



The Loss (and Gain) of Defensive Adaptations in Island Plants and Animals: A Comparative Review

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Abstract

Compositional differences between islands and continents had marked consequences for the evolution of island life. Regardless of their taxonomic rank, many island species lost defences that evolved in mammal-dominated ecosystems and gained new defences against bird-dominated islands. However, the study of island evolution has been taxonomically compartmentalised, with research on island animals and plants being conducted independently of one another. Thus, whether a common pattern in the evolution of island defences exists remains unclear. To help bridge this gap in our understanding, we conducted a comparative review of defensive adaptations in island animals and plants to (1) better understand differences in research effort between plants and animals, and (2) establish unified principles in the loss (and gain) of defences in island life. To do that, we manually screened 1600 studies extracted from Google Scholar. Of them, 127 were included in our review. The majority of studies focused on island animals. Most studies on the gain of defences focused on plants, while loss of defence was explored more thoroughly in animals. Differences in terminology and idiosyncrasies between animals and plants hindered our ability to compare research findings. Nonetheless, some commonalities have emerged. In particular, a general pattern of loss and gain of defences can be delineated. Insularity appears to promote the loss of non-bird-specific defences

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and the gain of bird-specific defences. This pattern though is clearer in plants than in animals and more research is needed to unify these two bodies of work.

5.1 Introduction

Early European naturalists were completely unprepared for what they encountered as they stepped ashore on oceanic islands. Their knowledge of the world's biota came mostly from continental Europe, where plants and animals looked and behaved in seemingly predictable ways. For example, continental birds tend to be small in size and quick to take to the air when confronted by predators. So it seemed safe to assume that island birds would be the same. However, continental generalisations about the natural world would leave them wholly unequipped for what they actually found. Instead of being 'normal' (i.e. small-bodied, flighted and alert to danger), many island birds looked exceedingly large, with wings often small to the point they ceased to function for flight (Carlquist 1974). Stranger still, they seemed to be completely oblivious to the dangers posed by human hunters and the predatory mammals we brought with us (Cooper et al. 2014).

The different nature of many island endemics would suggest that they have much to teach us about evolutionary ecology. However, for well over a century, these island 'oddities' were viewed by many researchers as scientifically static and phenomenalistic. What's more, hypothesised explanations for processes responsible for them were viewed as 'just-so stories' of natural history.

Many aspects of island biology can, and should, be approached using the general principles of the scientific method—in essence by erecting *a priori* hypotheses that are then tested empirically. When results fail to falsify these hypotheses, they should be tested further to solidify the understanding of repeated patterns in island evolution. If, on the other hand, they are inconsistent with hypotheses, previously accepted principles of island evolution should be modified or abandoned in favour of new hypotheses. Darwin's loss of dispersal ability hypothesis provides an illustrative example. Darwin hypothesised that the loss of vagility in island organisms resulted from selection against individuals that disperse into the surrounding sea. However, a review of the loss of dispersal ability in plant seeds revealed only limited support for the phenomenon (Burns 2019). Furthermore, when the loss of dispersal ability was observed, it usually arose from increases in seed size, rather than selection for reduced size or functionality of dispersal appendages (Burns 2018). Under these circumstances, the scientific method dictates that Darwin's hypothesis should be amended or abandoned, rather than continuing to be accepted as a 'just-so' story of natural history. One such alternative hypothesis is that the loss of dispersal in island organisms, when it is observed, arises as a passive by-product of selection for large size, rather than direct selection for reduced dispersal ability (i.e. the 'size constraints hypothesis', Burns 2019).

Although a priori hypothesis testing is an enormously powerful scientific tool, not all research into the island evolution should necessarily be shoehorned into the confines of this scientific method. Identifying unusual examples of island evolution, as early European naturalists did on oceanic islands (Darwin 1840), is in itself a valuable scientific method. Research in the psychology of new knowledge acquisition argues that human learning tends to occur in stages (Diederer and Fletcher 2021). The first stage is pattern recognition. For example, continental birds tend to be small, volant and vigilant. This leads to the second step of predicting what will be found in the future, say when we arrive on oceanic islands. The last and most important step is when new learning takes place. When exceptions are observed (e.g. island birds tend to be big, non-volant and naïve) it is known as a *prediction error*. This philosophical pathway of learning, known as the *prediction error paradigm*, or PEP for short, is not only a widely accepted theoretical construct that describes how the human mind learns, but it also forms the backbone of traditional natural history research that continues to be used productively (Burns and Low 2022).

The PEP can be a powerful tool in understanding island evolution, especially when ‘prediction errors’ accumulate and form a recognisable pattern themselves. While flightless birds are often iconic examples of such exceptions, ecologists soon recognised that other insular species shared similar traits. By comparatively assessing ‘prediction errors’ across multiple taxa, we might be able to develop unifying theories of island evolution.

5.2 Island Disharmony and Enemy-Specific Selection

A striking and widely appreciated aspect of island life is sharp changes in species composition. Some types of species that are common on continents, most notably mammals, are routinely absent from islands (Whittaker et al. 2017; Schrader et al. 2021). Conversely, other types of species, especially birds, dominate island ecosystems to an extent unparalleled on continents. These changes in species composition are collectively known as island disharmony, and island disharmony can have marked consequences for the evolution of island life. For instance, defence mechanisms evolved by animals and plants on continents often prove to be unnecessary or inadapt in insular environments (Hochberg and Moller 2001; Whittaker and Fernandez-Palacios 2007). This can lead to the loss of old defences evolved in mammal-dominated ecosystems and the gain of new defences against bird-dominated islands.

This happens because mammal and bird predators are morphologically distinct and forage in very different ways. Many mammals use olfactory cues, which are particularly advantageous while searching for food in low-light conditions or the darkness of night. On the other hand, birds have a more advanced visual system. Unlike mammals, which have two or three light receptors, birds have four light receptors that cover a greater range of wavelengths in electromagnetic radiation, including the UV spectrum (Kelber 2019). The anatomical structure of mammalian

and avian mouthparts is also quite different. Mammals have soft lips and gums, which are susceptible to damage by sharpened defensive structures at the first point of contact. Yet they also have teeth, which can be used to crush and dismember tougher types of prey. On the other hand, birds have keratinised bills that are more resistant to damage at the first point of contact and a gizzard instead of teeth for grinding harder food types.

Comparing the ways in which animals and plants have lost and gained defences after island colonisation could help us better understand the patterns under which island evolution operates. However, even though most hypotheses regarding island evolution can be applied similarly to both plants and animals, since its inception the study of island evolution has been taxonomically compartmentalised, with research on island animals being conducted independently of research on island plants. To help bridge this gap in our understanding of island evolution, we used a different methodological pathway. We conducted a comparative review of defensive adaptations in island plants and animals in an effort to: (1) better understand differences in research effort between plants and animals, and (2) establish unified principles in the loss (and gain) of defences in island life.

5.3 Methods

We ran eight distinct searches on Google Scholar using different keywords for both animals and plants. Four searches were equivalent between the two groups (taxon-nonspecific searches), while the other four focused on taxon-specific traits (taxon-specific searches). Traits were selected following Burns (2019) for plants and Baeckens and Van Damme (2020) and Whittaker and Fernandez-Palacio (2007) for animals (see the Supplementary Material for a full list of searches and Boolean operators). For each search, we inspected the first 10 pages of results ($n = 100$ studies).

We included all studies discussing the loss or gain of defence mechanisms. We defined a defence mechanism as any behavioural, morphological or physiological adaptation that enhances fitness by reducing the rate or intensity of predation, or by increasing tolerance to predation. Predation was defined as an inter- or intra-specific interaction that increases the fitness of one part (i.e. the predator) by decreasing the fitness of the other (i.e. the prey) (Minelli 2008). Interactions where the prey is killed by the predator, herbivory and parasitism will all be considered predation events. We considered loss of defence to occur when a defence mechanism originally present in the mainland ancestor is lost or reduced after island colonisation. Gain of defence occurs when a defence mechanism originally absent or reduced in the mainland ancestor is accentuated after island colonisation due to novel or higher predation pressures.

Studies were manually screened. We examined titles and abstracts first, then the full manuscript when needed. We did not set temporal or geographic ranges; however, we assessed only studies in English. Studies were screened by two

reviewers, FM (title & abstracts) and RC (full manuscript). Studies published by one of the authors were assessed by another reviewer at all stages.

5.4 Results

We inspected a total of 1600 studies, 800 per taxon. For animals, we found 112 studies investigating gain to or loss of defence against predators, 87 after removing duplicates. Another nine studies were removed after full-manuscript inspection ($n = 79$, Fig. 5.1). Of these, 11 explored potential gains of defence mechanisms, 66 investigated losses of defence mechanisms and 2 summarised both aspects (Fig. 5.1). For plants, 106 studies investigated loss to or gain of defence against predators, 56 after removing duplicates. Another four studies were removed after full-manuscript inspection ($n = 52$, Fig. 5.1). Of these, 25 explored gains of defence mechanisms, 17 explored losses of defence and 9 investigated both aspects (Fig. 5.1).

Most studies on gain of defences focused on plants (71.8%, p -value < 0.01). Considering only research articles, for animals, of the 11 studies investigating gain of defence (14.1% of total animal studies), four focused on defences gained against native predators, three birds and one con-specific reptile (i.e. defence against cannibalism, see Pafilis et al. 2011). Four studies focused on defences gained against introduced mammals, and three found no support for the gain of defence mechanisms in island animals (e.g. Itescu et al. 2017) (Fig. 5.1). For plants, of the 28 studies investigating gain of defence (53.8% of total plant studies), 25 focused on defences gained against native predators. Of these, 20 regarded birds, 2 reptiles and 3 mammals. Two studies focused on defences gained against introduced mammals, and one study found no support for gain of defence mechanisms in island plants (McGlone and Webb 1981) (Fig. 5.1).

Loss of defence was explored more thoroughly in animals (76.7%, p -value < 0.01). Considering only research articles, for animals, of the 66 studies investigating loss of defence (83.5% of total animal studies), 10 focused on defences lost to mammals, 10 on defences lost to reptiles, 1 on defences lost to birds and 36 on loss of defence to predators, regardless of their taxon. Nine studies found no support for loss of defence mechanisms (e.g. Van Damme and Castilla 1996; Le Saout et al. 2015) (Fig. 5.1). For plants, of the 20 studies investigating loss of defence (38.5% of total plant studies), 12 focused on defences lost to mammals and 5 on defences lost to birds, while 3 found no support for loss of defence mechanisms in island plants (e.g. Monroy and Garcia-Verdugo 2019; Moreira et al. 2021) (Fig. 5.1).

Tables 5.1 and 5.2 illustrate the traits that have so far been associated to insular loss and gain of defence in animals (number of traits = 14) and plants ($n = 13$). If animal- and plant-exclusive traits are excluded (i.e. behavioural traits and tolerance), a few parallels can be drawn. First, both animals and plants respond to changes in predation pressure by changing in size. In animals, increasing and decreasing sizes are both regarded as a loss of defence (Baeckens and Van Damme 2020). An exception is *Podarcis gaigae*, where gigantism is a defence against intra-specific

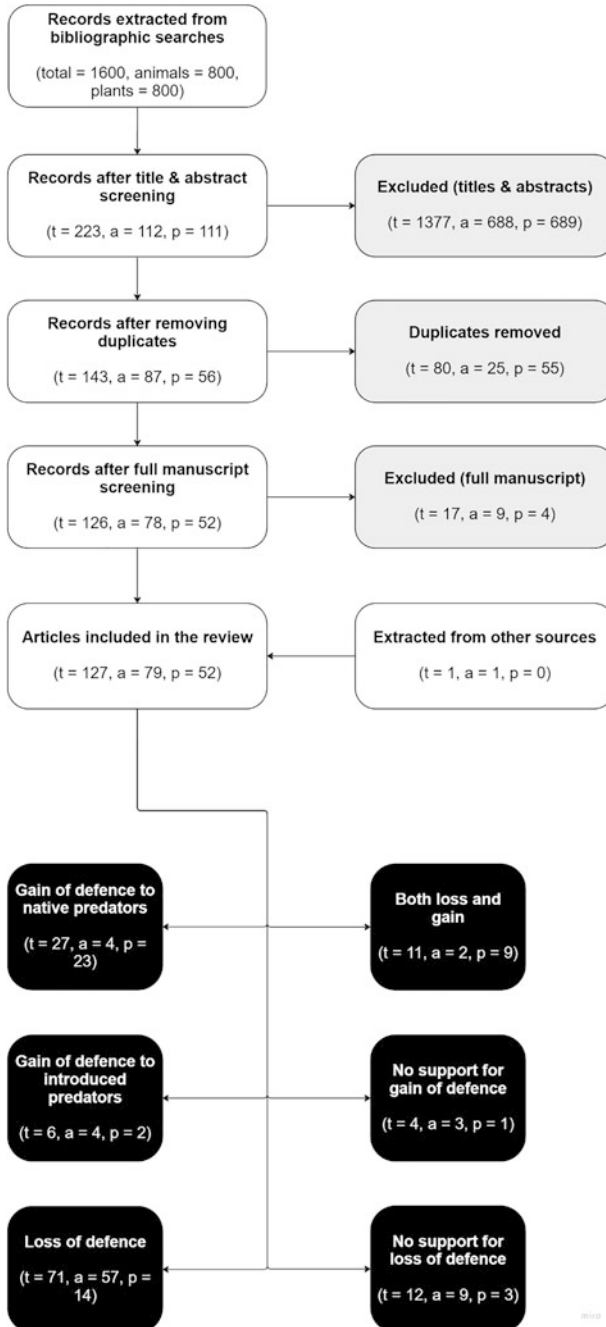


Fig. 5.1 Screening process of articles extracted from the literature search. White and grey boxes indicate, respectively, articles retained and excluded at each stage. Black boxes represent the final categories after full-manuscript assessment. At each stage, the total (t), animal (a) and plant (p) numbers of articles are provided

Table 5.1 List of studies that address the loss and gain of defence mechanisms in island animals, grouped by traits. The ‘pattern’ is what the authors demonstrated. The ‘potential process’ is what the authors suggested as the cause of the observed pattern but not necessarily demonstrated. ‘Category’ indicates whether the study supports loss of defence, gain of defence against native predators or gain of defence against introduced predators

Trait	Studied taxa	Island	Mainland	Pattern	Potential process	Category	Reference
Nocturnal activity	Santa Cruz Fox (<i>Urocyon littoralis santacruzae</i>)	Santa Cruz	California	Increased nocturnal activity in island foxes	Increased predation pressure	Gain of defence against native birds	Swarts et al. (2009)
Body size	Vertebrates	Islands worldwide		Island dwarfism and gigantism	Reduced predation pressure	Loss of defence	Adler and Levins (1994), Baeckens and Van Damme (2020), Baier and Hoekstra (2019), Benitez-Lopez et al. (2021), Blondel (2000), Case (1978), Case and Schwaner (1993), Crespin et al. (2012), Lawlor (1982), McNab (2002), Novosolov et al. (2012), Pafilis et al. (2011), Rotger et al. (2022), Rozzi and Lomolino (2017), Runemark et al. (2014), Runemark et al. (2015), Russell et al. (2011), Sale et al. (2009), Salvador and Fernandez (2008), Senczuck et al. (2014), Terborgh (2022), Zhu et al. (2020), Rozzi et al. (2023)

(continued)

Table 5.1 (continued)

Trait	Studied taxa	Island	Mainland	Pattern	Potential process	Category	Reference
	Skyros wall lizard (<i>Podarcis gaigae</i>)	Mesa Diavates and Lakonissi	Skyros	Island gigantism	Increased intra-specific predation pressures	Gain of defence against cannibalism	Pafilis et al. (2011)
Boldness	House mouse (<i>Mus musculus</i>)	Gough island and Isle of May		Island mice are bolder and more exploratory	Reduced predation pressure	Loss of defence	Gavrillidi et al. (2022), Gray and Hurst (1998), Stratton et al. (2021)
	Lizards	Islands worldwide		Island lizards are bolder	Reduced predation pressure	Loss of defence	Brock et al. (2015), Cooper et al. (2009, 2014), Cooper and Perez-Mellado (2010, 2012), Li et al. (2014), Runemark et al. (2014), Vervust et al. (2007)
	Macropodid marsupials	Various islands	Australia	Island populations are bolder	Reduced predation pressure	Loss of defence	Blumstein (2002)
	New Zealand robin (<i>Petroica australis</i>)	New Zealand		Less time allocated to assessing predation risk, but predator recognition is learned if exposed to mammals		Loss of defence and gain of defence against introduced mammals	Jamieson and Ludwig (2012), Maloney and McLean (1995), Muralidhar et al. (2019)
	Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>)	Svalbard islands	Norway	Island populations are bolder	Reduced predation pressure	Loss of defence	Reimers et al. (2011)

	Santa Cruz Fox (<i>Urocyon littoralis santacruzae</i>)	Santa Cruz	California	Island foxes are bolder	Reduced predation pressure	Loss of defence	Crooks and Van Vuren (1995)
	Gartersnake (<i>Thamnophis sirtalis</i>)	Beaver archipelago	Michigan	Increased boldness in island snakes	Reduced predation pressure	Loss of defence	Placyk (2012)
	Deer mouse (<i>Peromyscus maniculatus</i>)	Saturna Island	Canada	Island populations are bolder	Reduced predation pressure	Loss of defence	Baier and Hoekstra (2019)
	Birds	Islands worldwide		Island populations are bolder	Reduced predation pressure	Loss of defence	Blondel (2000), Cheke and Hume (2008), Frith (2013), Rasheed et al. (2017)
Colouration	Flying fox (<i>Pteropus rayneri</i>)	Solomon islands		Change in posterior colouration	Increased predation pressure	Gain of defence against native birds	Hamilton (2004)
	Lizards (genus <i>Podarcis</i>)	Mediterranean islands		Larger variance of dorsal colouration on islands	Reduced predation pressure	Loss of defence	Runemark et al. (2014)
	Birds	Islands worldwide		Larger variance of plumage colouration on islands	Reduced predation pressure	Loss of defence	Bliard et al. (2020)
	Strawberry poison frog (<i>Oophaga pumilio</i>)	Various islands	Costa Rica and Panama	Island frogs are more conspicuous	Higher predation pressure	Gain of defence against native birds	Dreher et al. (2015)
Physiological response	Galapagos iguanas (<i>Amblyrhynchus cristatus</i>)	Galapagos islands		Increased physiological response if exposed to predators	Increased predation pressure	Gain of defence against introduced mammals	Berger et al. (2007), Rodl et al. (2007)

(continued)

Table 5.1 (continued)

Trait	Studied taxa	Island	Mainland	Pattern	Potential process	Category	Reference
Reproductive output	Rodents	Islands worldwide		Reduced reproductive output on islands	Reduced predation pressure	Loss of defence	Adler and Levins (1994)
Age of maturity	Anole lizards	Antilles		Island anoles reproduce later	Reduced predation pressure	Loss of defence	Terborgh (2022)
	<i>Cavia intermedia</i>	Moleques do Sul	Brazil	Sexual maturity is reached later on islands	Reduced predation pressure	Loss of defence	Salvador and Fernandez (2008)
	Skyros wall lizard (<i>Podarcis gaigae</i>)	Mesa Diavates and Lakonissi	Skyros	Increased reproductive output on islands	Increased intra-specific predation pressures	Gain of defence against cannibalism	Pafilis et al. (2011)
Population density	Rodents	Islands worldwide		Higher population density on islands	Reduced predation pressure	Loss of defence	Adler and Levins (1994), Baier and Hoekstra (2019)
	Lizards	Islands worldwide		Higher population density on islands	Reduced predation pressure	Loss of defence	Novosolov et al. (2012), Novosolov and Meiri (2013), Pafilis et al. (2011), Siliceo-Cantero et al. (2017), Terborgh (2022)
	Birds	Greater and lesser Antilles		Higher population density on islands	Reduced predation pressure	Loss of defence	Terborgh (2022)
Tail autotomy	Lizards	Mediterranean islands		Reduced tail-shedding rates on islands		Loss of defence	Cooper and Perez-Mellado (2010), Pafilis et al. (2009)

Flocking behaviour	Birds	Islands worldwide		Flocking is lost or reduced on islands	Reduced predation pressure	Loss of defence	Beauchamp (2004)
Group size effect	Macropodid marsupials	Various islands	Australia	Group size effect is lost on islands		Loss of defence	Blumstein and Daniel (2002, 2003, 2005)
Visual and acoustic response	Macropodid marsupials	Various islands	Australia	Visual and/or acoustic predator recognition is lost on islands	Reduced predation pressure	Loss of defence	Blumstein et al. (2000), Blumstein (2002)
Olfactory response	Macropodid marsupials	Various islands	Australia	Olfactory predator recognition is lost on islands	Reduced predation pressure	Loss of defence	Blumstein (2002)
	Quolls (genus <i>Dasyurus</i>)	Astell island	Australia	Olfactory predator recognition is lost on islands	Reduced predation pressure	Loss of defence	Jolly et al. (2018)
	Lizards	Islands worldwide		Olfactory predator recognition is lost on islands	Reduced predation pressure	Loss of defence	Durand et al. (2012), Mencia et al. (2017), Monks et al. (2019), Mori and Hasegawa (1999), Van Moorleghem et al. (2019)
	Burrowing bettongs (<i>Bettongia lesueur</i>) and greater bilbies (<i>Macrotis lagotis</i>)		Australia	More wary when exposed to predators	Increased predation pressure	Gain of defence against introduced mammals	Blumstein et al. (2019)
Nest site	Orange-crowned warblers (<i>Leiothlypis celata sordida</i>)	Santa Catalina	California	Variance of nest sites increases on islands	Reduced predation pressure	Loss of defence	Hays et al. (2022)

Table 5.2 List of studies that address the loss and gain of defence mechanisms in island plants, grouped by traits. The ‘pattern’ is what the authors demonstrated. The ‘potential process’ is what the authors suggested as the cause of the observed pattern but not necessarily demonstrated. ‘Category’ indicates whether the study supports loss of defence, gain of defence against native predators or gain of defence against introduced predators

Trait	Studied taxon	Island	Mainland	Pattern	Potential process	Category	Reference
Branching architecture	Angiosperms	Madagascar	Africa	Very dense branching and small leaves in juveniles	Predation pressure from browsing birds	Gain of defence against native herbivore birds	Bond and Silander (2007), Grubb (2003)
	Angiosperms	New Zealand		Divarication. Higher tensile strength, thin twigs, wide-angle branches, three-dimensional-angled branching	Predation pressure from browsing birds	Gain of defence against native herbivore birds	Atkinson and Greenwood (1989), Bond et al. (2004), Burns (2019), Howard et al. (2022), Lee et al. (2009), Lusk et al. (2020), Maurin and Lusk (2020)
Spinescence	Angiosperms	Chatham Island	New Zealand	Island plants display smaller branching angles, shorter internodes and larger stems	Reduced predation pressure	Loss of defence	Kavanagh (2015)
	Angiosperms	Madagascar	Africa	Loss of spines	Reduced predation pressure	Loss of defence	Grubb (2003)
	Seed plants	New Zealand		Increased spinescence, spinescence increasing or	Predation pressure from	Gain of defence against native	Atkinson and Greenwood (1989), Burns (2014, 2019), Clark and Burns

				decreasing during ontogeny	browsing birds	herbivore birds	(2015), Lee et al. (2009), Ottaviani et al. (2020)
Angiosperms	New Zealand offshore islands	New Zealand	Loss of spines on islands	Reduced predation pressure	Loss of defence	Burns (2014, 2016a, b, 2019)	
Angiosperms	Channel Islands	California	Loss of spines on islands	Reduced predation pressure	Loss of defence	Salladay (2013), Salladay and Ramirez (2018)	
Leaf size and shape	New Zealand	New Zealand	Small leaves in juvenile plants	Predation pressure from browsing birds	Gain of defence against native herbivore birds	Atkinson and Greenwood (1989), Burns (2019)	
Angiosperms	Madagascar	Africa	Small leaves in juvenile plants	Predation pressure from browsing birds	Gain of defence against native herbivore birds	Bond and Silander (2007)	
Campanulaceae (genus <i>Cyanea</i>)	Hawaii		Juvenile leaves are deeply divided	Predation pressure from browsing birds	Gain of defence against native herbivore birds	Givnish et al. (1994), James and Burney (1997)	
Angiosperms	Mascarenes		Juvenile leaves elongated and smaller	Predation pressure from browsing	Gain of defence against native	Eskildsen et al. (2004), Hansen et al. (2003)	

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Table 5.2 (continued)

Trait	Studied taxon	Island	Mainland	Pattern	Potential process	Category	Reference
	Angiosperms	Channel islands	California	Island plants have larger leaves	giant tortoises	herbivore reptiles	Bowen and Van Vuren (1997), Salladay and Ramirez (2018)
	Angiosperms	Balearic and Canary islands		Native plants have smaller, thicker leaves than introduced plants	Reduced predation pressure	Loss of defence	Moreira et al. (2022)
Woodiness	Seed plants	Islands worldwide		Evolution of insular woodiness on islands	Reduced predation pressure	Loss of defence	Ottaviani et al. (2020), Zizka et al. (2022)
Colouration and crypsis	<i>Pseudopanax crassifolium</i>	New Zealand		Aposematic colouration in saplings, dishonest signal in seedlings	Predation pressure from browsing birds	Gain of defence against native herbivore birds	Burns (2019), Fadzly et al. (2009), Kavanagh et al. (2016)
	Angiosperms	Mascarenes		Juvenile leaves reddish or purple, inconspicuous	Predation pressure from browsing giant tortoises	Gain of defence against native herbivore reptiles	Eskildsen et al. (2004), Hansen et al. (2003)
	<i>Elaeocarpus hookerianus</i> , <i>Pseudopanax crassifolium</i> ,	New Zealand		Small inconspicuous leaves in juveniles	Predation pressure from	Gain of defence against native	Burns (2010, 2019), Fadzly et al. (2009), Fadzly and Burns

	New Zealand mistletoes and Scree plants									(2010), Lee et al. (2009)
Secondary metabolites	Angiosperms	Mascarenes		Higher levels of anthocyanins in juvenile leaves		Predation pressure from browsing giant tortoises	Gain of defence against native herbivore reptiles			Hansen et al. (2003)
	Angiosperms	New Zealand		Evolution of toxicity			Gain of defence against native herbivore birds			Batcheler (1989)
	<i>Tuja plicata</i>	Haida Gwaii archipelago	Canada	Reduced monoterpene concentration in island plants		Reduced predation pressure	Loss of defence			Vourc'h et al. (2001)
	Angiosperms	Santa Cruz	California	Reduced metabolites concentration in island populations		Reduced predation pressure	Loss of defence			Bowen and Van Vuren (1997), Watts et al. (2011)
	Angiosperms	Hawaii		Native plants are less toxic than introduced ones		Reduced predation pressure	Loss of defence			Grayson and Lennstrom (2022)
Latex exudation	<i>Argemone glauca</i>	Hawaii		Highly variable levels of latex exudation			Gain of defence			Barton (2014)
Prickles	Campanulaceae (genus <i>Cyanea</i>)	Hawaii		Juvenile leaves have denser prickles		Predation pressure from browsing birds	Gain of defence against native			Givnish et al. (1994), James and Burney (1997)

(continued)

Table 5.2 (continued)

Trait	Studied taxon	Island	Mainland	Pattern	Potential process	Category	Reference
	<i>Rubus croceacanthus</i> , <i>Glochidium obovatum</i> and <i>Zanthoxylum</i> <i>ailanthoides</i>	Kashima Island	Japan	Longer and denser prickles on island plants	Predation pressure from browsing mammals	herbivore birds	Takei et al. (2014a–c)
Leaf abscission	Poaceae	New Zealand		Evolution of leaf abscission	Reduced predation pressure	Loss of defence	Antonelli et al. (2011)
Twig cutting	Angiosperms	Haha-jima	Japan	Higher probability of twig cutting for endemic species	Reduced predation pressure	Loss of defence	Abe and Umeno (2011)
Flowering phenology	<i>Plectritis congesta</i>	Sidney Island	Canada	Island plants flowered later	Predation pressures from browsing mammals	Gain of defence against native and introduced mammals	Skaeni and Arcese (2020)
Fruit size	<i>Plectritis congesta</i>	Sidney Island	Canada	Island plants produced small, wingless fruits	Predation pressures from browsing mammals	Gain of defence against native and introduced mammals	Skaeni and Arcese (2020)
Tolerance	Bilberry (<i>Vaccinium myrtillus</i>)	Various islands	Norway	Island populations have higher tolerance	Predation pressures from browsing mammals	Gain of defence against introduced mammals	Dahlgren et al. (2007)

predation (Pafilis et al. 2011). Conversely, size reductions in plants are interpreted as defence mechanisms against insular browsing birds and reptiles (Burns 2019), while gigantism as a loss of defence (Salladay and Ramirez 2018; Zizka et al. 2022).

Secondly, both animals and plants appear to evolve or accentuate aposematic colouration in response to increased predation pressure on islands (Dreher et al. 2015; Kavanagh et al. 2016). In plants, increased predation stimulates cryptic colouration too (Hansen et al. 2003; Burns 2019), while animals increase colouration variance in response to predator release (Runemark et al. 2014; Bliard et al. 2020). Third, while two animal studies suggested predator release on island delays age of maturity (Salvador and Fernandez 2008; Terborgh 2022), a plant study found delayed flowering to be associated to increased browsing pressures (Skaien and Arcese 2020).

Several studies assessed how reduced predation pressure on islands can alter the reproductive output and population density of animals (Adler and Levins 1994; Baier and Hoekstra 2019; Terborgh 2022). However, we found no plant study addressing the matter. This is especially noteworthy since density-compensation and the production of fewer, bigger offspring are known patterns in plants (Burns 2019). Finally, while the relation between predation pressures and plant chemical defence received considerable attention (Hansen et al. 2003; Grayson and Lennstrom 2022), no similar study has been conducted in animals (but see Dreher et al. 2015).

5.5 Synthesis

Overall, from these results several important generalisations can be made. First, the animal and plant fields of research seem to be on fundamentally different conceptual pathways. This is proved by the significant relationship between the studied group (i.e. animals or plants) and the pattern investigated (i.e. loss or gain of defence, $\chi^2 = 24.26$, $df = 1$, p -value < 0.001). Research effort in animal studies has focused mostly on loss of defence. When gain of defence is addressed, it is often tied to introduced predators. Conversely, the majority of plant studies investigated gain of defences against native predators (Fig. 5.2).

Animals and plants interact with mammalian and avian predators in fundamentally different ways. When animals are attacked by birds or mammals, the result is often the death of the prey (i.e. predation *sensu stricto*). Therefore, the loss of anti-predatory behaviour in island animals may lead to population collapse. This is common to many oceanic archipelagos invaded by aggressive mammalian predators (Whittaker and Fernandez-Palacios 2007). By contrast, herbivores usually harvest non-lethal amounts of foliage. Plant extinctions are thus less likely (but see Moreira and Abdala-Roberts 2022) and understanding how island plants prevent herbivory became more important. Therefore, while animal research prioritised the loss of anti-predatory behaviours against introduced mammals, plant research focused instead on unusual adaptations to deter unique native island herbivores.

Second, despite the sharp difference in research priorities between the two fields, a general pattern on loss and gain of defences can be delineated. If work on

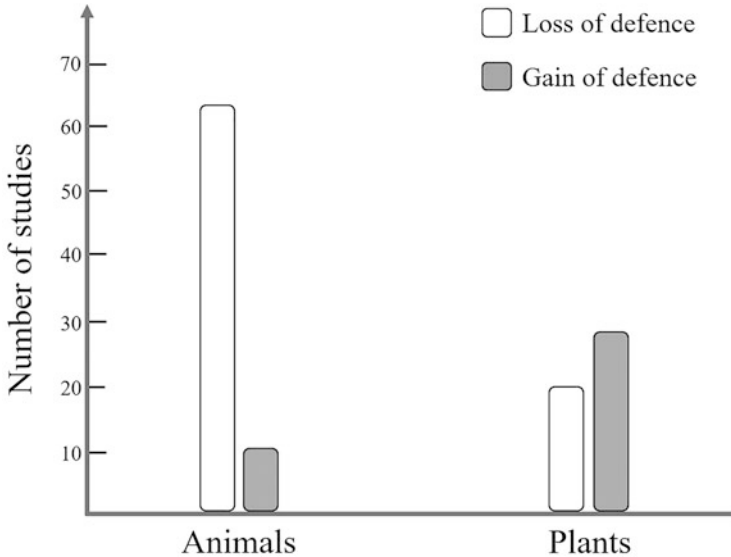


Fig. 5.2 Studies investigating loss and gain of defence in animals and plants. In animals, 66 studies investigated loss of defence and 11 gain of defence. In plants, 20 investigate loss of defence and 28 gain of defence. The two fields are on conceptually different pathways, as work on animals focuses mostly on loss of defence, while work on plants prioritises the study of gain of defence ($X^2 = 24.26$, $df = 1$, p -value < 0.001)

introduced predators is excluded, as insularity increases, species tend to lose defences against continental non-bird predators and gain defences against island bird predators (Fig. 5.3). This pattern is clear in plants. In animals, several studies suggest that a similar pattern might occur (Hamilton 2004; Swarts et al. 2009; Dreher et al. 2015), but the evidence is insufficient to draw a firm conclusion at this time.

Finally, when specific traits are considered, animals and plants seem to respond to insular pressures by changing in size, colouration and reproductive phenology. However, size responses are not consistent between the two groups. In animals, changes in body size are always regarded as a loss of defence. In plants, dwarfism is mainly viewed as a gain of defence and gigantism as a loss of defence. Furthermore, animal studies have only focused on whole-body size changes, while plant studies have mainly analysed the scaling of specific modules (i.e. body parts such as leaves and spines). As for colouration and reproductive phenology, the number of available studies is insufficient to delineate any general pattern, and the results gathered so far suggest no consensus between animals and plants.

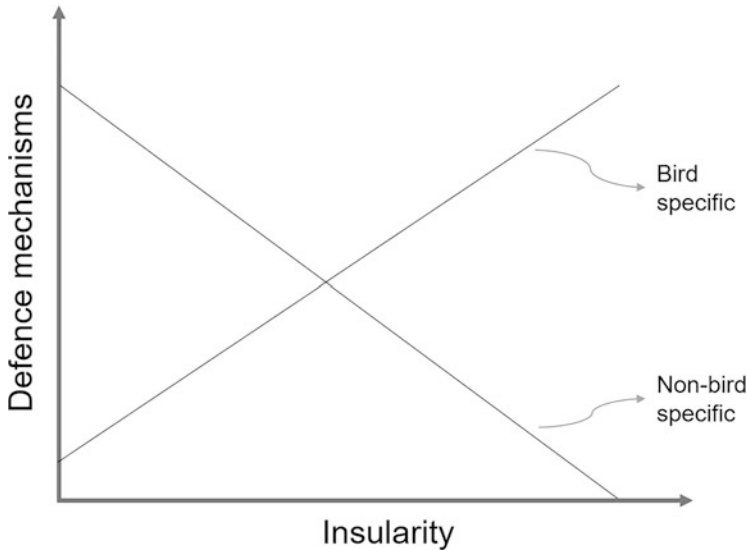


Fig. 5.3 Model illustrating a hypothetical common pattern of loss and gain of defences in island animals and plants. As insularity (i.e. area and isolation) increases, the number of non-bird-specific defences decreases (i.e. loss of continental defences) and the number of bird-specific defences increases (i.e. gain of insular defences). Given the work conducted so far, this pattern is clear in plants but not in animals, where additional studies on gain of defences are needed. The model only accounts for island native predators

5.6 Future Directions and Conclusions

There were approximately 30% more studies on animals than on plants. All animal studies focused on vertebrates, with one exception (Karagkouni et al. 2017). Among vertebrates, only two studies focused exclusively on amphibians, with none on fish. Similarly, plant studies address mostly angiosperms and, marginally, conifers. Among angiosperms, no taxon (e.g. genus or family) was comprehensively investigated. Overall, future work should focus on plants. Within animals, future work would benefit from focusing on invertebrates, amphibians and fish. Within plants, research effort should be redirected towards non-angiosperms and, more generally, on individual plant families, searching for consistent patterns of loss and gain of defence. Research effort was not homogenous among traits as well and some could receive more attention (e.g. colouration and chemical defences in animals and reproductive output and phenology in plants).

Despite a smaller body of work, plant studies explored the island defence syndrome more exhaustively (Fig. 5.2). Differences are largely due to a lack of studies on the gain of defence to native predators by animals, which is crucially needed for the development of the field. Conversely, plant research would benefit from focusing more on responses to multiple predators, an aspect so far

underappreciated. For instance, the multipredator hypothesis might help explain unusual patterns such as the comparable incidence of spinescent plants between islands and mainland Australia (Blumstein 2006; Meredith et al. 2019).

Future work would also benefit from overcoming differences in terminology. Only some defensive traits can be compared between animals and plants and a clear definition of defence mechanisms can help in identifying them. We propose defence mechanisms to be defined as any morphological or physiological adaptation that enhances fitness by reducing the rate or intensity of predation, with predation including only inter-specific interactions. We believe such a definition would render comparisons between animals and plants meaningful and would help us find unifying principles in the evolution of defences in island life.

In conclusion, research effort on the loss and gain of defence mechanisms on islands prioritised loss of defence in animals and gain of defence against native predators in plants. However, despite stark differences in focus, a potential unifying pattern can be delineated between the two groups. In particular, in plants, insularity promotes the loss of non-bird-specific defences and the gain of bird-specific defences (Fig. 5.3). If this applies to animals too is yet unclear; however, current work seems to indicate that a common pattern exists.

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