Are there general patterns in plant defence against megaherbivores?

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Field surveys were conducted to test whether plants deploy structural defences in ways that match the distribution of megaherbivores. In Western Australian scrublands, where adult plants are within the reach of megaherbivores, structural defences increased vertically and were deployed preferentially by adult plants. Conversely, in woodlands of Eastern Australia and California, where adult plants grow above the reach of megaherbivores, structural defences decreased vertically. Populations of closely-related taxa on offshore islands exhibited significant reductions in defence in the absence of megaherbivores. The results also demonstrate that island plant taxa can evolve vertical changes in defence after colonizing continents, where they are exposed to megaherbivores. Overall, the results of the present study illustrate a complex array of spatial patterns in plant defence that match the distribution and foraging behaviour of large mammals. When interpreted alongside previous work demonstrating similar spatial patterns in other types of plant defence, the results may help to unify our understanding of how megaherbivores have shaped the evolution of plant form and function. © 2013 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, 111, 38–48.


INTRODUCTION

Prickles, thorns, and spines are analogous structures that are commonly assumed to deter herbivory by large mammals, or ‘megaherbivores’ (Ronel & Lev-Yadun, 2012). Although they are derived from different tissues (prickles originate from epidermal tissue; thorns are modified twigs or branches; and spines are modified leaves, leaf parts or stipules, Cornelissen et al., 2003), all three can damage the mouthparts of megaherbivores, thus slowing rates of herbivory (Cooper & Owen-Smith, 1986; Hanley et al., 2007; Shipley, 2007). However, prickles, thorns, and spines are not always effective at deterring herbivores and they may serve other adaptive functions (Potter & Kimmerer, 1988; Rafferty, Lamont & Hanley, 2005).

If prickles, thorns, and spines are effective anti-herbivore adaptations, they should be deployed by plants in ways that match the foraging behaviour and distribution of megaherbivores. Unlike insects, which are small in size and often capable of flight, the large body size of megaherbivores places distinctive restrictions on where they can forage. They are typically too large to fly or climb proficiently, and so leaves at the top of tree canopies are generally safe from megaherbivores. Mammals are also poor over-water dispersers, and so they are usually absent from oceanic islands (Whittaker & Fernández-Palacios, 2007). Congruent patterns in the traits of interacting species are commonly referred to as ‘trait matching’ (Thompson, 2005) and the phenomenon has been demonstrated previously in several types of species interactions (Brodie, Ridenhour & Brodie, 2002; Burns, 2004; Anderson & Johnson, 2009; Martins & Johnson, 2013). If trait matching occurs between megaherbivores and plant structural defences, then prickles, thorns, and spines should be distributed nonrandomly in two spatial dimensions; they should

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be distributed both vertically and horizontally (geographically) in ways that maximize contact with mega herbivores.

Vertical variation in plant traits typically arises from ontogenetic changes in their production. Ontogenetic changes in plant morphology are collectively known as ‘heteroblasty’ and the phenomenon is commonly assumed to enhance physiological performance in changing environmental conditions as plants grow. Common examples include tank bromeliads (Meisner & Zotz, 2012, 2013), which produce leaves that cup-together to store water at maturity, and aquatic plants (Wells & Pigliucci, 2000), which produce different leaf forms when they are submerged and once they reach the water surface to help cope with associated changes in water flow. Putsive examples of heteroblasty in plant structural defences often involve flightless browsing birds that are now extinct (Greenwood & Atkinson, 1977; Fadzley et al., 2009; Fadzley & Burns, 2010). Accordingly, direct tests of whether heteroblasty can alter rates of herbivory are rare (Bond, Lee & Craine, 2004) and the link between heteroblasty and plant structural defence is controversial (Zotz, Wilhelm & Becker, 2011).

Geographical variation in plant traits typically results from geographical variation in the distribution and behaviour of interaction partners (Thompson, 2005). Although mammals are widely distributed across the globe, they are not adept at over-water dispersal, and so nonvolant mammals are usually absent from oceanic islands (Whittaker & Fernández-Palacios, 2007). Structural defences against mammalian herbivores should therefore be lost in plant taxa that colonize oceanic islands from continents and heteroblastic changes in the deployment of prickles, thorns, and spines should be reduced.

The present study reports the results of an exploratory analysis of trait matching between plant structural defences and the spatial distribution of mega herbivores. The production of prickles, spines and thorns by woody plants was quantified in two spatial dimensions to test whether they matched the distribution and foraging behaviour of large mammals. Four hypotheses were addressed:

1. Plant structural defences are deployed vertically (i.e. heteroblastically) in ways that match the foraging behaviour of large mammals.
2. Spinescence heteroblasty differs among vegetation types, such that prickles, thorns, and spines are produced progressively (later in ontogeny) in shrubs, where adult plants are vulnerable to mega herbivores. Conversely, they are produced retrogressively (earlier in ontogeny) in woodlands, where only juvenile plants are exposed to mega herbivores.
3. Spinescence heteroblasty is less pronounced on islands that are devoid of large mammals.
4. Undefended, island plant taxa evolve spinescence heteroblasty after colonizing continents where they are exposed to mega herbivores.

MATERIAL AND METHODS

Structural defences were measured in 16 plant taxa spanning seven biogeographical locales. Taxa were located in field searches that took place over the course of several days at each study site. During field searches, marked trails were traversed in search of plant species that produced prickles, thorns or spines. Once a structurally defended species was identified, a search was conducted for plants representing a range of ontogenetic stages (i.e. seedlings, saplings and adults). If plants appeared to exhibit patterned gradation in structural defence across life-history stages, these species were included in the study. In some sites (e.g. Paluma Range National Park), only one putative heteroblastic species could be identified. In other sites (e.g. Lesueur National Park), ten or more suitable species were found. In sites with many measurable species, analyses were restricted to the four most common species that collectively represented the widest range of phylogenetic backgrounds. Study sites were chosen to encompass a range of vegetation types, canopy heights and biogeographical histories. Island study sites were selected to facilitate comparisons with previously measured mainland taxa.

SOUTH-WEST AUSTRALIA

Four species were measured in ‘mallee’ scrubland in Lesueur National Park, which is located approximately 150 km North of Perth in South-West Australia (30°09′S 115°11′E). The area supports a highly diverse flora dominated by small-statured shrubs, which rarely grow above 2 m in height. Initial observations suggested that two species (Jacksonia furcellata, Fabaceae and Acacia stenoptera, Mimosoideae) produced leaves at early life-history stages but, as plants grew taller, they stopped producing leaves rather abruptly and, instead, produced rigid, photosynthetically active stems with very sharp tips (i.e. sharpened phyllodes). To quantify this potential pattern in defensive heteroblasty, 30 individuals from each species were selected haphazardly and their height above the ground and degree of structural defence was quantified (1 = leaves only; 2 = leaves and sharp phyllodes; 3 = sharp phyllodes only). To test whether levels of structural defence increased with plant height, separate Poisson
regressions with log link function were conducted for each species. All statistical analyses were conducted in the R environment (R Development Core Team, 2008).

Two additional species were measured at this site, which produced leaf spines rather than sharpened phyllodes. *Hakea auriculata* (Proteaceae), produced conspicuously sharp projections along its leaf margins, which appeared to increase in size and shape abruptly during ontogeny. To characterize vertical changes in the morphology of leaf spines, three measurements were made on five leaves collected from the top of 30 plants: (1) the length of the terminal leaf spine; (2) leaf length or the distance from the tip of the petiole to the base of the petiole and (3) leaf width, namely the maximum width perpendicular to the length measurement. Leaf length and leaf width measurements were multiplied to obtain an estimate of leaf area and measurements for each leaf were averaged within plants prior to statistical analyses. The height of each plant was also measured. Two statistical tests were conducted to test whether leaves became smaller and more structurally defended at maturity. Separate general linear models were used to test whether the length of the terminal spine increased with plant height, and whether leaf area declined with plant height. All three variables were ln-transformed prior to analyses to conform to assumptions.

*Banksia carolinoides* (Proteaceae) appeared to exhibit a similar pattern in defensive heteroblasty. However, juvenile plants appeared to be completely undefended. To characterize vertical changes in the density of leaf spines, the number of leaf spines on the uppermost five leaves on 30 plants was enumerated, along with their surface area, which was quantified as the product of their length and width (as defined above). Leaf spines were defined specifically as projections from the leaf margin formed an angle smaller than 90°. A general linear model was then conducted to test whether the density of leaf spines (number of leaf spines per leaf area) increased with plant height. Values for each leaf were averaged within plants prior to analyses and both variables were logarithm transformed to conform to assumptions.

EAST AUSTRALIA AND LORD HOWE ISLAND

Field measurements were made at three coastal localities in Eastern Australia, which spanned 15° of latitude and comprised a range of different forest types (temperate Eucalypt forest, subtropical littoral forest, tropical dry forest, and tropical rainforest). Parallel field searches were also made for several taxa on Lord Howe Island, which is located 600 km off the coast of Eastern Australia.

A single species, *Bursaria incana* (Pittosporaceae), was measured in tropical dry forest in Paluma Range National Park, which is located approximately 50 km North of Townsville, in North-east Queensland (19°10’S 146°15’E). Initial observations suggested that smaller plants produce sharp thorns, whereas larger plants were generally unarmed. The height of 30 plants was measured and, on the uppermost lateral branch of each plant, the length and width of the uppermost five leaves was measured and a search for the presence of thorns was conducted. A binomial regression with a log link function was then performed to assess whether thorn production (thorns absent = 0, thorns present = 1) varied with plant height. A general linear model was also conducted to assess whether leaf area varied with plant height (both variables were ln-transformed).

Three species were measured in Noosa Heads National Park, which is located 80 km North of Brisbane, in South-east Queensland (26°23’S, 153°06’E). *Banksia integrifolia* (Proteaceae), *Drypetes deplanchei* (Putranjivaceae), and *Wilkiea macrophylla* (Monimiaceae) all appeared to produce leaf spines as juveniles, whereas older plants were more poorly defended. The length and width of a sample of leaves from each species were measured and the total number of leaf spines that they contained was enumerated. Sample sizes varied among species. Three leaves from 30 plants were measured in *B. integrifolia*, three leaves from 22 plants were measured in *D. deplanchei*, and two leaves were measured on 30 plants of *W. macrophylla*. To test whether leaf spine densities declined with plant height, separate general linear models were conducted comparing leaf spine densities (number of leaf spines per leaf area) to plant heights for *B. integrifolia* and *W. macrophylla* (statistical analyses of *D. deplanchei* are described below). Values for each leaf were averaged within individual plants prior to analyses and all variables were ln-transformed.

Two taxa were assessed in temperate forest in Mt Keira National Park, which is located 10 km East of Wollongong, eastern New South Wales (34°24’S 150°51’E). Prickle densities were measured in a common liana species (*Smilax australis*, Smilaceae) and thorn densities were measured in a free-standing, small tree *Corposma quadrifida* (Rubiaceae). In *S. australis*, the total number of prickles occurring on a single haphazardly selected internode from 30 separate individuals was tallied. Internode length (mm) and diameter (mm) were also measured to calculate stem surface area. In *C. quadrifida*, the total number of thorns produced on the upper-most branch on 30 individuals was enumerated, along with plant height and the total length of each branch. To test whether
thorn densities declined with plant height, a general linear model was conducted comparing leaf spine densities (number of thorns per branch length) to plant heights. Both variables were ln-transformed and the statistical analyses of *S. australis* are described below.

Lord Howe Island is located 600 km East of Australia in the Tasman Sea (31°33′S, 159°05′E). Its flora and fauna are derived entirely via overwater dispersal and Lord Howe Island was devoid of mammals until last century. *Smilax australis* and *D. deplanchei* both occur naturally on the island, and so identical measurements to those made on the mainland were made for comparative purposes. General linear models were used to test whether relationships between prickle densities and stem sizes in *S. australis*, as well as relationships between leaf spine densities and plant height in *D. deplanchei*, differed between island and mainland populations. Study site (island versus mainland) was considered a fixed factor in both analyses. Plant height was used as the covariate in *D. deplanchei* and internode surface area (π × diameter × length) was used as a covariate in *S. australis*.

**CALIFORNIA AND SANTA CRUZ ISLAND**

Two pairs of taxa were measured in the Santa Monica Mountains, Southern California (34°05′N, 118°38′W) and on nearby Santa Cruz Island (34°02′N, 119°34′W). The area supports Mediterranean-type scrubland that is similar to South-west Australia (Rundel & Gustafson, 2005). However, unlike mallee scrublands, the vegetation here is substantially taller, and adult plants of measured species grew between 3–10 m in height. Santa Cruz Island is located approximately 40 km off the coast of Southern California and was separated from the mainland throughout the Pleistocene. Prior to human arrival, it housed only one large herbivorous mammal species (*Mammoth excilis*), which is not considered to have browsed extensively on woody plants but, instead, fed mainly on grasses (Schoenherr, Feldmeth & Emerson, 1999).

*Prunus ilicifolia* ssp. *lyoni* (Rosaceae) and *Quercus berberidifolia* (Fagaceae) were measured in the Santa Monica Mountains (mainland California) and *Prunus ilicifolia* ssp. *ilicifolia*, and *Quercus pacifica* were quantified on the Southern end of Santa Cruz Island. *Quercus pacifica* and *Q. berberidifolia* were formally classified under the same species name and have only recently been split taxonomically (Schoenherr et al., 1999). The length and width of three leaves from the upper-most, mature branch of 30 trees was measured, in addition to the total number of leaf spines, except for *P. ilicifolia* ssp. *ilicifolia* for which two or three leaves from 21 plants were measured. General linear models were used to test whether leaf spine densities differed between island and mainland plant populations. Study site (island versus mainland) was considered a fixed factor and plant height was used as the covariate in both analyses. Values for each leaf were averaged within individual plants prior to analyses and ln-transformed when necessary to conform to assumptions.

**RESULTS**

In the mallee scrublands of South-west Australia, *J. furcellata* and *A. stenoptera* showed convergent patterns in spinescence heteroblasty (Fig. 1). Poisson regression showed that structural defences increased with plant height (*J. furcellata*, *P* = 0.014; *A. stenoptera*, *P* = 0.003), with apparently palatable leaves being produced at initial stages of ontogeny, which were later lost in favour of rigid, sharp phyllodes. *Hakea auriculata* showed a similar pattern.

Figure 1. Spinescence heteroblasty in *Jacksonia furcellata* (A) and *Acacia stenoptera* (B), two shrub species from South-west Australia. Smaller plants produce leaves but, once plants grow above 0.1 m in height, leaf production stops, and plants instead produce sharp, rigid phyllodes (photosynthetically active stems).
in spinescence heteroblasty (Fig. 2). Leaf area declined with plant height ($P = 0.002$), whereas the length of the terminal leaf spine increased ($P < 0.001$). All three species therefore displayed a ‘progressive’ pattern in heteroblasty, wherein plants produce larger, less defended lamina at earlier stages of ontogeny and smaller, more defended lamina later in ontogeny.

In tropical forests in north-east Australia, thorn production declined with plant height in $B. incana$ ($P = 0.004$), whereas leaf size increased ($P < 0.001$). Similarly, leaf spine density declined with plant height in $W. macrophylla$ ($P < 0.001$). Therefore, both species exhibited a ‘retrogressive’ pattern in spinescence heteroblasty, with smaller, younger plants being more heavily defended than larger, older plants (Figs 3, 4).

$Banksia carlinoides$, which inhabits south-west Australia, and $B. integrifolia$, which inhabits north-east Australia, exhibited opposing forms of spinescence heteroblasty (Fig. 5). Leaf spine densities in $B. carlinoides$ increased progressively with plant height in mallee scrublands, where adult plants are exposed to megaherbivores ($P < 0.001$). On the other hand, leaf spine densities in $B. integrifolia$ decreased retrogressively with plant height and were absent in all plants above 3 m in height ($P < 0.001$), above which they reached a height refuge from megaherbivores.

Leaf spine densities declined with plant height in $D. deplanchei$ in both North-east Australia and Lord Howe Island (Fig. 6A; $P < 0.001$). The relationship for the Australian mainland had a marginally steeper slope than the Lord Howe Island relationship ($P = 0.054$). If their slopes are assumed to be similar, the intercept of the relationship for Lord Howe Island was marginally lower than the mainland ($P = 0.065$).

Prickle density declined with stem size in $S. australis$ (Fig. 6B; $P < 0.001$), and a clear difference in slope was observed between islands and the mainland ($P < 0.001$). Leaf spine density declined with plant height in $P. ilicifolia$ (Fig. 6C; $P < 0.001$) and a marginally significant difference in slope was observed between islands and the mainland ($P = 0.062$). If their slopes are assumed to be similar, the intercept for the mainland relationship was larger than the island relationship ($P < 0.001$). Leaf spine density declined with plant height in both $Q. berberidifolia$ and $Q. pacifica$ (Fig. 6D; $P < 0.001$). A clear difference in

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\text{Figure 2. Adult and juvenile leaf forms in } Hakea auriculata, \text{ a heteroblastic shrub species from South-west Australia (A). Smaller plants produce relatively large leaves, with comparatively small leaf spines (B). However, as plants grow taller, they produce leaves with smaller surface areas and larger, more rigid leaf spines (C).}
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\text{Figure 3. Spinescence heteroblasty in } Bursaria incana, \text{ a small tree that inhabits tropical dry forest in North-east Australia. Younger, smaller plants (illustration at left) produce smaller leaves and sharp thorns (black diamonds), whereas older, larger plants (illustration at right) are devoid of thorns (white diamonds) and produce larger leaves.}
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slope was observed between islands and the mainland ($P < 0.001$), with the mainland population showing a shallower slope than the island population.

Thorn production in *Coprosma quadrifida*, which is native to south-east Australia but evolved from a New Zealand ancestor, was strongly heteroblastic (Fig. 7). Thorn density declined linearly with plant height ($P < 0.001$), indicating that smaller plants exposed to megaherbivores were better defended than larger plants.

**DISCUSSION**

Plant structural defences matched the spatial distribution of megaherbivores, both vertically and geographically, in the 16 plant species investigated in the present study. The production of prickles, thorns, and spines varied with plant size, although their developmental directionality differed among vegetation types. In scrublands, structural defences were deployed preferentially in adult plants. In woodlands, they were produced by seedlings and saplings. These defences are consistent with the foraging behaviour of megaherbivores, which cannot reach the crowns of adult trees, yet can forage freely on adult shrubs.

Spinescence heteroblasty also showed consistent reductions on isolated islands that were devoid of large mammals. The loss of defence on islands worked in reverse in *C. quadrifida*, which likely evolved from an island ancestor without thorns, although it exhibited a clear pattern in spinescence heteroblasty in its native Australia.

Previous work has demonstrated that prickles, thorns, and spines can deter herbivory by large mammals (Cooper & Owen-Smith, 1986; Milewski, Young & Madden, 1991; Gowda, 1996; Obeso, 1997). Structural defences often restrict bite sizes and therefore reduce energy intake rates, which limits damage rather than inhibiting it altogether (Wilson & Kerley, 2003a, b; Cash & Fulbright, 2005; Hanley *et al*., 2007; Shipley, 2007). However, structural defences may not always be effective deterrents to megaherbivores (Rafferty *et al*., 2005). Prickles, thorns, and spines may also have different functional attributes. Thorns can serve as climbing implements in lianas (Putz, 1990) and they sometimes form domatia to house mutualistic ants (Stanton, Palmer & Young, 2005). Thorns might promote self-shading in arid environments, leaf spines could function as drip-tips in wetter environments, and phyllodes may enhance...
physiological function under certain environmental conditions (Forster & Bonser, 2009). Direct, quantitative evidence showing that structural defences deter megaherbivores has yet to be collected for many of the species investigated in the present study (Hanley et al., 2007; Rafferty, Lamont & Hanley, 2010 for several South-west Australia taxa), and so alternative explanations for the functioning of prickles, thorns, and spines cannot be ruled out. Although measurements were made in several continents, from a global perspective, sampling was restricted to just two localities. Additional work in other localities, particularly continents with different assemblages of megaherbivores (e.g. Africa and South America), would provide valuable new insight into the repeatability of observed patterns in plant defence against megaherbivores.

Many types of plant defence, including structural defences, are inducible (Karban & Baldwin, 1997). Several previous studies have shown that the production of prickles, thorns, and spines can be deployed plastically in response to the recent actions of megaherbivores (Gómez & Zamora, 2002; Young, Stanton & Christian, 2003). Therefore, vertical patterns in structural defence, as well as differences in spinescence heteroblasty between islands and continents, may not represent genetically fixed adaptations to megaherbivores. Instead, they could result from plastic responses to recent herbivory. Although plausible, this interpretation appears unlikely. Feral goats, sheep, cattle, and other large, herbivorous mammals have been introduced recently to both Lord Howe and Santa Cruz Islands, exposing plants to megaherbivores. However, island plant populations

Figure 6. Loss of spinescence heteroblasty in four plant taxa inhabiting islands devoid of megaherbivores. A, Drypetes deplanchei is a tree species that occurs in both North-east Australia and Lord Howe Island (LHI). Leaf spine densities show a sharper decline in density with plant height on LHI. B, Smilax australis is a liana species that occurs in both Eastern Australia and LHI, where produces fewer prickles. C, Prunus ilicifolia is a tree species that occurs in Western North America and Santa Cruz Island. Prunus ilicifolia subsp. ilicifolia shows a reduction in spinescence heteroblasty on Santa Cruz Island, relative to P. ilicifolia subsp. lyonii, which occurs on the California mainland. D, Quercus berberidifolia and Quercus pacifica are sister species of small tree that occur in western North America and Santa Cruz Island, respectively. Quercus pacifica shows a reduction in spinescence heteroblasty relative to Q. berberidifolia.
nevertheless produced lowered levels of structural defence, suggesting that reduced patterns in spinescence heteroblasty have a genetic basis. Furthermore, when grown in cultivation in areas devoid of megaherbivores, *B. integrifolia* continues to produce strongly spinescent juvenile leaves (K. C. Burns, pers. observ.).

Trait matching between megaherbivores and plant structural defences has been documented previously. For example, spine production in the Japanese shrub *Damnacanthus indicus* covaries with the distribution of Sitka deer (*Cervus nippon*). In regions where deer are present, *D. indicus* produces higher densities of larger spines compared to regions where deer are absent (Takada, Asada & Miyashita, 2001). White (1988) reported an ontogenetic pattern in prickle production similar to *S. australis*, wherein smaller, younger branches of *Aralia spinosa* are more heavily armed than larger, older branches. In a particularly insightful study, Kato, Ishida & Sato (2008) showed that Japanese nettle (*Urtica thunbergiana*) produces higher densities of stinging hairs where it is exposed to deer herbivory. It was also shown that stinging hair densities negatively affect deer herbivory and that their production has a genetic basis, suggesting herbivores can select for stronger defences in more vulnerable plant populations.

Although vertical variation in structural defences matched the distribution of megaherbivores, two distinct forms of spinescence heteroblasty were observed. In South-west Australia, structural defences were deployed progressively, or later in ontogeny. The opposite pattern was observed in North-east Australia, where structural defences were deployed retrogressively, or earlier in ontogeny. The dichotomy between the progressive and retrogressive forms of spinescence heteroblasty is best illustrated by the two *Banksia* species shown in Figure 5. Despite being closely related phylogenetically, the expression of spinescence heteroblasty is diametrically opposed in each species, which grow to different heights at maturity.

Island biotas often exhibit several consistent patterns in trait evolution. Changes in body size, loss of dispersal ability, and loss of defensive adaptations are common attributes of island animals (Lomolino et al., 2013). Although fewer studies have addressed these issues in plants, island plants could display repeated patterns in island evolution that are broadly similar to animals (Cody & Overton, 1996; Burns, Herold & Wallace, 2012). In an earlier study on Santa Cruz Island, Bowen & Vuren (1997) showed that both chemical and structural defences are lower relative to their mainland sister taxa. Vourch et al. (2001) showed that *Thuja plicata* seedlings on Haida Gwaii (i.e. Queen Charlotte Islands) are less defended chemically than conspecifics on the mainland. The results obtained in the present study build upon these studies by illustrating that the vestiges of structural defences evolving on the mainland can often be observed in earlier ontogenetic stages in island populations, in the form of relaxed patterns in spinescence heteroblasty (Alberch et al., 1979).

Paradoxically, other forms of heteroblasty are unusually common on highly isolated islands that are devoid of large mammals. The floras of Hawaii (Givnish et al., 1994), Madagascar (Bond & Silander, 2007), Mauritius (Eskildsen, Olesen & Jones, 2004), New Caledonia (Burns & Dawson, 2006), and New Zealand (Carlquist, 1974; Greenwood & Atkinson, 1977) are characterized by a preponderance of woody plants whose leaf morphology and branching architecture change markedly in ways that are very rarely displayed by woody plants on continents. One explanation for this ‘insular’ form of heteroblasty is that it assisted plants in coping with island environments physiologically (McGlone & Webb, 1981; Gould, 1993; Clearwater & Gould, 1994; Day, 1998; Howell, Kelly & Turnbull, 2002). Alternatively, insular heteroblasty might be linked to non-mammalian megaherbivores. Although large, isolated islands typically lack browsing mammals, they were often home to flightless, browsing birds, and tortoises (Whittaker & Fernández-Palacios, 2007). Birds and tortoises lack teeth and forage very differently from mammals, and several previous studies have shown that divaricate
branching and certain types of leaf morphology may deter toothless browsers (Bond et al., 2004; Fadzley & Burns, 2010). Interestingly, these forms of heteroblasty are often lost on the smaller, satellite islands flanking these large oceanic islands. These satellite islands (e.g. the Chatham Islands, which lie 600 km east of New Zealand) lacked toothless megaherbivores, thereby providing another putative example of the loss of plant defence on islands, similar to the loss of prickles and spines on Lord Howe and Santa Cruz Islands (Burns & Dawson, 2009; Fadzley et al., 2009; P. H. Kavanagh unpubl. observ.). Unfortunately, almost all toothless megaherbivores have been driven to recent extinction by human activities on isolated islands (Steadman, 2006; Johnson, 2009; Lee, Wood & Rodgers, 2010), rendering direct experimental tests of their relationship with insular heteroblasty all but impossible (Bond et al., 2004).

Similar trait matching patterns have also been observed in nonstructural plant defences (Boege & Marquis, 2005; Barton & Koricheva, 2010). Swihart & Bryant (2001) summarize vertical and geographical patterns in plant chemical defences that match the distribution and behaviour of mammalian herbivores. In hundreds of north-temperate plant species, chemical defences are deployed preferentially by juvenile plants, providing evidence for vertical trait matching. Ontogenetic changes in plant chemistry also vary geographically, with ontogenetic clines being strongest in colder, higher-latitude sites. Thus, similar to patterns in divaricate branching on oceanic islands, chemical defences are commonly deployed in a similar manner to the way that prickles, thorns, and spines are deployed.

Overall, the results obtained in the present study indicate that prickles, thorns, and spines can be produced through vertical and geographical space in ways that match the distribution and foraging behaviour of large mammals (Ronel & Lev-Yadun, 2012). Similar patterns in trait matching in plant defensive chemistry have been documented in other continental locales and similar patterns in putative defences (divaricate branching) have been documented in other insular settings. When interpreted jointly, these results suggest that congruent vertical and geographical trait matching between megaherbivores and plant defence could be common macroevolutionary phenomena.

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