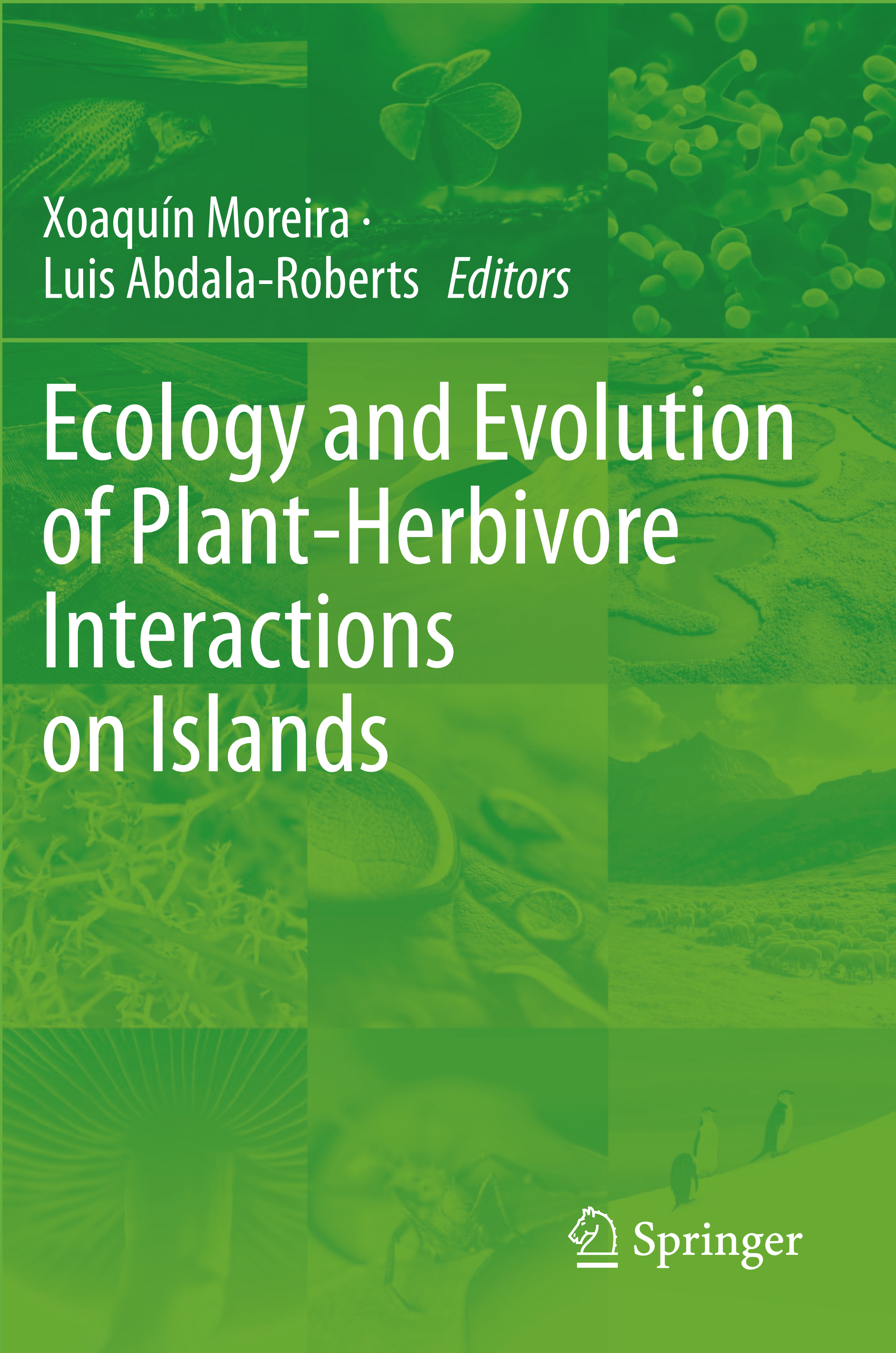
Ecological Studies 249



Xoaquín Moreira ·
Luis Abdala-Roberts *Editors*

Ecology and Evolution of Plant-Herbivore Interactions on Islands

Springer

Ecological Studies

Analysis and Synthesis

Volume 249

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Xoaquín Moreira • Luis Abdala-Roberts
Editors

Ecology and Evolution of Plant-Herbivore Interactions on Islands

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Editors
Xoaquín Moreira
Misión Biológica de Galicia (MBG-CSIC)
Pontevedra, Spain

Luis Abdala-Roberts
Departamento de Ecología
Universidad Autónoma de Yucatán
Mérida, Mexico

ISSN 0070-8356 ISSN 2196-971X (electronic)
Ecological Studies
ISBN 978-3-031-47813-0 ISBN 978-3-031-47814-7 (eBook)
https://doi.org/10.1007/978-3-031-47814-7

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To my daughters (Olivia, Marina), wife
(Silvia) and parents (Joaquín, Aurora)
—Xoaquín Moreira
To my dear family and friends, guiding forces
and teachers in life.
—Luis Abdala-Roberts

Foreword

Islands fascinate ecologists. In part, this is because a large portion of island plants and animals are endemic, and ecologists are drawn to unique biodiversity. Islands also have fewer species than found on the mainland. This simplification increases our ability to understand the forces structuring biological communities, otherwise so much more complex on the mainland. Islands also have well-defined borders and they are often replicated in archipelagos, both of which provide the opportunity to test ecological theory through natural and manipulative experiments.

Darwin and Wallace, in their published accounts of the natural history of tropical islands, revealed the possibilities of islands as laboratories for the study of ecology, evolution, and biogeography. These early accounts have since launched a host of studies focusing on island flora and fauna. Indeed, perhaps the most well-regarded theories in these fields, Evolution by Natural Selection and The Theory of Island Biogeography, have their roots in the early accounts of Darwin and Wallace.

This volume, for the first time, brings together research focusing on plant–herbivore interactions on islands. Herbivory is the most basic of ecological interactions, structuring all components of food webs through the transfer of energy, nutrients, and secondary metabolites from plants to animals. It is also the interaction that contributes to the success, or lack thereof, of agriculture. Thus, to understand island ecology, including the ability of humans to live sustainably on islands, one must understand the details of the interactions between plants and their herbivores on islands.

A largely untested hypothesis scattered throughout the island ecology literature is that plant–herbivore interactions on islands are qualitatively different from those on the mainland. Early natural history observations, and comparisons of plants and herbivores between mainland and islands, gave rise to this hypothesis, which has largely gone untested. Exploration of this hypothesis provides the basis for many of the chapters included in this volume.

When Charles Darwin first set foot on the island of Chatham of the Galapagos, on September 17, 1835, the first biological interaction he observed was that of herbivory. Amidst a rugged field of sharp lava, he encountered two giant tortoises, one feeding on a cactus pad. Having spent the last three years traveling along the coast of South America, Darwin recognized a uniquely different interaction (a "typical terrestrial" iguana foraging in the tidal zone for algae) and a uniquely different organism (extant giant tortoises were known only from other Pacific and Indian Ocean islands) as an herbivore. These observations were perhaps the first clue that interactions between plants and herbivores on oceanic islands might differ from those on the associated mainland.

We now know that, in addition to housing fewer total species than the neighboring mainland, they also can have or had a uniquely different collection of species than found on the mainland. Fossil evidence and historical accounts attest to a vertebrate herbivore fauna, depending on the island, of elephant birds, moas, and giant geese (all extinct), giant lemurs (also extinct), and giant tortoises and lizards, for example. Wholly, 61% of vertebrate global extinctions since 1500 have occurred on oceanic islands although they only represent ~6% of the land surface area. The evolutionary pressure represented by these animals may have led to unique physical defense and architectural traits in their botanical prey, now appearing to be anachronistic in their absence. Whether this applies to phytochemicals largely remains to be seen. Collectively, these missing interactions due to global herbivore extinctions challenge our ability to uncover the adaptive reasons for certain traits in island plants. For the most part, the role of invertebrate herbivores and diseases has received only limited research attention to the point that we do not know whether island and mainland faunas even differ let alone whether their impacts differ.

Interactions between plants and herbivores also serve as the foundation for tritrophic interactions. Long-term studies, some described here, of plants and their herbivores and the natural enemies of those herbivores reveal that trophic control of island herbivores is ever changing. The presence or absence of winter ice and catastrophic storms can add or remove species seemingly overnight. This vulnerability to gain or loss of important members in food webs allows for important insights into how ecosystems are structured.

The above understanding of island food webs is critically important for practical reasons. First, imbedded in any attempt toward sustainable crop production is the need for trophic control of herbivorous pests. Second, attempts to control or eradicate introduced species further require understanding of basic population biology and the role of trophic control. Introduced species have populated islands since humans first began visiting them, having profound effects on native species. This understanding is urgent given the global biodiversity crisis and that island endemism is 9.1 to 8.5 greater in plants and vertebrates, respectively, than on mainland.

The volume is both valuable and timely. It is valuable because herbivory is a foundational process for all ecosystems. Island research on herbivory has been conducted across the globe from East to West and from the Arctic to the Equator and into the Southern Hemisphere, offering a chance to reveal general principles. The contributing authors all are experts in the discipline of plant–herbivore interactions but bring a variety of viewpoints depending on their approach to studying these interactions. Most importantly, they provide insightful analysis of their particular question and discuss future directions.

This volume is timely because ecologists have been using islands as their laboratory to study plant–herbivore interactions for the last 70 years but there has been no compilation to date that summarizes their results. It is also timely in that many of the island systems currently under study, and to be studied, are heavily altered by introduced species. And even more so, islands are threatened by climate change, directly by changes in the abiotic environment and human agricultural expansion, and indirectly by sea level rise. Islands are indeed a microcosm of what is occurring to our planet globally.

River Falls, WI, USA

Robert J. Marquis

Preface

We met in the laboratory of Professor Kailen Mooney at the University of California-Irvine in 2012. At that time, we investigated plant–herbivore interactions from different perspectives, Luis focused on tritrophic mechanisms affecting herbivory and Xoaquín focused on plant induced defenses. For more than a decade, we have worked together, sharing projects and students, and in the process have gradually melded and enriched our perspectives: Luis gaining insight into plant traits underlying interactions and Xoaquín on tritrophic interaction mechanisms. It could be said that we belong to the same group but on two different continents.

The motivation to put together this book arose from several discussions we had in recent years. Specifically, in 2018, we began to extend our work on plant–herbivore interactions to island systems. The ecological and evolutionary effects of herbivores and their mechanisms remain poorly understood on islands, despite the known importance of plant–herbivore interactions for island ecosystems and abundant descriptive studies. The present volume seeks to synthesize recent findings and advance our knowledge on the ecology and evolution of plant–herbivore interactions. For one, it provides an up-to-date compilation of current research on herbivory and plant defenses on islands, including new studies testing classical predictions as well as work incorporating novel perspectives and approaches. In addition, it seeks to set the stage for a renewed research agenda on plant–herbivore interactions on islands that addresses key gaps in knowledge and launches a more integrative approach. One that centers on aspects such as plant defensive syndromes, community-level patterns of herbivory, and multi-trophic interactions, while combining plant–animal interaction ecology and community ecology approaches with island biogeographical frameworks. Finally, we think the book can also promote links between basic ecology and management by shedding knowledge that can inform the conservation and restoration of impacted island ecosystems. Overall, we hope that this book will be relevant and of interest to students and researchers devoted to the study of plant–herbivore interactions.

Pontevedra, Spain	Xoaquín Moreira
Mérida, Mexico	Luis Abdala-Roberts

Acknowledgments

First of all, we would like to thank all authors who enthusiastically contributed to this book. They did a great effort in both writing and reviewing the chapters. This book would not exist without their help. Second, we want to acknowledge all our previous mentors and colleagues who inspired our researcher careers, such as Kailen A. Mooney, Robert J. Marquis, Sergio Rasmann, and Ted C.J. Turlings, just to name a few. Third, we thank our institutions the Spanish National Research Council (CSIC) in Spain and the Autonomous University of Yucatán (UADY) in Mexico. Finally, we are very grateful to the staff of Springer Nature (Lars Koerner, Delphis F. Levia, Bibhuti Sharma) for their invaluable help during the whole editorial process.

Contents

Part III Tritrophic Interactions

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

1

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

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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.

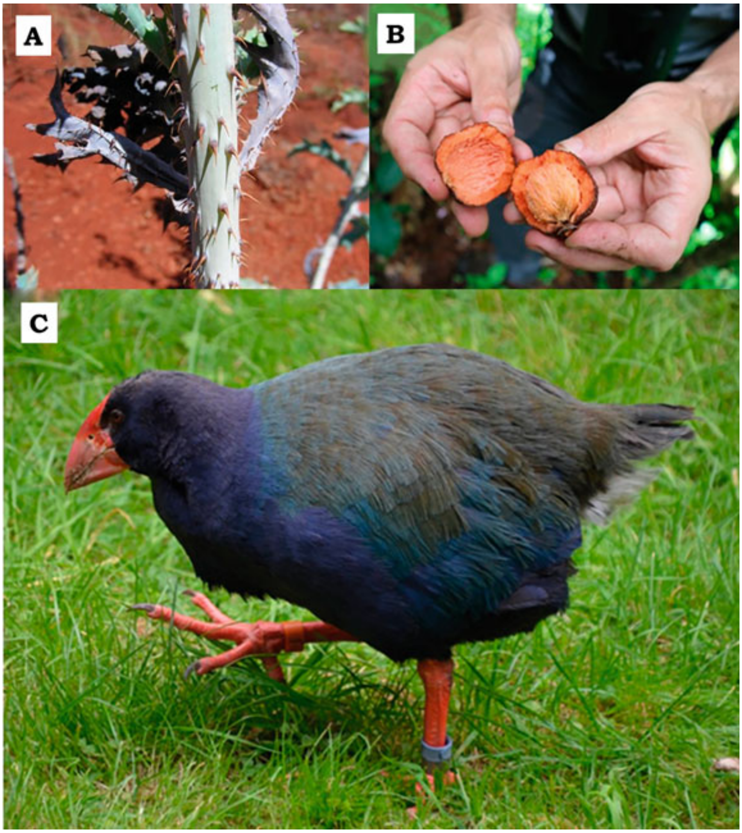

Fig. 1.1 (**a**) The Hawaiian Prickly Poppy (*Argemone glauca*), a spinescent plant species widely distributed in Hawaiian Islands (photo credit: Kasey Barton). (**b**) The rare and endemic palm *Hyophorbe vaughanii* (Arecaceae) in Mauritius bears large seeds within inconspicuous brown fruits that become 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

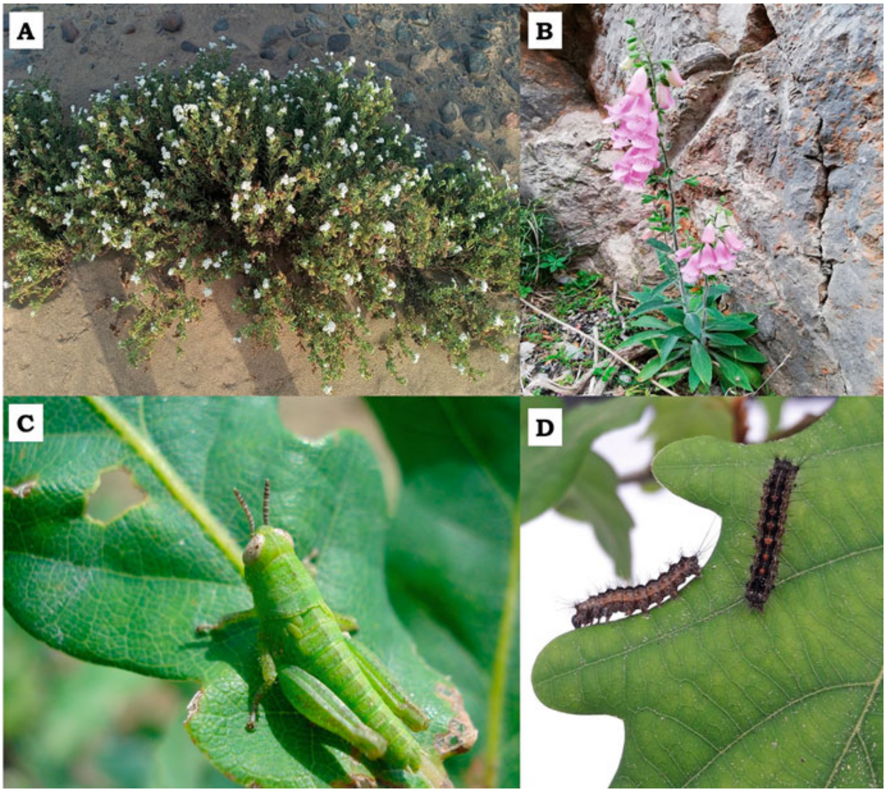

Fig. 1.3 (**a**) *Heliotropium ramosissimum*, an herbaceous perennial plant native to Canary Islands (photo credit: Xoaquín Moreira). (**b**) *Digitalis minor*, an herbaceous perennial plant endemic to Majorca and Menorca in Balearic Islands (photo credit: Miquel Capó). (**c**) Grasshopper (photo credit: 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.

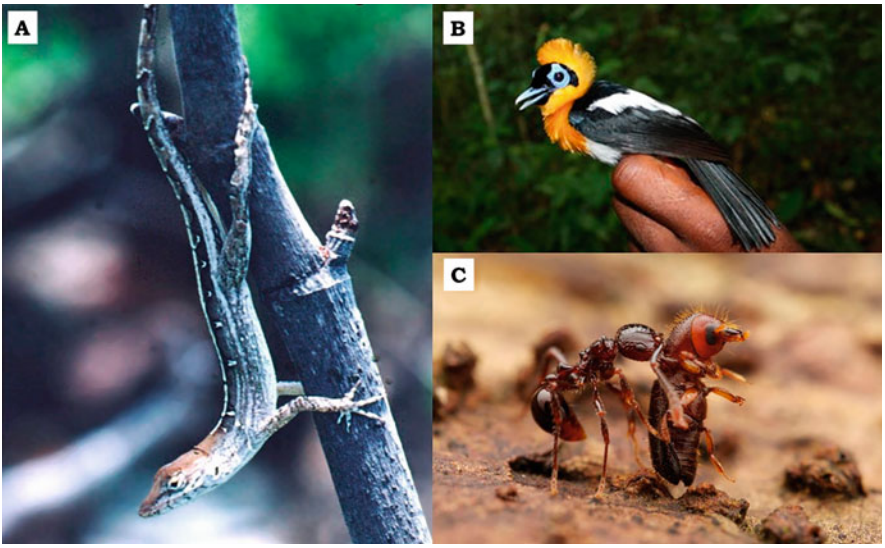

Fig. 1.4 (**a**) The brown anole (*Anolis sagrei*), a predatory lizard widely distributed in Bahamas Islands (photo credit: David Spiller). (**b**) The ochre-collared monarch (*Arses insularis*), an insectivorous bird species endemic to New Guinea (photo credit: Katerina Sam). (**c**) The predatory ant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

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Part I

Plant Defences

Spinescence and the Island Plant Defense Syndrome

2

Kasey E. Barton, Joanna K. Carpenter, Ana Flores, Llorenç Saez,
and Mohammed Armani

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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K. E. Barton (✉) · A. Flores
School of Life Sciences, University of Hawai'i at Mānoa, Honolulu, HI, USA
e-mail: kbarton@hawaii.edu

J. K. Carpenter
Manaaki Whenua – Landcare Research, Dunedin, New Zealand

L. Saez
Systematic and Evolution of Vascular Plants (UAB), Associated unit to CSIC, Faculty of Biosciences, Autonomous University of Barcelona, Bellaterra, Barcelona, Spain

M. Armani
College of Agriculture and Natural Resources, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana

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_2

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.

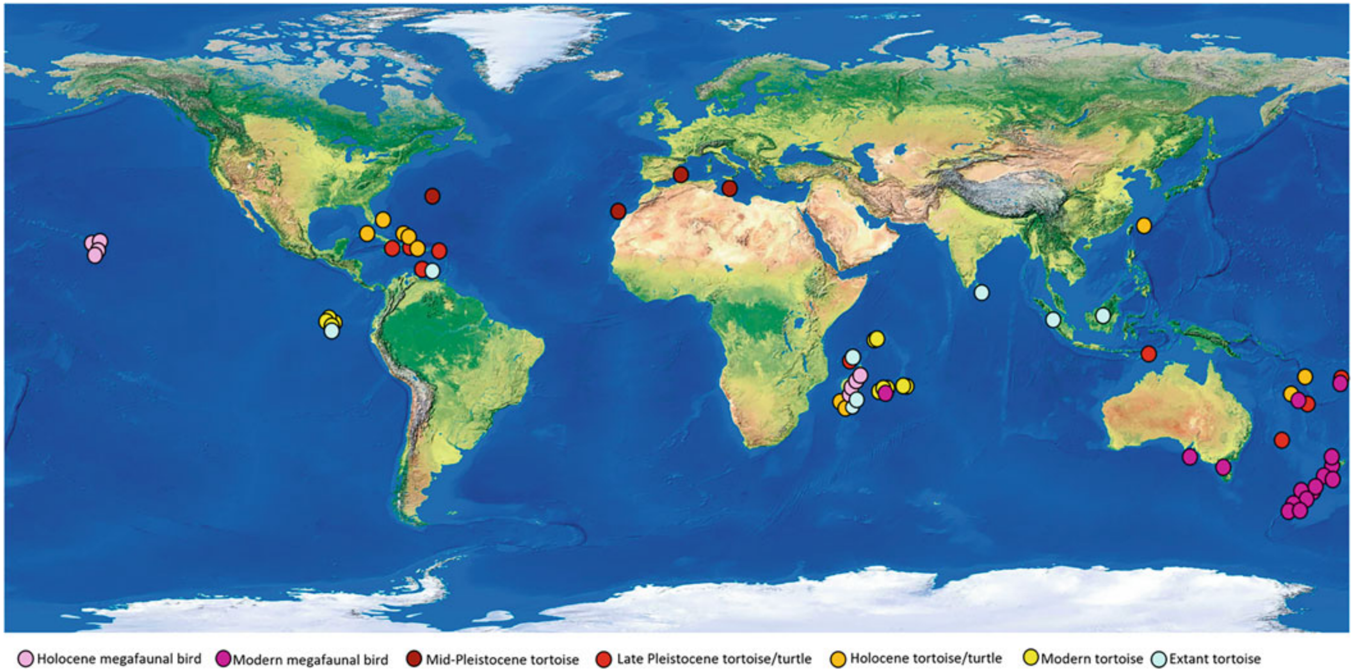

Fig. 2.1 Map showing distribution of extant and extinct megafaunal (>5 kg) non-toothed vertebrate herbivores on islands since the Mid-Pleistocene. Each dot represents one species. Colors represent whether each species was a bird, tortoise, or turtle, and when that species went extinct. Mid-Pleistocene 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.

Acknowledgments The authors thank Riccardo Ciarle for providing the Lord Howe and Norfolk Island species lists, as well as Carl Beierkuhnlein and Anna Walentowitz for providing the plant species list for the Canary Islands, and Julian Hume for sharing invaluable information on extinct vertebrate herbivores. The authors thank an anonymous reviewer for feedback.

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3

The Consequences of Species Extinctions and Introductions for Plant-Frugivore Interactions on Islands

Julia Helena Heinen and Michael Krabbe Borregaard

Abstract

Most recent vertebrate extinctions have happened on islands, often associated with the introduction of non-native species. This has led to drastic changes in island community compositions and their ecological functions, with unknown consequences for island ecosystems. Species interactions have been particularly strongly impacted, such as interactions between plants and the animals that eat fruits and thereby disperse seeds. Loss of seed dispersal may limit plant movement and recruitment success, increasing the risk of associated secondary extinctions of fleshy fruited plants. However, plants differ in the degree of their dependency on interactions with animals and there is very little direct empirical evidence that co-extinction has happened. Here, we provide an overview of what we know, and do not know, about the consequences of losing frugivore seed dispersers for island plants and discuss the main challenges for quantifying the problem.

3.1 Introduction

Islands provide unique opportunities for studying the structure and function of ecological communities. Because islands are isolated from immigration, and often small, their communities tend to be ecologically less complex than those of mainland ecosystems (Whittaker et al. 2017). Within these simpler communities, ecological release from predation and competition has enabled rapid evolution of a wide variety

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J. H. Heinen (✉) · M. K. Borregaard
Center for Macroecology, Evolution and Climate, Globe Institute, SUND Faculty, University of Copenhagen, Copenhagen, Denmark
e-mail: juliaheinen@sund.ku.dk

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_3

of extraordinary species, such as giant tortoises and flightless birds. As a consequence, islands are biodiversity hotspots that harbour 15–20% of all terrestrial species, many of which are endemic to islands, in spite of constituting only 3.5% of the earth's land surface (Whittaker et al. 2017). At the same time, they are hotspots of extinction, with 74% of all recently extinct vertebrates having gone extinct on islands (Tershy et al. 2015). Of these island extinctions, 86% are associated with the introduction of non-native species (Bellard et al. 2016), such as rats, cats, goats, and pigs, that predate on some native species and compete with others. The introduction of predators and competitors has eroded the benevolent conditions that characterized these native insular communities, with profound consequences for island biota (Whittaker and Fernandez-Palacios 2007; Drake and Hunt 2009).

The combination of species extinctions and introductions of both animals and plants have had secondary effects on the remnant communities, in many cases due to restructuring of species interaction networks. As a case in point, up to 90% of woody plants in the (sub-)tropics interact with animal species (mostly birds, mammals, reptiles, and invertebrates) that disperse their seeds by swallowing or carrying their fruits and dropping them elsewhere. This facilitates plant movement and may also directly improve seed germination through mechanical pulp removal and through chemical effects during gut passage (Fleming et al. 1987; Fleming and Kress 2013; Traveset 1998; Traveset et al. 2007; Valido and Olesen 2019; Falcón et al. 2020; Lim et al. 2020; Kissling et al. 2009). Loss of frugivores may thus impede the dispersal and reproduction of most island plants, raising the concern that this may lead to plant population declines and ultimately co-extinctions (Bond 1994; Brodie et al. 2014; Heinen et al. 2020; Fadini et al. 2009; Meyer and Butaud 2009).

Though potentially highly important, these secondary dynamics remain mostly conjecture, and a number of analytical and conceptual challenges make it difficult to empirically estimate the actual magnitude of the threat from loss of ecological interactions such as frugivory. Here, we provide an overview of what we know, and do not know, about the consequences for island plants of losing frugivore seed dispersers, and discuss the main challenges for quantifying the problem.

3.2 Vulnerability of Plant-Frugivore Interactions on Islands

By dispersing seeds, animals increase plant recruitment success and drive movement dynamics in plant populations, making plants less vulnerable to disturbances such as habitat loss and fragmentation (Fleming and Kress 2013). However, the many anthropogenic threats to both animals and plants combined can easily disrupt frugivory and seed dispersal interactions (Fleming and Kress 2013; Kaiser-Bunbury et al. 2010). We argue here that island communities are particularly vulnerable to plant-frugivore interaction loss, exacerbating the pressure on the integrity of island ecosystems.

On islands, the narrower breadth of available resources (e.g. different food sources or suitable habitat) has in many locations caused a wider range of organisms to supplement their diet with fruits (Kaiser-Bunbury et al. 2010; Traveset and

Richardson 2014), increasing the prevalence of frugivory. Some of these animals destroy the seeds, but many others end up playing a key ecological role as seed dispersers (Kaiser-Bunbury et al. 2010; Carpenter et al. 2020). One example is that of lizards, which, in contrast to the mainland, incorporate a sizable portion of fruit into their diets on many islands worldwide (Valido and Olesen 2019), including, for example, several geckos and skinks (e.g. *Phelsuma* spp. and *Leiolopisma* spp.) on the Indian Ocean island of Mauritius (Cheke and Hume 2008). Island communities may thus be characterized by many plant-animal interactions.

At the same time, island communities have relatively low species numbers, which also makes island plants particularly vulnerable to the effects of interaction loss (Kaiser-Bunbury et al. 2010; McConkey and O'Farrill 2016). In the larger interaction networks of mainland communities, the loss of any one species may be compensated for by interactions with other species, whereas in island communities, lost species often have few or no replacements (Fleming and Kress 2013; Kaiser-Bunbury et al. 2010; Fricke et al. 2018). Even small reductions in the absolute number of interactions may have important consequences, and a scenario where a plant species loses all possible seed dispersers is substantially more likely (Fleming and Kress 2013; Kaiser-Bunbury et al. 2010; McConkey and O'Farrill 2016). In addition, global extinctions are more common on islands relative to mainland (Tershy et al. 2015), even under population pressures that cause range reductions, which means that interaction loss in mainland systems is more often likely to be temporary.

Plants lose seed dispersal already before their seed dispersers go globally extinct, and even a moderate decline in the population size of a key seed disperser may negatively impact plant recruitment success and movement potential (Fleming and Kress 2013; McConkey and O'Farrill 2016). This may be particularly pronounced for island populations, characterized by low population sizes and limited distributions, and on many islands, hunting, habitat destruction, and competition and predation by introduced species have severely reduced the abundance of vertebrate seed dispersers (Heinen et al. 2018; Tershy et al. 2015), more so than in mainland ecosystems (Tershy et al. 2015). Such marked declines in disperser populations may eventually lead to "functional" extinction, in which a frugivore species persists, but no longer disperses seeds to an ecologically relevant degree; that is frugivore-mediated seed dispersal occurs so rarely that it does not affect plant population dynamics (McConkey and O'Farrill 2016).

More subtle and harder to detect pressures on plant-frugivore interactions are animal behavioural responses to ecosystem changes (Heinen et al. 2020, 2023; McConkey and O'Farrill 2016). As the population sizes of plants decrease rapidly on islands, some of the animals that depend on fruits may have to shift their diets to more common plants, resulting in a negative feedback cycle as already declining plant species lose reproductive potential (Fricke et al. 2018; Oleksy et al. 2021). In addition to abundance declines, interaction behaviour on islands can also be altered by introduced species (Heinen et al. 2023; Oleksy et al. 2021; Reinegger et al. 2021) because of their competitive advantage in ecosystems characterized by evolution under low competition (Whittaker and Fernandez-Palacios 2007). Many introduced fruiting plants offer attractive rewards (e.g. sweet, pulp-rich mango) that outcompete native plants for attracting frugivores (Linnebjerg et al. 2009; Oleksy et al. 2021). Such dietary shifts towards introduced plant species have already been described for Mauritius and Hawaii (Linnebjerg et al. 2009; Oleksy et al. 2021; Vizentin-Bugoni et al. 2019) and have the potential to reduce native plant seed dispersal and shift the ecological balance towards introduced plants, even in the absence of extinctions. Introduced non-native frugivores may also be sustained by non-native plants, further facilitating their invasion (Linnebjerg et al. 2009; Traveset and Richardson 2014) and driving a cascade of ecological effects that erode island ecosystems.

3.3 The Extent of Frugivore Change on Islands Globally and in Mauritius

Losses of vertebrate frugivores characterize many islands globally, although the extent differs geographically among islands, and has been particularly high on those islands that are isolated from the mainland, have small area sizes, and a higher maximum elevation (Heinen et al. 2018; Fig. 3.1). The pattern of preferential extinction of larger frugivores is globally consistent (Heinen et al. 2018). The same is true for frugivores that cannot fly (Fig. 3.2) (Heinen et al. 2018). The loss of many large frugivores from island communities has decreased their community-level mean body mass by 37% and maximum mass by 51% (Heinen et al. 2018), leaving only the smaller frugivores that likely cannot swallow and disperse the largest seeds (Fig. 3.3).

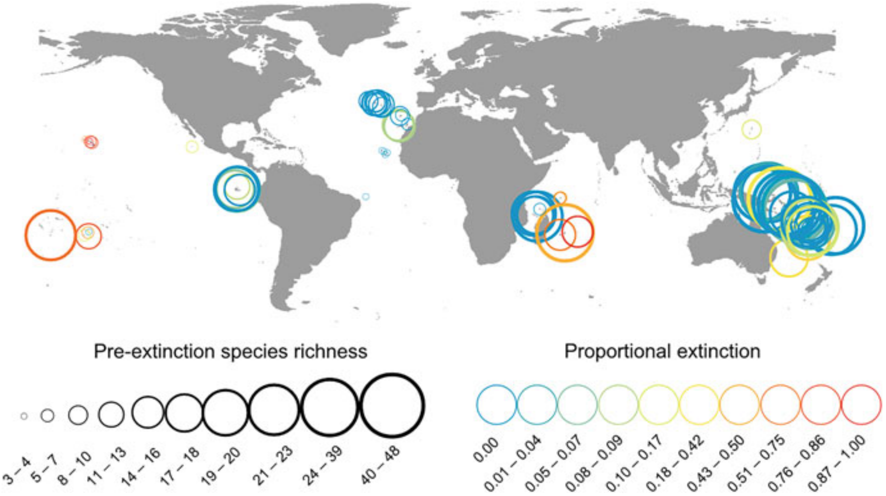

Fig. 3.1 Frugivore species richness (birds, mammals, reptiles) prior to human arrival and the proportion of this that has gone extinct on 74 islands within 20 archipelagos worldwide (Heinen et al. 2018)

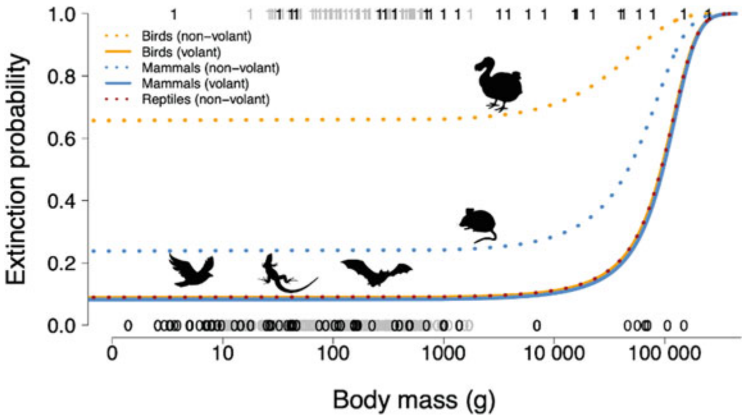

Fig. 3.2 Generalized linear mixed-effects model of extinction probability of insular frugivorous birds, mammals, and reptiles in relation to their body mass and ability to fly (adapted from Heinen et al. 2018)

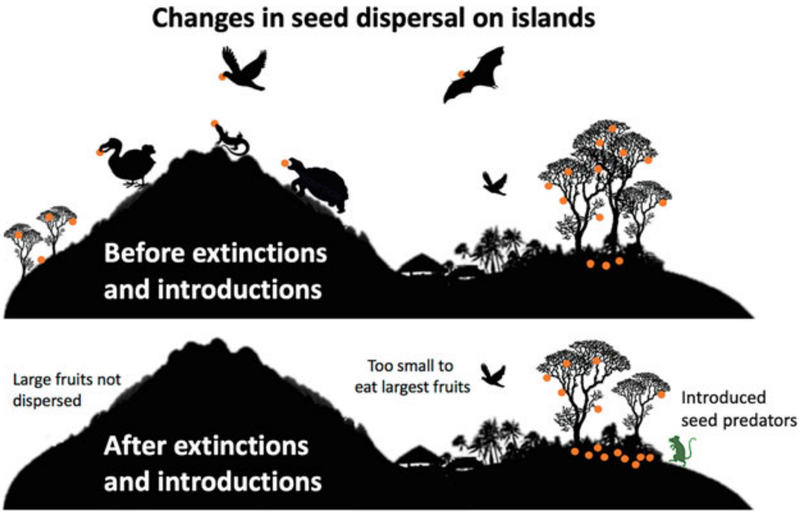

Fig. 3.3 Conceptual overview of the changes in seed dispersal on islands, showing the extinction of large frugivores, the loss of seed dispersal for large-fruited plants, and the introduction of non-native seed predators

Though extinctions and their local effect are relatively well-described, there is no similar global consensus on the effect of introductions of non-native species of frugivorous birds, mammals, and reptiles. However, a number of individual systems have been the focus of concerted research effort, and we thus here pay particular attention to case studies on a single well-studied island, where the local-scale effects of frugivore extinctions and introductions have been studied intensively: the

Western Indian Ocean island of Mauritius (Cheke and Hume 2008). Mauritius was one of the last islands in the world to be colonized by humans (in AD 1638), which means that its colonization history has been documented exceptionally well (Cheke and Hume 2008). The island is also severely affected by human activities, causing the loss of almost all of its native vegetation, the introduction of many non-native species, and many extinctions, including frugivores such as the iconic Dodo (*Raphus cucullatus*), giant skinks (*Leiolopisma mauritiana*), as well as an entire genus of endemic giant tortoises (*Cylindraspis* spp.) (Cheke and Hume 2008).

The frugivore community on Mauritius was substantially changed by extinctions and introductions (Box 3.1, Heinen et al. 2018, 2023). After human arrival, only 15 of the 26 known native frugivorous birds, mammals, and reptiles survived and 14 non-native frugivores established (Cheke and Hume 2008; Heinen et al. 2023). In particular, the extinction of many large Mauritian frugivores left only small native frugivores in the community. Large animals are particularly vulnerable to hunting and habitat loss because of their generally smaller population sizes and larger range sizes (Cardillo 2003; Dirzo et al. 2014). The remaining small-bodied native frugivores are unlikely to swallow and thus disperse the largest seeds (Heinen et al. 2018, 2023). This increases the risk that some Mauritian plant species may lose most or all of their native dispersers (Heinen et al. 2018, 2023), potentially putting them at risk of secondary extinction (Heinen et al. 2020). Indeed, a recent empirical study confirmed that the recruitment success of many native plants in one of the best-preserved forests (Brise Fer) is now very low (Albert et al. 2021). The many introduced frugivorous animals likely cannot replace extinct species as seed dispersers, as they frequently destroy the native seeds (Heinen et al. 2023).

In addition to being affected by disperser loss, many native plants suffer from competition for nutrients and water with introduced plants, lowering their fruit production (Bissessur et al. 2023; Monty et al. 2013). Intensive conservation efforts have reduced invasive species abundance and managed to bring back several critically endangered species from the brink of extinction and improved their IUCN status (e.g. Mauritius kestrel, pink pigeon, echo parakeet, Telfair's skink) (Cheke and Hume 2008). However, nearly all native frugivores remain rare and many seed dispersal interactions with native plants are likely functionally extinct.

3.4 Consequences of Seed Disperser Loss for Island Plants

The effects of loss of frugivore-mediated seed dispersal for island plants can be divided into two categories: those that affect plant recruitment success (e.g. seed handling and short-distance dispersal) and those that affect the population-level movement of plants (e.g. long-distance dispersal). There are three stages at which these processes are affected: functional limitation of the interaction, functional extinction of the interaction, and ultimately frugivore extinction.

The primary effect of disperser loss is on the recruitment success of plants (Fig. 3.4) (Fleming and Kress 2013). The very act of handling fruits by frugivores may be beneficial for seed germination. Seed handling by frugivorous vertebrates

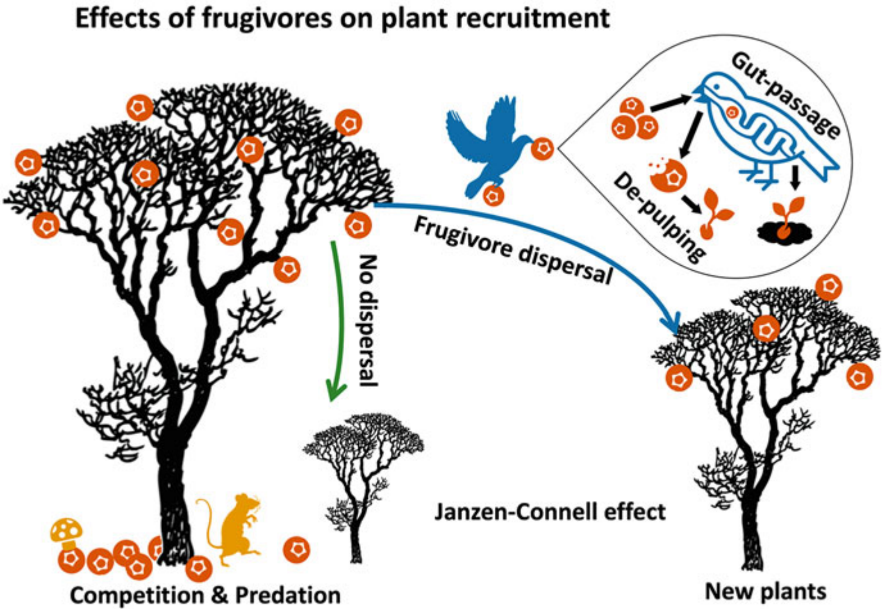

Fig. 3.4 Conceptual explanation of the effects of frugivores on plant recruitment. Frugivores can increase germination success by removing pulp from seeds or by passing seeds through their gut. Frugivores also contribute to the Janzen-Connell effect (Janzen 1970; Connell 1971), whereby plants that are dispersed further away from the mother plant suffer less predation and competition and therefore have higher chances of survival and reproduction. The young trees that are shown are similar in age, but one is suffering from competition near the mother tree which stunted growth and hampered fruit production

generally leads to removal of fruit pulp from the seeds by means of chewing, pecking, or ripping (Traveset 1998; Traveset et al. 2007). This in itself has been shown to increase seed germination because it can remove germination inhibitors present in the pulp and prevents seed destruction by insects, bacteria, and fungi attracted to the rotting pulp (Traveset 1998; Traveset et al. 2007). In addition to that, seeds that are swallowed can be abraded mechanically and/or chemically by passing through the intestinal system of animals, in some cases increasing germination success (Traveset 1998; Traveset et al. 2007). Finally, the faecal matter or oral ejecta pellet (Fig. 3.5) in which the seeds end up can provide a beneficial depositional environment for emerging seedlings (Traveset 1998; Traveset et al. 2007). Island and mainland frugivores both provide these services to plants. However, islands with lower species richness than mainland potentially provide plants with lower functional redundancy in these services.

Plant recruitment potential on islands has been changed by a shift in the types of frugivores (e.g. morphology, behaviour, ecological function) that are able to eat different fruits and handle them differently (Heinen et al. 2018, 2023). The over-representation of large-bodied frugivores (e.g. various species of giant tortoise)

Fig. 3.5 Evidence of plant-frugivore interactions between flying foxes (*Pteropus niger*) and endemic plants on Mauritius. (**a**) Mashed-pulp ejecta in the shape of the upper palate on the left and fruit with teeth marks on the right (*Mimusops maxima*). (**b**) Seed germinating while still stuck in the ejecta (*Labourdonnaisia glauca*). Both photos by Julia Heinen

among island extinctions (Fig. 3.2; Heinen et al. 2018, 2023) has left mostly small frugivores to disperse native seeds. These species may not be able to swallow (Heinen et al. 2023) or carry larger seeds (though they may be able to handle and depulp them), and they generally have smaller guts that can fit fewer seeds (Wotton and Kelly 2011, 2012). Introduced non-native frugivores may potentially take over the role of seed dispersers (Griffiths et al. 2011; Rodriguez 2006; Vizentin-Bugoni et al. 2019), but may handle seeds differently or predate on them (Carpenter et al. 2020; Heinen et al. 2023; McConkey and O'Farrill 2016), and may facilitate the spread of invasive non-native plants as well (Traveset and Richardson 2014; Linnebjerg et al. 2009). The reduction or loss of (mechanical) seed handling by native frugivores can therefore reduce the number of new plants in the population (McConkey and O'Farrill 2016), and for plants that strongly depend on frugivores for their population survival, this has the potential to result in plant co-extinctions (Fleming and Kress 2013).

In addition to the beneficial effects of mechanical seed handling (e.g. depulping, gut abrasion), the primary effect of frugivory is to move seeds away from the mother plant (Fleming and Kress 2013). Even short-distance movements of seeds have been shown to reduce the impact of host-specific parasites, diseases, and predators on seeds and seedlings, as well as reducing sibling competition associated with vicinity to the mother plant (Fig. 3.4, the Janzen-Connell effect, Janzen 1970; Connell 1971). The types of seed and seedling predators (including parasites and diseases) can be divided into "distance-responsive-predators" that kill seeds and seedlings near the mother tree (these may specialize on that particular species) and "density-dependent-predators" that kill them where they are most abundant (can be generalists) (Janzen 1970; Connell 1971). The mix of predator types contributes to a mixed distribution of plant species over the landscape, because each species is able to escape their own host-specific predators and diseases, and species that become common will suffer more host-specific predation (Janzen 1970; Connell 1971). The effects are predicted to be strongest in tropical and wet habitats due to higher pathogen abundance and

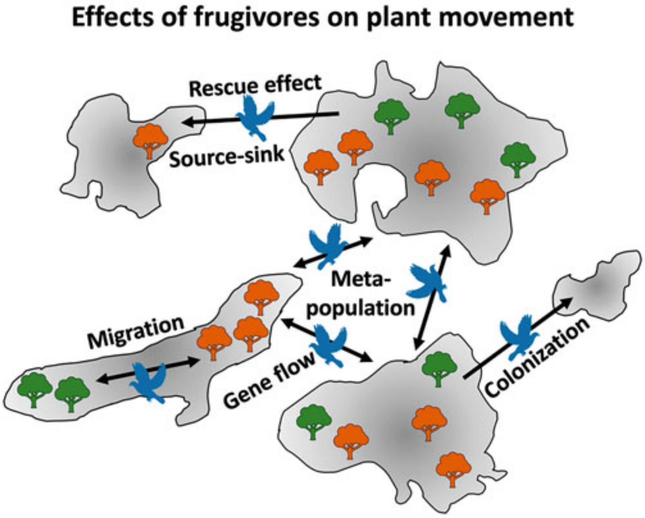

Fig. 3.6 Conceptual explanation of the effects of frugivores (blue) on plant movement at population level. Frugivores can spread seeds to new areas, assisting their colonization, or connect existing populations, facilitating migration, gene flow (green and orange genotypes), and metapopulation dynamics, or provide rescue effects and source-sink dynamics to locally declining plant populations

diversity (Janzen 1970; Connell 1971), which is also where frugivore-mediated seed dispersal is most common (Fleming et al. 1987; Fleming and Kress 2013; Kissling et al. 2009). Additionally, most islands of oceanic origin are (sub)tropical and characterized by many frugivore species (Heinen et al. 2018).

On islands, where communities are generally less diverse than on the mainland, seed predators (and pathogens) may be opportunistic generalists more often than specialists on the seeds of a single plant species, potentially making the density-dependent Janzen-Connell effect less strong in insular environments (Hansen et al. 2008). If abundance of seed predators is too low on islands, as is the case for both generalist and specialist frugivorous weevils in New Guinea lowland rainforest, they may be below a critical threshold to cause Janzen-Connell effects (Ctvrtecka et al. 2014). On the other hand, island plants that do rely on escape from density-dependent predation and competition may be more vulnerable than they would be on the mainland because the remaining habitats are too small to support viable populations (Hansen et al. 2008). On Mauritius, an experimental study of the Janzen-Connell effect for *Syzygium mamillatum* (Myrtaceae) showed strong negative distance-dependent effects on survival and growth of seedlings when they were close to their mother trees (Hansen et al. 2008). This was mainly due to fungi and insect damage, and it is unknown whether these are generalists or specialists (Hansen et al. 2008).

Though most seeds are dispersed over relatively short distances, frugivory occasionally leads to long-distance movements with population-level effects (Fig. 3.6) (Fleming et al. 1987; Fleming and Kress 2013). Sometimes plant seeds are moved far enough to colonize new islands, such as when birds and flying foxes transport ingested seeds of fleshy fruited plants from Sumatra or Java to the Krakatau islands (Whittaker and Jones 1994). These islands were completely sterilized by a volcanic eruption in 1880 (and again in 2019), but the native forests were quickly rebuilt, in part driven by frugivore-mediated dispersal from nearby forests (Whittaker and Jones 1994). Some island frugivores, especially those that can fly, occasionally travel to other nearby islands or have home ranges that extend across several islands, connecting multiple island populations (Zann 1992; Vidal et al. 2014).

Long-distance dispersal events (Fig. 3.6) contribute to island metapopulation dynamics and enable source-sink dynamics and rescue effects for connected locally declining sub-populations of plants (Amarasekare 2004; Nathan and Muller-Landau 2000; Nathan 2006; Rogers et al. 2021; Vidal et al. 2014). Reductions in seed dispersal would impede metapopulation dynamics, leading to reduced levels of gene flow and over time eroding genetic diversity (Fleming and Kress 2013; Moreno-Mateos et al. 2020; Rogers et al. 2021). This might result in negative eco-evolutionary feedback loops (Moreno-Mateos et al. 2020), with lower genetic diversity decreasing resilience to disturbances and reducing the adaptation to new environments (Fricke et al. 2022; Rogers et al. 2021). Therefore, the reduced movement potential of plants might limit their resilience to the effects of anthropogenic disturbances in the present and future and can affect the plant's ability to track environmental changes, such as global climate change (Fricke et al. 2022; Rogers et al. 2021).

The distance over which plants can now be dispersed is also affected by the loss of many large frugivores on islands (Heinen et al. 2018), because the remaining small frugivores can generally travel less far and have shorter gut retention times (Vidal et al. 2014; Wotton and Kelly 2011, 2012). Vertebrate seed dispersers that were unable to fly have been more vulnerable to extinction in the past, such as island birds that lost the ability to fly (Heinen et al. 2018), further exacerbating the reduction in plant movement potential. Some introduced non-native frugivores may be able to provide long-distance seed dispersal, but, as discussed before, they may also do so for invasive plants (Traveset and Richardson 2014).

The complete loss of frugivore-mediated seed dispersal following frugivore extinction could in theory lead to plant co-extinction (Fleming et al. 1987; Fleming and Kress 2013; Rogers et al. 2021). This is most likely for plants that depend on this for their reproduction, without alternative strategies or new interaction partners (Heinen et al. 2020). In turn, the loss of these plants could then cause further co-extinctions of other species that depend on them for their survival, with the potential to trigger extinction cascades and ecological collapse or shifts to alternative stable states (Fleming et al. 1987; Fleming and Kress 2013; Rogers et al. 2021).

3.5 Challenges in Identifying Effects of Disperser Loss on Plants

It is clear that the loss of frugivore seed dispersers may affect plant populations negatively, in particular in island communities. However, there are a number of challenges for identifying the exact extent of dispersal loss effects on islands. First, it is difficult to assess with high certainty whether species have gone extinct, and even more difficult to assess whether interactions are fully functionally extinct. Second, seed dispersal interactions are not always obligate and plants may have alternative strategies for reproduction or dispersal, making frugivore extinctions less problematic than we may assume. And, third, it is challenging to obtain suitable data for assessing the ecological consequences of disperser loss in-depth. Below, we review each of these three challenges in turn and they are summarized in Table 3.1.

3.5.1 Determining Species Extinctions, Functional Extinctions, and Co-extinctions

True extinction of plants and animals is difficult to determine with certainty because it requires the entire island to have been searched thoroughly for any remaining individuals, by those who have the skills to correctly identify them. Because of this, there are still people undertaking targeted searches for species such as the Tasmanian tiger (*Thylacinus cynocephalus*) and in some cases they are successful, such as with the recent rediscovery of the presumed extinct Fernandina island Galapagos tortoise (*Chelonoidis phantasticus*) (Jensen et al. 2022). The same regularly happens for plants, for example, through drone surveys of inaccessible mountain slopes in Hawaii (La Vigne et al. 2022). The motivation and funding necessary to do this may be higher for some species than others, leaving us with a broad range of confidence in the robustness of extinction status assessments. This in turn makes it difficult to determine whether plants have truly lost their frugivore seed dispersers, have been negatively impacted by this, or have suffered co-extinction as a consequence themselves.

Co-extinction of plants is often mentioned as an important consequence of losing frugivore seed dispersers, though we are not aware of any conclusive empirical evidence for this. Most of the known co-extinctions refer to parasites of which the hosts have gone extinct due to very strong obligate interactions, such as the two species of feather lice of the passenger pigeon (Dunn 2009). The idea of co-extinctions driven by disperser losses has caused concern for island plants with fruits characteristic of dispersal by extinct animals, such as fleshy fruits with large seeds that can be reached by ground-dwelling large animals (Guimarães Jr et al. 2008). These plants are believed to be on their way to co-extinction with a delayed effect.

A well-known, but untrue, story about disperser loss co-extinction comes from Mauritius. The extinction of the famous Dodo (about 360 years ago) was initially thought to have left the “Dodo tree” (tambalacoque, *Sideroxylon grandiflorum*,

Table 3.1 A concise summary of the challenges and implications of frugivore seed disperser loss on island plant populations

Aspect	Challenges and implications	References
Extinctions	Difficulty in determining true extinctions	Jensen et al. (2022), La Vigne et al. (2022)
	Lack of evidence for disperser loss co-extinctions	Baider and Florens (2006), Guimarães Jr et al. (2008), Heinen et al. (2018)
	Functional extinction may be hard to detect	Bissessur et al. (2023), Heinen et al. (2018, 2020), McConkey and O'Farrill (2016), Monty et al. (2013), Reinegger et al. (2021)
Alternative strategies	Some plants have alternative dispersal methods	Bond (1994), Heinen et al. (2020), Rogers et al. (2021), Vargas et al. (2015)
	Vegetative reproduction does not contribute to genetic diversity	Fleming et al. (1987), Fleming and Kress (2013), Rogers et al. (2021)
	Long-distance dispersal may be hindered without frugivores	Rogers et al. (2021), Whittaker and Jones (1994)
	Introduction of non-native species as replacements is complex	Griffiths et al. (2011), Heinen et al. (2023), Kaiser-Bunbury et al. (2010), Nogués-Bravo et al. (2016)
Data collection	Time-consuming and physically challenging	Robertson et al. (2006), Magurran and McGill (2010), Ramírez-Castañeda et al. (2022)
	Observer bias and limited observations of interactions	Magurran and McGill (2010)
	Limited funding and access to field sites	Ramírez-Castañeda et al. (2022)
	Misclassification, oversimplification, and generalization of traits and morphometrics	Dominy et al. (2003), Magurran and McGill (2010), Onstein et al. (2020), Schmidt et al. (2004)
	Difficulties in collecting data for extinct species	Baider and Florens (2006), Cheke and Hume (2008), Hume and Winters (2016), Heinen et al. (2018, 2020, 2023)

Sapotaceae) without a seed disperser, predicting its inevitable co-extinction in the near future (disputed by Baider and Florens 2006). This was because it has an exceptionally thick (~6 mm) woody endocarp around its seed that was incorrectly thought to need abrasion in the Dodo's strong, stone-filled crop to allow the seed to break through and germinate (Baider and Florens 2006). However, this appears not to have been the case as seeds can still be found germinating on the forest floor in absence of the Dodo (Fig. 3.7), although the tree is increasingly rare (possible causes discussed in Baider and Florens 2006).

There are several other rare plants in Mauritius that possess traits that suggest that their seeds used to be dispersed by frugivores that no longer exist. For example, the palm *Hyophorbe vaughanii* (Arecaceae) has very large, single seeds (2 cm diameter) embedded in large fruits (4 cm diameter) that have an inconspicuous brown colour

Fig. 3.7 Germinating seed of the "Dodo tree" (tambalacoque, *Sideroxylon grandiflorum,* Sapotaceae) on Mauritius, which was incorrectly thought to be at risk of disperser loss co-extinction after the Dodo disappeared. Photo by Julia Heinen

Fig. 3.8 Variations in morphology of a few native fruits in Mauritius. From left to right, top to bottom: *Syzygium mamillatum*, *Hyophorbe vaughanii*, *Tambourissa Tau* or *T. cordifolia*, *Pandanus barckayi*, *Ochna mauritiana*. Photos by Julia Heinen

until they fall to the ground where they ripen and break open to reveal their attractive bright orange pulp which seems to invite large ground-dwelling frugivores (e.g. giant tortoises or Dodos) that are no longer present to eat them (Fig. 3.8, see top middle). Co-extinction risk may be even harder to detect in plants that used to be dispersed by small frugivores and have no particular traits that indicate disperser loss. Disperser loss co-extinction is a particularly poignant example of the difficulty in obtaining convincing empirical evidence, as the effects of losing seed dispersers are hard to disentangle from other extinction drivers, and long generation times of plants may cause a delay in secondary extinctions.

Functional extinction may also be difficult to detect. In particular, functional extinction may be the result of, for example, a drastic reduction of fruit production, removing the potential for interaction even when both species are still abundant (Heinen et al. 2018; McConkey and O'Farrill 2016). This has been observed for several plants on Mauritius, which reduced fruit set as a response to intensified nutrient competition in environments heavily invaded by non-native plants (Monty et al. 2013). Control of invasive non-native plants may therefore be more important to prevent functional extinction of plants than restoring seed dispersal interactions (Bissessur et al. 2023). Destruction of flowers and unripe fruits by introduced animals (e.g. by macaques on Mauritius) may also cause functional extinction of seed dispersal interactions without initial loss of interaction partners (Reinegger et al. 2021). When seeds are dispersed by frugivores very rarely but successfully, this may still contribute to the reproduction and dispersal of plants often enough to affect their population dynamics, so that the ecological function is still maintained (Heinen et al. 2020; McConkey and O'Farrill 2016). Important questions for directing conservation efforts are "how often do seeds need to be dispersed to prevent plant extinction?", "how often do frugivores need to interact with the plants to achieve this?", and "how many frugivores are needed for functional seed dispersal interactions?". However, these are difficult to answer because they each require a lot of observations and in-depth studies that are very hard to do, such as on seed handling, gut passage, and germination, especially if fruits and frugivores are already rare. A clear overview of the factors that determine interaction functionality is thereby essential for determining whether functional extinction has taken place.

The Seed Dispersal Effectiveness (SDE) framework (Box 3.2) quantifies and qualifies many factors that are important in determining the contribution of individual seed dispersers to plant fitness (Schupp 1993; Schupp et al. 2010). This is a comprehensive framework that requires in-depth investigations into many different aspects of plant and frugivore morphology, behaviour, and ecology, such as germination experiments and gut passage timing. It is therefore difficult to collect enough information to use it for whole communities, even simplified island communities that provide ideal model systems.

Another simplified approach is that interaction functionality may be restored by increasing distributional range overlap between the interacting species, and by preventing disruptions of encounter rates between the species and success rates of interactions that do take place (Heinen et al. 2020). It is also important to be aware that to prevent or overcome functional extinction, general conservation management efforts may not always be adequate, such as fencing a habitat, and may require additional specific management efforts (Heinen et al. 2020). Obligate seed dispersal interactions are thereby a priority for restoration of functionality, because a lack of alternative dispersal strategies is most likely to cause negative secondary effects on plant populations (Heinen et al. 2020).

3.5.2 Alternative Modes of Reproduction and Dispersal

Not all plants that offer fleshy fruits or arils to frugivores depend on animals as their only means of dispersal, making it challenging to identify which interactions are obligate and/or at risk of negative consequences of disperser loss (Heinen et al. 2020; Rogers et al. 2021). There are at least two ways for plants to disperse to new sites. Their seeds may have multiple dispersal strategies that do not only make use of frugivores (diplochory), such as by wind, water, gravity, or external attachment to animals (Vargas et al. 2015). Alternatively, some plants can reproduce and spread vegetatively (e.g. root stems) in addition to producing fruits and can either switch between strategies as needed or rarely do so (Vargas et al. 2015). Functional traits of the plants can be used to help identify which plant-frugivore interactions are obligate without alternatives (e.g. presence of root stems or floating seeds) (Bond 1994; Heinen et al. 2020), but this is not always possible. At the same time, many frugivorous island animals appear to be opportunists and generalists that feed on many different plant species due to the scarcity of resources and strong dependency on what is available on their island, making many fruit-feeding interactions non-obligate from their point of view. It is challenging but important to find out whether frugivore-mediated seed dispersal is obligate, and if not, what alternative dispersal strategies are being used to evaluate whether plant populations are potentially negatively affected by frugivore extinctions (Heinen et al. 2020). Alternative strategies may not be sufficient in the long run because alternative seed dispersal will maintain the genetic recombination benefits of sexual reproduction, but vegetative reproduction will not (Fleming et al. 1987; Fleming and Kress 2013; Rogers et al. 2021). High genetic diversity can increase island plant resilience to the many threats on islands, such as changing climate, habitat loss from sea level rise, and human disturbance. Additionally, long-distance dispersal, such as colonization of islands, may be harder without animal seed dispersers (Rogers et al. 2021) like flying foxes that transport seeds to the Krakatau islands (Whittaker and Jones 1994). Such negative effects may take too long to detect due to the long generation time of plants. Many island plants have particularly slow generation times due to the lack of competition during their evolution (Robertson et al. 2006; Whittaker and Fernandez-Palacios 2007).

Another way for plants to overcome disperser loss is to gain new interactions with introduced frugivores (Heinen et al. 2023; Kaiser-Bunbury et al. 2010; Vizentin-Bugoni et al. 2019). These have in some cases been able to take over the role of extinct seed dispersers (Griffiths et al. 2011), but it is difficult to determine the full extent of the ecological impact of these species (Nogués-Bravo et al. 2016). It requires many thorough studies that take years to complete into whether they, for example, outcompete native frugivores, spread non-native plants, predate on seeds, or affect other native species on the island. This is not feasible at all. In the case of deliberately introducing non-native species to take over the role of extinct seed dispersers and restore island ecosystems, acting fast with the risk of potential unknown negative consequences is sometimes prioritized over doing nothing at all (Griffiths et al. 2011; Nogués-Bravo et al. 2016). For example, Aldabra giant tortoises *Aldabrachelys gigantea* are used to replace extinct giant tortoises *Cylindraspis* spp. in Mauritius and extinct ducks in Hawaii.

3.5.3 Obtaining Comprehensive Data

An important challenge is that it can take a lot of time to run experiments and collect the necessary comprehensive data to investigate the full extent of consequences of losing seed dispersers for island plants. Slow plant life history, as is characteristic for many island plants, can also add to the time required to obtain data. For example, it can take several years before dormant seeds germinate and for new plants to produce seeds of their own, limiting the feasibility of experiments on plant recruitment success and risking incorrect results (Robertson et al. 2006). The longer it takes to run germination experiments, the longer the exposure is to factors that risk its failure, such as fungal infections, drought, weeds, and ants or rats removing seeds. Collection of observational data is not only time-consuming but often physically challenging, walking through difficult terrain trying to find plants and animals and observe their behaviour. Reaching remote islands over rough oceans can be very challenging, dangerous (e.g. high wave boat landing on rocky shores of Round island in Mauritius), costly (e.g. helicopters), and time-consuming, with few opportunities to return which requires commitment to long stays (e.g. Aldabra in Seychelles). There is also a strong element of chance involved in obtaining observational data. The observer needs to spend enough time in the right place at the right moment to, for example, find plants with ripe fruits and to see a lizard quickly swallow one of them in the distance.

Then there is the challenge of correctly identifying both the animal and plant involved in the interaction, which requires a clear view of the species and proper training, experience, and access to literature, especially for plants. Evidence of interactions can be obtained through direct observations, where it may be hard to identify which fruit is eaten (e.g. trees may cross branches) and whether it is truly the fruit that was eaten (e.g. not the insect on it or leaf next to it, not only tasting and rejecting the fruit), or through indirect observations (Fig. 3.5a) of teeth markings on fruit or ejecta of hard parts of fruit pulp and seeds from the mouth (may be similar among species). In some cases, indirect evidence of successful seed dispersal can be clear, such as the germination of seeds embedded in ejecta of the only frugivorous bat on Mauritius (Fig. 3.5b). Determining the outcome of different seed handling events based on (field) observations, such as whether the seed is destroyed or dispersed viably, is challenging because it may be difficult to see or track and may vary depending on chance (e.g. chewing) and the context of the environment (e.g. whether there are other ripe fruits nearby). Rare interactions or dispersal events are especially hard to capture, risking a bias in any observations towards more common interactions (Magurran and McGill 2010). The lack of observational data is not a reliable way to exclude that an event occurs, and observation time influences the number of possible observations (Magurran and McGill 2010). The limited

Fig. 3.9 Variation in fruit sizes and shapes within one tree, for two different native species in Mauritius. (**a**) Fruits are very variable in size and shape with pear-shaped, round, and oval fruits from the same tree. (**b**) All fruits are similar in shape and size. Photos by Julia Heinen

number of species-level interactions within the relatively smaller communities on islands is therefore perhaps more feasible to identify than those on the mainland.

Data collection is especially challenging for researchers with very limited access to funding because they do not always have money to travel to and access specimen collections and herbaria or to conduct fieldwork, especially if this takes a lot of time, forcing prioritization (Ramírez-Castañeda et al. 2022). Many island nations have limited funding opportunities. Field-based data collected by local people is often used by researchers from other regions, not always benefitting those who collected the data, which poses ethical challenges (Ramírez-Castañeda et al. 2022).

The collection of plant and animal morphometrics and functional traits comes with challenges related to misclassification, oversimplification, or inappropriate generalization. This is especially the case when data is collected that represents whole species rather than individuals. Animal morphometrics, such as gape size (e.g. bill width) to determine the potential size of seeds that can be swallowed, are usually taken from adult individuals even though in nature there is usually a mix of animals with different ages and morphometrics. For example, adult Aldabra giant tortoise beak width may not be representative for the size of fruits that can be swallowed by the many smaller juveniles present on Aldabra Island. Strong sexual dimorphism can also make it challenging to come up with one measurement to represent a characteristic at the species level. Slight differences in measuring techniques and equipment used by different researchers can influence the accuracy of the data obtained (Magurran and McGill 2010). Under ideal circumstances, average morphometrics are based on hundreds of specimens to make them as representative as possible. However, these may not be easily accessible because they are spread out over collections worldwide that are not digitized, or they may be so rare that only one specimen is available. This can create variation in representativeness of data at species level depending on the amount of intraspecific variation within the characteristic, which may be more problematic for some types of studies than for others. For example, adult bird bill sizes might not vary as much within the species, but fruit size and shape can vary a lot within the species, even if they come from the same tree (Fig. 3.9). Comparing the same trait across different species can be difficult when species vary a lot in appearance, making it hard to identify what needs to be measured, such as fruit lengths for several native Mauritian plants (Fig. 3.8).

Categorical data can oversimplify characteristics and may be classified differently by different researchers. Fruit colour is an example of a plant trait that is often used in frugivory research which seems straightforward to collect but is challenging in reality. Many fruits have several colours (e.g. red with white dots, or berries that are either purple or white), change colour during their ripening process (e.g. green to red), or have colours that are difficult to define (e.g. turquoise). Proposed solutions are to reduce fruit colours to single basic colour terms (Dominy et al. 2003), assign primary and secondary colours, or use broader colour classifications such as "conspicuous" and "non-conspicuous" (Onstein et al. 2020; Schmidt et al. 2004). However, these colours are still assigned by researchers based on their own human vision, which may be less relevant for interactions with animals that have different types of colour vision (e.g. UV vision in birds) (Honkavaara et al. 2002). The choice of data to collect needs to be representative of the factors that influence plant-frugivore interactions. Some of these factors are very difficult or impossible to take into account, such as the smell of fruits.

Collecting data for extinct species is especially challenging because specimens and information about past interactions are often limited. For some islands, such as Mauritius, there are several historical drawings and descriptions of animals and what they ate (Box 3.1) (Cheke and Hume 2008). Reliability of these sources varies because many stories and drawings are based on second-hand accounts by people who were able to write and draw, and basic biological understanding was limited. In some cases, detailed scaled botanical drawings of fruits can be used to estimate fruit measurements for extinct plants or rare ones that do not produce ripe fruits anymore. Even behavioural information on interactions can sometimes still be inferred. For example, on Mauritius where specific berries were found in a pigeon crop and extinct giant tortoises were described eating "fallen apple-like fruits", which narrows down the possible plants (Hume and Winters 2016). In cases where only some parts of the animals remain, partial specimens or subfossils, some morphometrics that are available can be converted with calculations to others, such as lizard snout-vent length (Pough 1980; Meiri 2010) or tortoise curved carapace length to body mass (Heinen et al. 2018), or newly calculated based on large available datasets. Scientific articles that describe newly discovered extinct animals rarely have more than a few subfossil bones to work with and provide only measurements relevant to species identification instead of those that are relevant to their ecological roles (e.g. bill width), but often provide scaled images that can be used to derive them and compare the species to its closest relative. If no other information is available for extinct species, data from a morphologically similar, close taxonomically related species can be used as a substitute. The measurements can be either used directly for one substitute species or averaged across several species, or adjusted for described differences with the extinct species (e.g. 30% larger) (Heinen et al. 2018). There are many creative ways of overcoming challenges with data collection that need to be carefully considered because they may work better for answering some research questions than for others.

3.6 Conclusion

To conclude, the interactions between species, specifically frugivore-mediated seed dispersal, have been altered on islands worldwide due to extinctions and introductions of animals and plants. These changes can negatively impact the recruitment success and dispersal of island plants, which are particularly vulnerable due to limited alternative interaction partners in simple island communities. Extinctions of large, flightless frugivorous birds, mammals, and reptiles are most common on isolated and small islands, like Mauritius, where introduced frugivores are likely not good at replacing extinct species as seed dispersers and often destroy seeds. Before extinctions happen, declines in animal seed disperser abundance can already lead to "functional" extinction, where frugivores persist but do not disperse seeds enough to affect plant population dynamics. In addition to extinctions and functional extinctions, shifting animal behaviour, such as dietary changes towards common or non-native fruits, poses a threat to native plant-frugivore interactions that is difficult to detect.

The consequences of frugivore-mediated seed dispersal loss on island plants can be categorized into two main aspects: its impact on plant recruitment success involving seed handling (e.g. pulp removal and gut abrasion) and short-distance dispersal, and its influence on population-level plant movement encompassing long-distance dispersal (e.g. colonization and metapopulation dynamics).

However, there are several challenges in identifying the consequences of disperser loss on plants. Determining species extinctions, functional extinctions, and co-extinctions is difficult, and conclusive evidence is often lacking. Detecting functional extinction is particularly challenging without fully understanding the factors determining interaction functionality, for which a clear overview is lacking. Identifying which interactions are obligate and at risk from seed disperser loss is also complex. Furthermore, assessing dependency on animal seed dispersal is complicated by alternative dispersal strategies of plants, such as vegetative growth or seeds that can also be dispersed via wind, water, gravity, or attachment to animals.

Comprehensive data collection on plant-animal interactions presents challenges, including the time required, limited funding, and difficulties identifying species. Collecting data for extinct species is especially challenging due to limited specimens and interaction information. Overcoming the challenges researchers face in determining the causes, the extent, and the consequences of frugivore-mediated seed dispersal loss is crucial for gaining fundamental understanding of plant-animal interactions and for effective conservation and management strategies in island ecosystems. Furthermore, these challenges underscore the need for collaborative research, adaptive conservation strategies, and ongoing monitoring to address the impact of disperser loss on fragile island ecosystems.

Box 3.1 Extinctions and Introductions in the Mascarenes

When early mariners first arrived on remote oceanic islands such as Mauritius and Rodrigues, after months at sea and an odious diet of dried or salted food, they encountered an unspoilt ecosystem full of animals, the like of which they had never seen before. Birds, bats, and reptiles abounded, and there were so many giant tortoises that one could walk a hundred paces solely on their backs (Leguat 1708). The skies were full of flying foxes, giant lizards crawled on the ground and climbed the trees, and a variety of tame and colourful birds, several unable to fly, such as the famous Dodo, inhabited the forests (Cheke and Hume 2008; Hume 2017). Many of these species were described and illustrated, albeit somewhat poorly, with more emphasis placed on their culinary qualities than anything else (Leguat 1708; Cheke and Hume 2008). Hungry sailors easily caught these island inhabitants, since they had evolved in isolation from mammalian predators, and had no fear of humans (Hume 2017; Steadman 2006). The sailors did not arrive alone, and introduced livestock, which included the accidental introduction of black rats. Rats quickly established on the island along with cats, and goats, pigs, and exotic plants were left behind as a source of food for crews of the next visiting ships (Hume 2017; Steadman 2006). As island species have generally evolved in isolation from competition, they were unable to compete with the introduced rapidly spreading, opportunistic invasives, causing many of the endemic species to go extinct (Blackburn et al. 2004, 2009; Whittaker and Fernandez-Palacios 2007). Because of overwhelming human interference, island ecosystems on a global scale have suffered the same consequences as those in Mauritius and Rodrigues, and have been irreversibly damaged.

Parrot hunting on Mauritius (de Bry 1601)

Box 3.2 Seed Dispersal Effectiveness (SDE)

The Seed Dispersal Effectiveness (SDE) framework for quantifying and qualifying seed dispersal effectiveness outlines many factors that are important in determining how individual seed dispersers contribute to plant fitness (Schupp 1993; Schupp et al. 2010). Its purpose is to provide an organizing framework for the study of ecological and evolutionary consequences of seed dispersal rather than identifying functional extinction, but can be of use in this context to evaluate single plant-frugivore interactions. It states that the quantitative component of seed dispersal (number of seeds dispersed) depends on (1) the number of visits, influenced by frugivore local abundance and degree of frugivory, and (2) the number of seeds dispersed per visit, influenced by the number of fruits handled per visit, the handling behaviour and the frugivore body size (Schupp et al. 2010). The qualitative component of seed dispersal (probability of seed producing adult) depends on (1) the quality of seed treatment in mouth and gut, influenced by seed breakage and digestion, and the altered germinability; and (2) the quality of seed deposition, influenced by seed survival (herbivory and pathogens), seedling emergence (germination requirements), and the subsequent survival and growth (herbivory, pathogens, competition, and physiological requirements) (Schupp et al. 2010).

Acknowledgements Funding was provided by Carlsberg grant no. CF19-0695.

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4

Leaf Traits Linked to Herbivory in Lineages with Mediterranean-Macaronesian Distributions: Does an Island Syndrome in Plant Defence Exist?

Carlos García-Verdugo, Xoaquín Moreira, Juli Caujapé-Castells, and Jaume Flexas

Abstract

Island-mainland comparisons offer an excellent framework to improve our understanding about phenotypic evolution, including particular plant traits associated with defence against herbivores. In this chapter, we provide an overview of leaf phenotypic traits putatively related to plant defence on islands, with a focus on lineages spanning mainland Mediterranean and Macaronesian island distributions. The information available to date shows that Macaronesian plants inhabiting lowland island habitats typically display large leaves, high concentrations of phenolic compounds in leaves and low photosynthetic rates as compared to their mainland counterparts. Such phenotypic convergence provides strong evidence of an island syndrome, but does not support the prediction that, due to the evolutionary absence of large herbivores, Macaronesian plant endemics have systematically lost or lowered their defences as compared to closely related mainland species. We argue that biogeographical and climatic factors should also be considered to achieve a more complete understanding of insularity effects on the evolution of defence-related traits in plants.

C. García-Verdugo (✉)
Departamento de Botánica, Facultad de Ciencias, Universidad de Granada, Granada, Spain

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

J. Caujapé-Castells
Departamento de Biodiversidad Molecular y Banco de ADN, Jardín Botánico Canario 'Viera y Clavijo' – Unidad Asociada CSIC, Cabildo de Gran Canaria, Camino del Palmeral 15, Las Palmas, Gran Canaria, Spain

J. Flexas
Departament de Biologia, Universitat de les Illes Balears, Carretera de Valldemossa, Palma de Mallorca, Illes Balears, 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_4

4.1 Phenotypic Syndromes in Macaronesian Plants: Biogeographical Framework

Islands have inspired research questions since long ago because some of their biotic features seem strikingly different to what we observe on mainland areas (Darwin 1859; Wallace 1892). Thus, one of the first evolutionary patterns described on islands was that a large proportion of insular insects have 'lost' their ability to fly as compared to closely related insects of mainland areas (Darwin 1859). More recently, Carlquist (1966) suggested that certain suites of plant traits appear to evolve together as a response to common island conditions, following a pattern known as the 'island syndrome'. For plants, this syndrome has been linked to several life-history and quantitative traits, including breeding systems, dispersal ability and levels of anti-herbivore defences, among others (reviewed in Burns 2019; Baeckens and Van Damme 2020).

In the case of defence-related traits, one of the most remarkable biotic differences between most oceanic islands and their mainland source areas is the lack of large insular herbivores (Wallace 1892; Carlquist 1980). Theory predicts that low herbivore pressure on islands would generally result in a prominent component of the island syndrome: reduced levels of plant defence (Carlquist 1980; Bowen and Van Vuren 1997; Vourc'h et al. 2001, reviewed in Burns 2019). However, recent work on plants endemic to oceanic islands provides weak support for this prediction (Pardo et al. 2018; Monroy and García-Verdugo 2019; Moreira et al. 2019, 2022; Slazak et al. 2021), probably because studies comprise highly heterogeneous levels of herbivore pressure between island and mainland settings and some study traits can be evolutionarily shaped by factors other than herbivory (Monroy and García-Verdugo 2019; Moreira et al. 2021).

In this chapter, we review the available evidence on putatively defensive traits for a particular island-mainland system: the Macaronesian islands and their Mediterranean continental source area. The Macaronesian islands are composed of four volcanic archipelagos (Azores, Madeira, Canary Islands and Cape Verde) lying on the North Atlantic Ocean, of which the Canary Islands harbour the highest plant diversity (c. 600 taxa). From a climatic point of view, Late Pleistocene shifts from tropical to Mediterranean-type conditions within some island areas likely promoted active reciprocal biodiversity exchange between Macaronesian and mainland settings (Fernández-Palacios et al. 2011; García-Verdugo et al. 2019a; Caujapé-Castells et al. 2022). Up to five vegetation belts can be currently differentiated within each island, with Mediterranean-like thermophilous shrublands occupying lowland zones (Fernández-Palacios et al. 2011). Mediterranean-type habitats in Macaronesia are, however, characterized by particular features associated with the latitudinal location of the archipelagos. For instance, lowland zones experience subtropical conditions (i.e. narrow annual temperature range) and high exposure to UV radiation all year round (Utrillas et al. 2013; García-Verdugo 2014; see also Weigelt et al. 2013). Importantly, the Macaronesian flora has evolved in the absence of large herbivores until the arrival of human colonists (Gangoso et al. 2006; De Nascimento et al. 2020). In this regard, we could expect island endemic lineages to show clear phenotypic responses depicting herbivore release with respect to ungulate browsers (e.g. Bowen and Van Vuren 1997). Comparisons of insect diversity between both settings have been studied in less detail, but herbivore guilds such as beetles (Coleoptera) appear to exhibit low diversity (Becker 1992), which would also support the idea of reduced insect herbivore pressure on the island setting. Studies on Macaronesian plant lineages have comprised traits related to defence against browsers (i.e. spines) or chemical traits that could affect both browsing mammals and insect herbivores (i.e. secondary compounds) (e.g. Shmida and Werger 1992; Monroy and García-Verdugo 2019; Moreira et al. 2022). Even though levels of insect herbivore pressure are difficult to assess, browsing pressure by ungulates is generally shown as a major driving force in the evolution of insular plant defence (Bowen and Van Vuren 1997; Vourc'h et al. 2001), and hence we would expect Macaronesian endemics to have lost (or lowered, at least) traits related to anti-herbivory defence.

Alternatively, it is also possible that leaf phenotypes of insular plants have been shaped by multiple environmental cues and stochastic factors associated with the process of island colonization (Brandenburger et al. 2019; García-Verdugo et al. 2019b), which may result in phenotypic shifts between mainland and island settings that are not necessarily related to changes in herbivore pressure. If trait variation between Macaronesian and closely related Mediterranean taxa consistently follows a pattern of convergent evolution across lineages, the occurrence of an island syndrome would be supported (Burns 2019). Furthermore, if herbivory release is a key factor driving phenotypic evolution of Macaronesian taxa, we would expect convergent patterns towards reduced investment in mechanical and chemical defence across plant lineages. In addition to traits typically related to anti-herbivory defence, we also examine the information available from studies on resource-acquisition traits that may provide an integrated view on plant defence (Menzies et al. 2016). We focus this review on the Macaronesian islands because they provide an interesting framework to address this hypothesis and extend our observations to other island systems, particularly to those where island plants have evolved in the absence of large browsers and biogeographical connections between island and mainland taxa are well understood.

4.2 Leaf Traits Putatively Associated with Plant Defence: Insights from the Comparison Between Macaronesian and Mainland Mediterranean Plants

4.2.1 Spinescence

Researchers have recurrently noticed that some island plant species do not display spinescence (i.e. the physical defences in the form of spines, thorns or prickles), while their mainland relatives do (Carlquist 1980; Bowen and Van Vuren 1997; Burns 2014; reviewed in Burns 2019). If spinescence plays a role as a browsing deterrent, an intuitive explanation for this pattern is that evolution in the absence of browsers may have resulted in the loss or reduction of such mechanical defences.

In the case of the Canary Islands, Shmida and Werger (1992) noticed the ‘paucity of spines’ when Canarian and Mediterranean floras were compared. While this observation appears to suggest that selection for reduced spinescence has occurred in the Canary Islands, we are not aware of any study specifically testing the evolution of this trait between Macaronesian endemics and their mainland ancestors. Nevertheless, Moreira et al. (2022) analysed several phenotypic traits within an evolutionary framework (including spinescence) using a large set of endemic and non-endemic native species of the Balearic Islands (Mediterranean region) and the Canary Islands, which are two archipelagos differing in levels of browsing pressure in evolutionary terms (i.e. much higher in the former case). Contrary to expectations, comparisons between endemics and native non-endemics revealed no differences in spinescence. This trait, however, was the only one lacking phylogenetic signal in the study, which suggests that spinescence has been independently selected for in Mediterranean taxa (including Balearic Island endemics) across phylogeny. Although these results support the idea that levels of ungulate pressure on islands may account for spinescence, the main explanatory factors underlying the high incidence of plant spinescence in the Mediterranean area, including wind exposure, physiological response to reduce transpiration and herbivore deterrence, remain to be assessed (Terradas 1991; Tébar et al. 2004).

Studies from other regions similarly show that plant spinescence is far from being rare on islands relative to mainland areas. By comparing species lists for 18 island-mainland pairs around Australia, Meredith et al. (2019) did not find differences in this trait between settings. It has been suggested that spinescence in some island systems in the Pacific Ocean may be an anachronistic response to extinct avian browsers or tortoises (reviewed in Burns 2019). In addition, the introduction of exotic ungulates, particularly goats, has severely limited the natural distribution of many plant taxa in Macaronesia (Gangoso et al. 2006). Under this scenario, it is remarkable that some native, non-endemic species such as *Lycium intricatum* and *Launaea arborescens* are nowadays among the most common shrubs in lowland areas across the entire Canarian archipelago and most islands of Cape Verde, in the case of *L. arborescens*. Both are spiny species and share physiological traits to cope with drought such as being facultative deciduous (i.e. they drop their leaves under prolonged water shortage). The recent spread of these species suggests that strong pressure by exotic ungulates and xericity are important selective forces in lowland Macaronesian habitats.

In conclusion, loss of spinescence does not seem to be a generalized feature of island plants. Studies conducted to date indicate similar levels of spinescence on islands versus mainland areas, and in some cases even higher trait values for insular plants. Differences between Macaronesian and Mediterranean taxa could be due to selective patterns driven by herbivory on mainland areas, although other environmental factors cannot be discarded.

4.2.2 Leaf Size

Leaf size has been hypothesized as another plant trait related to levels of herbivore pressure (Burns et al. 2012; Kavanagh 2015). A comparison between New Zealand (as the mainland source area) and Chatham Island taxa by Burns et al. (2012) indicated a consistent pattern of increased leaf size for insular taxa. These authors suggested that larger leaves on the Chatham Islands could be due to (1) release from high herbivore pressure (i.e. browsing birds in New Zealand) as smaller leaf sizes could reduce foraging efficiency by herbivores (Brown and Lawton 1991), or (2) increased intra-specific competition for light in island tropical forests.

Comparisons of mainland Mediterranean versus Macaronesian congeners have frequently found larger leaf sizes for island plants (Ortega-Olivencia and Catalán 2009; García-Verdugo 2014; Moreira et al. 2022; Fig. 4.1). However, the explanatory hypotheses put forward by Burns et al. (2012) for the Chatham Islands flora do not seem to suit this system. First, the Mediterranean-type habitats of the Macaronesian islands typically consist of open shrublands. Hence, competition for light does not seem a plausible explanation for increased leaf size in this island setting. Second, and related to the first, there is good evidence that small leaf size is associated with xericity in Mediterranean-type habitats (Ackerly 2009; Peguero-Pina et al. 2014), rather than an anti-herbivore trait.

We propose two alternative explanations for the observed trend towards increased leaf size across Macaronesian plants that occur in lowland habitats. First, limited oscillation in temperature is related to increased leaf size at global scales (Wright et al. 2017), and one of the most remarkable abiotic differences between

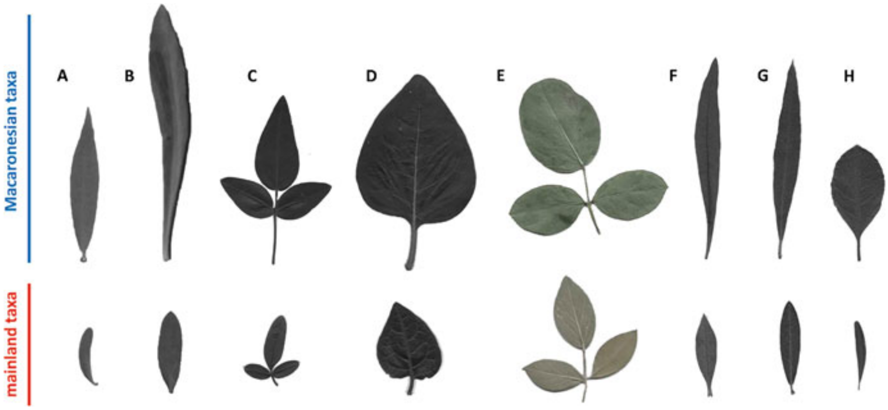

Fig. 4.1 Leaf size comparisons between island-mainland pairs of closely related species that are common components of Mediterranean-type habitats in Macaronesian and mainland settings. Leaf sizes are to scale and correspond with the following species pairs: (**a**) *Periploca laevigata–P. angustifolia*, (**b**) *Kleinia neriifolia–K. anteuphorbium*, (**c**) *Chrysojasminum odoratissimum–C. fruticans*, (**d**) *Withania aristata–W. frutescens*, (**e**) *Bituminaria bituminosa* var. *albomarginata–B. bituminosa* var. *bituminosa*, (**f**) *Globularia salicina–G. alypum*, (**g**) *Olea cerasiformis–O. europaea*, (**h**) *Rhamnus crenulata–R. lycioides*

Macaronesia and the Mediterranean mainland area is the much narrower temperature range of the islands (García-Verdugo 2014). Thus, climatic conditions could favour convergent patterns towards large leaf sizes across island taxa, whereas selection towards smaller leaf sizes would prevail in continental Mediterranean areas. A second factor, likely complementary to the first, is allometry. Macaronesian habitats tend to select for increased woodiness and plant size (Lens et al. 2013; García-Verdugo et al. 2014), and thus larger leaf sizes could be a by-product of selection on correlated traits (leaf and plant size; see discussions in Burns et al. 2012; Burns 2019).

4.2.3 Secondary Metabolites

Some of the first empirical studies on the evolution of plant defence on islands documented low levels of secondary metabolites for island taxa as compared to those measured in mainland counterparts (Bryant et al. 1989; Bowen and Van Vuren 1997; Vourc'h et al. 2001). However, the prediction that insular endemics have reduced chemical defences has received mixed support (Moreira et al. 2022; reviewed in Burns 2019; see also the meta-analysis by Moreira et al. 2021).

We examined the information available from common garden studies comparing Macaronesian and Mediterranean pairs of taxa (Fig. 4.2) and found limited support for this hypothesis. Specifically, phenolic compounds (i.e. total polyphenolics, condensed tannins), a popular choice in studies of plant defence (e.g. Bryant et al. 1989; Bowen and Van Vuren 1997), are similar (*Olea*, *Prunus*) or even higher (*Periploca*) on islands when compared to levels displayed by mainland counterparts (Fig. 4.2). Likewise, conspecific comparisons of Balearic versus Canarian populations of five plant species by Moreira et al. (2022) revealed higher total phenolic content (55% higher, on average) for taxa from the Canary Islands relative to Mediterranean taxa. Due to the antioxidant activity of such compounds (Karabourniotis et al. 2014) and the high exposure to UV radiation at lower latitudes, photoprotection could likely be the main role for these compounds in Macaronesian plants, rather than anti-herbivore defence (Rico et al. 2013; Monroy and García-Verdugo 2019).

On the other hand, additional work looking at specific compounds for which anti-herbivore effects have been demonstrated, such as the phenolic compounds oleuropein (Koudounas et al. 2015) and angelicin (Berenbaum et al. 1991), were shown to be lower on Canarian taxa (Fig. 4.2). In keeping with the expectation of the 'loss of chemical defence' hypothesis, this pattern suggests that mainland levels of anti-herbivory compounds have been lost as a consequence of insularity. One notable exception was provided by Pardo et al. (2018), in which Macaronesian populations of the laurel forest species *Prunus lusitanica* displayed significantly high levels of prunasin, a cyanogenic compound with anti-herbivore activity (Fürstenberg-Hägg et al. 2013). Given the recent expansion of *P. lusitanica* across its mainland distribution (García-Verdugo et al. 2013), contrasting levels of secondary compounds between settings could be due to neutral processes associated with

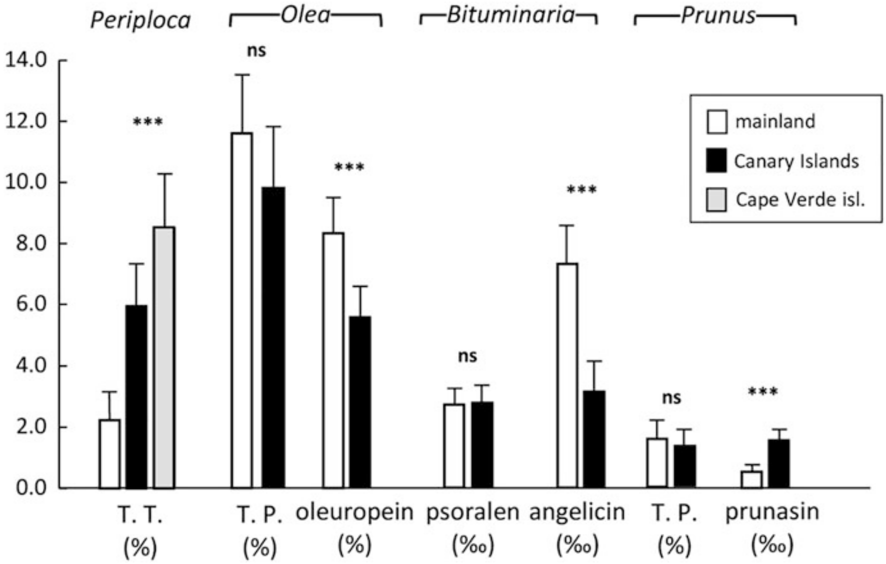

Fig. 4.2 Levels of putatively defence compounds in species pairs grown under common garden conditions. Statistical differences (***$p < 0.001$) are based on the results provided in each study. Data are extracted from: Monroy and García-Verdugo (2019) for *Periploca*, García-Verdugo et al. (2023) for *Olea*, Del Río et al. (2010) for *Bituminaria* and Pardo et al. (2018) for *Prunus*. *T.T.*, total tannins; *T.P.*, total phenolics

mainland bottlenecks (López-Goldar et al. 2019) or selective pressures in Macaronesian laurel forests exerted by phytophagous insect guilds (Pardo et al. 2018).

4.2.4 Photosynthetic Rates

Photosynthetic performance has never been considered a putative component of the island syndrome (see Burns 2019; Baeckens and Van Damme 2020). However, we believe that this trait could help provide an integrative view on plant defence, since CO_2 assimilation rates intrinsically lie at the core of defence theories (growth-defence trade-off; Herms and Mattson 1992; Wright et al. 2004) and carbon-based secondary metabolites are strongly related to photosynthetic patterns (Karabourniotis et al. 2014; Menzies et al. 2016).

Estimates of photosynthetic rates under common garden conditions have seldom been assessed in Macaronesian versus Mediterranean lineages. Considering the few studies available, there appears to be a clear tendency towards lower CO_2 assimilation rates in Macaronesian taxa (Fig. 4.3). Differences in photosynthetic rates suggest alternative resource-use strategies adopted in xeric habitats that differ in seasonality. Because photosynthesis in continental Mediterranean areas is strongly limited both by water availability (prolonged summer drought) and by temperature

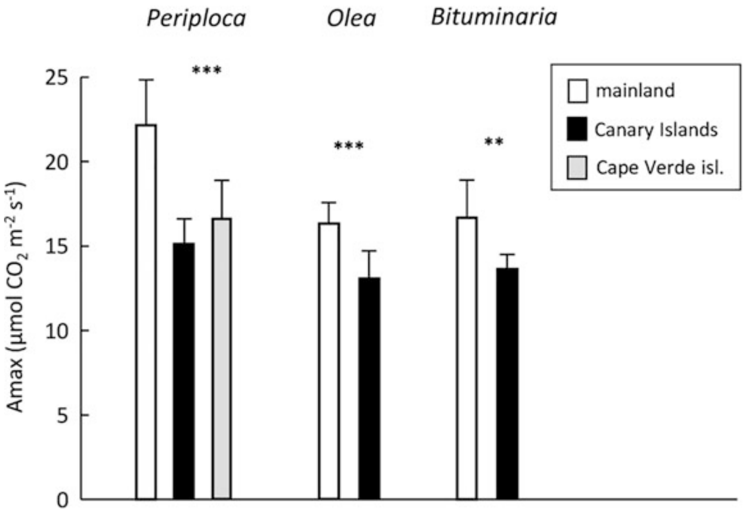

Fig. 4.3 Estimates of maximum photosynthetic rates (Amax) in species pairs grown under common garden conditions. Statistical differences (***$p < 0.001$) are based on the results provided in each study. Data are extracted from: García-Verdugo et al. (2020) for *Periploca*; Granado-Yela et al. (2011) and García-Verdugo et al. (2023) for *Olea*; Foster et al. (2015) and Valencia et al. (2016) for *Bituminaria*

(i.e. high in summer, low in winter), selection could have favoured higher photosynthetic rates (and related photosynthetic traits) to maximize growth during limited periods of optimal environmental conditions (Flexas et al. 2014). In agreement with this potential explanation, a recent study on *Periploca laevigata* showed that Macaronesian island sublineages tend to converge towards a leaf phenotype with low photosynthetic rates related to low climatic seasonality, whereas Mediterranean mainland populations displayed a specialized leaf phenotype characteristic of arid plants (i.e. high maximum photosynthetic rates, small leaves, amphistomaty, isobilateral mesophyll) (García-Verdugo et al. 2020).

Furthermore, differences in CO_2 assimilation rates could influence defence allocation. For example, a conservative resource-use efficiency in photosynthesis is typically associated with high investment in polyphenolic compounds with a protective role (Karabourniotis et al. 2014), which is in line with the pattern previously discussed for Macaronesian taxa inhabiting lowland habitats (see Sect. 4.2.3—Secondary Metabolites). Apart from implications in herbivore resistance, lower photosynthetic rates on Macaronesian plants could translate into limited herbivory tolerance. Traits such as compensatory growth or resprouting ability following herbivore attack (Fornoni 2011) may be limited on island taxa that display conservative rates of carbon storage and high construction costs for photosynthetic tissues (i.e. investment in large amounts of secondary compounds, large leaf sizes). Limited tolerance to herbivory might thus contribute to explaining why Macaronesian endemic plants are more negatively impacted by exotic browsing mammals than non-endemics (Cubas et al. 2019).

4.3 Synthesis and Future Considerations: A Syndrome Perspective

Based on the available evidence from empirical island-mainland comparisons, the hypothesis that Macaronesian plant endemics have lost their defences is still poorly supported. In turn, published studies point towards a repeated pattern of phenotypic convergence across Macaronesian plants inhabiting Mediterranean-type habitats that are characterized by large leaves, high concentrations of phenolic compounds in leaves and low photosynthetic rates as compared to those of mainland counterparts. We propose that this repeated pattern of evolution between mainland and island habitats constitute strong evidence for an island syndrome (sensu Burns 2019), but it also seems unlikely that the driving factors of this pattern are related to limited herbivore pressure on the Macaronesian islands.

In order to properly analyse emerging patterns in the context of plant-herbivore interactions, we argue that biogeographical and climatic factors should also be considered as potential contributing factors in any island system. In our study system, since most Macaronesian endemic lineages may have diverged from their closest mainland relatives around the onset of the Mediterranean climate (Plio-Pleistocene) (see the review by García-Verdugo et al. 2019c), we hypothesize that the identification of an island syndrome specifically related to plant defence should take into consideration the following points:

1. Some extant island traits might not be the result of selective patterns on the island setting itself, but rather correspond with traits developed by mainland ancestors before the establishment of the Mediterranean climate (García-Verdugo et al. 2020; Alonso et al. 2022). An evolutionary framework for inference of ancestral states of traits in the island-mainland system under study could be useful to understand where and how those traits evolved.
2. Total pools of phenolic compounds may reflect levels of protection against photodamage rather than chemical defence against herbivores (Karabourniotis et al. 2014). Specific secondary metabolites for which anti-herbivore effects have been demonstrated appear to be a preferable choice in studies seeking comparisons of defensive chemical traits between island and mainland settings.
3. Although we have evidence that large browsing mammals have not co-evolved with island plants in the study system, estimates of herbivore pressure from native insect guilds would help in understanding whether these play a role in the evolution of insular traits.

In conclusion, there is limited evidence that Macaronesian island lineages have lost their defence traits with regard to mainland counterparts. Emerging leaf phenotypic patterns could be mostly explained by disparate patterns of climate-driven selection between Macaronesian and mainland settings. Further research considering specific sets of defensive traits (i.e. spinescence, chemical compounds with demonstrated anti-herbivore effect) implemented into a phylogenetic or phylogeographical framework is needed to improve our knowledge on the evolution of plant defence. We encourage further investigation on island phenotypic syndromes in Macaronesian lineages and their continental ancestors, since the environmental conditions and the biogeographical history of plant lineages in this region clearly deviate from those of the study areas where most of the theoretical framework in plant defence has been built. We believe that these particular abiotic and biotic conditions will help to provide a complementary view on the evolution of island plant defence and stimulate research in other island systems.

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

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Riccardo Ciarle, Kevin C. Burns, and Fabio Mologni

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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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/978-3-031-47814-7_5.

R. Ciarle · K. C. Burns
School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand

F. Mologni (✉)
Department of Biology, University of British Columbia Okanagan, Kelowna, BC, Canada
e-mail: fabio.mologni@ubc.ca

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_5

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 (Diederen 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

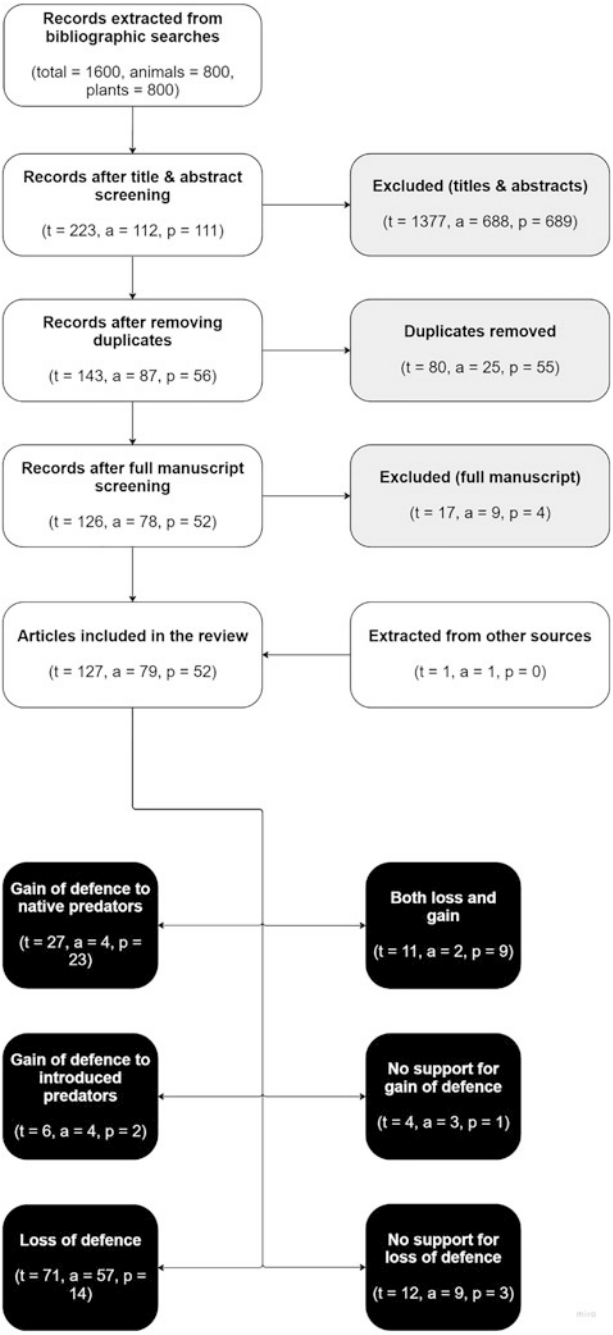

Fig. 5.1 Screening process of articles extracted from the literature search. White and grey boxes indicate, respectively, articles retained and excluded at each stage. Black boxes represent the final categories after full-manuscript assessment. At each stage, the total (t), animal (a) and plant (p) numbers 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 (*Urocyon littoralis santacruzae*)	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 (*Podarcis gaigae*)	Mesa Diavates and Lakonissi	Skyros	Island gigantism	Increased intra-specific predation pressures	Gain of defence against cannibalism	Pafilis et al. (2011)
Boldness	House mouse (*Mus musculus*)	Gough island and Isle of May		Island mice are bolder and more exploratory	Reduced predation pressure	Loss of defence	Gavriilidi 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 (*Petroica australis*)	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 (*Rangifer tarandus platyrhynchus*)	Svalbard islands	Norway	Island populations are bolder	Reduced predation pressure	Loss of defence	Reimers et al. (2011)

	Santa Cruz Fox (*Urocyon littoralis santacruzae*)	Santa Cruz	California	Island foxes are bolder	Reduced predation pressure	Loss of defence	Crooks and Van Vuren (1995)
	Gartersnake (*Thamnophis sirtalis*)	Beaver archipelago	Michigan	Increased boldness in island snakes	Reduced predation pressure	Loss of defence	Placyk (2012)
	Deer mouse (*Peromyscus maniculatus*)	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 (*Pteropus rayneri*)	Solomon islands		Change in posterior colouration	Increased predation pressure	Gain of defence against native birds	Hamilton (2004)
	Lizards (genus *Podarcis*)	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 (*Oophaga pumilio*)	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 (*Amblyrhynchus cristatus*)	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)
	Cavia intermedia	Moleques do Sul	Brazil	Sexual maturity is reached later on islands	Reduced predation pressure	Loss of defence	Salvador and Fernandez (2008)
	Skyros wall lizard (*Podarcis gaigae*)	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 *Dasyurus*)	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 (*Bettongia lesueur*) and greater bilbies (*Macrotis lagotis*)		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 (*Leiothlypis celata sordida*)	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)
	Angiosperms	Chatham Island	New Zealand	Island plants display smaller branching angles, shorter internodes and larger stems	Reduced predation pressure	Loss of defence	Kavanagh (2015)
Spinescence	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	Angiosperms	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 *Cyanea*)	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)

(continued)

Table 5.2 (continued)

Trait	Studied taxon	Island	Mainland	Pattern	Potential process	Category	Reference
					giant tortoises	herbivore reptiles	
	Angiosperms	Channel islands	California	Island plants have larger leaves	Reduced predation pressure	Loss of defence	Bowen and Van Vuren (1997), Salladay and Ramirez (2018)
	Angiosperms	Balearic and Canary islands		Native plants have smaller, thicker leaves than introduced plants		Gain 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	*Pseudopanax crassifolium*	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)
	Elaeocarpus hookerianus, *Pseudopanax crassifolium*,	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				browsing birds	herbivore birds	(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)
	Tuja plicata	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	*Argemone glauca*	Hawaii		Highly variable levels of latex exudation		Gain of defence	Barton (2014)
Prickles	Campanulaceae (genus *Cyanea*)	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
						herbivore birds	
	Rubus croceacanthus, *Glochidium obovatum* and *Zanthoxylum ailanthoides*	Kashima Island	Japan	Longer and denser prickles on island plants	Predation pressure from browsing mammals	Gain of defence against native deer	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	*Plectritis congesta*	Sidney Island	Canada	Island plants flowered later	Predation pressures from browsing mammals	Gain of defence against native and introduced mammals	Skaien and Arcese (2020)
Fruit size	*Plectritis congesta*	Sidney Island	Canada	Island plants produced small, wingless fruits	Predation pressures from browsing mammals	Gain of defence against native and introduced mammals	Skaien and Arcese (2020)
Tolerance	Bilberry (*Vaccinium myrtillus*)	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

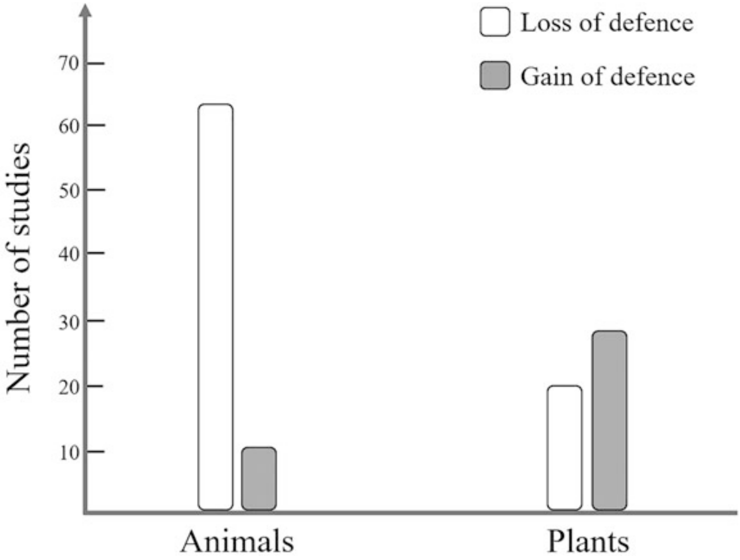

Fig. 5.2 Studies investigating loss and gain of defence in animals and plants. In animals, 66 studies investigated loss of defence and 11 gain of defence. In plants, 20 investigate loss of defence and 28 gain of defence. The two fields are on conceptually different pathways, as work on animals focuses mostly on loss of defence, while work on plants prioritises the study of gain of defence (X-squared = 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.

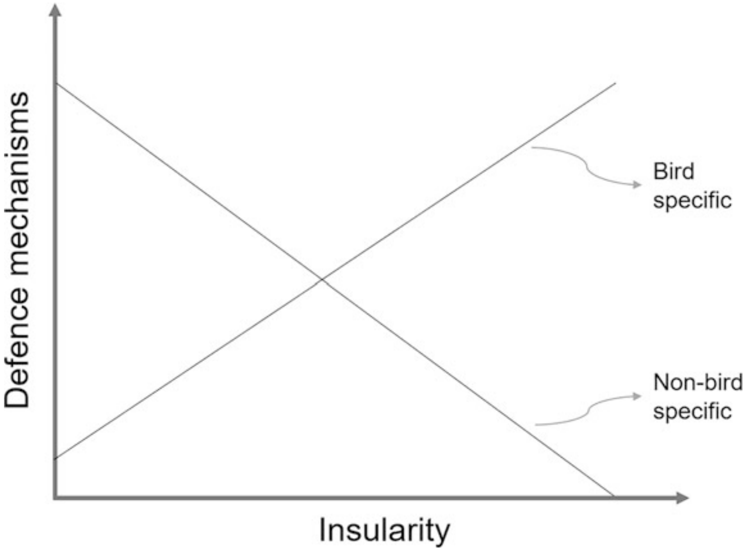

Fig. 5.3 Model illustrating a hypothetical common pattern of loss and gain of defences in island animals and plants. As insularity (i.e. area and isolation) increases, the number of non-bird-specific defences decreases (i.e. loss of continental defences) and the number of bird-specific defences increases (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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Part II

Plant–Herbivore Interactions

6

Impact of Non-native Mammalian Herbivores on Insular Plant Communities in the Canary and Balearic Islands

Miquel Capó, Joana Cursach, Elena Baraza,
Juana María González-Mancebo, Juan Rita, Marcelino del Arco,
and Jonay Cubas

Abstract

Biological invasions are a major cause of loss of biodiversity worldwide, particularly on islands. Introduced mammalian herbivores are among the most threatening of all invasive species, especially goats [*Capra hircus* (Linnaeus, 1758)], sheep [*Ovis orientalis aries* (Linnaeus, 1758)], mouflon (*Ovis orientalis musimon* [Pallas, 1762)], Barbary sheep [*Ammotragus lervia* (Pallas, 1777)], and rabbits [*Oryctolagus cuniculus* (Linnaeus, 1758)]. The vulnerability of insular plant communities, especially the endemic flora, is strongly influenced by their historic (and present) herbivory context, within which these introduced herbivores have played a key role. The effects of the introduction of mammals such as goats and rabbits are difficult to elucidate, as their introductions occurred thousands (or hundreds) of years ago and data on the previous status of the plant communities are not available. However, the present-day impacts of both of these herbivores on insular plant communities have been intensively studied. Herbivory can reduce the distribution area and constrain insular endemic species to inaccessible areas such as cliffs or islets, which impoverishes the original insular ecosystems and changes their species composition. Moreover, the

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M. Capó (✉)
Department of Natural Systems and Resources, Universidad Politécnica de Madrid, Madrid, Spain

Research Group of Plant Biology under Mediterranean Conditions, Departament de Biologia,
Universitat de les Illes Balears, Palma, Islas Baleares, Spain

J. Cursach · E. Baraza · J. Rita
Research Group of Plant Biology under Mediterranean Conditions, Departament de Biologia,
Universitat de les Illes Balears, Palma, Islas Baleares, Spain

J. M. González-Mancebo · M. del Arco · J. Cubas
Plant Conservation and Biogeography Research Group, Departamento de Botánica, Ecología y
Fisiología Vegetal, Universidad de La Laguna, La Laguna, Islas Canarias, 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_6

negative effects of these species on the insular native flora have led to the development of eradication and control programmes on many islands, with the aim to recover and protect native plants. Coordination between policymakers, managers, researchers, hunters and society is crucial in order to identify efficient solutions to protect and restore insular plant communities, effectively manage hunting activities and optimally limit the effects of introduced mammals.

6.1 Overview of Introduced Mammalian Herbivores on Islands

The establishment and expansion of invasive species are one of the most significant drivers of global change (Lenzner et al. 2020; Bello-Rodríguez et al. 2021), and these impacts are especially dramatic on islands where native species have often evolved in the absence of strong competition, herbivory, parasitism or predation (Courchamp et al. 2003). In particular, the introduction of exotic herbivores has provided evidence of profound changes in island ecosystems (Courchamp et al. 2003) and the degradation impact can remain for hundreds or thousands of years until the herbivores are eradicated (Chapuis et al. 2004; Garzón-Machado et al. 2010; Velamazán et al. 2017).

Goats, sheep and rabbits are considered huge threats to the conservation of insular biodiversity when they become feral in natural areas (Cubas et al. 2019; Mayol et al. 2017). The negative effects of these feral livestock on insular plant communities and endemic flora, such as predation of endangered species, impact on demographical structure or propagation of alien species, among others, have been intensively studied by several authors since the middle of the last decade (Sventenius 1946; Ceballos and Ortuño 1951; Nogales et al. 1992; Salgado-Luarte et al. 2019), but information on how ecosystems respond to their impact remains largely unresolved in many systems. For instance, effective regeneration of some trees and shrubs in some arid Australian ecosystems is suppressed in favour of the establishment of alien plants that are adapted to herbivory (Cooke 2012). Notably, amongst all introduced mammalian herbivores, goats and rabbits are included in the Top 100 world's worst invasive alien species list published by the International Union for Nature Conservation (IUCN) (Lowe et al. 2004) and their eradication is considered a key factor for ecological restoration around the globe (Priddel et al. 2000; Donlan et al. 2002; Bried et al. 2009; Capizzi 2020; Rita et al. 2022). The impact of introduced mammalian herbivores on insular vegetation, especially endemic plant species, varies depending on their palatability, resistance and defence strategies, and their ecological distribution, among other factors (Cubas et al. 2019; Capó 2021). These impacts become especially harmful when they severely feed upon narrow or endangered species (Carqué et al. 2004; Velamazán et al. 2017), leading in some cases to local or regional extinctions. For example, in regions such as Australia, introduced mammalian herbivores can locally eliminate all of the seeds of native shrubs and shift the herbaceous composition, even at low herbivore densities (Lange and Graham 1983; Bird et al. 2012).

Here, we present a review of the literature about the impact of introduced mammalian herbivores in two insular systems, namely the Canary and Balearic Archipelagos. We seek to elucidate these impacts relative to historical (pre-introduction) by describing communities of extinct herbivore paleofauna, as well as by providing a detailed analysis of how and when introduced mammalian herbivores arrived in these archipelagos and what are their impacts on insular plant communities and concretely on threatened species. In doing so, we also examine differences and similarities between systems in introduced herbivore impacts and potential explanatory factors (from geographical origin to ecosystem variation). Finally, we also present perspectives on how to advance future multidisciplinary research needed to achieve effective solutions for island ecosystem management and conservation.

6.2 Native Herbivore Paleofauna of the Studied Insular Systems

Knowledge on the origin of islands is essential to understand the processes that mediated the evolution of plant-herbivore interactions and therefore the vulnerability or capacity of native plant species to defend themselves against introduced herbivores. Generally, islands are classified into two types depending on their origin: oceanic, that is, islands that emerged through the surfacing of submarine folds due to geological pressure; and continental, that is, islands that originated by tectonic plate movements that fragmented and isolated the terrestrial surface (Rosenbaum et al. 2002).

Oceanic islands represent 5% of the terrestrial surface of Earth and are considered one of the most important refuges for endemic species per unit area (Kreft et al. 2008). In fact, a staggering 25% of the entire endemic flora is located on oceanic islands (Fernández-Palacios 2004). At the same time, they are also one of the most threatened areas of the world and have suffered 80% of all-known species extinctions since the year 1500 aC (Ricketts et al. 2005). In the case of the Canary Islands, an example of this type of island, fossils of a variety of native reptiles and micromammals have been found, such as tortoises (*Geochelone* spp.) from the Pliocene (5.3–2.6 Mya) (López-Jurado and Mateo 1993) and more recent fossils from the Holocene, such as giant lizards (*Gallotia* spp.) (Castillo et al. 1994), an unknown snake (*Boidae*) (Barahona et al. 1998), as well as micromammals such as a native mouse [*Malpaisomys insularis* (Hutterer, López-Martínez & Michaux 1988)] (Hutterer et al. 1988) and giant rats (*Canariomys* spp.) (Crusafont-Pairo and Petter 1964). Overall, however, this system has historically been characterized by the absence of ungulates, with the exception of a bovid (NAME) during the last 5 million years, which was also present in the Balearic Islands. Therefore, the island origins of the Balearic and Canary Archipelagos—and thus the evolution of their flora—were driven by two very different ecological scenarios. Thus, the ideas about the impact of introduced mammalian herbivores on oceanic (Canary Islands) and continental

(Balearic Islands) islands presented throughout this chapter must be interpreted within the context of their different biogeographic origins and processes.

In contrast, continental islands can preserve well-established ecosystems that were present on the continent at the time of fragmentation. After fragmentation and isolation, these newly isolated communities followed their own line of evolution under insularity. Many fossil records from the Plio-Pleistocene period (5.3–0.01 Mya) confirm the existence of endemic insular mammalian herbivores on the continental islands of the Mediterranean Basin, ranging from micromammals (Vogel and Sofianidou 1996) to artiodactyls (Croft et al. 2006; Bover et al. 2010). However, all of these species became extinct before the Holocene, probably due to abrupt climatic change or as a result of the arrival of humans to the islands (Bover et al. 2016). The Balearic islands represent a system of this type, for which fossil records of mammalian herbivores have been dated back to the Holocene 4035 ± 32 years BP (Bover et al. 2016), followed by more abundant records dated after the Messinian salt crisis caused by the closure of the Strait of Gibraltar and the drying of the Mediterranean Sea (5.9–5.3 Mya) (Krijgsman et al. 1999). During the salt crisis, the Balearic Islands were still connected to the continent, which allowed the transfer of new herbivores. The genus *Myotragus* spp., which represents small artiodactyls, arrived and established on the island of Mallorca at this time, becoming one of the most interesting ungulates among insular native mammals that are part of the Plio-Pleistocene fossil fauna of the eastern islands of the Balearic Archipelago (Bover et al. 2008). Progressive dwarfism and changes in dentition gave rise to a species endemic to Gymnesians, the extinct *Myotragus balearicus* (Bate, 1909) (Bover et al. 2008; Palombo et al. 2013; Winkler et al. 2013). The first colonizing human populations are thought to have arrived on the islands about 4000 years before the present, which almost coincides with the last fossil records of *M. balearicus* (Bover et al. 2016). The most plausible scenario is based on a continuum between the last natural populations of native *M. balearicus* and the human introduction of new mammalian herbivores, mainly goats, rats, rabbits and sheep (Mayol et al. 2017).

6.3 Endemic Flora of the Canary and Balearic Islands and Their Vulnerability

The Canary Islands are located 96 km off the west coast of Africa, in the Macaronesian region, and the maximum altitude is located on Tenerife Island at 3718 m a.s.l. The archipelago harbours 2260 wild species of vascular plants, of which 597 are endemic, within 29 genera (Data Bank of Canary Islands Government). Hence, a high proportion of the flora on the Canary Islands is endemic (del Arco and Rodríguez-Delgado 2018). The archipelago is home to more than 50% of the endemic flora of Spain and exhibits the highest endemicity rate in Europe (Beltrán et al. 1999). Moreover, this archipelago has one of the highest percentages of endemic plants in the world (Whittaker and Fernández-Palacios 2007), including many unique ecosystems such as *Euphorbia* scrub and shrublands, thermo-sclerophyllous woodland, dry, humid and temperate laurel forests, Canary pine forest, summit broom shrubland and a community of Teide violets. In terms of the vascular flora, circa 30% of all endemic species are estimated to be endangered (Caujapé-Castells et al. 2010) and this has the highest number of threatened plant species in Spain (del Valle et al. 2004).

The Balearic Archipelago, on the other hand, is located in the Western Mediterranean Basin. The maximum altitude is 1445 m a.s.l. (Mallorca). This Archipelago is home to 1551 plant species, of which 20 are endemic to the Thyrrenian Islands (including Corsica and Sardinia) and 140 are exclusive to the Balearic Archipelago (Rita and Payeras 2006; Sáez et al. 2013). The latest available version of the Balearic Islands flora red list considers 171 taxa under various categories of threat: high proportions of these threatened species are also endemic—56.5% in Mallorca, 17.7% in Menorca, 47.8% in Eivissa and 28.5% in Formentera (Sáez et al. 2017). The Archipelago encompasses many different habitats, including saltmarshes, temporary ponds, dunes, shrublands, forests and ravines. The disturbances caused by humans have changed over time; urbanization, construction of infrastructure and intensive agriculture in some areas and abandonment of agriculture in others, among other factors, are currently causing the loss or fragmentation of many habitats (Pons and Rullan 2014; Sáez et al. 2017).

Altogether, both archipelagos harbour a wide variety of endemic species and habitats of high conservation value due to endemism or rarity, all of which are currently being impacted to some degree by introduced mammalian herbivores. We will next describe how and when these herbivores arrived, their current population levels, and then analyse whether management strategies have been successful in mitigating these impacts and to what extent.

6.4 History of Exotic Mammalian Introductions and Current Status

Goats and sheep were probably introduced to the Canary Islands during the first millennium BC (Rando 2003; de Nascimento et al. 2020) while the European rabbit (*Oryctolagus cuniculus*) was introduced in the fifteenth century (de Abreu-Galindo 1977). Rabbits have the highest establishment success in the Archipelago (Nogales et al. 2006) and are present on all islands and habitats of the Archipelago, including the main islets—except for Montaña Clara, where they were successfully eradicated between 2000 and 2001 (Martín et al. 2002). Additional introduced mammals include the mouflon (*Ovis orientalis musimon*), which was introduced during 1970s to El Teide National Park (Tenerife), and Barbary sheep (*Ammotragus lervia*), introduced to Caldera de Taburiente National Park (La Palma) (Nogales et al. 2006). Both species have experienced substantial population increases over time, expanded to other ecosystems and been illegally trafficked to other islands from the same archipelago (La Gomera and Gran Canaria) (Rodríguez-Luengo, personal communication).

The introduction of exotic mammalian herbivores to the Balearic Islands coincides with the arrival of humans about 4000 years ago. Most of these animals were intentionally introduced as cattle for food purposes, such as goats and sheep (Campbell and Donlan 2005). These species were managed and used by humans for centuries, and some populations were evolutionarily driven to form varieties of domestic animals such as the goat variety known as '*Cabra mallorquina*' from Mallorca or '*Cabra eivissenca*' from Eivissa. The first of these species is now used for hunting purposes, while the other is still used for cattle (Mayol et al. 2017).

During human colonization 4000 years ago, several species of small mammals such as rabbits and rats were also introduced, which rapidly dispersed and colonized all islands of the Archipelago (Traveset et al. 2009). Rats also colonized small islands in the Archipelago, such as Dragonera, Cabrera, es Vedrà and Conillera. Whereas rabbits are currently abundant in the centre and southern part of the Island of Mallorca and are widespread on the other islands, being particularly harmful on small islands such as Formentera and Cabrera and the islets (Santamaría et al. 2007; Capó et al. 2020; Rita et al. 2022). In addition, other more recently introduced herbivores are becoming free-ranging, including the European fallow deer [*Dama dama* (Linnaeus, 1758)], which will probably expand across these islands in the near future (Pinya and Lassnig 2018).

More recently, significant land-use change occurred in the Balearic Islands during the 1960s with the shift from agriculture to tourism (Pons and Rullan 2014), which led to the abandonment of many populations of ungulates (mainly goats). As a result, feral populations of goats were established on the mountains and natural areas of Mallorca (Vives and Baraza 2010). Their high reproductive rate and lack of management allowed the populations to grow rapidly and led to overpopulation within a few decades (Mayol et al. 2017; Limpens et al. 2020). At present, the overpopulation of goats is considered one of the major threats to plant communities on these islands (Moragues et al. 2015; Mayol et al. 2017; Capó et al. 2021, 2022).

6.5 Impacts of Introduced Mammalian Herbivores on Both Insular Systems

The introduction of the first mammalian herbivores to the Canary and Balearic Islands is dated before the start of ecosystem studies, which makes it difficult to compare data of herbivory impacts before and after introductions. In addition, there is no information on the historical distribution of plant species that are currently constrained to areas inaccessible to herbivores (i.e., cliffs or mountain walls) and on potential plant species extinctions during the last few centuries. Hence, the richness and composition of the original plant communities could differ remarkably from the current vegetation—many insular endemic species could have disappeared or drastically reduced their populations due to the introduction of mammalian herbivores, as reported for other islands worldwide (Wood et al. 2017). Therefore, it is difficult to evaluate the ecological degradation due to introduced mammalian herbivores in most ecosystems, complicating the design of suitable vegetation restoration strategies. As an example, *Thesium psilotocladum* Svent was last seen on Tenerife in 1983. Since then, repeated searches in its classic localities have been unsuccessful.

Uncontrolled livestock has been pointed out as the main cause of the extinction of this species (Martín-Cáceres et al. 2004).

6.5.1 Impact of Herbivory by Feral Goats

Goats are considered one of the most pernicious invasive species on islands around the world (Lowe et al. 2004). Herbivory by goats can drive dramatic decreases in the population size of endemic plant species, with the remaining restricted to areas where herbivores find it difficult to access (Nogales et al. 1992; Pisanu et al. 2012) or eventually become extinct (Roemer et al. 2002; Genovesi and Shine 2004; Campbell and Donlan 2005; Garzón-Machado et al. 2010). They can also severely defoliate shrub species, causing severe damage on the plant (Chynoweth et al. 2013; Limpens et al. 2020; Capó et al. 2021) (Fig. 6.1). They can also indirectly affect endemic fauna such as insular lizards by altering their habitat and competing for resources (Nogales et al. 1992), invertebrate communities (Jauregui et al. 2008), as well as mutualistic interactions such as seed dispersion or pollination (Traveset and Richardson 2006; Capó et al. 2022).

In the Canary Islands, the presence of goats has contributed to the degradation of natural ecosystems and plant communities (Gangoso et al. 2006; Fernández-Lugo et al. 2013). This trend has continued since their introduction, mainly due to the economic benefits of the species for the aboriginal inhabitants and Europeans (Rando 2014). In fact, goats are feral on all of the Canary Islands, especially in specific areas defined as Natural Protected Areas. However, feral goats eradication programmes have been difficult to implement or continue for social reasons (Fernández-Lugo et al. 2013).

In the Balearic Islands, feral goats foraging areas are very stable during the year between 45 and 170 ha (Ibáñez et al. 2019). However, there is strong temporal variation in their diet depending on the season of the year and the type of vegetation they feed (Rivera-Sánchez 2014). Although it is not uncommon to see feral goat populations throughout the mountainous areas of Mallorca, these animals show a

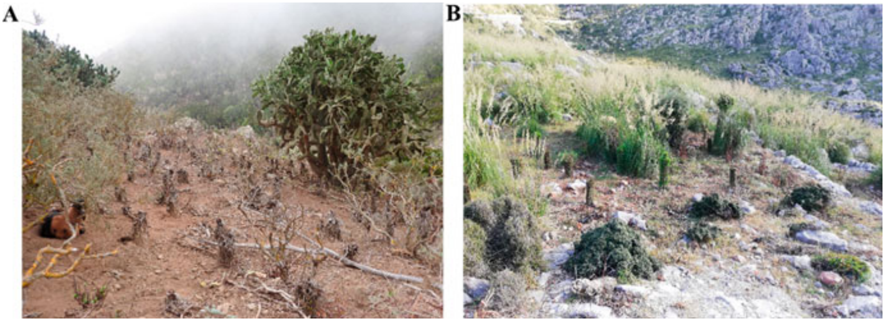

Fig. 6.1 Examples of plant communities on the Canary Islands (**a**) and Balearic Islands (**b**) that are severely affected by overpopulation of goats

preference for the highest and rockiest areas (Limpens et al. 2020). At the same time, these habitats are also hotspots of endemic flora, such as the mountain peaks of the northern mountain range (Moragues et al. 2015). Still, literature on the effects of goats on the Balearic Islands vegetation is scarce; only a few studies have reported severe threats to endemic species (Cursach and Rita 2012; Capó 2021) and vegetation at the population level, such as the case of *Euphorbia dendroides* L. (Capó et al. 2021), and at the community level, as observed in Es Vedrà islet (Capó et al. 2022). The impact of goats can also occur through indirect effects, such as the habitat disappearance due to soil erosion in the case of *Naufraga balearica* Constance & Cannon. Even though goats can favour *N. balearica* plant survival by predation of its competitor species, they also impact the species by increasing soil nitrification and erosion (Cursach et al. 2013).

6.5.2 Effects of the European Rabbit

Rabbits directly affect a large number of endemic and native plant species found on islands (Chapuis et al. 1995). These herbivores mainly predate seedlings and young individuals, making an assessment of their impact hard to detect in the short term (Cubas et al. 2018; Capó et al. 2021). These effects, however, are expressed over longer-term periods even after eradication and are intensified by impoverishment of the seed bank in the soil (Edwards and Crawley 1999; Bueno et al. 2011; González-Mancebo et al. 2019), especially due to the significant impact of rabbits on the juvenile stages of plants (Gómez-Aparicio et al. 2005; Irl et al. 2012; Cubas et al. 2017, 2018; Capó et al. 2021) and their influence on seed recruitment (Nogales et al. 1995, 2005; Martín et al. 2003).

In the Canary Islands, information on their ecological impacts in the archipelago was surprisingly scarce until recently (Garzón-Machado et al. 2010; Irl et al. 2012; Cubas et al. 2018, 2019, 2021; González-Mancebo et al. 2019) and their negative effects are considered a direct threat to many endangered and keystone insular species (Bañares et al. 2004, 2008, 2010; Carqué et al. 2004; Moreno 2008; Seguí et al. 2017). For instance, several key accompanying species of *Pinus canariensis* C. Sm. ec DC. in the Canarian pine forest (Bello-Rodríguez et al. 2019; Cubas et al. 2022) are now restricted to rupicolous areas due to the disappearance of all accessible populations to rabbits (Garzón-Machado et al. 2010).

The impacts of rabbits on insular endemic species have also been reported for the Balearic Islands, mainly in terms of fruit and seed predation or herbivory of vegetative structures (Santamaría et al. 2007; Capó et al. 2020). Specifically, the impact of rabbits on the endangered *Medicago citrina* (Font Quer) Greuter has been exhaustively investigated on the small islands of the Balearic Archipelago. Some studies have shown that this species is absent from the large island of Cabrera because both rats and rabbits consume seeds and seedlings arriving from surrounding islets (Latorre et al. 2013). Interestingly, and among the few successful cases, another study reported that new seeds of *M. citrina* germinated and a population of more than

2000 individuals established within a few years after eradication of rabbits on an islet close to Eivissa island (Rita et al. 2022).

6.6 Case Studies of Highly Threatened Endemic Species

On both archipelagos, there are many cases in which the impact of introduced mammalian herbivores comprises their conservation status (Moreno 2008; Bañares et al. 2010; Sáez et al. 2017). From this large number of species, we have selected three threatened endemic species whose most important threatening factor is introduced mammalian herbivores requiring urgent management strategies (i.e., fencing, herbivore population control) in order to guarantee their conservation.

6.6.1 *Cytisus supranubius* (Tenerife and La Palma, Canary Islands)

Cytisus supranubius (L.f.) Kuntze is considered a keystone species characteristic of alpine ecosystems in the Canary Islands (particularly on Tenerife), which should be considered vulnerable according to the general criteria established by the IUCN (Cubas et al. 2022). This species was considered to be in decline in the 1940s (Sventenius 1946), but the establishment of El Teide National Park in 1954 prohibited the human use of this species (previously used as pasture, for firewood and bedding for livestock). In addition, goats were eradicated within the limits of the National Park, which led to a dramatic reduction in herbivore pressure (Rodríguez-Delgado and Elena-Rosselló 2006). These important conservation measures led to a strong increase in the population of *C. supranubius* in subsequent years with a notable expansion in later decades, as demonstrated by the distribution maps of this species (del Arco and Rodríguez-Delgado 2018) and aerial photographs (Kyncl et al. 2006).

In the last 32 years, *C. supranubius* has experienced a 28.7% decline in its distribution (Cubas et al. 2022). This reduction is negatively correlated with temperature and positively correlated with precipitation. Climate change, especially prolonged droughts, is contributing to an increase in the mortality rate of this species (Olano et al. 2017). However, the most important factor that explains the decline of this species is the impact of European rabbit (Cubas et al. 2018). In a recent study including rabbit and mouflon exclusion plots across 13 sites of summit vegetation, Cubas et al. (2018) found that the European rabbit was the main cause for the decline in the Teide broom population. Outside the fences, the number of juveniles is almost non-existent (<2%) (Cubas et al. 2018). This suggests that exclusion of mouflon alone will not lead to recovery of the population structure of this species (Cubas et al. 2018). The present-day Teide broom shrublands without recruitment exhibit ageing of the shrubs and a high number of dead individuals (Cubas et al. 2018).

The impact of the European rabbit on the Teide shrubland can also operate through different pathways, in many cases involving complex mechanisms. For instance, one relates to an increase in the representation of clones within

C. supranubius populations. Rabbit seed herbivory increases the representation of clonally produced offspring, leading to reduced cross-fertilization by natural pollinators of this species, ultimately causing reduced seed viability due to inbreeding (Pérez de Paz et al. 2017). In many areas, these clones form large groups of shrubs with low vitality and lower reproductive output (Cubas 2020), thus reinforcing the direct negative effects of the European rabbit on vegetation regeneration in the Teide broom.

By impacting this species, rabbits also have indirect effects on the ecosystem. This can occur because *C. supranubius* is a major nitrogen fixer in the ecosystem (Wheeler and Dickson 1990; Pulido-Suárez et al. 2021), and reductions in its abundance consequently lead to a reduction in total soil nitrogen, and thus negative impacts on other plant species (Cubas et al. 2022). The presence of rabbit latrines has been also shown to alter the soil rhizobial populations within the ecosystem and can favour co-entrance of non-nodulating bacteria into the root nodules of plants, which can affect N-fixing symbiosis (Pulido-Suárez et al. 2021).

6.6.2 *Coristospermum huteri* and *Agrostis barceloi* (Mallorca, Balearic Islands)

Coristospermum huteri (Porta) L.Sáez & Rosselló and *Agrostis barceloi* (Porta) L. Sáez & Rosselló are endemic species to the Balearic Islands catalogued as Critically Endangered on both the Red List of Vascular Flora of Spain (Moreno 2008) and the Red List of Vascular Flora of the Balearic Islands (Sáez et al. 2017). These species are also classified at the highest threat level according to the Decree 75/2005 (Balearic Catalogue of Endangered Species, Special Biological Protection Areas) (BOIB 2005). These plants only occur at the summit of the highest mountain on Mallorca Island, Puig Major, at 1200–1400 m a.s.l. The summit of this mountain represents a hotspot of extremely narrow endemic species and other endangered plant species, as this unique site on the Balearic Islands has sufficient elevation to function as a suitable refuge in the present interglacial period (López-Pujol et al. 2013). However, herbivory pressure, mainly by feral goats, poses a major threat to the conservation of this site.

Coristospermum huteri is a perennial herb that inhabits limestone cliffs in shaded and slightly moist rocky areas; its entire population consists of ca. 400 individuals (of which more than 200 are transplanted individuals) distributed within an area smaller than 0.1 km^2 (Bibiloni et al. 2017). Its biology has not yet been fully studied, though this species has been reported to have extremely low genetic diversity (allozyme markers) (López-Pujol et al. 2013); this is a common rule for species with small population sizes, especially in island populations. Generally, the number of reproductive individuals is very low: only 9 individuals bloomed in 2006 (Forteza 2007), 3 in 2007, 2 in 2008, 12 in 2009, 5 in 2010, 13 in 2011 (López-Pujol et al. 2013), 12 in 2015 (Bibiloni et al. 2017) and 17 in 2022 (L. Sáez, personal communication). Anthropogenic threats have also affected the population of *C. huteri* over recent decades. Historical records indicate that the species was very abundant in the summit area (Bonafè 1979); however, plants could have been destroyed by construction of a radar facility for military purposes in 1958 (Sáez and Roselló 2004; Moragues et al. 2015). At present, the major threats are drought and herbivory by introduced mammalian herbivores, with the latter causing a reduction of up to 50% in the population during the late twentieth century (Mayol and Bibiloni 2005). Due to the poor conservation status of the species, recovery plans have been designed and implemented (BOIB 2008); several measures have been implemented in the last decades to avoid a decrease in the population sizes, mainly by controlling the impact of goat herbivory by fencing. To complement these efforts, control of competitor plant species inside the fenced area has also been implemented and plants were transplanted to increase the population. Globally, these management measures have improved the population size, but conservation actions must continue to reduce the impact of feral goats. A significant decrease in the feral goat populations would highly benefit the conservation of this species. In addition, other factors threaten the survival of the species, such as the low habitat availability and its very low reproductive performance.

Agrostis barceloi is a short rhizomatous perennial grass up to 30 cm in height that occurs in three subpopulations of an area of 170 m^2 (Sáez and Rosselló 2004; Massó et al. 2016). The rupicolous plant grows on shadow rock crevices and moist soils at the base of cliffs—generally north-facing—and is a tetraploid ($2n = 28$) species (Sáez and Rosselló 2000). Generally, the number of reproductive individuals is very low; the population size fluctuates widely over the years and the species undergoes clonal reproduction (Sáez and Rosselló 2004; Moragues et al. 2015). Previous studies reported no genotypic variability in this species, which can be attributed to a founder effect, the very small effective population size and a series of threats affecting the population (Massó et al. 2016). Predation of leaves and inflorescences certainly constitutes the major threat to the species; thus, conservation strategies including fencing and removal of competitor plants have been performed in recent years according to the Recovery Plan for this species (BOIB 2008). Indeed, fencing was initially very effective, as the number of inflorescences increased from 36 in 2007 to 1255 in 2008 (Moragues et al. 2015). Moreover, the habitat disturbance due to construction of the previously mentioned military installations in the 1950s and episodes of drought affect the persistence of the species (Sáez and Rosselló 2004; Massó et al. 2016). Overall, similarly to the case of *C. huteri* described above, ongoing management measures related to controlling the herbivory pressure are critical for the conservation of *A. barceloi*; demographic monitoring, improved knowledge of the biology of the species and creation of *ex-situ* collections are also essential for long-term conservation.

6.7 Multidisciplinary Perspectives and Recommendations

Management of introduced herbivores affects a variety of social stakeholders with contrasting points of view, which can lead to confrontational dynamics that inhibit policymakers from implementing interventions. Thus, it is crucial to include many

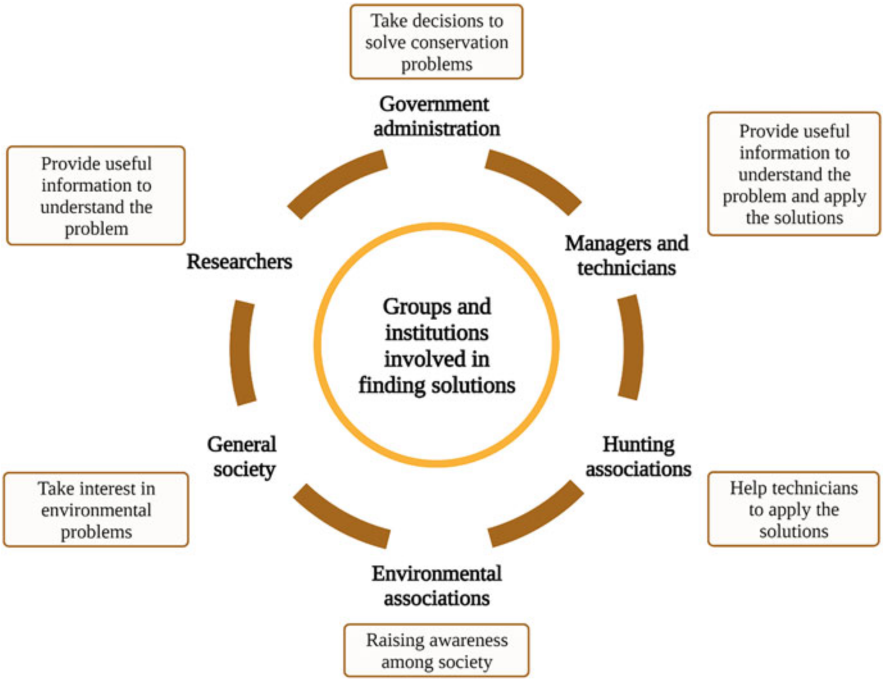

Fig. 6.2 Multidisciplinary scheme illustrating the major stakeholders implicated in the management of introduced mammalian herbivores and the roles they should play in application of suitable solutions

agents from society in order to properly manage multidisciplinary problems as the one presented in this chapter. In this section, we present the major social issues that must be considered in order to effectively manage and palliate the impact of introduced mammalian herbivores on both the Canary Islands and Balearic Islands (Fig. 6.2).

6.7.1 Government Administration

Conservation actions and decisions taken by environmental authorities can eventually be refused by society due to controversial social perception of mammalian herbivores on both archipelagos. For instance, in 2016, the Government of the Balearic Islands decided to eradicate the feral goats from a small islet located close to the island of Eivissa for conservation purposes. This decision translated into extraordinary recovery of the vegetation, especially of endemic plant species (Capó et al. 2022). However, at the same time, this decision was not well received by animalism parties and some citizens, and required judicial intervention (Rita 2016). This case illustrates how these policy actions are essential to consider a multidisciplinary point of view in order to guarantee their effectiveness in the long term.

6.7.2 Managers and Technicians

Environmental managers and conservationist technicians play an essential role in the creation of suitable strategies and programmes to address the impact of introduced mammalian herbivores. In some cases, complete eradication is difficult or even impossible; therefore, population control of the herbivores must be continuously performed to maintain the population density at low levels. This option is often difficult for several reasons, depends on the use of the area and an appropriate strategy needs to be designed (i.e., exclusion fences, hunting area, experimental areas, public-use areas, etc.) (Capó et al. 2021).

6.7.3 Researchers

Ongoing scientific studies must be carried out to generate new information that can help both government leaders and managers to design and implement efficient strategies. This information must also contribute to raising awareness to society through outreach activities and dissemination of results in non-scientific programmes, journals and media. Even though recent information has been generated to indicate which species and areas are more affected by introduced mammalian herbivores on both archipelagos (Cubas et al. 2018, 2019; Muñoz-Gallego et al. 2019, 2022; Limpens et al. 2020; Bello-Rodríguez et al. 2021; Capó et al. 2021, 2022; Ibañez-Álvarez et al. 2022; Rita et al. 2022), managers still demand more answers in order to design control and eradication programmes. Further studies must focus on disentangling the influence of introduced herbivores on the demographic structures, recruitment, germination and ecological interactions of threatened endemic species.

6.7.4 Hunting Associations

It is not rare that hunter authorities and associations take responsibility and collaborate with environmental management authorities with the purpose to control ungulate populations in order to prevent ecosystem and animal population degradation. However, common hunting techniques used to eradicate ungulates from islands (Campbell et al. 2004; Campbell and Donlan 2005) usually require hunters to be specially trained to optimize their fieldwork (Carrion et al. 2011). Hence, the collaboration of hunters with management programmes is desirable, under appropriate supervision by environmental authorities, to guarantee an optimal conservation strategy.

6.7.5 General Society and Environmental Associations

General society plays a key role in visualizing the importance of environmental problems and finding optimal solutions. In particular, environmental problems need to be communicated to urban areas, where it is very difficult to have a realistic perception of the problem and possible solutions. In this sense, it is very important that society knows and understands the importance of conserving valuable natural places, the serious problem of introduced herbivores and the limited management options that can be realistically applied (i.e., eradication of goats from islets or other crucial spots). Also, environmental associations can play a very important role in raising awareness among society about the problems of introduced herbivores on conservation of the natural heritage.

6.7.6 Animalism Versus Conservationism

The most defeating conflict that conservation managers face in terms of environmental policies is the confrontation between animalism and ecologism (López-i-Gelats et al. 2021). Animalism prioritizes the well-being of animals, frequently with a bias towards species that are phylogenetically close to humans or that have domestic traditions (Bailey 2015). In contrast, ecologism considers the ecosystem to be important as a whole (Baxter 1999). Hence, animalism and ecologism have opposing views on the role of introduced mammalian herbivores: animalism considers introduced herbivores as new members of the ecosystem that nature should adapt to, and considers killing the mammals as a crime. On the other hand, ecologists consider the introduced herbivores as a threat to the conservation of nature and that their elimination (with maximum effort to avoid unnecessary suffering) is necessary to guarantee the survival of native species of flora and fauna.

6.8 Conclusions and Final Remarks

This chapter reviews the current studies about the impact of non-native mammalian herbivores, notably goats and rabbits, on the ecosystems of the Canary and Balearic Archipelagos. The Canary Islands, due to their oceanic origins and lack of native mammalian history, appear to be more susceptible to these invasive species. In contrast, the Balearic Islands once housed native mammals like the bovid *Myotragus balearicus*, which potentially exerted evolutionary pressures on certain species but others seem to be vulnerable to herbivory. Anyway, the current proliferation of non-native mammal herbivores in both archipelagos poses significant threats to native plant communities due to overgrazing, with endemic species being especially vulnerable. To address these ecological challenges, comprehensive strategies are imperative. These should involve collaboration among a wide spectrum of stakeholders, ensuring a cohesive approach that factors in varied perspectives to counteract the adverse impacts of these invasive species effectively.

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7

Potential Benefits of Mammalian Herbivores on Insular Systems: The Case of Goats on Mediterranean Islands

Jordi Bartolomé and Bartomeu Seguí

Abstract

Mediterranean islands had long been the home of several mammalian herbivores in pre-human times, which differentiates them from other islands where such fauna was absent until its introduction as domestic species. Man colonized the Mediterranean islands thanks to goats, which was well-adapted to their climate. After several millennia of coexistence its role is generating controversy. Many studies have argued that some Mediterranean islands are suffering from overpopulation, which are seriously threatening landscapes, endemic plants, and reforestation. However, little is known about the ecosystem services they provide, whereby they not only provide food, but also maintain plant heterogeneity and diversity, prevent forest fires, conserve animal genetic heritage, benefit other animal species, and contribute to the maintenance of endemic plant resistance and tolerance to herbivory. The clues that these herbivores offer regarding the structure of pre-human ecosystems, as well as their equivalents after faunistic turnover in human times, is sometimes neglected. The conclusion is not only a call for caution when applying certain actions, such as eradication, but also for recognition of certain ecosystem functions as well as genetic, taxonomic, and social aspects.

J. Bartolomé (✉)
Department of Animal and Food Science Small Ruminant Research Group Universitat Autònoma de Barcelona 08193, Bellaterra, Spain
e-mail: jordi.bartolome@uab.cat

B. Seguí
Hunting Service Department of Economic Promotion and Local Development Consell de Mallorca, Palma, 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_7

7.1 The Singularity of Mediterranean Islands

Most Mediterranean islands ceased to be isolated from the continent for a period of 640 kyr at the end of the Miocene, during the so-called Messinian salinity crisis, which began 59 myr ago (Rouchy and Caruso 2006). This is transcendental for island ecosystems. At that time, extensive grasslands abounded on the continent and the large herbivores that regulated them diversified. Some of these managed to cross the saline desert that the Mediterranean basin had become and reached the islands. Once the Mediterranean basin had refilled, these populations began their own evolution in an insular environment, where the phenomena of dwarfism among large herbivores and gigantism among small ones were frequent. Some evolved towards generalist diets as a subsistence strategy, which would have a major effect on the vegetation (Winkler et al. 2013; Bethune et al. 2019). The ecological role of medium to large herbivores, as species offering clues to these ancient pre-human communities, seems to respond to a palaeoecological pattern that has also been recognized, by comparison, in extreme oceanic islands where large-sized birds took the role of mammals that could not colonize them (Seguí and Alcover 1999).

In terms of the composition of mammalian species, the Mediterranean islands during the Pleistocene were famous for hosting a large number of endemisms (Palombo 2008). Table 7.1 shows a list of species of large or medium sized mammalian herbivores recorded on different Mediterranean islands, almost all of which are extinct today.

Some of these species, being isolated, would have escaped the great extinctions that the large herbivores on the continent began to suffer 50,000 years ago, probably caused by overhunting at the hands of human hunters and gatherers (Martin 1984). However, it seems that the Mediterranean islands did not offer enough resources to support stable populations of hunters, so they surely did not colonize them (Cherry 1981). This long presence of certain medium and large herbivores on Mediterranean islands in pre-human times differentiates them from other islands in the world where such fauna was absent until their introduction as domestic species in modern times. Since the Miocene (25 Ma), Mediterranean flora has had to adapt to withstand disturbances such as droughts, fires, and herbivory, generating highly resilient vegetation. During the Neolithic (12,000 BP), a second great wave of invasion by man covered the continent, transforming grasslands into cereal fields, forests into pastures, and replacing many of the remaining large wild herbivores with domestic varieties. The Mediterranean islands would not escape this second wave and would be colonized by ranchers and farmers, who introduced species (e.g. goats and sheep) that were pre-adapted to the insular Mediterranean environment. The previous or contemporary disappearance of large or medium wild herbivores meant goats, or alternatively mouflons on some islands, could occupy a large part of their ecological niche as a medium-sized herbivore, even when replaced species was not a Bovidae. Some of these ancestrally introduced taxa were once described as new to science and/or considered endemic pre-human fauna for centuries (e.g. *Capra cretica*, *Ovis ophion*, *Capra dorcas*). Their taxonomy and biogeography have been revised as fossil and subfossil records have emerged. An East to West pattern of age of

Table 7.1 Large and medium size mammalian herbivores recorded on Mediterranean islands in pre-human times

Species	Islands	Period of extinction
Bison priscus siciliae	Sicily	Late Pleistocene
Bos primigenius siciliae	Sicily	Late Pleistocene
Candiacervus sp	Crete	Early Holocene
Cervus elaphus corsicanus	Corsica, Sardinia, and Sicily	Not extinct
Cervus elaphus siciliae	Sicily	Late Pleistocene
Ebusia moralesi	Eivissa	Late Neogene
Elephas chaniensis	Crete	Pleistocene
Elephas creticus	Crete	Pleistocene
Elephas creutzburgi	Crete	Pleistocene
Elephas cypriotes	Cyprus	Pleistocene
Elephas falconeri	Sicily	Middle Pleistocene
Elephas mnaidriensis	Sicily, Malta	Pleistocene
Elephas tiliensis	Tilos	Mid Holocene
Equus hydruntinus	Sicily	Mid Holocene
Etruria viallii	Sardinia	Late Miocene
Hippopotamus creutzburgi	Crete	Pleistocene
Hippopotamus melitensis	Malta	Pleistocene
Hippopotamus minor	Cyprus	Early Holocene
Hippopotamus pentlandi	Sicily, Malta	Mid Holocene
Hoplitomeryx	Gargano (paleo-island)	Early Pleistocene
Hypolagus sp	Eivissa	Early Pliocene
Hypolagus sp	Mallorca	Early Pliocene
Hypolagus sp	Sicily	Pleistocene
Leporidae indet	Menorca	Pliocene?
Macaca majori	Sardinia	Pleistocene
Mammuthus creticus	Crete	Pleistocene
Maremmia cf *M lorenzi*	Sardinia	Late Miocene
Megaloceros carburangelensis	Sicily	Late Pleistocene
Megaloceros cazioti	Corsica and Sardinia	Holocene
Myotragus balearicus	Mallorca, Menorca, Cabrera, and Dragonera	Mid Holocene
Nesogoral melonii	Sardinia	Early Pleistocene
Oreopithecus bambolii	Sardinia	Late Miocene
Oryctolagus aff *O lacosti*	Sardinia	Pleistocene
Prolagus sardus	Corsica and Sardinia	Late Holocene (eighteenth C)
Turritragus casteanensis	Sardinia	Late Miocene
Tyrrhenotragus gracillimus	Sardinia	Late Miocene
Umbrotherium azzarolii	Sardinia	Late Miocene

introduction of post-human caprine and ovine forms is detected (Seguí et al. 2005), the Eastern Mediterranean islands having been the first to suffer faunistic *turn over*, and the westernmost Balearic Islands, the last. An increasing degree of morphological divergence from agriotype/continental ancestral form is also recognized along this East to West introduction process.

7.2 Goats Helped Man to Invade the Mediterranean Islands

Goats and sheep, along with the first domesticated cereals and legumes, were well adapted to the dry Mediterranean climate and enabled Neolithic man to invade, through agricultural and livestock activity, nearly all the large islands of the Mediterranean basin (Broodbank 2006; Ramis 2017), even the smallest and frequently karstic ones (Leppard and Pilaar Birch 2016). The term "invade" is used here and is applied to man in the sense of a non-indigenous species that spreads rapidly, causing environmental damage (Simberloff and Rejmánek 2011, p 727). In this case, it is assumed that environmental damage refers, for instance, to the transformation of forests and grasslands into cultivated fields. This definition, equivalent to "non-native pest species", is often applied to goat populations on the islands to justify their eradication. The presence of goats on Mediterranean islands keeps the debate open as to what biological invasions are and how we should define alien and invasive species (Colautti and Richardson 2009). Moreover, new considerations are arising with regard to threats to and opportunities for feral animal forms in post-human ecosystems and their socio-environmental management on islands and in remote rural areas (López i Gelats et al. 2021; Rodríguez-Rodríguez et al. 2022; Barceló et al. 2022). These views are conditioned by the legality of designs and development models.

*Nevertheless, regardless of how goats and humans are categorized, the fact is that they reached the eastern Mediterranean islands together for the first time about 10,000 years ago (*Peltenburg et al. 2000*) and about 6000 years later they arrived on the last western islands (*Alcover 2008*). Ovicaprids now* tend to comprise a majority proportion of overall zooarchaeological assemblages on Mediterranean islands (Leppard and Pilaar Birch 2016). This preponderance of sheep and goats might be explicable because during the first steps of colonization, low demographic pressure enabled the establishment of extensive pastoral systems, which are usually characterized by specialization in one domestic group (e.g. Halstead 1996; Helmer 1992; Howell-Meurs 2001), and domestic caprine are a better-adapted species to a high mobility system (Ramis 2017). For several thousand years, goats have played an important role in the ecosystem service by providing food (such as meat, milk, and cheese) and leather to islanders (Hatziminaoglou and Boyazoglu 2004), and even today this is one of its main services on some Mediterranean islands (Hadjigeorgiou et al. 2002). During this time, goats have grazed year-round in the most inhabited islands with hardly any food supplement. Even the small islets have been used as corrals or seasonal pastures (Gizicki et al. 2018).

Early pastoral systems and their relationship with the hunting of pre-domestic or ancient domestic forms of ovicaprids is another subject to be considered with regard to Mediterranean islands. In Crete, for instance, the crossbreeding of domestic herds with live captured specimens of agrimi for the renewal of blood lines has been documented (Porter 1996), as has the mixed hunting-pastoral management of the Mallorcan goat, where domestic and feral goats (called "wild" in historical documents) have coexisted since at least the Middle Ages (Villalonga Morell 2020). In relation with these feral goats, traditional hunting with dogs and lasso (called *ca i llaç* in Catalan) is practised on the island and was described back in the nineteenth century by the archduke Ludwing Salvator (Salvator 1869–1884). The most traditionally used dogs are a half blood between *ca de bestiar* and *ca eivissenc*, two ancient autochthonous breeds (Payeras and Falconer 1998). Although it is unknown if this technique was already practiced in this way in antiquity, the use of dogs for hunting feral goats (agrimi) in Crete is well represented on vessels from the Minoan Bronze Age period (Eiring 2004). This indicates that goats have contributed to the supply of food since ancient times, not only as a domestic species but also as a hunting resource.

7.3 Domestic, Feral, and Wild Goats: A Contribution to Animal Biodiversity

The taxonomic identity of some insular, anciently isolated feral ovicaprid populations has been a matter of controversy up to the present, and heterogeneous criteria persist (Seguí et al. 2005; Gippoliti 2013; Seguí 2014; Duhart 2020). For instance, the classification of current mouflon populations on Mediterranean islands, such as *Ovis gmelini ophion* in Cyprus and *O. g. musimon* in Corsica and Sardinia, considers them both to be subspecies of their wild ancestor, *O. g. gmelini* by IUCN, (IUCN Red List, last accessed 18 March 2020), although they were probably translocated during the Neolithic, as ancestral sheep livestock by humans migrating from the Fertile Crescent to the Western Mediterranean (Portanier et al. 2022). On the other hand, Cretan agrimi and other insular goat populations introduced to Mediterranean islands were grouped as domestic goats and treated as a separate species from their ancestor, the bezoar (Shackleton 1997; Mannen et al. 2001; see IUCN Red List *op cit*), named *Capra hircus* and *Capra aegagrus*, respectively. However, genetic studies showed that it was a single species, and in 2003, the Bulletin of Zoological Nomenclature classified them as a subspecies, assigning the name *Capra aegagrus hircus* to the domestic variety and *Capra aegagrus aegagrus* to the wild one (ICZN 2003). This categorization is more consistent with the fact that animals of both subspecies can interbreed to produce fertile offspring and that domesticated individuals can become feral and behave like wild populations. Before then, some authors considered several island populations to be endemic subspecies of the bezoar (Schultze-Westrum 1963; Masseti 2009), namely the Cretan goat or agrimi (*C. a. cretica*), the Youra goat (*C. a. yourensis)*, and the Aegean goat (*C. a. pictus*), and therefore they were all considered a different species from the domestic goat (Kahila et al. 2002). Certain other Mediterranean islands, such as Montecristo and Mallorca, have also conserved populations of free grazing goats that have kept the debate about their wild or domestic origin alive for years (Masseti 2016). For example, Masseti (2014) associates the Mallorcan population to *C. a. yourensis* phenotype, with some genetic introgression as claimed by Seguí et al. (2005). However, genetic studies have established a criterion to group all introduced populations under the domestic form (Horwitz and Bar-Gal 2006), including agrimi, which may have been introduced to the islands in wild form and released as a food source, but subsequent introgressions with domestic animals would have influenced its genotype.

The historical identity of these insular caprine populations has shifted from the earliest classic taxonomic approach to be progressively substituted by molecular phylogeography (Gippoliti 2013). The genetic point of view seems have ultimately become the accepted position in recent biological listing, which has detracted efforts to conserve feral insular populations of goats that are considered domestic. However, genetic value and recognition as a genetic resource derived from agriotypes, plus adaptation to insular ecosystems, lead to other definitions and protected values that also fall within the framework of biodiversity (FAO 2007). Legal frameworks have come to create terms such as “own species” to refer to an autochthonous or anciently introduced species that is now integrated in insular ecosystems (e.g., Balearic hunting and river fishing act 6/2006); as well as “quasi endemic species” (Gippoliti 2013), supporting the underlying biological value of different taxa, from different points of view, and even shifting some arguments towards new scenarios (Gippoliti and Amori 2004). Limitations with regard to diffuse concepts, taxonomy, and definitions are being tested and revaluated on islands, which are once again serving as biological laboratories.

Below the species level, domestic goats have evolved for millennia into native breeds adapted to local environmental conditions (Park and Haenlein 2006; Vahidi et al. 2014). They have become one of the most adaptable livestock in the world and provide food resources to the human population. This has favoured diversity within the species, which today has more than 500 registered breeds (Zhang et al. 2018) and many of the Mediterranean islands have their own. Some of them, such as Pitiüsa and Ibicenca, are at evident risk of extinction (Camacho et al. 2011).

Islands are interesting scenarios where traces of ancient goat traits, historical introductions, and peculiar management systems can be found. For instance, it is assumed that insular goats are smaller than mainland wild bezoar goats (Horwitz and Bar-Gal 2006; Masseti 2009). These traits can be detected by genetic analysis as shown by the way some haplogroups are now restricted to certain islands, as is the case with Corsican and Sicilian breeds (Sardina et al. 2006; Naderi et al. 2007). The endangered Montecristo feral goat population is genetically separate from other goat breeds (Somenzi et al. 2022). The so-called “Mallorcan Wild Goat” also has a well-defined genetic identity despite its proximity to other peninsular breeds (Seguí et al. 2005; Martínez et al. 2015; Martínez et al. 2019) with a greater degree of genetic homogeneity and is a major contributor to the regional caprine genetic diversity (Ginja et al. 2017), without the influence of exotic breeds (Sevane et al. 2018).

On these Mediterranean islands, where goat rewilding occurred during antiquity, the breeds are viewed as having cultural, historical, scientific, and aesthetic virtues (Spagnesi et al. 1986; Altaba 2000; Seguí et al. 2005; Masseti 2009). The Girgentana and Maltese breeds have been reported as being the most differentiated from other South Italian breeds and have been proposed as high priority for conservation (Criscione et al. 2016). Also, the Skopelos breed, which is mainly reared in the Northern Sporades archipelago, shows high levels of genetic diversity, related with high levels of homozygosity as a result of the typical management practices, history, and demography of the insularization process (Michailidou et al. 2019). The mitochondrial diversity observed among island goats may be evidence of historical events or ancient diffusion that would have been lost elsewhere and hence should be preserved for the future management of genetic resources (Hughes et al. 2012). According to Cardoso et al. (2018) goats from Mediterranean islands display patterns of homozygosity that are similar to those found in continental populations, but they are a complex case because certain populations display a significantly higher level of homozygosity (e.g. Girgentana and Mallorcan wild goat) and others do not (e.g. Corse and Sarda). These authors concluded that the diversity of insular goat populations is modulated by multiple factors such as geographic distribution, population size, demographic history, trading, and breed management.

Some authors consider these breeds to be of no taxonomic interest, as they come from artificial selection, and that their contribution to biodiversity should be restricted to the livestock world (Mayol et al. 2017). However, reality shows that most goat populations, domestic or feral, are present in ecosystems, playing the role of large wild herbivores and therefore do have ecological value both on the mainland (Herrero et al. 2013) and on the islands (Seguin et al. 2001). In fact, goats have a remarkable ability to lose their domestic behaviour and become feral animals (Coblentz 1978). The social, environmental, and biological benefits of goats should also be recognized (Perevolotsky and Seligman 1998), including in island environments (Arévalo et al. 2012).

Early feralized insular populations of goats that lie on the boundary between natural/domestic taxa, that are at the interface of natural/anthropized environments and are affected by combined natural selection/anthropic management, are much more than local breeds and are original genetic resources. These taxa are increasingly neglected and have sometimes become endangered. As they are derived from populations that were isolated for long periods of time and thus developed long-standing links between genome and environment, as stated by Serranito et al. (2021), they are becoming a key topic in conservation of animal genetic resources (Alderson 2008).

A unique case is that of the Mallorcan goat, due to its dual profile as a source of meat and as game for hunters (Seguí 2014). The dual domestic-hunting component also implies a twofold administrative consideration of the two populations, which genetically come from the same background (Martínez et al. 2019). This goat is officially recognized as an autochthonous breed in danger of extinction and is recognized as such in the National Information System of Spanish Livestock Breeds (https://wwwmapagobes), but at the same time it is recognized as a hunting variety in Decree 91/2006 of the Balearic government and is included in the National Board of Trophy Hunting Homologation (Spanish Government), SCI, and CIC listings. The Balearic management plan for the breed combines scenarios, genetic monitoring, and selective breeding with big game hunting as a source of finance for breeders and hunting states, as well as providing meat.

7.4 Potential Contribution of Goats to the Maintenance of Plant Diversity, Heterogeneity, and Ecosystem Functions

Some authors argue that goat grazing management is a powerful ecological instrument for structuring plant communities, whereby livestock are used in ecosystem engineering by applying different grazing pressures to maintain heterogeneous landscapes (Perevolotsky and Seligman 1998; Arevalo et al. 2011). The "intermediate disturbance hypothesis" (Wilson 1994; Wilkinson 1999) is one of the most frequent suggestions for the maintenance of species diversity in ecological communities. This hypothesis assumes that a greater diversity of species is found under conditions of continuous, moderate disturbance, as opposed to the lack or excess of such disturbance. Roxburgh et al. (2004) added that the concept refers to a mechanism, or group of mechanisms, leading to stable long-term coexistence of species. Based on this hypothesis, goat grazing is often used to generate such disturbance worldwide, as reviewed by Rosa García et al. (2012). For example, moderate goat grazing is considered valuable for the conservation of some pastures dominated by native or endemic species on the Canary Islands (Fernandez-Lugo et al. 2009; Arevalo et al. 2011). Another example occurred on Pinta Island, where overgrazing by goats put the survival of the Galapagos tortoise (*Geochelone elephantopus*) at risk. The eradication of the goats, with the consequent elimination of the disturbance, led to a decline in plant diversity through homogenization of the landscape (Hamann 1993). Also, the eradication of feral goats on Nakoudo-jima, an oceanic island, enhanced expansion of the invasive shrub *Leucaena leucocephala* (Osawa et al. 2016). Similarly, on Round Island (Mauritius) eradication of introduced goats by 1978 and rabbits by 1986 led to an increased abundance of three threatened tree species (Bullock et al. 2002). However, unpredicted effects such as increasing rates of establishment of non-native plants have also occurred (Bullock et al. 2002).

Around the Mediterranean Basin, undergrazing may be an even more serious threat to rangelands integrity than heavy grazing (Perevolotsky and Seligman 1998). A review of the ecosystem services provided by ungulates in Mediterranean woody ecosystems (Velamazán et al. 2020) showed that a similar number of studies observe positive (26%) and negative (33%) effects on biodiversity, but positive effects of ungulates were reported mainly in shrublands. Dense forest eliminates or displaces heliophilous species that cannot grow under such intense shade, while in open spaces they suffer from high insolation, droughts, and grazing. This diverse floristic group develops very well in the Mediterranean scrub, a heterogeneous formation to whose maintenance goats contribute especially well. Montserrat (2009) describes in detail the ecological functioning of these formations and the key role played by goats in their maintenance. Bushes that are devoured by goats form hemispherical caps barely half a meter high. Heliophilous species form a tender grass under them, mainly in the peripheral crown of each bush, where it is fertilized by leaf litter and animal manure. Nocturnal cooling produces water sprays that are retained under the bush, providing a certain amount of hidden precipitation. These woody formations, which are practically attached to the ground, both cushion the erosive effects of torrential rains after long periods of drought and reduce the risk of fires. The species that form these caps are usually palatable to goats, such as *Olea europaea ssp sylvestris*, *Quercus coccifera*, *Quercus calliprinos*, and several species of spiny legumes, and the formations to which they give rise have a variety of names in the Mediterranean basin, such as “garrigue” in the West and “phrygana” in the East.

Although these open formations are considered stages of Mediterranean forest degradation, their diversity could be greater (Colombaroli and Tinner 2013) and their ecological value could also be similar to that of holm oaks or pine forests. Mediterranean scrub controlled by goats should be viewed as an important piece of a mosaic that they form together with holm oak and pine forests to guarantee the maximum biodiversity on the islands (Bartolomé et al. 2014). Their management needs to consider that biodiversity can decrease when pressure from herbivores ceases. A clear example of loss of diversity due to the abandonment of traditional agro-pastoral activities has been observed on Molat, in the eastern Adriatic (Sedlar et al. 2017), where garrigues and rocky pastures represented 75% of the territory in the early twentieth century but by the early twenty-first century barely amounted to 5%. Studies have revealed high biodiversity in the open vegetation units (mesophilous and rocky grasslands) followed by a small increase in semi-open vegetation (like garrigues) and a major decrease in the current closed vegetation (maquis and pine forest). These observed changes were correlated to island depopulation and the abandonment of rural activities.

Along the same lines, the current increase in shrub and woody cover on the islet of Dragonera (Balearic Archipelago) is attributed more to the cessation of agricultural and forestry activities than to the eradication of goats and rats a few decades ago (Ibañez-Álvarez et al. 2022). According to Oro et al. (2022), this increase has in turn caused a decrease in heliophilous plant species. These authors suggest that before man’s arrival the islet was inhabited by cave goats (*Myotragus balearicus*) and giant dormice mouse (*Hypnomys morpheus*), which subsequently became extinct. The effect of these herbivores would have predisposed the vegetation to support the arrival of goats and rats, which would play a similar role. This study has proposed the need to maintain herbivores, such as goats, even on small islets to avoid the phenomena of scrub encroachment associated with rural depopulation (Oro et al. 2022), although more studies are needed to decide if this proposal can be generalized.

The heterogeneous shrubland in Asinara National Park (Sardinia) is a semi-open maquis regulated by feral goats and donkeys roaming throughout the island. One of the contributions of these herbivores to the ecosystem is the dispersal of seeds attached to their fur (epizoochory) or in their faeces (endozoochory) (Treitler 2019). Both have an important role in plant dynamics, through seed input on the vegetation and on the soil seed bank. The most effective mechanisms for transporting seeds on animals usually occur in annual plant species and graminoids (Shmida and Ellner 1983), with Treitler observing that goats disperse a higher number of shrub diaspores while donkeys disperse more from grasses, indicating a complementary potential for seed dispersal among these two species.

Goat droppings contain a high number of viable seeds of certain species that they consume, and domestic goats may perform seed dispersal functions in the same way as other wild or extinct herbivores (Janzen 1986; Hansen et al. 2008). This phenomenon may explain the differences observed in the floristic composition of islands with or without goats without causing any change to the total amount of biodiversity. On the Cycladic islands, in the central Aegean Sea, Gizicki et al. (2018) found that plant assemblages on the islands without goats are characterized by relatively rare, native perennial species such as *Medicago arborea*, *Matthiola sinuata*, and *Atriplex halimus*. On the contrary, islands with goats are characterized by more annual, generalist, low-lying plant species, usually with sticky seeds, such as *Plantago coronopus*, *Tordylium apulum*, and *Phleum arenarium*. Hence, a decrease in the former would be compensated or even exceeded by an increase in the latter. Panitsa et al. (2006) studied data on the floral composition of 86 very small islets in the Aegean archipelago and found that grazed ones were richer in plant diversity than non-grazed ones. They attribute this greater richness of species to the fact that plant diaspores reach the islets through the skin and faeces of the goats that are annually transported by boat to graze on them. In addition, Snogerup and Snogerup (2004) classed 100 taxa as probably having been introduced by grazing animals to one or several islets in the same archipelago 45 of them had been on the islets for at least 10 years. And on the Balearic Islands, goats are the main seed dispersers of the ancient Mediterranean palm, *Chamaerops humilis* (Muñoz-Gallego et al. 2019). This dispersal effect is in general agreement with other studies conducted in semi-arid Mediterranean pasturelands (Alrababah et al. 2007). However, once goats are removed, the islands begin to lose some of these introduced species leading to an overall decline in alpha diversity (Gizicki et al. 2018).

Feral goats are currently one of the most important examples of unintentional “rewilding”, a term that considers multiple coexisting and confronted values, such as cultural heritage, conservationism, animal welfarism, and economic benefits (Prior and Brady 2017). The concept of rewilding is more functional than taxonomic, and hence feral goats have been proposed as possible proxies for extinct species, such as *Myotragus balearicus*, in the Balearic Islands (Palau 2020 p. 288). In this sense, Winkler et al. (2013) considers that *Myotragus balearicus* was an intermediate feeder, as goats are. Feral goats would be a better choice than domestic goats, as their diet tends to be more selective, like that of wild goats (Aldezabal and Garin 2000). This means animals are not forced to consume plant resources regardless of their quality or availability, as can be the case with domestic livestock.

7.5 Forest Fire Prevention Ecosystem Services

In the Mediterranean basin, the colonization of open spaces by pine forests used to be controlled by intensive grazing and especially by land clearance (Marty et al. 2003). In recent decades, changes in land-use practices have led to an increase in forest areas, including on Mediterranean islands (Cerabolini et al. 1996; Puddu et al. 2012; Keenan et al. 2015). This increase is caused by the abandonment of agricultural and pastoral land in remote and unproductive areas, together with a shift of human populations toward urban areas. In addition, on islands with heavy amounts of tourism, such as Mallorca (Barceló et al. 2022), urbanization has been described as a cause of major environmental and rural change (Binimelis and Ordinas 2012; Barceló and Seguí 2017, Barceló et al. 2017; Barceló Adrover et al. 2018).

The rural change has led to a greater accumulation of biomass in the undergrowth that, in turn, increases the risk of forest fires (Lasanta-Martínez et al. 2004). Increased fuel continuity has led to several large fires in recent decades, not only on the mainland, but also on the islands (Domenech 2015). In the past, livestock used to graze the undergrowth in search of resources, which in the Mediterranean basin are usually of poor quality (Bartolomé et al. 2019) but this did help to reduce the fire hazard. Grazing programs have recently been implemented in some dry Mediterranean forest regions with the explicit intention of reducing fire risk (Mancilla-Leytón et al. 2013; Lovreglio et al. 2014; Mena et al. 2016). This type of control of undergrowth by livestock is considered to be one of the most cost-effective approaches (Ruiz-Mirazo 2008; Casals et al. 2009). Due to their grazing behaviour and their ability to tolerate so many plant secondary compounds, goats are surely the most widely used animal (e.g. Mancilla-Leytón et al. 2013; Lovreglio et al. 2014). This is especially true when combined goats with equines, which are more efficient consumers of fine fuel represented by dry grasses, for reducing fuel phytovolume in undergrowth (Bartolomé Filella et al. 2016; Bartolomé et al. 2019, 2020).

The risk of forest fires is a great concern among local islanders. For instance, Cypriots feel that goat grazing benefits forests by reducing that risk and enhancing vegetation growth (Michaelidou and Decker 2005). This contrasts with the view that goats damage forests, which was so prevalent during the British Administration from the 1940s onward, to the point of promoting laws to eradicate feral goats from the island (Michaelidou and Decker 2005). This change in perception has also been observed in Corsica, where shepherds were previously blamed for starting fires to improve pastures, while livestock grazing is viewed today as an efficient means for preventing this major environmental risk (Flamant et al. 1999).

The Balearic Islands have some 200,000 hectares of forests, more than half of which are *Pinus halepensis, a* pyrophytic conifer. In recent decades, there has been an increase in forest land and at the same time in large forest fires (IFN4 2012). In Mallorca, pine seedlings have a survival rate after a fire of 23% without goats, while the rate is just 5% with them (Mayol et al. 2017), highlighting how useful grazing can be for control. Among ruminants, goats can reduce bush cover more efficiently than sheep or cattle (Sineiro 1982; Benavides et al. 2009). In Corsica, as in the SE of

France, The Livestock Farming Systems research programs carried out by the INRA explored the possibility of using grazing by small ruminants to prevent fire risk (Flamant et al. 1999). So, goats are useful for controlling the expansion of forest masses that can become fuel for large fires.

When populations of feral goats occupy mountain areas, they will commonly graze in the network of firebreaks. These strips are one of the most effective ways of reducing the spread and severity of wildfires and goats find them attractive due to the amount of regrowth produced by mechanical clearing. The reduction of the phytovolume effect can be enhanced with the implementation of water and salt points, as has been observed in Mallorca (Pareja et al. 2020). This shows that the use of goats for fire prevention does not necessarily require them to be domestic and driven by shepherds. So, when it comes to reducing fuel biomass, feral goats can compensate for the current lack of domestic livestock in certain regions. Moreover, the use of grazing to reduce fuel biomass does not imply any loss of biodiversity (Ruiz-Mirazo et al. 2011). Attracting feral goat populations to firebreaks would not only help to reduce the risk of fires and, consequently, to the mitigation of climate change, but would also entice these animals away from places where they could cause more conflict, such as gardens, roads, and crop fields (Pareja et al. 2020).

7.6 The Ecosystem Services Generated by Goat Hunting Reserves

Every year, millions of people participate in sport hunting activities around the world, and hunting-related expenditure along with wildlife-associated recreational services generates economic benefits, mainly for rural communities (Benson 2001). These benefits even exist on oceanic islands where most game species have been introduced. For instance, in Hawaii, hunters wish to maintain non-native game populations while other people are struggling against the damages caused by introduced species (Lohr et al. 2014). Smaller localized management plans might be the best way to alleviate human-wildlife conflicts caused by introduced game species (Madden 2004). Although sport hunting is condemned by animal rights activists as a clear example of cruelty to animals (Cantor 2014), it also has gained significant importance in recent decades in terms of sustainable development and biodiversity conservation (Díaz et al. 2008; Martinez-Jauregui et al. 2011). The Safari Club International argues that one of the best strategies for the conservation of wild species is to promote hunting (Ullmann 2014). According to Loveridge et al. (2007), this can be done in many ways, with the acquisition and protection of habitat being a major benefit.

The Mediterranean islands are characterized by a traditional hunting culture (Trantalidou 2011), which is surely directly related to the migratory routes of the many birds that use the islands as a resting area and which were a seasonal source of protein for the islanders (Falzon 2008). The importance of this hunting culture has been made manifest throughout history by the application of strict rules, often for the benefit of the local nobility (Cassar 2018). In recent decades, the activity has become a sport and also a means for obtaining products that are viewed as delicacies by the hunters themselves. In the future, this activity may well lead to more contemplative practices, such as birdwatching.

This hunting culture also affects the goats that roam free on many islands. Feral goats can serve as an economic and hunting resource (Forsyth et al. 2009). Some authors maintain that the first goats to be introduced by humans to the islands served more for hunting than any domestic purpose (Horwitz and Bar-Gal 2006). Throughout history, populations of feral goats have been maintained on many islands in the most remote places, where agriculture and livestock rearing were unfeasible (Villalonga Morell 2020). Certain traditional hunting techniques, such as the above-mentioned use of dogs and lassos in Mallorca, would have been developed as a result of these populations (Colom 2014). This is currently one of the few techniques that could lead to a form of hunting without killing, where the main attraction would be to admire how skilled trained dogs are at corralling goats on the island's cliffs.

This hunting culture requires the maintenance of a wild landscape, where the hunter feels part of nature. It is due to this need that hunting has its value in the conservation of ecosystems (Heffelfinger et al. 2013). Trophy hunting of goats is, in a way, equivalent to livestock management, whereby animal populations are controlled at low densities (Adrover et al. 2017). Hunting enclosures could be used to remove specimens that do not conform to the trophy pattern and thus maintain the genetic heritage. The decrease in domestic livestock on some Mediterranean islands has led to the proliferation of feral goat populations and this, in turn, has made it easier for some owners to obtain additional income from hunting activities (Mayol et al. 2017).

The "Mallorcan wild goat", popularly known as the Balearen boc, is reported in historic trophy collections (Oriani 2016) and was included in 2005 as a hunting trophy in the Saffari Club International list, which re-values the animal in the market. Since then, the island has attracted wealthy visitors who come in search of the prized hunting trophy. The hunting of a few tens of trophy specimens per year has made it possible to maintain a dozen large hunting reserves, which cover more than 15,000 ha of land and support very low stocking rates (less than 0.15 animals/ha) to prevent the trophy from diminishing in quality. Such a system combines the conservation of such an ancient and highly valued population as the "Mallorcan wild goat", with density control, genetic selection, economic wealth, and sustainable development for remote areas (Seguí 2014; Barceló et al. 2017; Rengifo Gallego 2019). As hunting activities are highly regulated and the use of a genetically monitored population for trophy hunting is technically complex, the national and local administrations are working very closely together to oversee the recovery, monitoring, and management of remote, abandoned areas. These areas do not serve any other uses, such as agriculture, livestock rearing, or forestry and can consequently almost be considered protected areas. This hunting activity is one of the alternatives to rural abandonment and ensures the maintenance of the Tramontana Mountain range, probably the most important area of natural beauty in Mallorca (Roque 2017).

7.7 Benefits for Other Animal Species

Management of goats on the islands is approached from different perspectives, including the interest in conserving native breeds and varieties as sources of food resources, the need to control their effects on the vegetation, and even attempts to eradicate a species that is considered bio-invasive since its introduction to the islands (Mayol et al. 2017; Gizicki et al. 2018). The conservation, control, or eradication of goats should be based on comprehensive analysis of their role in the insular ecology (Zavaleta et al. 2001). There is not always enough knowledge about the ecological relationships established between exotic and native species, and the possible risk of their removal causing further damage to other components of the ecosystem (Courchamp et al. 2003). For instance, the rabbits that were introduced by man to the Canary Islands are an important part of the diet of two native avian scavengers, the buzzard (*Buteo buteo*) and the raven (*Corvux corax*) (Nogales and Hernández 1997; Palacios-Palomar 2005). On the same islands, Gangoso et al. (2006), highlighted that goat carcasses help to maintain the population of three endangered endemic subspecies of avian scavengers: the Egyptian vulture (*Neophron percnopterus majorensis*), the Eurasian buzzard (*Buteo buteo insularum*), and the common raven (*Corvus corax canariensis*). The decline in extensive goat grazing activity is considered responsible for the decrease in the population of these species on the islands of Lanzarote and Fuerteventura (Martín and Lorenzo 2001). Sometimes, introduced taxa such as goats play a role as a "keystone species" with some native species depending on them (Myers et al. 2000; Gangoso et al. 2006). These episodes can even occur even on highly biodiverse oceanic islands, such as the Galapagos, where goat eradications led to a decline, rather than a recovery, of the endangered Galapagos Hawk (*Buteo galapagoensis*), because the species had come to depend on goat-altered habitats (Rivera-Parra et al. 2012).

Feral goats are considered a relevant species in some islands due to their role as food for different endangered raptors, such as the golden eagle (Aquila crysaetos) in Corsica and Sicily (Seguin et al. 2001) or in Sardinia (Sirigu et al. 2019). Before the arrival of humans, the scavenger species on Mediterranean islands, such as the Bearded vulture (*Gypaetus barbatus*), Black vulture (*Aegypius monachus*), Egyptian vulture (*Neophron percnopterus*), and Griffon vulture (*Gyps fulvus*) surely depended on native ungulates. Following humanization, these scavenger species probably switched their dietary preferences to domestic ungulates, and carcasses of goats and sheep form the bulk of their diet at present (Congost and Muntaner 1974; Donázar et al. 2002; Xirouchakis and Nikolakakis 2002). Ambitious conservation projects aimed at maintaining extensive herds of domestic ungulates as a widely available food resource have made it possible to recover these species in Corsica and Crete (Bearded vulture) and in Mallorca (Black vulture) (Thibault et al. 1992; Tewes et al. 1998). However, in the latter case, the view that feral goats are invasive and therefore need to be eradicated has led to the unprecedented situation of having to feed vultures artificially through volunteer campaigns (Capellà-Miternique 2020).

The Griffon vulture (*Gyps fulvus*) was very abundant in ancient times in Cyprus but nowadays it is the most threatened bird species on the island due, among other reasons, to the decrease in free roaming grazing animals (Kassinis 2013; Papadopoulos 2013). Successful action plans to re-establish safe population levels include the promotion of traditional livestock husbandry (Papazoglou and Charalambous 2013; Xirouchakis et al. 2021). Hellicar and Kirschel (2022) found that moderate grazing pressure in Cyprus in the past increased the richness of breeding bird species in lower scrub habitats, such as phrygana, because grazing plays an important role in maintaining habitat (Perevolotsky and Seligman 1998) heterogeneity. The authors argue that this is an example of the above-mentioned intermediate disturbance hypothesis. According to Gangoso (2006), goats and other introduced herbivores on islands (e.g. rabbits) should not be exclusively regarded as detrimental for conservation purposes.

Another group of fauna that benefits from the presence of goats in the Mediterranean basin are dung beetles, which take advantage of the constant rain of dry dung pellets scattered across the land. This group shows a clear correlation between grazing intensity and endemicity (Verdú and Galante 2002). These beetles cause the nutrients in the dung to quickly cycle through the ecosystem and act as a biological control agent for gastrointestinal livestock parasites (Truman Fincher 1973). Dung beetles, including those of Mediterranean islands, are highly endemic and comprise many species adapted to aridity and the use of dry dung pellets (Verdú and Galante 2002), such as *Thorectes balearicus*. The presence of humans and their herds on Mediterranean islands fosters their dispersal, as appears to have occurred with the 176 species of dung beetle on the circum–Sicilian islands (Tonelli et al. 2016). On the other hand, the complete absence of grazing animals, as on the island of Malta, may have contributed substantially to the disappearance of species associated with animal dung (Pivotti et al. 2011). Other arthropods that utilize dung to breed and which increased due to goat grazing on Mediterranean islands are Dipterans (Gizicki et al. 2018). Consequently, the conservation of grazing activity by pellet-dropping goats might help maintain the biodiversity of dung insects and their ecosystem services on Mediterranean islands.

7.8 Potential Contribution of Goats to the Maintenance of Endemic Plant with Traits Resistance and Tolerance to Herbivory

The remarkable contribution of islands to global plant biodiversity is mainly the result of the many range-restricted endemics found on them (Kier et al. 2009). On oceanic islands, these endemic plant species have evolved in the absence of mammalian herbivores (Courchamp et al. 2003). Increased endemism means that endemic plant species should be more heavily grazed than non-endemic species, indicating a lack of adaptation among the former to mammalian herbivory (Cubas et al. 2019). Thus, endemic plant species are considered vulnerable to grazing by generalist herbivores, hence the assumption that invasive goats constitute a threat to the endemic flora (Lowe et al. 2004) and many studies have highlighted their detrimental effects (e.g. Coblentz 1978; Chynoweth et al. 2013). Proposals and actions to avoid or reverse these effects are mainly the eradication or exclusion of goats (Myers et al. 2000; Cambell and Donlan 2005). These efforts have often been very successful, even in Mediterranean islands (Capizzi 2020), although the desired effects are not always achieved (Zavaleta et al. 2001).

The Mediterranean islands are one of the largest archipelagos in the world, with almost 10,000 islands and islets. The major environmental heterogeneity and long historical biogeography explain the high diversity of its vegetation. Although most of them are not oceanic islands, their degree of plant endemicity varies between 9% on the Balearic Islands to 18% on Crete, and with a plant richness that varies from just over 1500 species in the Balearic Islands to almost 2800 in Sicily (Médail 2016). Without a doubt, this is one of the reasons why the Mediterranean basin is considered a biodiversity hotspot. However, this richness of Mediterranean insular vegetation is linked to the presence of herbivores among pre-human fauna and the long-lasting influence of humans, who have shaped vegetation dynamics through burning, cutting, grazing, and ploughing (Schule 1993; Burjachs et al. 1994; Blondel 2008). It could therefore be assumed that the plant species endemic to the Mediterranean islands that evolved, first under pressure from Pleistocene and early Holocene megaherbivores, and later under pressure from human-introduced ovicaprids, possess tolerance or resistance traits or escape strategies and, probably, better withstand the grazing pressure than endemic species that have evolved on islands without this fauna. Indeed, Capó (2021) studied 97 Tyrrhenian or Balearic endemic taxa and observed that most of them present resistance or escape strategies. Concretely, a quarter of the species contain secondary compounds, such as alkaloids, glycosides, or coumarins and 13% present anatomical defences, mostly in the form of spines. One third are less than 5 cm tall and grow at ground level, which is considered an escape strategy, and the remaining quarter are able to grow in inaccessible places, such as cliffs or small islets. Similarly, another recent study by Moreira et al. (2022) found that insular taxa (endemics and non-endemic natives) across Balearic and Canary Islands were more defended (thicker and smaller leaves with less nutrients) than exotic species introduced from the mainland. It should be noted that herbivory tolerance strategies, such as compensatory growth, have not been considered in these studies and may be a further factor in some cases. Some native shrubs of the Balearic Islands, such *Buxus balearica*, *Juniperus oxycedrus*, and *Ephedra fragilis,* could maintain their growth rate and biomass ratios under simulated herbivory by stimulating sprout production (Bartolomé et al. 2019).

In 2005, the Mediterranean Island Plant Specialist Group published a list of the 50 endemic plants that are on the brink of extinction (de Montmollin and Strahm 2005). The list shows only nine species whose survival is considered to be related to grazing, especially by goats. Of these nine species, six are indicated to be negatively affected by grazing. *Minuartia dirphya* is endemic to the peaks of Euboea and is considered severely threatened by grazing from goats and sheep, and from fires lit by shepherds. *Ligusticum huteri* is endemic to the highest peaks of Mallorca and has a rhizome that enables it to resprout when its leaves are consumed. Although feral goats are considered one of the main threats, it is also noted that drought and herbivory by insects are the main causes of their recession (Forteza 2007). *Ribes* *sardoum*, endemic to Sardinia, with unknown defensive mechanisms against herbivory, is considered affected by uncontrolled livestock grazing, although it is observed that its decline is also due to low seed viability (de Montmollin and Strahm 2005). *Aethionema retsina* on the island of Skiros and *Convolvulus argyrothamnos* from Crete are species without any efficient grazing protection and which are eaten by goats (de Montmollin and Strahm 2005). However, they both have a certain ability to evade grazing as they are adapted to grow in the rocky crevices of coastal cliffs. *Bupleurum kakiskalae* is another of Crete's rarest plants and grows on a few calcareous cliffs, but specialists point out that most seeds fall to the ground below the cliffs where the young seedlings are destroyed by goats (de Montmollin and Strahm 2005). However, the list contains three species that are well adapted, or even require a certain degree of herbivory. *Salvia veneris* is a species endemic to Cyprus that has leaves growing in a basal rosette, which is unusual in the genus *Salvia*, and is thought to be an adaptation to grazing by goats. *Lysimachia minoricensis*, endemic to Menorca, seems to owe its recession to the abandonment of rural activities, and attempts at re-introduction have only been successful in areas that were previously disturbed by fire or grazing. Finally, *Naufraga balearica,* from Corsica and Mallorca, requires a certain grazing pressure to avoid competition with other species (Cursach et al. 2013).

All these response strategies to herbivory can also be useful in the face of other disturbances, such as droughts or fires, and it is likely that they have been maintained in part thanks to the ancient grazing of livestock introduced by man.

7.9 Conclusions

With the information available to date, it can be concluded that a multidisciplinary approach involving scientists, hunters, farmers, animal rights campaigners, policy makers, rangers, and local communities is required for the design of future sustainable management of goat grazing on Mediterranean islands. For this goal, Rodríguez-Rodríguez et al. (2022) proposed several criteria of interest: (a) the value of genetic conservation in the case of extinct wild ancestors, (b) the niche occupancy criterion and, finally, (c) a cultural criterion. Here, we propose extension of the genetic criterion to a wider morphogenetic approach that also considers both the values in terms of original genetic resources, and in terms of isolated, ancient populations with particular genotypic and phenotypic features in their different goat lineages. Regarding the niche occupancy criterion, we propose its exploration and application in consideration of island size and the pre-human fossil record on the presence or absence of medium or large herbivores, plant endemicity, and acquired strategies by plants to evade herbivory. Regarding the cultural criterion, we propose that it should be applied in consideration of the socioeconomic and socioenvironmental opportunities that the management of goats can provide in terms of benefits for other animal species, ecosystem services, forest and landscape structure and diversity, and fire prevention.

7.10 Epilogue

There are different opinions about the management of mammalian herbivores that have been established on the Mediterranean islands for millennia, as is the case of goats. Many arguments have been based on the damage of goats on island ecosystems and the assumption that this impact can be generalized to all islands. Surprisingly, the Convention on the Conservation of European Wildlife and Natural Habitats recommended consideration, as a rule, of feral ungulates as an invasive alien species on Mediterranean and Macaronesian islands without considering that the two regions have completely different histories of herbivory (Council of Europe 2015). Following this recommendation, eradication has come to be viewed as an essential part of conservation, which contrasts with other international disposals like those of the Convention on Biological Diversity or of the Food and Agriculture Organization for genetic resource protection. Less radical discourses advocate determination of each region's carrying capacity, or only eliminating feral goats, or those that do not belong to quasi endemic or well-defined breeds. Currently, new discourses are appearing around the idea that goat grazing on Mediterranean islands is compatible with or even necessary to ensure high levels of biodiversity, landscape maintenance, and the provision of externalities. In this review, we have compiled studies and exposed management scenarios that reinforce this idea, with the purpose of highlighting how the ecological interactions established between native and introduced species a long time ago are complex, and their reduction or disappearance could provoke further unpredicted changes to ecosystems.

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8

Ecology and Evolution of Plant-Enemy Interactions during Early Colonization: Messages from a Land-Rising Archipelago

Peter A. Hambäck, Lars Ericson, and Johan A. Stenberg

Abstract

Plant-enemy interactions on islands are shaped by ecological and evolutionary processes during the history of the islands. It is, however, rare to be able to observe the foundational phases on islands, but opportunities exist in areas with land-rising coastlines, such as in parts of the Baltic Sea. Using several plant-enemy systems, a pattern appears where low-defended plants are typically dominating on young islands and on shores of older islands. One reason for this pattern is that the main seed sources are plants from sites with low enemy attack rates and with high reproductive output. Later on in succession, once herbivore populations become established and attack rates increase, selection acts to increase plant resistance traits. Even though the number of studied plant species is still low, it is apparent that processes during foundational phases may be complex and simplified explanations for current patterns may be hard to find.

P. A. Hambäck (✉)
Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden
e-mail: peter.hamback@su.se

L. Ericson
Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

J. A. Stenberg
Department of Plant Protection Biology, Swedish University of Agricultural Sciences, Alnarp, Sweden

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_8

8.1 Introduction

Islands have fascinated biologists for a long time, not only because of the often unique fauna and flora on isolated islands but also because islands potentially represent replicated and large scale evolutionary or ecological experiments (e.g., Darwin 1859; MacArthur and Wilson 1967; Simberloff 1976; Wardle et al. 1997; Gillespie and Roderick 2002; Whittaker et al. 2014). There are many good examples where general ecological or evolutionary theories have been tested using islands as independent units, isolated by water, in natural experiments (e.g., Wardle et al. 1997; Wardle et al. 2012), following accidental introductions (e.g., Fukami et al. 2006; Maron et al. 2006; Towns et al. 2009), or even by actively manipulating island features or species compositions (e.g., Simberloff 1976; Hambäck et al. 2004; Losos et al. 2004; Herrel et al. 2008). Perhaps the most classical examples include effects of patch size and isolation, encapsulated in the Island Biogeography Theory, where larger islands are predicted to harbor a higher species diversity following a power law (MacArthur and Wilson 1967). Larger islands also harbor longer food chains (Holt et al. 1999), which may in turn result in differences in the strength of species interactions and in trait evolution (Oksanen et al. 2010; Moreira and Abdala-Roberts 2022).

When using islands for testing ecological or evolutionary theories, it is important to remember that observations depend not only on island size but also on the geological and colonization history of the island (Gillespie and Roderick 2002; Strandmark et al. 2020). Unfortunately, few studies exist on the colonization and successional changes during early island formation, compared with the large number of studies on colonization dynamics and successional changes on mainland systems involving plants, animals, and their interactions (e.g., Brown and Gange 1989; Davidson 1993; Carson and Root 1999). Island studies have mainly compared communities and species traits between islands with different characteristics or position and used theories of colonization dynamics to make conjectures about prior ecological and evolutionary processes (e.g., Darwin 1859; MacArthur and Wilson 1967). Whereas these comparisons have yielded important conclusions about potential evolutionary processes, it is important to note that the historical trajectory leading to island formation (such as tectonic processes, volcanism, and relative sea level changes) may affect the build-up of communities and species interaction networks. The outcome may be that evolutionary trajectories and community patterns show differences between island types as well as compared with mainland communities (Stuart et al. 2012). Studying the foundational phases during the build-up of plant-herbivore networks is difficult in most parts of the world, but opportunities exist in areas where islands are formed either by volcanic processes (e.g., Surtsey outside Iceland, Leblans et al. 2014; Magnusson et al. 2014; Ilieva-Makulec et al. 2015), or in areas such as the Baltic Sea where land-rising processes continuously create young islands ready for colonization.

The Baltic Sea is perhaps the most island-rich area in the world, including hundreds of thousands of islands varying in size and age, where ecological processes have been studied using space-for-time substitutions (e.g., Carlsson et al. 1990;

Stenberg et al. 2006) or by following interactions over time (e.g., Zhan et al. 2022). The land-uplift creating these islands is a consequence of an isostatic rebound since the end of the latest ice age (10,000 years ago) when the ice suppressed the tectonic plates. Land uplift is still close to 1 cm per year in the northernmost parts, but decreases to the south and is even negative in the southernmost part due to tilting plates (Steffen and Wu 2011). The archipelagos in the Baltic Sea have attracted the attention of geologists and biologists for more than a hundred years, resulting in pioneering research including the first derivation of the species-area relationships (Arrhenius 1921), the role of chance in shaping species distributions (Palmgren 1921), and studies on the change of species numbers with increasing island height and isolation (Valovirta 1937). In addition, more recent studies have used these islands to study ecological and evolutionary consequences from trophic interactions, such as the role of feral minks (*Neovison vison*) for prey abundance (Nordström and Korpimäki 2004; Fey et al. 2009), how variation in prey size among islands affect morphological traits in populations of the common European Viper (*Vipera berus* L.) (Forsman 1991), the role of selection and random processes for color polymorphism in the meadow spittlebug (*Philaenus spumarius*, Halkka et al. 2001), and foundational work on metapopulation ecology (Hanski 1999).

In this chapter, we review research that has used land-uplift islands in the Skeppsvik archipelago, in the northern part of the Baltic Sea, to study the foundational phases of plant-enemy interactions involving herbivorous insects and pathogenic fungi on islands. These islands provide a great opportunity to study the colonization of both plants and their natural enemies because land uplift, simplified biota, and the homogenous geology in the archipelago create a predictable, tractable, and well-replicated colonization process (Valovirta 1937). Moreover, because the geological age is correlated with island height, where approximate arrival of different species is well established, these islands provide an opportunity to study how species traits and interactions with enemies change along a successional gradient. We first set the stage by describing important aspects of the geological history and plant succession in this system before introducing our study species, three early successional forb species. We then describe how each of these plant species interact with their main enemies and how these interactions change over time due to both ecological and evolutionary processes and in relation to island features such as wind exposure, size, and geological age.

8.2 Setting the Stage: Plant Colonization and Succession

The Baltic Sea is characterized by its richness of islands along the coasts, often forming archipelagos of various extent, such as the broad band stretching from Stockholm to Helsinki and a similar smaller band in the transition between the Bothnian Sea and the Bothnian Bay (Fig. 8.1). These islands are comparatively young, since they were under water during the latest glaciation, when land was suppressed by the heavy inland ice. Other common characteristics of the Baltic Sea are the brackish water, the virtually absence of tide (around 10 cm in the central

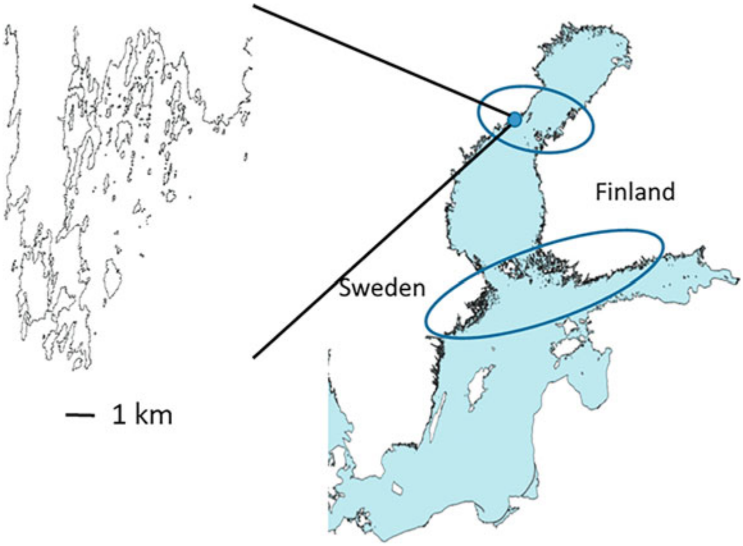

Fig. 8.1 Map of the Baltic Sea, which contains hundreds-of-thousands of islands of various sizes, and a detailed map of the Skeppsvik archipelago. Marked areas in the large map indicate major archipelagoes, such as the band of islands from the Stockholm Archipelago with 30,000 islands to the Åland Islands and the Archipelago Sea with more than 40,000 islands (lower oval) and the Kvarken area between Umeå and Vaasa (upper oval)

parts), and a seasonal sea-level variation formed by wind and air pressure. The young age and the low salinity makes the Baltic Sea hostile for most organisms adapted to marine or freshwater habitats, which has resulted in a species poor fauna and flora and few endemic plants (Jerling 1999; Jonsell and Karlsson 2004).

Variation in geology and in the force of land ice have resulted in widely different island types in different parts of the Baltic Sea, where Archean rock islands dominate the northern fringe of the Baltic proper (Stockholm-Helsinki), and wave-washed moraine islands dominate further north along the Bothnian Sea and Bothnian Bay. Plant succession dynamics differ between these island types and is typically more predictable on moraine islands. On these islands, the colonization process mirrors the littoral position (height above sea level) in contrast to Archean rock islands where species composition is more governed by edaphic conditions. The bedrock on the Archean rock islands causes finer soil fractions to be washed away by storm waves, causing fertile sites to be patchily distributed on lee sides and in sheltered depressions. So, although the long-term successional trajectory from open shores to deciduous thickets to forest (*Pinus sylvestris*) is predictable, the outcome is typically a fragmented vegetation where chance has played an important role during soil accumulation. In contrast, the soil on moraine islands is more stable and less washed away during storms, offering available space for plants to colonize as soon as the islands emerge, resulting in a more predictable colonization pattern (open shore,

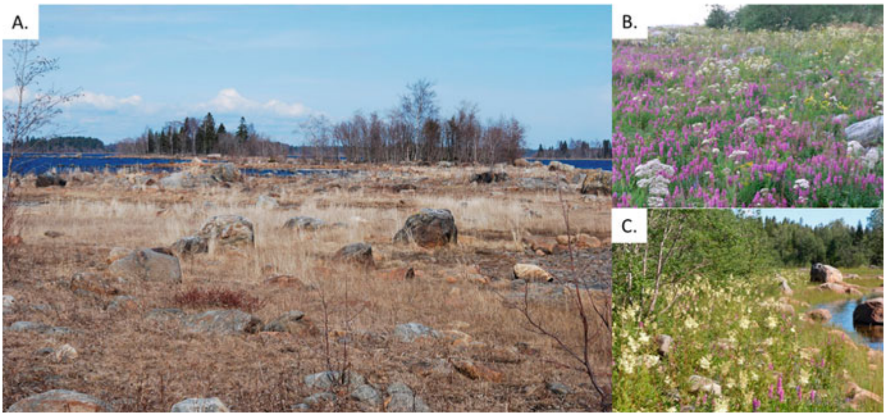

Fig. 8.2 (**a**) The successional gradient illustrated from the grass and forb dominated habitats on recently emerged land, to deciduous trees (*Alnus incana*, *Sorbus aucuparia*, and *Betula pendula*) further back in the photo and finally to spruce and pine forests on the oldest islands (in the background). (**b**) In the outer part of the archipelago, waves and ice scouring delay shrub and trees colonization creating broad open shores dominated by species-rich forb communities. Close to water extensive stands of *Lythrum salicaria* are succeeded by tall herb communities with dense stands of *Filipendula ulmaria*. (**c**) In the inner part of the archipelago, lower disturbance allows trees to colonize closer to the shore and resulting open shores are narrower than in the outer part. The lower part of the graminoid-dominated shore with single *Lythrum salicaria* plants is followed by *Filipendula ulmaria* in front of the deciduous fringe. Photo: Lars Ericson

deciduous fringe, coniferous forest) with a continuous increase in species richness paralleling successional age.

Our focal system, the Skeppsvik archipelago, is a well-studied but relatively small archipelago at the transition between the Bothnian Sea and Bothnian Bay (Fig. 8.1), consisting of around 100 islands with ages up to about 1000 years (sizes 0.08–0.3 km^2, Carlsson-Granér et al. 2014). Skeppsvik is a drumlin archipelago, thus with moraine origin, where young islands are colonized by graminoids such as *Deschampsia bottnica*, *Juncus gerardi*, and *Festuca rubra*, and forbs like *Tripolium vulgare* and *Lythrum salicaria*. After about 50 years, the first shrubs appear (*Hippophaë rhamnoides*, *Myrica gale*, and *Salix* spp.) followed by a deciduous tree stage (*Alnus incana*, *Sorbus aucuparia*, and *Betula pendula*) before Norway spruce (*Picea abies*) takes over the central parts of older islands (Fig. 8.2a, see also Carlsson-Granér et al. 2009). However, the successional pattern also varies between islands depending on exposure. In the outer parts, inundation combined with wave and ice action can strongly delay colonization of shrubs and trees and promote a vegetation dominated by extensive and dense stands of tall herbs (Fig. 8.2b). In less exposed sites, inwards in the archipelago, the vertical extension of the open shore is narrower (Fig. 8.2c), diminishing the available space for many littoral species and resulting in more fragmented plant populations. This gradient has also implications for the occurrence of plant natural enemies as they may be washed away during high-water periods on exposed islands in the outer parts of the archipelago and less so on sheltered shores in the inner parts.

8.3 Focal Plants and Enemies

Our focal species include the three forb species, *Lythrum salicaria* (purple loosestrife), *Filipendula ulmaria* (meadowsweet), and *Silene dioica* (red campion) (Fig. 8.3). A commonality for these species is that population sizes are largest on younger islands in the outer part of the archipelago and decline on older islands further inwards. Whereas all three species are able to regenerate on exposed islands in the outer parts of the archipelago, more sheltered sites further inwards have strongly reduced regeneration of both *L. salicaria* and *S. dioica*. Consequently, large *L. salicaria* plants on sheltered shores are mainly relicts from earlier more exposed conditions. By contrast, *F. ulmaria* may regenerate also on open, sheltered shores by germinating on exposed ground during low water levels. Seed dispersal and establishment of these species involve a large random component, where founders come from other islands in the archipelago with variable genetic backgrounds. This random component creates a landscape level mosaic of plant traits. Once established on an island, the population size increases rapidly (Carlsson

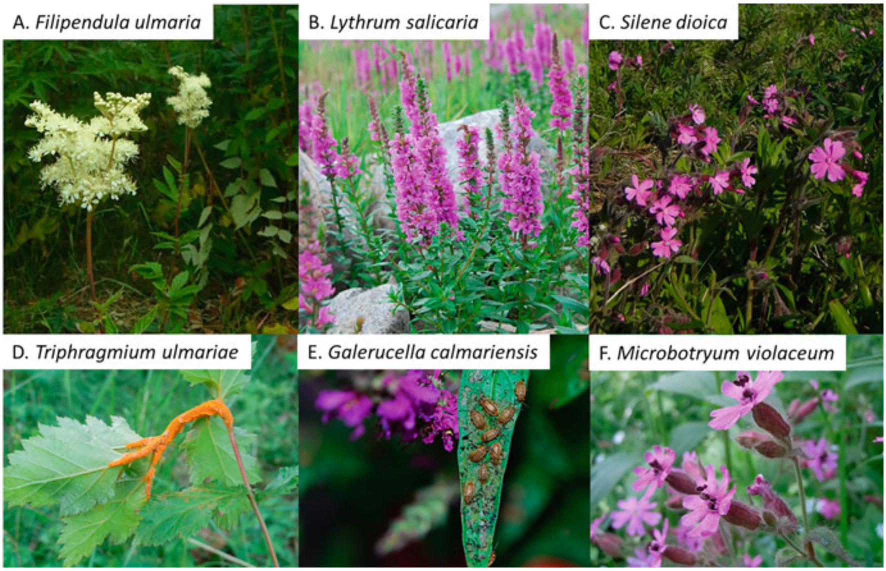

Fig. 8.3 Focal species and some of their main enemies. *Filipendula ulmaria* (meadowsweet) is mostly favored when colonization of woody plants is delayed by wave and ice action and may dominate shores by forming extensive stands. *Lythrum salicaria* (purple loosestrife) is among those 10 species that first colonize islands and heavily depends on disturbance for its establishment. *Silene dioica* (red campion) also colonizes younger islands but is more abundant within the exposed border of deciduous trees. Photo: Lars Ericson

et al. 1990), and population structure may be reinforced because pollination and seed dispersal on the shore may occur over very short distances which limit genetic remixing (as shown for *S. dioica*, Giles et al. 1998; Ingvarsson and Giles 1999).

The main enemies attacking *Filipendula ulmaria* are the host specific rust pathogen *Triphragmium ulmariae* (Fig. 8.3d) and the univoltine leaf beetles *Galerucella tenella* and *Altica engstromi*. The rust is non-systemic and reinfects plants annually through over-wintering teliospores, which may disperse between islands through wave action (Burdon et al. 1995). Following successful infection, the rust forms orange-colored aecial infections that distort stems and petioles. The leaf beetles overwinter as adults in the litter and attack plants during early summer and then strongly reduce plant growth and fitness (Stenberg et al. 2006; Stenberg et al. 2007). Young *G. tenella* larvae preferentially feed on flower buds whereas older larvae also consume leaves. *Altica engstromi* skeletonizes the entire plant. Whereas *A. engstromi* is monophagous on *F. ulmaria*, *G. tenella* also feed on other Rosaceae (Stenberg and Axelsson 2008; Stenberg et al. 2008).

The main enemy affecting *Lythrum salicaria* is again a leaf beetle (*G. calmariensis,* Fig. 8.3e) with a similar life cycle as *G. tenella* (Hambäck et al. 2000). Young *G. calmariensis* larvae preferentially feed within flower buds, whereas older larvae may completely defoliate the host plant before pupating in the ground (Lehndal et al. 2016). Both *Galerucella* beetles are in turn attacked by the parasitic wasp *Asecodes parviclava*, with parasitism rates ranging up to almost 100% (Stenberg et al. 2007). Flowers of *L. salicaria* are also commonly attacked by a flower-feeding weevil (*Nanophyes marmoratus*), but densities of this species are rarely high enough to cause serious damage to the plant (Hambäck 2021).

Finally, the main enemy affecting population densities of *Silene dioica* is a sterilizing anther-smut fungus generally known as *Microbotryum violaceum* (*Ustilago violacea*, Microbotryales, Fig. 8.3f, Giles et al. 2006). Recent studies have shown that anther smuts on Caryophyllaceae hosts are not true smuts but closer related to rusts. They form a monophyletic group of host specific taxa and our species is now referred to *M. silenes-dioicae* (Kemler et al. 2020). This fungus is dispersed by pollinators, mainly bumblebees, visiting infected flowers and then moving spores to uninfected plants. Because the infection is systemic, infection may ultimately lead to strong population declines of the host plant.

8.4 Arrival of Plant Enemies and Eco-Evolutionary Feedbacks

Early colonizing propagules on exposed shore lines have a high probability of coming from plants with a low resistance to both insect attacks and pathogen infections, for two reasons. First, inundation and wave-wash reduce enemy survival on these exposed sites and thereby create enemy-free areas where there is no selective advantage for plants resistant to either insect or pathogen attacks. Second, likely propagule sources are often from other similarly exposed shorelines with low enemy pressure and where plant populations consequently have low resistance and vigorous reproductive output (Lehndal et al. 2016).

The successional processes following colonization are both similar and different between plant species, but have perhaps been best described for *S. dioica* (Carlsson-Granér et al. 2014). Following establishment on young islands, the *Silene* populations rapidly grow in size until later successional species restrict the distribution to the areas close to the water where new land is continuously created out of the sea. The anther-smut fungus typically does not colonize the very young populations but instead expands on islands of intermediate age where the prevalence may be high, though also highly variable. This variability in disease prevalence seems to be an effect of the processes during foundation of the populations, where small-scale dispersal and kin-selection due to pollination by plant neighbors create high intra-population variation at small spatial scales (Giles and Goudet 1997; Ingvarsson and Giles 1999). Such heterogeneity persists under long-term infection, despite a potential of the fungus to select for more resistant genotypes with small flowers and shorter stigmas (Giles et al. 2006). A plausible explanation is high population turnover where new colonists originate mainly from populations with low infection or from recently colonized islands that have never been exposed to the disease (Carlsson-Granér et al. 2014).

Similar to *S. dioica*, *F. ulmaria* populations are largest and most extensive on intermediately aged islands and become more scattered, fragmented, and smaller, on older islands. Moreover, and again similar to *S. dioica*, propagules giving rise to early colonizing *F. ulmaria* plants generally arrive from other early successional communities and have a low resistance to natural enemies. Their survival is possible due to low attack rates caused by limited overwintering capacities of enemies in these highly disturbed habitats. These low defended plants may also have a competitive advantage compared with more defended plants by flowering early and by producing more floral shoots. With time, enemies (both fungi and insects) will establish and cause strong directional selection on *F. ulmaria* traits. Stenberg et al. (2006) investigated defense traits in plants collected from islands with different ages, showing that plants from older islands contained higher concentrations of both condensed tannins, chlorogenic acids, and (+)-catechin (Fig. 8.4a) and also had a lower growth rate. Concomitantly, it was also apparent that *G. tenella* females laid fewer eggs and consumed less leaf mass on plants sourced from older island (Fig. 8.4b). This higher resistance in older plant populations has several consequences, including lower beetle densities on older islands (Hambäck and Ericson, unpubl), shifts in the beetle diet with population age (Stenberg et al. 2008), and reduced seed-set (Fig. 8.5). When *G. tenella* beetles were given a choice to feed on *F. ulmaria* and *Rubus arcticus* (Arctic bramble), another potential host plant, it was apparent that beetles preferred *R. arcticus* when the alternative was a *F. ulmaria* plant from an older island but not so when the alternative was a *F. ulmaria* plant from a younger island (Fig. 8.4c, Stenberg et al. 2008). Thus, it seems that the beetles, by inflicting natural selection for stronger resistance in its main host plant, also modify the relative profitability of their different food plants.

F. ulmaria population development is also affected by pathogens, particularly the rust pathogen *Triphragmium ulmariae* (Fig. 8.3d). Using a 30-year data set, Zhan et al. (2022) showed that both disease prevalence (% infected plants) and disease

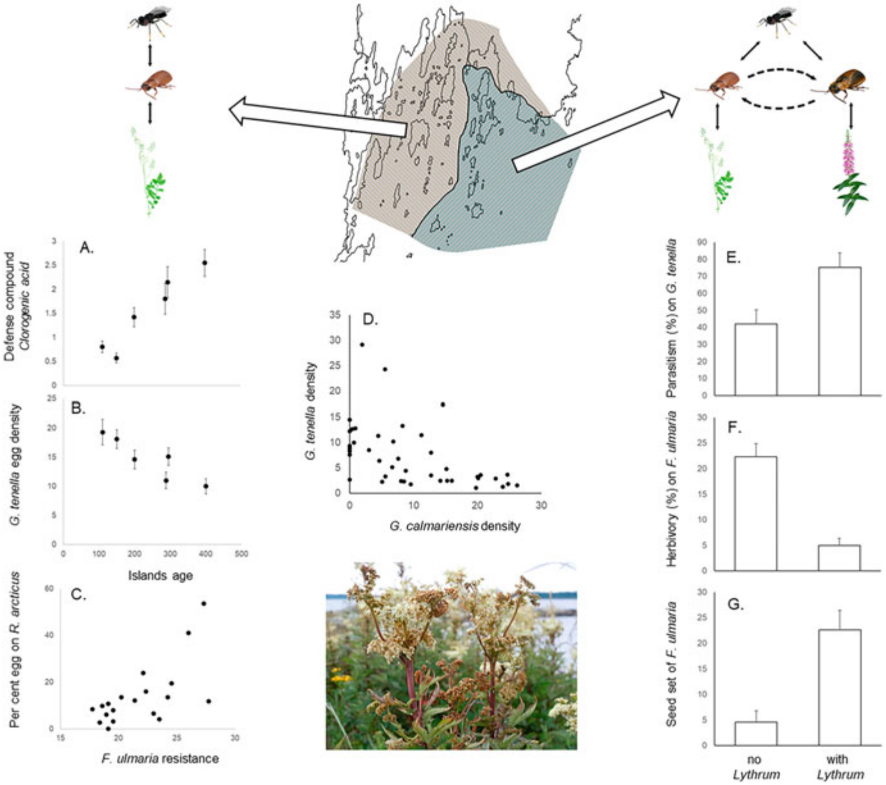

Fig. 8.4 *Lythrum salicaria* only occurs in the eastern part of the archipelago, which has consequences for indirect interactions between this species and *Filipendula ulmaria* through a shared parasitoid on two leaf feeding beetles (*Galerucella calmariensis* and *G. tenella*) that are negatively related among sites (**d**). On islands with both plant species, parasitism rates were higher on *G. tenella* (**e**), which had the consequence that herbivory was lower (**f**) and seed set of the host plant *F. ulmaria* was higher (**g**). On islands with only *F. ulmaria*, defense compound concentrations were higher on older islands (**a**), which reduced egg laying rates (**b**) and caused beetles to start laying eggs on an alternate host (**c**, *Rubus arcticus*). Redrawn from Stenberg et al. (2006, 2007, 2008). Photo: Lars Ericson

severity of *T. ulmariae* on *F. ulmaria* decreased over time, but also that the growth rate of the plant population was negatively affected by higher disease incidence and severity. These effects are likely consequences from the strong effect from infection on the survival of plant seedlings (Ericson et al. 2002), but effects on the evolutionary trajectory is unknown. Moreover, a complicating pattern is that disease severity shows large variations over time, which cause evolutionary hot-spots and cold-spots to vary among islands (Smith et al. 2011).

The *Lythrum salicaria* system illustrates an additional feature of plant-herbivore interactions in these early successional communities. Plants on young islands are again less damaged by beetles, in this case the leaf beetle *G. calmariensis* (Lehndal

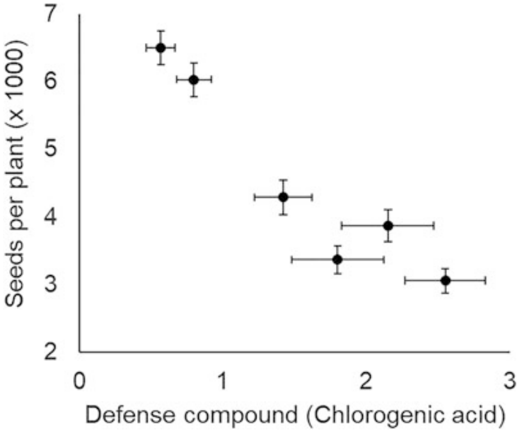

Fig. 8.5 Relationship between defense compound concentration in plant leaves (from Stenberg et al. 2006) and plant seed set of *Filipendula ulmaria* grown in a common garden ($n = 30$ for each island)

et al. 2016), but this effect seems to depend on island features such as exposure. The mechanism appears to be that winter survival rates are strongly reduced on exposed islands because high water floods during winter wash away grass litter, the main overwintering habitat of the beetles. On older islands, by contrast, the litter, with the over-wintering adults, often remains higher on the shore even on exposed islands leading to increased winter survival. As a consequence, *L. salicaria* plants on these shores may be completely defoliated during peak years of *G. calmariensis*, except when growing inside shrubs such as *Salix* or *Myrica gale*. In this case, the mechanism underlying the lower herbivory seems to be that beetles are less able to locate *L. salicaria* plants when growing in shrubs, thus providing an associational refuge, and the consequence is lower herbivory (Hambäck et al. 2003). Although the difference may be somewhat counteracted by a higher larval mortality outside the shrubs, caused by lady-bird beetles, both flowering frequency and seed-set may be an order of magnitude higher on plants inside compared with outside the shrub patches (Hambäck et al. 2000). Further inwards in the archipelagos, such *L. salicaria* plants may be the only survivors from earlier large populations, when increasing shelter prevents successful seedling establishment.

Research has also shown indirect interactions between the plant-beetle systems involving *L. salicaria* and *F. ulmaria* which vary as a function of island features (Fig. 8.4d), including spill-over parasitism from wasps attacking *G. calmariensis* on *L. salicaria* to attacking *G. tenella* on *F. ulmaria* (Hambäck et al. 2006). This process was discovered because *L. salicaria* is absent from the western parts of the archipelago where the sheltered, litter-covered shores exclude successful seedling survival. We found that parasitism rates by *Asecodes parviclava* on *G. tenella* were higher on islands with both *L. salicaria* and *G. calmariensis* present (Fig. 8.4e). At the same time, parasitism rates on *G. calmariensis* were lower on islands with than without *F. ulmaria*. Stenberg et al. (2007) identified that this pattern arose because flowering plants of *F. ulmaria* are more attractive to the wasp than flowering plants of *L. salicaria*. *Filipendula ulmaria* produces more nectar, and probably more easily accessible nectar to wasp females due to different floral structures, compared to *L. salicaria*. Thus, on islands with both plants there is an asymmetric movement of wasps from *L. salicaria* to *F. ulmaria*. At the same time, wasp mortality is likely higher after attacking *G. tenella* compared with *G. calmariensis*, because the former beetle species has a greater capacity to encapsulate wasp eggs (Fors et al. 2016), but those surviving still increase total parasitism rates. Because wasp parasitism also reduces the beetle population, at least of *G. tenella*, there is an indirect effect on leaf damage and seed set of *F. ulmaria* (Fig. 8.4f, g, Stenberg et al. 2007).

8.5 Synthesis

The observed patterns suggest some common trajectories for the early successional development of plant-enemy interactions on land-rising islands in the Skeppsvik archipelago. Most importantly, plant populations on new islands typically experience a period of enemy-free time before herbivores and pathogens can establish because of high wave disturbance and flooding. This period allows plants with low resistance to establish because founding seeds typically arrive from nearby low-resistance populations which have also enjoyed enemy-free time. As islands grow older and changing physical conditions allow enemies to establish, natural selection will increasingly favor investment in resistance traits, albeit often at the cost of reduced capacity to produce seeds. This trajectory may, however, depend on the order of plant colonization to islands, as a consequence from parasitoid-mediated indirect interactions between two of the study plants. If *L. salicaria* establish prior to *F. ulmaria*, herbivore damage on *F. ulmaria* may be lower due to parasitoid-mediated indirect effects, possibly reducing the selective advantage of more resistant plants. One key message following the important role of bi- and tritrophic interactions is that the strength and direction of selection may vary even over the small spatial scales prevailing in the Skeppsvik archipelago and that the outcome of these interactions are difficult to grasp without detailed study. This insight indicates the need to incorporate a spatial perspective when discussing island biota. At an ecological scale, it is necessary to view colonization on islands from a metacommunity perspective involving local dynamics and migration processes (sensu Leibold et al. 2004), but also to realize that selection dynamics will vary spatially among islands in a geographic mosaic of islands (sensu Thompson 1994) with different successional maturity.

8.6 Conclusions

Although islands have been important as study systems for basic eco-evolutionary theories, classical island biogeography theory alone often fails to explain evolutionary patterns of plant-herbivore interactions (Moreira et al. 2021). The reasons for these shortcomings may include a lack of knowledge about colonization patterns, founder effects, and historic evolutionary processes that cannot be inferred from features such as island size and distance alone. Rising archipelagos, with their predictable and repetitive colonization processes, offer unique possibilities to go beyond classical island biogeography and more fully exploit the processes leading to the current complexity of plant-enemy interactions. Because islands differ in isolation, exposure and other physical characteristics within archipelagos, new perspectives may be incorporated and perhaps even serve as a bridge between island biogeography, metacommunity models, and the geographic mosaic perspective of co-evolution.

Founder effects are obviously important in all studies of island ecosystems because colonizing species and genotypes are not a random set of potential candidates but depend on both isolation and species traits. The Skeppsvik archipelago is evidently different compared to many oceanic islands because founder populations are in comparatively close vicinity, which results in a metacommunity dynamic that is more dominated by reciprocal migration events than by local dynamics. In that sense, birth-death dynamics of populations on these islands likely resemble mainland systems more than oceanic islands. On the other hand, and similar between the land-rising islands and oceanic islands, populations are more strictly spatially defined compared with mainland systems because the matrix is completely inhospitable. This isolation may reduce genotype introgression and thereby increase the rate of population differentiation.

Whereas these processes are important to study for understanding the community development on islands, these archipelagoes also represent a bridge between small-scale, and often artificially constructed, mesocosm studies and large-scale dynamics in natural ecosystems. For example, plated bacterial microcosms (Koskella et al. 2011) and arthropod mesocosms (Masier and Bonte 2020) have been used as experimental "islands" to promote our understanding of evolutionary processes similar to those addressed in this review. Whereas these studies may provide a road-map for the type of processes whereby local and regional processes may affect ecological and evolutionary patters, land-uplift islands allow us to study corresponding process in a natural setting and across longer time scales. Future research will benefit from building further bridges between these different approaches to reach a more holistic understanding of plant-enemy interactions over both ecological and evolutionary time scales.

Acknowledgements We are grateful to the large number of field assistants and collaborators that have been involved in data collection during the years. Financial support has also been received from the Swedish Research Councils NFR and VR.

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9

Island Features and Abiotic Factors as Drivers of Insect Leaf Herbivory on Islands

Xoaquín Moreira, Carla Vázquez-González, Beatriz Lago-Núñez, and Luis Abdala-Roberts

Abstract

Herbivory is a dominant interaction across the globe and has shaped within- and among-species variation in both plant and herbivore traits. Islands are not the exception, and several studies have documented cases where native herbivores such as mammals, tortoises, crabs, birds and to a lesser extent insects exert strong effects on insular plant traits and abundance, and in some cases drive speciation. Nonetheless, we still know little about the drivers of herbivory on islands, in particular the influence of classically studied geographical or physical island features and the virtually unstudied influence of abiotic factors. In particular, more isolated (i.e. distance to mainland), geologically older and smaller islands are predicted to lead to decreases in herbivore abundance and richness which would in turn lead to lower herbivory. In addition, islands found in more humid or warmer climates and with soil types that promote productivity should exhibit higher herbivory. In this chapter, we aim at investigating the effects of island physical factors such as island size, isolation and geological age, as well as abiotic factors (namely, climate and soil), on insect herbivory for 76 plant species found across 6 archipelagos (17 islands in total) in Europe. Contrary to expectations, we found no significant relationship between herbivory and island features (area, isolation and geological age), as well as no association between herbivory and

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X. Moreira (✉) · B. Lago-Núñez
Misión Biológica de Galicia (MBG-CSIC), Pontevedra, Galicia, Spain

C. Vázquez-González
Misión Biológica de Galicia (MBG-CSIC), Pontevedra, Galicia, Spain

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, USA

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

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_9

climate. The only exception was a significant relationship between herbivory and soil characteristics where plants growing under silty soils exhibited lower levels of leaf damage, indicating that soil physical features could play a bottom-up role in shaping herbivory patterns on island. Overall, our findings provide little support for predicted effects of island features and climate on insect leaf herbivory levels but some evidence for soil abiotic controls. These findings call for further studies involving larger taxa and island sample sizes combined with robust controls on plant traits, phylogeny and insect feeding guilds across broader abiotic gradients.

9.1 Effects of Island Physical Features on Herbivory

Islands cover a very small fraction of the planet's land surface (ca. 5%) but harbour nearly a third of the species found in biodiversity hotspots and exhibit extremely high species endemism levels (Myers et al. 2000). Classically, research on islands has focused on geographical factors (e.g. size, isolation, geological age; MacArthur and Wilson 1967) and evolutionary processes (e.g. speciation and in situ radiations; Schluter 2001) driving species diversity (reviewed by Whittaker et al. 2017). Less studied, however, are the effects of insularity features on species interactions (Holt 2010; Schoener et al. 2016), in particular herbivory (Moreira and Abdala-Roberts 2022), and this gap has limited our understanding of the ecological and evolutionary consequences of insularity on species and communities.

Herbivory is a ubiquitous force shaping plant and herbivore species traits and biodiversity (Marquis 1992; Cyr and Pace 1993; Futuyma and Agrawal 2009; Turcotte et al. 2014). Islands are not the exception, and several studies have documented cases where native herbivores such as insects, mammals, tortoises, crabs and birds exert strong effects on insular plant traits and abundance (e.g. Terborgh et al. 2006; Terborgh 2010; Kavanagh 2015), as well as promote speciation (Losos et al. 1998; Grant and Grant 2006). Nonetheless, we still know little about the drivers of herbivory on islands, in particular the influence of geographical or physical features such island area, isolation and geological age or abiotic factors (Moreira and Abdala-Roberts 2022). For example, greater island isolation (i.e. distance to mainland) and geological age and smaller island area usually lead to predictable decreases in herbivore abundance and richness (Carlquist 1974; Grant 1998) which should in turn lead to lower herbivore pressure. Likewise, islands found in more humid or warmer climates (Weigelt et al. 2013) or with geological features that result in more fertile soils (Pillon et al. 2010) should exhibit higher herbivore pressure.

Several challenges must be addressed to robustly test for insularity effects on herbivory. Critically, there is a need for well-replicated studies both within and among insular systems (e.g. archipelagos, Moreira and Abdala-Roberts 2022). Meta-analysis partly offsets this limitation but can be constrained in power or inference due to inherent variation among studies. Second, studies are needed that span herbivory measurements on multiple plant species and include different herbivore groups to increase inference and identify commonalities and differences within and among taxa, particularly for damage by speciose invertebrate guilds (Schoener 1989; Burns 2019; Moreira et al. 2021).

9.2 A Case of Study across Insular Systems in Europe

In this chapter, we aim at investigating the effects of island physical factors such as island size, isolation and geological age, as well as abiotic (namely climate and soil) factors, on insect leaf herbivory for 76 plant species (38 herbs, 25 shrubs and 13 trees; Fig. 9.1) found across six archipelagos (17 islands in total) in Europe

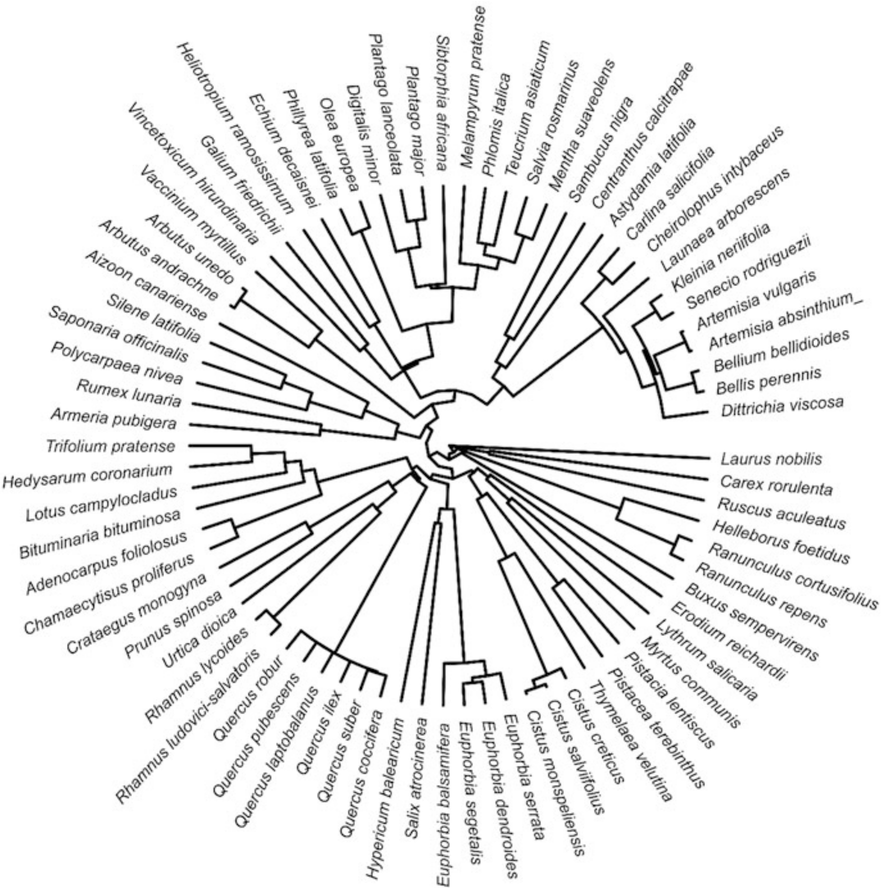

Fig. 9.1 Phylogenetic tree of the studied plant species from an updated mega-tree derived mainly from a phylogeny for seed plants by Smith and Brown (2018) and a phylogeny for pteridophytes by Zanne et al. (2014) using the V. phylomaker package in R (Jin and Qian 2019)

Fig. 9.2 List of the 17 insular systems used in this study. 1. Gotland, 2. Sálvora, 3. Ons, 4. Cíes, 5. La Gomera, 6. Tenerife, 7. Gran Canaria, 8. Lanzarote, 9. Formentera, 10. Ibiza, 11. Majorca, 12. Menorca, 13. Corsica, 14. Sardinia, 15. Sicily, 16. Lesbos, 17. Crete

(Fig. 9.2). Specifically, we asked: (*i*) Do island area, distance to mainland and geological age predict herbivory? Following theory, we expected lower herbivory on islands that are smaller, more isolated and of more recent origin. (*ii*) Do abiotic factors, namely climate and soil characteristics, correlate with herbivory? Here, we expected higher herbivory in warmer and wetter (and less seasonal) insular systems, as well as in islands with more fertile soils. The novel test of drivers of herbivory on islands in this chapter helps pave the road towards bridging theory on island biogeography and species interactions and a better understanding of insularity effects on herbivory.

At the end of the growing season (before leaf senescence in the case of deciduous species), we surveyed insect leaf herbivory in the 17 islands (Fig. 9.2). These estimates provided an assessment of cumulative herbivory over the growing season, after most damage during the spring and summer had occurred. For each island, we selected at least one population (range: 1–3) of herbaceous or woody native or insular endemic plant species (range: 4–19 species per island). Each population was composed of at least 10 individuals. For each population, we randomly sampled 4–5 plants separated by 2 m. This sampling effort resulted in 76 plant species and 740 individual plants across the study. In the case of woody species, we collected only juvenile trees or shrubs with <1.8 m height. For each plant, we randomly collected up to 15 leaves distributed throughout the plant canopy. Leaves were taken

Table 9.1 Description of the eight climatic variables from the WorldClim database and the nine soil variables in the topsoil (0–5 cm deep) from the SoilGrids database used to estimate abiotic conditions of each plant population

Variable	Description	Units
BIO1	Annual mean temperature	°C
BIO4	Temperature seasonality (standard deviation *100)	[dimensionless]
BIO5	Maximum temperature of warmest month	°C
BIO6	Minimum temperature of coldest month	°C
BIO12	Annual precipitation	mm
BIO13	Precipitation of wettest month	mm
BIO14	Precipitation of driest month	mm
BIO15	Precipitation seasonality (coefficient of variation)	[dimensionless]
BLDFIE	Bulk density (fine earth fraction)	kg m^{-3}
CECSOL	Cation-exchange capacity (fine earth fraction)	cmolc kg^{-1}
CRFVOL	Coarse fragments (volumetric)	cm^3 cm^{-3}
ORCDRC	Organic carbon content	g kg^{-1}
PHIHOX	pH index (H_2O solution)	[dimensionless]
PHIKCL	pH index (KCl solution)	[dimensionless]
CLYPPT	Clay content (gravimetric)	kg kg^{-1}
SLTPPT	Silt content (gravimetric)	kg kg^{-1}
SNDPPT	Sand content (gravimetric)	kg kg^{-1}

to the laboratory where they were photographed to estimate the percentage of leaf area consumed by insect herbivores using the professional mobile application BioLeaf—Foliar Analysis™ (Brandoli Machado et al. 2016).

To assess climatic and soil conditions present at each sampling site, we used eight bioclimatic variables of the WorldClim database (http://www.worldclim.org/) at 1 Km^2 resolution (Hijmans et al. 2005) and nine soil variables in the topsoil (0–5 cm deep) from the SoilGrids database (http://www. soilgrids1km.isric.org) at 250 m^2 resolution (Hengl et al. 2017) obtained from the geographical coordinates of each site (see Table 9.1 for variables used). Rather than testing for associations between each abiotic variable and herbivory which would inflate Type I error, we summarized climatic variables and soil variables (separately in each case) using principal component (PC) analysis (PROC FACTOR, rotation = varimax in SAS 9.4) and used the standardized *z*-scores of these PCs to examine the relationships between these factors and herbivory (see ahead) (Moreira et al. 2014). Two axes explained 82% of the variance (54% and 28%, respectively) in the 8 climatic variables across sites. PC1 (hereafter "temperature") was positively related to minimum temperature of the coldest month and negatively related to temperature seasonality. PC2 (hereafter "precipitation") was positively related to annual precipitation and precipitation of the wettest month. Similarly, two axes explained 73% of the variance (52% and 21%, respectively) in the nine soil variables across sites. PC1 ("PC1 soil" hereafter) was positively related to soil pH (in H_2O and KCl solutions) and bulk density and negatively related to organic carbon content. PC2 ("PC2 soil" hereafter) was negatively related to silt content.

For all statistical analyses, we averaged population values within each island for species with multiple populations per island in order to have one value per species per island. First, we tested for associations between herbivory and island features by running a linear mixed model that included island size, isolation and geological age as predictors of leaf damage. Second, we tested the association between herbivory and abiotic conditions by running two linear mixed models, one including climatic PCs and the other soil PCs as predictors of herbivory. In all the above models, we included plant species, species taxonomic family, and the archipelago as random factors to account for species repeated measures (i.e. when species were sampled on more than one island), shared evolutionary history of plant taxa, and insular system, respectively. In all these models, we squared-root transformed herbivory to achieve normally distributed residuals. We ran all statistical analyses in R software version 4.2.1 (R Core Team 2020). We implemented linear mixed models using the *lmer* function from the *lmerTest* package (Kuznetsova et al. 2017). We visualized bivariate graphs to depict associations between herbivory and predictors by plotting predicted values obtained from each model using the *augment* function from the *broom.mixed* package (Robinson 2014). We built all graphs using ggplot (Wickham 2016).

Overall, the amount of leaf area removed by insects was low (mean ± SE: 3.11 ± 0.29%, range: 0–15%). These levels of insect damage are comparable to those reported in previous studies on islands across temperate areas (reviewed by Moreira et al. 2021). For example, Moreira et al. (2019) found that the percent leaf area removed by insect leaf chewers on holm oaks growing in Mediterranean islands was approximately 2.5%. Similarly, Shin et al. (2021) found that the percent leaf area removed by insect leaf chewers in three woody species across 18 islands in South Korea varied from 2.59% to 4.15%. That said, work with native herbivores, in particular insects, remains limited and calls for more work describing frequency and magnitude of insular plant damage by leaf-chewing insects as well as other guilds. This could include intra- and inter-specific comparisons and tests of underlying drivers given by plant traits while controlling for phylogenetic inertia.

Contrary to expectations, we found no significant relationship between herbivory and island area (Fig. 9.3a), isolation (Fig. 9.3b) or geological age (Fig. 9.3c). Classic theory predicts stronger plant-herbivore interactions in larger, older and less isolated island (MacArthur and Wilson 1967). In comparison, past studies provide support for predictions in some but not all cases (Moreira et al. 2021). For instance, Arnold and Asquith (2002) found that the proportion of leaf area consumed by caterpillars increased with island size on eight artificial forested islands at Panama, but island isolation had no effect on herbivory. Shin et al. (2021) found that herbivory by external feeders in three tree species groups (*Mallotus japonicus*, *Prunus* species and *Quercus* species) increased with island size on 18 islands in southwest Korea, whereas herbivory by external feeders decreased with isolation. In addition, Borges and Brown (1999) found that geologically older but smaller islands in Azores had more herbivore species than the two most recent ones. In addition, these authors found that herbivore species richness was negatively correlated with distance to mainland (Borges and Brown 1999). In contrast, Becker (1992) found that herbivore

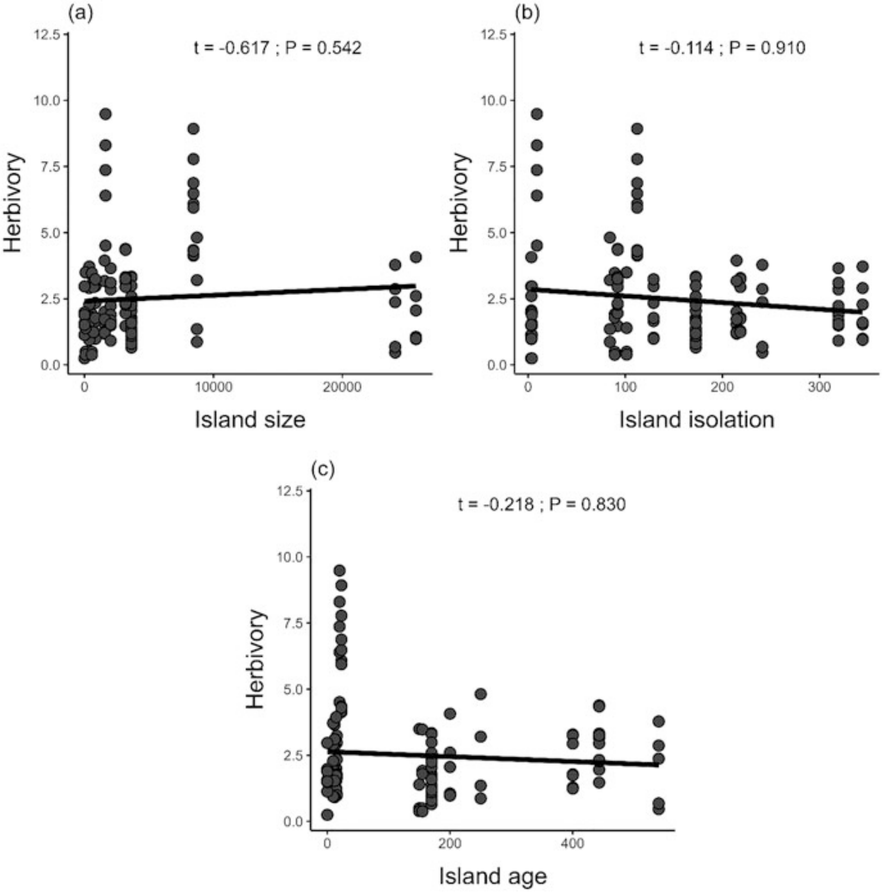

Fig. 9.3 (**a**) Island size (km^2), (**b**) isolation (km to mainland) and (**c**) geological age (millions of years) as predictors of the percentage of leaf area consumed by insect herbivores for 76 plant species found in 17 European islands. T- and *P*-values are shown. Circles represent plant population predicted values obtained from the corresponding linear mixed model

species richness was not significantly correlated with island area in a global study including Canary Islands, Galapagos, Mediterranean Islands and California Channel Islands. Our findings, while negative, add to this mix of findings which suggest that we are still at an initial stage in understanding the effects of these drivers and further work is needed to try to achieve some degree of generalization. In particular, work in tropical regions where herbivory rates are expected to be higher (Coley and Barone 1996) are needed, ideally including more plant species per island.

Likewise, we found no significant relationship between herbivory and climatic variables, namely temperature- and precipitation-related factors (Fig. 9.4a and b). Other factors held constant, warmer and more humid climate would be predicted to support more species and greater abundances of insect herbivores and thus exhibit

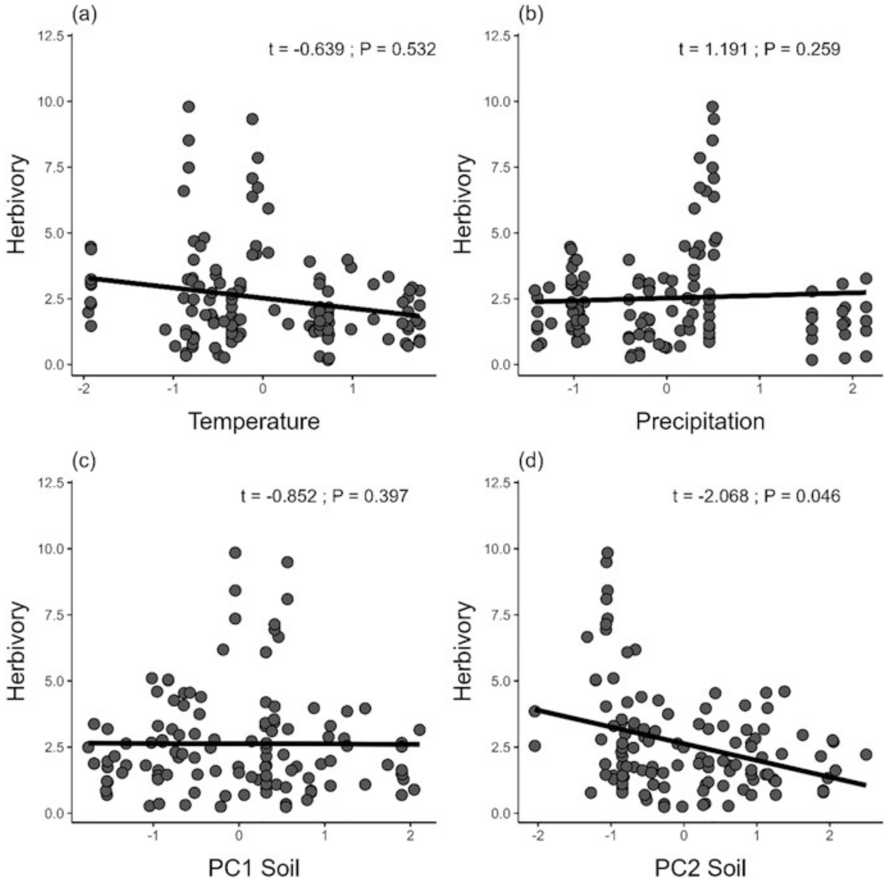

Fig. 9.4 (**a**) Temperature, (**b**) precipitation, (**c**) PC1 soil and (**d**) PC2 soil as predictors of the percentage of leaf area consumed by insect herbivores for 76 plant species found in 17 European islands. Climatic and soil variables were grouped based upon principal component analyses so the x axis shows the standardized *z*-scores of the first two principal components from each analysis (*see text*). T- and *P*-values are shown. Circles represent plant population predicted values obtained from the corresponding linear mixed model

higher herbivore pressure (Lemoine et al. 2013; Hamann et al. 2021). Studies testing for abiotic controls on insular herbivory are scarce, with one exception being a study by our group who similarly to this study reported that climatic factors did not explain leaf herbivory in holm oaks (*Quercus ilex*) distributed across several islands in the Mediterranean basin (Moreira et al. 2019). Results from this chapter add to this pattern across a broad range of species in terms of both ecology and taxonomy, suggesting climatic controls are weak or absent across the insular systems studied. While there was 2.4-fold variation in mean annual temperature and 1.9-fold variation in annual precipitation, perhaps variation was not large enough to detect significant trends. The inclusion of islands across a broader latitudinal range would product a more appropriate and robust design to test for climatic controls on insular herbivory (Weigelt et al. 2013; Harter et al. 2015).

Contrary to climatic variables, we detected a significant negative relationship between herbivory and PC2 soil (but not PC1 soil, Fig. 9.4c), indicating that plants growing under silty soils had lower levels of leaf damage (Fig. 9.4d). Higher levels of silt, other soil features held constant, are typically associated with more water retention and air circulation which favour productivity (Wyckhuys et al. 2017). While theory predicts lower levels of herbivory in nutrient-limited soils due to slower plant growth and increased allocation to defences (Coley et al. 1985; Endara and Coley 2011), plants simultaneously allocate to both growth and defences under increased nutrient availability (Hahn and Maron 2016). The rationale behind this is that trade-offs between growth and defence are weak or lacking under high resource availability, and therefore plants can maximize both functions simultaneously (Sampedro et al. 2011). While speculative, it would be interesting to test for such trade-offs, at least with correlational analyses, across study systems with a broader range of (or contrasting) soil (and climatic, see above) conditions to determine whether patterns consistent with trade-offs (negative growth-defence correlations) are present and if they are modulated by abiotic conditions. This would help to better understand soil abiotic controls over herbivory via endogenous plant resource constraints.

9.3 Synthesis and Outlook

Overall, our findings provide little support for predicted effects of island features and climate on insect leaf herbivory levels for the studied taxa and insular systems. This runs counter to patterns found on mainland in both temperate and tropical areas (Cyr and Pace 1993; Turcotte et al. 2014), suggesting that herbivory in insular systems, at least in temperate areas such as the Mediterranean basin and Macaronesia, is not governed by these predictors. The only evidence found for abiotic controls was given by soil variables related to texture and water retention such as silt content, warranting further investigation in the context of more in depth-analyses of largely overlooked soil factors (Strahlhofer et al. 2021). At the same time, further studies involving larger taxa and island sample sizes combined more robust controls on plant traits, phylogeny and insect feeding guilds across broader abiotic gradients are needed before reaching stronger conclusions. These types of assessments are under way by our group and promise to yield valuable insight into the drivers of herbivory in islands.

Acknowledgements We are grateful to Nikos Fyllas, Nikos Piperakis, Lucía Martín-Cacheda, Cristina Alonso, Ignacio Vicente-Díez, Jonay Cubas, Andrea Galmán, Miquel Capó, Luis Sampedro, Marc Gibernau and Torbjörn Lindell for help in field sampling. This research was supported by two grants from the Spanish Ministry of Science and Innovation (PID2022-141761OB-I00, EUR2023-143463) and two grants from Galician Innovation Agency (IN607A 2021/03 and the Oportunius Program) to XM. CVG was supported by a postdoctoral fellowship from the Xunta de Galicia-GAIN/Fulbright (IN606B 2021/004).

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Part III

Tritrophic Interactions

Food Web Dynamics on Bahamian Islands

10

David A. Spiller, Thomas W. Schoener, and Jonah Piovia-Scott

Abstract

We here summarize and integrate findings in our studies of food-web interactions on Bahamian islands conducted over a 40-year timespan. Results obtained in a series of field experiments, taken together, provide compelling evidence that predatory lizards reduce herbivory and thereby have a positive indirect effect on plants, even though lizards also reduce web spiders which eat herbivores. Two exogenous factors, hurricanes and allochthonous resource pulses, play a significant role in structuring island communities and produce major temporal fluctuations in food-web dynamics. Following hurricanes, herbivory increased substantially on severely damaged plants due at least in part to enhanced susceptibility of resprouting foliage to herbivores. The top-down effect of lizards on herbivory was stronger after the hurricanes than before. Allochthonous resource pulses in the form of seaweed deposition events cause a sequential series of bottom-up and top-down effects that propagate throughout the food web. In the short-term, lizards shift from eating local prey (including terrestrial herbivores) to eating mostly marine detritivores, leading to increased herbivory and weakening the trophic cascade from lizards to plants. In the long-term, decomposing seaweed adds nutrients to plants, increasing their growth rate, and a numerical response by lizards to marine detritivores strengthens the trophic cascade.

D. A. Spiller (✉) · T. W. Schoener
Department of Evolution and Ecology, University of California, Davis, CA, USA
e-mail: daspiller@ucdavis.edu

J. Piovia-Scott
School of Biological Sciences, Washington State University, Vancouver, WA, USA

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_10

10.1 Introduction

Understanding how various factors influence species interactions in food webs is a central goal in ecology (Schoener 1989; Borer et al. 2005; Abdala-Roberts et al. 2019). One of the most influential concepts is the "trophic cascade" (Terborgh and Estes 2010), which can be broadly defined as the propagation of impacts by consumers on their prey downward through food webs (Estes et al. 2011). Indeed, many empirical studies have shown that the eradication of a single apex predator species caused dramatic changes in community structure and ecosystem functioning (Estes et al. 2011). The canonical theory for such trophic cascades assumes that consumers eat species in only the next level down, causing strong unimpeded top-down forcing (Oksanen et al. 1981). However, many food webs are reticulate, with consumers feeding on species in multiple trophic levels, and contain other complexities that can weaken trophic cascades (Polis and Strong 1996; Finke and Denno 2004; Cuny et al. 2021). Another theoretical assumption is that the system is at equilibrium or at least at a temporary steady state. Conversely, many studies have found that environmental perturbations can lead to substantial variation in the strength of trophic cascades, with important consequences for the food webs in which they are embedded (Piovia-Scott et al. 2017a).

Islands can serve as excellent model systems for studying food-web processes for three reasons. First, because they often vary in community composition, comparisons between islands with focal species present or absent can be used as replicated "natural experiments" (Diamond 1983) to test hypotheses on the functional role of those species in the food web. Second, island communities have fewer species and less spatial heterogeneity than mainlands, increasing the feasibility of identifying the key drivers of food-web dynamics (Wardle 2002). Third, islands are well-defined isolated areas and thus can be used as independent replicates in manipulative experiments designed to test food-web theory (e.g., Hambäch et al. 2004).

We have been studying food-web interactions on Bahamian islands for over 40 years. Our early studies focused on the top-down effects of predatory lizards on species in lower levels during a time period (throughout the 1980s and early 1990s) when no hurricane had a major impact on any of our study sites. Subsequently (1996 to present) hurricane frequency has increased substantially (Goldenberg et al. 2001; Kossina et al. 2020), and several hurricanes have passed directly over or close to our study islands, having devastating impacts on their communities. In the first section of this chapter, we will summarize our early studies on the basic structure and dynamics of our study system, focusing on how food-web complexity influences the cascading effects of lizards. The following sections will delineate the effects of hurricanes and allochthonous resource pulses on food-web dynamics, centering on how bottom-up processes associated with these environmental perturbations influence the trophic cascade at different time scales.

10.2 Food-Web Structure and Dynamics

To investigate the effect of predatory lizards on species in lower trophic levels, we used two complementary methods: (1) comparative studies on small islands with lizards present and absent and (2) experimental studies in which lizard densities were manipulated within enclosures on a large island and lizard introductions onto small islands initially without them. The most abundant lizard on our study islands is *Anolis sagrei*, a small species which eats a wide variety of arthropods, including carnivores, herbivores, and detritivores (Schoener 1968; Pringle et al. 2019). Observational and manipulative studies therefore centered on this species unless stated otherwise.

10.2.1 Comparative Studies

We began by counting annually the number of web spiders on approximately 100 islands with lizards either present or absent in the Exuma Cays, an archipelago in the central Bahamas consisting of approximately 50 relatively large islands surrounded by hundreds of smaller islands where we counted the spiders (Fig. 10.1). Analysis of the first two annual censuses showed that web-spider density was about ten times higher on no-lizard than on lizard islands (Schoener and Toft 1983; Toft and Schoener 1983), suggesting that lizards have a strong negative effect on spiders. Subsequent experimental work corroborated this causal link (Spiller and Schoener 1988, 1994), and long-term studies revealed that the interaction strength of lizards on spiders was related to island area (Schoener et al. 2016) and annual variation in the interaction strength was related to rainfall (Spiller and Schoener 1995, 2008).

These results prompted us to ask, does the top-down effect of lizards propagate further down the food-web? Because lizards feed on both carnivorous spiders and herbivorous arthropods and spiders eat herbivorous arthropods, lizards are "intraguild predators" (Polis et al. 1989). We proposed two different models in which the top-down effect of lizards on plants could be either positive or negative, depending on the relative interaction strength of lizards vs. spiders on herbivores (Fig. 10.2). In Model A the effect of lizards on herbivores is stronger than the effect of spiders on herbivores; the dominant pathway has two links connecting three trophic levels, and thereby the indirect effect of lizards on plants is positive. In Model B the effect of spiders on herbivores is stronger than the effect of lizards on herbivores; the dominant pathway has three links connecting four trophic levels, and thereby the indirect effect of lizards on plants is negative.

To investigate the indirect effect of lizards on plants (via herbivory), in 1984, we measured the amount of leaf damage on *Conocarpus errectus* (buttonwood), one of the most common species on our study islands. Buttonwood occurs as two different color morphs with "silver" or "green" leaves, containing high and low density of trichomes, respectively. Silver and green morphs are often intermingled on the same island. We collected large samples of leaves on 74 islands with lizards either present

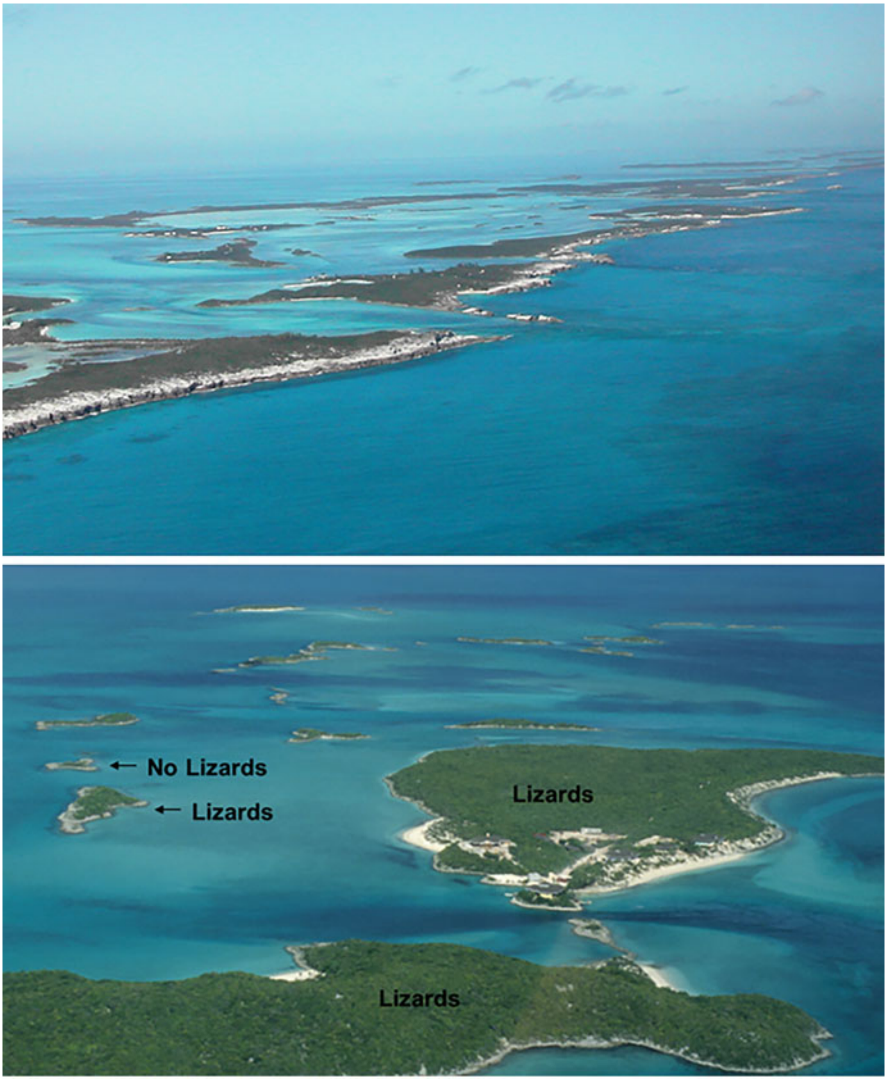


Fig. 10.1 *Top*: Aerial photograph of the Exuma Cays, an archipelago in the central Bahamas consisting of approximately 50 relatively large islands surrounded by hundreds of smaller islands. *Bottom*: A closer view of a segment of the Exuma Cays. Lizards were present on all large islands and were present or absent on small islands. Photographs taken by David Spiller

or absent and measured percent of leaf area damaged in the lab (Schoener 1988). Results showed that leaves were 1.5 times more damaged on no-lizard islands than on lizard islands, supporting Model A (Fig. 10.2), and green leaves were 1.4 times more damaged than silver leaves, indicating that the top-down effect of lizards and plant defense are equally important factors controlling herbivory. Web-spider

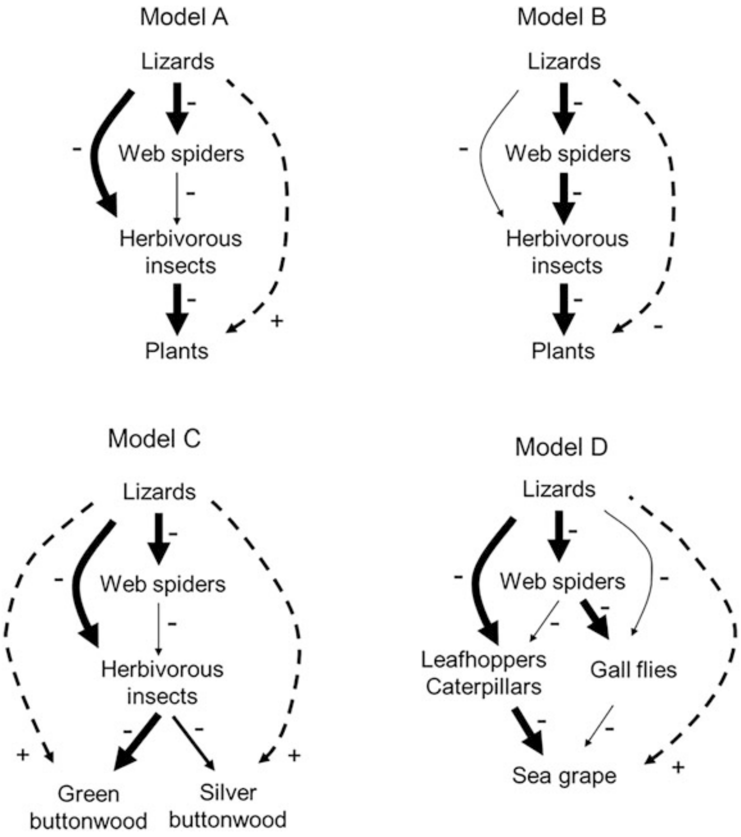


Fig. 10.2 Food-web interaction modules with intraguild predation in which lizards eat web spiders, and both lizards and web spiders eat herbivorous insects. Solid lines represent direct effects proportional to their thicknesses. Dashed lines represent the indirect effect of lizards on plants. In Model A the effect of lizards on herbivores is stronger than the effect of web spiders on herbivores, and thereby the indirect effect of lizards on plants is positive. In Model B the effect of lizards on herbivores is weaker than the effect of web spiders on herbivores, and thereby the indirect effect of lizards on plants is negative. Model C represents our interpretation of the comparative study on small islands of buttonwood leaf damage for green and silver color morphs containing leaves with low and high densities of trichomes, respectively. Model D is our interpretation the enclosure-experiment results in which the effect of lizards on leafhoppers and caterpillars is strong, whereas the effect of web spiders on gall flies is strong (see text for more explanation)

density was not correlated with leaf damage (Schoener 1988), indicating that the effect of lizards on herbivory is stronger than that for spiders, as in Model A. Model C (Fig. 10.2) is our interpretation of this study showing that the negative direct effect of herbivores is stronger for green than for silver morphs. Analysis of variance showed that the effect of lizards on leaf damage did not differ significantly between color morphs, indicating the positive indirect effect of lizards was the same magnitude for the two morphs. In addition to the study of leaf damage, Schoener (1987) found that the frequency of the silver morph was higher on no-lizard islands than on lizard islands, suggesting that chronically greater herbivory on no-lizard islands selected for silver morphs, or induced the production of trichomes. Later lab experiments (Agrawal and Spiller 2004) showed that silver leaves were less damaged than green leaves by two different herbivorous arthropods common on our study islands, an adult flea beetle (*Chaetocnema brunnescens*) and a bagworm lepidopteran (*Biopsyche* sp.).

10.2.2 Field Experiments

We conducted a series of controlled field experiments designed to test the top-down effect of lizards on spiders and plants and to elucidate the mechanisms. In the first experiment, we manipulated lizard density within six enclosures on a large island (Staniel Cay); three enclosures were selected randomly to have lizards removed and the other three had lizards present at their natural density serving as controls. The study site was located on a sandy bluff covered with dense scrubby vegetation 0.5–1.5 meters high, predominately *Coccoloba uvifera* (sea grape). During the experiment (May 1985 to November 1988), we counted numbers of web spiders at about 3-month intervals and measured amounts of damage that accumulated on large samples of sea grape leaves tagged each year**.**

Results showed the mean number of web spiders was three times higher in lizard-removal enclosures than in controls with lizards (Spiller and Schoener 1988). Dietary analysis of lizards and web spiders in the enclosures showed a moderate overlap in the size distribution and taxonomic composition of arthropods, but there were significant differences. Lizard diets contained larger arthropods and more Homoptera and Lepidoptera (which are predominantly herbivorous) than web-spider diets (Spiller and Schoener 1990a). Araneae (spiders) were frequently eaten by lizards, but not by web spiders. Lizards reduced food consumption by *Metepeira datona* (the most abundant web-spider species), and the reduction was stronger for large prey (>4 mm body length) than for small prey (≤4 mm). Lizards also reduced the biomass of large arthropods caught in aerial sticky traps, but not the biomass of small arthropods. These results revealed that lizards are both predators and competitors of web spiders and thereby intraguild predators, having both direct and indirect negative effects on web spiders. We suggest that the direct effect of predation by lizards is stronger than competition because they greatly reduced short-term survivorship of web spiders (Spiller and Schoener 1988, 1990a).

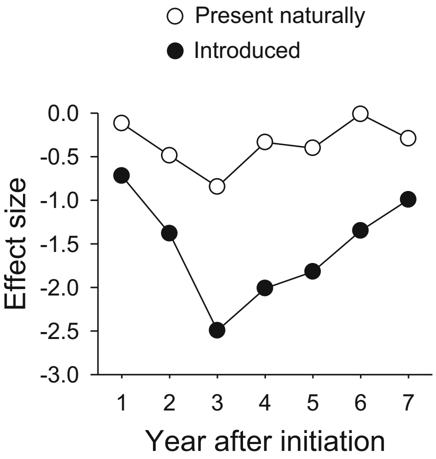
We analyzed three different categories of leaf damage: scars (necrotic areas), holes (entirely missing areas), and galls (Spiller and Schoener 1990b). In the field we observed scars produced by homopterans (leafhoppers) and holes produced mostly by caterpillars; galls were produced by the cecidiomyiid midge *Ctenodactylomyia watsoni*. Scar damage was 2.2 times higher in lizard-removal enclosures than in controls. Hole damage was 1.7 times higher in lizard-removal enclosures than in controls. In contrast, gall damage was 1.7 times higher in controls with lizards than in lizard-removal enclosures. Total leaf damage was 2.0 times higher in lizard-removal enclosures than in controls. We suggest that the effect of lizards on leafhoppers and caterpillars was strong relative to the effect of spiders because these relatively sedentary herbivores are easily caught by lizards, but not in spider webs, whereas the effect of web spiders on gall flies (searching for oviposition sites) was stronger because they are frequently caught in spider webs but not by lizards. We propose that because web-spider density was higher in lizard-removal enclosures than in controls, reduced gall damage in removals was caused by higher predation by web spiders. Our experimental results can be delineated by a composite of Models A and B (Model D, Fig. 10.2). Because scars and holes accounted for most of the total leaf damage, lizards reduced total herbivory, thereby having a positive effect on sea grape.

To tease apart the effects of lizards and web spiders, we conducted a 2 × 2 factorial enclosure experiment with four treatments ($n = 3$ for each): (1) Controls with lizards and spiders unaltered (natural densities), (2) lizards removed and spiders unaltered, (3) spiders removed and lizards unaltered, (4) both lizards and spiders removed (Spiller and Schoener 1994). This experiment was conducted on Staniel Cay, the large island where the previous experiment was performed. The experiment ran from 1989 to 1992 and data collection followed the same procedures as described for the previous experiment. Results showed that spider density was 1.5 times higher in lizard-removal enclosures than in controls. Web spiders reduced the biomass of small arthropods (mostly flies) caught in aerial sticky traps. Hence, by reducing web-spider density, lizards had an indirect positive effect on small flies. Total leaf damage was 3.3 times higher in treatments with lizards removed than in those with lizards unaltered. We found no significant effect of web spiders on any type of leaf damage. An objective of the experiment was to test the direct negative effect of web spiders on gall flies, as depicted in Model D (Fig. 10.2). However, galls were extremely rare during this experiment, making it unfeasible to detect the effect of web spiders.

We used a system of small islands located in the Abacos (northern Bahamas) to conduct a seven-year experiment to test the direct and indirect effects of introducing the lizard *A. sagrei* on the food web (Schoener and Spiller 1996, 1999). Eight islands without lizards were blocked into four pairs, according to vegetated area (amount of land covered by vegetation), and lizards were introduced onto one island (selected randomly) from each pair. The experiment included four other islands containing lizards naturally (one in each block) that were used to ascertain if and when the food-web elements on the introduction islands converged to those with lizards present naturally. Lizard introduction caused a rapid and devastating effect on web-spider density; within 2 years web-spider density on introduction islands converged to about the same level as on islands with lizards present naturally and remained there until the end of the experiment (Schoener and Spiller 1996). During the last 6 years of the experiment, mean web-spider density was 80% lower on islands with lizards introduced than on no-lizard islands and was 86% lower on islands with lizards present naturally than on no-lizard islands.

We measured herbivory on buttonwood which occurred on all the study islands (Schoener and Spiller 1999). The trajectory of total leaf damage on introduction

Fig. 10.3 Effect sizes of lizards on leaf damage computed as ln (mean damage on islands with lizards present [naturally or introduced]/ mean damage on islands without lizards)



islands was intriguing. Three years after initiation of the experiment, leaf damage plummeted on introduction islands and was 92% lower than on no-lizard islands; surprisingly, at this time leaf damage was 57% lower on introduction islands than on islands with lizards present naturally. Towards the end of the experiment, leaf damage in the two treatments with lizards (present naturally and introduced) started to converge. Figure 10.3 shows the stronger effect size of lizards on introduction islands than on islands with lizards present naturally, which maximized 3 years after initiation of the experiment. We posit that initially islands without lizards contained herbivorous insects that lacked antipredator traits and thereby were more vulnerable to lizards than those on islands with lizards present naturally where the vulnerable herbivores had been depleted by lizards. We suggest that when lizards were first introduced onto no-lizard islands they feasted on the vulnerable herbivores, causing amounts of leaf damage to drop below the level on islands with lizards present naturally (which contained fewer vulnerable herbivores). Then after several years most of the vulnerable herbivores were depleted on the introduction islands, which were replaced by less-vulnerable herbivores, and leaf damage converged to the level on islands with lizards present naturally.

The number of large arthropods (>4 mm body length) caught in aerial sticky traps did not differ significantly between treatments, but the number of small arthropods (≤4 mm) was significantly higher on islands with lizards than those without lizards. A separate analysis of hymenopteran parasitoids, which were predominantly small (usually 1–2 mm), showed they were significantly more abundant on islands with lizards than those without lizards (Schoener et al. 1995). In a later experiment at the same site (Schoener et al. 2002), we found a negative correlation between parasitoid abundance and web-spider density, suggesting that higher web-spider density on no-lizard islands reduced parasitoid abundance. Hence, because parasitoids often prey on herbivorous insects, web spiders may have both a direct negative effect on herbivorous insects and an indirect positive effect via their negative effect on parasitoids. This may be one reason why the effect of web spiders on total herbivory is weak.

10.3 Hurricanes

In October 1996, we had just finished our annual survey of the biota inhabiting small islands located offshore the north and south sides of the very large island Great Exuma, when the eye of Hurricane Lili pasted directly over the study site (Spiller et al. 1998). Because Lili's approach was from the southwest, islands on the south side of Great Exuma were exposed to the full force of the storm surge, the most destructive component of the hurricane, whereas islands located on the north side were much more protected. The surge removed most of the standing biomass of vegetation on the exposed islands, whereas damage to the vegetation on the protected islands was minimal. In the week following the storm, we found that all lizard and spider populations were exterminated on exposed islands; in contrast, no lizard population and only small populations of spiders were exterminated on protected islands.

As part of an ongoing food-web study, we had measured amounts of leaf damage on buttonwood for three consecutive years before the hurricane (Spiller and Agrawal 2003). During the hurricane, all study shrubs on exposed islands were reduced to stumps by the surge and regenerated by sprouting during the following year. Damage on the sprouted foliage was high and we frequently found moth larvae (*Collomena filifera* and other unidentified species) consuming the leaves. Some shrubs were completely defoliated, and a few which were defoliated repeatedly apparently died due to herbivory following the hurricane rather than by the direct impact from the hurricane. We observed that on exposed islands buttonwood with silver leaves before the hurricane sprouted green leaves the year after and then reverted to producing silver leaves the following year. In addition, the sprouted foliage appeared to be very lush, possibly because the leaves were larger, more tender or contained more nitrogen. Measurements of leaf damage before and after the hurricane showed that herbivory increased on devastated islands exposed to the storm surge but not on relatively undamaged shrubs on protected islands, suggesting that foliage sprouting on severely damaged shrubs was more susceptible to herbivores than new foliage on undamaged shrubs. Abundance of moths caught in sticky traps on exposed islands was very low a few months following the hurricane and then increased markedly after 12 months. We hypothesized that increased herbivory on exposed islands was caused by two factors: low predator abundance and increased susceptibility to herbivory of leaves on damaged shrubs.

To test the second factor, we conducted a controlled field experiment: Hurricane damage was simulated by pruning shrubs on replicated islands (Spiller and Agrawal 2003). The experiment showed that herbivory was significantly higher on pruned shrubs than on unaltered control shrubs. Leaf size was larger, percent nitrogen was higher, and leaf toughness and trichome density were lower on pruned shrubs than on controls. The experimental results indicate that enhanced herbivory on exposed

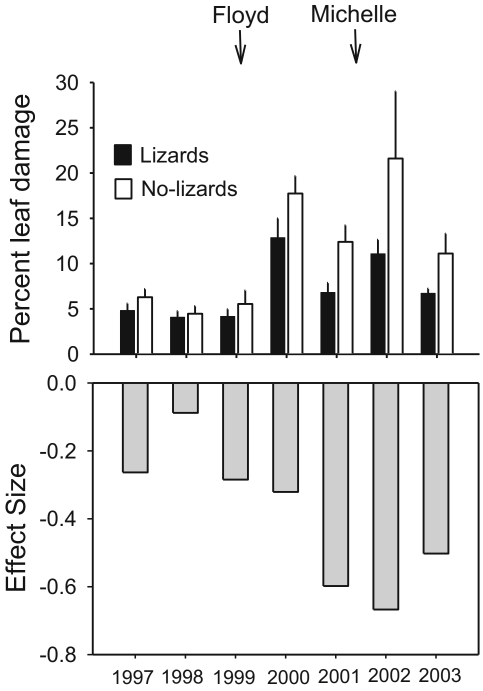


Fig. 10.4 *Top*: Mean percent of total leaf area damaged on islands with and without lizards before and after hurricanes Floyd and Michelle struck the study site. Error bars are standard errors. *Bottom*: Effect sizes of lizards on leaf damage computed as in (mean damage on islands with lizards/mean damage on islands without lizards)

islands following Hurricane Lili was caused, at least in part, by increased susceptibility of the sprouted foliage to herbivorous arthropods, but the reduction of predators may have also been important.

We also conducted long-term food-web studies on small islands in a semi-protected bay offshore Great Abaco which took a direct hit by Hurricane Floyd in September 1999. Lizards were exterminated on some but not all of the study islands. Leaf damage on buttonwood was measured before and after the hurricane on islands which either had lizards present or absent continuously both before and after the hurricane (Spiller and Schoener 2007). The year after Floyd, leaf damage increased on both lizard and no-lizard islands. In 2001 the site was hit by Hurricane Michelle and leaf damage increased again the following year (Fig. 10.4, top). The negative effect size of lizards on herbivory was 2.5 times stronger during the disturbance period (2000–2003) than before (Fig. 10.4, bottom). Overall abundance of lizards was 30% lower during the disturbance period than before, and abundances of web spiders and hymenopteran parasitoids were respectively 66% and 59% lower. We suggest that increased herbivory observed on all islands was caused, at least in part, by the overall reduction in predation by both lizards and arthropods; increased herbivory could have also been caused by increased susceptibility of the foliage to herbivory (as found in Spiller and Agrawal 2003), but that factor was not tested in the study. We hypothesize that magnification of the lizard effect on herbivory following disturbance was caused by reduced compensatory predation by arthropods on islands without lizards. A second hypothesis is that herbivores colonizing islands following the disturbances were more vulnerable to lizard predation than those present before the disturbances. The generality of the second hypothesis will be discussed below (Sect. 10.5.2).

In a third study, we focused on the effect of the moth *Achyra rantalis* feeding on the plant *Sesuvium portulacastrum* on small islands with and without lizards in the Exuma Cays (Spiller et al. 2016). The plant is a fast-growing prostrate vine inhabiting shorelines, and consequently moths are highly vulnerable to being consumed by lizards which frequently forage close to the ground. Measurements of moth abundance were on average > 4 times higher on no-lizard than on lizard islands. The site was impacted by Hurricanes Floyd and Michelle; the centers of the storms passed nearby causing moderate disturbance. Lizards were not exterminated on any study islands, but large proportions of the study plants growing on shorelines were washed away. Immediately following each hurricane percent cover over the ground by *S. portulacastrum* was reduced to about the same low level on all islands. However, regrowth rate following Floyd and Michelle was significantly higher on lizard islands than on no-lizard islands, presumably caused by lizards controlling moths after the hurricanes. Moths were much more abundant on no-lizard islands and were observed infesting plants following the hurricanes, apparently impeding regrowth of vines on the damaged plants. In fact, on some no-lizard islands where moths were exceptionally abundant, percent cover decreased further the second year after the disturbances, which was evidently caused by intense herbivory on the remaining vines. Hence, lizards increased the recovery rate ("ecological resilience" sensu Pimm 1991, Gunderson 2000) of the plants.

10.4 Marine Subsidies

The influence of resource subsidies (the flow of nutrients and organisms across habitat or ecosystem boundaries) on recipient food webs has received a bourgeoning amount of attention (Polis et al. 1997, 2004; Marczak et al. 2007; Leroux and Loreau 2008; Subalusky and Post 2019; Scherer-Lorenzen et al. 2022). Resource subsidies may vary temporally, arriving in pulses (Yang et al. 2008, 2010), which can produce a variety of effects on recipient food webs (Anderson et al. 2008; Holt 2008; Takimoto et al. 2009; Leroux and Loreau 2012).

In the Bahamas, large amounts of seaweed are deposited on shorelines in the fall following tropical storms and early cold fronts. We hypothesized that this seaweed deposition represents a pulsed resource subsidy (sensu Sears et al. 2004, Yang et al. 2008) that is consumed by detritivores, which are eaten by predatory lizards; those predators also consume terrestrial herbivores. Additionally, seaweed washed high onshore during storms may decompose directly into the soil and fertilize plants. We hypothesized that the marine-based resource pulse would enhance terrestrial herbivory in the short-term when the lizards switch from eating herbivores to marine detritivores, weakening the trophic cascade from lizards to plants. In the long-term, we hypothesized that lizards would respond numerically to marine subsidies

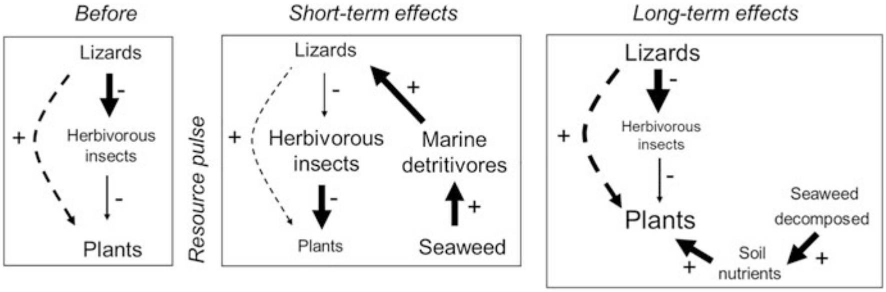


Fig. 10.5 Food-web modules showing the hypothesized short-term and long-term effects of a resource pulse (seaweed deposition). Solid lines represent direct effects proportional to their thicknesses. Dashed lines represent the indirect effect of lizards on plants (a trophic cascade). For each food-web element, the change in font size is proportional to its change in abundance over time. *Before the pulse*: A moderate top-down effect by lizards on herbivorous insects leads to a moderate trophic cascade. *Short-term effects*: Lizards switch to eating mostly marine detritivores, leading to increased herbivores, and thereby weakening the trophic cascade. *Long-term effects*: Lizards proliferate due to a delayed reproductive response, caused by consumption of copious detritivores in the past. The seaweed becomes decomposed and marine detritivores die off, and subsequently the lizards switch back to eating mostly herbivores, strengthening the trophic cascade. Also, the decomposed seaweed adds nutrients to the soil, fertilizing the plants

and then switch back to eating mostly herbivores as the marine detritivores decline, strengthening the trophic cascade. These hypotheses are depicted in Fig. 10.5.

We tested our hypotheses on large islands in the Exumas where we added seaweed to six shoreline plots and removed seaweed from six other plots for 3 months during fall 2006; all plots were repeatedly monitored for 12 months after the initial manipulation (Spiller et al. 2010). Three months after the initial manipulation, biomass of amphipods (the major marine detritivores) was 79 times higher in plots with seaweed added than in plots with seaweed removed, and lizards were observed eating the amphipods. Stable isotope analysis revealed a shift in lizard diet composition toward more marine-based prey in subsidized plots. Wright et al. (2013) showed that lizard individual growth rate was higher in subsidized plots. Buttonwood leaf damage was 70% higher in subsidized than in removal plots after 8 months, but subsequent damage was about the same in the two treatments. After 12 months, buttonwood leaf nitrogen content was 18% higher and foliage growth rate was 70% higher in subsidized plots. We suggest two sequential causal pathways for the effects of marine subsidies on terrestrial plants: (1) *The predator-diet-shift effect*: Lizards shift from eating local prey (including terrestrial herbivores) to eating mostly marine detritivores, leading to increased herbivory and thereby weakening the trophic cascade from lizards to plants and (2) *The fertilization effect*: Seaweed adds nutrients to plants, increasing their growth rate (Spiller et al. 2010). Because herbivory did not become lower in subsidized plots than in unsubsidized plots during the course of the experiment, there was no evidence that marine subsidies strengthened the trophic cascade in the long-term (as depicted in Fig. 10.5), possibly because the experiment needed to run for a longer period of time. Predatory arthropods also increased in the subsidized plots, including the large ant *Camponotus tortuganus*. Buttonwood petioles contain extrafloral nectaries that attract ants which in turn eat herbivorous arthropods (Piovia-Scott 2011). Hence, reduced leaf damage in subsidized plots may have been caused by both lizards and ants switching to eating mostly marine detritivores.

To test the interactive effects of marine subsidies on predation by lizards and ants, we conducted an experiment (Piovia-Scott et al. 2011) on 12 small islands in the Exumas. Lizards were present on six islands and absent from six islands, and seaweed treatments (added or removed) were assigned to half the islands with and without lizards. On each island, 11–12 buttonwood branches were randomly assigned to have ants excluded with Tanglefoot® adhesive or unaltered. After 7 months, the experiment showed that on islands without marine subsidies, the effect of only lizards or only ants on leaf damage was weak, but with both together leaf damage was markedly reduced. The effect size of both predators together was three times the additive effects of each one alone, making the interactive effect of lizards and ants synergistic (Sih et al. 1998). We suggest that the synergistic effect was linked to temporal partitioning of activity time by the two predators; lizards (*A. sagrei*) are diurnal whereas the dominant ants (*C. tortuganus*) are nocturnal. Hence, herbivores could avoid *A. sagrei* by feeding at night and avoid *C. tortuganus* by feeding during the day, but they could not allocate activity times to avoid both types of predators. Lizards did not affect the abundance of ants, implying that temporal partitioning may reduce the frequency of antagonistic interactions between the different predators. On islands with marine subsidies, lizards and ants alone tended to reduce leaf damage, but the synergistic effect on herbivory was eliminated, presumably because both lizards and ants switched from eating herbivores to eating marine detritivores, as found in the previous experiment. In this experiment there was no evidence that marine subsidies strengthened the trophic cascade in the long-term (as depicted in Fig. 10.5), but again this experiment may have not run long enough to reveal this process.

To test the short and long-term effects of marine subsidies, we conducted a 5-year experimental study on 32 small islands in Abaco (Piovia-Scott et al. 2019; Wright et al. 2020). In this experiment, we manipulated the frequency and magnitude of pulses of seaweed deposition on islands with or without experimentally introduced populations of lizards. There were four seaweed input treatments: (1) a single large addition in the first year, (2) three small annual additions (adding up to the same total as the single large addition), (3) three large annual additions, and (4) controls with no seaweed input. In the short-term (the first year of the experiment), inputs of marine subsidies weakened the effect of lizards on buttonwood leaf damage and growth, presumably associated with a lizard diet shift from herbivores to marine detritivores. This short-term weakening of cascading effects on plants was more pronounced in treatments with higher subsidy magnitude (1 and 3). However, in the long-term (after the first year), inputs of marine subsidies strengthened the lizard effect on leaf damage and growth. This long-term effect was more pronounced in the high frequency input treatments 2 and 3. We posit the long-term effect operates via two pathways: (1) a numerical response by lizards (Wright et al. 2020) and (2) plant fertilization, whereby increased quality of foliage for herbivores leads to increased herbivory on no-lizard islands, but not on islands with lizards. This occurs because herbivores are free to respond numerically to fertilization on no-lizard islands, but not on islands with lizards which keep herbivores at a low level. Note that this explanation is consistent with the exploitation ecosystems hypothesis (Oksanen et al. 1981).

In addition to these experiments, we conducted a comparative study of natural variation in seaweed deposition and terrestrial food-web components using 29 shoreline plots located on large islands in the Exumas. Results of this study showed lizard density, leaf damage and nitrogen content, and foliage growth were significantly higher in plots with high amounts of subsidies than in those with low amounts of subsidies (Spiller et al. 2010). The natural variation in seaweed deposition appeared to be habitual, linked to topographical features of the shoreline plots. Hence, in this case the seaweed deposition "treatment" occurred more like a continuous long-term press than a pulse. A path analysis on leaf damage provided evidence that marine subsidies enhanced the top-down effect of lizards on plants (seaweed increases lizard abundance which increases their effect on herbivory); however, the bottom-up fertilization effect was stronger than the top-down lizard effect (Piovia-Scott et al. 2013).

10.5 Discussion

10.5.1 Food-Web Structure of the Study System

The results of our studies, taken together, provide compelling evidence that predatory lizards reduce herbivory and thereby have a positive effect on plants, even though lizards also reduce web spiders which eat herbivores. We conclude that the effect of lizards on herbivores is stronger than the effect of web spiders on herbivores because the major herbivores are more vulnerable to lizards than to web spiders. Dial and Roughgarden (1995) studied the effects of *Anolis* lizards on a large, complex food web of arthropods and associated herbivory in a Puerto Rican rain forest. They removed several arboreal *Anolis* species (mostly *A. evermanni* and *A. stratulus*) from the canopy of seven tabonuco trees (22–29 meters in height!); seven similar tabonuco trees with *Anolis* present at their natural densities were the controls. The experiment showed that lizards reduced the abundance of both predacious and herbivorous arthropods and reduced the frequency of leaf damage. Several lines of evidence indicate that higher herbivory in lizard-removal trees was caused by greater abundances of large herbivorous arthropods which were eaten more frequently by lizards than by predatory arthropods which typically ate smaller prey. The results obtained in Dial and Roughgarden's field experiment are remarkably similar to our findings, even though their study was conducted on a much larger island with a more complex food web.

Mooney et al. (2010) performed a meta-analysis on 113 experiments (predominantly on mainlands) documenting the effects of insectivorous vertebrates on predacious arthropods, herbivorous arthropods, and plants. They predicted that because insectivorous vertebrates are intraguild predators, feeding on both predacious and herbivorous arthropods and predacious arthropods feed on herbivores, the effect of the vertebrate predators on predacious arthropods should be stronger than their effect on herbivores. However, they found that the effect of vertebrate predators was on average about the same for predacious and herbivores arthropods, and they indirectly reduced plant damage and increased plant biomass. This and other analyses indicated that intraguild predation does not weaken the trophic cascade, as expected according to some theory (Mooney et al. 2010). We contend that effects of insectivorous vertebrates on predacious arthropods, herbivorous arthropods, and plants are generally consistent with Model A (Fig. 10.2).

Body size appears to play an important role in structuring food webs (Schoener 1989; Petchey et al. 2008; DeLong et al. 2015). We posit that top-down effects of vertebrate predators are usually stronger than arthropod predators because vertebrate predators are larger, and thereby can eat a broader range of herbivorous arthropods, including those that are too big for most predacious arthropods. In addition, because they are generally smaller than vertebrates, arthropod predators are eaten by a wider range of predators and are more susceptible to physical disturbances caused by the weather which frequently reduce their abundance, weakening their top-down effect (Schoener and Spiller 2003). Social ants may be the exception that proves the rule (Mooney 2007; Piovia-Scott 2011). Cooperative foraging may enable ants to capture prey larger than those captured by solitary predatory arthropods and group defense may protect them from predators.

We did find evidence that intraguild predation by lizards on web spiders caused an indirect positive effect on gall-making flies and other small insects caught in sticky traps which may have slightly weakened the trophic cascade. In addition, Piovia-Scott et al. (2017b) found that lizards reduced the abundance of other predatory arthropods. However, intraguild predation may not always dampen the trophic cascade. We found evidence that web spiders reduced the abundance of hymenopteran parasitoids which often prey on herbivores; therefore, lizards may indirectly increase parasitoids by eating web spiders. This four-level interaction chain (lizards-spiders-parasitoids-herbivores) within the food web may strengthen the trophic cascade from lizards to plants.

Furthermore, interactions between different types of predators may not always be antagonistic, dampening the trophic cascade. We found that the effects of diurnal lizards and nocturnal predatory ants on plants were synergistic (Piovia-Scott et al. 2011), possibly because herbivorous arthropods had no “escape in time” from predation. Synergistic effects of multiple predators on prey may also be caused by different predators foraging in different places within the prey’s habitat (Sih et al. 1998). We suggest that on our study islands overall levels of herbivory are controlled by a suite of predator species preying upon multiple herbivore species.

10.5.2 Temporal Variability in Food-Web Dynamics

Numerous abiotic and biotic factors can change food-web dynamics at different time scales (Piovia-Scott et al. 2017a). We found that food webs on Bahamian islands were profoundly impacted by two exogenous factors, hurricanes and allochthonous resource pulses. Both of these factors can play a major role in structuring island communities (Whittaker 1995, 2000; Polis et al. 1997, 2004; Fukami et al. 2006) and as discussed below can produce major temporal fluctuations in food-web dynamics.

Following hurricanes, herbivory increased substantially in all of our studies (Spiller and Agrawal 2003; Spiller and Schoener 2007; Spiller et al. 2016). We propose that these high levels of herbivory following hurricanes were caused by two factors. The first is increased susceptibility to herbivorous arthropods of resprouted foliage on severely damaged plants, which is linked to increased nitrogen and reduction of defensive traits (Spiller and Agrawal 2003). Other studies have found that plants heavily damaged by physical disturbances were more susceptible to herbivory, including resprouting plants on the bank of a river following a major flood (Nakamura et al. 2005, 2006) and resprouting plants following fire (Stein et al. 1992; Knapp et al. 1999). The second factor causing higher herbivory following hurricanes is a reduction in predators. Following catastrophic disturbance by Hurricane Lili on exposed islands, all predators were exterminated (Spiller et al. 1998), giving the colonizing herbivores a “predator-free window in time.”

In addition to increased herbivory, we found that following moderate disturbances by hurricanes, when lizards were not exterminated, the top-down effect of lizards on leaf damage was stronger after hurricanes than before (Fig. 10.4). We suggest that herbivores colonizing islands following the disturbances were more vulnerable to lizard predation than those present before the disturbances. There may be a trade-off between dispersal ability and vulnerability to predators among herbivore species. For example, studies of river food webs following scouring floods (Wootton et al. 1996; Power et al. 2008) showed that early herbivorous colonizers, such as tuft-weaving midges and mayflies, are more vulnerable to predators than later arriving herbivores, such as armored caddisflies; subsequently, when predators arrive they deplete the vulnerable herbivore species and the river becomes dominated by the protected herbivore species. In addition to a change in species composition, when predators colonize an area they may cause phenotypic changes in herbivore traits within species that decrease their vulnerability (e.g., they spend more time avoiding predators and less time feeding), known as a trait-mediated indirect effect (Schmitz et al. 2004; Schoener and Spiller 2012). Furthermore, natural selection may favor herbivore individuals that are less vulnerable to predators but also less efficient at consuming plants, leading to a rapid eco-evolutionary response (Schoener 2011). These processes may also be applicable to the results of our lizard introduction experiment on small islands in which the effect size of introduced lizards on leaf damage was initially much stronger than the effect size of lizards naturally present (Fig. 10.3). We suggest that before introduction these islands contained naïve herbivores vulnerable to lizard predation, which were devoured by lizards within a few years, and subsequently the effect size decreased.

Spiller et al. (2018) proposed a mechanistic conceptual framework for how food webs recover from natural physical disturbances, based on our island studies and empirical studies on other types of physical disturbances (including fires, floods, and volcanic eruptions). We found evidence for a general pattern of island food-web succession generated by two processes: 1) Sequential recovery/colonization of successively higher trophic levels. This creates "herbivore-free time" for rapid plant growth and subsequent "predator-free time" for herbivores and 2) tradeoffs between successional stage and susceptibility to consumers in which early successional species (or phenotypes within a species) are more susceptible than later successional species (or phenotypes). Thus as consumer species colonize an island, they may change the species or phenotypic composition of their food supply from highly productive and vulnerable items to less productive and vulnerable items, thereby weakening both bottom-up and top-down effects in the food web.

Allochthonous resource pulses in the form of seaweed deposition events have multiple temporally varying effects on Bahamian island food webs. In the short-term, all of our experiments found evidence for the "predator-diet-shift effect" in which lizards shift from eating local prey (including terrestrial herbivores) to eating mostly marine detritivores, leading to increased herbivory and thereby weakening the trophic cascade from lizards to plants (Spiller et al. 2010; Piovia-Scott et al. 2011, 2019). In the long-term, we found evidence for two other mechanisms: 1) The "fertilization effect" in which seaweed adds nutrients to plants, increasing their growth rate (Spiller et al. 2010), as well as increasing herbivory (Piovia-Scott et al. 2013) and 2) a numerical response by lizards to marine subsidies strengthens the trophic cascade from lizards to plants (Piovia-Scott et al. 2019). Hence, allochthonous resource pulses can cause a sequential series of bottom-up and top-down effects that propagate throughout the food web.

In the Bahama Islands, the most significant seaweed deposition events occur during hurricanes when massive amounts of seaweed are washed high upon the shoreline into the vegetation. By providing nutrients to the plants and prey subsidies to the secondary consumers, such events occurring at a low frequency may have a favorable impact on island communities in the long term. However, in the short term, we have found that herbivory increases following hurricanes via increased susceptibility to herbivores of the foliage on severely damaged plants and following seaweed deposition when predators switch from eating herbivores to marine detritivores. In addition to the recent increase in hurricane frequency and intensity, which is expected to continue due to climate change (Kossina et al. 2020), during the last decade there has been a dramatic increase in the amount of *Sargassum* seaweed in the Atlantic Ocean with unprecedented amounts washing ashore more and more frequently (Rafael et al. 2019; Wang et al. 2019). Hence, the compounding effects of increasing frequency of hurricanes and seaweed deposition may lead to chronic intense herbivory on islands, particularly when hurricanes reduce predator abundances.

During this time of increasing frequency of many types of disturbances, strategies for sustainable management of ecosystems should focus on maintaining resilience (Pimm 1991; Gunderson 2000; Pace et al. 2015). We have found that predators increase the recovery rate of producers following disturbance, implying that maintaining key species interactions embedded within food webs may mitigate the negative impacts of global change on island ecosystems.

10.6 Conclusions

We have found that predatory lizards reduce herbivory and thereby have a positive indirect effect on plants on Bahamian islands. Food-web complexity can influence the cascading effects of lizards. For example, intraguild predation by lizards on spiders (which also eat herbivores) may weaken the cascade. However, interactions between different types of predators may not always be antagonistic, dampening the trophic cascade. We found that the positive effects of diurnal lizards and nocturnal predatory ants on plants were synergistic, possibly because herbivorous arthropods had no "escape in time" from predation. Two exogenous factors, hurricanes and allochthonous resource pulses, play a significant role in structuring island communities and produce major variation in food-web dynamics.

Acknowledgements We thank A. Agrawal, J. Kolbe, J. Losos, L. Morrison, G. Takimoto, C. Toft (deceased), A. Wright, and L. Yang for their collaboration. We were kindly assisted in Abaco by the Pinder family and Friends of the Environment and in the Exumas by the people of Staniel Cay and N. Bottomley. We extend our gratitude to The Bahamas Ministry of Agriculture and Fisheries for permission to conduct this research and National Science Foundation and University of California, Davis for support.

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Impact of Predators on Arthropod Herbivores and Herbivory along Mountain Ranges on Islands Versus Mainland

11

Katerina Sam, Anna Mrazova, Marketa Houska Tahadlova, Jan Kollross, and Heveakore Maraia

Abstract

Trophic interactions between plants, herbivorous arthropods, and their predators are complex and prone to trophic cascades. Understanding these interactions is important, yet they received little attention especially for marine islands. Nevertheless, marine islands offer systems where species interactions are tractable, and their underlying drivers can be explicitly assessed. Herbivory and predation rate are expected to be lower on islands relative to mainland given the lower abundance and diversity across trophic levels. In addition, herbivory and predation are expected to be higher at low elevations due to reduced abiotic stress and more stable abiotic conditions. However, elevational clines in biotic and abiotic conditions may vary on islands relative to mainland, setting the stage for differential gradients on each landform type. Indeed, mountainous islands provide a key opportunity to test how insularity shapes trophic interactions along abiotic clines and departures from these patterns relative to mainland. To address this, we conducted a meta-analysis of predator exclusion studies on both landform types aimed to test for the strength of predation pressure on arthropod communities and herbivory. Our findings indicate that insectivorous vertebrates significantly reduce arthropod abundances and herbivore damage, and such effect was stronger overall on islands than on mainland but did not vary significantly with elevation for either landform type. This latter result could be explained by stronger effects of vertebrates on invertebrate predators at low elevations, thus dampening predator effects on herbivory at low elevation via intra-guild predation. In contrast, mean effects of invertebrate predators, i.e. ants, on herbivory did not differ

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K. Sam (✉) · A. Mrazova · M. Houska Tahadlova · J. Kollross · H. Maraia
Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic

Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic

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_11

between mainland and islands (though significant increases in herbivores and herbivory were found on mainland but not islands), but did show a significant decrease with elevation which was statistically indistinguishable across landform types. Combined, these results show strong contingency in responses based on the type of predator type and counter predictions of weaker top-down control on islands, at higher elevations, and further suggest no qualitative differences in elevational clines in predation pressure across environment types. These findings deserve attention in future mechanistic tests with different types of predation, herbivory, and plant traits.

11.1 Introduction

Marine islands represent unique environments, which are defined as land surrounded by water bodies; that is, smaller than the continent of Australia (Fernández-Palacios et al. 2021; Whittaker and Fernández-Palacios 2007; Whittaker et al. 2017). Although marine islands represent only 7% of the land surface (Sayre et al. 2019), it is estimated that they host ca. 20% of the global biota (Kier et al. 2009). They are hotspots for endemic biodiversity (Kier et al. 2009), due to their origin, unique long-term isolation, ecological dynamics, and occurrence of specific ecological niches. Despite the significant contribution of oceanic islands to global biodiversity and ecological processes (Kueffer and Kinney 2017), existing studies have focused mostly on the survey of insular species richness (Blackburn et al. 2016; Borregaard et al. 2016; Sadler 1999; Whittaker et al. 2014). Investigations of trophic interactions are scarce, although they play a crucial role in global diversity patterns, particularly on islands. For example, the potential loss of endemic species from an island can inevitably impact other trophic levels, similar to the migration of an invasive species to an island. Accordingly, we have a poor understanding of the effects of insularity on species interactions and resulting community structures and ecosystem processes (Hunter 2001; Oksanen and Oksanen 2000).

Islands are often mountainous, with resulting elevational gradients in species interactions and ecosystem functioning. Along the mountain ranges, abiotic factors are fundamental in shaping ecological communities and trophic interactions (Pellissier et al. 2012). Multiple factors change predictably with increasing elevation, shaping species abundance, composition, and richness, though rates of change or even the strength of abiotic clines may vary between mainland and island systems. For example, temperature on mainland decreases by an average of approximately 0.68 °C for each 100 m increase in elevation (Barry and Chorley 2009). Precipitation clines in mainland systems depends on the elevational range, in some cases increasing or decreasing with elevation and in others showing humped-shaped patterns (Pepin et al. 2022). In contrast, island mountains are typically moist and, in some cases, show little variation in precipitation across the elevational gradient (Barry 1992; Whiteman 2000). Other abiotic factors varying with elevation (e.g. condensation zone), and on island vs. mainland, can be important determinants of trophic interactions and lead to different outcomes.

Previous work has reported on differences in elevational clines in species abundance and diversity between mainland and island systems (Grytnes and McCain 2007; Lomolino 2001; McCain and Grytnes 2010). For example, elevational patterns in community structure and species richness on islands often change more steeply than on mainland. The peaks of diversity are typically significantly higher on the islands then on mainland (McCain 2005). Both on islands and mainland, elevational patterns in species richness fall into several common patterns: decreasing, low plateau and mid-elevation peak (McCain and Grytnes 2010). For example, birds, plants, and insects display all four common patterns of elevational species richness—in the case of birds the frequency being evenly distributed (McCain 2009; McCain and Grytnes 2010), whereas for reptiles the predominant pattern is decreasing richness with elevation (McCain 2009). However, differences can be observed also within taxa, with insectivorous birds often following mid-elevational patters and frugivores having highest richness and abundance in lowlands (Sam et al. 2019). On islands, the mid-elevational peaks are pushed to higher elevations, with relatively smaller communities of mountain taxa (McCain 2005). On mainland, the low-elevation plateau or mid-elevation peak at lower parts of the gradients are more typical. Non-flying small mammals (e.g. rodents, shrews, and tenrecs) almost ubiquitously display mid-elevational peaks in diversity (McCain 2005), whereas in flying mammals (i.e. bats), elevational patterns were evenly split between decreasing and mid-elevational peaks (McCain 2007). The fact that different animal species of different abundances meet at certain elevations of islands surely shape top-down forces, i.e. regulation of prey by predators. Simultaneously, specific environmental conditions affect available resources, diversity, and plant characteristics (bottom-up forces) (Hooper et al. 2005).

The study of top-down and bottom-up forces in terrestrial ecosystems has been always a central question in ecology and conservation (Banse 2007; Grange and Duncan 2006; Hunter 2001; Pace et al. 1999; Polis 1999; Terborgh et al. 1999), yet they have been rarely studied along elevational clines. Top-down processes in terrestrial systems can have fundamental effects on population demography and community composition (Ripple et al. 2001; Roemer et al. 2002; Rudolf and Rasmussen 2013). On the other hand, at places where plants are well mechanically or chemically directly protected (i.e. strong bottom-up control), the trophic cascades between predators and produces might be relatively weak. The relative importance of top down to bottom-up forces might be contrasting not only along the elevational gradients, but also between the mainland and islands as predator effects and plant defences are expected to be weaker on islands. However, the understanding of how these biotic interactions along elevational gradients affect community processes is mostly lacking (but see Hunter 2001; Oksanen and Oksanen 2000). This is especially true for insular communities, as they differ from the mainland communities, and receive very limited attention (Martín-Queller et al. 2017).

To fill in these knowledge gaps, we aim to synthesise the effect of vertebrate and invertebrate predators on arthropods and in turn on herbivory damage along elevational gradients and compare such gradients between oceanic islands and mainland. To this end, we performed a meta-analysis of predator exclusion experiments and analysed predator effect sizes on arthropods and herbivory from studies conducted at different elevations on oceanic islands or on mainland.

11.1.1 Arthropod Herbivores, Herbivory, and Plant Defences along the Elevational Gradients of Islands

Herbivorous arthropods comprise a quarter of the total insect species on Earth, including more than nine orders: Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, Phasmida, and Thysanoptera (Shin et al. 2021). The abundance of host plant individuals or plant biomass is the main resource affecting the distribution of arthropod herbivores and their population dynamics (Dempster and Pollard 1981; Marques et al. 2000). Due to the lack of host plants, the relative abundance of herbivorous insects is in general slightly higher on the mainland than on islands (Nilsson and Ebenman 1981). On islands, in contrast to mainland, herbivorous insects cause most of the herbivory damage, as the islands are typically not occupied by large herbivores. Despite their importance, the studies on arthropod herbivores causing leaf damage on marine island plants are rare (but see Arnold and Asquith 2002; Nakamura et al. 2008).

As plants develop defences against herbivores in direct proportion to arthropod herbivory (Janzen 1973; Rhoades 1979), the production of defences decreases when herbivores are absent. Consequently, insular endemic plant species that evolved in the absence of herbivores were predicted to possibly lack defences against herbivory (Terborgh 2009). This hypothesis, although widely accepted, has been rarely tested. Surprisingly, the current state of knowledge fails to consistently support the theory that insular plants are less defended due to the lower abundances and diversity of herbivores on islands. For example, Bowen and Van Vuren (1997) found substantial variation in chemical, structural, and morphological defences between island endemic plants and their closest mainland relatives, with almost all differences were in the direction of reduced defences in island taxa. However, phylogenetically controlled analyses showed that insular plant taxa (endemics and non-endemic natives) invest more in mechanical defences and have a similar content of chemical defences compared to mainland species (Moreira et al. 2021). Naturally, other factors might play a role. For example, a study performed in Korea showed that two herbivorous feeding guilds were affected differently: The external feeder's activity was more explained by the distance of the island from the mainland while the activity of the internal feeder was affected by the area of the island (Shin et al. 2021).

Along elevational gradients, studies typically report the highest abundance of herbivorous arthropods at low elevations (e.g. Collins 1980; Wolda 1987; Sam et al. 2017), while several studies showed the highest arthropod abundance at mid-elevations (Janzen 1973; Ghosh-Harihar 2013). Importantly, there does not seem to be differences between the elevational patterns in abundances of herbivorous arthropods between mainland and insular systems, and the elevational decrease in abundance seems to be rather general pattern. However, not only abundance, but also community composition and body size tend to change along elevation, affecting the prey availability to insectivorous predators and the herbivory rate. While lowland communities tend to host larger insects (Sam et al. 2017; Terborgh 1977), several studies found that leaf chewers of some plant species have larger body sizes with increasing elevation in tropical forests (Brehm et al. 2019; Houska Tahadlova et al. 2023). Larger arthropod herbivore consumes more plant tissue, and they are more profitable for larger predators.

Similar to elevational patterns in abundance of herbivorous arthropods, herbivory has also been shown to decrease with elevation (e.g. Alonso 1999; Louda 1982; Metcalfe et al. 2014; Poveda et al. 2012; Sam et al. 2020; Suzuki et al. 2013). However, other studies have found increases (e.g. Bito et al. 2011; Koptur 1985; Matías and Jump 2015; Zhang et al. 2016) or no change (Hódar and Zamora 2004; Lay et al. 2013) in herbivory with elevation. Lowland plants are expected to be less nutritious and better defended (Coley and Aide 1991; Galmán et al. 2018; Pellissier et al. 2012; Pellissier et al. 2016), consistent with patterns of higher herbivory at low elevations. This prediction has been supported by the work of Garibaldi et al. (2011) and Pellissier et al. (2012) but not by the study conducted by Bito et al. (2011) in Australia, and by Sam et al. (2020) and Volf et al. (2020) on the island New Guinea. Thus, general conclusions about ecology of elevational gradients are far from definitive (especially with insufficient data support from islands) with growing evidence that results are not consistent across time and space (Andrew et al. 2012; Moreira et al. 2018). A recent review called not only for a critical re-evaluation of the evidence for geographic gradients in plant-arthropod herbivore interactions but also for the development of a new mechanistic framework for predicting the patterns that do exist (Moreira et al. 2018).

11.1.2 Insectivorous Predators on Islands

Insectivorous predators shape interactions at lower trophic levels and at the same time respond to environmental conditions differing along an elevational gradient. Some predators may be completely missing from some islands or certain elevations. As a result of the absence of predators, the herbivorous insects would strongly suppress the growth of plants, especially those depending on indirect plant defences involving predators, rather than direct defences. Arguably, the most important predators of arthropod herbivores on islands are birds, bats, lizards, ants, or spiders. They all differ in their abilities to colonise and inhabit different islands and their elevations, in their energy needs and diet breadth.

Birds: Insectivorous birds, as highly mobile flyers, are omnipresent predators colonising islands relatively easily. Yet, the species richness of island bird communities is often reduced and accompanied by greater population densities of some species in relation to those found in similar mainland habitats (George 1987; Wright 1981). In tropical forests, insectivorous birds are estimated to consume between 100 kg to 176 kg of insect (ha^{-1} year^{-1}), while consumption of temperate insectivorous birds is estimated to be between 35 and 137 kg of insect (ha^{-1} year^{-1}) (Nyffeler et al. 2018). A trend similar to this latitudinal pattern can be expected also along elevational gradients, and less diverse and simplified fauna of insectivorous birds is typically observed at higher elevations. Due to the high energy needs of insectivorous birds, islands might represent suboptimal habitats. Various insectivorous bird species were reported to change their feeding habits while in denser populations on islands than on the mainland (Nilsson and Ebenman 1981) or coping with low arthropod diversity on islands by expanding their diet of flowers and nectars. The observed widening of diet may also imply that relative predation pressure on insect might be actually greater on islands than on the mainland. Further, supplementation of insect prey with other types of food is likely to increase with increasing elevation, as arthropods represent relatively scarcer food resources at high elevations (Sam et al. 2017). Indeed, this theoretical pattern was partially supported, showing a low elevation plateau in predation pressure along insular elevational gradients (Houska Tahadlova et al. 2023; Tvardikova and Novotny 2012). Yet, it remains unclear whether the predation pressure on arthropods is actually higher on islands than on the mainland, as it depends on rarely studied densities of both involved trophic levels.

Bats: Bats often represent most of the mammals on oceanic islands (Jones et al. 2009). A report shows that 60% of all bat species live on islands and 25% of them are island endemics, while 8% of all bats are single-island endemic species (Jones et al. 2009). Along the elevational gradients of islands, the abundance and richness of bats, and insectivorous bats more specifically, decreases drastically. Islands harboured a less diverse and structurally simplified bat fauna, similar to birds. On the other hand, islands that are far from the mainland are especially species-poor (Meyer and Kalko 2008). This decline in species richness was associated with compositional shifts towards assemblages strongly dominated by frugivores with good dispersal abilities. Members of other ensembles, most importantly gleaning bats, were much less common or absent on islands (Meyer and Kalko 2008). Unlike in birds, there is puzzlingly low diet plasticity in insectivorous bats in general, thus bats do not adjust their feeding to resources and do not supplement their food with other resources when insects are rare. All this might indicate that bats might not have strong direct and immediate effect on measurable herbivory damage, as gleaners who would feed on insect folivores, might be mostly missing on islands. However, bats may have long term effect on herbivory by feeding on adult lepidopterans. Manipulative studies focusing on the effect of insectivorous bats on herbivore arthropods and herbivory damage on marine islands are basically absent to our knowledge.

Ants: Ants contribute 10–20% of world animal biomass (Hölldobler and Wilson 1990). As they are found in all forest strata and serve as ecosystem engineers and are able to feed as herbivores, scavengers, and predators, they represent an important but complicated taxon in terms of trophic interactions. Similar to other arthropod groups, they are virtually ubiquitous on marine islands, as they can fly or float (Hölldobler and Wilson 1990; Karley et al. 2004; Wilson and Regnier Jr 1971). Once on the islands, some species can reach extremely high population abundances but subsequently decline (Morrison 2016). Similar to other taxa mentioned, for ant species richness (closely tied to abundance), two general patterns have been observed across elevational gradients: either a decline with increasing elevation (Brühl et al. 1999) or mid-elevational peak (Munyai and Foord 2012). However, their impact on herbivorous arthropods and herbivory is difficult to predict, as the species composition and the ecological functioning of individual ant species vary along various environmental gradients (Wiescher et al. 2012) as well as on different islands (Morrison 2016).

Lizards: They can reach high densities following predator and competitor release due to their relatively low energetic costs, which can be up to 10 times lower than those of endotherms (Pough 1980; Spiller and Schoener 1998; Schoener and Spiller 2010). Lizards may also increase their densities by diversifying their diets (Buckley and Jetz 2007; Olesen and Valido 2003). While the partitioning of energy between lizard species of different sizes is constant between islands and the mainland, island lizard populations use more energy than mainland lizard populations. Ecological differences between islands and the mainland may contribute to the higher energy use by island populations. For example, Olesen and Valido (2003) suggest that islands have fewer arthropods available to lizards and hence a high frequency of herbivorous lizards. Lizards eating at a lower trophic rank have the potential to reach higher population densities (Pough 1973). Along elevational gradients, the diversity and abundance of lizards decrease with increasing elevation, which leads to much higher predation pressure in lowland sites (Fu et al. 2007).

Spiders: The role of foliage-dwelling spiders in insular ecosystems is similar yet different in certain aspects to ants. Their ability to travel on island might follow same faith as in ants and they also act as herbivore as well as intraguild predators. However, hunting strategies (and/or diet specialisation) in spider assemblages seem to determine whether spiders (i) partition prey resources with vertebrate predators and what prey or prey size will be most impacted by them; (ii) act as prey to vertebrate predators; (iii) are intraguild predators (Finke and Denno 2005). The main difference to ants is supposedly in abundances and lower versatility in the resource acquisition but also in terms of body size and prey size, respectively. Further, spiders serve as almost equally important food source as herbivorous arthropods for insectivorous birds (Mooney et al. 2010). Spider body size does not seem to resemble particular trend in abiotic conditions following changes of elevation (Houska Tahadlova et al. 2023). Thus, the net effect of spiders in top-down control of herbivores is remarkably hard to predict, further, studies focusing on spiders on (insular) elevational gradients are extremely scarce.

11.2 Manipulative Experiments Studying the Effect of Predators on Lower Trophic Strata on Islands

To evaluate the effect of predators on arthropods and herbivory at different elevations on islands and the mainland, we conducted an extensive survey of the literature on manipulative field studies where (i) insectivorous vertebrates (i.e. birds, bats, lizards) and ants were experimentally excluded individually or in combination with either field cages and netting and sticky barriers respectively, (ii) matched with appropriate open-access controls, and (iii) the effects of their removal were measured on herbivory on terrestrial plants and/or naturally occurring arthropod populations or communities. On Web of Science (all collections) and Google Scholar, we searched the terms “bird AND exclosure”, “bat AND exclosure”, “ant AND exclosure” and “lizard AND exclosure”. Further details of the methods and analyses used are mentioned in Sam et al. (2022). In total, we analysed 486 individual experiments from 157 publications in which either vertebrates or ants were manipulatively excluded. The datasets we analysed spanned a latitude of −41.2 to 64.23 degrees (mean ± SE = 19.82 ± 3.32) and altitudes of 0 to 3700 m a.s.l. (650.4 ± 150). While 421 experiments were conducted on mainland, only 61 were conducted on marine islands. The shortest experiments lasted 7 days and the longest lasted 96 months (9.56 ± 1.1 months). Exclosures ranged from 0.1 m^2 to 1000 m^2 (35.14 ± 1 m2).

Tests were based on unweighted natural log response ratios LRR (Curtis and Wang 1998; Hedges et al. 1999) calculated from mean responses in the presence or absence of a predator (ant or vertebrate). LRR is an effect size measurement that quantifies the results of experiments (i.e. response variables) as the log-proportional change in between the means of the variable in treatment (in the absence of insectivorous predators, $\bar{Y}$I-) and in control group (in the presence of insectivorous predators, $\bar{Y}$I+) and was thus calculated as (ln[$\bar{Y}$I−/ $\bar{Y}$I+]). To compare the ratio of mesopredators (i.e. predatory arthropods) to herbivores in the presence (P:HI+) and absence (P:HI-) of insectivorous predators, we used a log response ratio as ln([PI-:HI−/ PI+:HI+). It is important to note, that we calculated LRR the classical way (as ln(experimental mean/control mean); e.g. Curtis and Wang 1998, Hedges et al. 1999).

Vertebrate exclusion drove increases in arthropod abundance, both herbivorous and predatory and the magnitude of these responses, on average, were in most cases similar and significant (except on herbivorous arthropods on islands, i.e. CI overlapping zero) on both islands and mainland (Fig. 11.1a), i.e. no difference between landform types in vertebrate exclusion effects (Table 11.1). However, vertebrate predator exclusion, on average, led to a significantly greater increase in herbivore damage on islands (by 119%) than on the mainland (by 23% mainland (Table 11.1, Fig. 11.1a), i.e. stronger top-down pressure on island ecosystems (albeit no difference between landform types in vertebrate effects on herbivorous arthropods; Table 11.1).

On the other hand, and also contrarily to expectations, we found no evidence of significant elevational gradients in vertebrate exclusion effects on either herbivorous arthropods or herbivory (Fig. 11.2B, E), a pattern that was consistent across landform types, i.e. no elevation by landform type interaction (Fig. 11.2B, E). In contrast, there was a significant elevational gradient in vertebrate exclusion effect sizes on predatory arthropods, for which vertebrate exclusion had stronger effects at low than at high elevation (Fig. 11.2C), a pattern consistent across landform types (Fig. 11.2C). Inconsistently with above-mentioned patterns, we found a significant interaction on the predator:herbivore ratio whereby vertebrate exclusion effects

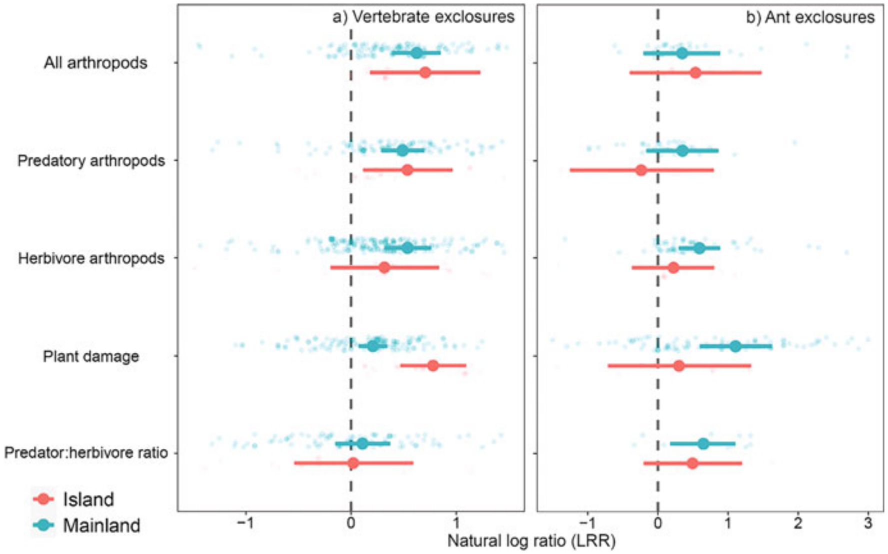

Fig. 11.1 Plot showing how the abundance of all arthropods, predatory arthropods, herbivorous arthropods, herbivory, and predator-herbivore natural log ratio responds to the ant (**a**) and vertebrate exclusion treatments (**b**) on islands (red) and mainland (**b**). The duration of the experiment is included in individual models in cases where response variables were affected by this study feature. The X-axis shows the mean effect sizes of natural log ratios (LRR = ln(exclosure/control)) with 95% CI of individual response variables. Effect size values above zero indicated that the absence of predators due to the exclusion treatments is harmful to plants, as the abundance of arthropods in exclosures increased and potentially caused increased herbivory damage to plants. Note the different scales on the x-axes in parts (**a**) and (**b**)

weakened with elevation on islands whereas they strengthened with elevation on mainland (Fig. 11.2D).

Ant exclusion drove increases in herbivorous arthropods, herbivory, and the predator:herbivore ratio on mainland but not islands (CI overlapping zero; Fig. 11.1b, Table 11.1), but there was no significant difference in the mean effect size between landform types, i.e. arthropod and herbivory responses were overall similar across islands and mainland (Table 11.1). On the other hand, we found significant decreases in the strength of ant exclusion effects on herbivory with elevation, a pattern that was statistically indistinguishable across landform types, i.e. no elevation by landform interaction (Fig. 11.3E). Likewise, there was a trend for weaker effect sizes with elevation for herbivorous arthropods, albeit non-significant, and no significant elevation by landform type interaction (Fig. 11.3B). In addition, there were no elevational gradients as well as no interaction for either predatory arthropods or the predator:arthropod ratio (Fig. 11.3C, D). It is important point out lower number of studies which led to highly variable effect sizes.

Table 11.1 The response (LRR ± 95% confidence intervals) of the number of all arthropods, predatory arthropods, herbivore arthropods, plant damage, and predator:herbivore ratio to (**a**) vertebrate and (**b**) ant exclosure at the island and mainland (land type). A significant increase in the response variable in exclosures respectively to the controls is indicated by asterisks in the Increase (4th) column. The difference between the land types for a given response variable is indicated as a *P* value in the last column of the table

	LowCI	LRR	HighCI	Increase (by %)	Response	Land type	Land type effect (*P* value)
A) vertebrate exclosure							
	0.192	0.708	1.230	**102.9***	Total arthropods	Island	0.784
	0.396	0.628	0.856	**87.3***		Mainland	
	0.119	0.538	0.962	**71.3***	Predatory arthropods	Island	0.843
	0.283	0.489	0.694	**63.1***		Mainland	
	-0.202	0.318	0.820	37.4	Herbivore arthropods	Island	0.429
	0.317	0.537	0.758	**71.0***		Mainland	
	0.465	0.784	1.090	**118.9***	Plant damage	Island	**<0.001**
	0.071	0.207	0.344	**23.1***		Mainland	
	-0.539	0.030	0.597	3.0	Predator: herbivore ratio	Island	0.716
	-0.153	0.108	0.373	11.5		Mainland	
B) ant exclosure							
	-0.429	0.534	1.477	70.5	Total arthropods	Island	0.733
	-0.196	0.352	0.888	42.1		Mainland	
	-1.254	-0.223	0.808	-20.0	Predatory arthropods	Island	0.307
	-0.148	0.355	0.865	42.6		Mainland	
	-0.381	0.228	0.805	25.7	Herbivore arthropods	Island	0.276
	0.288	0.594	0.893	**81.1***		Mainland	
	-0.998	-0.012	0.958	-1.2	Plant damage	Island	0.080
	0.443	0.827	1.195	**128.5***		Mainland	
	-0.207	0.501	1.219	65.1	Predator: herbivore ratio	Island	0.697
	0.191	0.656	1.108	**92.7***		Mainland	

11.3 Discussion and Conclusions

Islands commonly have fewer species than comparable mainland areas (Rosenzweig 1995; Whittaker and Fernández-Palacios 2007). Despite this general rule, several authors have observed that trophic cascades play out very differently on oceanic islands than in continental areas (Oksanen et al. 2010; Terborgh 2009), and differences in trophic cascades have been observed also along insular elevational gradients (Houska Tahadlova et al. 2023; Sam et al. 2015). Yet, some emergent patterns appear based on the analysed manipulative experiments. We found that in general, arthropod abundances tend to increase more, yet non-significantly, in absence of vertebrate predators and ants on islands than on the mainland. The abundance of all arthropods increased by 70% vs. 42% on the island vs. on the

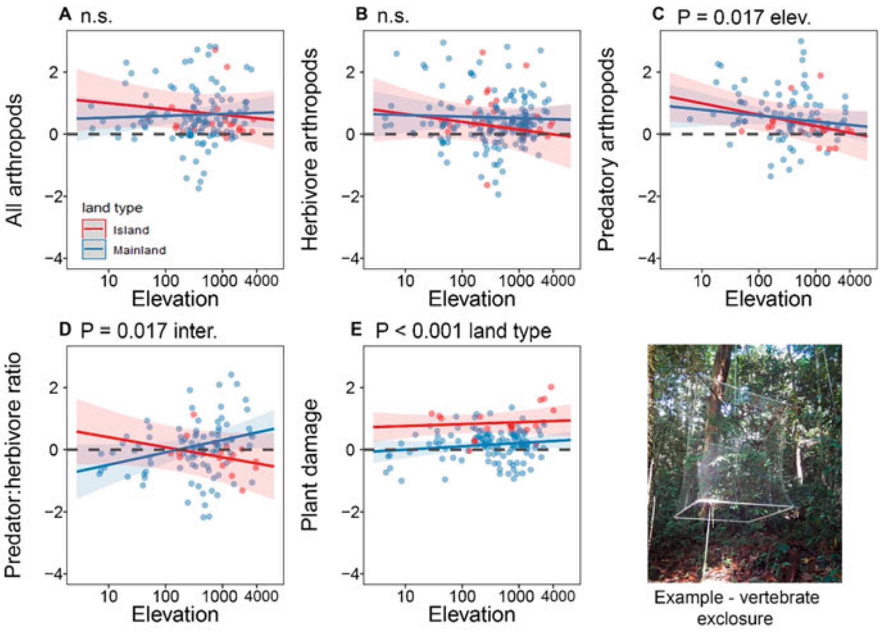

Fig. 11.2 The effect sizes (LRR, on Y axes) of insectivorous vertebrate predator exclusions along elevation and on different land types (effect of the exclusion of vertebrates on the island in red, on the mainland in blue) on various response variables (**A-E**). Elevation had a significant effect on the change of the abundances of predatory arthropods after the predators were excluded (**C**). Elevation had no significant effect on the change of abundances of all arthropods (**A**), herbivorous arthropods (**B**), and plant damage (**E**). The interaction between elevation and land type (island or mainland) had a significant effect on the change in ratio between all predatory arthropods and all herbivorous arthropods (**D**). Y-axes show the natural log ratios (LRR = ln(exclosure/control)) of individual response variables. Log-scaled elevation was used in models and the actual elevation was plotted on the x-axes to ease the visual interpretation of the results. Values above zero (0) indicate increase of response variables in exclosures respectively to the controls. Values below zero indicate decrease of the response variables in exclosures respectively to the controls. The overall increase and its significance are mentioned in Table 11.1 and Fig. 11.1. Latitude was used in all models as the first covariate. The insect on the bottom right shows an example of vertebrate exclosure on a sapling in the forest understory

mainland in ant exclosures, and by 103% vs. 87% respectively in vertebrate exclosures. This finding supports the hypothesis that arthropod prey might be under higher predation pressure on islands than on the mainland (Polis et al. 1997). Yet, it is important to note that our findings run counter to relatively higher vertebrate pressure but same or even relatively lower ant pressure on islands than on mainland. This trend in vertebrates is in parallel with observations that many predators on islands are forced to change their diet and include the plant material, even though they can afford to be fully insectivorous on the mainland (Nilsson and Ebenman 1981). Despite no comparable studies exist, strength of other interactions,

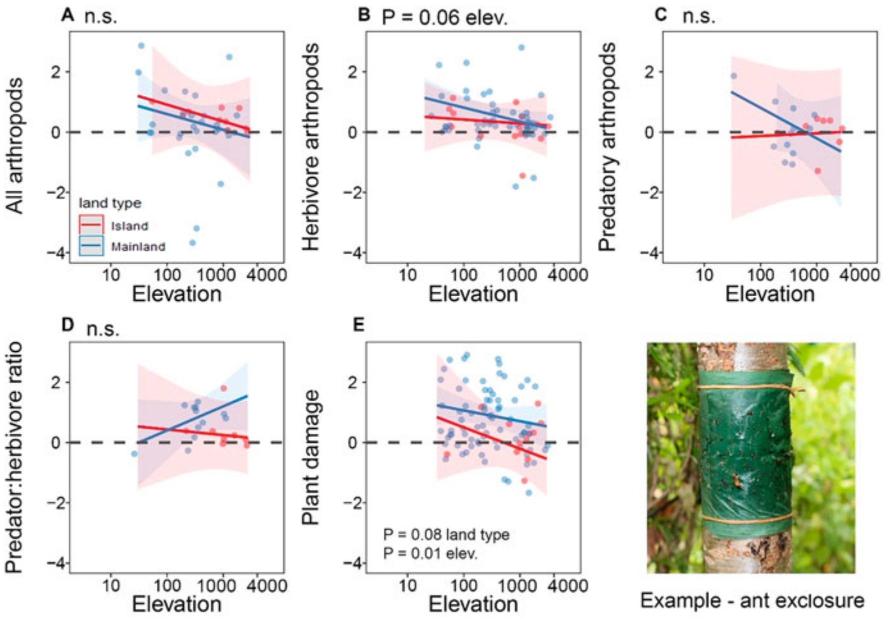

Fig. 11.3 Effect sizes (LRR, on Y axes) of insectivorous vertebrate predator exclusions along elevation and land type (effect of the exclusion of ants on islands in red, on mainland in blue) on various response variables (**A-E**). Elevation had a significant effect on the change of the abundances of herbivorous arthropods (**B**). Elevation had no significant effect on the change of the abundances of all arthropods (**A**), predatory arthropods (**B**), and the ratio between all predatory arthropods and all herbivorous arthropods (**D**). Elevation, as well as land type, had a significant effect on the change herbivory (**E**). Y-axes shows the natural log ratios (LRR = ln(exclosure/control)) of individual response variables. Log-scaled elevation was used in models and the actual elevation was plotted on the x-axis to ease the visual interpretation of the results. Values above zero (0) indicate increase of response variables in exclosures respectively to the controls. Values below zero indicate decrease of the response variables in exclosures respectively to the controls. The overall increase and its significance are mentioned in Table 11.1 and Fig. 11.1. Latitude was used in all models as the first covariate. The Insect on the bottom right shows an example of vertebrate exclosure on a sapling in the forest understory

measured this time as parasitism rate, was slightly but not significantly higher on islands (Santos et al. 2011).

However, the predation pressure from ants as well as vertebrate predators differed across trophic guilds of arthropods. Specifically, abundances of herbivorous arthropods increased significantly on the mainland, and not on the island, in the absence of both groups of our focal predators. Abundances of predatory arthropods (mostly spiders) increased significantly, both on the island and mainland, in the absence of vertebrate predators but not in the absence of ants. These results of experimental exclusion of vertebrate predators thus support the earlier observational studies, which showed that islands without naturally occurring lizards had extraordinarily high densities of spiders (Schoener and Spiller 2010; Toft and Schoener 1983), implicating important effects of intraguild predation.

We found that herbivory damage increased more on islands than on the mainland in vertebrate predators exclosures. Our results thus imply that vertebrate predators are more strongly controlling trophic cascades on islands than on the mainland. Two factors might be contributing to this pattern. First, the ability and need of vertebrate predators to broaden their diet breath on islands might be indicating higher predation pressure on individual arthropods on islands than on the mainland. Second, island plants might invest in different defences than mainland plants, relying more in cheaper indirect defences. Further, higher stochasticity of dispersal in herbivorous arthropods might be forcing the herbivores to survive on suboptimal host plants (Moreira et al. 2021), to which the respective herbivore species cause relatively higher damage once they learn to overcome their defences. In correspondence to predictions that island plants are relying more on indirectly induced defences and the help of predators rather than their own constitutive defences, it is expected that herbivory damage would be higher on islands than on the mainland if the insectivorous predators disappear. Similarly, according to island biogeography theory some organisms tend to increase their body size on islands compared with their mainland counterparts. Vertebrate insectivores are known to prefer larger prey (Karp and Daily 2014; Singer et al. 2017), as the searching time supposedly decreases with increasing prey body size. Such a phenomenon may lead to larger changes in leaf damage in case of absence of vertebrate predators.

Furthermore, theoretically, as food web diversity (a combined function of the number of trophic levels, species per level, and within-trophic-level foraging strategies) increases, both the number and importance of higher trophic levels increase as they maintain diversity (Terborgh 2015). This leads to an increased number of predator–prey interactions, and a corresponding rise in the relative importance of predation in structuring the community (Chan and Banks-Leite 2020; Roels et al. 2018). As a result, more diverse communities should be structured primarily by predation, while competition should play a predominant role in less diverse food webs (Preisser 2007). Contrary to these expectations, empirical studies seem to support the exact opposite patterns, in other words, less diverse communities ("food chains") are more likely to show strong top-down control (e.g. (Belovsky and Slade 1993; Halaj and Wise 2001; Mazia et al. 2009), while more diverse communities ("food webs") tend to diffuse top-down control and be more affected by bottom-up factors (e.g. Faveri et al. 2008; Gruner 2004). In line with the empirical observations, we found that herbivory damages in predator free space significantly increased on island, and this increase was significantly higher than on mainland. However, to our knowledge, there is not a single study focusing on the trade-off between indirect induced defences and constitutive defences, or body size-based approach in plants comparing insular systems and the mainland.

After the exclusion of ants, the herbivory damage increased significantly from controls on mainland but not on islands, despite the increase was not significantly different between the land types. Despite ants being relatively good dispersers, we might have been comparing islands with relatively lower richness and abundance of ants and contrasting them with the mainland where ants had more rich communities. Additionally, the mainland ant communities could be more predatory than those on islands (Janzen 1973), thus further causing stronger pressure. Further, we lack information on the role of other small predators (e.g. spiders) and their interactions with ants on islands. Nonetheless, it is difficult to pair the observed trend in the change in herbivory with the absence of ants, without having more studies and information on their diet on islands. Along the elevational gradient, the relative change in plant herbivory damage decreased towards higher elevations in ant exclosures while there was no observed pattern in herbivory damage in vertebrate exclosures.

Along the elevational gradient, the relative change in plant herbivory damage decreased towards higher elevations in ant exclosures while there was no observed pattern in herbivory damage in vertebrate exclosures. This elevational pattern within ant exclosures was detectable both on the mainland and islands despite the overall increase in herbivory was significantly higher in exclosures than in controls only on the mainland. The resulting elevational patterns from ant exclosures are in line with the expectation that ant abundance and diversity, and thus the predation and effect on plants is higher at lower elevation, in warmer conditions. In other words, ants seem to be protecting plants effectively from herbivorous damage on the mainland but not on islands and always more in lowlands than highlands. This pattern might be solely due to the insufficient number of manipulative experiments on islands. On several islands, ants were observed to be effectively protecting the plants from herbivory in the lowlands and not in the highlands, where plants lost their extrafloral nectaries due to the disappearance of herbivores and ants with increasing elevation (Keeler 1985). The observed elevational pattern was expected, as the abundances and species richness of predatory ants are high in lowlands of any land type.

11.4 Synthesis and Outlook

Our findings indicate that vertebrate insectivores define the herbivory damage of plants on islands, and they do it even more strongly on islands than on the mainland. However, the effect of vertebrate predators on plant damage doesn’t change with an elevation of any land type. This runs along the patterns showing that attack rates by birds on dummy prey do not change with increasing elevation (Roslin et al. 2017). Ants do not seem to be very important predators of arthropods on islands, and all their measurable effects were detectable only in lowlands. However, for more conclusive results, more studies specifically focusing on the manipulative experiments with various predators, conducted under standardised design on the mainland and island would be needed. Other experiments should focus on the trophic interactions on young and distant islands which are rarely studied. Further attention would also deserve the loss of “ant structures” on plants and interactions of ants and other mesopredators (e.g. spiders), which might be even more predatory on islands than on the mainland (e.g. beetles—Becker 1975). Specialisation and generalism of insect herbivores on insular systems, as well as the trade-off in different types of plant defences on islands, would be other questions worth investigating.

Acknowledgements We are grateful to Inga Freiberga who assisted the collection of the data from literature. All authors are thankful for financial support from the University of South Bohemia and European Research Council Starting Grant, BABE No. 805189.

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Pest Control in Coffee: A Tri-trophic Comparison between a Mainland and an Island Agroecosystem

12

John Vandermeer, Zachary Hajian-Forooshani,
Iris Saraeny Rivera-Salinas, and Ivette Perfecto

Abstract

The practical requirement of pest control in agriculture is an evident application of principles of tri-trophic ecological interactions—plant (crop), herbivore (pest), and predator (natural enemy). We analyze the coffee agroecosystem and four of its main pests, the coffee berry borer, the coffee leaf miner, the green coffee scale, and the coffee leaf rust, comparing a mainland site (Mexico) and an island site (Puerto Rico). In addition to the direct trophic, competitive, and mutualistic interactions, there are a variety of indirect higher order interactions, many of which qualitatively increase the complexity of the organizational structure. We explore how the basic nodes of the natural enemy network remain relatively constant between mainland and island, but their frequency and, especially, the complications of their interconnections are dramatically different. The coffee berry borer is preyed upon by numerous species of ants at both sites with an indirect effect of larger ants interfering with smaller ants, the latter of which are able to penetrate the coffee seed through the holes the borer makes and prey on the larvae and eggs of the berry borer. While the larger ants do indeed impede the berry borer directly, their indirect effect of excluding the smaller ants counters this effect. Similarly, in Puerto Rico Anolis lizards, effective predators on the

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J. Vandermeer (✉)
Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

School for Environment and Sustainability, Ann Arbor, MI, USA
e-mail: jvander@umich.edu

Z. Hajian-Forooshani
German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Institute of Computer Science, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

I. S. Rivera-Salinas · I. Perfecto
School for Environment and Sustainability, Ann Arbor, MI, USA

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_12

berry borer, tend to avoid areas dominated by specific species of ants, a pattern not seen at the mainland site. The coffee leaf miner is extremely common in Puerto Rico and quite rare in Mexico, for reasons unknown. Its adults are attacked by the common coqui frogs and anoline lizards, again with the indirect effect of some species of ants involved. The scale insect is common in Mexico but mainly associated with a specific species of Azteca ants, providing refuge for predatory beetle larvae and thus enhancing control of this pest across the entire landscape. In Puerto Rico the coffee leaf miner is present but only very rarely reaches pest status. The coffee leaf rust has a variety of potential biological control elements at both sites, yet only on Puerto Rico do they (the control elements) reach significant status, perhaps an element in the dramatic difference between the mainland and island site in terms of the importance of the coffee leaf rust.

The practical requirement of pest control in agriculture is perhaps the most evident application of the idea of tri-trophic ecological interactions—plant (crop), herbivore (pest), and predator (natural enemy). Detailed study with a narrow focus is made possible by the artificial (in principle, experimental) setting of both plant and herbivore, such that the complexities of the higher trophic levels can be studied in distinct, but planned, agroecological contexts. Certain cultivated plants which tend to have similar herbivores from place to place, have been effectively placed in particular sites (farms) and provide a unique scientific opportunity for the investigation of trophic interactions. They can be used effectively as replicated treatments of focal trophic modules in a variety of specified ecological contexts, structured by both management and associated biodiversity. Here we focus on the similarities and differences associated with a tropical mainland site and a tropical island site in structuring the complexity of four focal tri-trophic systems, each associated with four of the major recognized pest species of coffee.

Since the publication of island life (Wallace 1892), the science of ecology has been attendant to obvious patterns that occur when comparing the flora and fauna of islands to their counterparts on nearby mainland areas. The evident balance between arrival of species (immigration) and local extinction of species, first advocated by Levins and Heatwole (1963) and eventually formulated into an elegant graphical framework by MacArthur and Wilson (1963), in what remains a common discourse about island biogeography. Yet tropical island travelers frequently note more than just a relative paucity of species on islands. It is frequently the case that evident structural details are obvious (Vitousek et al. 2013), including structural elements of trophic connections (Gravel et al. 2011).

Our focus is on the coffee agroecosystem at a mainland site in Mexico and an island site in Puerto Rico. The coffee agroecosystem is a novel ecosystem (Hobbs et al. 2009, 2013; Morse et al. 2014; Perfecto and Vandermeer 2015; Lewis et al. 2019). In these cases, the study of community structure confronts the challenge (and opportunity) of not only explaining extant spatial and organizational patterns (e.g., species abundance distributions, species area curves, spatial clusters of species, etc.), but also the realities of recent, sometimes concurrent, interactions among the species of concern. Indeed, there has been burgeoning interest in novel ecosystems for this very reason (Solórzano et al. 2021; Teixeira et al. 2021; Ammar et al. 2021; Rinkevich 2021), and their likely volatile nature, being far from equilibrium, makes them important candidates for the study of regime change as we move from mainland to island in our focus.

In particular, the coffee agroecosystem has received considerable attention from ecologists (Vandermeer et al. 2010, 2019; Zewdie et al. 2020, 2021; Avelino et al. 2006, 2012, 2022; Philpott et al. 2007, 2008). Our work has been explicitly aimed at understanding the pest control aspects of this system from a community ecology perspective (e.g., Vandermeer et al. 2010, 2019; Vandermeer and Perfecto 2019; Perfecto et al. 2003, 2021), a subject that, we argue, has essential spatially explicit dynamics associated with its complex organizational structure. Although frequently unrecognized by practitioners, we argue it is nevertheless critical to understanding the persistence of the system, given its recent assembly (little more than two centuries old in the Neotropics), yet remarkably persistent elements (Vandermeer and Perfecto 2019; Perfecto and Vandermeer 2020).

The use of the network metaphor has become ubiquitous in ecology. In our restricted use, we consider the complications of a single trophic level, the consumers, predators, or pathogens, of the coffee pests. It is clear from previous work in both Mexico (Vandermeer et al. 2010, 2019) and (Hajian-Forooshani et al. 2020; Perfecto et al. 2021) that the natural enemies of the pests (third trophic level) exist within dynamical constraints among them. It is those dynamical constraints we suggest are highly variable and take on distinct meanings on islands as opposed to mainland cases. We herein review some of those complexities, comparing the mainland site in the southwestern Chiapas (Mexico) to the island site in the central mountains of Puerto Rico.

12.1 The Organizational Complexity of the System

There are at the base of the network, four evident tri-trophic systems: (1) a leaf miner (*Leucoptera coffeela*) and its enemies, (2) a seed predator (*Hypothenemus hampei*) and its natural enemies, (3) a sap sucker (*Coccus viridis*) and its natural enemies, and (4) a fungal pathogen (*Hemileia vastatrix*) and its natural enemies. The natural enemies exist at various scales of organizational complexity, forming a network containing more than just direct trophic connections, perhaps best characterized as a hypergraph (Golubski et al. 2016; González et al. 2021). Because the backbone primary producer is coffee, we can define very specific patches of vegetation in the broader landscape that contain this hypergraph. The system is a complicated spatial mosaic at various scales, from meters (Vandermeer and Perfecto 2023) (i.e., the patch scale), to the patches or spirals formed by a multi-Turing process at the level of hectares (i.e., the farm scale), to the variability from farm to farm at the level of kilometers (i.e., the landscape scale) (Perfecto and Vandermeer 2020).

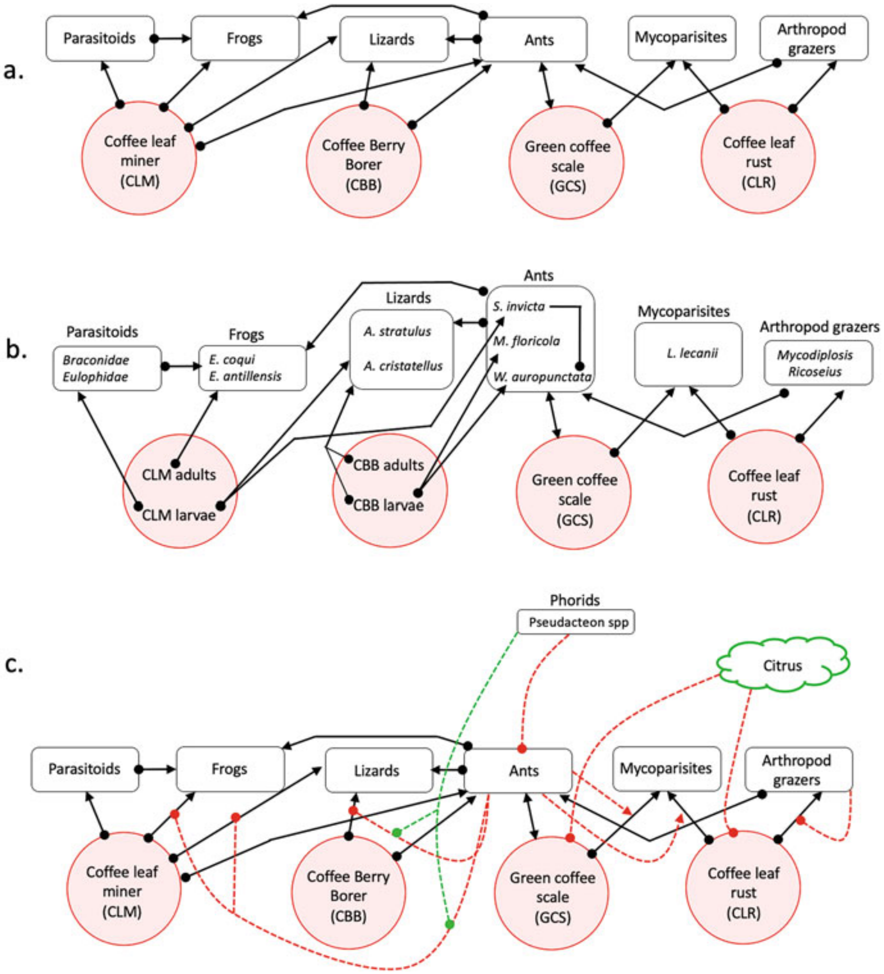

Fig. 12.1 The four main coffee herbivores and their main natural enemies. (**a**) basic functional groups; (**b**) main species in the functional groups and their connection to the life stages of the herbivores; (**c**) basic hypergraph of the system including currently known hyperlinks (nonlinear rates)

A keystone functional group in this general narrative is the community of ants, nesting and foraging both arboreally (in coffee bushes and shade trees) and terrestrially (on the ground). They create a spatial "pilot pattern" (Vandermeer and Jackson 2018) into which the other natural enemies of the coffee pests are constrained. Thus, the community ecology of ants partially determines the spatial pattern of the natural enemies that impact the pests of the agroecosystem.

The simplest level of organizational complexity is the system of "guilds" or "functional groups," in this case the herbivores and the predators (Fig. 12.1a). It includes the four main coffee pests: the coffee berry borer (CBB), the coffee leaf miner (CLM), the coffee leaf rust (CLR), and the green coffee scale (GCS), along with five functional levels of natural enemies, namely: vertebrate predators, arthropod predators/parasitoids, mycoparasites, and ants (De la Mora et al. 2008; Vandermeer et al. 2010, 2019; Gonthier et al. 2013; Pak et al. 2015; Morris et al. 2018; Hajian-Forooshani et al. 2023). As we move from the mainland situation to the island situation, the functional groups maintain much of their integrity, but their internal structure becomes significantly changed, and, especially important, the pattern of interconnections among them changes dramatically. In network science one might characterize the system as having consistent basal nodes (the state variables, pests, are the same from place to place), but variable higher trophic nodes and wiring (the manner in which the other state variables occur and are interconnected) varies dramatically. This variability in network configuration must, however, be understood under a framework of strong spatial patterning of the system, much of which is driven, directly and indirectly, by ants (Vandermeer et al. 2019; Vandermeer and Perfecto 2020).

Each of what we refer to as functional groups is composed of various species, some of which have specialized roles in the overall system, leading to the second level of organizational complexity (Fig. 12.1b). Some components of community structure fit well within the framework of functional groups (e.g., parasitoids of leaf miners), while others contain individual species that in the end engage in species-specific “functions” (as we noted above, we use the phrase functional groups only for convenience of presenting levels of organizational complexity).

In addition to the direct trophic, competitive, and mutualistic interactions (or, first order interactions, as in Fig. 12.1a and b), our research has uncovered a variety of indirect higher order interactions, many of which qualitatively increase the complexity of the organizational structure (Fig. 12.1c). For example, lizards eat CLM larvae, but their consumption rate of CLM is decreased when within spatial clusters of the electric ants (Perfecto et al. 2021), a phenomenon evident in Puerto Rico but virtually lacking entirely in Mexico. This is a second order interaction. In addition, the presence of the phorid fly parasitoids (*Pseudacteon* spp.) that attack some of the ant species (at least *S. invicta* and *L. iniquum* in Puerto Rico and *A. seriaceasur* in Mexico), in addition to having a direct interaction with the ants, also initiate a third order interaction by disrupting other interactions in the system. For example, *S. invicta* ants in Puerto Rico and *A. seriaceasur* ants in Mexico decrease the attack rate of the CBB (second order interaction), but the phorid flies interfere with this action of the ants (the phorids decrease the ants’ ability to interfere with the CBB’s ability to attack the coffee). This is a third order interaction, sometimes referred to as trait-mediated cascades (Liere and Larsen 2010; Hsieh et al. 2012, 2022; Greeney et al. 2015; Haggerty et al. 2018; Wood et al. 2020) and have been shown to have important community-level effects (Schmitz et al. 2004; Haggerty et al. 2018; Bairey et al. 2016; González et al. 2021), and also resonates in complex ways with spatial pattern formation (Seifan and Kadmon 2006).

12.2 The Coffee Berry Borer

Perhaps the most directly obvious of the four pests is the infamous coffee berry borer (CBB), due to its habit of drilling directly into the seed, which is the basic commodity that goes to market. It emerged as a major pest in the 1980s and is regarded as far more important, on most farms, than any of the other pests. A variety of natural enemies have been reported, including the fungus *Bauvaria bassiana* (De La Rosa et al. 2000), Anole lizards (Monagan Jr et al. 2017), birds and bats (Williams-Guillén et al. 2008; Karp et al. 2013), and parasitic hymenoptera (Gómez et al. 2005; Howard and Infante 1996). However, by far the most obvious natural enemies are ants.

There is now a substantial literature documenting the general category "ants" as major predators on this seed-eating herbivore (Morris and Perfecto 2016; Morris et al. 2015; 2018; Armbrecht and Gallego 2007; Larsen and Philpott 2010; Philpott and Armbrecht 2006; Philpott et al. 2008, 2012; Gonthier et al. 2013; Bustillo et al. 2002; De la Mora et al. 2015). Some rather casual observations can easily convince one that, at least in coffee farms in Mexico, the *Azteca* ants are major predators of (or at least antagonists to) the CBB (Perfecto and Vandermeer 2006; Gonthier et al. 2013; Pardee and Philpott 2011). It takes the CBB approximately 1–2 h to completely burrow into the fruit, which means it is unprotected and unable to escape the predacious activity of the ants during that window of time. If *Azteca* and some other ants encounter a berry borer trying to burrow into a seed, they grab the borer by its posterior end and pull it out of the fruit.

A number of smaller species of ants are also known predators of CBB (Gonthier et al. 2013; Morris et al. 2018). These species offer considerable regulatory potential since they can enter the coffee seed through the hole that the borer made (Larsen and Philpott 2010). One group is the twig-nesting complex, including the genus *Pseudomyrmex* (at least three species are common), and *Procryptocerus scabriusculus*, all adept at entering hollow arboreal structures since they normally nest in hollow twigs (Larsen and Philpott 2010). Other small arboreal ants capable of entering the hole made by the CBB include the arboreally nesting *Solenopsis picea*, which nests in superficial structures, such as moss, surrounding the branches of the coffee bushes (Morris and Perfecto 2016). In addition, a variety of ground foraging ants, small enough to enter the CBB's hole include *Pheidole protensa*, and a variety of other species in that same genus. Of particular interest is the well-known *Wasmannia auropunctata* (the electric ant or the "little fire ant"), which nests and forages on both the ground and arboreally (Yitbarek et al. 2017a, b; Morris and Perfecto 2016). It is extremely abundant on Puerto Rican coffee farms and plays, we think, an important role not only for control of the CBB, but, as discussed below, for two of the other pests as well.

In Mexico, *Azteca* clearly dominates over the smaller species in the system, reducing their nest density (and thus overall population density) significantly (Jiménez-Soto et al. 2013). Although *Azteca* are not present in Puerto Rico, another species fills some of its role, specifically with respect to controlling the CBB, the invasive tropical fire ant *Solenopsis invicta*. Similar to *Azteca*, *S. invicta* is too large to enter the bored berry but acts to repel adult CBB attempting entrance to the berry.

In one study, examination of the scars made by the berry borer and extrapolating as to the role of smaller ants (especially *Monomorium floricola*, *Pheidole morens*, *Brachymyrmex heeri*, and *W. auropunctata*), allowed for the separation of the CBB's attack from its survival. Indeed, the larger *S. invicta* seems to reduce the attack of CBB, while the smaller ants reduce its survival (i.e., after having entered the seed, what is its reproductive success). Thus, these two ant types (large and small) had a combined effect of reducing the CBB damage, although through distinct mechanisms (Newson et al. 2021).

In sum, a variety of ant species are predators on the CBB, both in Mexico and Puerto Rico, suggesting that "ants" represent an excellent natural enemy to regulate the CBB. However, the foregoing natural history suggests that the system is not so simple. While several of the smaller arboreal species (*Pseudomyrmex* spp., *S. picea*, *P. scabriusculus*, and *W. auropunctata* in Mexico and *M. floricola, P. morens, B. heeri, and W. auropunctata* in Puerto Rico) could be effective predators on adults, larva and pupa of CBB after it burrowed in the seed, they are effectively unable to engage in such predation if *Azteca* (in Mexico) or *S. invicta* (in Puerto Rico) are around. Fruits that are not harvested tend to dry out and fall to the ground, providing a refuge for the beetles during the dry season, but also being exposed to the potential predation from the smaller ground foraging ants. Yet those smaller ants have dramatically reduced populations if they are forced to compete with *larger ants*. In other words, the whole system seems to be operating in a complicated fashion with potential predators interfering with one another, but perhaps acting in an "emergent" fashion to at least partially regulate this key herbivore. It is worth noting that despite the dramatic differences in the specific identity of the ant species involved, a similar biological control story involving ants seems to emerge for both Mexico and Puerto Rico. These similarities and differences are summarized in a comparison network graph in Fig. 12.2.

The system is complicated by the fact that the electric ant, *W. auropunctata,* is also regarded as a pest (it stings harvest workers and thus is reported to reduce harvest efficiency). It seems that the only agents with the potential to control it are other ants (Fig. 12.2), particularly the imported fire ant (*S. invicta*), also considered a pest, and the big-headed ant (*Pheidole megacephala)* (Vázquez Moreno et al. 2012; Pérez-Consuegra et al. 2018). The latter is also a non-native ant and seems to compete with *S. invicta* on the ground, although the relationship between these two is not well-understood. The dynamics of this subsystem have been partially documented, including, for example, the formation of spatial pattern through complex interactions between *S.invicta* and the *W. auropunctata* (Perfecto and Vandermeer 2020; Vandermeer and Perfecto 2020), the different foraging strategies of the two ants on the CBB (Newson et al. 2021), and the effect of *W. auropunctata* as both predator of the CBB and antagonist of other predators of the CBB, mainly lizards (Perfecto and Vandermeer 2020a; Perfecto et al. 2021; Monagan Jr et al. 2017). It is worth emphasizing the special place of *W. auropunctata* as the "worst pest anyone has ever seen" (personal information from several farmers) and as a demonstrated natural enemy of CBB (and the coffee leaf miner), a classic ecological contradiction that an honest management program needs to consider. It is both pest

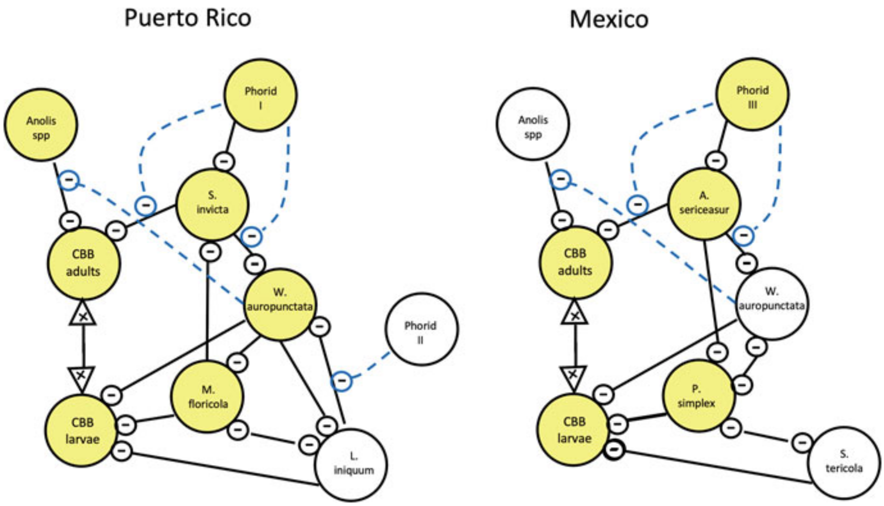

Fig. 12.2 The regionally distinct communities associated with the coffee berry borer (CBB) in Mexico and Puerto Rico. Links between organisms denote interactions, with arrowheads (triangles) showing positive effects and circles negative effects. The interaction networks are constructed from observations by the authors in both field and laboratory settings. Dotted blue lines are trait-mediated indirect interactions. Yellow filled circles represent relatively common organisms in each agroecosystem. *Solenopsis invicta, Wasmannia auropuctata, Pseudomyrmex simplex, Monorium floricola, Linepethema iniquum, Solenopsis tericola,* and *Azteca sericeasur* are all ants. The case of *L. iniquum* is displayed because of its interesting interaction with *W. auropunctata*, which is thought to be a major predator of the CBB, yet the interaction between the two species is strongly affected by a phorid (Yitbarek et al. 2017a, b). The various species of ants tend to fall into two functional groups, *S. invicta* (Puerto Rico) and *A. sericeasur* (Mexico) are larger ants that are unable to penetrate the hole made in the coffee berry by the borer, whereas all the other species are small and can do so. While the particular species composition is sometimes the same in the two sites (e.g., *W. auropunctata*), oftentimes the species are distinct but their functional property of preying on larvae of the CBB is the same (e.g., *L. iniquum* and *S. tericola*, both of which are displayed here as symbolic of many other small species at each of the sites)

and a natural enemy of pest. Recently the importance of yet another species of ant, *Monomorium floricola* has been reported as forming an intransitive loop with the other two dominant species (*S. invicta* and *W. auropunctata*), complicating this story considerably (Vandermeer and Perfecto 2023).

In addition to ants, it is well known that the potential for several species of *Anolis* to act as an effective predator of the CBB a force in both Mexico and Puerto Rico (Monagan Jr et al. 2017), documenting what most farmers understand to be the case. At the scale of a whole farm, there is a negative relationship between *W. auropunctata* and *Anolis* (Perfecto et al. 2021), presumably due to the lizard's avoidance of general areas where *W. auropunctata* are common (Perfecto and Vandermeer 2020a; Perfecto et al. 2021). Further, a spatial mosaic pattern tends to form, presumably due to the complicated Turing-like effects of the parasitic phorid flies acting on the ants, the *Azteca* in Mexico and the *S. invicta* in Puerto Rico, coupled with an intransitive structure emerging from that Turing-like effect, plus the competitive effect of the fire ants on the electric ants in Puerto Rico (Vandermeer and Perfecto 2020; 2023). Surveys on one of the farms in Puerto Rico where this effect was studied suggest that *Anolis* lizards avoided the patches dominated by electric ants, which is a spatial pattern that in turn emerges from the complicated dynamics involving *S. invicta*, *W. auropunctata*, *Monomorium floricola*, and phorid flies in Puerto Rico (Vandermeer and Perfecto 2023). Therefore, the phorid fly/S.invicta/ *W. auropunctata*/*M. floricola Anolis* lizard combination has its own spatially explicit context (Vandermeer and Perfecto 2020; Vandermeer and Perfecto 2023; Perfecto et al. 2021) that will ultimately determine the biological control of the CBB, through the multiple pathways of predation on both adults (outside and inside berries) and brood (inside berries) by the two ants and the lizards. While Anoline lizards are obviously potential predators of the CBB in Mexico, the dramatic difference in population densities of lizards between Puerto Rico, where virtually every coffee bush contains a lizard, and Mexico where they are difficult to find, suggests that the lizards are a far more important predator in Puerto Rico than in Mexico (Monagan Jr et al. 2017).

12.3 The Leaf Miner System

The coffee leaf miner (*Leucoptera coffeella,* Lepidoptera: Lyonetiidae, hereafter CLM) is of main concern for coffee production in various locations. In Puerto Rico it is responsible for 20–40% loss in production and in Mexico for up to 12% (Dantas et al. 2021). It is a specialist on *Coffea*, and its damage significantly reduces photosynthetic rates, frequently resulting in defoliation (Guerreiro Filho 2006). The CLM adult oviposits its eggs on the surface of the coffee leaves. Seven to twelve days later the larva hatches and burrows into the coffee leaf where it starts feeding on the palisade parenchyma of the leaf (usually for about 12 days) (Pereira et al. 2007; Guerreiro Filho 2006). During this stage, larvae create the "mine," the characteristic damage that defines this pest. During the last larval instar, the larva emerges from the mine and begins cocoon construction, a process taking about an hour, and leaving the larvae quite vulnerable to visual predators. The adult emerges from the cocoon 5 days later. The different life stages of the CLM are vulnerable to different natural enemies at each stage. The eggs are also vulnerable to generalist predators such as ants (Lomeli-Flores et al. 2009), the larvae inside the mines are susceptible to parasitoids (Gallardo Covas 1988; Lomeli-Flores et al. 2009), and the transition between larvae and pupae, where the larvae are unprotected while building their cocoon, are vulnerable to predation by lizards, ants, and frogs. The pupae may also be susceptible to predation by small ants and parasitoids. Finally, the adults are prey of lizards and frogs (Beard et al. 2021), although the apparent night flights of adults probably restricts the impact of lizards. However, the extent to which natural enemies affect each other and the impact of these potential interactions on the CLM dynamics remains enigmatic.

In Mexico, the potential pool of natural enemies is expected to be more diverse in comparison to Puerto Rico because of its mainland status. Studies on the community of natural enemies in Mexico have identified 22 species of parasitoids and another 17 predators (Lomeli-Flores et al. 2009), but this is likely an underrepresentation of the diversity of predators on the CLM (cite?). Among the natural enemies, predatory wasps have been shown to play an important role and are responsible for the mortality of up to 69% of the CLM (Lomeli-Flores et al. 2009), actively infesting both egg and larval stages. In addition, ant communities, which can be relatively diverse in coffee agroecosystems, have been shown to be one of the most important predators of this pest—e.g., twig-nesting ants prey on the eggs and pupal stages (De la Mora et al. 2008) of the CLM, and other arboreal ants have been reported to prey on eggs, larvae, and pupae of this pest (Lomeli-Flores 2009).

In comparison, the diversity of potential natural enemies in Puerto Rico is lower than in Mexico. A survey of parasitoids in 1985 showed the presence of only six parasitoids causing rates of parasitism from 19.5–23.5% (Gallardo Covas 1988). Other important predators in Puerto Rico are the native coqui frogs (*Euleutherodactylus* spp.) and the lizards (*Anolis* spp.), both known for being important generalist predators (Beard et al. 2021). Anoline lizards are especially abundant in coffee agroecosystems (Borkhataria et al. 2012). Furthermore, there is a dramatic difference in population density of these lizards, with Puerto Rico housing extremely large local densities relative to Mexico (Monagan Jr et al. 2017). Comparing lizards to frogs, the latter are believed to be important predators specifically of the adult stage of the CLM since both are nocturnal, while lizards are more likely to prey upon the larvae when they are spinning their protective cocoon, which seems to be done exclusively during the daylight hours (personal observations). Both types of vertebrate predators are seemingly more important in the island agroecosystems than on the mainland sites.

Ants are also important predators of the CLM in both mainland and island sites. The diversity of ants on coffee farms in Mexico is estimated to be well over 150 species in comparison to approximately 30 in Puerto Rico (personal observations). A recent study found that the presence of the invasive (in Puerto Rico) ant *Wasmannia auropunctata* is negatively related with the abundance of *Anolis* spp. in Puerto Rico (Perfecto and Vandermeer 2020a; Perfecto et al. 2021). Additionally, patches with high densities of *W. auropunctata* and low densities of *Anolis spp* had higher number of CLM mines, than patches with low densities of *W. auropunctata* and high densities of *Anolis* spp. (Perfecto et al. 2021). The reduced co-occurrence, of *W. auropunctata* and *Anolis* spp., suggests an antagonistic interaction between the two, where *W. auropunctata* may be modifying the behavior of the lizards, mainly by harassing them, causing them to flee the areas where it is dominant, consequently reducing anoline predation on the CLM (Perfecto et al. 2021). Comparative studies of this relationship are not available due to the relative rarity of both Anoline lizards and *W. auropunctata* in Mexico (part of its native range).

The negative effects of exotic ant species may also affect the community of native ants which plausibly could be better at the controlling of the CLM. Preliminary results of surveys on the CLM in coffee agroecosystems suggest higher damage by the CLM in plants dominated by *W. auropunctata* or *Solenopsis invicta* compared to plants dominated by native ants (personal observations). We speculate that the differing status of CLM in Mexico and Puerto Rico may be related to the diversity of predators in each system, clearly linked to well-known patterns of biodiversity on islands.

12.4 The Scale Insect System

Casual observations leave little doubt that the green coffee scale (GCS) has dramatically different population dynamics on the mainland versus the island. In Mexico, there are frequently significant concentrations of GCS on leaves and some bushes are completely covered with them, something very rarely seen in Puerto Rico. However, in both cases any local concentration of scale insects is associated with some species of mutualistic ants (Rivera-Salinas, unpublished data). Particularly large concentrations of scale insects are associated with the ant *Azteca seriaceasur* in Mexico (Perfecto and Vandermeer 2006; Vandermeer and Perfecto 2006; Livingston et al. 2008; Vandermeer and Perfecto 2019), although a variety of other species also provide mutualist havens albeit not to the same extent as *A. seriaceasur*.

There is a strong spatial component associated with the scale insect in Mexico which is not easily observable in Puerto Rico. In the former site, the beetle *Azya orbigera* is a voracious predator of both larvae and adults of the GCS. Beetle larvae produce waxy filaments that allow them to evade attack by the ants and thus find much sustenance on leaves and branches containing large numbers of GCS. Beetle adults, contrarily, have no such protection and thus have no protection against the ants as they seek out their food, (Vandermeer et al. 2010). These basic natural history observations set up a dramatic expectation regarding spatial patterns. GCS disperse by wind (the first instar larvae are known as crawlers, the main dispersal form). Consequently, some individuals find themselves at a distance far removed from the mother scale who, for the most part, must have been under the protection of one of the ant protectorates. If the distance is too great, the probability of being attacked by the adult predatory beetle is far greater than that of being discovered by an ant worker and thus coming under the protection of the ants. But the extant range of ant foraging is itself partly dependent on where the concentrations of GCS happen to be. Thus, first instar GCS, probably dispersing more or less randomly from their nascent patch. Those that disperse from within a high-density patch are not likely to encounter predatory beetles immediately, since they will most likely remain within the spatial area tended to by their ant associates and thus remain under ant protection. Contrarily, those whose dispersal is initiated from an area removed significantly from a high-density patch, perhaps from a mother GCS that has managed, by chance, to escape beetle predation even though not under ant protection, are not likely to immediately find ant protectors. This basic structure leads to the prediction that the pattern in the field should be "hysteretic," with two critical transitions, one from very low scale populations jumping to very high populations and another from very high

GCS populations jumping to very low populations, with a hysteretic zone and alternative equilibria, in between. This expected pattern is evident in Mexico associated with the ant *A. sericeasur* (Vandermeer and Perfecto 2019) but clearly not found associated with any of the ant species in Puerto Rico (unpublished data).

Under some circumstances ant protective effects on GCS may not have to do with predation, but with the indirect effects of removing the honeydew produced by the GCS, effectively making survival and instar metamorphosis more efficient by reducing incidence of fungi covering the adults (Jha et al. 2012). Although direct evidence is lacking, the fact that the ants (in the case of *A. seriaceasur* in Mexico) remove honey dew at a rate sufficient to avoid build-up of secondary fungal growth may also affect the build-up of the scale pathogen *Lecanicillium lecanii*. It is certainly plausible that the GCS, under protection from the ants, are "cleaned" regularly by the ants, until a critical transition is reached where the ants cannot keep up with excessive honeydew production, thus leaving some individual GCS particularly susceptible to attack by the fungal pathogen, clearly a mechanism for the spatial patterns observed (Vandermeer and Perfecto 2019). However, other studies suggest that the ants have an opposite effect by promoting to some extent the dispersal of *L. lecanii* conidia (Jackson et al. 2012a).

The relationships between ants, GCS, and the latter's pathogens observed at the mainland sites appear to be considerably different in Puerto Rico. In Mexico *L. lecanii* attacking GCS is clearly density-dependent as would be expected for any disease (Jackson et al. 2012a). In contrast, casual observations in Puerto Rico, plus testimony from farmers, suggest that the dramatic epizootics of *L.lecanii* on scale insects are virtually independent of the density of the scale insects. Indeed, in Puerto Rico it is relatively common to find coffee leaves with a single GCS insect completely covered with *L. lecanii*, an observation rarely if ever made in Mexico. Yet, it seems that the biodiversity of sap-sucking Hemipterans is actually quite large in Puerto Rico (personal observations), even though the particular species, *C. viridis*, never seems to gain the prominence it does in Mexico. The potential for production of L. lecanii would thus seem larger in Puerto Rico, a point of some importance as we turn to a discussion of the coffee leaf rust system.

12.5 The Coffee Leaf Rust System

The coffee leaf rust (CLR) is a fungal pathogen that has followed coffee to nearly every region of cultivation, having just recently reached Hawaii, where initial reports suggest devastating impacts on production. From early epidemics of CLR in Ceylon in the late 1800s to the more recent "big rust" epidemic in Central America in 2012, the variable and often destructive dynamics of this fungal pathogen around the globe has long puzzled plant pathologists and agricultural practitioners. Understanding the underlying mechanisms driving CLR infection dynamics has proven elusive although it is an area of active research (Avelino et al. 2006, 2012; Belachew et al. 2020). While an intersection of ecological, economic, and sociological factors likely contributed to the realization of the "Big Rust" epidemic in Central America

(McCook and Vandermeer 2015; McCook 2019), it has been difficult to pinpoint a singular or most dominant contributing factor. Some research suggests the potential importance of abiotic factors in structuring the dynamics of the pathogen (Avelino et al. 2015), but other research has shown that climatic factors alone are insufficient (Bebber et al. 2016). Our team's work (Jackson et al. 2012a; Vandermeer et al. 2014, 2019; Hajian-Forooshani et al. 2016, 2020, 2023), in contrast with many phytopathologists, seeks to understand the system with a focus on the top-down components, that is, the natural enemies.

The CLR and its community of natural enemies has notably distinct dynamics on a mainland site (Chiapas, Mexico) compared to an island site (Puerto Rico) (Hajian-Forooshani et al. 2016, 2023). The two sites seem to experience dramatically differently dynamics of CLR even though they have similar timelines in terms of both the arrival of coffee and the pathogen (cite?). Southern Mexico recently experienced a devastating CLR epidemic while Puerto Rico has yet to experience an island-wide epidemic, although similar local epidemics have occurred in the past (at the level of a single farm or closely grouped farms). It has been suggested that top-down trophic control of the CLR is far more important in Puerto Rico than in Mexico (Hajian-Forooshani et al. 2016, 2023; Hajian-Forooshani and Vandermeer 2022). That is, the community of natural enemies contains the main controlling agents keeping the CLR pathogen at relatively benign levels in Puerto Rico but fails to do so in Mexico. As to why this is the case or how extensive the pattern may be, we await further research results and hope to stimulate similar research agendas in other areas of coffee cultivation.

Two of the natural enemies are shared on the mainland site and the island: *Lecancillium lecanii*, a generalist fungal parasite that attacks both other fungi and insects, and *Mycodiplosis hemileiae,* a fly larva that is a rust specialist (attack rates by *L.lecanii* and *M. hemileiae* were 60% and 32.2% in Puerto Rico but only 8.7% and 3.8% in Mexico in one study; Hajian-Forooshani et al. 2016). In some farms on Puerto Rico over 80% of the coffee trees had *L. lecanii* attacking CLR year-round, while in Mexico *L. lecanii* exhibited strongly seasonal dynamics where an upper limit of only about 20% of plants would have *L. lecanii* for a short period of time (Hajian-Forooshani et al. 2023). The dynamics of the natural enemy community in Puerto Rico are notably more complicated than those in Mexico, due in part to Puerto Rico having two additional common natural enemies, namely, a group of gastropods which consume CLR spores (Hajian-Forooshani et al. 2020), and a community of mites that consume and reproduce in lesions CLR spores (Hajian-Forooshani and Vandermeer 2022; Hajian-Forooshani et al. 2023).

The dramatically different dynamics of shared consumers in both regions begs the question of what factors may be driving these differences. Similar to other facets of the main-land/island coffee agroecosystems elaborated in this chapter, the context in which these tri-trophic modules are embedded impacts their dynamics. Figure 12.3 shows the hypothesized interaction networks (informed by a combination of laboratory experiments and field observations) centered on the CLR in Mexican and Puerto Rican agroecosystems.

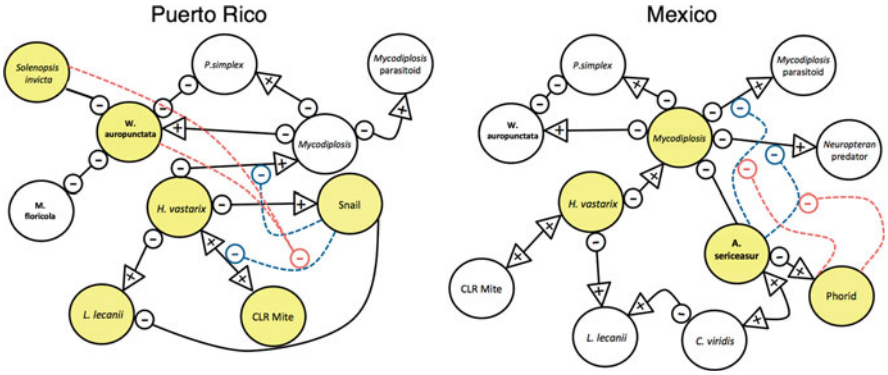

Fig. 12.3 The regionally distinct communities associated with the coffee leaf rust in Mexico and Puerto Rico. Links between organisms denote interactions, with arrowheads (triangles) showing positive effects and circles negative effects. Note that interaction networks are constructed from observations by the authors in both field and laboratory settings. Dotted blue lines are trait-mediated indirect interactions, dotted red lines represent trait-mediated indirect interaction cascades. Yellow filled circles represent relatively common organisms in each agroecosystem. *Solenopsis invicta*, *Wasmannia auropuctata*, *Pseudomyrmex simplex*, *Monorium floricola*, and *Azteca sericeasur* are all ants

Just as in other tri-trophic components of the coffee agroecosystems discussed in this chapter, ants play an important role in structuring the tri-trophic modules associated with CLR (see Fig. 12.1). In Mexico, *Azteca sericeasur*, whose spatial pattern sets the stage for a variety of other interactions in the system (Vandermeer et al. 2008, 2019), influences the dynamics of the CLR in complicated and context-dependent ways. This is illustrated by the simultaneous positive and negative forcing *Azteca* has on different components of the natural enemy-CLR-coffee tri-trophic interaction. On the one hand, prior work has shown how *Azteca* builds populations of scale insects which are alternative resources for *L. lecanii*, resulting in local increases in *L. lecanii* which attack CLR (see Vandermeer et al. 2010; Jackson et al. 2012a, b, 2016). On the other hand, preliminary surveys suggested that sites with *Azteca* were associated with reduced numbers of *M. hemileiae* (Hajian-Forooshani et al. 2016). This suggests that *Azteca* has both indirect positive (through promoting *L. lecanii*) and indirect negative (through reducing *M. hemileiae*) effects on coffee. Preliminary analysis suggests that the net effect of *Azteca* on the CLR tends to be indirectly negative on coffee—sites with *Azteca* are associated with higher amounts of CLR. We speculate that this may be the result of a trophic cascade whereby *Azteca* reduces *M. hemileiae* thus releasing CLR locally in space.

While *Azteca* is absent in Puerto Rico, other ants (especially *S. invicta*) fulfill similar roles ecologically, with clear implications for the dynamics of the CLR via their effects on the natural enemies. Additionally, the contexts of agroecosystem management have important implications for the dynamics of these complex interaction networks (see Fig. 12.1). One such management factor that we hypothesize is important in structuring tri-trophic dynamics is the intercropping of citrus with coffee. In large-scale surveys across the coffee producing region of Puerto Rico, it is evident that inter-cropping with citrus influences the ant communities found on coffee farms as well as the density of their *Hemipteran* mutualist partners. Furthermore, the CLR experiences higher levels of attack by *L. lecanii* when citrus is present (unpublished data). Together, results from these surveys suggest that citrus promotes elevated amounts of *L. lecanii* which then spill over to attack the CLR.

While multiple studies now highlight differences in the relative abundance of natural enemies when comparing Puerto Rico to Mexico, there are still gaps in our understanding of the implications of these differences for CLR dynamics. While our working hypothesis is that these differences in enemy communities drive the large-scale qualitative dynamics of the CLR, a detailed understanding of the action of natural enemies is still an area of active research. For example, the natural enemies *M. hemelia*, *L. lecanii*, and the rust mites are all associated with a reduction in spore load as the CLR progresses (unpublished data). Furthermore, multiple co-occurring natural enemies seem to have a synergistic effect in reducing CLR-spores. These observations are currently under study.

12.6 Conclusion

We presented a comparison of the particular case of a novel tri-trophic ecosystem as it exists at a site in southern Mexico as compared to the island site of Puerto Rico. Even though the basic elements of the system are the same (four particular pest species, which is to say the herbivore level of the tri-trophic structure plus a taxonomically diverse yet functionally similar natural enemies, which is to say the predator level of the tri-trophic structure), we see dramatic differences between regions. Although our studies have been concentrated at only two sites, our experience in other neighboring sites (Cuba in the Caribbean and other large farms in Mexico, Nicaragua and Costa Rica) suggest to us that these patterns are indeed representative of a mainland/island comparison. Using a consistent "habitat background" (the ecosystem called the coffee farm) and a stable and consistent lowest trophic level (the coffee plant), it seems that the trophic connections we have uncovered are representative of how this level of trophic complexity plays out in an island/mainland framework.

Casting these observations in a classic trophic dynamic framing, one important and highly cited ecosystem function is "control from above," which is to say, the control of a population (its size, distribution, rate of growth, etc.) is affected from the trophic level above it—predators control prey, herbivores control plants, pathogens control hosts. In particular, the control of herbivores by the community of predators and pathogens is an essential ecosystem function and clearly an ecosystem service when dealing with agroecosystems—the biological control of pests. Furthermore, it is a striking example of how basic ecological knowledge can enrich our understanding of an applied system leading, we propose, to an enlightened approach to the fundamental problem of pest control.

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Epilogue

The content of this volume spans diverse types of research on plant-herbivore interactions on islands from around the world, ranging species- to community-level, different spatial and temporal scales, as well as basic to more applied work. These investigations provide different and yet complementary perspectives on ecological and evolutionary patterns and processes relating to plant-herbivore interactions on islands. For example, reported patterns often depart from classical expectations of lower herbivore pressure (and lower plant defences) on islands and point to strong present or past pressure by native herbivores, as well as shifts in suites of plant traits selected upon on islands. In addition, some types of plant traits are seemingly more common on islands than on mainland and this relates to differences in herbivore composition, in some cases strongly dictated by herbivore extinctions. At the same time, these studies also highlight our poor understanding of the defensive role of many physical and chemical plant traits on islands and whether these have evolved due to herbivore pressure or some other factors specific to islands. In addition, this volume also illuminates on the temporal and spatial processes driving herbivory on islands, including the role of metapopulation and successional dynamics. Indeed, given their physical features (isolation, clear boundaries), islands are particularly well suited to study the influence of temporal and spatial processes underlying herbivory patterns. In this case, studies show how temporal build up in herbivory on islands shapes plant trade-offs between defences and reproduction and in turn propagule pressure spatial dynamics which shape plant island colonization. We are only starting to understand how herbivory plays into these spatiotemporal dynamics. Finally, this volume provides novel perspectives on the influence of multi-trophic interactions, also with a focus on factors shaping predation pressure on islands and how these might differ relative to mainland. Importantly, they highlight the role of seasonal patterns of resource inputs to island systems which shape food webs and ecosystem function. They also point to how spatial changes in predator abundance or species composition shape predation pressure on herbivores on islands relative to mainland, pointing, for example, the key role of clinal variation in abiotic factors. We still, however, lack a good understanding of the drivers of insularity effects on predator communities and

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https://doi.org/10.1007/978-3-031-47814-7

behaviour shaping predation pressure, and often their consequences for plants (e.g. defences) remain poorly studied.

Following from these findings, we next develop what in our view are important research views and approaches for future work. In each case, we provide examples of how their adoption can illuminate and build on patterns reported in this volume.

A Multivariate View on Plant Defences on Islands

Plant defence research has emphasized the importance of assessing multiple (rather than single) traits to examine patterns of trait co-expression patterns (i.e. syndromes) and how different traits jointly contribute to plant defence (Agrawal and Fishbein 2006; Moreira et al. 2020). Adopting this approach is especially important and timely in island ecology research to uncover plant defensive syndromes associated to islands. It has been used by a few with respect to island plant traits associated with resource use and acquisition (García-Verdugo et al. 2020), but its application to anti-herbivore defensive traits is lacking (Moreira and Abdala-Roberts 2022). This could allow to test or detect the potential breakdown of mainland syndromes as a function of differences in herbivore abundance or composition, including both extant and extinct fauna granted that historical data are available. This would also illuminate on plant trait patterns reported in this volume (see García-Verdugo et al. chap. 4), namely to better understand plant bottom-up controls on herbivory via plant resource allocation trade-offs between defensive and functional or reproductive traits which in turn shape propagule pressure (e.g. Hambäck et al. chap. 8), as well as the evolution of complex defensive phenotypes in plants due to selection by different groups of herbivores, extant and extinct (e.g. see Barton et al. chap. 2, Heinen and Borregaard chap. 3) as well as introduced ones (e.g. Capó et al. chap. 6).

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Understanding Variability in Top-Down Pressure

The drivers of variation in predation have been largely ignored in many island systems, even though they can provide particularly well-suited arenas to understand the factors that drive predation pressure and its impacts on herbivory and plants (Moreira and Abdala-Roberts 2022). Past work has argued that top-down effects of predators on herbivores should be weaker on islands than on mainland because predators are more prone to extinction than lower trophic levels (e.g. due to smaller population sizes) (Holt 2010), or because herbivores are better able to escape from their natural enemies on islands upon feeding on new host plants found in insular systems (Denno et al. 1990). Additionally, authors of this volume report on the effects of physical disturbances and seasonal inputs shaping predation pressure, either directly or via changes in bottom-up forcing (e.g. in Spiller et al. chap. 10, Hambäck et al. chap. 8). More research is needed on factors involved in spatial (e.g. colonization dynamics, environmental filtering, or biotic and abiotic resource availability affecting predator abundance) or temporal (e.g. seasonal changes in habitat features affecting predation) processes. This will yield a deeper mechanistic understanding into spatiotemporal variability in predation explaining herbivory and plant traits on islands, and differences relative to mainland (e.g. in Vandermeer et al. chap. 12).

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Collecting Multi-Trophic Data

By necessity, plant-herbivore research often involves measuring both plant traits and herbivory to explain the role of herbivores in shaping variation in plant defence allocation and ultimately their evolution (Marquis 1992; Agrawal 2007; Futuyma and Agrawal 2009). Still, tests of insularity effects on herbivory and plant defences have often failed to incorporate both types of data, making it difficult to test ecological and evolutionary predictions (Moreira et al. 2021). Adding to this, tri-partite measurements also including predation or some proxy of predation pressure are even rarer but ultimately needed to more robustly test theory. One of the few exceptions is work on the Bahamian islands, synthesized by Spiller et al. (chap. 10), showing dampening of predator effects on plant defences via herbivory suppression. By integrating data across trophic levels we can better understand how insularity shapes herbivory and plant defences, potentially contributing to explain many of the patterns reported in this volume.

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Identifying Abiotic Drivers across Trophic Levels

We also call for future work with increased emphasis on abiotically-driven variation in ecological communities and species interactions. This can illuminate on the causes behind abiotically-driven clinal variation in herbivory and predation within and across islands as well as relative to mainland (e.g. Sam et al. chap. 11), the identification of abiotic factors (or factor combinations) with highest explanatory power (Moreira et al. chap. 9), and the role of abiotic disturbances (Spiller et al. chap. 10). Assessing these abiotic influences across scales (e.g. microhabitat to landscape, within and across islands or mainland) can shed light on patterns reported in several chapters of this volume.

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https://doi.org/10.1007/978-3-031-47814-7

Merging Biogeography and Evolutionary Ecology of Herbivory

Historical and broad-scale factors such as geological age, history of colonization, island size, physical heterogeneity, and geographical isolation have been well studied with respect to their effects on community structure, speciation, and population ecology (Losos and Ricklefs 2009; Valente et al. 2014). However, there is little work on the biogeographical drivers of herbivory (and other interactions as well) on islands, reflecting the separate paths biogeographic and evolutionary ecology research have followed. For example, recent work has shown macroclimatic variation (Weigelt et al. 2016), productivity and soil type (Pillon et al. 2010), and species invasions (Craven et al. 2019) shape community structure and ecosystem processes on islands, but little do we know how they affect herbivory (Moreira and Abdala-Roberts 2022) and its resulting influences on communities and ecosystems. Moreira et al. in this volume (chap. 9) provide one of the few attempts testing the influence of island physical features and macroclimatic variation on herbivory patterns on European islands. We are yet, however, to uncover macroecological drivers of herbivory on islands.

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