size on islands has been demonstrated quantitatively. Larger seeds in fleshy-fruits may limit the range of dispersal vectors available to a plant as well as reducing the number of fruits eaten during a feeding period (Wheelwright, 1985; Levey, 1987). Furthermore, seed number scales negatively with seed size (Niklas, 1994; Henery & Westoby, 2001) and producing fewer seeds reduces the likelihood of long distance dispersal (Nathan, 2006).

RMA regression of island seed size against mainland seed size produced a scaling relationship that differed from isometry. In particular, a slope parameter greater than one suggests the size of insular seeds increases disproportionately with increasing seed size. The majority of small seeded taxa in the dataset rely on wind dispersal while species with larger seeds generally produced fleshy fruits. Anemochorous species may experience stronger constraints on maximum seed size due to the aerodynamics of wind dispersal (Greene & Johnson, 1993). While in fleshy fruited species (and zoochorous species in general) seed size may be less tightly constrained, allowing greater size increases without impeding the probability of successful dispersal. Birds often display size increases on islands and size coupling between fruits and frugivores is common (Clegg & Owens, 2002; Burns, 2013). Therefore, putative selection pressures for increased seed size may be less constrained in fleshy-fruited taxa. Analysis of dispersal mode reflected this, as fleshy-fruited taxa showed greater size increases on islands than dry-fruited taxa. However, dry-fruited taxa still displayed a tendency for larger seeds on islands. Furthermore, patterns in seed size persisted even after accounting for differences in taxonomic distance and phylogeny between island-mainland pairings, suggesting selection for increased in seed size is strong on islands (see Cody & Overton, 1996).

Work on animals suggests the depauperate nature of island communities may increase intraspecific competition and promote insular size changes (Grant, 1965; Case, 1978; Lomolino, 2005). This situation may also apply to plants. Larger seed sizes may promote a competitive advantage due to the increased nutrient reserves, which produce larger, more competitive seedlings (Leishman *et al.*, 1995; Moles & Westoby, 2004). Evidence also suggests that larger seed sizes increase plant survival at later life stages (e.g. sapling stage - Moles & Westoby, 2004).

Selection early in ontogeny may also influence size patterns evident at later life stages. In animals, adult body size is strongly influenced by size at birth and a recent investigation suggests body size patterns on islands may reflect selection acting on birth size (Aubret, 2012). A parallel situation may be

occurring in plants. The probability of seedling establishment increases with seed size (Moles & Westoby, 2004). Seed size is strongly correlated with traits evident later in ontogeny, such as plant height and stem size (Corner, 1949; Leishman *et al*., 1995; Moles & Westoby, 2004). Many herbaceous lineages develop woodiness on islands and recent research suggests an increase in leaf size is common (Carlquist, 1974; Burns *et al*., 2012). As a result, it could be that selection first acting on seeds may facilitate evolutionary changes at later life history stages.

My results suggest that selection favours increased seed size on islands, regardless of dispersal mode, growth form and evolutionary history. Several processes may explain this macroevolutionary trend. First, increasing seed size may reduce propagule mortality associated with unfavourable dispersal into the ocean (see Darwin, 1859; Carlquist, 1974). Second, it may provide competitive advantages post-dispersal and increase the likelihood of establishment. The sizes of plant traits are also known to scale allometrically with one another (Niklas, 1994), so selection acting on seeds may facilitate size changes in other traits and this deserves further attention. Direct investigations of potential processes are now needed, in addition to global analyses of seed size to establish whether the observed pattern is universal.

Chapter 3 - Sexual size dimorphism in island plants: the niche variation hypothesis and insular size changes

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Abstract

The niche variation hypothesis predicts insular populations exhibit increased sexual size dimorphism (SSD), to minimize intraspecific competition. Although many animal taxa conform to this prediction, insular patterns of SSD have yet to be investigated in plants. Here, I tested for differences in SSD of dioecious plants that colonised four island groups (Kermadec, Three Kings, Chatham, and Auckland Islands) from New Zealand. Using herbarium collections, I quantified leaf and stem sizes of 263 individuals from 28 dioecious taxa. I developed a novel analytical technique to explore changes in the direction of SSD on islands. Lastly, I tested for evolutionary size changes of male and female plants on islands. The degree of SSD did not vary predictably between insular and mainland taxa, contrary to predictions of the niche variation hypothesis. Furthermore, the direction of SSD was not predictable on islands, while it was consistently female biased on the mainland. Our results suggest that selection favours increased size of both sexes on islands and that SSD is unpredictable for insular plants.

Introduction

Sexual size dimorphism (SSD) is common in birds (Santiago-Alarcon & Parker, 2007; Székely, 2007), insects (Stillwell *et al.*, 2010), reptiles (Wikelski & Trillmich, 1997; Pearson *et al.*, 2002), and mammals (Dayan & Simberloff, 1998; Lindenfors, 2007). Morphological differences between the sexes are often striking and become more pronounced on islands (Ebenman & Nilsson, 1982; Dayan *et al.*, 1989; Dayan & Simberloff, 1998; Pearson *et al.*, 2002). SSD is also common in many species of dioecious plants (separate male and female individuals, Bond & Midgley, 1988; Obeso, 2002; Kavanagh *et al.*, 2011; Barrett & Hough, 2013). Islands typically house high numbers of dioecious taxa and insularity is known to promote distinct evolutionary changes in island plant populations (Carlquist, 1966, 1974; Bawa, 1980, 1982; Baker & Cox, 1984; Thomson & Brunet, 1990). However, insular patterns of SSD associated with dioecy remain unknown.

The niche variation hypothesis predicts that morphological variability scales positively with niche breadth (Van Valen, 1965). A further prediction under this hypothesis is that morphological variability increases on islands (see Meiri *et al.*, 2005). Insular populations face fewer competing species and increasing morphological variability may facilitate occupation of available niche space (as advocated to explain size changes of insular animals, Grant, 1965; Lomolino, 2005). SSD is a major component of morphological variability within a population and is also predicted to increase on islands (Ebenman & Nilsson, 1982; Meiri *et al.*, 2005). Additionally, SSD may increase in response to elevated levels of intraspecific competition (Rothstein, 1973; Shine, 1989). The prediction of increased SSD on islands is supported in studies of birds (Ebenman & Nilsson, 1982), mammals (Dayan & Simberloff, 1998; Simberloff *et al.*, 2000) and snakes (Pearson *et al.*, 2002). Alternatively, SSD may become less pronounced on islands, contrary to predictions of the niche variation hypothesis. This may result from reduced habitat diversity, resource abundance, gene flow, or taxon cycle fluctuations (see Ricklefs & Bermingham, 2002; Meiri *et al.*, 2005).

The niche variation hypothesis makes specific predictions regarding morphological variation associated with niche breadth. Therefore, tests for increased SSD on islands should consider traits that are related to niche occupation (e.g canine size in carnivores, Meiri *et al.*, 2005). In plants, leaf size is a suitable trait as it is correlated with climatic conditions and competitive ability (Parkhurs & Loucks, 1972; Grime *et al.*, 1997; Diaz *et al.*, 1998; Moles & Westoby, 2000; Westoby *et al.*, 2002; Thuiller *et al.*, 2004; Ackerly & Cornwell, 2007). SSD in leaf size is also common in many unrelated groups of dioecious plants (Bond & Midgley, 1988; Kavanagh *et al.*, 2011; Barrett & Hough, 2013). Investigating SSD of stem diameter ('stem size' hereafter) may also be informative. Leaf and stem sizes are often related allometrically (Corner, 1949; Niklas, 1994) and differences in SSD between leaves and stems may help elucidate the action of selection.

Here, I provide the first test for differences in SSD between related island and mainland plants. I measured leaf and stem sizes of 28 dioecious taxa, comprising 14 island-mainland comparisons, from four island groups (Kermadec, Three Kings, Chatham, and Auckland Islands) surrounding New Zealand. First, I tested for an increase in the degree of SSD on islands, as predicted by the niche variation hypothesis. Second, I developed a novel analytical technique to test for differences in the direction of SSD (female or male biased) between related mainland and insular plants. Lastly, I tested for sex specific size changes of plants on islands as differences between the sexes may provide insight into patterns of insular SSD.

Methods

The three main islands of New Zealand (North, South and Stewart Islands) are encircled by numerous smaller islands, that vary in age (Gibbs, 2006). The flora of these offshore islands consists mainly of taxa that have dispersed over-water from New Zealand (Wardle, 1991). Although many of these islands were once connected by land bridges, I focused on the Kermadec, Three Kings, Chatham and Auckland islands, as they remained isolated from the main islands during the Pleistocene (see Appendix A1). Specifically, populations from Raoul Island (Kermadec group), Great Island (Three Kings group), Chatham Island (Chatham group), and Auckland Island (Auckland group) were included (see figure 3.1).

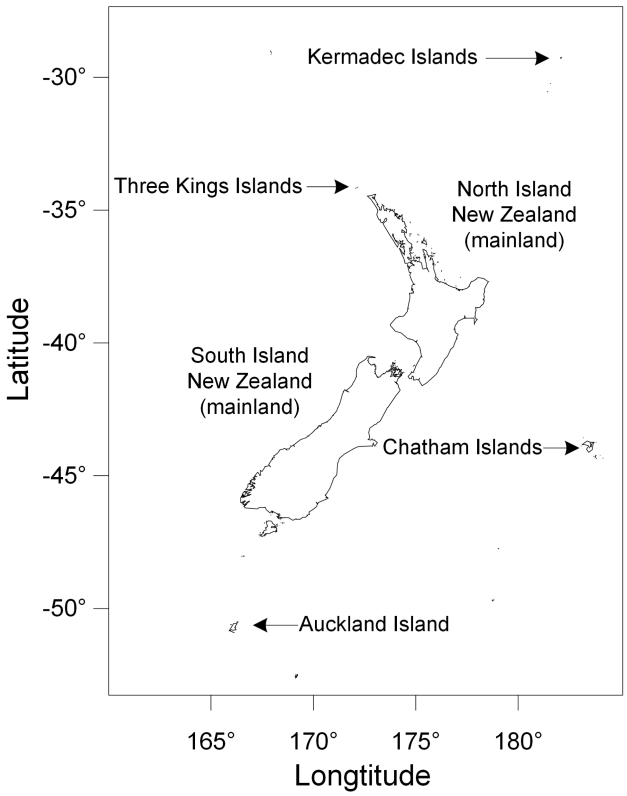

Figure 3.1 Map of study islands surrounding New Zealand

To characterize SSD in insular and mainland plants, I used herbarium material. This allowed efficient collection of a diverse dataset. Material was examined from the national herbarium at Te Papa Tongarewa (the National Museum of New Zealand), the herbarium at Auckland Museum and the Allan Herbarium at Landcare Research. Analysis was restricted to dioecious woody taxa in an effort to mitigate any effect drying may have on stem measurements. I sampled insular taxa with conspecific mainland populations and island endemics with known mainland relatives. This allowed for a broad scale test incorporating the greatest number of island-mainland comparisons possible. I ascertained mainland relatives for Chatham Island species using the recent molecular analysis by Heenan *et al.* (2010). In this study, DNA sequence data were used to identify the closest relatives for 35 taxa endemic to the Chatham Islands. In other cases, phylogenetic analyses were not available to help determine insular and mainland relatives. Two pairings were separated at species but not genus level. In these cases, the mainland taxon chosen is the most likely relative based on morphological similarities (*Piper melchior* and *P. excelsum*; *Coprosma acutifolia* and *C. tenuifolia* – see Dawson & Lucas, 2011). In all other instances, the insular taxa were a variety or subspecies of well-known mainland species (Allan, 1961). When collating mainland data, I only included specimens collected from mainland areas as close as possible to the island in question in an effort to minimise any effect of environmental differences associated with latitude. The dataset consisted of 263 specimens, representing 14 island-mainland taxonomic pairings (see Table 3.1).

Due to the modularity of plant structure, a single parameter is difficult to obtain when quantifying plant size. Additionally, when testing predictions of the niche variation hypothesis it is important to consider traits that are related to niche occupation. I chose to use the size of leaves and stems (diameter) as these measures are easily obtained from herbarium sheets, leaf size is correlated with climatic conditions and competitive ability, and SSD in leaf size is common (Corner, 1949; White, 1983; Bond & Midgley, 1988; Midgley & Bond, 1989; Grime *et al.*, 1997; Diaz *et al.*, 1998; Thuiller *et al.*, 2004; Ackerly & Cornwell, 2007; Kavanagh *et al.*, 2011). Stems must support the weight of

leaves, so leaf and stem sizes are likely to be associated allometrically (Corner, 1949; Niklas, 1994). Stems must also support flowers, fruits and dispersers. Investigating differences in SSD between leaves and stems may provide insight into the processes responsible for observed patterns. As destructive sampling (i.e. removal of leaves) would restrict the use of specimens in the future, digital vernier callipers were used when making measurements (accurate to 0.01mm). Leaf size was estimated by quantifying leaf length (linear distance between leaf tip and base of petiole) and leaf width (maximum distance perpendicular to length measurement at widest point of leaf) on four randomly selected, fully expanded, leaves per specimen. The area of an ellipsoid ($A = \pi \times L/2 \times W/2$) was then used to approximate leaf area. Differences in leaf shape between study taxa may complicate the use of certain leaf area estimation techniques. However, all island-mainland comparisons are made between closely related taxa making any difference in shape minimal (see analyses described below). Stem diameters were measured 10 mm towards the base of the specimen from the point of petiole attachment of the second and fourth randomly selected leaves. Leaf and stem measurements were then averaged within each specimen prior to analyses.

Due to the nature of herbarium collections, species were represented by a variable number of specimens. Collections for dioecious plants also contain a variable number of specimens for each sex. At least five specimens of each sex were measured (see Cornelissen *et al.*, 2003), where possible, for all study taxa (mean ± SE = 4.7 ± 0.125). The use of herbarium specimens allowed a diverse dataset to be utilised, however environmental effects are difficult to discount. Analyses were conducted that accounted for individual variation within taxa to minimise any effect of differences in sampling technique and environmental conditions between individual herbarium specimens (see analyses described below). Although all major herbaria in New Zealand were visited, sample sizes for males within a few study taxa were not ideal. In order to assess the significance of this, I ran Levene tests for homogeneity of variance between male and female data for each study taxa individually. There was no significant difference in variance between male and female leaf size

data for any study taxa. Three taxa displayed unequal variance between male and female stem size data. In all three cases only two specimens represented males. Therefore, I ran all analyses a second time, only including taxa with at least three samples or more for each sex.

SSD can be quantified many different ways. A common technique is to calculate the ratio of male size to female size (e.g. Delph *et al.*, 1996; Wikelski & Trillmich, 1997; Meiri *et al.*, 2005). However the analysis of SSD ratios can be problematic, particularly when a dataset displays both male and female biased SSD. Therefore, I followed the recommendations of Smith (1999) and quantified SSD as the ratio of the larger sex to that of the smaller sex. Ratios were then subtracted from one to provide an index of the degree of SSD (Lovich & Gibbons, 1992; Fairbairn & Shine, 1993; Smith, 1999; Santiago-Alarcon & Parker, 2007). Mean values for female and male traits could be used, however, the use of mean values may be problematic. As SSD may arise from differences in maturation rates between the sexes, incorporating individual variation may be important (the use of mean values per sex would not account for this). Therefore, I implemented a bootstrapping procedure, which randomly selected one individual of each sex when calculating ratios. After 10,000 iterations mean ratios for each of our study taxa were calculated. Differences in SSD between mainland and insular pairings were tested for with the Wilcoxon matched pairs test. Phylogenetic relatedness between pairs in our dataset makes a phylogenetic correction method appropriate (Felsenstein, 1985). However, a lack of phylogenetic hypotheses for our study taxa precluded the use of such techniques. Eight of the insular-mainland pairings in our dataset were from the genus *Coprosma*. I chose to analyse these taxa alone, as well as the pooled dataset, to test for any effect this may have on overall results.

Table 3.1 Sexual Size Dimorphism indices for insular and mainland study taxa. SSD index = 1 - (larger sex/smaller sex), see methods for detailed description.

Island Location	Insular taxa	SSD index		Mainland taxa	SSD index	
		Leaves	Stems		Leaves	Stems
Auckland Island	*Coprosma ciliata*	0.849	0.102	*Coprosma ciliata*	0.692	0.161
Auckland Island	*Coprosma foetidissima*	0.118	0.076	*Coprosma foetidissima*	0.833	0.198
Auckland Island	*Coprosma perpusilla subsp. subantarctica*	0.346	0.061	*Coprosma perpusilla subsp. perpusilla*	0.508	0.256
Chatham Island	*Coprosma propinqua var. martinii*	0.072	0.155	*Coprosma propinqua var. propinqua*	0.621	0.03
Chatham Island	*Coprosma acerosa*	0.194	0.263	*Coprosma acerosa*	0.158	0.134
Chatham Island	*Piper excelsum subsp excelsum*	0.055	0.058	*Piper excelsum subsp excelsum*	0.039	0.021
Chatham Island	*Coprosma chathamica*	0.449	0.166	*Coprosms repens*	0.62	0.271
Chatham Island	*Plagianthus regius subsp. chathamicus*	0.115	0.428	*Plagianthus regius subsp. regius*	2.157	0.179
Kermadec Islands	*Coprosma acutifolia*	0.209	0.171	*Coprosma tenuifolia*	0.506	0.069
Kermadec Islands	*Piper excelsum subsp psittacorum*	0.568	0.164	*Piper excelsum subsp excelsum*	0.039	0.021
Three Kings Islands	*Piper melchior*	0.101	0.23	*Piper excelsum subsp excelsum*	0.039	0.021
Three Kings Islands	*Coprosma macrocarpa subsp. macrocarpa*	0.323	0.244	*Coprosma macrocarpa subsp. minor*	0.2	0.072
Three Kings Islands	*Alectryon excelsus subsp. grandis*	0.249	0.129	*Alectryon excelsus subsp. excelsus*	0.711	0.131
Three Kings Islands	*Streblus smithii*	0.144	0.121	*Streblus banksii*	0.827	0.105

While the analyses described above test for differences in the degree of SSD between mainland and island pairings, changes in which sex is larger (direction of SSD) are not accounted for. I implement a novel analytical technique to identify the direction of SSD for related insular and mainland taxa (Fig. 2). The angle, α, of a line connecting male and female points can take any value in the range 0-360° and describes which sex is larger in island and mainland settings. For example, angles less than 90 degrees indicate that SSD is female biased for both mainland and insular taxa (females have larger size on mainland (x-axis) and on island (y-axis) - see Fig 3.2). While angles between 90 and 180 degrees indicate male biased SSD on islands and female biased SSD on the mainland (male point higher than female on y-axis, female point higher than male on x-axis). After calculating angles connecting male and female points (14 male-female pairings) for both leaves and stems, I conducted Rayleigh's test of uniformity to test whether the distribution of angles was non-random. I then calculated the circular mean and von Mises bootstrapped 95% confidence intervals.

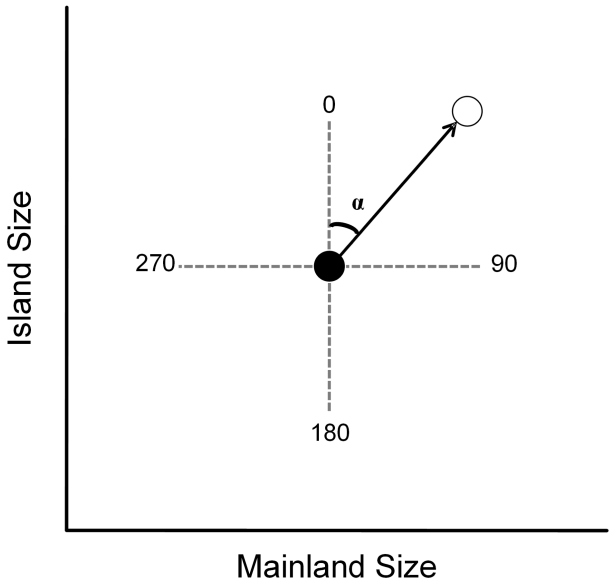

Figure 3.2 Diagrammatical representation of insular and mainland SSD. The closed circle represents males and open circle females, for a hypothetical species. The angle of the line between male and female points, α, describes which sex is larger in mainland and island situations.

Lastly, I ran reduced major axis regression (RMA) of island size (leaves and stems) against mainland size, separately for males and then females. Differences in environmental conditions between specimens may influence leaf size and variation in stem age between specimens may influence stem diameter. Therefore, a bootstrapping procedure was implemented to account for among individual variation. One male and female individual were randomly selected from each taxon and then RMA used to calculate slope and intercept parameters. After 10,000 iterations, mean slope and intercept parameters were calculated. Data were logarithmically transformed prior to analysis to conform to normality assumptions. Incorporating this analysis allowed for differences in mainland-to-island size change between the sexes to be detected. All analyses were carried out in the R environment for statistical computing and circular statistics were calculated using the R packages *Circular* and *CircStats* (Lund & Agostinelli, 2009; Agostinelli & Lund, 2011; R-Development-Core-Team, 2011). RMA analyses were conducted using the package *smatr* (Warton *et al.*, 2012b).

Results

There was no consistent difference in degree of SSD of leaves between island and mainland pairings (Figure 3.3A). Wilcoxon matched pairs test showed there to be no significant difference in SSD of leaves between islands and mainland for either the pooled dataset or *Coprosma* taxa (W = 80, *P* = 0.0906; *Coprosma,* W = 30, *P* = 0.1094). Similarly, degree of SSD of stems displayed no discernable pattern when insular and mainland pairs were compared (Figure 3.3B). Wilcoxon matched pairs test showed there to be no significant difference in SSD of stems between islands and mainland (W = 30, *P* = 0.1726; *Coprosma*, W = 16, *P* = 0.8438).

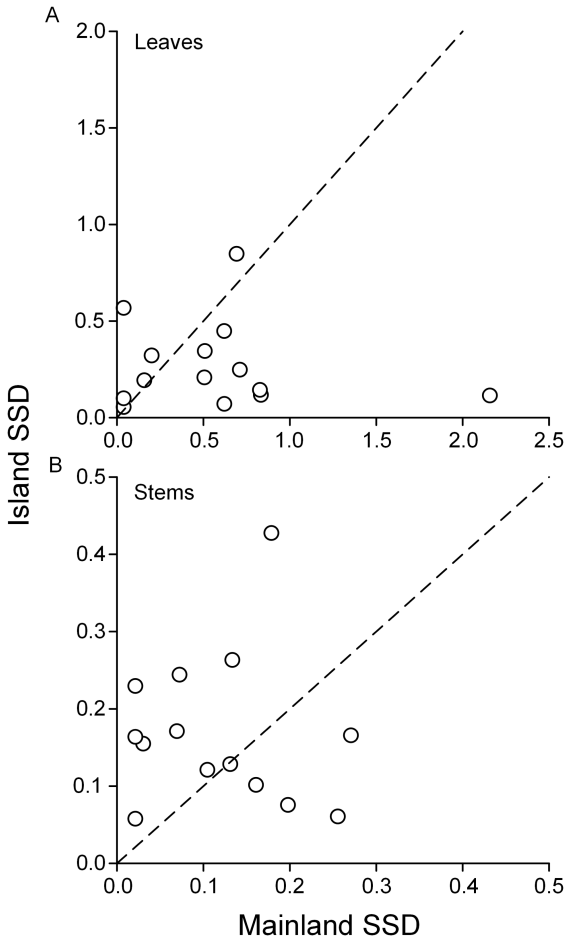

Figure 3.3 Relationship between degree of SSD in leaf (A) and stem size (B) of insular taxa and their corresponding mainland relative. SSD = 1 - (larger sex/ smaller sex). The dotted line represents isometry (points above the line indicate greater degree of SSD on islands; points below the line indicate greater degree of SSD on the mainland).

Results of Rayleigh's test of Uniformity indicated lines joining male and female points did cluster about a mean direction, for both leaf and stem analyses (leaves, $P = 0.0037$; stems, $P = 0.011$; see Figure 3.2 & 3.4). The confidence interval of the mean direction for leaves encompasses 90°, suggesting SSD in leaf size is not consistently female or male biased on islands (mean = 86.178; 95% CI = 56.568-113.840). However, it suggests female leaves are consistently larger for mainland taxa as angles higher than 180° are outside of the 95% confidence interval (see Figure 3.4A). Analysis of stem size data produced analogous results. SSD in stem sizes was not consistently male or female biased on islands (mean = 63.492; 95% CI = 35.917-110.293). However, as values above 180° are not contained within the confidence interval, this suggests female stem size is consistently larger than male stem size on the mainland (Figure 3.4B).

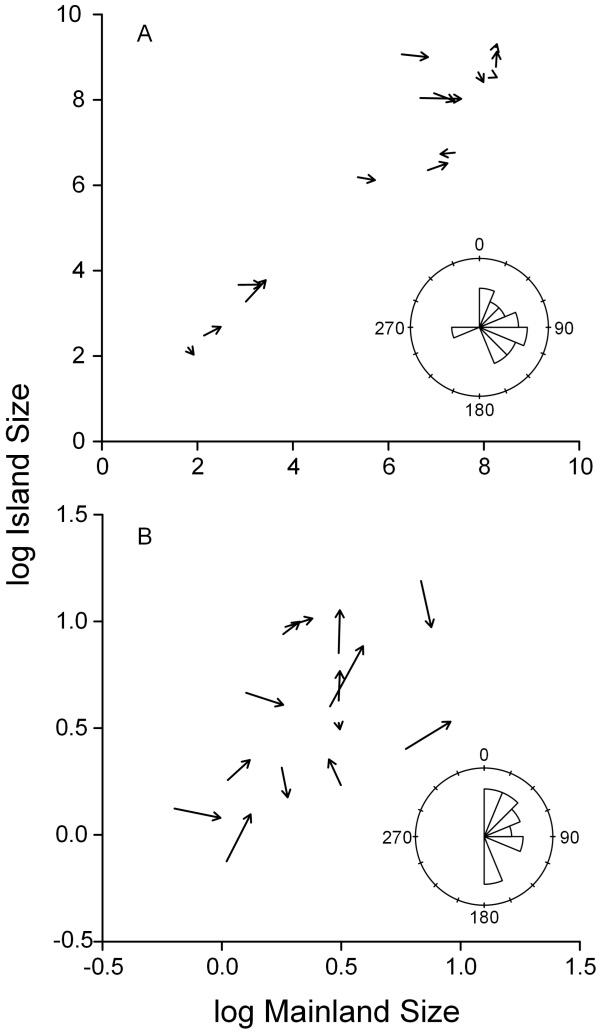

Figure 3.4 The direction of SSD for insular and mainland leaf (A) and stem size (B). Arrows represent lines between male and female points, the angle of the line indicating the direction of SSD for related mainland and insular taxa (see Figure 1). Rose diagrams display the frequency distribution of line angles.

Male and female leaf sizes were consistently larger on islands. The slope of the RMA analysis was greater than one and the majority of points fall above the line of isometry (see Table 3.2 & Figure 3.5A). However, the intercept for female values is slightly below zero, while the intercept for male values is marginally greater than zero. Stem sizes were also larger on islands for both males and females, with slope parameters greater than one for both sexes (see Table 3.2 & Figure 3.5B).

Analyses only including taxa with at least three or more specimens for each sex produced identical results (see Appendix A2).

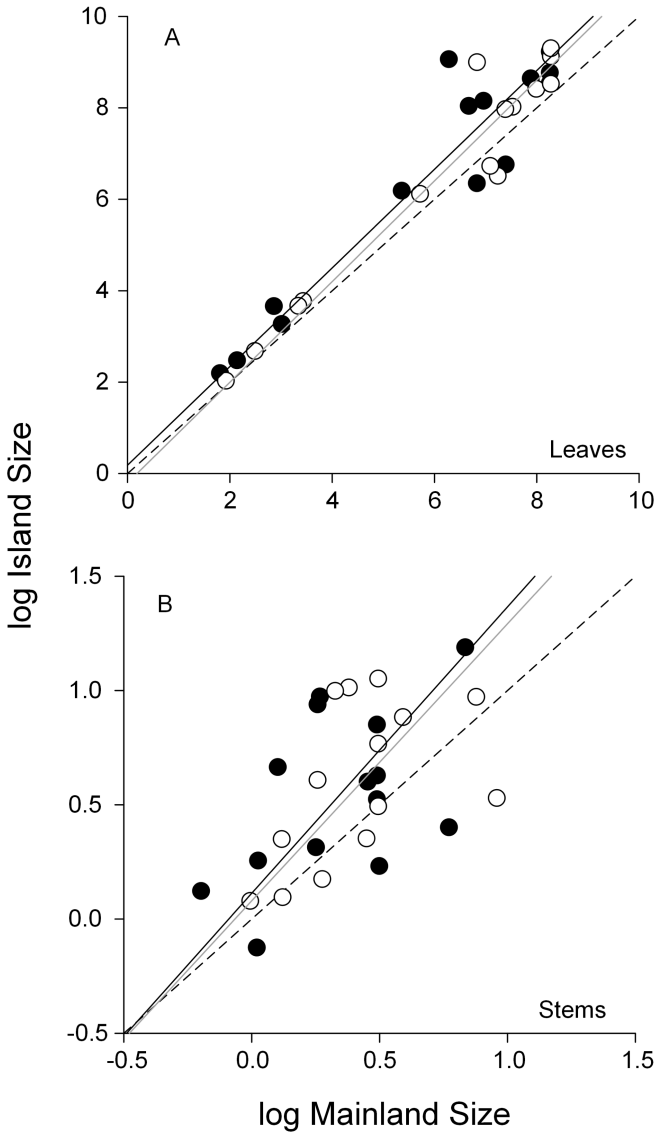

Figure 3.5 Relationship between leaf (A) and stem size (B) of 14 island-mainland comparisons. Males are represented by closed circles, females by open circles. The dotted line represents isometry (points above the line of isometry indicate larger size on islands; points below the line indicate larger mainland size). Solid lines are result of RMA regression, black lines represent males and grey lines represent females (see Table 3.3).

Table 3.3 Results from RMA analyses of insular and mainland leaf and stem sizes. Slope and intercept parameters are given for male and female individuals.

		Slope	**Intercept**
Trait	**Sex**	Mean value ± SD (95% CI)	Mean value ± SD (95% CI)
Leaves			
	Female	1.101 ± 0.046 (1.100-1.102)	-0.203 ± 0.303 (-0.209 to -0.197)
	Male	1.079 ± 0.045 (1.079-1.080)	0.184 ± 0.278 (0.178-0.189)
Stems			
	Female	1.212 ± 0.416 (1.204-1.220)	0.080 ± 0.186 (0.077-0.084)
	Male	1.253 ± 0.315 (1.246-1.259)	0.113 ± 0.133 (0.110-0.0115)

Discussion

SSD did not vary predictably between islands and the mainland. This is inconsistent with predictions of the niche variation hypothesis, suggesting it does not apply to dioecious plants. However, SSD was consistently female-biased on the mainland. Female plants often outcompete males and leaf size scales positively with competitive ability (Thuiller *et al.*, 2004; Sanchez-Vilas *et al.*, 2011; Barrett & Hough, 2013). Selection may also favour larger stems in females in order to support the weight of seeds and structures that aid the seed dispersal process (Kavanagh *et al.*, 2011). This may promote SSD in leaf size due to allometry between leaves, stems and accessory structures (Corner, 1949). Alternatively, selection for differences in plant architecture between the sexes may promote efficient pollen capture and dispersal (see Midgley, 2010).

Both the direction and the degree of SSD were not predictable for insular plants. Environmental differences between islands may be important, as many plant traits vary predictably along environmental gradients (Diaz *et al.*, 1998). Environmental variables scale strongly with latitude (Clarke & Gaston, 2006; Kreft & Jetz, 2007), however a recent test found consistent size increases of plants on islands separated by more than 20° latitude (see Burns *et al.*, 2012). Similarly, my results displayed consistent increases in the size of both sexes,

across all islands. Experiments on *Drosophila* suggest changes in SSD are not predictable when both sexes are under selection for increased size simultaneously (Reeve & Fairbairn, 1996). This may also apply to dioecious plants.

In dioecious species, reproductive costs are higher for females than males (Bazzaz *et al.*, 1987). For example, males may allocate 10-15% of resources to reproduction while this figure can reach 40% in females (Wallace & Rundel, 1979). Differences in growth rates between the sexes have also been linked to reproductive costs (Jing & Coley, 1990). While both sexes illustrated a tendency for larger leaves on islands, this was not as strong in females (intercept parameter less than zero). Differences in reproductive expenditure may result in male individuals having more resources available for vegetative growth. Therefore, selection acting to increase leaf size on islands may be slightly more constrained in females, leading to unpredictable patterns of SSD.

A recent test for size changes of insular plants in the south-west Pacific suggested that selection might be acting specifically on leaf size (Burns *et al.*, 2012; but see Kavanagh & Burns, 2014). This is consistent with my results and increasing leaf size may have important consequences for insular flora. For example, differences in herbivore communities between islands and mainlands may promote evolutionary changes in leaf size. Small leaves are thought to deter browsing by large herbivores, however islands typically house fewer herbivore species than comparable mainland areas (Carlquist, 1974; Bond *et al.*, 2004; Lee *et al.*, 2010). This reduction in herbivory pressure may relax selection for smaller leaves. The depauperate nature of islands increases levels of intraspecific competition and this has been attributed to size changes of insular animals (Grant, 1965; Case, 1978; Lomolino, 2005). It may also promote increases in leaf size. Increasing leaf size may provide a competitive advantage to insular plants, as plants with larger leaves tend to have wider distributions and are more competitive (Carlquist, 1974; Bond *et al.*, 2004; Lee *et al.*, 2010). Consequently, stem sizes may increase via correlated evolution with leaf size.

SSD did not vary predictably between insular and mainland plants, contrary to predictions of the niche variation hypothesis. However, leaves and stems of both sexes were consistently larger on islands. Larger leaves may be selectively advantageous where intraspecific competition is high and herbivores are scarce. Stem sizes may then increase via correlated evolution with leaves. Male and female plants may respond to selection for increased size at different rates, perhaps due to differences in reproductive costs, and this deserves further attention. The majority of island-mainland comparisons in the dataset were between fleshy-fruited taxa (see Appendix A3). Results were consistent for the one comparison between taxa with wind-dispersed seeds, however future analyses are needed to determine if life-history traits influence insular patterns of SSD. Furthermore, incorporating estimates of divergence times, differences in environmental conditions, and extending analyses to a global scale will further our understanding of SSD in island plants.

Chapter 4 - Herbivory and the evolution of divaricate plants: structural defenses lost on an offshore island

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Abstract

Many island plants are characterised by unique morphology. For example, the high branching angles and small leaves of divaricate plants are a common feature of the New Zealand flora. The divaricate growth form may be an adaptation to deter browsing by extinct avian herbivores (moa); alternatively aspects of the insular climate may be responsible. However, our understanding of the selective pressures responsible for the high branching angles and small leaves of divaricate plants is incomplete. Here, I tested for differences in traits associated with the divaricate growth form between plants from Chatham Island and the New Zealand mainland. Moa never reached the Chatham Islands and its flora is derived from plants on mainland New Zealand. Therefore, I predicted Chatham Island plants to have lost morphological adaptations that may have deterred moa herbivory. Traits were quantified on 316 individuals in the field, allowing for 12 island-mainland taxonomic comparisons. Chatham Island plants consistently produced smaller branching angles, larger leaves, shorter internodes, and larger stems than related mainland plants. Results are therefore consistent with the hypothesis that selection for small leaves and high angled branching may be relaxed on the Chatham Islands due to an absence of moa. Smaller branching angles and larger leaves may offer a competitive advantage to Chatham Island plants.

Introduction

Many island plants are characterized by leaf and shoot morphology that is uncommon in mainland floras. For example, the divaricate growth form (small, widely spaced leaves, narrow stems, and high branching angles) is a feature of more than 50 species from 16 families in New Zealand (Greenwood & Atkinson, 1977). Plants sharing similar traits are also common in Madagascar ('wire plants' - see Bond & Silander, 2007). Large birds were dominant herbivores in both New Zealand (Moa - Aves: Dinornithiformes) and Madagascar (Elephant birds – Aves: Aepyornithidae), leading to the hypothesis that the divaricate growth form is an adaptation to deter large avian browsers (Greenwood & Atkinson, 1977; Bond *et al.*, 2004; Bond & Silander, 2007). Although direct tests are not possible (due to the extinction of elephant birds and moa), feeding trials with extant ratites support the anti-herbivore hypothesis (Bond *et al.*, 2004). Alternatively, the high branching angles and small leaves may be an adaptive response to wind, cold, temperature fluctuations (McGlone & Webb, 1981), or a mechanism to avoid photoinhibition (Howell *et al.*, 2002; Christian *et al.*, 2006).

Moa were present on the main islands of New Zealand (North and South Islands, 'mainland' hereafter – see Figure 1) until hunting and habitat loss lead to their extinction less than 1000 years ago (Holdaway & Jacomb, 2000). However, many of the offshore islands surrounding the mainland were never reached by moa (see Greenwood & Atkinson, 1977). For example, moa were not present on the Chatham Islands, yet the flora of the islands is derived primarily from taxa that arrived via overwater dispersal from the New Zealand mainland (Heenan *et al.*, 2010). These dispersal events are estimated to have occurred approximately 3 Ma, long after the diversification of moa in New Zealand (Bunce *et al.*, 2009; Heenan *et al.*, 2010). While anti-herbivore defenses may be under strong selection on the mainland (New Zealand), selection for these traits may be relaxed after island colonization. For example, plant-ant mutualisms that deter insect herbivores are often lost on islands (Janzen, 1973; Rickson, 1977) and morphological and chemical defenses are absent or less effective (Bryant *et al.*, 1989; Bowen & VanVuren, 1997; Vourc'h

et al., 2001). Chatham Island plants tend to display reduced levels of heteroblasty when compared to related mainland plants, potentially due to an absence of moa herbivory (Burns & Dawson, 2009). A similar situation may be occurring with divaricating plants (see Greenwood, 1992), however this is yet to be tested.

Despite four decades of investigation, the functional significance of divaricate traits remains unresolved (Greenwood & Atkinson, 1977; McGlone & Webb, 1981; Day, 1998; Howell *et al.*, 2002; Bond *et al.*, 2004; Bond & Silander, 2007). The absence of moa on the Chatham Islands, along with climatic similarities and the flora being derived from plants on the New Zealand mainland, offers a unique opportunity to further test the anti-herbivore hypothesis. Under the anti-herbivore hypothesis, it is suggested that the high branching angles and small leaves of divaricate plants would make feeding difficult and unproductive for browsing birds (Greenwood & Atkinson, 1977; Bond *et al.*, 2004). Therefore, selection for these traits may be relaxed on the Chatham Islands. This may also apply to species that are not strictly defined as divaricate. For example, a plant with higher branching angles and smaller leaves than a co-occurring plant should be better defended against browsing birds, regardless of growth form.

I predicted Chatham Island plants to have lost morphological adaptations thought to deter moa herbivory. Branching angles, internode lengths and the sizes of leaves and stems were quantified on 316 individuals, representing 12 island-mainland comparisons from nine families and a range of growth-forms. First, I tested for differences in branching angles between related Chatham Island and mainland plants, as high angled branching may have made feeding difficult for moa (see Bond *et al.*, 2004). Second, I tested for differences in scaling relationships between internode length and leaf size, as small widely spaced leaves make feeding unproductive for large avian browsers (Bond *et al.*, 2004). Lastly, I tested for differences in the size of leaves and stems between Chatham Island and mainland plants.

Methods

Numerous smaller islands surround the main islands of New Zealand (North and South Island). One group of satellite islands is the Chatham Islands, located 850 km to the east of the main islands of New Zealand at 44°S (see Figure 4.1). The flora of the Chatham Islands consists mainly of taxa that have dispersed overwater from New Zealand. The islands also have a long history of isolation, emerging between 3.0 and 2.0 Ma and remaining isolated from the main islands of New Zealand during the Pleistocene (Heenan *et al.*, 2010). Compared to locations at similar latitude on the New Zealand mainland, the Chatham Islands experience similar mean temperatures (Chatham Is = 11.4° C; Christchurch = 12.1° C), slightly more annual rainfall (Chatham Is = 855 mm; Christchurch = 648 mm), higher average wind speeds (Chatham Is = 25 km/h; Christchurch = 15 km/h), more days per year with gale force winds (Chatham Is = 16; Christchurch = 3) and fewer frost days per year (Chatham Is = 4; Christchurch = 70; (National Institute of Water and Atmospheric research, 2014).

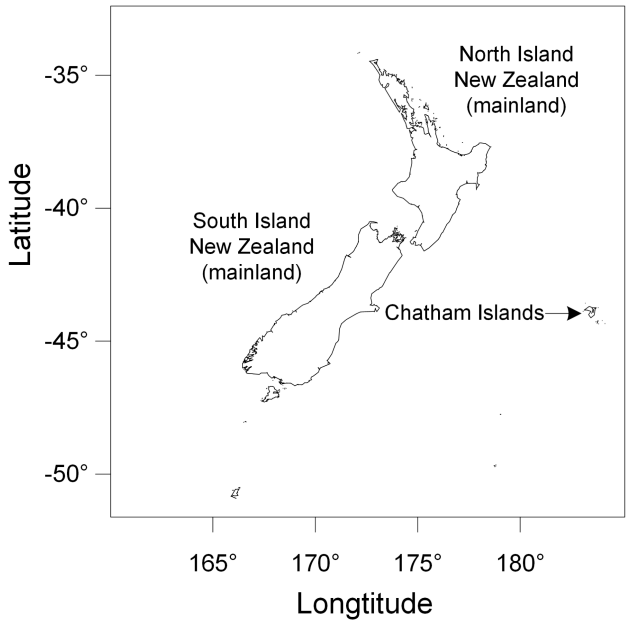

Figure 4.1 Map of New Zealand and Chatham Islands

Data were collected on Chatham Island in February 2013 and plants were sampled in Ocean Mail Scenic reserve (43°44.73'S, 176°23.91'W), Henga Scenic reserve (43°51.0′ S 176°33.2′ W), Mt. Chuddleigh Reserve (43°43.57'S, 176°33.94' W), and Nikau Bush Scenic reserve (43°45.7′ S 176°34.8′W). Mainland samples were collected from Otari Wilton's Bush (41°14′ S, 174°45′ E), Nelson Lakes National Park (41°48′ S, 172° 50′ E), Wellington Eastern Walkway (41°19.86' S, 174°49.77′ E), Keith George Memorial Park (41°08.36′S, 175°00.18′E), Castle Point Scenic Reserve (40°54.32′S, 176°13.25′E), Lowes Bush Scenic Reserve (41°00.03′S, 175°35.91′E) and Titahi Bay (41°06.40′S, 174°50.10′E). Where possible, at least 10 adult individuals were sampled per taxon (mean ± SE =13.74 ± 0.37). Differences in leaf and branching traits are often associated with light conditions (Cornelissen *et al.*, 2003). Therefore, only plants growing in well-lit areas were sampled. On each individual, two terminal stems were randomly selected and the following traits were measured: stem length, internode length, branching angle, stem diameter, and leaf size. I chose to focus on the aforementioned traits, as they have often been associated with adaptations to deter browsing by moa (Greenwood & Atkinson, 1977; Bond *et al.*, 2004; Bond & Silander, 2007). Five branching events were randomly selected and angles were measured to the nearest degree using a protractor. When fewer than five branching events were present, all were measured. Three fully expanded leaves from each stem were randomly selected for leaf area measurements. Leaf size was estimated by quantifying leaf length (linear distance between the leaf tip and the base of the petiole) and leaf width (maximum distance perpendicular to the length measurement at the widest point of the leaf). The area of an ellipsoid ($A = \pi \times L/2 \times W/2$) was then used as a proxy for leaf area. Stem diameter was measured at the base of each stem, 1 cm towards the stem tip to avoid any swelling at the node. Leaf and stem measurements were taken using digital vernier calipers (accurate to 0.01 mm). Measurements were then averaged within each individual prior to analyses.

Determining mainland relatives for taxa endemic to Chatham Island was achieved using the recent molecular analysis by Heenan *et al.* (2010). In this

study, DNA sequence data were used to identify the closest relatives on mainland New Zealand for 35 taxa endemic to the Chatham Islands. In one instance, two insular taxa (*Coprosma propinqua var. martinii* and *C. aff martini*) were descended from the same mainland taxon (*C. propinqua var. propinqua*), yet they display remarkably different growth habits (*Coprosma propinqua var. martinii* is an upright shrub to small tree growing in swamps and bogs; *C. aff martini* is a prostrate to decumbent shrub restricted to sand dunes - see Heenan *et al.*, 2010). Therefore, they were treated as independent comparisons. In two cases, the Chatham Island taxa were undifferentiated taxonomically from well known mainland taxa.

To test for differences in mean branching angle between related Chatham Island and mainland plants I first ran Watson-Williams tests, equivalent to a t-test for circular data (see Jammalamadaka & SenGupta, 2001), for each taxonomic pairing. Following this, I conducted Rayleigh's test of uniformity on the pooled Chatham Island data, and then mainland data, to test whether the distribution of branching angles was non-random in each location (see Jammalamadaka & SenGupta, 2001). The circular mean and von Mises bootstrapped 95% confidence intervals were also calculated for Chatham Island and mainland branching angles. Lastly, I conducted a Watson-Williams test on the pooled Chatham Island and mainland branching angles.

The density of leaves on a stem could be quantified in a variety of ways. One option is to take the ratio of leaf size to internode length, providing an indication of the gap between adjacent leaves (Kelly, 1994). However, the use of ratios in statistical analyses can often be problematic (see Smith, 1999). To avoid the potential complications associated with the analysis of ratios, scaling relationships between leaf size (dependent variable) and internode length (independent variable) were used. Reduced major axis regression (RMA) of leaf size and internode length was carried out separately for Chatham Island and mainland data. RMA was utilized instead of Ordinary Least Squares (OLS) regression due to variables being subject to sampling and measurement error (see Price & Phillimore, 2007). Resulting slope and intercept parameters indicate whether leaf sizes differ for a given internode length between Chatham

Island and mainland plants. Mean values for Chatham Island and mainland taxa could be used when calculating regression parameters. However, the use of mean values per taxon ignores among-individual variation. This may be particularly important when analyzing plant traits that are potentially influenced by differences in age or growing conditions between individuals. In order to account for this a bootstrapping procedure was implemented (see Kavanagh *et al.*, 2011). During each bootstrap replicate one individual was randomly selected from each taxon and RMA was used to obtain slope and intercept parameters. After 10,000 iterations mean slope and intercept parameters were calculated, along with associated standard deviations and 95% confidence intervals.

Lastly, leaf and stem sizes were compared between related Chatham Island and mainland taxa. To test for size differences in leaves and stems between island and mainland taxa the RMA procedure described above was implemented (Chatham Island trait size as dependent variable and mainland trait size as independent variable). Secondly, I ran ANCOVA to test for differences in the allometric scaling of leaf and stem sizes. Leaf size was treated as the dependent variable, stem size as a covariate and location (island or mainland) as a fixed factor.

Leaf size and internode data were natural logarithm-transformed to conform to assumptions. All analyses were conducted in the R environment for statistical computing (R Development Core Team, 2013). RMA analyses were conducted with the smatr package (Warton *et al.*, 2012b). Watson-Williams tests, Rayleigh's tests of uniformity, circular means and von Mises bootstrapped 95% confidence intervals were calculated with the CircStats package (Lund & Agostinelli, 2009).

Table 4.1 Average branching angles and Watson-Williams test results for related Chatham Island and mainland plants (growth forms are for mainland taxa). Adult individuals were sampled in all cases. Average island and mainland angles across all taxa ('All' – bottom row of table) are based on species averages.

Mainland taxa	Growth form	Branching angle	Chatham Island taxa	Branching angle	Watson-Williams test
Coprosma propinqua	Divaricate shrub	79.515	*Coprosma propinqua var. martinii*	43.261	$F_{(1, 27)} = 254.74$, $p<0.001$
Coprosma propinqua	Divaricate shrub	79.515	*Coprosma aff. martinii*	48.774	$F_{(1, 26)} = 152.324$, $p<0.001$
Leptecophylla juniperina	Shrub to small tree	49.871	*Leptecophylla robusta*	38.541	$F_{(1, 26)} = 28.582$, $p<0.001$
Plagianthus regius subsp. regius	Tree	53.124	*Plagianthus regius subs. chathamicus*	51.483	$F_{(1, 25)} = 0.158$, $p = 0.694$
Coprosma repens	Small tree	59.493	*Coprosma chathamica*	40.846	$F_{(1, 27)} = 64.2528$, $p<0.001$
Melicytus alpinus	Shrub	55.615	*Melicytus chathamicus*	33.909	$F_{(1, 26)} = 97.102$, $p<0.001$
Piper excelsum	Small tree	48.154	*Piper excelsum*	41.983	$F_{(1, 26)} = 6.529$, $p = 0.017$
Hebe elliptica	Shrub	44.445	*Hebe barkeri*	56.394	$F_{(1, 23)} = 11.733$, $p = 0.002$
Myrsine divaricata	Divaricate shrub	69.528	*Myrsine chathamica*	42.133	$F_{(1, 26)} = 131.436$, $p<0.001$
Corokia cotoneaster	Divaricate shrub	65.824	*Corokia macrocarpa*	42.842	$F_{(1, 24)} = 61.67$, $p<0.001$
Coprosma acerosa	Prostrate shrub	74.988	*Coprosma acerosa*	69.875	$F_{(1, 27)} = 2.283$, $p = 0.142$
Olearia virgata	Divaricate shrub	43.679	*Olearia traversiorum*	40.189	$F_{(1, 23)} = 1.435$, $p = 0.243$
All	-	60.293	All	45.800	$F_{(1,22)} = 9.445$, $p = 0.006$

Results

Mean branching angles were significantly different in 9 of the 12 Chatham island-mainland comparisons and the majority displayed lower branching angles for Chatham Island taxa (see Table 4.1). Results of Rayleigh's test of uniformity indicated that branching angles did cluster about a mean, for both mainland and Chatham Island plants (mainland – $P < 0.001$; Chatham Island – $P < 0.001$). The Watson-Williams test indicated that Chatham Island and mainland branching angles were significantly different (see Table 4.1), and average branching angles were lower for Chatham Island taxa (Chatham Island: mean = 45.800°, 95% CI = 41.310°-51.243°; mainland: mean = 60.293°, 95% CI = 53.598°-67.681°; see Table 4.1 & Figure 4.2).

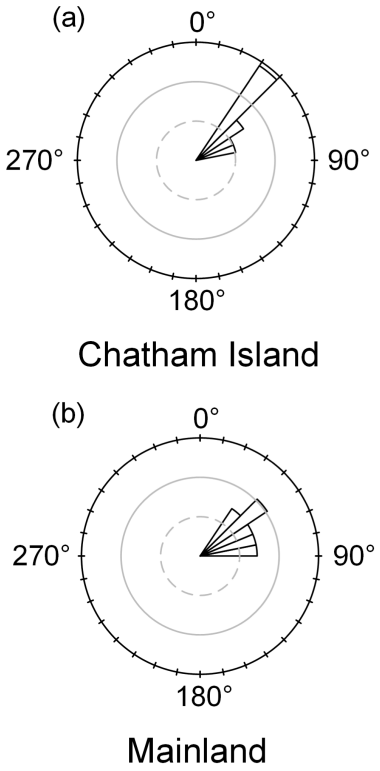

Figure 4.2 Rose diagrams representing average branching angles for (a) Chatham Island and (b) mainland taxa. Dashed grey circles indicate a frequency of 1; solid grey circles a frequency of 4; and the outer black circle a frequency of 8 (i.e. 8 taxa). Mainland: mean = 60.293°, 95% CI = 53.598°-67.681°. Chatham Island: mean = 45.800°, 95% CI = 41.310°-51.243°

Leaf sizes scaled positively with internode lengths (see Figure 4.3). However, the relationship differed for island and mainland plants. The slope parameter was 2.329 (see Table 4.2) for Chatham Island taxa and the intercept value was greater than zero. For mainland plants, the slope parameter was marginally smaller (2.213) and the intercept parameter was less than zero (see Table 4.2). These results suggest that Chatham Island taxa consistently produce larger leaves than mainland taxa for a given internode length (see Figure 4.3).

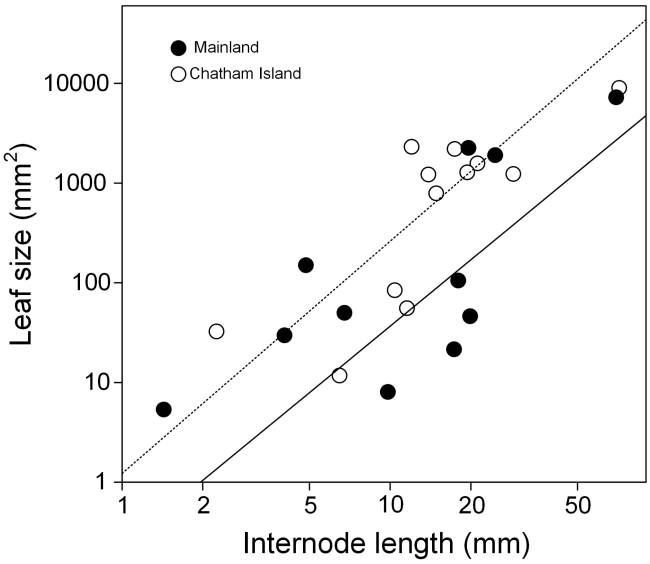

Figure 4.3 Relationship between leaf size and internode length for mainland and island plants. Closed circles are mainland taxa and open circles are insular taxa. The dotted line represents RMA results for island plants, the solid line for mainland plants. Both axes are logarithm transformed.

Chatham Island leaf sizes scaled positively with mainland leaf sizes (Chatham Island leaf size as dependent variable, mainland leaf size as independent variable; slope = 0.952). However, the intercept parameter of the RMA analysis was greater than zero (1.703, see Table 4.2). This indicates that leaf sizes were consistently larger for Chatham Island taxa. Results were similar in the analysis of stem sizes (see Table 4.2). Leaf sizes scaled positively with stem sizes ($F_{1,19} = 42.146$, $P < 0.001$), relationships had similar slopes ($F_{1,19} = 0.068$, $P = 0.797$) and intercepts ($F_{1,20} = 0.359$, $P = 0.556$) for Chatham Island and mainland datasets.

Table 4.2 Results of RMA regression analyses. In leaf size - internode length comparisons, leaf size was the dependent variable and internode length was the independent variable. In comparisons of leaf and stem size between Island and mainland plants (two bottom rows of table), Chatham Island data were the dependent variable and mainland data the independent variable.

		Slope	Intercept
Trait	**Location**	**Mean value ± SD (95% CI)**	**Mean value ± SD (95% CI)**
Leaf size v Internode length	Island	2.329 ± 0.187 (2.325 - 2.332)	0.088 ± 0.555 (0.077 - 0.0989)
Leaf size v Internode length	Mainland	2.213 ± 0.156 (2.21 - 2.216)	-0.648 ± 0.390 (-0.656 to -0.641)
Stem size	Island v Mainland	0.974 ± 0.421 (0.966 - 0.982)	1.124 ± 1.313 (1.10 - 1.15)
Leaf size	Island v Mainland	0.952 ± 0.045 (0.951 - 0.953)	1.703 ± 0.186 (1.699 - 1.706)

Discussion

High branching angles, small leaves that are widely spaced, and narrow stems may have deterred moa herbivory (Greenwood & Atkinson, 1977; Bond *et al.*, 2004). Chatham Island plants tended to have lower branching angles, larger leaves, smaller spaces between leaves, and stouter stems than related mainland plants. These results suggest that the absence of moa on the Chatham Islands has relaxed selection for morphology thought to deter browsing moa.

The wide angled branching of divaricate plants may be a response to browsing moa, making shoots difficult for birds to swallow (see Greenwood & Atkinson, 1977; Bond *et al.*, 2004; Bond & Silander, 2007). Chatham Island plants tended to display lower branching angles than mainland relatives (see Figure 4.2), even in cases where the mainland taxa were not described as divaricate (Allan, 1961). The absence of moa on Chatham Island may have relaxed selection for high branching angles. Branching angle also influences overall plant architecture and light capture efficiency (Honda & Fisher, 1978).

Simulation models suggest that trees with tall narrow crowns (i.e. small branching angles) are more competitive (Borchert & Tomlinson, 1984). Evolutionary changes on islands are often associated with increased intraspecific competition (Grant, 1965; Case, 1978; Lomolino, 2005) and this may also contribute to evolutionary changes in plant branching angles.

Results of a recent investigation into evolutionary changes of island plants suggest that selection is acting to increase leaf size (Burns *et al.*, 2012; but see Kavanagh & Burns, 2014). Chatham Island plants tended to produce larger leaves than mainland relatives, consistent with the results of Burns *et al.* (2012). Furthermore, Chatham Island taxa produced larger leaves for a given internode length. Selection may favour small, widely spaced leaves on the mainland to deter large browsers (e.g. moa) by making feeding unproductive (Bond *et al.*, 2004; Lee *et al.*, 2010). The absence of moa on the Chatham Islands may have relaxed selection for small, widely spaced leaves. Selection may then favour increased leaf size as plants with larger leaves are more competitive and occupy wider distributions (Schmitt & Wulff, 1993; Grime *et al.*, 1997; Westoby *et al.*, 2002; Thuiller *et al.*, 2004). Stem sizes of Chatham Island plants were also larger than those of mainland relatives. Stems provide biomechanical support for leaves and the two traits are often associated allometrically (Corner, 1949; Niklas, 1994). Therefore, stem size may increase via correlated evolution with leaves.

The high branching angles and small leaves of divaricating plants may provide tolerance to wind and frost (McGlone & Webb, 1981), improve light capture efficiency (Day, 1998) and reduce photoinhibition (Howell *et al.*, 2002). Compared to locations at the same latitude on the New Zealand mainland, the Chatham Islands have similar mean temperatures but are much windier (National Institute of Water and Atmospheric research, 2014). A reduction in leaf size and number is associated with increased tolerance to wind stress (Stokes *et al.*, 1995; Niklas, 1996). Yet, Chatham island taxa consistently displayed larger, more closely spaced leaves than related mainland plants. The wide-angled branching of divaricate plants may provide a 'frost-screen'; protecting interior leaves from frost damage (McGlone & Webb, 1981). The

Chatham Islands experience fewer frost days than comparable mainland areas. However, tests are yet to demonstrate significant climate based benefits to traits associated with the divaricate growth form (Kelly & Ogle, 1990; Darrow *et al.*, 2001; Howell *et al.*, 2002; Christian *et al.*, 2006).

Chatham Island plants consistently produced larger leaves, smaller spaces between leaves, lower branching angles, and stouter stems than related mainland plants. These results are consistent with the prediction that an absence of moa has relaxed selection for plant traits that deter moa herbivory. Furthermore, increasing leaf size and reducing branching angles may provide a competitive advantage in response to elevated intraspecific competition. Insular climate has been advocated as an alternative to the anti-herbivore hypothesis for the evolution of divaricate plants (see McGlone & Webb, 1981). However, structural differences between related Chatham Island and mainland plants are inconsistent with predictions of the climate-based hypothesis. While direct tests are not possible, the results of this study lend further support to the anti-herbivore hypothesis for the evolution of the divaricate growth form. Furthermore, results were consistent among island-mainland pairings regardless of whether mainland taxa were defined as divaricate. Increased tensile strength of stems may be a further adaptation to deter browsing moa (Bond *et al.*, 2004; Bond & Silander, 2007). Future studies comparing stem tensile strength between Chatham Island and mainland plants may provide further insights into the importance of this defensive strategy. Investigations including a variety of growth forms and island systems are now needed, in addition to further cafeteria-style experiments, to establish the importance of moa herbivory in the evolution of structural traits in the New Zealand flora.

Chapter 5 - The ontogeny of signal honesty: new insights from an aposematic tree

Abstract

Young animals often have less energy to devote to defense and are therefore more likely to utilize dishonest defensive signals. Here, I demonstrate dishonest defensive signals (i.e. aposematism) in plants for the first time, by investigating signals on both the upper and lower surfaces of leaves, which have hitherto been neglected. I demonstrate that *Pseudopanax crassifolius* (Araliaceae), a tree species that is endemic to New Zealand, produces leaves with marginal teeth that peak in size during the sapling stage of development. However, warning coloration on upper leaf surfaces peaked at the seedling stage, providing a dishonest signal of defense. Signals on lower leaf surfaces peaked in the sapling stage, providing an honest defensive signal later in ontogeny. Marginal teeth and all warning coloration were absent in adults, after they grow above the reach of the largest known native megaherbivores (Moa – Aves: Dinornithiformes). Overall results illustrate the importance of considering the changing perspective of herbivores as plants develop and unify our understanding of dishonest signals in plants and animals.

Introduction

Dishonesty is common in animal-signaling systems (Searcy & Nowicki, 2005; Rowell *et al.*, 2006). Furthermore, rates of dishonesty often vary predictably through ontogeny. Human children begin to lie at an early age (Lee, 2013). However, rates of dishonesty tend to decline in early adulthood (Jensen *et al.*, 2004; Evans & Lee, 2011; Levine *et al.*, 2013). While lying in humans is an action carried out intentionally and may be tightly linked to theory of mind (Lee, 2013), other forms of dishonest signaling also decline through ontogeny in non-human animals. For example, small male green frogs (*Rana clamitans*) produce dishonest signals of size more frequently than large males (Bee *et al.*, 2000). Nestlings of *Laniocera hypopyrra* resemble toxic caterpillars (both morphologically and behaviourally), however individuals lack these traits later in ontogeny (Londono *et al.*, 2015). Young male birds often delay plumage maturation, thus providing a dishonest signal of sex (Rohwer *et al.*, 1980; Hawkins *et al.*, 2012). Similar patterns of dishonest signaling may also occur in plants. However, the honesty of signaling through plant ontogeny has yet to be investigated.

Animals often advertise their level of defense to predators by being brightly coloured (i.e. aposematism) (Mappes *et al.*, 2005). Similarly, recent research suggests aposematism may also be common in plants (Lev-Yadun, 2001, 2003; Lev-Yadun & Ne'eman, 2004; Lev-Yadun & Gould, 2007; Fadzly *et al.*, 2009; Cooney *et al.*, 2012). Specifically, structural defenses of many plant species are brightly colored, making them conspicuous to vertebrate herbivores (Lev-Yadun, 2001; Fadzly *et al.*, 2009). The viewing perspective of terrestrial herbivores changes as plants grow vertically and this may influence the production of aposematic signals by plants. For example, when leaves are aposematic, the changing perspective of herbivores may select for signals on upper (adaxial) and lower (abaxial) leaf surfaces to be produced at different ontogenetic stages. However, the potential for lower leaf surfaces to signal to herbivores viewing leaves from below has not been investigated. Furthermore, aposematism is generally considered to be reliable, providing an honest signal of defense (Summers & Clough, 2001; Lev-Yadun, 2003; Bezzerides *et al.*,

2007; Cooney *et al.*, 2012). However, changes in herbivore perspective and antiherbivore defense through plant ontogeny may influence the honesty of warning signals.

Many plant species display a reduction in defense once above the reach of browsing animals (Gowda & Palo, 2003; Burns, 2014). Similarly, the strength of aposematic signals may decline as plants grow vertically and fewer herbivores are able to receive the visual signal. When leaves are aposematic this relationship may vary between upper and lower leaf surfaces. Aposematic signals on upper leaf surfaces may peak when plants are small and terrestrial herbivores of all sizes are able to receive the signal (see Figure 5.1). However, early in ontogeny plants tend to have large root:shoot ratios and lack sufficient resources for investment in structural defense (Boege & Marquis, 2005; Hanley *et al.*, 2007). Consequently, aposematic signals on upper leaf surfaces may peak when plant defenses are poorly developed, providing a dishonest signal (see Figure 5.1). Selection may favor aposematism on lower leaf surfaces to peak later in ontogeny. For example, when plants are of intermediate height the leaves are likely to be within reach of browsing animals and lower leaf surfaces may be visible to the greatest number of herbivores (see Figure 5.1). Plants of intermediate height are likely to have sufficient resources for the production of structural defenses (see Boege & Marquis, 2005) and aposematism on lower leaf surfaces may tend to be a reliable, honest signal.

Pseudopanax crassifolius (Sol. ex A.Cunn) C. Koch. is a heteroblastic tree endemic to New Zealand and individuals go through a predictable series of morphological transitions (Gould, 1993). Leaves of seedlings (individuals < 10 cm tall) are cryptically colored and saplings (10-300 cm tall) produce leaves with marginal teeth and associated aposematic spots (see Figure 5.2a; Fadzly *et al.*, 2009). However, leaves of adults (> 300cm tall) lack these antiherbivore defenses (Gould, 1993; Fadzly *et al.*, 2009). Structural defenses during the sapling stage and cryptically colored seedlings may have reduced rates of herbivory by extinct browsing birds (Moa – Aves: Dinornithiformes; Greenwood & Atkinson, 1977; Fadzly *et al.*, 2009). *P. crassifolius* is not known to produce aposematic signals on lower leaf surfaces. However, color contrast from

background vegetation may provide a signal to herbivores viewing leaves from below (see Figure 5.2b).

Here, I investigate ontogenetic changes in aposematic signals and the potential for aposematism on upper leaf surfaces to be dishonest in *P. crassifolius*. First, I used piecewise regression to test for changes in the production of teeth through plant ontogeny. Piecewise regression was used as the production of structural defense is predicted to increase early in ontogeny, and then decline once above the browsing height of moas (Greenwood & Atkinson, 1977; Fadzly *et al.*, 2009). I then tested whether the strength of aposematic signals on upper leaf surfaces peaked early in plant ontogeny, providing a dishonest signal of defense (see Figure 5.1). The colors of lower leaf surfaces may be aposematic, however this has not yet been tested. I tested for color contrasts of lower leaf surfaces from background vegetation using an avian vision model. I then tested whether the contrast of lower leaf surfaces peaked at intermediate plants heights, providing an honest signal of defense.

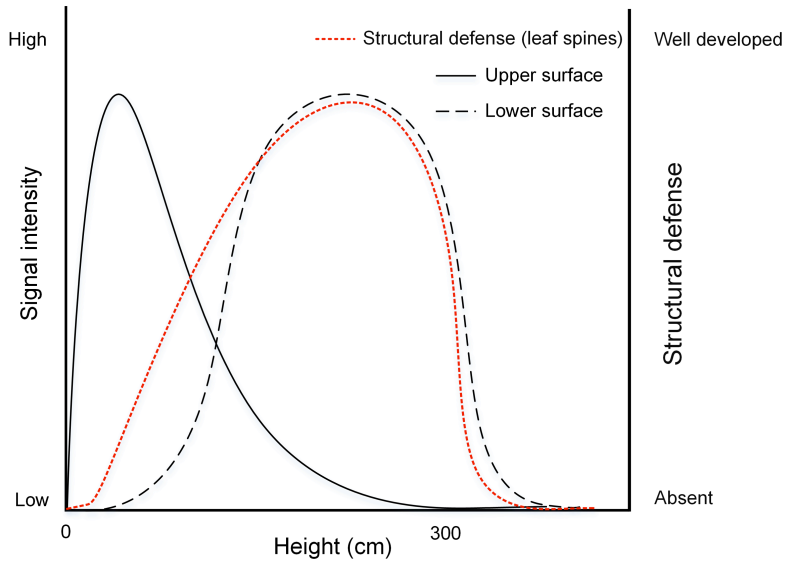

Figure 5.1 Diagrammatical representation of hypotheses. Signaling on upper leaf surfaces is predicted to peak early in ontogeny (solid line) when structural defenses are poorly developed (dotted red line). However, signals produced on lower leaf surfaces are predicted to peak later in plant ontogeny (dashed line) when structural defenses are well developed. Structural defenses and signaling of lower leaf surfaces decline once individuals attain a height refuge from herbivory.

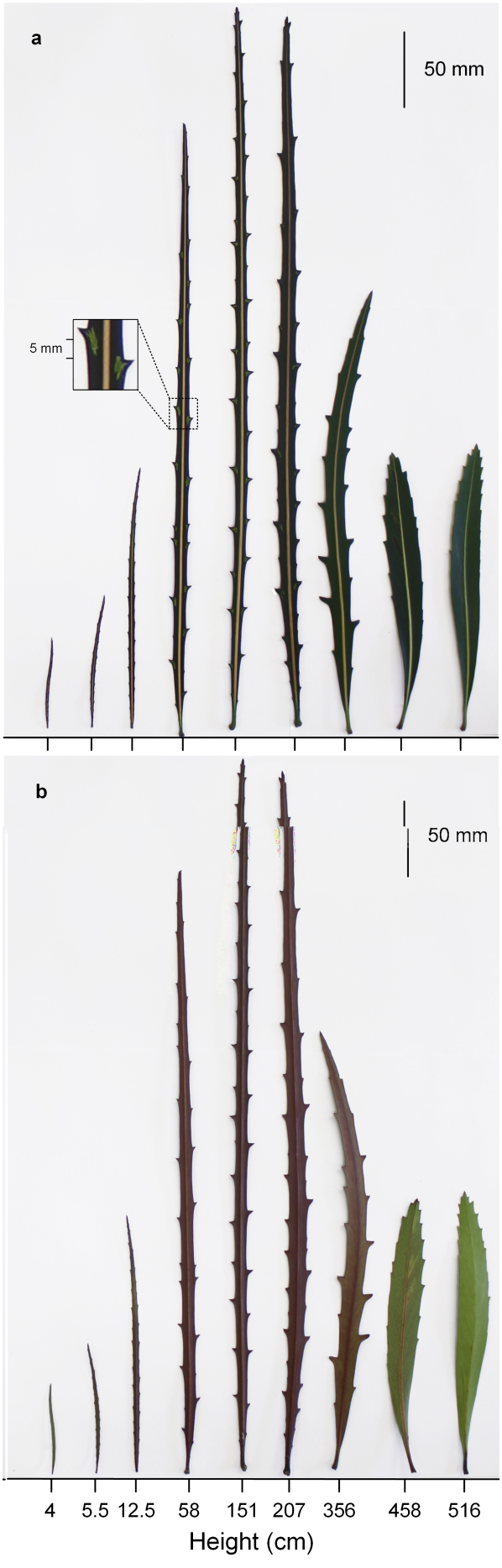

Figure 5.2 Upper (a) and lower (b) leaf surfaces of typical leaves produced by *P. crassifolius* though plant ontogeny, from seedling to adult. The inset box in panel (a) illustrates a magnification of marginal teeth and associated aposematic spots.

Methods

Pseudopanax crassifolius individuals were sampled in Nelson Lakes National Park, South Island, New Zealand (41°48'S, 172°50'E) in May 2014. Individuals were randomly selected, height (cm) was measured with a 10m measuring tape and the youngest fully expanded leaf was removed for analysis. The final dataset consisted of 113 individuals ranging from 3 – 526 cm tall, capturing all four ontogenetic stages of leaf morphology described for *P. crassifolius* (Gould, 1993).

Upper leaf surface

Leaves were scanned using a Canoscan 8400F color image scanner at 600 dpi. On each leaf, the size of four randomly selected teeth and their associated aposematic spots were measured using the image analysis software Image J (Schneider *et al.*, 2012). I quantified the size of marginal teeth by drawing a polygon around the tooth margin and calculating its area (mm^2). Adjusting the threshold level of the image allowed aposematic spots to be selected and the area calculated. When a single marginal tooth had multiple small aposematic spots associated with it, all were measured and the combined area was calculated. Tooth size and spot size data were then averaged within leaves prior to analyses.

If teeth are produced in response to moa herbivory, tooth size is predicted to decline above the browsing height of moa. Therefore, I tested for scaling relationships between tooth size and plant height using piecewise regression. I used an iterative approach, following Crawley (2007), where the breakpoint value was determined by the model with the lowest residual MSE (mean squared error). Seedlings (<10cm) were not included due to an absence of marginal teeth (see Fadzly *et al.*, 2009). Therefore, the dataset consisted of 86 individuals (12.5 – 526 cm tall). Tooth size data were logarithm transformed prior to analysis to conform to model assumptions.

Previously, it has been suggested that 'saplings' (10-300 cm tall) produce both marginal teeth and aposematic spots (Fadzly *et al.*, 2009). However, individuals taller than 3 m may still produce marginal teeth (see (Gould, 1993)). I used a Generalized Linear Model (GLM) with a binary response function to test

whether the presence of aposematic spots was determined by tooth size, plant height, or an interaction between tooth size and height. I then tested the prediction that the strength of aposematic signals on upper leaf surfaces will peak early in ontogeny (see Figure 5.1). One option would be to test for scaling relationships between the size of aposematic spots and plant height. However, the size of leaves and marginal teeth varies through ontogeny (Gould, 1993), potentially constraining the size of aposematic spots. Therefore, I calculated signal intensity as the percentage of spot size relative to tooth size (signal intensity = 100 × spot size/tooth size). Ordinary Least Squares (OLS) regression could then be used to test for scaling relationships between signal intensity and plant height. However, the use of OLS regression minimizes the sum of squared variation in the Y direction and is not appropriate when measurement error in X and Y variables is likely (Price & Phillimore, 2007). To avoid these confounding sources of bias, I ran Reduced Major Axis (RMA) regression. Leaves without aposematic spots provide a signal intensity value equal to zero and were omitted from RMA analyses as their inclusion created a highly skewed distribution (logistic regression analyses described above account for ontogenetic changes in the presence/absence of aposematic spots). Signal intensity was square root transformed to conform to model assumptions.

Lower leaf surface

Anthocyanin is commonly responsible for red pigmentation in leaves and differences in anthocyanin concentration strongly influence leaf optical properties (Neill & Gould, 2000). Therefore, I measured anthocyanin content of lower leaf surfaces using an opti-sciences CCM-200 chlorophyll content meter that was adapted (by the manufacturer) to calculate anthocyanin content index ((ACI; see Schreiber & Wade, 2007)). Three measurements were taken per leaf, one at the midpoint of the leaf and 3cm either side of the first measurement. When leaves were too small for this protocol, the entire surface of the probe was covered with the leaf and three consecutive measurements were taken. ACI measures were then averaged within leaves prior to analyses.

To determine if changes in ACI would result in differences in perception by moa I used reflectance properties of leaves.

Due to the potential degradation of leaves over time, a subsample of leaves was randomly selected for reflectance measurements. This ensured reflectance properties obtained reflected values of fresh leaf tissue (within 24hrs of collection). To ensure all stages of *P. crassifolius* ontogeny were captured in the subsample, I randomly selected at least five individuals from the following height classes: 0-10 cm (n = 7), 11-100 cm (n = 6), 101-200cm (n = 6), 201-300 cm (n = 5), 301 + cm (n = 5). Reflectance spectra of the lower surface of *P. crassifolius* leaves were measured with an Ocean Optics USB2000 spectroradiometer and Xenon Pulse X2 lamp Ocean Optics light source (Dunedin, FL, USA). Leaves reflectance properties were measured as the proportion of a diffuse, Teflon-based, white reflectance standard. The fiber optics probe was mounted inside a matte black plastic tube to exclude ambient light. The angle of illumination was fixed at 45° to minimize glare and the distance between the probe and leaf surface was fixed at 1cm. Spectra were calculated between 300 to 700nm at 5nm intervals with SpectraSuite software. Three measurements were made per leaf (as for anthocyanin indices above) and reflectance spectra were then averaged for each leaf. Reflectance spectra for the lower leaf surface of five common co-occurring trees (*Carpodetus serratus, Griselinia littoralis, Kunzea ericoides, Nothofagus fusca, Nothofagus solandri* and *Raukaua simplex*) were also measured using the same protocols (three leaves per species). The reflectance spectra for these species were then averaged to provide a 'background canopy reflectance'.

I assessed color contrasts of *P. crassifolius* leaves and background canopy according to avian vision. Specifically, I plotted reflectance data in three-dimensional tetrahedral color space. Exact spectral discrimination data are not available for moa, therefore I used the V model based on its closest living relative, *Strithio camelus* (ostrich) (Turvey *et al.*, 2005). Euclidian distances of *P. crassifolius* points from average background canopy were calculated. Greater Euclidean distances between *P. crassifolius* leaves and background canopy represent greater color contrasts. To test whether ACI

scales with contrast of *P.crassifolius* leaves from background foliage I carried out OLS regression of Euclidean distances against ACI. A reflected inverse transformation was used on Euclidean distance data to conform to normality assumptions. Regression parameters were then used to predict Euclidean distances for all 113 leaves based upon ACI values. ANOVA of observed versus predicted values was carried out to test the robustness of Euclidean distance predictions. I then carried out piecewise regression of predicted Euclidean distances (dependent variable) and plant height (independent variable).

Lastly, I tested for scaling relationships between the size of marginal teeth and ACI. Seedlings (<10cm) were not included in this analysis due to an absence of marginal teeth. Therefore, a sub-sample of 86 individuals (12.5 – 526 cm tall) was used. Scaling relationships were tested for using RMA regression and tooth size data were logarithm transformed to conform to assumptions.

All analyses were carried out in the R environment for statistical computing (R-Development-Core-Team, 2011). The smatr package was used for RMA regression (Warton *et al.*, 2012) and the pavo package was used for the analysis of reflectance data (Maia *et al.*, 2013). Break-point regression was carried out using an iterative approach (see Crawley, 2007).

Results

Initially, the size of marginal teeth scaled positively with plant height (break-point regression: slope = 0.006; see Figure 5.3; R^2 = 0.435; $p < 0.001$). However, above a height of 377 cm (break-point value with lowest Mean Squared Error- MSE) tooth size scaled negatively with increasing plant height (slope = -0.007; see Figure 5.3a)

Upper leaf surface

The probability of aposematic spots being produced increased with the size of marginal teeth (b = 1.873; z = 5.395; $p < 0.001$; Generalized Linear Model). Plant height did not influence the probability of aposematic spot presence (b = 0.001; z = 0.394; p = 0.694; GLM), as aposematic spots are not produced at the lower and upper ends of the height spectrum (see Fig 5.3b). However, there was a significant interaction between tooth size and plant height, indicating a decrease in the probability of aposematic spots being produced with increasing tooth size and plant height (b = -0.006; z = -4.715; $p <$ 0.001; GLM). Furthermore, signal intensity (SI = 100 × spot size/tooth size) scaled negatively with plant height and peaked early in plant ontogeny (Reduced Major Axis regression: R^2 = 0.610; $p < 0.001$; slope = -0.064; intercept = 18.015; see Fig 5.3b).

Lower leaf surface

Euclidean distances of *P. crassifolius* leaves from background vegetation (obtained from tetrahedral color space based upon avian vision model – see materials and methods) scaled positively with Anthocyanin Content Index (ACI; R^2 = 0.554; $p < 0.001$; Ordinary Least Squares regression). Therefore, increased ACI resulted in greater contrasts of leaves from background foliage. Reflectance data were not available for all leaves in the dataset (see materials and methods). Therefore, I predicted Euclidean distance values based upon ACI measurements for cases where reflectance data were not available. Estimates of Euclidean distance calculated using the regression equation did not differ significantly from observed values ($F_{1,56}$ = 0; p = 1; ANOVA), indicating that estimates accurately reflect real Euclidean distance measures. Piecewise regression of predicted Euclidean distances initially scaled positively with plant height (R^2 = 0.692; $p < 0.001$; slope = 0.003; see Fig 5.3c). However, above a height of 138 cm (breakpoint value with lowest MSE) Euclidean distances scaled negatively with increasing plant height (slope = - 0.0007; see Fig 5.3c).

Lastly, the size of marginal teeth scaled positively with ACI (RMA regression: $R^2 = 0.234$; $p < 0.001$). This indicates that *P. crassifolius* leaves with greater contrasts from the background foliage also produced larger teeth.

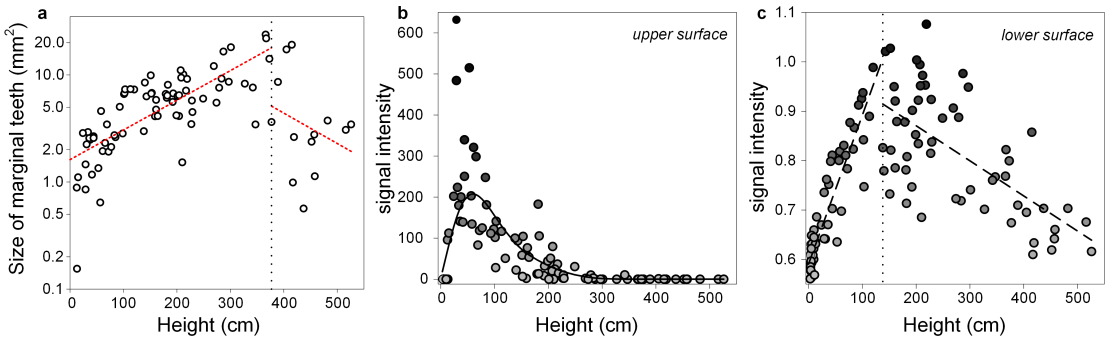

Figure 5.3 Variation in the size of marginal teeth (a) and intensity of signals produced on upper (b) and lower (c) surfaces of leaves through plant ontogeny. The dashed red lines in panel (a) represent the result of piecewise regression analysis. The dotted vertical line is at the breakpoint of height = 377 cm. Tooth size data were natural logarithm transformed to conform to assumptions. Upper leaf surface (b) signal intensity calculated as size of aposematic spots relative to marginal teeth (signal intensity = 100 × spot size/tooth size). The black line is a smoothed spline (df = 7). Lower leaf surface (c) signal intensity is the contrast of leaves from background vegetation based on avian vision (see methods for detailed description). Dashed lines are the result of piecewise regression; the dotted vertical line is at the breakpoint of 138 cm.

Discussion

The production of marginal teeth by *P. crassifloius* varied through ontogeny, consistent with predictions based on moa herbivory (Greenwood & Atkinson, 1977; Atkinson & Greenwood, 1989). Furthermore, the contrast of lower leaf surfaces from background foliage scaled positively with the size of marginal teeth. This suggests optical properties of lower leaf surfaces may be aposematic, providing a reliable signal of defense to herbivores viewing leaves from below. Conversely, the strength of aposematic signals on upper leaf surfaces peaked early in plant ontogeny when marginal teeth are poorly

developed. Selection may favor signal intensity to be highest early in plant ontogeny, as the signal is likely to be viewed most frequently by potential herbivores when plants are small in stature. For example, the tallest (3 m at full stretch; Berentson, 2012) and the shortest (50 cm tall; Berentson, 2012) moa species are likely to have co-occurred with *P. crassifolius* (Allan, 1961; Worthy, 1990). Thus, the aposematic signals on upper leaf surfaces would have been visable to the widest range of browsing moa (juveniles and adults of both species) early in plant ontogeny. Furthermore, analysis of moa coprolites suggests plants less than 1 m tall accounted for much of their diet (Wood *et al.*, 2008).

The contrast of signals with the background environment strongly influences signal effectiveness. For example, the contrast of aposematic animals with the background determines rates of predator avoidance (Aronsson & Gamberale-Stille, 2009) and the contrast of fruits with background foliage increases fruit detection by birds (Burns & Dalen, 2002; Schaefer *et al.*, 2006). Anthocyanin concentration in lower cell layers of *P. crassifolius* leaves varied through ontogeny and scaled positively with the contrast of leaves from background foliage. The contrast with background foliage peaked during the sapling stage and scaled positively with the size of marginal teeth. Therefore, optical properties of lower leaf surfaces potentially provided a reliable signal of structural defense to moa. While the largest moa species is suggested to have been approximately 2 m tall (3 m at full stretch), there was extreme sexual size dimorphism with males half the size of females (Worthy & Holdaway, 2002; Berentson, 2012). Juveniles and sub-adults are also thought to have accounted for more than 25% of some moa populations (Turvey & Holdaway, 2005). Therefore, selection may have favored the contrast of lower leaf surfaces from background foliage to peak at intermediate heights, when the greatest number of browsing moa would have been likely to receive the signal effectively.

Alternatively, lower cell layers may contain high concentrations of anthocyanins to maximize photosynthetic efficiency in low-light environments (Smith, 1909; Hughes *et al.*, 2008). One functional explanation is that anthocyanins in the lower epidermis may reflect red light back into the

mesophyll, maximizing light capture (Hughes *et al.*, 2008). The total amount of ambient light increases vertically within a forest and ambient light levels are lowest at the forest floor (Pukkala *et al.*, 1991; Endler, 1993; Terborgh & Mathews, 1999). However, anthocyanin concentrations in lower cell layers of *P. crassifolius* leaves were lowest early in plant ontogeny, but increased with increasing plant height. Anthocyanins are also suggested to play a photoprotective role when shade-adapted plants are exposed to intermittent high-intensity sunlight (Gould *et al.*, 1995). However, the anatomy and morphology of juvenile *P. crassifolius* leaves is typical of a sun-adapted, xeromorphic plant (Gould, 1993). Therefore, it is unlikely that physiological functional explanations can fully account for the ontogenetic changes I observed in *P. crassifolius*.

The intensity of aposematic spots on the upper surface of *P. crassifolius* leaves peaked when marginal teeth were small. Furthermore, the probability of aposematic spots being present decreased with increasing plant height and tooth size. This suggests aposematic spots may be providing a dishonest signal of defense. During early stages of ontogeny plants tend to have large root:shoot ratios and may lack sufficient resources for structural defense (Boege & Marquis, 2005; Hanley *et al.*, 2007). Therefore, dishonest warning signals may provide an effective deterrent to herbivores when plants are vulnerable but resource limited. To my knowledge, this is the first time dishonest aposematism has been documented in a plant species.

Dishonesty is common in signaling systems and is often employed by individuals that would suffer adversely if signals were honest. For example, young male animals frequently mimic females to reduce the risk of injury caused by confrontation with older males (Forsyth & Alcock, 1990; Saetre & Slagsvold, 1996; Shine *et al.*, 2000; Whiting *et al.*, 2009; Hawkins *et al.*, 2012). Furthermore, individuals producing dishonest signals are often resource limited or disadvantaged compared to honest signalers (Steger & Caldwell, 1983; Backwell *et al.*, 2000; Bee *et al.*, 2000; Wilson *et al.*, 2007; Valkonen *et al.*, 2014). Aposematic signals produced by *P. crassifolius* were dishonest early in ontogeny, when defenses were poorly developed. However, individuals at later

ontogenetic stages tended to produce honest signals of defense. Aposematism often develops later in ontogeny due to an absence of defense at earlier life-history stages (Grant, 2007; Fadzly *et al.*, 2009; Higginson & Ruxton, 2010; Valkonen *et al.*, 2014), perhaps due to energetic requirements of growth early in ontogeny (Nylin *et al.*, 2001; West *et al.*, 2001; Boege & Marquis, 2005; Ojala *et al.*, 2007). Early stages of aposematism may tend to be dishonest in both plants and animals, with signal reliability increasing as defenses fully develop. Future studies of aposematism that consider variation in signals through ontogeny, and the changing perspective of signal receivers, will further our understanding of warning signal reliability.

Chapter 6 - General discussion

Overall, the results of this thesis provide further insights into the evolution of plants on islands. First, seed sizes (Chapter 2) of insular plants were consistently larger than those of mainland relatives. Furthermore, differences in life-history traits did not influence the island-mainland seed size relationship. Second, the results of Chapter 3 suggest selection is acting to increase the size of both sexes of dioecious plants simultaneously on islands. Third, traits associated with the divaricate growth form (Chapter 4) have been secondarily lost on the Chatham Islands. Lastly, *P. crassifolius* (Chapter 5) displayed predictable changes in aposematic signaling and defense through ontogeny, potentially in response to unique insular herbivores.

Islands are renowned for producing repeated evolutionary pathways. This has been documented many times, particularly in the animal literature (e.g. the island rule, see Van Valen, 1973b; Lomolino, 2005). However, insular plants have received less attention and our understanding of predictable evolutionary changes in island plants is incomplete. For example, well-known phenomena, such as the evolution of woodiness on islands, remain unresolved with multiple hypotheses proposed (Darwin, 1859; Wallace, 1880; Carlquist, 1974; Bohle *et al.*, 1996; Givnish, 1998). Plants are modular organisms and selection acting on one trait may cause a correlated evolutionary response in another. Therefore, the results of this thesis may shed light on the processes responsible for macroevolutionary changes of plants on islands.

In the following discussion I address the broader implications the results of this thesis have for our understanding of the evolution of island plants.

Insular size changes in plants

Recent research suggests selection is acting to increase leaf size on islands (Burns *et al.*, 2012). Results of Chapters 3 and 4 are consistent with the findings of Burns *et al.* (2012), suggesting evolutionary increases in leaf size are common on islands. In dioecious taxa there was a consistent increase in leaf size of both sexes on islands (Chapter 3). Furthermore, plants of a variety of growth forms displayed consistent increases in leaf size on the Chatham Islands (Chapter 4). The depauperate nature of islands increases levels of

intraspecific competition and this is suggested to contribute to size changes of insular animals (Grant, 1965; Case, 1978; Lomolino, 2005). Similarly, increased intraspecific competition may influence evolutionary changes in leaf size. Selection may favour increases in leaf size on islands, as plants with larger leaves have wider distributions and are more competitive (Schmitt & Wulff, 1993; Grime *et al.*, 1997; Westoby *et al.*, 2002; Thuiller *et al.*, 2004).

Seeds are arguably the earliest life-history stage to experience strong selective pressures on islands. For example, a reduction in dispersibility of island seeds has been noted in as few as five generations after island colonization (Cody & Overton, 1996). In Chapter 2, I provided the first test for macroevolutionary changes in island seed size and results suggest a repeated tendency for seed sizes to increase on islands. Size patterns evident in mature individuals may be a response of selection acting earlier in ontogeny. For example, adult body size is strongly influenced by size at birth in a variety of animal taxa (Olsson & Madsen, 2001; Kaplan & Phillips, 2006; Ong, 2006; Garant *et al.*, 2007; Wilson *et al.*, 2009). Furthermore, a recent investigation suggests body size patterns of insular tiger snakes are a result of selection acting on birth size (Aubret, 2012). The same may be true in plants, as seed size is correlated with a number of plant traits evident later in ontogeny. For example, plant height and stem size are correlated with seed size (Corner, 1949; Leishman *et al.*, 1995; Moles *et al.*, 2004). Furthermore, seed size strongly influences seedling establishment and survival at later life-history stages (Moles & Westoby, 2004).

Hypotheses for the evolution of insular woodiness suggest that selection may favour overall changes in plant size on islands (see Darwin, 1859; Wallace, 1880; Carlquist, 1974; Bohle *et al.*, 1996; Givnish, 1998). However, they neglect the modularity of plant structure and the potential for woodiness to evolve due to selection acting on other plant traits. Furthermore, the action of selection may vary through plant ontogeny. Herbaceous colonists of islands are suggested to obtain a competitive advantage by developing secondary woodiness (Darwin, 1859; Carlquist, 1974; Givnish, 1998). Selection may first act on seeds to promote a competitive advantage, as larger seeds produce

larger, more competitive seedlings (Leishman *et al.*, 1995; Moles & Westoby, 2004). Later in ontogeny selection may favour larger leaves, due to competitive ability being positively associated with leaf size (Grime *et al.*, 1997; Westoby *et al.*, 2002; Thuiller *et al.*, 2004). Stems must provide mechanical support for leaves and seeds and the sizes of these traits are associated allometrically (Corner, 1949; Niklas, 1994). Therefore, selection acting to increase seed and leaf sizes may cause a correlated evolutionary response in stem size. Furthermore, seed size is positively associated with plant height (Leishman *et al.*, 1995; Moles *et al.*, 2004). Selection acting on other plant traits may facilitate the evolution of woodiness due to the structural support it provides. Previous hypotheses for the evolution of woodiness have neglected the possibility for the action of selection to vary with ontogeny. Investigating evolution in specific plant traits, at different stages of ontogeny, may improve our understanding of the processes responsible for overall size changes in island plants.

Unique herbivores

Plants often evolve unique adaptations to deter herbivores. For example, many plants produce prickles, thorns, or spines to deter mammalian browsers (Brown & Lawton, 1991; Ronel & Lev-Yadun, 2012). Furthermore, recent research suggests aposematism (warning signals) may be common in plants (Lev-Yadun, 2001, 2003; Lev-Yadun & Ne'eman, 2004; Lev-Yadun & Gould, 2007; Fadzly *et al.*, 2009). Islands are renowned for housing unique herbivore communities (e.g. Moa-nalos of Hawaii, Elephant birds of Madagascar, and Moa of New Zealand). Although many insular herbivores are now extinct, some of the unique traits expressed by island plants may be anti-herbivory adaptations.

Several features of the New Zealand flora are suggested to be adaptations to deter browsing moa (see Atkinson & Greenwood, 1989b). For example, the remarkable series of morphological transitions (heteroblasty) displayed by *P. crassifolius* may have evolved in response to moa herbivory. The leaf morphology of juveniles is suggested to have deterred browsing moa,

while adult morphology is more ordinary, perhaps due to attaining a height refuge (Greenwood & Atkinson, 1977; Fadzly *et al.*, 2009). The divaricate growth form is another unique characteristic of the New Zealand flora. More than 50 species in New Zealand, from a diverse range of lineages, produce the small leaves, high branching angles and narrow stems that characterize divaricate plants (Greenwood & Atkinson, 1977). This growth form may also be an evolutionary adaptation to deter browsing moa (Greenwood & Atkinson, 1977; Bond *et al.*, 2004). Plants sharing similar characteristics are also common in Madagascar, where Elephant birds were a dominant component of the herbivore fauna (Bond & Silander, 2007). Alternatively, it is suggested that the divaricate growth form is an adaptation to environmental conditions (McGlone & Webb, 1981; Howell *et al.*, 2002; Christian *et al.*, 2006). Similarly, environmental adaptations are suggested as alternative explanations for the unique morphology of *P. crassifolius* (Gould, 1993).

Anti-herbivore defenses are often lost on islands, perhaps due to a reduction in herbivory pressure (Janzen, 1973; Rickson, 1977; Bowen & VanVuren, 1997; Vourc'h *et al.*, 2001; Burns, 2014). *Pseudopanax chathamicus* is endemic to the Chatham Islands and is derived from a *P. crassifolius* ancestor (Heenan *et al.*, 2010). *P. chathamicus* lacks pronounced ontogenetic colour changes and morphological transitions in leaf morphology (Fadzly *et al.*, 2009). This suggests an absence of moa on the Chatham Islands has relaxed selection for traits that may have deterred browsing moa. The results of Chapter 5 further support the anti-herbivory hypothesis for the morphology of *P. crassifolius*. Juveniles produced structural defenses, however investment in defense declined once individuals were above the height of moa. Furthermore, investment in aposematic signals was consistent with the potential feeding behavior of moa.

The results of Chapter 4 provide further support for the hypothesis that the divaricate growth form is an adaptive response to moa herbivory. Plants on Chatham Island produced larger leaves, shorter internodes, smaller branching angles, and stouter stems than related mainland plants. Furthermore, these results were inconsistent with climate-based hypotheses. This suggests an

absence of moa on Chatham Island has relaxed selection for divaricate traits. The occurrence of unrelated plants sharing similar features on Madagascar also suggests that the unique features of divaricate plants may have deterred large avian browsers (Bond & Silander, 2007).

Conclusions & Future directions

Insularity is known to promote novel evolutionary changes in plants. However, the modularity of plant structure has not been appreciated in the past. By examining a range of trait specific changes in island plants the results of this thesis further our understanding of the action of selection on islands.

The results of Chapters 3 and 4 suggest that selection may be acting to increase leaf size on islands. Allometry between the size of leaves and stems may promote increased woodiness due to mechanical requirements of stems to support leaves. Furthermore, results of Chapter 2 suggest selection is acting to increase seed size on islands. A recent investigation suggests body size patterns of insular animals may be a reflection of selection acting on birth size (Aubret, 2012). The same may be true in plants and this deserves further attention. The evolution of insular woodiness suggests selection may be promoting overall size changes on islands. However, selection acting on specific plant traits, at different stages of ontogeny, may be facilitating this evolutionary pathway.

The unique herbivores of islands have often been suggested to play an important role in the evolution of insular plants. However, the significance of insular herbivory is frequently questioned, with physiological explanations suggested as alternatives. The results of Chapters 4 and 5 add further support to the role of herbivores in the evolution of island plants. Furthermore, results were inconsistent with physiological explanations. Rates of extinction are often high on islands and many insular herbivores are now extinct. However, feeding trials with extant relatives of extinct insular herbivores (see Bond *et al.*, 2004) may improve our understanding of the role herbivory played in the evolution of island plants.

Appendices

Appendix A: Chapter 3 supplementary material

Appendix A1. Physical geography of the island groups included in the study.

	Kermadec	Three Kings	Chatham	Auckland
Island area (km^2)	30	7	966	625
Distance from New Zealand mainland (km)	900	55	800	465
Climatic Conditions	subtropical	subtropical	cool-temperate	subantarctic
Average Temperature (°C)	19	17	11	8
Total Precipitation (mm)	1500	1800	1,100	1750

Appendix A2. Results of analyses after removing taxa with n < 3 for any sex.

Degree of SSD

Wilcoxon test results:

Trait	W	*P*
Leaves	41	0.1934
Stems	13	0.1602

Direction of SSD

Rayleigh's test of uniformity, mean angles and von Mises bootstrapped confidence intervals

	Rayleigh's test		
Trait	*P*	Mean angle	95% C.I
Leaves	0.012	97.86	69.58-125.86
Stems	0.036	67.36	34.27-119.99

RMA analyses of island and mainland leaf and stem sizes

		Slope	Intercept
Trait	Sex	Mean value ± SD (95% CI)	Mean value ± SD (95% CI)
Leaves			
	Female	1.073 ± 0.05 (1.072-1.074)	-0.213 ± 0.324 (-0.22 to -0.207)
	Male	1.025 ± 0.046 (1.024-1.026)	0.286 ± 0.273 (0.281-0.292)
Stems			
	Female	1.433 ± 0.351 (1.426-1.439)	-0.074 ± 0.157 (-0.077 to -0.071)
	Male	1.174 ± 0.612 (1.162-1.186)	0.034 ± 0.234 (0.03-0.039)

Appendix A3. Growth forms, seed dispersal modes, and pollination syndromes of study taxa.

Insular taxa	Growth form	Seed dispersal mode	Pollination syndrome	Mainland taxa
Coprosma ciliata	Shrub	Fleshy fruit	Wind	*Coprosma ciliata*
Coprosma foetidissima	Shrub	Fleshy fruit	Wind	*Coprosma foetidissima*
Coprosma perpusilla subsp. subantarctica	Shrub	Fleshy fruit	Wind	*Coprosma perpusilla subsp. perpusilla*
Coprosma propinqua var. martinii	Shrub	Fleshy fruit	Wind	*Coprosma propinqua var. propinqua*
Coprosma robusta	Tree	Fleshy fruit	Wind	*Coprosma robusta*
Macropiper excelsum subsp excelsum	Shrub	Fleshy fruit	Wind	*Macropiper excelsum subsp excelsum*
Coprosma chathamica	Tree	Fleshy fruit	Wind	*Coprosms repens*
Plagianthus regius subsp. chathamicus	Tree	Wind	Insect	*Plagianthus regius subsp. regius*
Coprosma acutifolia	Tree	Fleshy fruit	Wind	*Coprosma tenuifolia*
Macropiper excelsum subsp psittacorum	Shrub	Fleshy fruit	Wind	*Macropiper excelsum subsp excelsum*
Macropiper melchior	Shrub	Fleshy fruit	Wind	*Macropiper excelsum subsp excelsum*
Coprosma macrocarpa subsp. macrocarpa	Shrub	Fleshy fruit	Wind	*Coprosma macrocarpa subsp. minor*
Alectryon excelsus subsp. grandis	Tree	Fleshy fruit	Insect	*Alectryon excelsus subsp. excelsus*
Streblus smithii	Tree	Fleshy fruit	Wind	*Streblus banksii*

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