

2 Differences in Defence

Islands often house very different assemblages of predators than continents. Given their poor colonisation potential, mammalian predators are often replaced by other types of predators with greater dispersibility, such as birds. As a result, prey species on islands regularly lose defences against predators that are absent from islands, and readjust their anti-predatory adaptations to suit those that are present.

Are island plants similar to island animals? When freed from attack by mainland herbivores, do island plants lose defensive adaptations commonly deployed by their continental counterparts? On islands housing unusual 'toothless' herbivores, do island plants consistently evolve traits to cope with them?

Two types of data are needed to answer these questions. First, herbivore occurrence patterns need to be established to determine which islands were colonised by particular types of herbivores and which ones were herbivore-free. Second, the effects of particular plant traits on the behaviour of different types of herbivores need to be determined. Both types of data can then be integrated to test the hypothesis that island plants consistently adjust their defensive adaptations to suit co-occurring herbivore faunas. Straightforward as it seems, how plant defensive adaptations evolve on isolated islands is infrequently documented, poorly understood, and, in some cases, highly contentious.

ISLAND HERBIVORES

Insects are arguably the most abundant and widespread herbivores on the planet (Strauss & Zangerl 2002). They have co-evolved with plants for 400 million years and have had a significant influence on the evolution of plant form and function. However, insect herbivores will

not be the focus of this chapter, both because their biogeographic distributions are comparatively difficult to establish relative to vertebrates, and because trait-based relationships between plants and particular types of insects are more complicated. For the same reasons, a wide assortment of other types of herbivores, including viruses, bacteria, fish and fungi, await further study. Instead, this chapter will focus on terrestrial vertebrate herbivores.

Mammals are the largest vertebrate herbivores on the planet and have similarly profound impacts on plant ecology and evolution to insects (Danell & Bergström 2002). Not surprisingly, many plants possess adaptations to deter mammalian herbivores (see Hanley et al. 2007). When mammal-defended plants initially colonise islands from the mainland, founding populations carry these defences with them. But because mammals are poorly equipped for overwater dispersal, they rarely occur on isolated islands and plant defences against mammals lose their usefulness. On the other hand, plants colonising many large, oceanic islands were greeted by avian and reptilian herbivores. Although relatively unimportant on most continents, these 'toothless' herbivores dominated many island ecosystems prehistorically.

Unfortunately, vertebrate herbivore faunas have undergone radical transformations in the Anthropocene, not just on continents, but especially on islands (Steadman 2006). Native vertebrate herbivores have been eliminated from many islands and replaced intentionally with continental herbivores. So the herbivore faunas that occur on islands today are often a poor reflection of the circumstances under which island floras evolved.

Given their recent disappearance, identifying repeated patterns in plant defence against native vertebrate herbivores requires an understanding of prehuman herbivore distributions, which can be acquired in several ways. Some isolated islands were discovered relatively recently by peoples with written language. For many of these islands, such as the Galapagos, Mauritius, and Socotra, there are written descriptions of island faunas at the time of human contact. Other islands were discovered by peoples without written language

and lack written descriptions of the animals they once housed. Under these circumstances, paleontological excavations of subfossil bones, similar to those in Liang Bua on Flores Island, are needed to establish the types of herbivores that were once present.

Tortoises

Eighty Ma, reptiles were the most important vertebrate herbivores on the planet. But, since then, reptiles have declined in importance as herbivores, especially after the extinction of dinosaurs 65 Ma. Giant tortoises, the largest-bodied herbivorous reptiles alive today, can no longer be found on continents. However, a very different situation emerges on some oceanic islands, where giant tortoises were exceedingly common prehistorically. Early European explorers were astounded by the enormous densities of tortoises on the islands where they occurred (Cheke & Hume 2008). Given their numerical dominance, native plants may have evolved specific defences against tortoise herbivory.

Several aspects of the morphology and physiology of giant tortoises place clear constraints on how they interact with plants. First, tortoises do not have teeth, so they cannot chew their food. Instead, they must swallow their food more or less whole. As a result, they are likely to have difficulty consuming stiff, oversized, or spinescent leaves. They also have keratinised bills instead of sensitive lips and gums, so their first point of contact with food plants is more impervious to damage than mammalian mouthparts.

Second, reptiles can see across a broader spectrum of wavelengths than mammals. Most herbivorous mammals (e.g., ungulates) have just two light receptors in their eyes, which limits the wavelengths of light they can use to discriminate their food (Jacobs et al. 1998). On the other hand, reptiles possess four light receptors and are therefore able to detect a wider range of wavelengths (Bowmaker 1998). As a result, tortoises are more likely to rely on visual cues to locate palatable plants; therefore, selection could favour plants with traits that make them more difficult to detect visually.

Third, giant tortoises have a limited capacity to access leaves produced above the forest floor, given their heavy bodies and thick shells. So, leaves and shoots located higher up in plant canopies are free from danger. Plant defences against tortoises are therefore likely to be deployed preferentially by small-statured plants and during early ontogenetic stages in taller-statured plants.

Birds

With only a handful of exceptions (e.g., the hoatzin, *Opisthocomus hoazin*: Opisthocomidae), strongly herbivorous birds have given up the ability to fly for several reasons. Plants are generally less nutritious than animal prey, so herbivores need to consume larger quantities of foliage to survive. The weight of this foliage adds to the mass of birds during digestion, which negatively impacts their capacity to fly. Plant leaves and stems also require prolonged processing times, which can only be achieved in long digestive tracts, which are necessarily characteristic of large-bodied species. Weighed down by their herbivorous lifestyle, leaf-eating birds tend to be large bodied and, in most cases, have become flightless.

Several species of herbivorous ratites currently inhabit continents in the southern hemisphere, including the ostrich (*Struthio camelus*: Struthionidae) in Africa, rhea (*Rhea* spp.: Rheidae) in South America, and emu (*Dromaius novaehollandiae*: Casuariidae) in Australia. Their comparatively low diversity and restricted distribution makes them relatively unimportant herbivores on a global scale. However, prior to the wave of extinctions at the outset of the Anthropocene, giant birds were important herbivores on many oceanic islands. Most of these species colonised islands as small-bodied omnivores and subsequently evolved into giant, flightless browsers (e.g., Mitchell et al. 2014; Yonezawa et al. 2017). Lineages that have travelled down this evolutionary pathway towards herbivory include Galliformes (Sylviornithidae) in New Caledonia, water fowl (Anatidae) in Hawai'i and ratites (Palaeognathae) in Madagascar and New Zealand.

Despite their differences in appearance, giant tortoises and herbivorous birds actually forage in similar ways using analogous mouth parts. Both taxa lack teeth, so they cannot chew and they have keratinised bills instead of soft lips, so they are less susceptible to damage at the initial point of contact with food plants. With four visual receptors, they both see well and are likely to be more visually orientated foragers than mammals. Because they can no longer fly, they are also restricted to foraging from the ground, so foliage located higher up in plant canopies is out of reach.

Islands without Vertebrate Herbivores

Although many large, oceanic islands housed toothless herbivores, smaller islands often lacked vertebrate herbivores altogether, perhaps because small islands were insufficient in area to sustain viable populations (MacArthur & Wilson 1967). Plants on herbivore-free islands are released from selection by vertebrate herbivores altogether, regardless of which ocean they occur in, or from where they accumulated their respective floras.

DETERRENTS TO HERBIVORY

Chemistry

Plants utilise a variety of chemical compounds to deter herbivores and protect leaves (Agrawal & Weber 2015). One of the most common are tannins, which bind to digestive enzymes and dietary proteins, thus inhibiting their functioning (see Farmer 2014). Cyanogenic glycosides are another type of toxic secondary metabolite, which, when consumed by herbivores, is converted by enzymatic activity into hydrogen cyanide, an extremely potent poison (Vetter 2000). Alkaloids are a heterogeneous group of chemicals including caffeine, nicotine and strychnine that can have a variety of deleterious effects on animals (see Fester 2010; Walters 2011). Conifers often produce resins in response to attack, which can contain terpenes that are toxic to many types of herbivores (Krokene et al. 2010; Thimmappa et al. 2014).

A diverse range of plants also secrete latex when wounded, which can interfere with the foraging behaviour of herbivores, as well as contain toxic secondary chemicals (see Huber et al. 2015).

Spinescence

Another deterrent to vertebrate herbivory is sharp, ridged projections on or around vulnerable plant tissues. Spinescence can arise developmentally from several different plant tissues, each with its own terminology. Spines are modified leaves or stipules, thorns are modified twigs or branches, and prickles are derived from epidermal tissue. Regardless of their anatomical origin, prickles, thorns, and spines are functionally convergent traits that influence the behaviour of vertebrate herbivores (Cornelissen et al. 2003). Instead of deterring herbivory completely, spinescence tends to limit damage by large herbivores by reducing harvesting rates (Wilson & Kerley 2003a, 2003b; Cash & Fulbright 2005; Hanley et al. 2007; Shipley 2007).

Spinescence is often argued to be more effective in deterring mammalian browsers than avian browsers, which seems logical given that mammals have soft lips and gums that can be damaged more easily by sharp plant parts (Greenwood & Atkinson 1977; Bond & Silander 2007; Lee et al. 2010). However, some particular types of spinescence could be effective at deterring toothless browsers. Because birds and tortoises lack teeth and cannot chew, they cannot grind up food prior to ingestion. Therefore, leaves with sharp, rigid spines projecting from their margins may be difficult for toothless herbivores to swallow whole, and thereby constitute an effective deterrent to herbivory. Dense networks of thorns produced along the extremities of plant canopies (i.e., distally) could also protect leaves located within their inner recesses (i.e., proximally).

Branching Architecture

The way plants are branched might also deter herbivores. Most woody plants produce new branches at relatively shallow angles. As a result, their growth can be concentrated in particular directions, most often

upwards. However, *divaricate* plants produce branches at consistently wide angles, leading to less directional growth and a distinctive wiry appearance.

The evolutionary origins of divaricate branching are an enigma but it has evolved independently in many lineages. One explanation is that the growth form evolved to enhance physiological performance, or to help plants cope with past climatic conditions (see McGlone & Webb 1981; Howell et al. 2002). Alternatively, it could have also evolved as a deterrent to vertebrate browsers (Carlquist 1974; Greenwood & Atkinson 1977; Atkinson & Greenwood 1989; Bond & Silander 2007).

Divaricate branching may protect plants in several ways. First, the twigs of divaricate species are often strongly reinforced, increasing the effort required to remove leaves (i.e., high tensile strength, see Bond et al. 2004a). Second, branches that are attached at right angles stretch out over greater distances when pulled from their tips, further increasing the energy required by browsers to remove their leaves with a plucking motion. Third, right-angled branches, which give rise to a 'zig-zag' appearance, would make larger segments of stems difficult to swallow whole (Bond & Silander 2007). Lastly, branches at the extremities of divaricate plants often have lower leaf densities than branches towards their centre. Therefore, the outer branches themselves could impede access to a majority of leaves produced by divaricate plants (Atkinson & Greenwood 1989). In some species, these outer branches are very rigid and have sharpened tips, which might further prohibit access to leaves located in their inner recesses (i.e., 'porcupine plants', Burns 2016a, see also Charles-Dominique et al. 2017).

Leaf Heteroblasty

Defences are often deployed differentially throughout a plant's lifetime (Zotz et al. 2011). For example, many trees are better defended chemically at early stages of development, when they are still within reach of vertebrate herbivores (see Swihart & Bryant 2001). Similarly,

spinescent plants tend to produce prickles, thorns, and spines preferentially at early ontogenetic stages, and many divaricate plants lose their wiry appearance when they grow above a certain height (see Dawson 1988; Zotz et al. 2011; Burns 2013a).

Leaf morphology can also be heteroblastic. Divaricately branched trees always produce smaller leaves at earlier stages of ontogeny. Although juvenile microphyly could have a physiological explanation, it could also have been selected for by herbivores (Bond et al. 2004a). By reducing the energetic return to browsers that harvest leaves individually using a plucking motion, small juvenile leaf sizes might show rates of herbivory.

Leaves might also be coloured in ways that help protect them from attack (Lev-Yadun 2016). Some plants produce non-photosynthetic pigments in their leaves that radically alter their appearance and could make them more difficult for herbivores to locate. An object's conspicuousness results from a combination of its own reflectance properties and the reflectance properties of the background in which it lives. So, the more similar an object appears to its surroundings, the more difficult it is to locate. *Crypsis* refers to phenotypic similarity between a palatable object and unpalatable, inanimate objects, such as rocks or leaf litter (Kellner et al. 2011). *Mimicry* is a conceptually similar phenomenon. However, in this instance, evolution favours phenotypic similarity between a palatable object and a less-palatable, living organism (Barlow & Wiens 1977; Gianoli & Carrasco-Urra 2014; Scalon & Wright 2015; but see Blick et al. 2012). *Aposomatism* refers to the opposite phenomenon, when structural defences such as spinescence are conspicuously coloured to advertise their presence (Lev-Yadun 2016). If leaf colours evolved to thwart flightless vertebrate herbivores, we might expect colour-based defence to be heteroblastic in trees that grow above animal reach at maturity.

In addition to leaf size and colour, variability in the morphology of leaves can be more pronounced at early ontogenetic stages, perhaps for defensive purposes. Animals often forage by developing a 'search

image' for appropriate food resources (Tinbergen 1960; Punzalan et al. 2005). Pronounced variability in size, shape, colour, or symmetry of leaves could prohibit a herbivore's ability to form a search image for palatable prey and thereby form a viable defence (Brown & Lawton 1991; Lev-Yadun 2016). Although few studies to date have tested the search image disruption hypothesis in plants, Dell'Aglio et al. (2016) found that *Heliconius* butterflies use leaf shape as a cue for foraging and oviposition, driving negative frequency dependent selection on leaf shape in *Passiflora* vines. This could potentially also apply to ground-dwelling, vertebrate herbivores.

Plant Protection Mutualisms

An alternative strategy of plant defence is to develop mutualistic associations with animals that protect the plant from harm. For example, many plants (e.g., *Acacia* spp: Fabaceae) provide shelter in the form of hollow stems or thorns for stinging ants to inhabit. Ants that inhabit these structures then protect their homes from attackers. Other plants provide food for ants, in the form of glycogen-rich Müllerian bodies, or extra-floral nectaries that secrete sugary secretions. Plant protection mutualisms can be an extremely effective plant defence and may involve a variety of arthropods, including ants and mites (Beattie 1985; Rico-Gray & Oliveira 2007; O'Connell et al. 2010; Ward & Branstetter 2017).

SYNDROME PREDICTIONS

Immigrants to islands often come from larger landmasses where their ancestors were subject to vertebrate herbivores, mammalian or otherwise. If the newly colonised island is devoid of vertebrate herbivores, they may often possess defunct defensive adaptations. Assuming defensive adaptations are costly to produce, and if resources previously devoted to vertebrate defences can be diverted elsewhere (e.g., growth, reproduction), evolution will favour the loss of defence (Lahti et al. 2009). This prediction can be clearly illustrated by a Venn

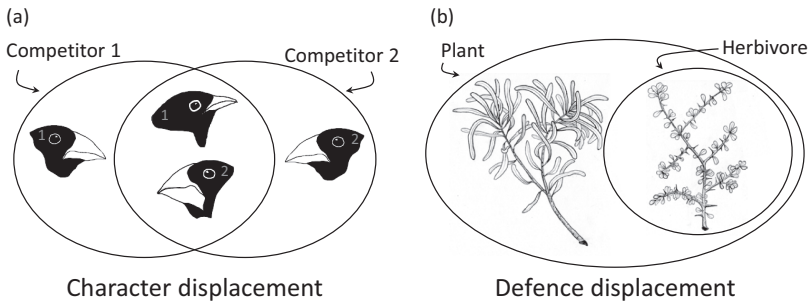


FIGURE 2.1 Venn diagrams illustrating character displacement and defence displacement. (a) Character displacement predicts that competing species diverge morphologically in sympatry to avoid competition for resources (see Schluter 2000; Chase & Leibold 2003). This is illustrated by two species of seed-eating finch (labelled 1 and 2), which have similar morphologies when they occur in allopatry, but in sympatry they evolve differences in bill morphology that promote differences in the use of food resources. Species 1 evolves a small bill to specialise on small seeds, while species 2 evolves a large bill to specialise on large seeds. (b) Defence displacement predicts that plant defences are deployed only in sympatry with herbivores. The large ellipse illustrates the total spatial distribution of a hypothetical plant species. The small ellipse illustrates the portion of its spatial distribution where it co-occurs with a hypothetical herbivore. The ellipse representing the herbivore sits entirely within the ellipse representing the plant, because the herbivore must co-occur with the plant in order to survive. Where the plant occurs sympatrically with the herbivore (e.g., close to the ground on continental landmasses), it evolves defensive adaptations for protection (e.g., thorns). However, in the absence of herbivore-mediated selection (either on isolated islands or when plants grow above the reach of mammalian herbivores on continents), plants are predicted to reinvest the energetic costs of defence elsewhere and become 'defenceless'. Illustration reprinted with permission from Burns (2013a)

diagram similar to those illustrating competitive displacement (i.e., *defence displacement*; Fig. 2.1).

Alternatively, defensive adaptations against toothless herbivores should evolve convergently on islands that housed giant tortoises or browsing birds. Assuming avian and reptilian herbivores forage analogously, three types of defensive adaptations might be more prevalent on 'toothless-browser islands'. First, spines along the

edges of leaves should be more common than large thorns produced on woody stems (i.e., *insular spinescence*). Second, traits associated with divaricate branching, including high tensile strength, right-angled branches that have large displacement distances when pulled, and branching patterns that create a cage-like outer structure, should be more prevalent. Third, traits associated with leaf heteroblasty (e.g., microphyllly, crypsis, mimicry, aposematism, and leaf-shape heterogeneity) should be produced preferentially at earlier ontogenetic stages.

Mutualisms only function when both players in the interaction co-occur in space and time. If a key partner is missing, the mutualistic relationship unravels because mutualistic services cannot be delivered. For example, in the absence of frugivores, the seeds in fleshy fruits will not be dispersed. In the case of plant protection mutualisms, the production of extra-floral nectaries, Müllerian bodies, or hollow stems will only be effective in deterring herbivory in the presence of stinging ants. Many isolated islands either have depauperate ant faunas or lack native ant mutualists. Under these circumstances, selection should favour the loss of mutualistic adaptations towards plant protectors and the dissolution of the plant protection mutualism.

HYPOTHESIS TESTING

Islands with Toothless Herbivores

Madagascar

Madagascar was attached to the ancient super-continent Gondwana 160 Ma. However, it began its geological journey towards insularity soon thereafter by rifting away into the Indian Ocean while still attached to India and the Seychelles (see Goodman & Jungers 2014). It became an island approximately 80 million years later and now lies 400 km east of Mozambique in the Indian Ocean.

The prehistoric herbivore fauna of Madagascar was truly exceptional. It housed two types of toothless browsers, both giant tortoises (*Aldabrachelys spp.*: *Testudinidae*) and 'elephant birds' (*Aepyornis* and *Mullerornis spp.*: *Aepyornithidae*). Unlike other islands that once

housed toothless browsers, Madagascar was also home to multiple types of large mammalian browsers. Subfossils from several species of hippopotamuses have been discovered (*Hippopotamus lemerlei*, *Choeropsis madagascariensis*: *Hipopotamidae*), in addition to approximately 17 species of giant lemurs (e.g., *Megaladapis* spp.: *Megaladapidae*, *Archaeoindris* spp.: *Palaeopropithecidae*), many of which had strongly herbivorous diets (Goodman & Jungers 2014).

Malagasy plants display a variety of traits that may have protected them against toothless browsers. Bond and Silander (2007) recorded more than 50 species from 36 genera and 25 families that exhibit divaricate-like branching patterns. While similar in many ways to divaricately branched plants from New Zealand, Malagasy divaricates tend to produce greater quantities of leaves at their extremities, rather than concentrating leaf production in their inner recesses, as they tend to do in New Zealand. Bond and Silander (2007) therefore referred to them as 'wire plants' rather than divaricates. Comparisons with related species in Africa showed that they have thinner twigs, smaller leaves, and wider branch angles. Their leaves also have higher tensile strength and greater lateral displacement when pulled.

Many Malagasy plants are spinescent, although the incidence of spinescence in Madagascar is lower than in comparable habitats in Africa (Grubb 2003). Spinescence in many plant taxa (e.g., *Diospyros aculeata*: Ebenaceae; *Euonymopsis humbertii*: Celastraceae; *Rinorea spinose*: Violaceae) occurs along leaf margins, which is consistent with the insular spinescence hypothesis. However, many other spinescent plants produce large, widely spaced thorns on branches (e.g., Didiereaceae, Crowley & Godfrey 2013). Furthermore, thorns are often produced well above the reach of tortoises and elephant birds, perhaps to deter arboreal lemur species that climb trees to feed on leaves in forest canopies.

Madagascar's unusually diverse vertebrate herbivore fauna complicates comparisons of plant defensive adaptations with other isolated islands. In particular, the presence of mammalian herbivores confounds tests for convergence in plant defensive adaptations against

toothless browsers. Given that nearly all of these herbivores are extinct, matching putative defensive adaptations to particular types of herbivores may now be impossible.

Mascarene Islands

Approximately 1,000 km off the east coast of Madagascar lies the first in a series of oceanic islands extending in an arch stretching in a north-easterly direction across the Indian Ocean. Reunion (2,512 km²) is the largest and closest island to Madagascar, followed by Mauritius approximately 175 km to the north-east (1,865 km²), and Rodrigues, a further 500 km east (104 km²). The Mascarene Islands were created by a 'hot spot' in the earth's crust, where magma escapes from the earth's mantle and then cools. As volcanic debris builds up, it breeches the ocean's surface to form islands, which in the case of the Mascarenes have moved slowly in a north-east direction on the African plate. Therefore, larger, younger islands are located farthest south-west, closest to the hot spot.

The three main Mascarene Islands have related floras that are derived from overseas dispersal, mainly from Madagascar and Africa. They also housed similar assemblages of vertebrate herbivores in their recent past (Cheke & Hume 2008). Giant tortoises occurred on all three main islands (*Cylindraspis* spp.). Dodos (*Raphus cucullatus*: Columbidae) occurred on Mauritius, and a related species, the Rodrigues solitaire (*Pezophaps solitaria*: Columbidae) occurred on Rodrigues Island. However, the extent to which they browsed on leaves is unclear, and their diets may have been dominated by fruits and bulbs, rather than leaves (Cheke & Hume 2008).

The incidence of leaf spinescence in the Mascarenes has yet to be quantified and compared with archipelagos. Similarly, the comparative incidence of divaricate branching has also yet to be established. However, leaf heteroblasty is common (Friedmann & Cadet 1976). Many species of woody plants that are endemic to the Mascarenes produce juvenile leaves that differ markedly in size, shape, and colour to their adult leaves.



FIGURE 2.2 Silhouettes of species displaying leaf heteroblasty in the Mascarene Islands (left column), New Caledonia (middle column), and New Zealand (right column). Juvenile leaves are shown on the left and adult leaves are shown on the right. Leaf heteroblastic species in all three archipelagos fall into distinct morphological categories: dissected (top row), microphyllous (middle row), and elongate (bottom row). (1) *Quivisia heterophylla*: Meliaceae, (2) *Securinega durissima*: Phyllanthaceae, (3) *Elaeodendron orientale*: Celastraceae, (4) *Codiaeum peltatum*: Euphorbiaceae, (5) *Atractocarpus rotundifolius*: Rubiaceae, (6) *Streblus pendulinus*: Moraceae, (7) *Elaeocarpus hookerianus*: Elaeocarpaceae, (8) *Hoheria sexstylosa*: Malvaceae, (9) *Elaeocarpus dentatus*: Elaeocarpaceae. The silhouettes are not drawn to scale.

The morphology of juvenile leaves fall into three distinct categories (Fig. 2.2). The juvenile leaves of some species are similar in shape to adult leaves, yet they are markedly smaller (i.e., ‘microphyllous’). Other species produce heavily lobed, compound or palmate leaves at early ontogenetic stages (i.e., ‘dissected’). However, the most

common ontogenetic shift in leaf morphology is characterised by juvenile leaves that are markedly longer and thinner than adult leaves (i.e., 'elongate'). Interestingly, long, thin juvenile leaves are often coloured differently than adult leaves. While adult leaves tend to be more uniformly green, elongate juvenile leaves often produce brightly coloured mid-veins.

Hansen et al. (2003) tested whether conspicuously coloured, juvenile leaves have higher concentrations of chemical defences. In a thorough screen of many heteroblastic species from the Mascarenes, they found no evidence that juvenile leaves were better defended chemically than adult leaves. Therefore, the bright colouration associated with many juvenile leaves could not be interpreted as an aposematic warning of elevated chemical defence. Nevertheless, giant tortoises tend to avoid consuming juvenile leaves in favour of adult leaves.

Eskildsen et al. (2004) offered adult and juvenile leaves of a number of heteroblastic species, as well as a number of co-occurring homoblastic species, to giant Aldabran tortoises (*Aldabrachelys gigantea*: Testudinidae). They found that tortoises consistently avoided juvenile leaves. Yet, why tortoises avoid juvenile leaves remains unclear. It could be that microphyllous leaves provide a lower energetic return to consumers. Highly dissected leaves could complicate the process of acquiring search images for palatable plant species. The conspicuously coloured mid-veins of elongate, juvenile leaves may signal greater tensile strength. However, these hypotheses have yet to be tested and additional study is needed to pinpoint the characteristics of juvenile leaves that tortoises find less palatable.

Socotra

Like Madagascar, Socotra sits on an ancient granite block that was once part of eastern Gondwana. However, it lies north of Madagascar, 100 km east of the Horn of Africa. It became isolated from the Arabian Peninsula much later, approximately 18 Ma (Van Damme & Banfield 2011; Culek 2013). It currently supports 800 species of plants, 37% of which are endemic (Van Damme 2009).

Fossil or subfossil evidence for large vertebrate herbivores has yet to be found on Socotra. However, there is a long history of human occupation and exploitation of the island, and an ancient text written approximately two millennia ago describes Socotra as the home of tortoises. The text mentions two tortoise taxa in particular, one that occurred at higher elevations and another that occurred in lowland areas (see Farmer 2014).

Large thorns (<2 cm long) are rare in the flora of Socotra, which is striking given its close proximity to mainland Africa, where large thorns are commonplace (Farmer 2014). However, many plant species on Socotra produce smaller-sized prickles, thorns, or spines. Notable examples occur in several genera in the Acanthaceae (*Barleria*, *Blepharis*, *Justicia*) and Lamiaceae (*Leucas*). Spinescent Socotran plants tend to be small in stature and often have a distinctive branching pattern whereby proximal leaves are protected by outward-pointing, spinescent stems (Fig. 2.3). Plants with similar morphological characteristics also occur in New Zealand and have been referred to as ‘porcupine plants’ (Burns 2016a). Quantitative comparisons between the incidence of different types of spinescence on Socotra and nearby



FIGURE 2.3 A spinescent shrub species from Socotra (*Neuracanthus aculeatus*: Acanthaceae) that produces dense networks of spines along the exterior of its canopy, which may have protected the leaves below from tortoise herbivory. (photo taken by Edward Farmer)

Africa have yet to be conducted, but are needed to test the insular spinescence hypothesis explicitly.

More distinctive spinescent structures are produced by other Socotran taxa. For example, *Tragia balfouriana*: Euphorbaceae produces poisonous, spinescent structures similar to the stinging nettle (*Urtica* spp.). Endemic species of *Hibiscus*: Malvaceae produce sharpened hairs that become dislodged from leaves when they are disturbed mechanically and rain down from the canopy on objects below (Farmer 2014). Heterophylly and heteroblasty are also commonplace. Most notably, frankincense (*Boswellia elongatata*: Burseraceae) produces long, narrow lanceolate leaves as juveniles, and then much larger, pinnately compound leaves as adults. This shift in morphology between juveniles and adults is similar to the elongate juvenile leaves produced by many heteroblastic species in the Mascarenes, as well as New Zealand and New Caledonia (Fig. 2.2). However, the overall incidence of leaf heteroblasty in the Socotra flora is unclear, and whether the size and shape of juvenile leaves conform to the three types of morphological transitions present on other toothless-browser islands is unknown.

Hawai'i

The world's most isolated oceanic archipelago is located 3,500 km from the west coast of North America in the eastern Pacific Ocean. The Hawai'ian Islands are a hot spot archipelago similar to the Mascarene Islands. They consist of four main islands and numerous smaller islands that stretch in a north-westerly direction away from the hotspot (18° 55' 12.00" N, -155° 16' 12.00" W). Younger islands are larger and located closer to the hot spot than older islands (Hawai'i: 0.4 Ma, 10,433 km²; Maui: 0.8–1.3 Ma, 1,883 km²; O'ahu: 2.6–3.75 Ma, 1,545 km²; Kauai: ~ 5.1 Ma, 1,431 km²; Walker 1990; Neal & Trewick 2008).

No evidence for giant tortoises has ever been unearthed from Hawai'ian sediments. Instead, subfossils of two evolutionary lineages of avian herbivores have been found. Unfortunately, all but one failed

to escape extinction following human arrival approximately 1,600 years ago. The first lineage is known as 'moa-nalo' and evolved from dabbling ducks (*Anatidae*). Several species of moa-nalo are currently recognised, and their subfossil remains have been found on all of the major islands except for Hawai'i (Slikas 2003). Moa-nalo were strongly herbivorous and may have specialised on ferns (James & Burney 1997).

The second lineage of avian herbivores was superficially similar to the moa-nalo, but evolved from geese rather than ducks. The largest species, the giant Hawai'i goose (*Branta rhuax*: *Anatidae*), was restricted to the youngest island (Hawai'i) and weighed approximately 8 kg. The nēnē-nui (*Branta hylobadistes*) was a slightly smaller species that inhabited many of the older islands in the archipelago (Paxinos et al. 2002). A third species, the nēnē (*Branta sandvicensis*) is the only endemic *Branta* species to escape extinction. Although capable of flight, the nēnē spends most of its time foraging on the ground, and, until recently, it occurred on all of Hawai'i's major islands.

Spinescence has long been argued to be uncommon in the Hawai'ian islands (Carlquist 1980). However, there are several notable exceptions. The Hawai'ian nightshade or popolo (*Solanum incompletum*: *Solanaceae*) is a distinctive-looking, endemic plant that produces remarkably large, conspicuous spines on both the upper and lower surfaces of its leaves, which appear bright red to human eyes.

Cyanea (*Campanulaceae*), the largest genus in the Hawai'ian Islands, contains many spinescent species. Of the 55 taxa considered by Givnish et al. (1994), 15 produce thorn-like prickles, a trait that evolved autochthonously on at least four occasions. Prickles are strongly heteroblastic in many of these species and are produced preferentially when plants are small, during early ontogenetic stages. Heteroblasty in spinescence is also frequently associated with heteroblastic shifts in leaf shape. Many spinescent species produce deeply lobed leaves at earlier ontogenetic stages, which is similar to the 'dissected' class of juvenile leaves in the Mascarenes.



FIGURE 2.4 Prickles produced by *Rubus hawaiiensis* (Rosaceae). Photo taken by Philip Thomas

Carlquist (1980) used the Hawai'ian raspberry, or akala (*Rubus hawaiiensis*: Rosaceae), as an example of the loss of herbivore defence on islands, as adult plants tend to lack structural defences, unlike its closest mainland ancestor, *Rubus spectabilis* (Morden et al. 2003). However, upon closer inspection, younger plants can be strongly spinescent (Fig. 2.4), which may have helped protect them against herbivory by giant ducks and geese. Some species in the genus *Rubus* use recurved prickles as aides for climbing other plants for structural support (e.g., *Rubus australis*), so spinescence in *R. hawaiiensis* may have a functional significance that is unrelated to herbivory. However, Randell et al. (2004) showed that the prickles produced by *R. hawaiiensis* are straight rather than recurved.

The Hawai'ian prickly poppy (*Argemone glauca*: Papaveraceae) is another notable spinescent plant species in Hawai'i. It produces prickles on leaves, stems, and fruits, in addition to latex when wounded. Barton (2014) showed that prickles were produced in similar densities throughout ontogeny. However, Hoan et al. (2014) showed

that increased prickly densities could be induced by mechanical damage and that on younger plants the magnitude of prickly induction was higher.

Galapagos

The Galapagos is another 'hot spot' archipelago that has been volcanically active for over 20 Ma. Located 900 km off the Pacific coast of South America, islands in the Galapagos do not align in an arch like the Hawai'ian Islands or the Mascarenes. Instead, the 20 or so islands that make up the archipelago are distributed more contiguously.

Although devoid of large browsing birds, many islands in the Galapagos supported giant tortoises (*Chelonoidis* spp.), while others appear to have never housed tortoise herbivores. As a result, convergence in plant defence in the presence of toothless browsers, and the loss of defence on islands without vertebrate herbivores (i.e., defence displacement) can be tested among islands within the archipelago. This unique set of circumstances makes the Galapagos an especially interesting place to investigate repeated patterns in the evolution of plant defence. However, quantitative investigations of structural defences against vertebrate herbivores have yet to be conducted (*c.f.* Adersen & Adersen 1993).

There is a long history of speculation that the morphology of 'prickly-pear' *Opuntia* cacti varies among islands according to the distribution of herbivores (Nicholls 2014). There are six species of *Opuntia* in the Galapagos, all of which are a preferred food of giant tortoises. Stewart (1911) speculated that the morphology of *Opuntia* cacti covaried with the distribution of giant tortoises. On islands that supported tortoises in the recent past, juvenile *Opuntia* cacti tend to produce long spines that are rigid and sharp. However, once they grow above the reach of giant tortoises, their pad-like stems apparently produce soft, bristle-like spines. A very different pattern emerges on islands that failed to receive tortoise colonists. On herbivore-free islands, *Opuntia* species seem to be smaller statured or prostrate, and markedly less spinescent overall (Dawson 1966).

New Zealand

New Zealand is a continental archipelago comprised of two main islands and hundreds of smaller islands located approximately 1,500 km east of Australia. Like Madagascar and Socotra, it was previously connected to the supercontinent Gondwana. However, it began to rift away from Australia c. 83 Ma, becoming completely independent in its current latitudinal position c. 40 Ma. Although some components of New Zealand's flora and fauna may have been present at the time it split from Gondwana, much of New Zealand's flora is derived via overwater dispersal, mostly from Australia (see Gibbs 2006).

New Zealand was a land dominated by birds prior to the arrival of humans (Lee et al. 2010). In addition to flightless rails (e.g. takahe, *Porphyrio* spp.) and herbivorous geese (*Cnemidornis* spp.), New Zealand was home to an unparalleled diversity of giant, flightless ratites with strongly herbivorous diets. Eight species of 'moa' are currently recognised (Dinornithiformes), all of which went extinct soon after human arrival approximately 750 years ago (McCulloch & Cox 1992; Tennyson & Martinson 2006). Measured in generations of woody plants, this change in the ecology of New Zealand has occurred very recently, too recently for evolution to favour the loss of defensive adaptations geared specifically towards toothless browsers.

Chemical defences in the New Zealand flora are poorly understood. Pollock et al. (2007) conducted cafeteria-style experiments using ostriches (*S. camelus*) as a surrogate for extinct avian herbivores. They found that ostriches tend to avoid plants with high levels of phenolics. However, the effects of plant chemistry on consumption rates were overshadowed by the effects of leaf size and branching architecture.

Divaricate branching is an outstanding feature of the New Zealand flora. Although plants with this distinctive growth form occur elsewhere on the planet, it appears to be unusually common in New Zealand. Nearly 10% of all woody plant species native to New Zealand are divaricately branched and the growth form has evolved independently in 17 plant families, including both angiosperms and

gymnosperms (Greenwood & Atkinson 1977; Dawson 1988). Although the incidence of divaricate branching seems unusually high in New Zealand, quantitative biogeographic comparisons of the incidence of divaricate branching have never been conducted.

A mechanistic explanation for the seemingly high incidence of divaricate branching in New Zealand is highly contentious. Divaricate branching could enhance physiological performance in specific environmental conditions, some of which may have been more prevalent in the recent past. For example, it could promote foliar frost tolerance, light capture, or prohibit photo-inhibition (e.g., Day 1998; Howell et al. 2002; Christian et al. 2006). However, empirical evidence for a link between divaricate branching and plant physiological performance is equivocal (Gamage & Jesson 2007).

There is a long history of speculation that divaricate branching evolved as a defence against avian browsers (Carlquist 1974; Greenwood & Atkinson 1977). Unfortunately, direct tests of this hypothesis are no longer possible because the putative selection agents are now extinct. However, Bond et al. (2004a) demonstrate that the shoots of several divaricately branched plant species are attached to stems more strongly than their non-divaricately branched relatives. They suggest that the increased tensile strength of stems, coupled with their low energetic yield given the small size and sparse spacing of leaves, would make it difficult for a toothless browser to make a living foraging on divaricate plants.

In food choice experiments using surrogate ratite browsers (emus, *D. novaehollandiae*), Bond et al. (2004a) found that divaricate plants tend to be avoided in favour of non-divaricate plants (see also Pollock et al. 2007). This provides strong, albeit indirect, support for the moa hypothesis. Although moa and emu could have foraged similarly, the avian browsers that inhabited New Zealand display a wide diversity of cranial and bill morphology and likely foraged in different ways (Attard et al. 2016). As a result, we will never know the extent to which emu are an accurate surrogate for moa in food choice experiments.

Divaricately branched tree species tend to be strongly heteroblastic. Younger plants are divaricately branched and as they mature they abruptly begin to produce larger leaves, shorter internodes, and shallower branch angles. Transition heights between divaricately branched juveniles and adults typically occur approximately 3 m above the ground, which broadly corresponds to the height of the tallest known moa species (see Greenwood & Atkinson 1977; Atkinson & Greenwood 1989), and is therefore consistent with the defence displacement hypothesis. However, in this instance, plants are separated from herbivores vertically, rather than biogeographically.

In contrast to divaricate branching, spinescence is not a prominent feature of the New Zealand flora (Box 2.1). Only 12 native taxa produce prickles, thorns, or spines (Fig. 2.5). However, in eight of these species, spinescence is associated with leaves, which is proportionally higher than its incidence in Africa (Milton 1991).

Many spinescent plant species around the globe deploy prickles, thorns, and spines plastically. After being damaged mechanically, plants often increase the production of spinescent structures (Obeso 1997; Gómez and Zamora 2002; Gödel et al. 2016). This allows plants to deploy prickles, thorns, and spines strategically, at times and places where they may be more likely to be attacked by herbivores. Leaf spinescence in some New Zealand plants, which were subject to toothless rather than mammalian browsers, can also be induced by mechanical damage (Box 2.2).

Leaf heteroblasty is a notable feature of the New Zealand flora. A large number of woody plant species from diverse phylogenetic backgrounds produce differently shaped leaves through ontogeny. Some produce microphyllous juvenile leaves, often in conjunction with divaricate branching (e.g., *Carpodetus serratus*: Rousaceae; *Pennantia corymbosa*: Pennantiaceae; *Sophora microphylla*: Fabaceae). Others produce long, thin juvenile leaves (e.g., *Elaeocarpus dentatus*: Elaeocarpaceae; *Knightia excelsa*: Proteaceae), or highly dissected and/or deeply lobed juvenile leaves (*Raukaua simplex*: Araliaceae). Categories of leaf shape at the juvenile phase in New Zealand

BOX 2.1 Insular spinescence

There are 12 currently recognised spinescent plant taxa in New Zealand (Table B2.1, see also Burns 2016a). Some taxa, such as *Pseudopanax* spp.: Araliaceae, likely evolved to become spinescent autochthonously. However, other taxa (e.g., *Discaria toumatou*: Rhamnaceae; *Eryngium vesiculosum*: Apiaceae; *Rubus* spp.: Rosaceae; *Urtica* spp.: Urticaceae) also occur in Australia, and therefore could have evolved spinescent structures prior to their arrival in New Zealand.

Spinescence can arise developmentally from several types of plant tissues, including leaves (spines), stems (thorns), and epidermal tissue (prickles). Two-thirds of spinescent plant taxa in New Zealand produce leaf spines. Given that birds lack teeth and cannot chew, leaf spines may be particularly effective at deterring bird browsers, more so than thorns or prickles located on branches.

Is the incidence of leaf spines unusually common in New Zealand? Two-thirds of spinescent plant lineages in New Zealand deploy

Table B2.1 *Native species of spinescent plants in New Zealand and type of spinescence*

Species	Type of spinescence
* <i>Aciphylla</i> spp.	Leaf spines
<i>Aristotelia fruticosa</i>	Thorns
<i>Carmichaelia odorata</i>	Thorns
<i>Discaria toumatou</i>	Thorns
<i>Eryngium vesiculosum</i>	Leaf spines
<i>Leptecophylla juniperina</i>	Leaf spines
<i>Meliccytus alpinus</i>	Thorns
<i>Olearia ilicifolia</i>	Leaf spines
* <i>Podocarpus</i> spp.	Leaf spines
* <i>Pseudopanax</i> spp.	Leaf spines
* <i>Rubus</i> spp.	Prickles on leaves & stems
* <i>Urtica</i> spp.	Poisonous spines on leaves & stems

* Genera containing multiple spinescent species

BOX 2.1 (cont.)

spinescence in close association with leaf tissues (Table B2.1). Milton (1991) provides comparable figures for spinescent plants in Southern Africa, where leaf spines were produced by approximately 23% of spinescent taxa, across a range of habitats, including forests, deserts, and grasslands. A binomial test for differences in the proportion of species producing leaf spines between regions indicates that leaf spinescence is unusually common in New Zealand ($p = 0.002$).



FIGURE 2.5 *Olearia ilicifolia*: Asteraceae, a spinescent plant species endemic to New Zealand.

plants are generally consistent with those found on the Mascarene Islands (microphyllous, elongate, dissected, Fig. 2.2).

Elaeocarpus hookerianus: Elaeocarpaceae provides a particularly striking example of leaf heteroblasty. Juvenile plants produce leaves with a remarkable range of shapes, from elliptical to linear with irregular and asymmetric lobbing (Fadzly & Burns 2010, see also Day & Gould 1997; Day et al. 1997). Another striking feature of *E. hookerianus* is that its juvenile leaves have high concentrations of

BOX 2.2 Induced spinescence

Induced defence is common in spinescent plants that are exposed to mammalian herbivory (Barton 2016; Coverdale et al. 2018). When damaged by herbivores, spinescent plants inhabiting continents often increase investment into prickles, thorns, and spines. To test whether plant species that are endemic to islands with toothless herbivore islands might also display induced defences, the size of lateral leaf spines was compared between damaged and undamaged saplings of a spinescent plant species from New Zealand.

Pseudopanax crassifoliosus: Araliaceae is a common tree species in New Zealand. It commonly grows alongside hiking trails, which are periodically cleared of overhanging vegetation. This sometimes removes the apical meristems of *P. crassifoliosus* saplings, many of which survive to produce new leaves.

To test for the induction of leaf spines following damage, I measured the length (mm) of the largest leaf spine on the youngest mature leaf of 25 damaged plants growing alongside trails traversing Nelson Lakes National Park, New Zealand (41°48' S, 172°50' E). Spine size in the youngest mature leaf on the closest undamaged plant located nearby was also measured ($n = 25$).

The size of lateral leaf spines covaries with several aspects of leaf morphology. Lateral leaf spines increase in size with both leaf area and the stature of juvenile plants. To control for these potentially confounding effects, leaf width (mm) and plant height (cm) were also measured.

A general linear model was then used to test for differences in spine size between damaged and undamaged plants. Relative spine size (spine length \cdot leaf width⁻¹) was used as the dependent variable. Damage was considered a fixed factor with two levels (i.e. damaged vs undamaged) and plant height was used as a covariate. Relative spine size was log transformed to conform to assumptions prior to analyses.

Results showed that spine size increased with plant height ($F = 4.277$, $p = 0.044$), at similar rates (i.e., similar slopes) for both damaged and undamaged plants ($F = 0.736$, $p = 0.396$). However, damaged plants had a higher intercept than undamaged plants ($F = 22.973$, $p < 0.001$),

BOX 2.2 (cont.)

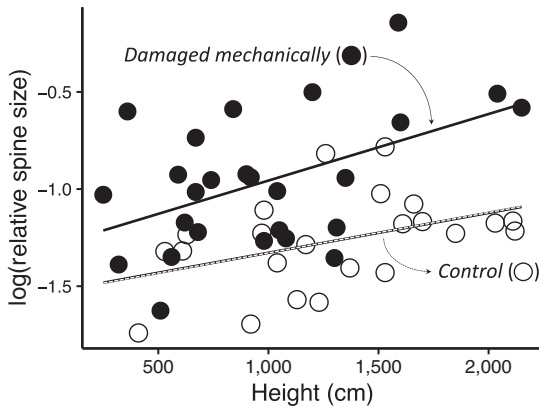


FIGURE B2.2 Induced defences in lancewood (*Pseudopanax crassifolius*: Araliaceae). Relative spine size (spine length \cdot leaf width⁻¹, y-axis, log transformed) is plotted against plant height (x-axis) in damaged (black circles, solid line) and undamaged (white circles, dashed line) plants.

indicating that damaged plants induced larger leaf spines following damage (Fig. B2.2). All analyses were performed in the R environment (R Core Team 2013).

accessory pigments (e.g., anthocyanins) leading to leaf hues ranging from green to mottled brown or even black to the human eye. When quantified from the perspective of birds, spectrographic analysis indicates that juvenile leaves would have been difficult to distinguish visually against a background of leaf litter (Fadzley & Burns 2010). On the other hand, adult leaves are regularly oblong, appear green to human observers, and stand out clearly against litter.

New Caledonia

Several thousand kilometres north of New Zealand lies an isolated island with a similar geologic history. New Caledonia separated from Australia 65 Ma, moving in a north-easterly direction into the tropical

Pacific. It has an exceedingly diverse flora that was subject to several types of large herbivores prehistorically. In addition to herbivorous tortoises (Hawkins et al. 2016), New Caledonia was also home to at least one species of giant, flightless, browsing bird (*Sylviornis neocaledoniae*: Sylviornithidae; Worthy et al. 2016).

Very little is known about how New Caledonian plants may have defended themselves against toothless herbivores. However, leaf heteroblasty is commonplace (Burns & Dawson 2006). A diverse range of species abruptly change leaf morphology during development. The juvenile leaves can also be placed in the three morphological categories present in both New Zealand and in the Mascarene Islands, i.e., dissected, elongate, and microphyllous (Fig. 2.2). Leaf heteroblasty therefore appears to be a convergent phenomenon on several toothless browser islands distributed across the globe. However, a formal quantitative investigation for congruence in leaf heteroblasty among the Mascarenes, New Caledonia, and New Zealand and other toothless browser islands have yet to be conducted.

Islands without Vertebrate Herbivores

Chatham Islands

Approximately 4 Ma, the Chatham Islands uplifted above the Pacific Ocean, 650 km east of New Zealand. The present-day archipelago, which is comprised of one large island (Chatham Island) and several smaller islets, has never been connected to a larger landmass and its flora is derived entirely by over-water dispersal from nearby landmasses, mostly from New Zealand. No evidence has ever been found for the existence of flightless vertebrate herbivores on the Chatham Islands prehistorically. The defence displacement hypothesis therefore makes clear predictions for the Chatham Islands. Selection should favour the loss of defensive adaptations against avian herbivores in species that evolved from ancestors in New Zealand, where they were exposed to avian herbivores.

Greenwood and Atkinson (1977) compared the number of divaricately branched species inhabiting coastal regions of New

Zealand to that found on the Chatham Islands. They found that divaricate plants were less prevalent on the Chatham Islands, as well as several other oceanic islands that flank New Zealand, suggesting a repeated pattern in the loss of divaricate branching in the absence of avian herbivores. However, an alternative explanation could be that the number of divaricate species on herbivore-free islands results from selective immigration, if divaricate plants are relatively poor over-water dispersers.

To explore Greenwood and Atkinson's (1977) conclusions further, Kavanagh (2015) compared leaf size and branching architecture in Chatham Island plant species to their closest relatives in New Zealand. He found that Chatham Island plants consistently produced larger leaves, shorter internodes, and narrower branch angles than their ancestors in New Zealand. Consequently, in the absence of selection from toothless browsers, Chatham Island plants appear to have evolved the loss of divaricate branching (Fig. 2.6; Box 2.3).

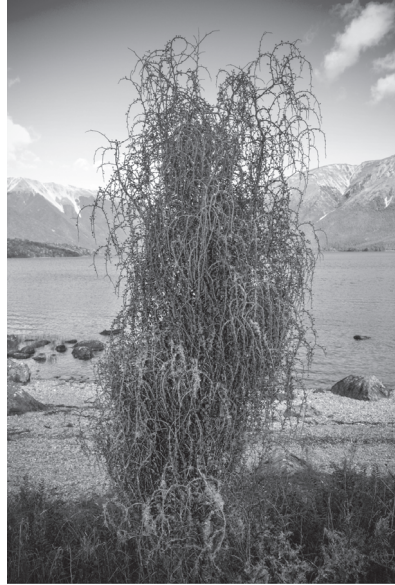
Spinescence is rare among plants on the Chatham Islands. However, several endemic species evolved from spinescent ancestors in New Zealand. For example, two species of speargrass (*Aciphylla dieffenbachia* and *A. traversii*: Apiaceae) occur on the Chatham Islands, both of which are derived from spinescent ancestors in New Zealand. Burns (2016a) compared leaf compression strength and the size of terminal leaf spines between Chatham Island and New Zealand taxa and found that *A. dieffenbachia* produces less-rigid leaves with smaller terminal spines. Box 2.4 illustrates similar results for sister species of *Leptecophylla*: Ericaceae.

While leaf shape heteroblasty is common in New Zealand, it is rare on the Chatham Islands (Burns & Dawson 2009). Two tree species that are endemic to the Chatham Islands produce heteroblastic leaves (*Dracophyllum arboretum*: Ericaceae; *Coprosma chathamica*: Rubiaceae). However, differences between the morphology of juvenile and adult leaves in both of these species differ markedly from the categories of morphological change found in the Mascarene Islands, New Caledonia, and New Zealand (Burns & Dawson 2009). All three

(a)



(b)



(c)



(d)

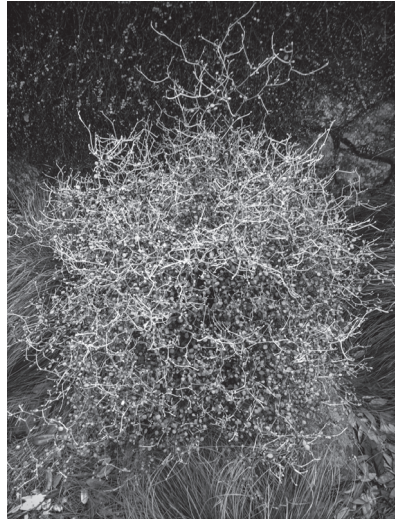


FIGURE 2.6 Photographs of three shrub species endemic to the Chatham Islands, which lacked vertebrate herbivores prehistorically: (a) *Myrsine chathamica*: Primulaceae; (c) *Corokia macrocarpa*: Argophyllaceae; (e) *Melicytus chathamica*: Violaceae

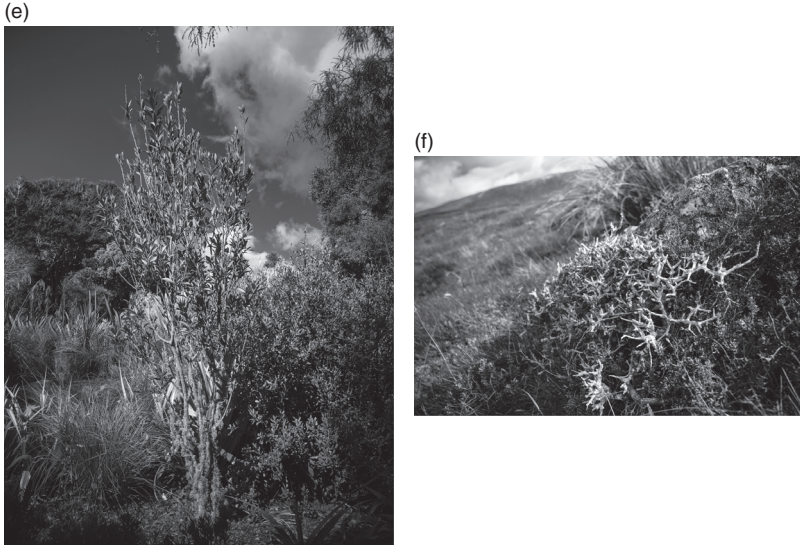


FIGURE 2.6 (cont.) Alongside are their closest ancestors in New Zealand, where they were subject to avian herbivory throughout their evolutionary history: (b) *Myrsine divaricata*; (d) *Corokia cotoneaster*; (f) *Melicytus alpinus*. All three Chatham Island endemics illustrate an evolutionary loss of divaricate branching (Kavanagh 2015), including a decline in leaf tensile strength (Box 2.3).

Chatham Island species produce juvenile leaves that are similarly shaped, but much larger than adults. Therefore, in addition to the loss of divaricate branching, spinescence, and leaf colouration, selection also appears to have favoured the loss of leaf heteroblasty on the Chatham Islands, or at least the type of heteroblasty found on other isolated islands.

Iceland

Three hundred kilometres east of Greenland lies a large, volcanic island that was devoid of large vertebrate herbivores prior to the arrival of humans (Darlington 1957; Bryant et al. 1989). Plant communities growing at similar latitudes in Asia, Europe, and North America are subject to a wide assortment of vertebrate herbivores, including

BOX 2.3 Loss of tensile strength in divaricate shrubs

The tensile strength of leaves produced by divaricate plants in New Zealand tends to be higher than their non-divaricate relatives (Bond et al. 2004a). This suggests that avian herbivores that forage for leaves individually using a plucking motion would have to pull harder to remove leaves of divaricate species. If this hypothesis is correct, then increased leaf tensile strength should be lost in populations on islands that lacked avian herbivores.

The Chatham Islands are a geologically young archipelago that acquired its flora entirely by over-water dispersal, mostly from New Zealand. To test for the loss of leaf tensile strength in divaricate plants in the absence of avian herbivory, the force required to remove the leaves of three divaricately branched species in New Zealand were compared to their sister species on the Chatham Islands, which lacked avian herbivores. Heenan et al. (2010) illustrated that the closest ancestor of three Chatham Island species, *Corokia macrocarpa*: Argophyllaceae, *Melicytus chathamicus*: Violaceae, and *Myrsine chathamica*: Primulaceae are the divaricately branched New Zealand endemics *Corokia cotoneaster*, *Melicytus alpinus*, and *Myrsine divaricata*, respectively. To compare their tensile strength, a single leaf from 17–30 plants of each species was measured using a force metre. Leaf size (leaf length·leaf width) was also measured as a coarse estimate of the energetic return to potential consumers. Measurements were made in Nelson Lakes National Park, New Zealand, and several forest reserves on Chatham Island (see Cox & Burns 2017 for site descriptions). Leaf tensile strength (Newtons, N) was then divided by leaf area (cm²) and compared between species pairs using separate linear models.

Results showed that relative leaf tensile strength tended to be higher in New Zealand (Fig. B2.3). Ratios between tensile strength and leaf area differed in all three comparisons (*C. cotoneaster* [n = 20] vs *C. macrocarpa* [n = 30], $t = 2.148$, $p = 0.037$; *M. alpinus* [n = 17] vs *M. chathamicus* [n = 30], $t = 10.895$, $p < 0.001$; *M. divaricata* [n = 30] vs *M. chathamica* [n = 30], $t = 4.813$, $p < 0.001$). Therefore, relative to their size, the leaves of New Zealand species were more difficult to remove

BOX 2.3 (cont.)

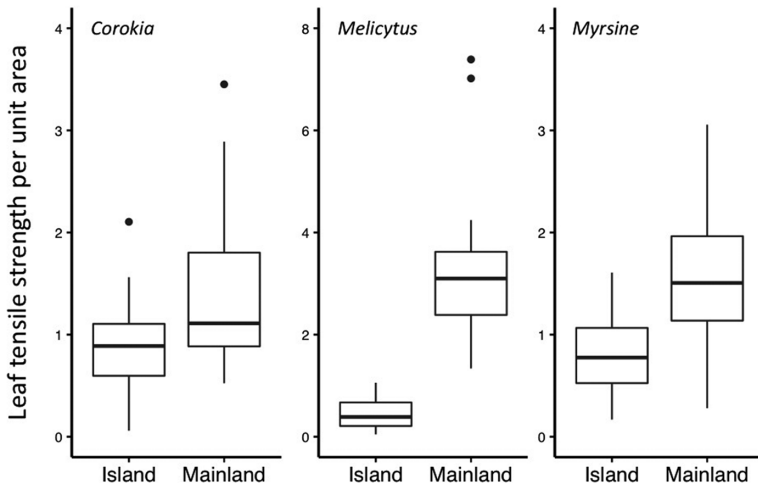


FIGURE B2.3 Relative foraging costs in three shrub species endemic to the Chatham Islands (labelled 'Island' on the x-axis), which evolved from divaricate ancestors in New Zealand (labelled 'Mainland' on the y-axis). The ratio between the force required to remove a leaf from its stem (N) and its area (cm^2) is shown on the y-axes. Relative foraging costs were statistically higher in New Zealand for all three taxonomic pairings.

than Chatham Island species. This suggests that selection has favoured higher foraging costs in New Zealand, where plants were exposed to avian herbivores (i.e., defence displacement). The data were courtesy of Bart Te Manihera Cox.

deer and caribou (Cervidae). Prehistorically, the diversity of large herbivores in these regions was even higher (Martin & Klein 1989).

Chemical defences are common in high latitude forests and scrublands, with smaller, younger plants typically being better defended than larger, older plants (Swihart & Bryant 2001). Bryant et al. (1989) compared chemical defences between Icelandic birch

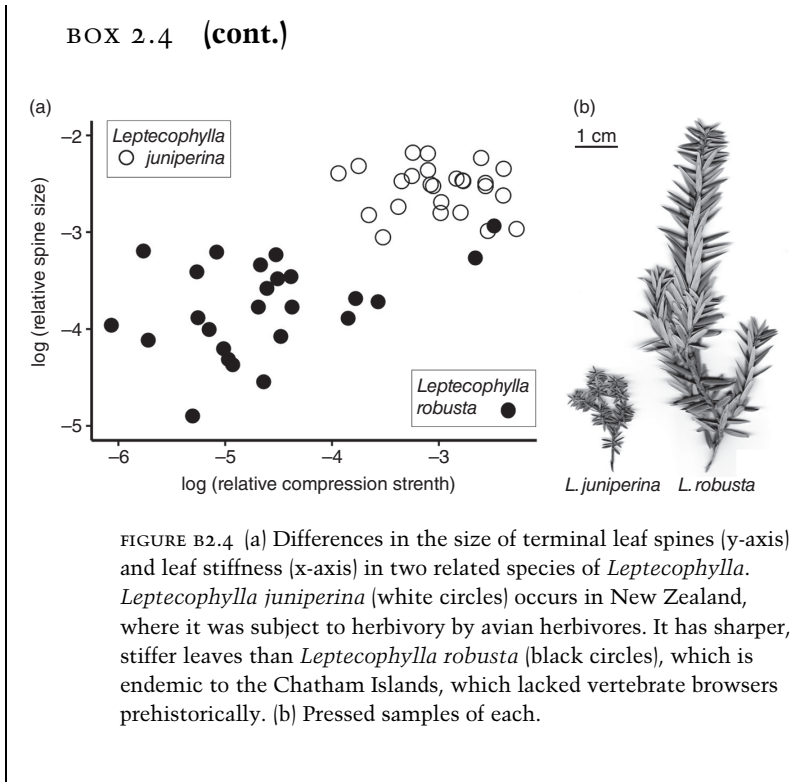
BOX 2.4 Loss of spinescence in *Leptecophylla*

Leptecophylla juniperina: Ericaceae is a widespread shrub species in New Zealand that produces small, needle-like leaves, which could have been difficult for avian browsers to swallow whole.

Leptecophylla robusta, is a closely related species that is endemic to the Chatham Islands, which lacked large, avian herbivores. Molecular evidence indicates that *L. robusta* recently diverged from *L. juniperina* after dispersing to the Chatham Islands (Heenan et al. 2010).

To test whether *L. robusta* has evolved to become less spinescent than *L. juniperina* in the absence of avian herbivory in the Chatham Islands, leaf rigidity (i.e., compression strength) and the size of terminal leaf spines were compared between taxa. Measurements were made on a single leaf from 25 individuals of *L. robusta*, in several forest reserves on the Chatham Islands (see Cox & Burns 2017 for site descriptions) as well as 25 individuals of *L. juniperina* from Nelson Lake National Park, South Island, New Zealand. Leaf compression strength was measured in Newtons (N) as the amount of force required to buckle leaves when compressed longitudinally. The length of the terminal leaf spine was measured to the nearest 0.01 mm using a dissecting microscope. Both leaf compression strength and the size of terminal leaf spines covary passively with leaf size, so both variables were scaled by leaf area (leaf length·leaf width) prior to analyses. To test whether *L. juniperina* produces sharper, more-rigid leaves than *L. robusta*, separate linear models were conducted on each variable. Both variables were log transformed prior to analyses to conform to assumptions.

Results showed that spinescence was higher in New Zealand (Fig. B2.4). *L. juniperina* had longer terminal spines ($t = 8.423$, $p < 0.001$) and stiffer leaves ($t = 11.320$, $p < 0.001$) than *L. robusta*. Selection therefore seems to have favoured the evolution of softer leaves with smaller terminal spines in the absence of vertebrate herbivores (i.e., defence displacement). The data were courtesy of Bart Te Manihera Cox.



(*Betula pubescens*: Betulaceae) and a handful of related birch species from Finland, Siberia, and Alaska and found that young plants from Iceland had lower concentrations of internode resins and triterpenes than similar-statured plants sourced on continents. In a series of food choice experiments, they also offered island and mainland birch plants to snowshoe hares (*Lepus americanus*: Leporidae), a common arctic herbivore in Europe, Asia, and North America. Results showed that hares consistently preferred less-defended birch seedlings. Results from Bryant et al.'s (1989) thorough study therefore provide compelling evidence that selection has shaped the chemical signatures of island plants and they are now more susceptible to vertebrate herbivory.

Haida Gwaii

Previously known as the Queen Charlotte Islands, the Haida Gwaii archipelago is located in the Pacific Ocean off the north-west coast of North America. They sit at a similar latitude to Iceland, but have a very different geologic history. Haida Gwaii was connected to what is now northern Canada during the last glacial–interglacial period. However, it failed to acquire a diverse vertebrate fauna. A single subspecies of caribou (*Rangifer tarandus dawsoni*: Cervidae) managed to colonise the islands naturally. However, it was a relatively unimportant herbivore, as it was restricted to the largest island in the archipelago, Graham Island. Other islands in the archipelago have experienced between 15,000 and 30,000 years of isolation from vertebrate herbivores.

The region supports conifer forest dominated by a handful of tree species. Vourc'h et al. (2001) compared the chemical signatures of western red cedar (*Thuja plicata*: Cupressaceae) from Haida Gwaii to those on the mainland. They found that island plants had lower concentrations of terpenes and were therefore more poorly defended than mainland plants. When subjected to browsing by black-tailed deer (*Odocoileus hemionus sitkensis*: Cervidae), island plants were attacked more frequently, similar to Icelandic birch.

Lord Howe Island

Lord Howe Island is a small volcanic island located 600 km east of Australia. It has never been connected to a larger landmass and was devoid of vertebrate herbivores prior to human arrival. However, the bones of a distinctive, horned tortoise (*Meiolania platyceps*: Meiolaniidae) have been found in sediments dating to the Pleistocene (Gaffney 1996). The island was uninhabited prehistorically, so, unlike other island megafauna, it did not meet its demise at the hands of human hunters or their mammalian castaways. Instead, it went extinct thousands of years ago for unknown reasons and the island's flora has evolved in the absence of vertebrate herbivores ever since. Morphologically, the tortoise had a strongly domed shell and likely could not reach any more than 0.5 m

above the ground (Gaffney 1996). Therefore, selection for plant traits aimed at deterring toothless herbivores would have been restricted to low-growing plants in the forest understory.

There are three spinescent plant taxa on Lord Howe Island, all of which are only slightly differentiated taxonomically from populations in Australia. *Smilax australis*: Smilacaceae is a liana that produces rigid prickles along its stems. *Alyxia ruscifolia*: Apocynaceae is a shrub that produces spade-shaped leaves that end in a sharp terminal spine, and *Drypetes deplanchei*: Putranjivaceae is a rainforest tree, whose seedlings produce holly-shaped leaves with sharp spines along their margins.

Burns (2013a; 2016b) compared the production of spinescent structures between island and mainland populations in all three taxa. In mainland populations of *S. australis*, smaller, younger stems had greater prickle densities than larger, older stems. However, on Lord Howe Island, plants were basically unarmed. Somewhat different results were obtained for *A. ruscifolia* and *D. deplanchei*. In these species, younger plants produced more spinescent leaves than older plants, both on the island and on the Australian mainland. However, spinescence was higher in Australia and mainland plants continued to produce spinescent leaves later into ontogeny than island plants.

California Islands

Situated less than 30 km off the coast of southern California lies an archipelago of 12 islands that are collectively known as the California Islands. Although they are weakly isolated in space, there is no evidence that they were connected to the mainland during the Pleistocene. Instead, they appear to have been isolated from North America for many more millennia (Johnson 1978). During this time, they have acquired a very distinctive fauna that is characterised by a lack of large herbivores, with one exception. Archaeological evidence indicates that it was once home to a dwarfed proboscidean, *Mammuthus exilis*: Elephantidae. Previous work suggested that its diet was comprised of grasses (Schoenherr et al. 2003). However, more recent research suggests that it may have been a browser, with a diet focused on leaves and

twigs (Semprebon et al. 2016). Standing approximately 1.75 m tall, it was substantially smaller than its closest mainland relative, the Columbian mammoth (*Mammuthus columbi*), which stood well over 4 m tall (Agenbrood 2010). Therefore, it is uncertain whether trees and shrubs inhabiting the California Islands were completely free from the effects of vertebrate browsers, or whether they were subject to browsing by a single species of smaller-statured herbivore.

In a pioneering study of the loss of defence in island plants, Bowen and Van Vuren (1997) compared structural and chemical defences between populations of six species of trees and shrubs inhabiting Santa Cruz Island and the adjacent mainland. Spinescence was reduced in five out of six study species, while chemical defences showed weaker and less consistent changes. When fed to sheep, island plants were consumed in greater quantities than mainland plants, indicating that island plants were more poorly adapted to vertebrate browsers. Salladay (unpublished material, Herbivory Defense of Island Plants and their Mainland Relatives, Berkeley, CA) repeated Bowen and Van Vuren's (1997) study with nine species from a different island, Santa Catalina, and obtained similar results.

Burns (2013a) compared heteroblastic shifts in the production of leaf spines between plants on Santa Cruz Island and the adjacent mainland. Results showed that spine densities were highest in younger plants and declined as plants matured. However, spine densities declined more rapidly in island plants. Burns (2013a) interpreted this as an early, incomplete stage in the evolutionary loss of leaf spines. However, in light of recent paleontological evidence (Semprebon et al. 2016), an alternative explanation could be that selection has favoured a shift towards earlier production of adult leaves in a manner consistent with the reach height of the dwarfed mammoths.

Islands without Plant Protectors

Hawai'ian Islands

The Hawai'ian Islands lack native ants, so plants colonising the archipelago with extra-floral nectaries are unable to attract them as plant

protection mutualists. Keeler (1985) showed that three native species (*Passiflora foetida*: Passifloraceae; *Ipomea indica*: Convolvulaceae; *Pteridium aquilinum*: Polypodiaceae), which produce extra-floral nectaries elsewhere in their range, do not produce extra-floral nectaries in Hawai'i. Therefore, in the absence of ants, they appear to have lost their extra-floral nectaries. Keeler (1985) also compared the incidence of extra-floral nectaries among thousands of introduced, native, and endemic species in the Hawai'ian flora. Results showed that fewer endemic species produced extra-floral nectaries than native species, and that fewer native species produced extra-floral nectaries than introduced species.

Ogasawara Islands

The Ogasawara Islands (formally known as the Bonin Islands) are located 1,000 km south of Japan in the western Pacific. They were created approximately 45 Ma when the Pacific plate began to subduct under the Philippine Sea plate. The resulting volcanic activity created an archipelago of around 30 islands, which received their floras via over-water dispersal, mainly from Japan.

The archipelago has a depauperate ant fauna (Sugiura et al. 2006). However, it was colonised by *Hibiscus tiliaceus*: Malvaceae, which produces extra-floral nectaries across its wide distribution spanning the western Pacific and Indian Oceans. A closely related species, *Hibiscus glaber*, is endemic to the archipelago and likely evolved from a common ancestor with *H. tiliaceus* in the recent past. It lacks extra-floral nectaries, suggesting selection has favoured the loss of extra-floral nectaries in the absence of mutualistic partners.

Interestingly, many species of ants have colonised the islands following the arrival of humans and some visit the extra-floral nectaries of *H. tiliaceus*. As a result, *H. tiliaceus* is rarely attacked by *Rehimena variegata* (Lepidoptera: Pyralidae), an endemic moth species that feeds on flowers. On the other hand, ants rarely visit *H. glaber*, presumably because they no longer provide energetic reward in the form of extra-floral nectar, and this endemic species is attacked frequently by *R. variegata*.

The Antilles

Cecropia (Urticaceae) is a genus of trees distributed throughout much of the neotropics and the islands in the Caribbean. A distinctive feature of most species in the genus is their mutualistic association with ants, most frequently in the genus *Azteca*: Formicidae. Most species of *Cecropia* produce Müllerian bodies at the base of leaf petioles, which are consumed by ants, who in turn vigorously defend plants against herbivores, as well as structurally parasitic plants (i.e., vines and lianas). However, islands in the Caribbean typically have less diverse herbivore communities, as well as fewer species of vines and lianas. Consistent with reductions in herbivore densities on islands, populations of *Cecropia* on Puerto Rico, Grenada, St Vincent, St Lucia, Barbados, Martinique, Dominica, and Guadalupe rarely produced Müllerian bodies (Janzen 1973; Rickson 1977). However, Trinidad and Tobago, two larger islands located closer to South America that house more diverse ant communities, support *Cecropia* plants that produce copious quantities of Müllerian bodies.

CONCLUSIONS

Overall results provide mixed support for syndrome predictions. On one hand, islands devoid of vertebrate herbivores repeatedly show evidence for defence displacement. Plant traits linked to mammalian herbivores are typically lost on islands devoid of vertebrate herbivores. Coniferous trees on Iceland and Haida Gwaii invest less in chemical defences than their mainland counterparts. Spinescent plants in Australia and California invest less in prickles, thorns, and spines after they colonise offshore islands. Plant traits that are thought to be effective at deterring toothless browsers also show evidence of defence displacement. Plants that colonised the Chatham Islands from New Zealand have repeatedly lost leaf spinescence, divaricate branching, and heteroblasty (including both leaf shape variation as well as apparently cryptic and aposematic leaf colouration).

Evidence for convergence in putative defensive adaptations against avian and reptilian herbivores on toothless browser islands is more equivocal. Contrary to some earlier accounts, spinescence is not absent from the floras of Hawai'i and New Zealand. It is also a conspicuous feature of the floras of the Galapagos and Socotra. Spinescence on these islands tends to be associated with leaves (i.e., spines) rather than stems (i.e., thorns), which may have been particularly effective at deterring toothless herbivores that would have had to swallow them whole. Divaricate branching is common in New Zealand and Madagascar, but it is curiously absent from Hawai'i. However, a global-scale analysis of the incidence of heteroblasty has yet to be conducted, so whether it has evolved convergently on islands with toothless browsers is untested. Evolutionary convergence in leaf heteroblasty is perhaps the most consistent characteristic of islands that once housed toothless browsers, being similarly common on the Mascarene Islands, New Zealand, and New Caledonia.

Comparatively fewer studies have investigated changes in plant protection mutualisms on islands. However, all available information points to the consistent loss of extra-floral nectaries and Müllerian bodies on islands where plant protectors (e.g., ants) are absent. Therefore, on islands that lack plant protectors, selection for plant protection mutualisms appears to be relaxed and structures facilitating plant protection mutualisms are repeatedly lost evolutionarily. However, few studies have tested for the loss of plant protection mutualisms to date, despite much interest in the phenomenon in general.

Although great advances have been made towards a better understanding of plant defence on islands, many important questions remain. One obvious, overarching deficiency is that nearly everything we know comes from islands in the Indian or Pacific Oceans, and in particular New Zealand and its surrounding islands. Work in other archipelagos (e.g., Macaronesia) is needed to determine whether defence displacement occurs consistently across the globe. Another serious obstacle is the changes to herbivore communities brought

about by humans. Given that many island mega-herbivores are now extinct, direct experimental tests of how plant traits affect the behaviour of toothless herbivores are often impossible. However, future study of plant defence in the Galapagos could be particularly informative, as it provides an unparalleled opportunity to explore variation in defensive adaptations among islands relative to one of the few toothless herbivores to escape extinction.