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PERSPECTIVE

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A roadmap for future research on insularity effects on plant–herbivore interactions

Abstract

State of the art: Theory predicts that herbivore pressure should be weaker on islands than on the mainland, owing to lower herbivore abundance and diversity because of dispersal constraints and environmental filtering. As a result, plants on islands should invest less in defences against herbivory. Although early empirical studies supported these predictions, recent systematic island–mainland comparisons have questioned this paradigm, with some studies reporting either no difference between islands and mainland or higher herbivory and plant defences on islands. Current data therefore appear to be unsupportive of predictions on insularity effects on plant–herbivore interactions, calling for more research to reassess predictions and to test underlying mechanisms for observed patterns.

Research opportunities: To meet this challenge, a renewed research programme based on the accrual of studies with specific features is needed. These should include more robust experimental designs with replication within and across systems, integrative and more nuanced assessments of plant defensive phenotypes and herbivory, a food web approach that considers the multitrophic context in which plant–herbivore interactions are embedded, and a consideration of historical factors (e.g., island origin and biogeographical factors, defensive anachronisms).

Outlook: This new research programme will require integration of evolutionary ecology research on plant–herbivore interactions with island biogeography, palaeoecology and community ecology to understand the influence of factors acting at different scales, from local factors driving herbivory and plant defences to historical processes and regional drivers of species composition determining species traits and their interactions.

1 | STATE OF THE ART OF INSULARITY EFFECTS ON PLANT–HERBIVORE INTERACTIONS

Islands cover close to 5% of the land surface of the planet but sustain *c*. 30% of the species found in biodiversity hotspots and have extremely high species endemism (Myers et al., 2000). In addition, it is estimated that insular endemic floras comprise a staggering 20% of the diversity of vascular plant species described to date (Tershy et al., 2015; Veron et al., 2019). These patterns of diversity and species composition were the subject of much interest for early naturalists and ecologists (MacArthur & Wilson, 1967), and modern research has provided evidence on the ecological and evolutionary processes acting under long-term isolation that have promoted speciation and diversification on islands (Whittaker et al., 2017). Evolutionary processes include local adaptation combined with founder effects that promote divergence among islands or between islands and the mainland, resulting in insular diversification (Losos & Ricklefs, 2009; Schluter, 2001). In addition, ecological factors and environmental filtering shape community assembly as a function of species traits in relation so insular biotic and abiotic conditions (Carvajal-Endara et al., 2017; Craven et al., 2019). Within each of these contexts, species interactions play a major role in shaping insular population dynamics and maintenance of biodiversity, on the one hand (Pringle et al., 2019; Schoener et al., 2016), and diversification via adaptive radiations, on the other (Grant & Grant, 2006; Losos et al., 1998; Percy, 2003). Understanding the effects of species interactions on species variation, biodiversity and ecosystem stability is more important than ever to conserve and manage insular species and ecosystems, as because these are being impacted disproportionately by global change (Harter et al., 2015; Russell & Kueffer, 2019).

Herbivory is a ubiquitous interaction across the globe (Karban, 1992; Turcotte et al., 2014) and has substantial effects on insular community structure and ecosystem function (Fuller et al., 1984; Terborgh et al., 2001), as well as on insular plant and herbivore trait evolution and diversification (Burns, 2019; Carvajal-Endara et al., 2020). Theory and early empirical work posited that herbivore pressure should be weaker on islands than on mainland as a result of lower herbivore abundance and diversity owing to dispersal constraints and environmental filtering (Atkinson, 1989; Carlquist, 1974; Grant, 1998). Consequently, plants on islands are expected to be less well defended, and several observational studies have reported findings in line with this prediction (e.g., Bowen & Van Buren, 1997; Burns, 2014; Carlquist, 1974; Vourc'h et al., 2001). However, a number of studies conducted during the last decade have producd mixed findings (Table 1); some have reported no difference between islands and the mainland, whereas others have found higher herbivory and/or plant defences on islands (e.g., Burns, 2019; Monroy & García-Verdugo, 2019; Moreira et al., 2019; Pardo et al., 2018). Further, a recent meta-analysis of 21 studies comparing mainland versus insular plant populations found that vertebrate herbivory (mainly by introduced mammals) was greater on islands. Invertebrate herbivory and physical and chemical plant defences (see Glossary) did not differ between islands and the mainland (although physical defences tended to be higher on islands) (Moreira et al., 2021). Thus, although studies remain limited, the patterns obtained so far, based on available data, do not provide a consistent picture and, in many cases, are unsupportive of predictions. Further research is called to achieve greater generalization and reassess the predictions and underlying mechanisms shaping current patterns.

2 | KNOWLEDGE GAPS AND RESEARCH OPPORTUNITIES

We call for a reassessment of current theory and a new phase of research on insularity effects on plant–herbivore interactions. Studies should fill key gaps in knowledge while conducting robust and systematic comparisons to test for insularity effects unambiguously and to identify factors underlying the observed patterns. Below, we describe what we believe are some of these key gaps or limitations and the corresponding challenges to be met. Many of the points made for plant–herbivore interactions are applicable to other types of ecological interactions (e.g., pollination, seed dispersal) for which similar limitations in insularity research exist. In this sense, the proposed research programme addresses to a large extent the effects of insularity on species interactions as a whole.

2.1 | Study design features

2.1.1 | Research gap

Most studies to date have been restricted to specific systems or regions (80% in temperate areas; Figure 1) and often to comparisons using a single plant species and one island versus mainland site (Table 1; Moreira et al., 2021). Although meta-analytical tools can be used to compare patterns across multiple systems, there are intrinsic limitations in doing so, and reaching strong conclusions is frequently limited by heterogeneity among studies.

2.1.2 | Challenges

Individual studies that span multiple systems and regions are needed to overcome system-specific idiosyncrasies. By using more robust designs (i.e., island and mainland sites within and among regions; Figure 2a) and consistent methodologies, one can increase inference and reach stronger conclusions about the effects of insularity on herbivory and plant defences. In this sense, we identify several basic study features needed to address this challenge: (1) compare multiple mainland and island sites and include multiple islands in each system; (2) conduct these replicated comparisons across systems within a region (e.g., Mediterranean basin) and in multiple regions; and (3) use consistent methodologies across systems (e.g., plant tissue sampling, herbivory measurements and standardized chemical analyses). Ultimately, data collected across systems and regions will allow more robust broad-scale (and even global) analyses. Geographically broader studies can also start to disentangle different sources of variation (e.g., historical or physical factors; see next subsection) in plant defences within and among systems.

2.2 | Physical and historical factors

2.2.1 | Research gap

The influence of physical and biogeographical features on mainland–island differences in plant–herbivore interactions has been little studied. Specifically, there are key differences in island physical features and geological origin (e.g., continental vs. oceanic islands), in addition to historical factors that shape species composition and interactions on islands versus the mainland (Gillespie, 2016; Valente et al., 2014). For example, recent work has highlighted the importance of considering macroecological factors, such as island size and abiotic factors, in addition to historical processes related to island age or colonization history (Craven et al., 2019), to understand contemporary patterns of plant (and herbivore) diversity and composition, which, in turn, determine species interactions and vice versa. More recent historical factors also include human impacts upon arrival in insular systems in the last millennia or centuries. The vertebrate communities presently found in many insular systems are very different from those found before human arrival, with many species of vertebrate herbivores currently extinct. As a result, many insular plant species exhibit defensive (or seed dispersal) anachronisms, such as in New Zealand forests (Burns, 2016, 2019) or mediterranean (e.g., Balearic and Canary Islands) shrublands (Capó et al., 2021; Cubas et al., 2019; Irl et al., 2012) shaped by extinct species of birds or ungulates, respectively. Likewise, introductions of non-native mammals in the last few centuries could also affect patterns of plant defence investment (Moreira et al., 2021).

2.2.2 | Challenges

Research is needed to address the macroecological and biogeographical factors shaping plant–herbivore interactions on islands. To fill this gap, we call for plant defence and herbivory studies that: (2) account for historical and physical features of islands, such as size, isolation and geological age (*sensu* island biogeography theory, see Glossary; Figure 2b); (2) consider the influence of abiotic factors shaping plant traits and herbivory (e.g., climate, soil conditions); and (3) adopt palaeoecological approaches to uncover defensive

TABLE 1 Review of the literature reporting plant defences (chemical or physical traits) and herbivory (invertebrate or vertebrate) in mainland versus insular plant populations (Moreira et al., 2021)

				Plant defence		Herbivore type	
Study identity	**References**	**Number of islands**	**Plant species**	**Chemical**	**Physical**	**Invertebrate**	**Vertebrate**
1	Moreira et al. (2019)	Multiple	*Quercus ilex*	+		−	
2	Monroy and García-Verdugo (2019)	Multiple	*Periploca laevigata*	+			
3	Bowen and Van Buren (1997)	Single	Six species	−	−		+
4	Meredith et al. (2019)	Multiple	Several species		0		
5	Pardo et al. (2018)	Multiple	*Prunus lusitanica*	+			
6	Kavanagh (2015)	Multiple	11 species		−		
7	Watts et al. (2011)	Multiple	*Eschscholzia californica*	−			+
8	Salladay and Ramirez (2018)	Single	10 species	0	−		+
9	Bond and Silander (2007)	Single	several species		+		
10	Monagan Jr et al. (2017)	Single	*Coffea arabica*			0	
11	Hoan et al. (2014)	Single	*Argemone glauca*		+		
12	Shimazaki and Miyashita (2002)	Multiple	*Viburnum dilatatum*	−	−	+	
13	Farnsworth (1991)	Multiple	Two species			+	
14	Hambäck et al. (2004)	Multiple	*Vaccinium myrtillus*				+
15	Bryant et al. (1989)	Single	*Betula pubescens*				+
16	Suissa and Barton (2018)	Single	*Argemone glauca*		+		
17	Vourc'h et al. (2001)	Single	*Thuja plicata*	−			+
18	Burns (2014)	Multiple	16 species		−		
19	Pardo and Pulido (2017)	Multiple	*Prunus lusitanica*		+	+	
20	Burns (2019)	Multiple	Three species		−		
21	Burns (2016)	Multiple	*Aciphylla dieffenbachia*		−		

Key: + = increased plant defences or herbivory on insular plants; − = decreased plant defences or herbivory on insular plants; 0 = no insularity effects on plant defences or herbivory

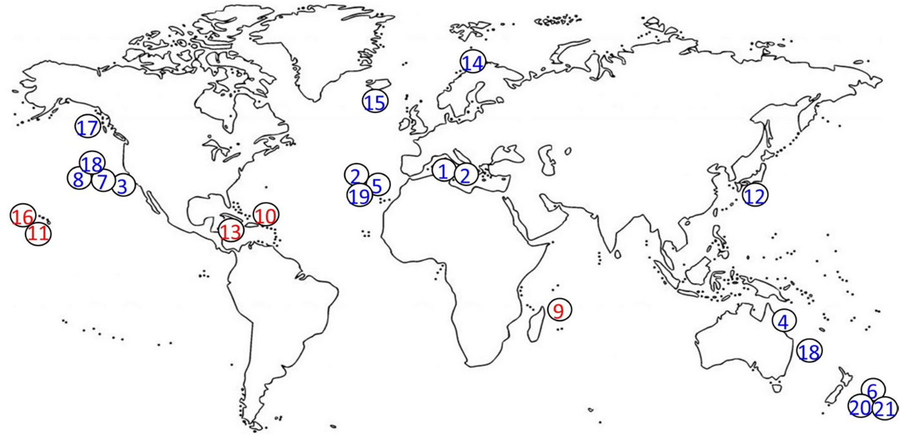

FIGURE 1 Map showing the main insular systems of the 21 studies used in a recent meta-analysis comparing plant defences and herbivory in mainland versus insular plant populations (Moreira et al., 2021). The numbers in circles represent the study identities included in Table 1. Red numbers represent tropical regions (those between 23.5° N and 23.5° S, i.e., between the tropics of Cancer and Capricorn) and blue numbers temperate regions (those from 23.5 to 66.5° N and from 23.5 to 66.5° S, i.e., between the tropics and the polar circles)

anachronisms. This research agenda could take advantage of systems for which historical processes are well understood (e.g., Hawaiian archipelago, Galapagos Islands, Canary Islands, some Mediterranean islands) to test concrete hypotheses about the influence of biogeographical factors on present-day variation in plant defences and herbivory. This knowledge could then inform subsequent work in other less-studied systems, in addition to broader-scale (and even global) analyses to identify commonalities and differences.

2.3 | Integrative assessments of plant (and herbivore) defences

2.3.1 | Research gap

Work on plant defences, including insularity studies, has usually considered single plant traits, whereas simultaneous assessments of multiple defensive traits or strategies are less common (Table 1; Figure 1). Research has shown that although plant defences are costly and that their redundancy can select against the expression or maintenance of multiple defences (Herms, 2002), in many cases plants express multiple defences simultaneously as a result of selection favouring the co-expression of a broad array of traits to cope with multiple attacking herbivore species (Pellissier et al., 2016; Whitehead et al., 2021). Accordingly, this can result in so-called defence syndromes (see Glossary; Agrawal & Fishbein, 2006; Moreira et al., 2020).

2.3.2 | Challenges

Research needs to move beyond the study of single plant traits to assessing multiple traits and defensive syndromes to achieve more realistic and integrative assessments of the effects of insularity on plant defensive phenotypes (Figure 2c). In this sense, we identify three research opportunities to address this gap: (1) start by measuring multiple types of plant defensive traits (e.g., physical, chemical and nutritional) and strategies (e.g., constitutive vs. induced defences, tolerance vs. resistance); (2) study multiple plant taxa simultaneously within each system (with appropriate controls for life-form, genetic relatedness, etc.) to increase inference and test for trait co-expression patterns within and among species (i.e., syndromes); and (3) in doing so, use multivariate statistical tools (ordination techniques and co-inertia analyses; Galmán et al., 2021; Pellissier et al., 2016) to identify and test explicitly for variation in plant defences under a multivariate perspective. Likewise, increased attention to herbivore counter-defences and plant–herbivore co-evolutionary processes shaped by insularity is also warranted to gain a more integral view of how plant–herbivore evolution is shaped by insularity. In both cases, experimental work to control for environmental variation and test for genetically based variation (e.g., greenhouse, common gardens) and to manipulate plant defences (e.g., induction experiments, herbivore bioassays) is essential to complement field-based information and to assess whether trait complexes or syndromes underlie reistance.

2.4 | Invertebrate herbivory and guild comparisons

2.4.1 | Research gap

Insularity research to date has been strongly biased toward vertebrate herbivory (close to 70% of the studies; Table 1; Moreira et al., 2021). However, invertebrate herbivory, which can be equally or even more ecologically important, may exhibit patterns that do not necessarily match those for mammals or other vertebrates (e.g.,

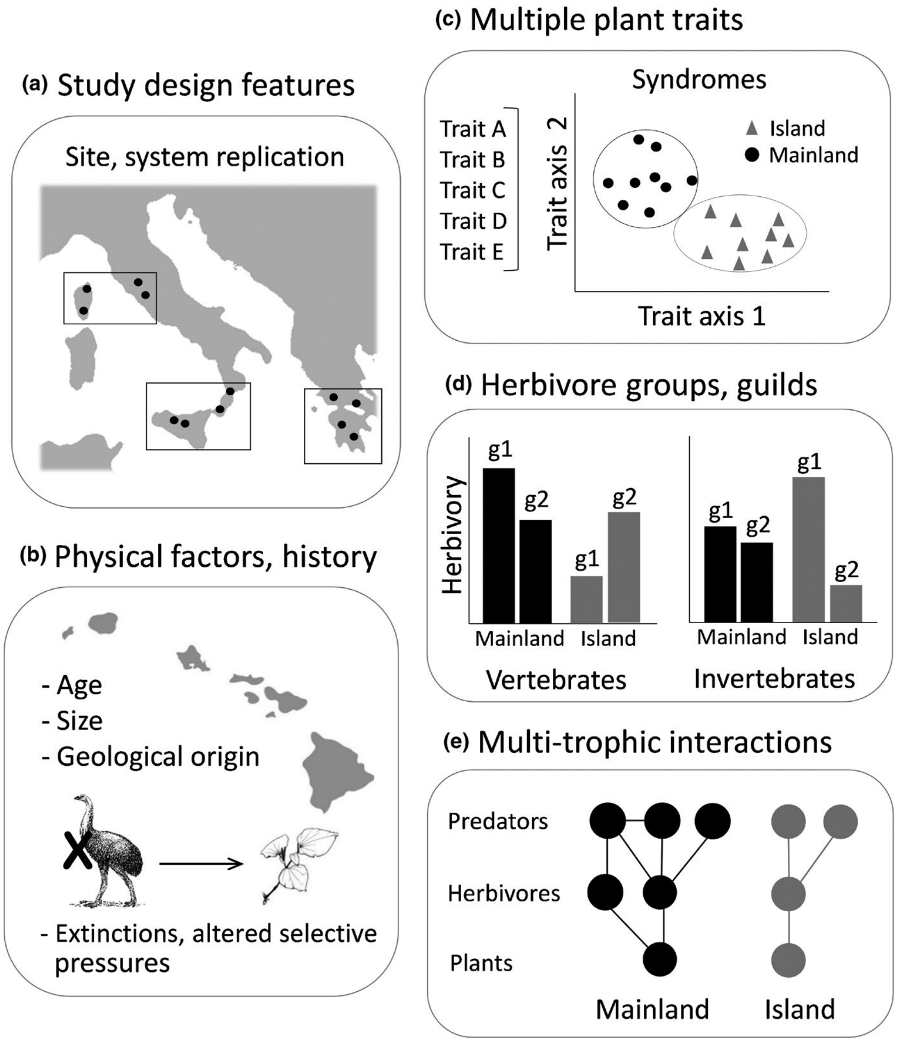

FIGURE 2 Diagram depicting novel features to incorporate in studies on insularity effects on plant–herbivore interactions. (a) Previous studies have frequently compared the mainland with a single island and have lacked site replication within each environment; more robust designs are needed that include multiple islands within a given system and replicate sites (dots = sites) on both the mainland and islands and, when possible, multiple systems. (b) Island physical features (e.g., size, age, geological origin) and historical factors (e.g., history of colonization, species extinctions) are usually not considered and can shape present-day patterns of herbivory and plant defences. (c) Most work has focused on one or a few plant defensive traits separately; studying multiple plant defensive traits and an explicit analysis of multivariate patterns of expression (defensive syndromes) are needed for a comprehensive assessment of the effects of insularity on plant defensive phenotypes. (d) Historically, studies have been biased toward vertebrate herbivory (e.g., mammals) and the impacts of single herbivore species; work that addresses invertebrate herbivory is needed, in addition to measurements that differentiate damage by different vertebrate and invertebrate herbivore species or guilds (g = guild). (e) Finally, most work has not considered the food web context in which plant–herbivore interactions are embedded; a consideration of multi-trophic interactions (e.g., predator effects on herbivores and plants, intraguild predation) is required for a robust understanding of how insularity affects plant defences and herbivory

birds, reptiles) owing to differences in animal dispersal ability, abiotic tolerance and dietary breadth, in addition to community-level differences (i.e., species composition and diversity) (Burns, 2019). For example, relative to invertebrates, most vertebrate herbivores are highly generalist in their eating habits and would therefore overcome reductions in host-plant availability owing to lower plant diversity on islands. In addition, mainland insect species pools are highly diverse and presumably have greater species redundancy than vertebrate pools (Gillespie & Roderick, 2002). This could buffer against herbivore species loss (e.g., owing to reduced area) or low dispersal (owing to isolation) on islands or could increase the probability of islands receiving herbivore species that can feed successfully on insular plants (i.e., a sampling effect; Schoener, 1989), possibly leading to weaker effects of insularity on invertebrate (e.g., insect) herbivory. Although these expectations could apply to many systems, it is also important to recognize that there are several systems in which native insular herbivores, both invertebrate (e.g., crabs) and vertebrate (e.g., tortoises, birds), exert overwhelming pressure on insular plants (Garzón-Machado et al., 2010; Terborgh, 2010). Accordingly, predictions on insularity effects and expected differences by herbivore group could change in these systems depending on the patterns observed on islands for specific groups of plants and animals.

2.4.2 | Challenges

The above examples highlight the uncertainty about invertebrate herbivore responses to insularity and how they compare to vertebrate herbivore patterns (Figure 2d). In this regard, we identify two study features to address this gap: (1) conducting simultaneous measurements of herbivory by vertebrates and invertebrates; and (2) within each group, assessing herbivory by different species or feeding guilds (e.g., leaf chewers, leaf miners, seed predators). The latter would be especially important in the case of highly diverse invertebrate (e.g., insect) communities to tease apart species- or guild-specific variation in insularity effects and herbivore traits explaining any such differences. As for plant defence assessments (see section 2.3), studies that address these features would ideally involve multispecies comparisons whereby several plant taxa and their associated herbivore faunas are studied concomitantly. Plant species could be selected based on a priori knowledge about contrasting levels of vertebrate versus invertebrate herbivory, in addition to evidence of attack by multiple feeding guilds.

2.5 | Multi-trophic dynamics

2.5.1 | Research gap

Studies on the effects of insularity on plant–herbivore interactions have largely neglected the effects of predators and parasitoids. However, research across many systems has shown that addressing plant–herbivore interactions without considering these top-down effects (and associated food webs) can lead to an incomplete or even erroneous understanding of the causes of variation in herbivory rates, herbivore traits and plant defence evolution (Abdala-Roberts et al., 2019). Although several studies have looked at how multi-trophic interactions (see Glossary) within insular systems affect herbivores and plants (e.g., Piovia-Scott et al., 2011; Spiller et al., 2016), island–mainland comparisons are lacking. The few empirical and theoretical studies conducted to date have argued that top-down effects of predators and parasitoids on herbivores should be weaker on islands than on the mainland (Holt, 2010; Santos et al., 2011; Terborgh, 2010). It has been argued that species in higher trophic levels are more prone to extinction (e.g., owing to smaller population sizes), such that low-diversity insular systems are more likely to lack predators and parasitoids (Holt, 2010). In addition, herbivores could be better able to escape from their natural enemies upon feeding on new host plants (e.g., endemics) found in insular systems but not the mainland (Denno et al., 1990), for instance, by sequestration of novel plant toxins found on islands to which predators or parasitoids are not adapted (Schoener et al., 1995; Spiller & Schoener, 1990).

2.5.2 | Challenges

The above predictions have not been tested and require studies addressing the effects of insularity on plant–herbivore interactions in multi-trophic contexts (Figure 2e). In this sense, we identify three study features to meet this challenge: (1) a greater emphasis on describing natural enemy communities and measuring predation and parasitism levels on focal herbivore species or guilds; (2) an increased consideration of plant traits known or suspected to mediate multi-trophic interactions (e.g., extra-floral nectar, domatia, volatile organic compounds; Nell & Mooney, 2019; Rudgers & Strauss, 2004); and (3) measuring herbivore traits that are likely to play a role in multi-trophic interactions (e.g., aposematism, sequestration of plant chemical compounds; Singer et al., 2014). By addressing these features and traits, multi-trophic interactions can be included to achieve a more robust understanding of the causes of mainland–island patterns in herbivory and plant defences.

3 | OUTLOOK

Over the last century, an increasing rate of species and population extinctions has taken place world-wide (Ceballos et al., 2015; Dirzo et al., 2014), with insular ecosystems being especially impacted by global change drivers (Caujapé-Castells et al., 2010; Myers et al., 2000). We argue that systematic studies aimed at understanding how insularity shapes species traits and their interactions across more systems will contribute to a better understanding of human impacts on island biodiversity and ecosystem function. For example, information on genetically and plasticity-based variation in defensive traits of insular plant taxa and insect herbivore counter-defences can help to predict and manage the impacts of invasive herbivores or plants (via shared herbivores) that are functionally or phylogenetically close to insular taxa. Likewise, knowledge on herbivore guild composition and the relative impacts of native versus non-native vertebrate and invertebrate herbivores on native plants can inform pest control practices and conservation programmes for threatened (e.g., endemic) or ecologically important (e.g. foundational species) insular plants and herbivores. In addition, knowledge on multi-trophic interactions can provide insight on trophic controls determining species co-existence and community structure on islands, as well as on how human impacts on food webs lead to species extinctions. Much promise lies ahead in future research that considers these types of features in order to reassess classic predictions and reach an expanded and more robust theory of insularity effects on plant defences and herbivory.

GLOSSARY

Island biogeography: Field that examines the historical and ecological (physical, abiotic and biotic) drivers of community structure (e.g., species diversity) on islands.

Defence syndrome: Suite of defensive traits that are co-expressed in a group of species and that differ from trait co-expression patterns found in other sets of species.

Chemical defences: Plant secondary compounds with chemical properties (e.g., phenolics, terpenoids, alkaloids) that can act as repellents or toxins to herbivores or can reduce plant digestibility.

Physical defences: Plant physical traits (e.g., thorns, spines, trichomes, fibre content) that deter herbivores, reduce their consumption or decrease their survival.

Multi-trophic interactions: Interactions involving species located across three or more trophic levels (e.g. plant-herbivore-predator).

KEYWORDS

abiotic factors, community ecology, defence syndromes, herbivore guilds, island biogeography, multi-trophic interactions

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AUTHOR CONTRIBUTIONS

X.M. and L.A.-R. conceived the idea and wrote the manuscript.

BIOSKETCHES

Xoaquín Moreira and Luis Abdala-Roberts are interested in the ecological and evolutionary processes that occur among different trophic levels (plants, herbivores and natural enemies) and predict how future global change might influence not only each species individually, but the various interactions as a whole.

DATA AVAILABILITY STATEMENT

This study does not include data.

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BIOSKETCHES

Xoaquín Moreira and Luis Abdala-Roberts are interested in the ecological and evolutionary processes that occur among different trophic levels (plants, herbivores and natural enemies) and predict how future global change might influence not only each species individually, but the various interactions as a whole.

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