Spinescence and the Island Plant Defense Syndrome

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Abstract

Island plants are predicted to have weak or absent defenses as part of the island plant syndrome. Evidence supporting the weak island defense prediction stems largely from observations of intense damage from invasive mammalian herbivores on islands. However, this evidence is misleading because most oceanic island plants have not evolved with native mammalian herbivores, and so should not have evolved defenses against them. In contrast, many islands have been home to other native vertebrate megafaunal herbivores, including flightless birds, tortoises, and turtles, many of which are now extinct or rare and therefore easy to overlook as agents of selection for island plant defenses. We review the evidence that island megaherbivores have selected for spinescence in island plants, supplementing published data with new estimates of spinescence for island floras varying in historical legacies of megafaunal herbivores. While the proportions of spinescent species are generally low, there are many spinescent island plants, likely functioning in defense against extant herbivores or persisting as defense anachronisms, no longer functioning due to the losses of native island

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megaherbivores. Future research exploring the evolvability of spinescence, including rates of losses or gains as herbivory selection pressure shifts, will be particularly enlightening for assessing island plant defenses in response to complex and variable historical legacies of megafaunal herbivory.

2.1 Introduction

Island floras are famously unique, characterized by biotic disharmony and high rates of endemicity (König et al. 2021). Whether island plant phenotypic diversity is also unique and distinct compared to that of continental floras, as predicted by island plant syndrome theory, remains an open question (Burns 2019). Island plant syndromes are proposed to have evolved convergently in response to shared island features, such as weak seasonality, mild climates, and relatively low disturbance regimes, in addition to distinct species interactions resulting from biotic disharmony, including generalized reproductive strategies and presumed relaxation in antagonistic interactions (Burns 2019). Recent and ongoing research testing whether island plants lack anti-herbivore defenses as part of an island plant syndrome has begun to cast doubt (Moreira et al. 2019, 2021; Meredith et al. 2019) on this previously widely claimed prediction (Bowen and VanVuren 1997; Carlquist 1974). Ideally, tests of island plant defenses would incorporate direct measures of defense traits in conjunction with damage patterns of native herbivores (Moreira and Abdala-Roberts 2022). However, island biotas are among the most endangered in the world with disproportionate numbers of species extinctions (Fernández-Palacios et al. 2021), resulting in the loss of many native island herbivores. Islands are also heavily invaded, and non-native herbivores, particularly mammals, are well-documented threats to island plants (Courchamp et al. 2003; Caujapé-Castells et al. 2010). Vulnerability to invasive mammalian herbivores does not itself provide robust evidence that island plants lack defenses because defenses generally have high specificity and target the native herbivores with which the plants evolved (Agrawal and Heil 2012). Thus, we should expect plants on islands without native mammalian herbivores to have weak defenses against mammals, but this does not preclude the presence of defenses that target other guilds of herbivores, such as insects, mollusks, crabs, reptiles, and birds. We focus here on synthesizing the evidence for island plant physical defenses, specifically spinescence because of its important role in deterring megaherbivores, in the context of defense against native island herbivores.

2.2 Spinescence Background

Spinescence is a type of structural defense, including spines as modified leaf parts (midribs, petioles, leaf tips), thorns as modified branches, and prickles as outgrowths of epidermal tissues, with convergent roles in defense against herbivores (Cornelissen et al. 2003; Bell and Bryan 2008; Hanley et al. 2007). The evolution of spinescence and diversification of spinescent lineages have been linked to simultaneous diversification of mega- and medium-sized herbivores in Africa (Charles-Dominique et al. 2016), Asia (Zhang et al. 2022), and the Neotropics (Dantas and Pausas 2022). In addition to its well-documented role in deterring mammalian herbivores (Cooper and Owensmith 1986; Cooper and Ginnett 1998; Lefebvre et al. 2022), spinescence can also reduce invertebrate herbivory by interfering with insect and mollusk mobility (Isermann and Rooney 2014; Kariyat et al. 2017).

Although prickles, spines, and thorns are generally thought to function exclusively in defense, it has also been suggested that they contribute to other ecophysiological functions. For example, thorns have been suggested to assist with heat dissipation and photo-protection in desert plants (Nobel 1988), and prickles are anatomically similar to trichomes (Bell and Bryan 2008), potentially functioning in photo-protection and water balance. Induction of elevated prickle density under high light (Barton 2014) supports the prediction that spinescence alleviates light stress. The prevalence of spinescent species in open habitats, such as savannas, may further indicate a role of spinescence in tolerance to high light conditions, although spinescence in sunny habitats is generally interpreted as evidence for construction costs limiting spinescent plants from shady understories where carbon costs exceed defense benefits (Charles-Dominique et al. 2016). The potential multifunctionality of spinescence has so far been directly investigated in only a few species and so warrants further examination.

Spinescence is thought to be a costly form of plant defense because resources invested in construction cannot be recycled (Hanley et al. 2007). Furthermore, modification of photosynthetic tissues into spinescent structures imposes an opportunity cost via lost photosynthetic capacity, leading to a trade-off between spinescence and an acquisitive leaf economic strategy (Armani et al. 2020b). Spinescence costs have been suggested via correlated reductions in growth rate (Armani et al. 2020b) and reproductive output (Gómez and Zamora 2002). Because defense costs are contingent on resource availability (Herms and Mattson 1992), further research is needed to refine predictions about the evolution of spinescence in island habitats. Furthermore, because resource availability and thus presumably defense costs (Boege and Marquis 2005) shift throughout plant ontogeny (developmental stages associated with phase change (Jones 1999), a developmental framework will be particularly informative.

The expression of spinescence commonly varies through plant ontogeny. Species can vary in the onset of spinescence during seedling development (Armani et al. 2020a), and later across vegetative phase change in species with dramatic morphological variation during phase change, typically referred to as heteroblasty (Zotz et al. 2011). Ontogenetic variation in spinescence is also common in non-heteroblastic species (Barton and Koricheva 2010). The prevalence of obvious ontogenetic shifts in plant defenses in island plants has been previously highlighted, particularly in Aotearoa New Zealand (Burns and Dawson 2009; Clark and Burns 2015). Spinescence often decreases during ontogeny, which is interpreted to reflect a need for spinescence during juvenile stages to defend against ground-dwelling tortoises and flightless birds, followed by escape as plants outgrow the reach of the herbivores later in ontogeny (Burns 2014, 2016a, 2016b). However, ontogeny represents a phase change and so is not strictly tied to plant height, and ontogenetic patterns in spinescence have also been observed in short-statured herbs. For example, prickly poppies are rosettes, and the density of leaf prickles varies considerably across ontogeny in the Hawaiian prickly poppy, both in their constitutive expression and in their inducibility by simulated herbivory (Hoan et al. 2014).

2.3 Spinescence in Island Plants

The predicted loss of spinescence as part of the island plant syndrome has three key assumptions: (1) spinescence does not function in defense against the herbivores native to islands (extant and extinct), such as insects, mollusks, crabs, birds, and reptiles; (2) spinescence is costly in the absence of herbivory, and therefore it should be selected against; and (3) spinescence plays no other role beyond defense, which could separately select for its persistence in island plants. As discussed in the previous section, spinescence costs and multifunctionality (assumptions 2 and 3) have only been examined in a few species and rarely on islands. Thus, the validity of these assumptions is uncertain, and future research should target these for critical insights about the evolvability of island spinescence. In contrast, considerable evidence exists to assess the first assumption that spinescence does not play a defensive role on islands, and we focus on this evidence for the remainder of this chapter.

2.3.1 Native Vertebrate Herbivores on Islands

All islands have native herbivores, including various invertebrates such as insects, mollusks, and land crabs. In addition, many islands harbored rich and fascinating guilds of native vertebrate herbivores prior to human arrival, which can be considered island megafauna due to their size (Hansen and Galetti 2009), and many of which are now extinct (Fig. 2.1). Avian herbivores include flightless megafaunal browsers like the nine species of moa (Order: Dinornithiformes) in Aotearoa New Zealand (26–230 kg; Wood 2020), elephant birds (Order: Aepyornithiformes) in Madagascar (108–643 kg; Hansford and Turvey 2018), and *Sylviornis neocaledoniae* in New Caledonia (27–34 kg; Worthy et al. 2016). Smaller avian herbivores include the infamous dodo (*Raphus cucullatus*) in Mauritius, takahē (*Porphyrio hochstetteri*) and kākāpō (*Strigops habroptilus*) in Aotearoa New Zealand, endangered nēnē (*Branta sandvicensis*), and the extinct, large flightless moanalo and nen-nui (Order: Anseriformes) in Hawaiʻi (Walther and Hume 2016; Baldwin 1947; Black et al. 1998). Most other insular vertebrate herbivores were tortoises and turtles. Many islands across the Indian Ocean, Caribbean, and Pacific Ocean contained giant tortoises or turtles (Rhodin et al. 2015), which could reach high densities and were important ecosystem engineers (Gerlach et al. 2013). In the south Pacific, meiolaniid turtles filled the niche of giant tortoises (White et al.

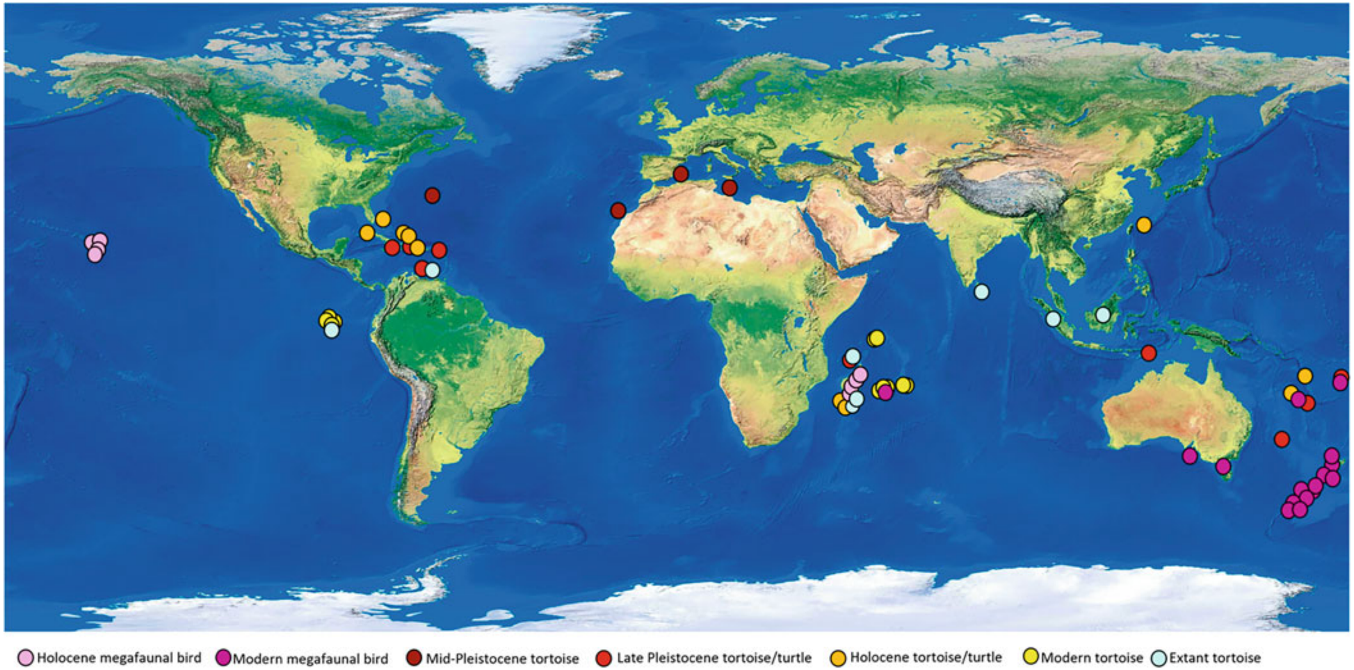

Fig. 2.1 Map showing distribution of extant and extinct megafaunal (>5 kg) non-toothed vertebrate herbivores on islands since the Mid-Pleistocene. Each dot represents one species. Colors represent whether each species was a bird, tortoise, or turtle, and when that species went extinct. Mid-Pleistocene refers to 780,000–125,000 years before present (ybp), Late Pleistocene refers to 125,000–12,000 ybp, Holocene refers to 12,000–450 ybp (prior to 1500 AD), and modern refers to species that have gone extinct since 1500 AD. Data for this map come from multiple sources (Rhodin et al. 2015; Wood 2020; Worthy et al. 2016; Hansford and Turvey 2018; Hume and Walters 2012)

2010). Stable isotope studies have confirmed that these turtles had a terrestrial, herbivorous diet (White et al. 2010), but their role in shaping the floras of these islands is almost entirely unconsidered. Some islands are also home to smaller reptilian herbivores, including iguanas in the Bahamas (Knapp and Alvarez-Clare 2016) and skinks in the Solomon Islands (Hagen and Bull 2011). Furthermore, some islands have native mammalian herbivores, including lemurs (extant and extinct) in Madagascar (Crowley and Godfrey 2013) and the extinct bovids *Myotragus* and *Ebusia* (Bover et al. 2016; Moyà-Solà et al. 2022) and the giant rabbit *Nuralagus* (Bover et al. 2008) in the Balearic Islands.

The majority of these herbivores are now extinct, but they spent millennia subsisting on the flora of the islands they inhabited and presumably acted as selective forces. Now, ungulates such as goats, deer, and pigs have been introduced to most of these islands, and research into the large impacts that these novel, mammalian herbivores have had on the flora has eclipsed the ghosts of herbivores past (Burns 2010), likely driving the widespread idea that island floras are naïve to herbivory and undefended. For example, most bioassays used to infer island plant defenses rely on non-native herbivores, usually mammals introduced to islands, and non-native mammalian preference for island compared to introduced plants is generally interpreted as evidence that island plants have weak defenses (Bowen and VanVuren 1997; Salladay and Ramirez 2018; Pollock et al. 2007; Cubas et al. 2019). However, characterization of the defensive role of island plant traits requires preference and performance data of native herbivores because they are the agents of natural selection for island plant defenses. For example, examination of host plant preferences through natural browsing of native island vertebrate herbivores, the Galapagos Tortoises (*Chelonoidis niger*), revealed that they feed on introduced plants disproportionately to their abundance, suggesting that unpalatability has evolved in native island plants to deter these native vertebrate herbivores (Blake et al. 2015). Unfortunately, most vertebrate herbivores on islands have undergone dramatic declines and even extinctions, which limit our understanding of island plant-herbivore interactions (McGlone and Clarkson 1993; Hansen and Galetti 2009; Rhodin et al. 2015). In some cases, related vertebrate herbivores have been used as proxies, assuming ecological equivalence between extinct and extant species, such as giant tortoises (Hunter et al. 2013; Moorhouse-Gann et al. 2021). However, because variability among species limits their ecological equivalence, careful consideration of morphology, feeding behavior, and distribution is needed to validate these substitution approaches.

2.3.2 Evidence for Spinescence in Island Plants

Despite a growing body of research characterizing island plant defenses (Moreira et al. 2021), relatively little focus has been on spinescence. Most studies to date have compared spinescence on native species on islands versus continents, or native versus non-native continental species naturalized on islands, and these have provided mixed evidence that spinescence is less common or reduced in island plants compared to continental plants (Table 2.1). For example, woody plants native to the Channel Islands generally have fewer and smaller leaf spines than continental California plants (Bowen and VanVuren 1997; Salladay and Ramirez 2018), and similar patterns are reported for plants from Madagascar versus continental South Africa (Bond and Silander 2007). However, prickles have similar frequencies in offshore Australian islands (Meredith et al. 2019) and greater densities in native Hawaiian species (Suissa and Barton 2018; Hoan et al. 2014) compared to continental species, potentially indicating meaningful variability between types of spinescence (spines, thorns, and prickles) evolving in island versus continental plants.

A major constraint of the island-continental comparison approach, particularly if it depends on measures of contemporary herbivory, is that it overlooks historical legacies of extinct, endemic vertebrate herbivores as sources of selection for defenses in island plants. Rather than focusing on island-continental comparisons, a shift in approach that compares defenses among island floras would shed light on the considerable complexity relating to the variable presence of megafaunal herbivores on islands. For example, spinescence frequency is higher in New Zealand than in the nearby Chatham Islands, consistent with selection by ratites (moa) in New Zealand, which never dispersed to the Chatham Islands (Burns 2016b). For islands with multiple native vertebrate herbivores, the timing of extinction may be relevant, as detected in a comparison of spinescence in the Canary versus Balearic Islands (Moreira et al. 2022). Both archipelagos were home to giant tortoises that went extinct in the Middle Pleistocene (Rhodin et al. 2015), but the Balearic Islands were also home to native bovids and giant rabbits that went extinct around the same time (Bover et al. 2008, 2016, 2019; Moyà-Solà et al. 2022), and the greater frequency of spinescence in Balearic than Canary Island plants (Moreira et al. 2022) may be the consequence of the combined selection from native tortoises and mammals. Incorporating heterogeneity among islands in their historical legacies of vertebrate herbivory may thus provide much-needed nuance to the study of island plant syndromes and could reveal the extent to which spinescence in island plants is a defense anachronism, left over from now-extinct herbivores (Burns 2010; Wallace 1889). Such an island-focused approach might also reveal that island conditions and species interactions are heterogeneous to the extent that convergent evolution leading to an island plant syndrome has not occurred, and rather, that island floras are diverse and do not differ in systematic ways from continental plants.

A significant limitation to applying a historical framework for the study of island plant syndromes is that we have little information about the mode or rate of spinescence evolution, beyond the rapid evolution associated with bovid co-diversification in Asia and Africa (Charles-Dominique et al. 2016; Zhang et al. 2022). The evolution of spinescence is especially unclear in island floras, although it has been reported that prickles, for example, evolved four times within 3.7 million years in the Hawaiian lobeliads (Givnish et al. 1994). Notably absent are predictions about the timeframe in which spinescence is lost or reduced under the absence of positive selection pressure by herbivores. In a comparison of congeneric species of *Aciphylla* in Chatham Islands where there are no known native vertebrate

Table 2.1 Summary of studies reporting spinescence in island plants, including comparisons of island versus continental plants, native versus non-native plants naturalized on islands, and characterization of island species alone. For each study, the focal archipelago, plant growth form and number of species, and the native vertebrate herbivore (extant or, more commonly, extinct) present on the focal islands are reported, as are the type of spinescence identified and the spinescence trait quantified for the comparison. The difference in spinescence between island and continental (native or non-native naturalized on islands) species is reported with respect to directionality alone (C > I, I > C, or I = C)

Reference	Archipelago	Growth form (no. spp)	Native vertebrate herbivore	Spinescence type	Trait	Trait comparison outcome
Island versus continental						
Bowen and VanVuren (1997)	California Channel Islands	Woody (12)	*Mammuthus exilis*	Spines	Number, length	C > I
Salladay and Ramirez (2018)	California Channel Islands	Woody (12)	*Mammuthus exilis*	Leaf spines	Number, length	C > I
Burns (2014)	Channel	Woody (4)	None	Leaf spines, prickles	Density	C > I
Burns (2016a)	Lord Howe	Woody (1)	Turtles	Leaf spines	Length	C > I
Bond and Silander (2007)	Madagascar	Woody (50)	Ratites	Not reported	Presence	C > I
Suissa and Barton (2018)	Hawaii	Herb (4)	Geese	Prickles	Density	I > C
Tindall et al. (2016)	New Zealand	Variable (5145)	Ratites	Variable	Presence	I = C
Meredith et al. (2019)	Australia offshore	Variable (1129)	Not reported	Not reported	Presence	I = C
Native versus non-native island						
Moreira et al. (2022)	Canary (Can), Balearic (Bal)	Woody (42)	Tortoise (Can), bovids and rabbit (Bal)	Not reported	Presence	I > C
Hoan et al. (2014)	Hawaii	Herb (2)	Geese	Prickles	Density	I > C
Native island only						
Lems and Holzapfel (1968)	Canary	Woody (5), herb (2)	Tortoise	Prickles	Presence	N/A
Barton (2014)	Hawaii	Herb (1)	Geese	Prickles	Density	N/A

Givnish et al. (1994)	Hawaii	Woody (18)	Geese	Prickles	Presence	N/A
Crowley and Godfrey (2013)	Madagascar	Woody (12)	Giant lemurs	Spines	Presence	N/A
Kavanagh et al. (2016)	New Zealand	Woody (1)	Ratites	Leaf spines	Length	N/A

herbivores, with species in New Zealand, the size and compression strength of spines are lower in Chatham Island species (Burns 2016b). Although it is unknown when *Aciphylla* colonized Chatham Islands in the several million years since they emerged (Heenan et al. 2010), it is feasible that the evolutionary relaxation took upwards of a million years or more. Furthermore, it is notable that spinescence was not lost entirely from the Chatham Island species, but was rather reduced in size. Whether a shift in selection regime associated with novel positive selection due to introduced herbivores could lead to increases in spinescence for these Chatham Island species remains unknown but would be fascinating to explore. Similar reductions, and not losses, have been described for spinescence in species of other islands (Salladay and Ramirez 2018; Bowen and VanVuren 1997; Burns 2014), emphasizing that spinescence is often reduced, but not lost, from island plants. In all cases, the timing and rate of evolutionary change remains unexplored.

2.4 Case Study

To investigate whether new insights may emerge through comparisons among island floras that consider the historical legacies of megafaunal herbivores, we collected new data on the frequency of spinescence for six island floras (Table 2.2). Our compilation included small islands in the South Pacific, Lord Howe and Norfolk Islands, as well as large archipelagos very isolated from continents, Vanuatu and the Solomon Islands. Temperate floras were represented by the Canary and Balearic Islands. Islands were selected primarily with the goal of capturing a range of native vertebrate herbivory histories. Solomon and Norfolk Islands represent herbivore-free islands with no known native vertebrate megafauna. Giant tortoises or turtles were historically present in the Canary, Balearic, and Lord Howe Islands, but considerable time has passed since their estimated extinctions in the Mid- and Late Pleistocene eras (Rhodin et al. 2015). The Balearic Islands are notable as the only representative island with native bovids and giant rabbits, although they have also been extinct since the Pleistocene (Bover et al. 2016). Vanuatu stands out for a relatively recent extinction of their megafauna meiolaniid-horned turtles, within an estimated 3000 years (White et al. 2010). This focal group of islands thus showcases how variable native megafauna are across islands, calling into question the overly simplistic expectation that island plants face convergent evolution due to shared conditions.

Spinescence for the focal island floras was determined through examination of digitized herbarium and living plant images, primarily using Plants of the World Online (POWO 2022), Global Biodiversity Information Facility (Flemons et al. 2007), or personal experience. Vascular seed plant species lists were acquired from published floras (Table 2.2). Only native terrestrial species were included, and variability among subspecies, varieties, or populations was excluded. Because of this focus on the species scale and due to a lack of images for some taxa, the total species examined may be less than the total species richness, and the number of species examined for each flora is reported (Table 2.2). Spinescence includes thorns, spines, and prickles, but because it is not always possible to accurately differentiate

Table 2.2 Islands examined in the case study. Island characteristics and vascular plant species lists were compiled from various floras and online resources (see text for details). Spinescence was determined through examination of digital herbarium and live plant photos. Megafauna predicted to be browsers are considered native vertebrate herbivores, and for those that went extinct, the predicted time since extinction is reported in years (Rhodin et al. 2015; Hawkins et al. 2016; White et al. 2010; Bover et al. 2019; Bover et al. 2008; Moyà-Solà et al. 2022)

Archipelago name	Biogeography/ ocean	Total area (km^2)	Isolation (km)	Species richness	Spinescence (of spp)	Native vertebrate herbivores	Sources
Vanuatu	Tropical South Pacific	12,199 (83 islands)	1750	1636	4.0%	Horned turtles (3000)	Plunkett et al. (2022)
Solomon Islands	Tropical South Pacific	28,446 (~1000 islands)	1867	1342	5.4%	None	Neall and Trewick (2008), 'Flora of the Solomon Islands' (2022)
Canary Islands	Temperate Atlantic, Macaronesia	7436 (8 islands)	100	1467	3.5%	Tortoise (200,000)	del Arco Aguilar et al. (2010), Beierkuhnlein et al. (2021)
Balearic Islands	Temperate Mediterranean Sea	5040 (7 islands)	192	1507	4.3%	Bovids (4300), Giant rabbit (Mid-Pleistocene), Tortoise (200,000)	Sáez et al. (2011)
Lord Howe Island	Temperate Tasman Sea	14.55	570	171	3.9%	Tortoise (Late Pleistocene)	Green (1994)
Norfolk Island	Temperate South Pacific	35 (2 islands)	761	124	4.0%	None	Green (1994)

among these traits in herbarium specimens, spinescence was assigned as a binary variable (presence/absence) at the species level, and the frequency of spinescence as a percentage of total species examined is reported (Table 2.2). Vegetative spinescence was the focus, and species with spinescence only on fruits or other reproductive tissues were not counted.

Spinescence is relatively uncommon in the six island floras, ranging from 3.5% in the Canary Islands to 5.4% in the Solomon Islands. Considering the narrow range of variability in spinescence for our focal island floras, no obvious patterns emerge with respect to island megafauna presence or time since extinction (Table 2.2). Whether these frequencies are low compared to continents, as predicted for island plant syndromes, requires similar data for continental floras. For example, our results correspond well with recent estimates of spinescence for 5145 native species in New Zealand and Australia, 3.9% and 4.2% respectively, providing evidence for similar spinescence in island and continental floras (Tindall et al. 2016). In contrast, the frequency of spinescence has been reported to be about three times higher at 11.5% for 1852 species from Southern Africa (Charles-Dominique et al. 2016). Even higher spinescence frequencies have been reported for small species pools in South Africa, ranging from 31.6% to 45.8% across different plant communities (Bond and Silander 2007). Spinescence seems to be particularly common in African plants, even reaching high frequencies in islands near Africa, as shown by 12.5% spinescence for plants on Madagascar (Bond and Silander 2007). Comparable data for spinescence frequency for temperate continental regions are not available. Clearly, additional evidence is needed to robustly examine the link between megafauna (extant and historical) and the evolution of spinescence, both among islands, and in comparison with continents.

2.5 Spinescence in Island Plants: Conclusions

Spinescence in island plants is not particularly common, but is also not absent. While spinescence is largely linked to browsing by large mammals, especially bovids, on continents, spinescence in islands has likely evolved in response to browsing by other megafauna, namely giant tortoises, turtles, and birds. Although reptiles and birds are beaked and thus less likely to be deterred by spinescence while browsing, their mouths and digestive tracts are soft-tissued, and so are likely to be vulnerable to damage and irritation following consumption (Burns 2019). The extinction of most of the world's island megafauna makes it nearly impossible to investigate the deterrent properties of spinescence, but substitution bioassays with extant ratites and the few remaining giant tortoise species offer promising opportunities (Eskildsen et al. 2004; Pollock et al. 2007). Furthermore, plasticity in spinescence in response to native herbivory has rarely been considered (Hoan et al. 2014) and could be prevalent, even emerging in species that appear to lack spinescence until browsed, as has been reported for *Echium* in the Canary Islands (Lems and Holzapfel 1968). Most importantly, a shift away from non-native mammalian browsers is needed to properly investigate island plant defenses. Considering the lack of evolutionary history with native mammalian herbivores, we should not predict island plants to have evolved defenses against them, and yet vulnerability to invasive mammals is often interpreted as evidence for weak island plant defenses. To assess island plant defenses, it is critical to examine native island herbivores or biologically meaningful proxies with similar morphologies, diets, and feeding behaviors. Of course, invasive mammals are a major threat to native island plants (Courchamp et al. 2003; Caujapé-Castells et al. 2010), and so these interactions warrant examination in this context, but not to shed light on island plant defenses.

Historical legacies of island megafauna are complex, including human-driven and natural extinctions over long timespans (Rhodin et al. 2015; Wood et al. 2017; Louys et al. 2021). Predicting whether island plants should have lost their defenses following extinction of island megafauna requires a better understanding of the tempo of spinescence evolution, and in particular, the rate of spinescence loss. Moreover, conditions under which spinescence may persist even in the absence of positive selection pressure from herbivory need to be considered, including multifunctionality in abiotic stress tolerance and the absence of allocation costs. Indeed, both of these aspects could explain a general trend in high defense investment for island plants despite reduced herbivory (Moreira et al. 2021). Accounting for multifunctionality, weak or absent allocation costs, and defense against under-appreciated microfauna such as skinks, crabs, and mollusks, might yet reveal that island spinescence is not quite the defense anachronism it has been suggested to be (Wallace 1889; Burns 2010), and that diverse sources of selection pressure maintain spiny island plants today.

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