1 Introduction: Ecology and Evolution of Plant-Herbivore Interactions on Islands

Luis Abdala-Roberts and Xoaquín Moreira

Abstract

Islands provide singular yet powerful natural settings for testing ecological and evolutionary hypotheses and have been particularly informative for disentangling the drivers and consequences of species interactions. Damage to plants inflicted by vertebrate and invertebrate herbivores represents an especially strong and ubiquitous force on island life which early on caught the attention of biologists. There are numerous biotic and abiotic factors that potentially explain herbivory patterns on islands, and yet many of these remain elusive or have simply not been tested. This book seeks to integrate current research on plant-herbivore interactions on islands, including both syntheses and empirical studies, shedding new insight and pointing to candidate mechanisms that explain variability in herbivory patterns on islands. Specifically, this book addresses research testing for patterns of variation in herbivory in relation to different types of plant traits associated with vertebrate and invertebrate herbivory on islands, as well as toisland features or processes classically studied in population ecology or island biogeography but less tested on plant-herbivore interactions. These include island area or distance to mainland, temporal (e.g., successional) and spatial (e.g., metapopulation) dynamics, and herbivore invasions or extinctions. Novel insight is gained by establishing links between or jointly testing these drivers, as well as by harnessing ecological complexity such as through the study of food web dynamics to explain herbivory and plant trait variation on islands. Likewise, several chapters deliver new syntheses that uncover novel patterns and can help

L. Abdala-Roberts (✉)
Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Mérida, Yucatán, México

X. Moreira
Misión Biológica de Galicia (MBG-CSIC), Pontevedra, Galicia, Spain

X. Moreira, L. Abdala-Roberts (eds.), *Ecology and Evolution of Plant-Herbivore Interactions on Islands*, Ecological Studies 249,
https://doi.org/10.1007/978-3-031-47814-7_1

pave the way for future empirical studies. Overall, these studies contribute to understanding how biotic and abiotic factors acting at different temporal and spatial scales shape plant-herbivore interactions on islands, and in turn how such effects influence island biological systems.

1.1 Islands as Model Systems in Ecology and Evolution of Species Interactions

Islands have long marveled natural historians, ecologists, and evolutionary biologists given the beauty of their landscapes and biological peculiarities (Darwin 1859; Wallace 1880; Warren et al. 2015; Whittaker et al. 2017). Within the scientific realm, the relative simplicity of their biotic systems and unique physical and geographic features (Diamond 1983) have made them especially amenable for studying ecological and evolutionary processes shaping species diversity and speciation (Losos and Ricklefs 2009; Gillespie 2016), metapopulation dynamics (Hanski 1999, 2010), and ecosystem processes (Oksanen et al. 2010; Young et al. 2010), to name a few. In particular, they have provided fertile ground for testing effects of biotic and abiotic or physical factors on species interactions, including the role of invasions (e.g., Henneman and Memmott 2001; Funk and Throop 2010; Pringle et al. 2019), island area and trophic complexity (e.g., Schoener et al. 2016), and disturbances (reviewed by Spiller et al. 2018), as well as the evolutionary consequences of these and other factors acting on species interactions (reviewed by Grant 1998; Terborgh 2010; Burns 2019). Insight gained has shown that island biological systems are strongly shaped by species interactions.

The study of species interactions on islands stems back to early descriptive work spanning pairwise interactions (e.g., pollination, herbivory; Wallace 1857; Darwin 1862, 1909) to food webs (e.g., Darwin 1839; Summerhayes and Elton 1923). Nonetheless, formal assessments (i.e., quantification) of species interactions did not come until the last third of the twentieth century, building on early work in iconic systems and expanding to other systems around the globe (Burns 2019; Moreira et al. 2021). These studies included, for example, work on the role of competition (and island physical features) in bird community assembly in Southeast Asia (Diamond 1975) and on trait evolution and speciation of Darwin finches in the Galapagos (Grant and Grant 1998; Carvajal-Endara et al. 2020), the evolution of plant reproductive traits linked to pollinators and seed dispersers across different systems (Barrett et al. 1996; Burns 2019), drivers of food web dynamics spanning the Caribbean (e.g., Bahamas; Spiller and Schoener 1994) and Southeast Asia (e.g., New Guinea; Houska Tahadlova et al. 2023) to the Arctic (e.g., Bear Island; Hodkinson and Coulson 2004), and the study of herbivory and plant defensive traits across several regions including islands in the Indian Ocean (e.g., Mauritius, Maldives), the Hawaiian Islands, and New Zealand (Terborgh 2010; Burns 2019; Barton et al. 2021). More recently, there have also been theoretical developments expanding on classical theory to explicitly consider species interactions (e.g., Holt 2010; Gravel et al. 2011).

1.2 Herbivory on Islands

In this book, we focus on herbivory as a prominent interaction on islands. Plants and herbivores together represent more than half of the macroscopic diversity on the planet (Strong Jr et al. 1984; Turcotte et al. 2014) and are strongly influenced by insularity and at the same time profoundly shape life on islands. Early descriptive work (e.g., Janzen 1973, 1975; Carlquist 1974; Becker 1975; Bowen and Van Buren 1997), consistent with biogeographical models predicting lower herbivore abundance and diversity on islands (MacArthur and Wilson 1967; Simberloff and Wilson 1969), found that plants inhabiting islands were less defended, presumably as a result of lower herbivore pressure (reviewed by Terborgh 2010). However, studies that followed depicted a more complex picture (Moreira et al. 2021). Indeed, some groups of vertebrate herbivores native to islands (e.g., tortoises, crabs, and birds) can reach high abundances and often dominate insular systems, thereby presumably exerting strong selection on plants (reviewed by Terborgh 2010; Burns 2019). In addition, paleoecological data strongly suggest that in many cases extinct vertebrate herbivores played a key role in shaping plant resistance- and dispersal-related traits (i.e., anachronisms; McGlone and Clarkson 1993; Givnish et al. 1994; Bond and Silander 2007; Kavanagh 2015). Still, for many systems we have a poor understanding of the role that extinct as well as extant island herbivores have played in shaping plant evolution on islands (Burns 2019). Further obtention and synthesis of present-day and paleoecological data on herbivory and plant traits are needed, including less studied (and yet ubiquitous) insect herbivory. Crucially, empirical work is needed that jointly tests for variation in plant traits, herbivory, and associated food web dynamics to piece together patterns of variation at each level and uncover species interaction mechanisms. An explicit consideration of island physical (area, age, etc.) and abiotic (soil, climate) features to link interaction patterns and dynamics with biogeographical factors (Moreira and Abdala-Roberts 2022; Obrist et al. 2022) is also needed to bridge evolutionary ecology and island biogeography research. Toward reaching these goals, data syntheses and empirical tests involving multiple systems (e.g., within a region) will increase explanatory power and yield more robust patterns and tests of candidate mechanisms.

1.3 Chapters Overview: Novel Tests and Views

This book integrates current research addressing the above challenges while yielding new perspectives on insularity effects on plant-herbivore interactions. First, it delves into patterns of variation in plant traits (Part I), including physical defenses (Chap. 2), dispersal-related traits (Chap. 3), chemical and functional traits (Chap. 4), and a broad overview of losses and gains of plant (and animal) defenses on islands (Chap. 5). In addition, the impacts of introduced herbivores on the traits, abundance, and community structure of island plants are also addressed (Chaps. 6 and 7). Then, this volume turns to patterns of variation in herbivory (Part II), including temporal dynamics of island colonization and metapopulation processes shaping plant-herbivore interactions (Chap. 8), and a cross-system phylogenetically controlled test of island abiotic and physical drivers of insect herbivory (Chap. 9). Lastly, the content addresses food web-level dynamics to understand variation in herbivory and plant traits (Part III), including work on the role of island abiotic disturbances and resource pulses on predation by lizards (Chap. 10), predation pressure along elevational clines in island mountain ranges (Chap. 11), and food web dynamics shaping predation pressure in island and mainland agroecosystems (Chap. 12). We next describe in more detail the main findings of each chapter.

Part I focuses on biotic and abiotic factors or phenomena shaping plant traits, populations, and communities on islands. Namely, Barton et al. (Chap. 2) review evidence for associations between island megafauna and the occurrence of plant spinescence (Fig. 1.1a), including comparisons across systems with different historical legacies of herbivore pressure. They find that the incidence of spinescence is rather low on islands, but that there are still numerous island plants which bear this trait, for which there is currently no apparent function. Results are discussed in the context of evolutionary pressure by extinct megafauna and the persistence of defensive anachronisms. Relatedly, Heinen and Borregaard (Chap. 3) review the incidence and consequences of frugivore extinctions for island plants and put forward evidence for such dynamics from a model system (Mauritius) (Fig. 1.1b). They report a disproportionately higher (recent) extinction rate of large-bodied frugivores on islands (relative to mainland), suggesting acute ecological and evolutionary impacts on island floras due to frugivore species losses. Like Barton et al., they also discuss the role of dispersal anachronisms and their specificity in explaining evolutionary outcomes and ecological impacts. Then, García-Verdugo et al. (Chap. 4) provide a case study of variation in leaf physical and chemical traits across mainland Mediterranean sites and Macaronesian islands for several plant taxa. They show that insular plants have larger leaves, higher amounts of secondary metabolites, and lower photosynthetic rates, suggesting convergence toward a leaf functional-defensive syndrome which appears to be unrelated to herbivory. In addition, also synthesizing plant trait patterns, Carlie et al. (Chap. 5) provide an assessment of losses and gains of defenses for island plants across the globe and show a trend for a loss of defenses against non-bird herbivores (which are more common or only present on mainland) and gain of defenses against dominant island vertebrate herbivores which are often birds (Fig. 1.1c). They also find that insularity is associated with changes in other plant traits such as size (e.g., dwarfism), which could be potentially evolutionarily linked to herbivory. Finally, Capó et al. (Chap. 6) and Bartolomé and Seguí (Chap. 7) provide contrasting (and yet complementary) views on the impacts of introduced (non-native) mammalian herbivores on island plant traits and communities. The former reports on evidence for marked impacts on native plant traits, abundance, and distribution, emphasizing effects on island endemics (Fig. 1.2), whereas the latter points to ecosystem services provided by introduced mammals on islands.

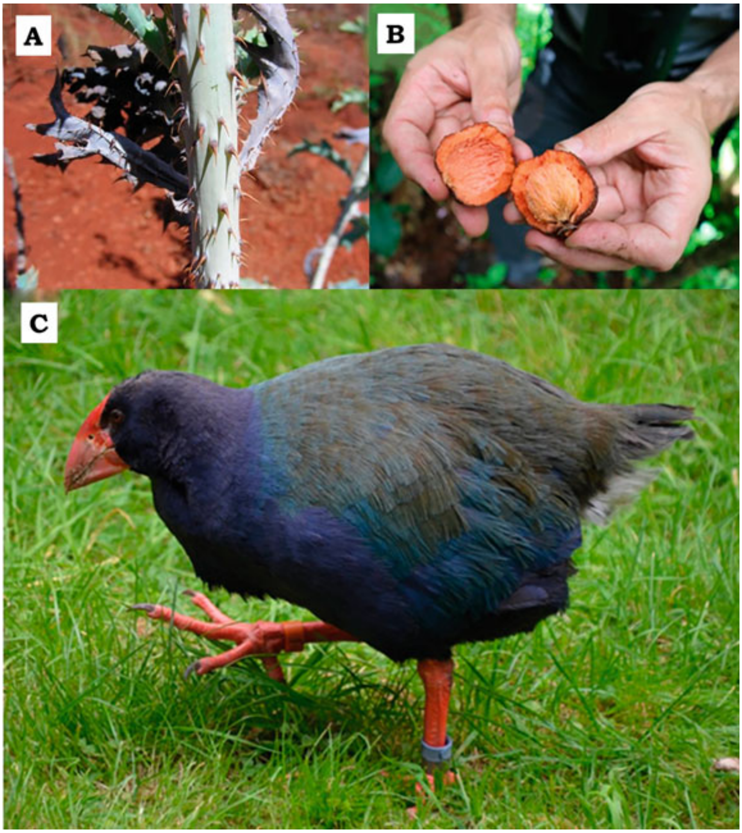

Fig. 1.1 (**a**) The Hawaiian Prickly Poppy (*Argemone glauca*), a spinescent plant species widely distributed in Hawaiian Islands (photo credit: Kasey Barton). (**b**) The rare and endemic palm *Hyophorbe vaughanii* (Arecaceae) in Mauritius bears large seeds within inconspicuous brown fruits that become vibrant orange upon ripening on the ground, potentially attracting extinct ground-dwelling frugivores (such as giant tortoises or Dodos) (photo credit: Julia Heinen). (**c**) The South Island takahē (*Porphyrio hochstetteri*), a flightless herbivorous bird indigenous to New Zealand (photo credit: Fabio Mologni)

Part II addresses insularity effects on patterns of herbivory. First, Hambäck et al. (Chap. 8) provide a temporal perspective on variation in herbivory and its reciprocal link with plant traits in land-rising coastlines of the Baltic region. They show a build-up in plant defenses with increasing herbivory from early plant colonization to later successional stages. Increased defenses in turn correlate with reduced reproduction in adult plants, thereby affecting propagule production and dispersal to other islands and therefore metapopulation dynamics which end up feeding back to affect succession dynamics and associated herbivory patterns. Then, Moreira et al. (Chap. 9) provide a phylogenetically controlled evaluation of the effects of island physical and abiotic features on insect leaf herbivory for 76 plant species distributed across several European insular systems (Fig. 1.3a–d). They report, however, no

Fig. 1.2 Increase in vegetation cover and diversity before (**a**) and after (**b**) a drastic reduction of goat populations in Es Vedra (islet close to Eivissa, Balearic Islands). Pictures were taken the same day in May 2016 (**a**) and 2017 (**b**). Photo credit: Joan Rita

effects of island area or abiotic (climatic) factors on herbivory patterns across islands.

Finally, Part III addresses plant-herbivore interactions on islands from a food web perspective, also folding in abiotic forcing and management perspectives. Spiller et al. (Chap. 10) synthesize findings from their studies on the impacts of predatory lizards (Fig. 1.4a) on herbivory and plants in the Bahamas and emphasize the key role exogenous factors play in shaping temporal variation in food web dynamics. Specifically, they find that resprouting after damage caused by hurricanes leads to higher herbivory and in turn higher predation, whereas seaweed deposition causes shifts in lizard diet which weaken predation but in the long term increases predation by boosting plant growth and lizard population sizes. Then, Sam et al. (Chap. 11) similarly look at the role of abiotic forcing on predation pressure, in this case analyzing data from insectivorous bird and ant exclusion studies conducted along elevational clines on islands and mainland sites across the globe. For predation by birds (Fig. 1.4b), they found stronger effects on herbivory on islands than on mainland but no evidence of elevational clines in predation effects for either islands or mainland. Effects of ants (Fig. 1.4c), on the other hand, do not differ between islands and mainland (though tended to be stronger in the latter) and exhibited elevational clines that were similar in both landform types. Interestingly, vertebrates had stronger effects on invertebrate predators at low elevations in both islands and mainland, suggesting intra-guild predation dampens herbivory clines similarly across environment types. Finally, Vandermeer et al. (Chap. 12) compare food web dynamics associated with plant pests in island versus mainland coffee farms. They find baseline similarities in coffee-associated food webs across island (Puerto Rico) versus mainland (Mexico) coffee agroecosystems, but substantial differences in the relative frequency of species and interactions. Importantly, ant species modulate trophic interactions in complex ways which differ on islands versus mainland. They act as predators of berry borers and as mutualists of scale insects, but the latter interaction is more common on mainland and indirectly drives greater suppression of

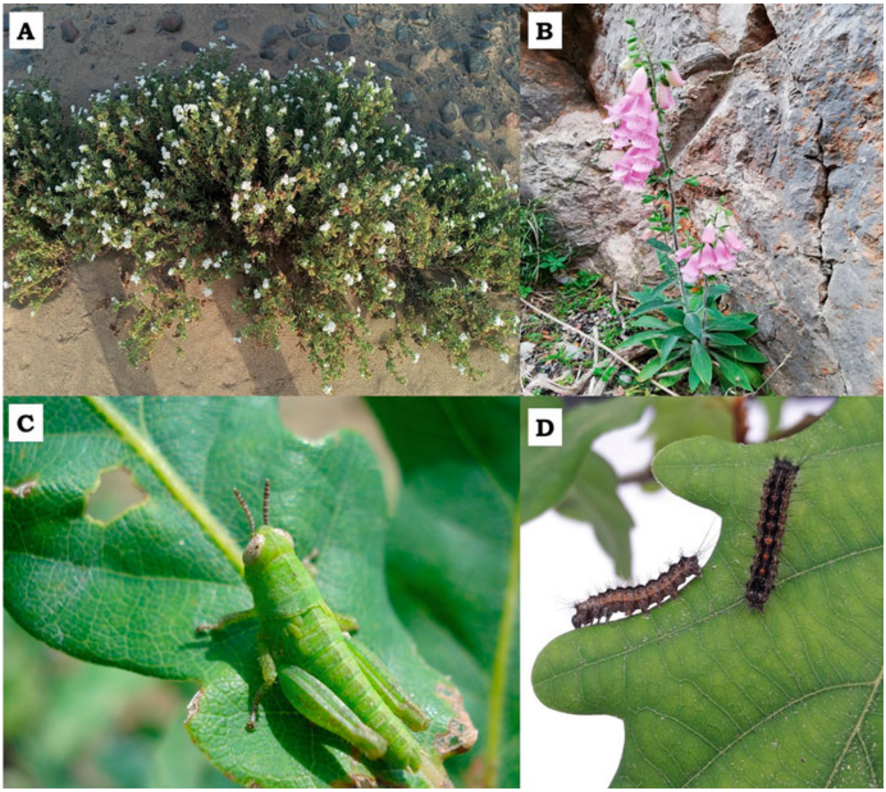

Fig. 1.3 (**a**) *Heliotropium ramosissimum*, an herbaceous perennial plant native to Canary Islands (photo credit: Xoaquín Moreira). (**b**) *Digitalis minor*, an herbaceous perennial plant endemic to Majorca and Menorca in Balearic Islands (photo credit: Miquel Capó). (**c**) Grasshopper (photo credit: Bastien Castagneyrol) and (**d**) larvae of *Lymatria dispar* (photo credit: Thomas Damestoy) feeding on leaves of the English oak *Quercus robur*, a species widely distributed across islands of western Europe

borers. Ant-mediated interactions also appear to play out differently for coffee-pathogen interactions, with higher disease incidence on mainland than on island farms. Further, lizards can also be important predators on island farms but rare on mainland.

Overall, we hope this volume positively impacts the field by stimulating research aimed at understanding how island biotic and abiotic factors shape plant-herbivore interactions, as well as species interactions overall, both ecologically and evolutionarily, and the resulting impacts on species traits, communities, and ecosystems. What we learn about species interactions, herbivory in particular, can be used to better understand and manage island biological systems, as well as those found on mainland.

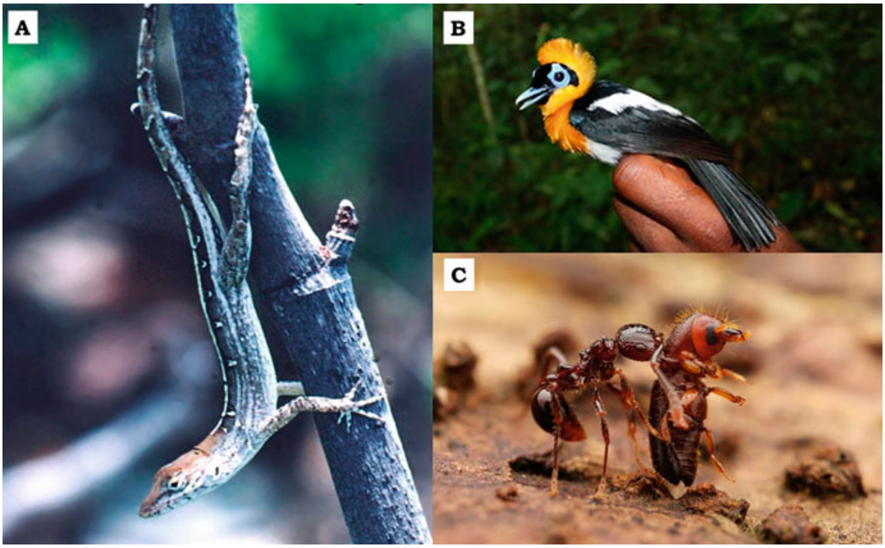

Fig. 1.4 (**a**) The brown anole (*Anolis sagrei*), a predatory lizard widely distributed in Bahamas Islands (photo credit: David Spiller). (**b**) The ochre-collared monarch (*Arses insularis*), an insectivorous bird species endemic to New Guinea (photo credit: Katerina Sam). (**c**) The predatory ant *Pristomyrmex quadridens* attacking the island pinhole borer (*Xyleborus perforans*) in New Guinea (photo credit: Philipp Hönle)

References

Barrett SCH, Harder LD, Worley AC (1996) The comparative biology of pollination and mating in flowering plants. Philos Trans R Soc B 351:1271–1280

Barton KE, Westerband A, Ostertag R, Stacy E, Winter K, Drake DR, Fortini LB, Litton CM, Cordell S, Krushelnycky P, Kawelo K, Feliciano K, Bennett G, Knight T (2021) Hawai'i forest review: synthesizing the ecology, evolution, and conservation of a model system. Perspect Plant Ecol Evol Systemat 52:125631

Becker P (1975) Island colonization by carnivorous and herbivorous coleoptera. J Anim Ecol 44: 893–906

Bond WJ, Silander JA (2007) Springs and wire plants: anachronistic defences against Madagascar's extinct elephant birds. Proc R Soc B 274:1985–1992

Bowen L, Van Buren D (1997) Insular endemic plants lack defences against herbivores. Conserv Biol 11:1249–1254

Burns KC (2019) Differences in defence. In: Burns KC (ed) Evolution in isolation: the search for an island syndrome in plants. Cambridge University Press, Cambridge, pp 43–84

Carlquist S (1974) Island biology. Columbia University Press, New York, NY

Carvajal-Endara S, Hendry AP, Emery NC, Neu CP, Carmona D, Gotanda KM, Davies TJ, Chaves JA, Johnson MTJ (2020) The ecology and evolution of seed predation by Darwin's finches on *Tribulus cistoides* on the Galápagos Islands. Ecol Monogr 90:e01392

Darwin CR (1839) Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world: under the command of Capt. Fitz Roy, R.N. Columbia University Press, London

Darwin CR (1859) On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life. John Murray, London
Darwin CR (1862) On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing. Kessinger Publishing/John Murray, London
Darwin CR (1909) The voyage of the beagle. P.F. Collier, New York, NY
Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, MA, pp 342–444
Diamond JM (1983) Laboratory, field and natural experiments. Nature 304:586–587
Funk JL, Throop HL (2010) Enemy release and plant invasion: patterns of defensive traits and leaf damage in Hawaii. Oecologia 162:815–823
Gillespie RG (2016) Island time and the interplay between ecology and evolution in species diversification. Evol Appl 9:53–73
Givnish TJ, Sytsma KJ, Smith JF, Hahn WJ (1994) Thorn-like prickles and heterophylly in Cyanea: adaptations to extinct avian browsers on Hawaii? Proc Natl Acad Sci USA 91:2810–2814
Grant BR, Grant PR (1998) Hybridization and speciation in Darwin's finches: the role of sexual imprinting on a culturally transmitted trait. In: Howard DJ, Berlocher SH (eds) Endless forms: species and speciation. Oxford University Press, Oxford, pp 404–422
Grant PR (1998) Evolution on islands. Oxford University Press, New Yok, NY
Gravel D, Massol F, Canard E, Mouillot D, Mouquet N (2011) Trophic theory of island biogeography. Ecol Lett 14:1010–1016
Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford
Hanski I (2010) Incorporating the spatial configuration of the habitat into ecology and evolutionary biology. In: Cantrell S, Cosner C, Ruan S (eds) Spatial ecology. CRC Press, London, pp 167–188
Henneman ML, Memmott J (2001) Infiltration of a Hawaiian community by introduced biological control agents. Science 17:1314–1316
Hodkinson ID, Coulson SJ (2004) Are high Arctic terrestrial food chains really that simple? – The Bear Island food web revisited. Oikos 106:427–431
Holt RD (2010) Towards a trophic island biogeography: reflections on the interface of island biogeography and food web ecology. In: Losos JB, Ricklefs RE (eds) The theory of island biogeography revisited. Princeton University Press, Princeton, NJ, pp 143–185
Houska Tahadlova M, Mottl O, Jorge LR, Koane B, Novotny V, Sam K (2023) Trophic cascades in tropical rainforests: effects of vertebrate predator exclusion on arthropods and plants in Papua New Guinea. Biotropica 55:70–80
Janzen DH (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687–708
Janzen DH (1975) Behavior of *Hymenaea courbaril* when its predispersal seed predator is absent. Science 189:145–147
Kavanagh PH (2015) Herbivory and the evolution of divaricate plants: structural defences lost on an offshore island. Austral Ecol 40:206–211
Losos JB, Ricklefs RE (2009) Adaptation and diversification on islands. Nature 457:830–836
MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ
McGlone MS, Clarkson BD (1993) Ghost stories: moa, plant defences and evolution in New Zealand. Tuatara 32:1–21
Moreira X, Abdala-Roberts L (2022) A roadmap for future research on insularity effects on plant-herbivore interactions. Glob Ecol Biogeogr 31:602–610
Moreira X, Castagneyrol B, García-Verdugo C, Abdala-Roberts L (2021) A meta-analysis of insularity effects on herbivory and plant defences. J Biogeogr 48:386–393
Obrist DS, Hanly PJ, Brown NEM, Ernst CM, Wickham SB, Fitzpatrick OT, Kennedy JC, Nijland W, Reshitnyk LY, Darimont CT, Starzomski BM, Reynolds JD (2022) Biogeographic features mediate marine subsidies to island food webs. Ecology 13:e4171

Oksanen L, Oksanen T, Dahlgren J, Hambäck P (2010) Islands as test of the green world hypothesis. In: Terborgh J, Estes J (eds) Trophic Cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington DC, pp 163–178

Pringle RM, Kartzinel TR, Palmer TM, Thurman TJ, Fox-Dobbs K, Xu CCY, Hutchinson MC, Coverdale TC, Daskin JH, Evangelista DA, Gotanda KM, Man in't Veld NA, Wegener JE, Kolbe JJ, Schoener TW, Spiller DA, Losos JB, Barrett RDH (2019) Predator-induced collapse of niche structure and species coexistence. Nature 570:58–64

Schoener TW, Spiller DA, Piovia-Scott J (2016) Variation in ecological interaction strength with island area: theory and data from the Bahamian archipelago. Glob Ecol Biogeogr 25:891–899

Simberloff DS, Wilson EO (1969) Experimental zoogeography of islands: the colonization of empty islands. Ecology 50:278–296

Spiller DA, Schoener T, Piovia-Scott J (2018) Recovery of food webs following natural physical disturbances. Ann N Y Acad Sci 1429:100–117

Spiller DA, Schoener TW (1994) Effects of top and intermediate predators in a terrestrial food web. Ecology 75:182–196

Strong Jr DR, Lawton JH, Southwood TRE (1984) Insects on plants: community patterns and mechanisms. Oxford

Summerhayes VS, Elton CS (1923) Contributions to the ecology of Spitsbergen and Bear Island. J Ecol 11:214–286

Terborgh J (2010) The trophic cascade on islands. In: Losos JB, Ricklefs RE (eds) The theory of island biogeography revisited. Princeton University Press, Princeton, NJ, pp 116–142

Turcotte MM, Davies TJ, Thomsen CJM, Johnson MTJ (2014) Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. Proc R Soc B 281:20140555

Wallace AR (1857) On the natural history of the Aru Islands. Ann Mag Nat Hist. Supplement to volume 20

Wallace AR (1880) Island life; or, the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates. Macmillan, London

Warren BH, Simberloff D, Ricklefs RE, Aguilée R, Condamine FL, Gravel D, Morlon H, Mouquet N, Rosindell J, Casquet J, Conti E, Cornuault J, Fernández-Palacios JM, Hengl T, Norder SJ, Rijsdijk KF, Sanmartín I, Strasberg D, Triantis KA, Valente LM, Whittaker RJ, Gillespie RG, Emerson BC, Thébaud C (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. Ecol Lett 18:200–217

Whittaker RJ, Fernández-Palacios JM, Matthews TJ, Borregaard MK, Triantis KA (2017) Island biogeography: taking the long view of nature's laboratories. Science 357:eaam8326

Young HS, McCauley DJ, Dunbar RB, Dirzo R (2010) Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. Proc Natl Acad Sci USA 107:2072–2077