Heteroblasty on Chatham Island: a comparison with New Zealand and New Caledonia

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Abstract: We used a comparative approach to investigate heteroblasty in the Chatham Islands. Heteroblasty refers to abrupt changes in the morphology of leaves and shoots with plant height. Common on isolated islands such as New Caledonia and New Zealand, which once had flightless, browsing birds, heteroblasty is hypothesised to be an adaptation to deter bird browsing. The Chatham Islands are a small archipelago located 800 km off the east coast of New Zealand, which has clear floristic links to New Zealand. However, unlike New Caledonia and New Zealand, the Chathams never had flightless, browsing birds. We investigated heteroblasty on the Chatham Islands by: (1) comparing height-related changes in leaf morphology and branching architecture in several plant taxa with heteroblastic relatives on the New Zealand mainland; (2) characterising changes in leaf morphology in heteroblastic tree species endemic to the Chathams; and (3) comparing overall trends in leaf heteroblasty on the Chathams with New Caledonia and New Zealand. Reversions to homoblasty were observed in the three Chatham Island taxa with heteroblastic relatives on the New Zealand mainland. However, two endemic tree species were clearly heteroblastic; both produced dramatically larger leaves as juveniles than as adults. Inter-archipelago comparisons showed that this trend in leaf morphology is rare among heteroblastic species in New Caledonia and New Zealand. Therefore, while some of our results were consistent with the hypothesis that heteroblasty is an adaptation to avoid bird browsing, other processes also appear to have shaped the expression of heteroblasty on Chatham Island.

Keywords: browsing; coevolution; island; leaf; moa; morphology; ontogeny

Introduction

The New Zealand flora has many distinctive attributes. Divaricate branching patterns (wire plants) and abrupt changes in leaf morphology during ontogeny (leaf heteroblasty) are several examples of plant traits that are common in New Zealand, but comparatively rare in other parts of the world (see Dawson 1988). Many attributes of the New Zealand flora are also shared with other isolated islands. For example, divaricate branching is common in Madagascar (Bond & Silander 2007), and leaf heteroblasty is widespread in Hawai'i (Givnish et al. 1994; Hansen 1996), the Mascarene Islands (Friedmann & Cadet 1976; Hansen et al. 2003) and New Caledonia (Burns & Dawson 2006). Identifying the ecological conditions shared by isolated islands with these distinctive floral attributes may lead to a better understanding of why these evolved.

Several hypotheses could explain the high incidence of leaf heteroblasty in New Zealand. First, developmental changes in leaf morphology could help plants cope with changing environmental conditions as plants grow vertically in forested environments (Day 1998; Winn 1999; Wells & Pigliucci 2000; Darrow et al. 2001, 2002;

Burns 2005). Second, island heteroblasty could be an adaptation to avoid herbivory (Greenwood & Atkinson 1977). Isolated islands typically lacked native mammalian herbivores, having instead toothless browsers such as giant tortoises (e.g. Mascarene Islands – Eskildsen et al. 2004) or flightless birds (Hawaiian moa-nalo – James & Burney 1997; Malagasy elephant birds – Bond & Silander 2007; New Caledonian *Sylviornis* – Harrison 1989; New Zealand moa – Worthy & Holdaway 2002). These unusual browsers are now mostly extinct, so direct investigations of animal browsing as an explanation for insular heteroblasty are no longer possible (but see Hansen et al. 2003; Bond et al. 2004; Eskildsen et al. 2004; Pollock et al. 2007). Nevertheless, if heteroblasty on isolated islands evolved in response to flightless, toothless browsers, heteroblastic changes should be similar on islands where they occurred. Conversely, islands lacking these large browsers should show reduced incidences of heteroblasty and/or reversions to homoblasty, if these features evolved in response to browsers.

The Chatham Islands are a small group of oceanic islands located 800 km east of New Zealand. There are clear floristic links between the Chathams and New

Zealand, and the Chatham Island flora probably originated by dispersal from New Zealand (see Trewick 2000; Trewick et al. 2007). Most plant taxa on the Chatham Islands have close relatives on the New Zealand mainland, although there are notable exceptions (e.g. *Myosotidium hortensia*). However, unlike New Zealand, the Chathams lacked large, vertebrate browsers. Dawson (1991) and Greenwood (1992) commented that plant taxa that are heteroblastic in New Zealand appear on the Chatham Islands to have reduced morphological differentiation between adult and juvenile plants. However, quantitative analyses of heteroblasty on the Chatham Islands have not been conducted, and it remains unclear whether the form of heteroblasty present on the Chatham Islands is distinct from other isolated islands, such as New Zealand and New Caledonia.

Here, we quantitatively evaluate heteroblasty on the Chatham Islands. We conducted field surveys for heteroblastic species on Chatham Island, as well as similar surveys on the New Zealand mainland for comparative purposes. These data were then used to answer four questions: (1) Do species with closely related heteroblastic relatives in New Zealand show reversions to homoblasty on the Chatham Islands? (2) Are there differences in branching architecture between *Pseudopanax chathamicus* and *P. crassifolius*? (3) Are there endemic species on the Chatham Islands that appear to have evolved heteroblasty in situ? (4) Do overall trends in heteroblasty on the Chatham Islands differ quantitatively from New Caledonia and New Zealand?

Materials and methods

Chatham Island is the largest of approximately 10 islands that make up the Chatham Islands, which collectively cover 966 km^2. The archipelago is oceanic in origin and may have been uplifted above sea level as recently as 4 million years ago (H.J. Campbell, GNS, unpubl.). The climate is windy, wet and cool year-round. Mean annual temperature at the capital (Waitangi) is approximately 11°C (mean monthly range 7–14°C, July–January). Precipitation ranges from 600 to 1500 mm annually. The flora consists of approximately 320 native plant species, 37 of which are endemic and 200 are naturalised (Given & Williams 1984). Although most of the original forest has been converted to pasture in the past century, several remnant forest patches have been fenced recently to allow for natural forest regeneration. Given and Williams (1984) give more detailed information on the geology, environment and natural history of the Chatham Islands.

Searches for heteroblastic woody plants were made by traversing forest tails in Henga Forest Reserve (43°51.0'S, 176°33.2'W), a 177-ha remnant forest patch on the central west coast of Chatham Island, and Nikau Forest Reserve (43°45.7'S, 176°34.8'W), a 19-ha forest patch near the

northern coast of the island. We adopted Ray's (1990) definition of 'metamorphic' heteroblasty, which refers to species with sudden rates of morphological change along a plant's vertical axis. Species displaying abrupt changes in size and shape (i.e. at least a twofold difference in area, lobing, or circularity) along their vertical axis were classed as heteroblastic. Nomenclature follows Allan (1961) and amendments in Connor & Edgar (1987).

For each heteroblastic species, we collected 5–10 leaves from 5–10 juvenile and adult plants. From the pool of leaves collected from each individual plant, three were randomly selected for analyses. Therefore, measurements of leaf morphology for each treatment combination were based on sample sizes between 15 and 30 leaves. Leaf morphology was measured following Burns & Dawson (2006). Leaf outlines were traced onto drawing paper, which were then converted to high-resolution, black and white images with an hp scanjet 5400c computer scanner (Hewlett-Packard Co., USA). Images were imported into ImageJ (Abràmoff et al. 2004) and three dependent variables, total leaf area (cm^2), leaf lobing (the dissection index: perimeter/√area), and leaf circularity (length/width) were used to characterise the morphology of each leaf. Leaf length was measured as the maximum distance from the leaf tip to the base of the petiole parallel to the midvein. Leaf width was measured as the maximum distance perpendicular to the midvein. The dissection index is a simple measure of two-dimensional shape complexity that is highly correlated with more complex measures of leaf lobing, such as fractal dimension (McLellan & Endler 1998).

Three Chatham Island species have closely related taxa on the New Zealand mainland that are strongly heteroblastic. *Pseudopanax chathamicus* is endemic to the Chatham Islands, but is closely related to *P. crassifolius*, which is strongly heteroblastic (Mitchell & Wagstaff 1997; Leon Perrie, Te Papa, pers. comm.). *Plagianthus regius* occurs in New Zealand and on Chatham Island, where it is designated as a distinct subspecies (var. *chathamica*). *Muehlenbeckia australis* is a liana that occurs in both New Zealand and on Chatham Island. Mainland forms of these three taxa were collected from either Otari Wilton's Bush (North Island) or Nelson Lakes National Park (South Island), using the same field-sampling techniques. Detailed descriptions of both sites can be found elsewhere (Burns & Dawson 2005, 2006). Comparisons of juvenile and adult leaf morphology between archipelagos were made with two-way ANOVA. Life history stage (juvenile vs adult) and archipelago (Chatham Island vs New Zealand) were each treated as fixed factors. Separate analyses were conducted for leaf area, circularity, and lobing using the general linear model procedure in SPSS (2002). Data were log$_{10}$ transformed to conform to assumptions when necessary.

Differences in branching architecture between *Pseudopanax chathamicus* and *P. crassifolius* were

assessed by comparing the number of branching events on plants < 3 m tall in both archipelagos. We traversed the circular track through Nikau Reserve (Chatham Island) and the peninsula track in Nelson Lakes National Park (New Zealand), stopping every 5 m in Nikau Reserve and every 10 m in Nelson Lakes. At each stop, we counted the

Figure 1. Juvenile and adult leaves of *Muehlenbeckia australis* (A), *Coprosma chathamica* (B), *Plagianthus regius* var. *chathamica* (C), *Dracophyllum arboreum* (D) and *Pseudopanax chathamicus* (E) from Chatham Island. The coin is 20 mm in diameter.

number of branching events on the nearest *Pseudopanax* plant located > 1 m from the track. The perpendicular direction off the track was alternated between sampling points. The change in sampling interval was necessitated by differences in population density and the size of sampling areas (n = 100 in Nelson Lakes, n = 67 on Chatham Island). Differences in branch number between archipelagos were assessed using a Poisson log-linear model in SPSS (2002). The number of branching events displayed by plants was used as a response variable and archipelago was treated as the single predictor variable with two levels (i.e. New Zealand – *P. crassifolius* and Chatham Island – *P. chathamica*).

We encountered two additional heteroblastic species on Chatham Island, *Coprosma chathamica* and *Dracophyllum arboreum* (Fig. 1), which lack unambiguous mainland relatives for comparative purposes. So for these species, we confined our comparisons between juvenile and adult leaf morphology in the Chatham Islands. We conducted one-way ANOVA, using life history stage (juvenile vs adult) as a single fixed factor, to compare leaf size and shape between juvenile and adult leaves. As with the previous analyses, separate tests were conducted for leaf area, circularity, and lobing, using the general linear model procedure in SPSS (2002), and data were $\log_{10}$ transformed to conform to assumptions when necessary.

Multivariate analyses were used to compare overall morphological transitions between juvenile and adult leaves in the Chatham Islands to morphological transitions in both New Caledonia and New Zealand. Data for New Zealand and New Caledonia were taken from Burns & Dawson (2006). To characterise changes in the size and shape of juvenile and adult leaves, average leaf area, circularity, and lobing of juvenile leaves of each species were divided by average values from adult plants. Juvenile-to-adult ratios of leaf area, lobing, and circularity were then subject to discriminant function analyses. This analysis generates a reduced number of variables or functions from original measurements of leaf size and shape that best delineate morphological differences between regions. Data were $\log_{10}$ transformed to conform to assumptions prior to analyses.

Results

Morphological transitions between juvenile and adult leaves of *Muehlenbeckia australis* differed between Chatham Island and New Zealand (Figs 1 & 2). Leaf area showed a statistical interaction between archipelago and life history stage (see Table 1). This resulted from substantial increases in leaf area between juvenile and adult leaves in New Zealand, while juvenile leaves were indistinguishable from adult leaves on Chatham Island. An interaction between morphology and life history stage was also observed in leaf circularity. Adult leaves were
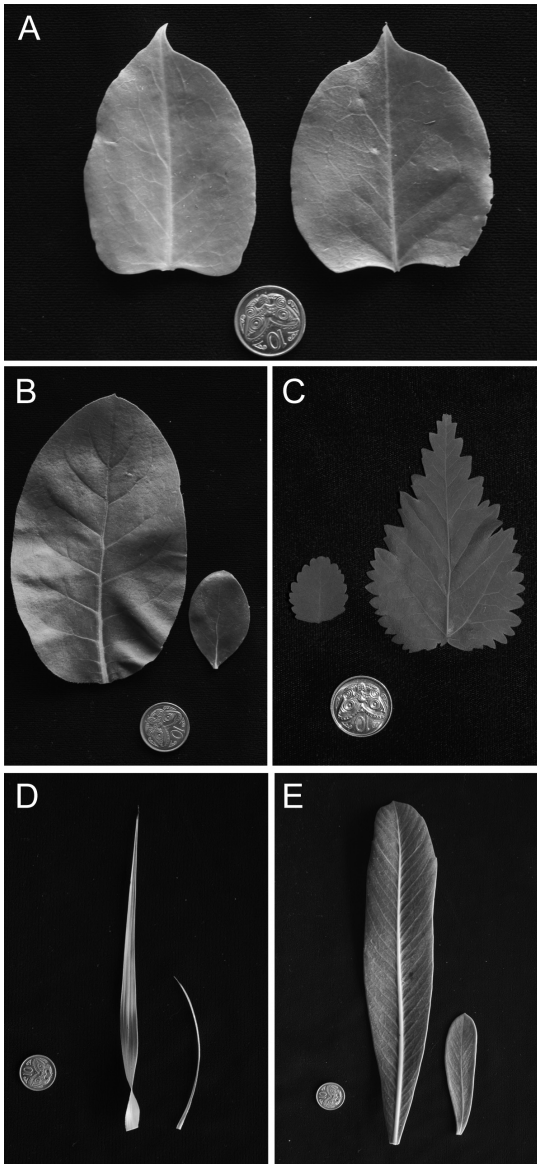
less circular than juveniles on the mainland, but adult and juvenile leaves were more similar in shape on Chatham Island. An independent effect of archipelago was observed in leaf lobing, indicating that leaves were less lobed on Chatham Island than in New Zealand.

Statistical interactions between archipelago and life history stage were observed for all three morphological measures in *Plagianthus regius* (Table 1). Juvenile leaves were smaller than adult leaves in both archipelagos, but differences in leaf size were less pronounced on Chatham Island (Figs 1 & 2). Similarly, juvenile leaves were more circular and more lobed than adults, but these differences were more pronounced in New Zealand.

Similar results were observed in comparisons between *Pseudopanax chathamicus* and *P. crassifolius* (Table 1, Figs 1 & 2). Juvenile leaves of *P. chathamicus* were much bigger than adult leaves, while differences in leaf size were less pronounced in *P. crassifolius*. Juvenile leaves of both species were less circular and more lobed than adults, but these differences were less pronounced on Chatham Island.

Branch number differed between *Pseudopanax chathamicus* and *P. crassifolius* (Wald $\chi^2 = 33.953$, df = 1, $P < 0.001$). Of the 67 *P. chathamicus* seedlings sampled, 36 were un-branched. Most multi-stemmed plants showed a single branching event, but some plants branched more than once, reaching a maximum of seven branches. Conversely, 91 out of 100 *P. crassifolius* seedlings were unbranched (Fig. 3). Of the nine multi-branched

P. crassifolius seedlings, seven showed obvious signs of herbivory damage and appeared to have branched in response to deer browsing. No obvious signs of browsing were observed on Chatham Island.
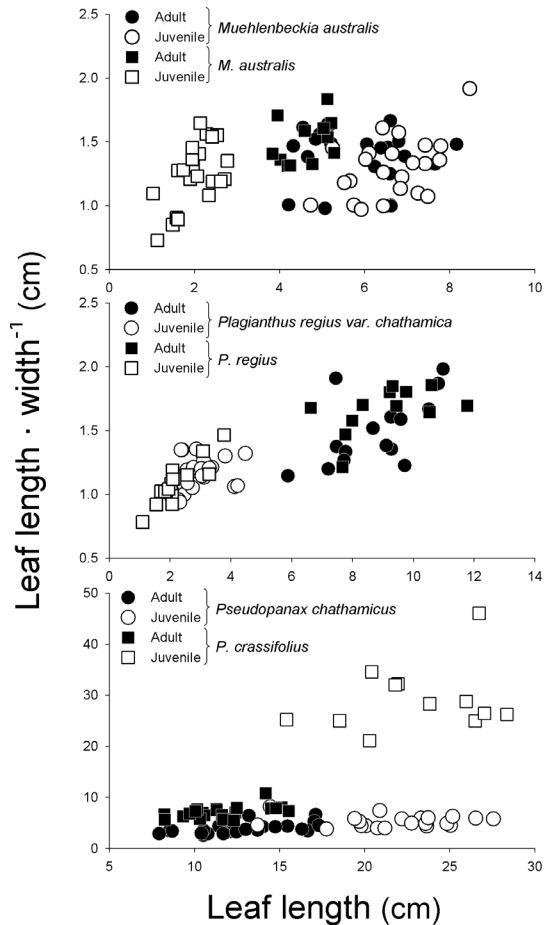

Figure 2. Differences in the size and shape of juvenile (open symbols) and adult (closed symbols) leaves of *Muehlenbeckia australis* (top), *Plagianthus regius* (middle) and *Pseudopanax chathamicus/crassifolius* (bottom). The ratio of leaf length to leaf width is shown on the *y*-axis (larger values reflect longer, narrower leaves). Leaf length is shown on the *x*-axis and is a coarse reflection of leaf size. Chatham Island taxa are shown as circles and New Zealand taxa are shown as boxes. Juvenile leaves on the Chatham Islands are more similar in size and shape to adults compared with their New Zealand counterparts.

Table 1. Results from general linear model analyses of leaf morphology.

|		Area	Circularity	Lobing
Muehlenbeckia	Archipelago	$F_{1,78} = 306.109$***	$F_{1,78} = 0.529$	$F_{1,78} = 4.701$*
	Life history stage	$F_{1,78} = 44.905$***	$F_{1,78} = 10.123$**	$F_{1,78} = 0.474$
	Archipelago × life history stage	$F_{1,78} = 130.478$***	$F_{1,78} = 4.153$*	$F_{1,78} = 0.050$
Plagianthus	Archipelago	$F_{1,63} = 11.270$**	$F_{1,63} = 0.481$	$F_{1,63} = 0.020$
	Life history stage	$F_{1,63} = 520.566$***	$F_{1,63} = 96.676$***	$F_{1,63} = 5.861$*
	Archipelago × life history stage	$F_{1,63} = 7.811$**	$F_{1,63} = 7.024$*	$F_{1,63} = 7.665$**
Pseudopanax	Archipelago	$F_{1,77} = 236.144$***	$F_{1,77} = 659.749$***	$F_{1,77} = 1041.845$***
	Life history stage	$F_{1,77} = 21.368$***	$F_{1,77} = 362.000$***	$F_{1,77} = 523.713$***
	Archipelago × life history stage	$F_{1,77} = 18.734$***	$F_{1,77} = 143.595$***	$F_{1,77} = 255.133$***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
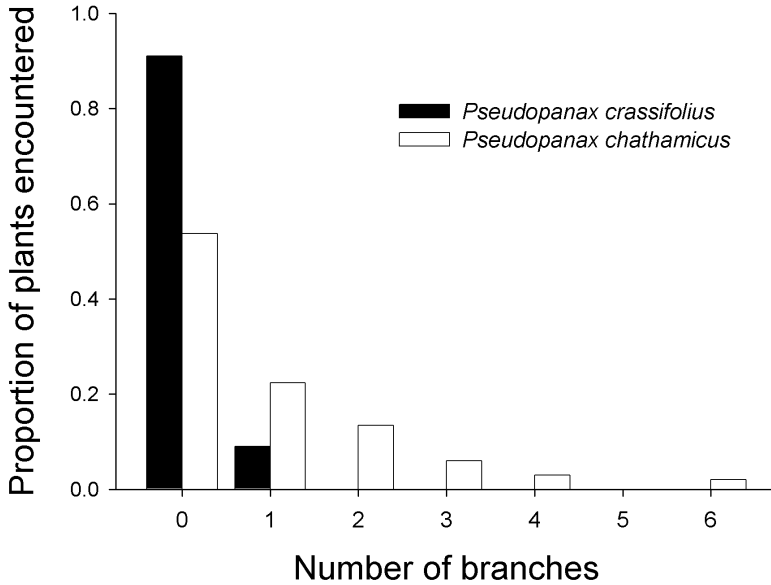
Figure 3. Frequency (*y*-axis) of *Pseudopanax crassifolius* (dark bars) and *P. chathamicus* (open bars) juvenile plants with different numbers of branching events (*x*-axis).
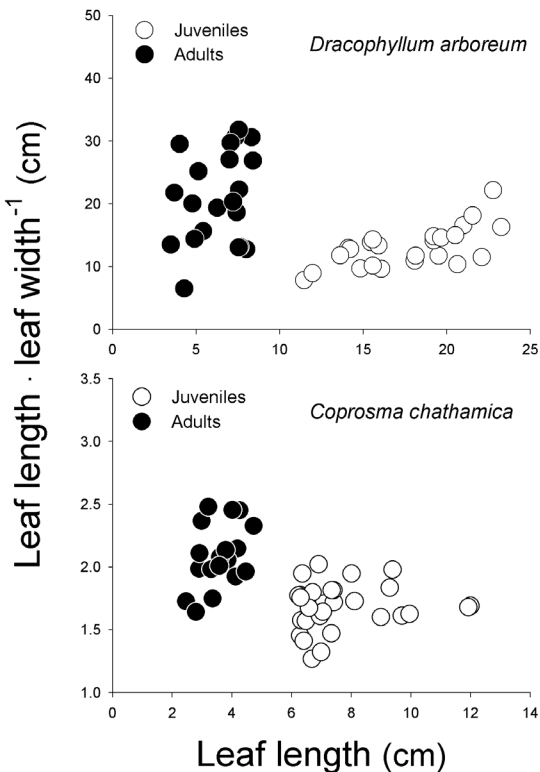
Two tree species that are endemic to the Chatham Islands, *Coprosma chathamica* and *Dracophyllum arboreum*, exhibited obvious heteroblastic changes in leaf morphology (see Fig. 1). Both species showed similar morphological differences between juvenile and adult leaves (Fig. 4). Juvenile leaves of *C. chathamica* were larger ($F_{1,45} = 281.422$), more circular ($F_{1,45} = 40.582$) and less lobed ($F_{1,45} = 41.664$) than adults. Juvenile leaves of *D. arboreum* were also larger ($F_{1,43} = 364.951$, more circular ($F_{1,43} = 20.497$) and less lobed ($F_{1,43} = 25.953$) than adults. (All $P < 0.001$.)

The first two functions generated by discriminant function analyses were able to differentiate the archipelagos (Wilk's $\lambda = 0.587$, $P = 0.009$). The first discriminant function accounted for 88.9% of variance that could be attributed to archipelago groupings (eigenvalue = 0.588). This first function was negatively correlated with the ratio of adult to juvenile leaf area ($r = -0.539$), positively correlated with the ratio of adult to juvenile

Figure 4. Differences between the size and shape of juvenile (open symbols) and adult (closed symbols) leaves of *Dracophyllum arboreum* (top) and *Coprosma chathamica* (bottom). The ratio of leaf length to leaf width is shown on the *y*-axis (larger values reflect longer, narrower leaves). Leaf length is shown on the *x*-axis and is a coarse reflection of leaf size. Juvenile leaves are larger and wider in both species, which is atypical of morphological changes in most heteroblastic species in New Caledonia and New Zealand.

leaf lobing ($r = 0.502$), and weakly associated with the ratio of adult to juvenile leaf circularity ($r = 0.076$). The second discriminant function accounted for an additional 11.1% of morphological variation (eigenvalue = 0.073). Juvenile–adult transitions in morphology were similar in New Caledonia and New Zealand, but more distinct on Chatham Island (Fig. 5).

Discussion

Reductions in the expression of heteroblasty on the Chatham Islands were observed in all three species with heteroblastic relatives in New Zealand. Juvenile leaves of *Muehlenbeckia australis* on Chatham Island were virtually indistinguishable from adult leaves, in contrast to this species in New Zealand. Juvenile leaves of *Pseudopanax chathamicus* were much larger, more circular, and lacked the sharp serrations present on the longer, thinner leaves of *P. crassifolius*. Reversions to homoblasty in *Plagianthus regius* were less pronounced. These results are generally consistent with the hypothesis that heteroblasty on islands such as New Caledonia and New Zealand evolved in response to browsing by large, flightless birds (Greenwood & Atkinson 1977).

One explanation for a weaker reversion to homoblasty in *Plagianthus regius* is that it is a more recent immigrant to the Chatham Islands, where it has had less time to adjust evolutionarily to the absence of browsers. Alternatively, processes other than bird browsing, such as selection by environmental conditions (McGlone & Webb 1981; Kelly & Ogle 1990), may be important. For example, changes in leaf and shoot morphology during ontogeny could help plants cope with vertical changes in environmental conditions such as shade (Jones 1995; Gamage & Jesson 2007), frost (Darrow et al. 2001) or wind (Burns 2005).

Analyses of branching architecture showed that *Pseudopanax chathamicus* began branching much earlier than *P. crassifolius*. *P. crassifolius* is typically rooted by a single stem and only begins to branch once plants grow above 3 m, which coincides with the height of the largest known moa species (Greenwood & Atkinson 1977). The juvenile leaves of *P. crassifolius* are remarkably long and stiff, and have sharp serrations along their margins. Extant ratites swallow leaves by first positioning them in their bill and then snapping their head forwards to orient them down their oesophagus (see Bond et al. 2004). The long, serrated leaves of *P. crassifolius* may have impeded this process and made them difficult to swallow. Once above 3 m, adult *P. crassifolius* plants begin to branch and produce less rigid leaves that lack serrations (see Gould 1993). Therefore, the unbranched habit of juvenile plants may represent a greater investment in vertical growth, to help plants reach a height refuge from moa browsing. In the absence of moa, earlier branching in *P. chathamicus* may assist in spreading leaves over larger horizontal areas, increasing interception of diffuse light in the forest understorey. However, plant branching architecture is known to vary with a wide range of environmental variables (see Barthélémy & Caraglio 2007), so this interpretation
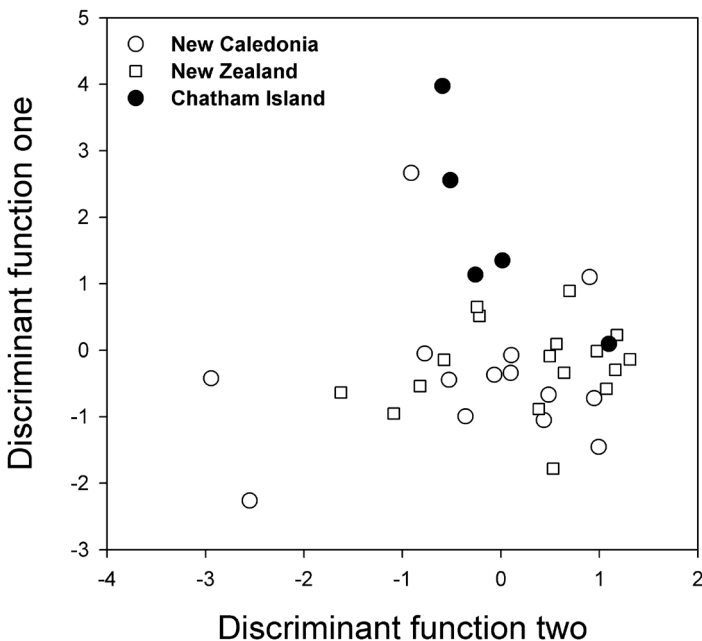

Figure 5. Discriminant function analyses of differences between adult and juvenile leaf area, circularity, and lobing in New Caledonia, New Zealand and Chatham Island. Heteroblastic transitions are more similar in New Caledonia and New Zealand than on Chatham Island.

remains speculative.

Plagianthus regius has a strongly divaricate branching habit in New Zealand. Although we encountered *P. regius* juveniles with divaricate-like branching in the Chatham Islands, this habit appeared to be less pronounced than in New Zealand (see also Cockayne 1902; Dawson 1991; Greenwood 1992). *Muehlenbeckia australis* commonly grows as a liana in New Zealand, yet juvenile plants are often densely matted, with long, thin stems that are consistent with the 'wire plant syndrome' (sensu Bond & Silander 2007). Chatham Island plants appear to have lost this branching pattern and most plants stood erect. Although extant ratites tend to avoid consuming 'wire' plants (Bond et al. 2004), divaricate branching might also serve a physiological function (see Darrow et al. 2002; Howell et al. 2002). Future work would benefit from direct quantitative comparisons of branching architecture between archipelagos.

Although the three species investigated here show consistent trends towards homoblasty, two endemic tree species, *Coprosma chathamica* and *Dracophyllum arboreum*, are strongly heteroblastic. Both species suddenly switch from producing large juvenile leaves to small adult leaves at maturity. Inter-archipelago comparisons of leaf shape showed that transitions from large-leaved juveniles to small-leaved adults are quite rare in New Zealand and New Caledonia, where heteroblastic trees and shrubs typically produce smaller leaves as juveniles (Burns & Dawson 2006). Only a small number of species show shifts from large to small leaves during ontogeny. For example, *Grevillea gillivrayi* is a native of New Caledonia that produces large leaves on stems located < 2 m from the ground. [This species is represented by the data point located in closest proximity to the Chatham Island species depicted in Fig. 5]. However, it suddenly begins to produce long, vertically orientated flower stalks at maturity, which bear smaller leaves (Burns & Dawson 2006). Large browsers typically prefer large leaves over small ones (Bond et al. 2004; Pollock et al. 2007), so this form of heteroblasty is unlikely to serve an anti-herbivore function. Smaller adult leaves may instead be a biomechanical adaptation, generating less mechanical stress on flowering stalks in high winds. A similar explanation may apply to *C. chathamica* and *D. arboreum* on Chatham Island, which is almost continuously buffeted by high winds. Therefore, the morphology of these species seems to argue against browsers as the sole process responsible for leaf heteroblasty on isolated islands.

Overall results illustrate consistent reversions to homoblasty in three Chatham Island plant species with heteroblastic relatives on the New Zealand mainland. These results are broadly consistent with the hypothesis that insular heteroblasty evolved as an adaptation to deter herbivory by browsing birds that are now extinct. However, heteroblasty is not uncommon on the Chatham Islands and the prevalent form of leaf heteroblasty is uncommon in New Caledonia and New Zealand. Therefore, results suggest that multiple processes may have shaped the evolution of heteroblasty on Chatham Island. Although direct tests of the moa-browsing hypothesis are no longer possible, future inter-archipelago comparisons may help to refine our understanding of this unusual characteristic of isolated islands.

Acknowledgements

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