LOSS OF DEFENSE IN PLANTS

Title page

Are island plants really poorly defended? No support for the loss of defense hypothesis in domatia-bearing plants

M. Biddick^{1*}

¹Terrestrial Ecology Research Group

Technical University of Munich

Freising, Germany.

<https://orcid.org/0000-0002-1196-5698>

*Correspondence: matt.biddick@tum.de

Running title: LOSS OF DEFENSE IN PLANTS

Article type: Research article

Abstract: 139 words.

Main text: 1502 words.

References: 30

Figures: 2

LOSS OF DEFENSE IN PLANTS

25 1. Abstract

26 The loss of defense hypothesis posits that island colonizers experience a release from
 27 predation on the mainland and subsequently lose their defensive adaptations. While support
 28 for the hypothesis is abundant, it has never been tested in domatia-bearing plants. Leaf
 29 domatia are cave-like structures produced on the underside of leaves that facilitate a
 30 defensive mutualism with predatory and fungivorous mites. I tested the loss of defense
 31 hypothesis in six domatia-bearing taxa inhabiting New Zealand and its offshore islands. No
 32 support for the loss of defense hypothesis was found. Changes in domatia investment were
 33 instead associated with changes in leaf size – a trait that has been repeatedly observed to
 34 undergo rapid evolution on islands. Overall results demonstrate that not all types of defense
 35 are lost on islands, suggesting a higher-resolution approach is needed when studying the
 36 evolution of defense on islands.

37 **Key words:** plant defense; island syndrome; insular evolution; New Zealand; plant-arthropod
 38 mutualism.

40 2. Introduction

41 Island organisms can often differ from their mainland counterparts in remarkable yet
 42 predictable ways. Collectively, these ecological, morphological, and behavioural differences
 43 comprise what is known as the ‘*island syndrome*’ [1-3]. One of the most remarkable trends
 44 comprising the island syndrome is the loss of defensive adaptations. The loss of defense
 45 hypothesis posits that island organisms lose defensive adaptations after colonizing isolated
 46 islands because they no longer provide a fitness benefit in the absence of mainland predators
 47 [4]. For instance, many endemic island birds like the Dodo of Mauritius exhibit no fear of
 48 mammalian predators – including humans (unfortunately to their detriment). In fact, almost
 49 half of the endemic avifauna of the New Zealand archipelago went extinct following the
 50 introduction of mammalian predators [5, 6]. Similar behavioural shifts are seen in other prey
 51 taxa like insular foxes, wallabies, and lizards [7, 8]. However, defensive adaptations are not
 52 only lost in island animals.

53 Many island plants have also lost defensive adaptations [2, 9, 10]. While prey animals
 54 change in response to the absence of mainland predators in their new environment, plants
 55 change in response to absent mainland herbivores [11]. Leaf spines, for example, are

LOSS OF DEFENSE IN PLANTS

effective physical deterrents of grazing ungulates like deer and cattle [12, 13]. However, on the California Channel Islands where ungulates have historically been absent (until recent introductions), many endemic plants produce larger leaves, fewer spines, and less phenol compounds than their most closely related mainland sister taxa [14]. Another remarkable loss of defense is seen in *Pseudopanax crassifolius* (lancewood) from New Zealand. Lancewood saplings produce long, hardened leaves with lateral leaf spines that are advertised with aposematic colouration [15]. Thought to deter large (now extinct) browsing birds called *Moa* [16], these morphological adaptations have been lost in populations of *P. crassifolius* inhabiting the Chatham Islands some 800km away (where *Moa* were absent) [17]. However, not all forms of plant defense are physical.

Some plants produce cave-like structures on the underside of their leaves known as domatia that facilitate a defensive mutualism with predatory and fungivorous mites [18, 19]. Leaf domatia provide a refuge for oviposition and shelter from the environmental extremes of leaf surfaces, which mites in turn protect via the consumption of herbivorous arthropods and fungal pathogens [20]. Some 2000 taxa of domatia-bearing plants belonging to 227 plant families have been described [21]. Intriguingly, no study has documented whether this defensive mutualism is lost on islands. To test this formally, I quantified domatia production in six cosmopolitan taxa inhabiting the New Zealand mainland and its surrounding offshore islands (figure 1).

3. Methods

(a) Data collection

Data collection was conducted between June 2018 and April 2019. Individuals were chosen haphazardly while walking through easily accessible forest sections. Only fully expanded, mature leaves were measured. Leaf length was measured as the longest linear distance from the most proximal to the most distal point of the leaf lamina using a digital calliper. Leaf width was measured as the widest distance across the leaf lamina perpendicular to the leaf length measurement. Leaf area was calculated as the product of leaf length and leaf width. Although more accurate methods of estimating leaf area exist [e.g., using leaf shape correction factors or leaf scanners, 22]), leaf $\times$ width calculations sufficed for the purpose of this analysis as it is not concerned with among species differences in leaf size. Couched in

LOSS OF DEFENSE IN PLANTS

other terms, any errors associated with leaf area estimates are consistent between island-mainland comparisons. Further, many of the islands included in this study are protected by the Department of Conservation, who maintain strict standards about the type of sampling that can be conducted on them. Domatia were then counted either by eye or USB microscope (for smaller domatia).

To expand upon data gathered in the field, pressed herbarium specimens from the Auckland War Memorial Museum Herbarium were measured. The Herbarium houses an extensive collection of high quality, preserved specimens of both indigenous and exotic plants spanning the full geographic extent of the New Zealand landmass – including its offshore islands. To standardize our sampling across specimens, 3 leaves per specimen were measured using the same methodology outlined above. Leaves were chosen haphazardly, and care was taken to not damage specimens (i.e., gloves and minimal calliper–specimen contact). Mainland sampling was conducted in the Kaimai-Mamaku Forest Park in Tauranga (37°41'S, 175°45'E). This site was chosen because the Kaimai Ranges span a large latitudinal extent of the north-eastern corner of New Zealand, and therefore represent the probable source pool for many island populations.

(b) Data analysis

To test for mainland-island differences in domatia production, I conducted species-wise Welch *t*-tests. Data were left untransformed as the Welch *t*-test is robust to violations of unequal variance. The same approach was used to test for mainland-island differences in leaf size. All analyses and data visualization were conducted in the R environment (v. 3.0.1) using the ‘tidyverse’ collection of packages [23].

4. Results

No evidence for the loss of defense hypothesis was observed, with 2 taxa exhibiting marginally reduced domatia production under insular conditions, 2 taxa exhibiting no change, and 2 taxa showing increased domatia production (table 1, figure 2). Island populations of *C. rhamnoides* exhibited marginally higher rates of domatia production relative to mainland populations. Changes in domatia production were instead associated with changes in leaf size on islands (table 1).

LOSS OF DEFENSE IN PLANTS

Table 1. Results of species-wise Welch t-tests analysing mainland-island population differences in leaf size and domatia production. Samples sizes are denoted in parentheses for mainland and island populations, respectively. Significant p -values ≤ 0.05 are denoted in italics.

species	leaf size			leaf domatia		
	T	p	insular change	T	p	insular change
<i>Coprosma repens</i> (30, 332)	-6.81	< 0.01	decrease	-2.44	0.02	decrease
<i>Coprosma rhamnoides</i> (64, 204)	9.77	< 0.01	increase	1.93	0.05	increase
<i>Coprosma robusta</i> (52, 60)	2.34	0.02	increase	-1.49	0.14	no change
<i>Coprosma lucida</i> (62, 245)	4.42	< 0.01	increase	2.56	0.01	increase
<i>Elaeocarpus dentatus</i> (80, 89)	0.88	0.38	no change	-2.49	0.02	reduce
<i>Vitex lucens</i> (30, 36)	4.43	< 0.01	increase	0.82	0.42	no change

5. Discussion

Many previous studies have documented the loss of defense adaptations in island organisms, and loss of defense is considered more generally to constitute part of the ‘island syndrome’ [1-3]. However, findings from this study demonstrate that not all types of defense are lost on islands. Only a marginal reduction in leaf domatia production was observed in two of the six taxa considered. The remaining taxa either showed no change or, contrastingly, increased domatia production on islands.

Why aren’t leaf domatia lost on islands? The putative explanation for defense loss in island organisms is the absence of mainland predators. For instance, mammals are typically poor dispersers and thereby lack the ability to colonize remote islands. Plants that have historically been defended against such mammalian predators, and subsequently colonize isolated islands, are freed from this predation pressure, and no longer benefit from the production of physical deterrents like thorns, spines, and prickles. The mites inhabiting leaf domatia, on the other hand, protect plants against insect and fungal attack – both of which disperse readily to islands [24].

Another potential explanation is that the islands considered in this study, and the flora inhabiting them, are too young to exhibit the loss of defense phenomenon. Indeed, previous work has demonstrated the effect of island age and time since divergence on phylogeographic patterns [25, 26]. Most of the islands considered here are continental break offs from the larger New Zealand landmass. As such, they are relatively young in comparison to true oceanic islands like Hawaii or Mauritius. This could explain why a marginal decrease in

LOSS OF DEFENSE IN PLANTS

domatia production was observed in some taxa. Further, many islands are only weakly isolated from the New Zealand mainland, such that gene flow between island and mainland populations may exist, dampening the signal of an otherwise real effect [see 27 for discussion].

Contrary to the loss of defense hypothesis, changes in domatia production were instead associated with changes in leaf size on islands. Prior work has demonstrated that leaf size in woody plants obeys the island rule [28] – a ubiquitous pattern in island evolution whereby species converge on intermediate sizes on islands. Changes in domatia production in island populations may therefore be explained by changes in leaf size if both traits are allometrically related (though allometrically-linked traits have been shown to evolve independently [29]).

In conclusion, island plants are not ‘poorly defended’ *per se*. Rather, they tend to lose adaptations to predators and competitors that are absent on the isolated islands they colonize. Because insect and fungal attack are still very much a threat on islands, the mutualistic relationship of plants with predacious and fungivorous mites facilitated by leaf domatia remains advantageous. Future work should test whether other types of defensive mutualisms are lost or reduced on islands, such as those with ants. Finally, the loss of defense hypothesis should be amended to reflect *changes* in defense rather than its loss. While island endemics are often poorly defended against introduced mammalian predators, many are exceptionally well protected against (now extinct) avian predators [30].

Data accessibility

Data related to this article can be found at doi:10.5061/dryad.rv15dv48q.

Author contributions

M.B collected the data, conducted analyses, and wrote the manuscript.

Competing interests

The author declares no competing interests.

Funding

LOSS OF DEFENSE IN PLANTS

171 M.B is generously funded by the Alexander von Humboldt Foundation as a Fellow.

172 Acknowledgements

173 I am indebted to KC Burns for his mentorship early in my academic career. I thank Ewen
174 Cameron and all staff at the Auckland War Memorial Museum for providing access to the
175 remarkable Herbarium. I am grateful have had access to the decades-worth of specimens
176 collected by the Auckland Botanical Society. Lastly, I thank J. Schmack for her ongoing love
177 and support.

178

179 6. References

- 180 [1] Baeckens, S. & Van Damme, R. 2020 The island syndrome. *Current Biology* **30**, R338-
181 R339.
- 182 [2] Burns, K.C. 2019 *Evolution in isolation: the search for an island syndrome in plants*,
183 Cambridge University Press.
- 184 [3] Whittaker, R.J. & Fernández-Palacios, J.M. 2007 *Island biogeography: ecology, evolution,*
185 *and conservation*, Oxford University Press.
- 186 [4] Monroy, P. & García-Verdugo, C. 2019 Testing the hypothesis of loss of defenses on
187 islands across a wide latitudinal gradient of *Periploca laevigata* populations. *American journal*
188 *of botany* **106**, 303-312.
- 189 [5] Holdaway, R. & MacPhee, R. 1999 Extinctions in near time: Causes, contexts, and
190 consequences.
- 191 [6] Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. 2004 Avian
192 extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955-1958.
- 193 [7] Blumstein, D.T. & Daniel, J.C. 2002 Isolation from mammalian predators differentially
194 affects two congeners. *Behavioral Ecology* **13**, 657-663.
- 195 [8] Cooper Jr, W.E., Pyron, R.A. & Garland Jr, T. 2014 Island tameness: living on islands
196 reduces flight initiation distance. *Proceedings of the Royal Society B: Biological Sciences* **281**,
197 20133019.
- 198 [9] Carlquist, S. 1974 *Island biology*. Columbia University Press, New York.
- 199 [10] Kavanagh, P.H. 2015 Herbivory and the evolution of divaricate plants: structural defences
200 lost on an offshore island. *Austral Ecology* **40**, 206-211.
- 201 [11] Vourc'h, G., Martin, J.-L., Duncan, P., Escarré, J. & Clausen, T.P. 2001 Defensive
202 adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and
203 island populations. *Oecologia* **126**, 84-93.
- 204 [12] Cooper, S.M. & Ginnett, T.F. 1998 Spines protect plants against browsing by small
205 climbing mammals. *Oecologia* **113**, 219-221.
- 206 [13] Cooper, S.M. & Owen-Smith, N. 1986 Effects of plant spinescence on large mammalian
207 herbivores. *Oecologia* **68**, 446-455.
- 208 [14] Bowen, L. & Van Vuren, D. 1997 Insular endemic plants lack defenses against herbivores.
209 *Conservation Biology* **11**, 1249-1254.
- 210 [15] Kavanagh, P.H., Shaw, R.C. & Burns, K.C. 2016 Potential aposematism in an insular tree
211 species: are signals dishonest early in ontogeny? *Biological Journal of the Linnean Society*
212 **118**, 951-958.

LOSS OF DEFENSE IN PLANTS

- 213 [16] Fadzly, N. & Burns, K. 2010 Hiding from the ghost of herbivory past: evidence for crypsis
214 in an insular tree species. *International journal of plant sciences* **171**, 828-833.
- 215 [17] Burns, K. & Dawson, J.W. 2009 Heteroblasty on Chatham Island: a comparison with New
216 Zealand and New Caledonia. *New Zealand Journal of Ecology*, 156-163.
- 217 [18] AGRAWAL, A. 1997 Do leaf domatia mediate a plant–mite mutualism? An experimental
218 test of the effects on predators and herbivores. *Ecological Entomology* **22**, 371-376.
- 219 [19] Agrawal, A.A. & Karban, R. 1997 Domatia mediate plantarthropod mutualism. *Nature*
220 **387**, 562-563.
- 221 [20] Grostal, R. & O'Dowd, D.J. 1994 Plants, mites and mutualism: leaf domatia and the
222 abundance and reproduction of mites on *Viburnum tinus* (Caprifoliaceae). *Oecologia* **97**, 308-
223 315.
- 224 [21] Brouwer, Y.M. & Clifford, H.T. 1990 An annotated list of domatia-bearing species. *Notes*
225 *from the Jodrell Laboratory*, 1-33.
- 226 [22] Lin, S., Niklas, K.J., Wan, Y., Hölscher, D., Hui, C., Ding, Y. & Shi, P. 2020 Leaf shape
227 influences the scaling of leaf dry mass vs. area: a test case using bamboos. *Annals of Forest*
228 *Science* **77**, 1-15.
- 229 [23] Wickham, H. 2017 The tidyverse. *R package ver 1*, 836.
- 230 [24] Simberloff, D. 1981 What makes a good island colonist? In *Insect life history patterns*
231 (pp. 195-205, Springer.
- 232 [25] Cox, B.T.M. & Burns, K. 2017 Convergent evolution of gigantism in the flora of an
233 isolated archipelago. *Evolutionary Ecology* **31**, 741-752.
- 234 [26] Emerson, B. 2002 Evolution on oceanic islands: molecular phylogenetic approaches to
235 understanding pattern and process. *Molecular ecology* **11**, 951-966.
- 236 [27] Welch, J.J. 2009 Testing the island rule: primates as a case study. *Proceedings of the Royal*
237 *Society B: Biological Sciences* **276**, 675-682.
- 238 [28] Biddick, M., Hendriks, A. & Burns, K. 2019 Plants obey (and disobey) the island rule.
239 *Proceedings of the National Academy of Sciences* **116**, 17632-17634.
- 240 [29] Biddick, M., Hutton, I. & Burns, K. 2019 Independent evolution of allometric traits: A
241 test of the allometric constraint hypothesis in island vines. *Biological Journal of the Linnean*
242 *Society* **126**, 203-211.
- 243 [30] Gibbs, G.W. 2006 *Ghosts of Gondwana: the history of life in New Zealand*, Craig Potton
244 Publishing.

LOSS OF DEFENSE IN PLANTS

Figure 1. Study area. (a) Remote islands off the east coast of the New Zealand ‘mainland’ were used to test the loss of defense hypothesis. (b) Leaf domatia are cave-like structures produced on the underside of leaves that facilitate a defensive mutualism with predacious and fungivorous mites (example of tuft domatia in *Carpodetus serratus* shown, photo credit: Morgan Ngata). Open circles denote individual offshore islands.

LOSS OF DEFENSE IN PLANTS

Figure 2. Leaf domatia production (y-axis) and leaf size (x-axis, logarithm-transformed) in six cosmopolitan plant taxa inhabiting the New Zealand mainland (red) and its offshore islands (green). Black arrows and asterisks denote significance and direction of change in each trait on islands.