



A meta-analysis of insularity effects on herbivory and plant defences

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Abstract

Aim: Plants on islands are often subjected to lower levels of herbivory relative to those found at mainland sites. As a consequence, island plants are predicted to exhibit lower levels of physical or chemical defences, which renders them more susceptible to introduced herbivores. Yet, instances of high pressure by superabundant herbivores native to islands have been reported in many insular systems, which presumably would result in heightened plant defences. To date, no quantitative review has been conducted to determine how common these contrasting patterns are and their implications for the evolution of plant-herbivore interactions.

Location: Islands worldwide.

Taxon: Plants, insects, molluscs, mammals.

Methods: We conducted a meta-analysis of insularity effects on herbivory and plant defences by including studies that involved island-mainland comparisons of the same plant species in both environments (90% of cases), or insular endemics versus mainland congeners (10% of cases). We tested for differences between mammalian and invertebrate (mollusc or insect) herbivory as well as between plant chemical and physical defences by specifying comparisons based on the type of herbivore (vertebrate or invertebrate) or plant trait included in the study.

Results: Mammalian herbivory was significantly higher on islands than on mainlands. In contrast, no significant effect was observed on invertebrate herbivory. In addition, we found no significant difference in either plant physical or chemical defences between insular and mainland plants, though physical defences tended to be higher for plants on islands.

Main conclusions: All analysed mammal studies focused on species introduced to islands, suggesting greater susceptibility of insular plants to exotic mammals, whereas the lack of effects in the case of invertebrate herbivory suggests no difference in susceptibility to molluscs or insects between insular and mainland plants. Interestingly, plant trait patterns suggest a trend for increased physical defences by insular plants, possibly due to heightened pressure by exotic mammalian herbivores on islands, whereas chemical defences appear uncorrelated to differences in herbivory. These



findings call for further experimental and observational studies measuring defences and herbivory for multiple sympatric plant species occurring at both mainland and island sites within a system, or comparing insular endemics to congeneric mainland species.

KEYWORDS

chemical defences, insect herbivores, islands, mainland, mammalian herbivores, meta-analysis, physical defences

1 | INTRODUCTION

Knowledge gained from research on island systems has contributed to important advances in biogeography, macroecology and evolutionary biology, including speciation mechanisms (Losos & Ricklefs, 2009), spatial patterns of biodiversity (Borregaard et al., 2017; Kreft et al., 2008; MacArthur & Wilson, 1967), and drivers of ecosystem function (Oksanen Oksanen et al., 2010; Terborgh, 2010). Islands have characteristics that facilitate tests of the effects of physical habitat features, such as area, isolation and topographical heterogeneity on biodiversity, speciation and species interactions (Carlquist, 1974; MacArthur & Wilson, 1967; Warren et al., 2015). Additionally, variation in historical factors, such as geological age or species colonization histories mean that island systems are ideal testbeds for studies examining mechanisms of community assembly (Chase et al., 2000; Gillespie, 2004).

Early theory relating insularity and the evolution of plant-herbivore interactions hypothesized that sea barriers have resulted in lower herbivore abundance and diversity on islands, which, in turn, has led to less herbivory in insular plant communities (Bowen & Van Buren, 1997; Carlquist, 1974; Vourc'h et al., 2001). Because plant defences are energetically costly (Herms & Mattson, 1992), insular plants are thought to have evolved lower defences or even lost them completely (discussed in Carlquist, 1974; Janzen, 1979). Initial research supported this prediction (e.g. Bowen & Van Buren, 1997; Bryant et al., 1989; Vourc'h et al., 2001), showing that insular plants exhibited lower physical defences (e.g. spines) against mammalian herbivory compared to their mainland counterparts (e.g. Funk & Throop, 2010). Additional research has shown dramatic effects of introduced mammalian herbivores on some insular species, particularly endemics (e.g. Cubas et al., 2019), which was taken as evidence that insular plants are poorly defended and thus highly susceptible to these taxa (reviewed by Terborgh, 2010). In contrast, a number of studies have documented cases where native insular herbivores (e.g. tortoises, crabs and birds) are highly abundant and exert strong pressure on insular plants, presumably because predators are rare or absent in these systems (e.g. Cubas et al., 2018; Garzón-Machado et al., 2010; Terborgh, 2010; Terborgh et al., 2006). These findings suggest that lower overall herbivore diversity and abundance on islands may not necessarily be conducive to weaker pressure on plants in systems, especially

where *particular* taxa of native insular herbivores are abundant leading to higher defences on islands for some plant species.

The question of how insularity has shaped herbivory-plant defence outcomes can be approached in several ways. A number of recent studies have compared herbivore or plant traits for plant species found on both islands and nearby continental sites, providing a so-called 'intraspecific' assessment of insularity effects. These studies have reported mixed findings, including no difference between islands and mainland sites to higher herbivory and/or plant defences on islands (e.g. Burns, 2019; Monroy & García-Verdugo, 2019; Moreira et al., 2019; Pardo et al., 2018). While capitalizing on controlling plant species identity by using populations of the same species found in each environment. These types of studies draw on a more restricted evaluation of mainland-island differences due to reduced genetic pools involving single species, as well as idiosyncrasies in focal species histories. Accordingly, replicated experiments involving multiple plant species or meta-analytical tests across a number of species are needed to help generalize individual species-level findings and reach stronger inference about plant intraspecific insularity patterns. Another powerful approach involves interspecific comparisons of island endemics with mainland congeners (e.g. Hoan et al., 2014), although studies are scarce because of issues relating to the design of robust tests (e.g. species replication, accurate identification of island-mainland congeneric species pairs). As evolutionary histories are important drivers of plant anti-herbivore defence traits, some researchers have compared endemic versus non-endemic species on islands finding that endemics are generally more palatable to introduced mammalian herbivores (Cubas et al., 2018, 2019). These studies support the idea that relaxed herbivore selection has played a more important role for insular endemics because their evolutionary history is more tightly linked to low herbivory under insularity, whereas non-endemic natives have likely experienced higher levels of herbivory throughout their evolutionary history at mainland sites.

Research has been somewhat biased toward studies focusing on vertebrate herbivory and physical defences (e.g. spines, thorns; see above), with less work examining invertebrate herbivory and plant chemical defences (but see Burns, 2019; Monroy & García-Verdugo, 2019; Moreira et al., 2019; Pardo et al., 2018). Phytophagous insect communities are more diverse and in many cases less dispersal-limited relative to species-poorer vertebrate guilds (e.g. non-volant mammals), and it is therefore less clear how they have shaped the evolution of plant anti-herbivory traits in

insular systems. Most recent invertebrate studies relate to intraspecific comparisons (e.g. Moreira et al., 2019), with only a few exceptions comparing island endemics to mainland congeners.

Our overall aim was to quantify changes in plant defences and herbivory between mainland and islands (hereafter 'insularity effect'). Specifically, we tested whether patterns differed between vertebrates (mostly mammals) and invertebrates, or based on whether physical or chemical defences were measured. We interpret our results in light of several plausible explanations and highlight important research gaps that should be addressed. To our knowledge, this study represents the first quantitative assessment of mainland versus island differences in herbivory and plant defences using meta-analytical tools. In doing so, we provide a first step towards synthesizing the available information on this subject and identifying incipient patterns.

2 | MATERIALS AND METHODS

We conducted an extensive literature search in the ISI Web of Knowledge database using the following search criteria: '(Plant OR tree OR shrub) AND (herbivore OR herbivores OR herbivorous) AND (defence OR defense) AND (island OR insular)'. We retained only articles, book chapters, reviews, theses, dissertations and abstracts published in English. To further limit the search to relevant papers, we filtered outputs to consider only the following research areas: plant sciences, environmental sciences, ecology, agriculture, forestry, evolutionary biology and entomology. This search spanned published work from 1940 to June 2019. In addition, we also surveyed cited studies found in review articles about plant-herbivore interactions on islands (e.g. Burns, 2014, 2019; Terborgh, 2010). In total, our search yielded 332 papers (see the PRISMA flow chart, Appendix S1: Figure S1). To be included in our analysis, studies had to meet the following criteria: (a) report some measure of herbivory (percent, frequency of damage) and/or plant physical or chemical defences for species growing on islands versus plants of the same species or a congeneric species growing in continental sites, and (b) that the study reported treatment (islands versus mainland) level means, some measure of variability (i.e. variance, standard error or standard deviation), and sample sizes in the text, figures, tables or appendices.

After applying the above criteria, the resulting dataset consisted of 211 study cases from 21 studies (i.e. 21 papers out of the initial 332) from the primary literature published between 1989 and 2019 in 18 scientific journals and one book chapter (see list of references in Appendix S2). Almost all these studies (>90%) compared the same plant species (one or more species in each case) at island versus mainland sites (i.e. intraspecific comparisons), and in all these cases the studied taxa were native to both environments (i.e. none of them were exotic species introduced to islands). The remaining few cases involved comparisons of an endemic insular species with a mainland congener. Study cases (k) represented data points, that is, island versus mainland comparisons, drawn

from a single primary study (n), where a single study may have one or more study cases (i.e. comparisons). The occurrence of more than one study case in a given study took place when more than one herbivory or plant defence response was measured and/or more than one island site was tested (against a mainland site), in which case the number of study cases in a given study equalled the number of responses by the number of island versus mainland comparisons. For each study case, we compiled the following information: plant identity and growth form (herbaceous or woody), island features (size, geological age, isolation), type of herbivore (insects, mammals or molluscs), and type of plant defence (chemical or physical). Physical defences included spine length and density, thorn density, prickle density, and specific leaf area (proxy for toughness), whereas chemical defences analysed included concentrations of phenolic compounds, terpenes, cyanogenic glycosides, and alkaloids. For each study case, we estimated insularity effect sizes using Hedges' *d* metric and a 95% confidence interval (CI) (Hedges, 1981) with the 'metafor' package 1.9-8 version in R 3.2.3 (R Core Team, 2019; Viechtbauer, 2010). Hedges' *d* was calculated as the standardized mean difference between island and mainland values such that negative values indicate that herbivory and defences had lower mean values on insular plants compared to mainland plants, whereas positive values indicate the inverse.

First, we estimated the overall mean effect size and 95% CI across all studies to assess whether there was a mean effect of insularity on herbivory and plant defences. An effect size was considered significant if its CI did not overlap with zero (Koricheva et al., 2013). Second, we investigated whether insularity effects on herbivory were contingent on herbivore type (mammals, insects or molluscs) by running a model including herbivore type as a moderator and estimating the mean effect sizes and 95% CIs model for each type of herbivore. Similarly, we also investigated whether insularity effects on plant defences were contingent on the type of plant defence (chemical or physical) by running a model including defence type as a moderator and estimated the mean effect sizes and 95% CIs model for each type of defence. We also ran preliminary analyses including island features (size, geological age, and distance to mainland) as these may affect insularity effects on defences (there was not enough data to run these analyses for herbivory). Results indicated that none of these features influenced relative differences in insularity effects between defence types (size: $Q_M = 3.65$, $p = 0.056$; distance to mainland: $Q_M = 1.85$, $p = 0.174$; age: $Q_M = 3.09$, $p = 0.079$), and we therefore report results from models without these variables. In all these models, we performed multi-level error meta-analyses (Nakagawa et al., 2017) with the *rma.mv* function of the R package metafor v. 2.0-0 (R Core Team, 2019; Viechtbauer, 2010). We included the primary reference and the study case (nested within primary reference) as random factors to account for non-independence among multiple effect sizes drawn from a single reference. We conducted several additional analyses to test whether our findings were robust and not affected by non-independence among effect sizes and publication bias (Appendix S3: Figures S2,S3; Appendix S4: Figures S4-S6).

3 | RESULTS

The overall mean effect size of insularity (i.e. mean difference between island versus mainland) on herbivory was positive ($2.40 \pm [-1.46; 6.27]$), but not significant (Figure 1). However, the meta-analysis model indicated that this effect was marginally significantly contingent on the herbivore type (insularity by herbivore type interaction: $Q_M = 5.30$, $p = 0.071$), whereby a significant positive effect of insularity was found for mammalian herbivory (i.e. island > mainland) while insect and mollusc herbivory patterns were more variable across studies and there was no significant effect in either of these cases (Figure 1).

The overall mean effect size of insularity on plant defensive traits was not significant ($1.21 \pm [-0.85; 3.27]$) (Figure 2). However, the meta-analysis model similarly showed that insularity effect on plant defences was contingent on the type of trait (insularity by trait type interaction: $Q_M = 4.04$, $p = 0.044$), whereby insularity tended to show a positive (albeit non-significant) effect for physical defences (Figure 2), whereas for chemical defences there was no clear pattern (Figure 2).

4 | DISCUSSION

Our results showed that mammalian herbivory was greater on islands than on the mainland whereas no significant effect was observed on

invertebrate herbivory. In addition, plant physical defences tended to be higher on island plants relative to mainland plants (though not significantly), whereas no pattern whatsoever was observed for chemical defences. These patterns are unresponsive of predicted declines in herbivory and plant defences on islands relative to mainland, and suggest differential mechanisms driving insularity effects on vertebrate relative to invertebrate herbivores, as well as on plant physical compared to chemical defensive traits. We next discuss plausible explanations for these findings and point to empirical studies necessary for robustly testing the ecological and evolutionary consequences of insularity on plant-herbivore interactions.

4.1 | Insularity effects on herbivory

Mammalian herbivory was greater on islands than on the mainland, and all the studies included in our analysis involved introduced species of ungulates or rodents. Introduced rabbits (*Oryctolagus cuniculus*), feral goats (*Capra aegagrus hircus*), cattle (*Bos bos taurus*), and deer (species of the family *Cervidae*) had been historically absent from islands until a few centuries ago and their introduction has been highly detrimental for insular plant communities (Bowen & Van Buren, 1997; Cubas et al., 2018, 2019; Garzón-Machado et al., 2010; Irl et al., 2012; Terborgh et al., 2010). Insular plant species, particularly endemics, have historically evolved in the absence of mammalian herbivory and

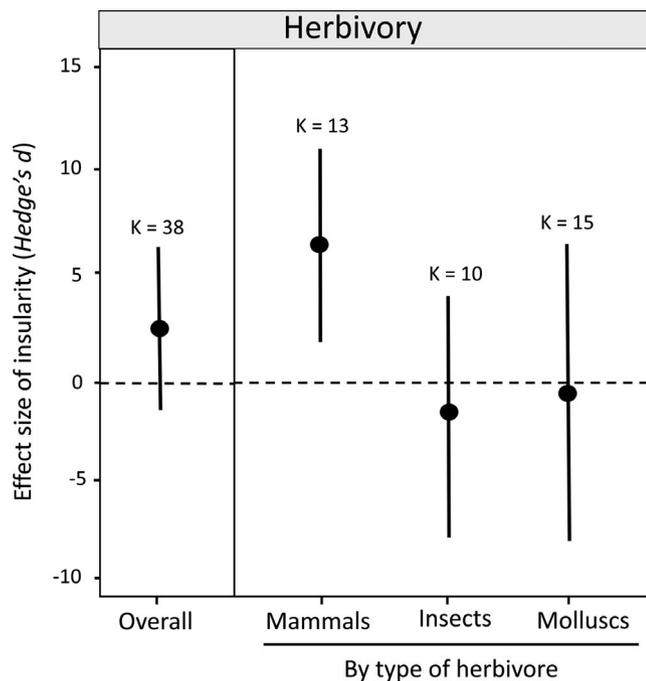


FIGURE 1 Mean effect size of insularity on herbivore damage grouping all types of herbivores (i.e. overall effect) or separated by type of herbivore (insects, mammals or molluscs). Dots and error bars represent model parameter estimates and corresponding 95% bias-corrected confidence intervals (CI). K = number of study cases. The horizontal dashed line centred on zero represents the null hypothesis (i.e. no difference in herbivory between continental and insular plants). Effect sizes are considered significant if the 95% CI does not include zero

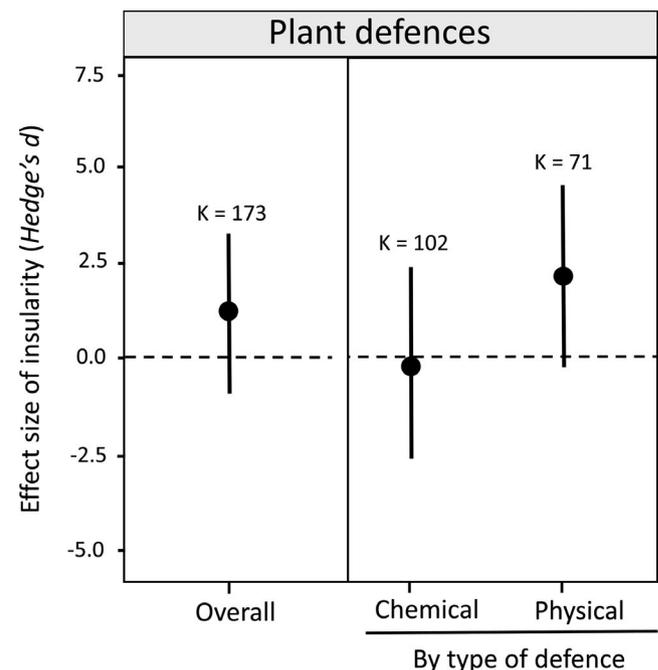


FIGURE 2 Mean effect size of insularity on plant defences grouping all traits (overall effect) or separated by type of defence (physical or chemical). Dots and error bars represent model parameter estimates and corresponding 95% bias-corrected confidence intervals (CI). K = number of study cases. The horizontal dashed line centred on zero represents the null hypothesis (i.e. no difference in defences between continental and insular plants). Effect sizes are significant if the 95% CI does not include zero

are therefore expected to have lower (or even lack) defences against these herbivores (Bowen & Van Buren, 1997; Cubas et al., 2019; Funk & Throop, 2010; Terborgh, 2010), contributing to increased impacts by mammalian herbivores. Our results fit this expectation by showing that insular plants exhibited higher levels of herbivory by introduced mammals, but at the same time contradict it as insular plants also tended to exhibit higher physical defences. This apparent contradiction could be explained by insular plants evolving increased defences due to a recent history of strong selection by introduced mammals and/or due to higher levels of induced defences (see discussion ahead). Levels of herbivory could remain higher on islands despite heightened plant defences as mammalian populations can rise unchecked by predators or pathogens (reviewed by Terborgh, 2010). Nonetheless, it is difficult to pair these herbivory and plant trait patterns as in many cases results from each came from different studies, an important limitation in our analysis. To adequately test these possibilities, studies are needed which compare defence levels and vertebrate herbivory on populations of focal species originating from islands versus those from mainlands, or insular taxa versus mainland congeners planted in reciprocal transplant experiments where the presence of herbivorous mammals is manipulated (for a related example, see Skainin & Arcese, 2020). Likewise, comparisons of herbivory on insular plant taxa with contrasting defence levels can also yield valuable insight (e.g. endemics versus non-endemics; see Cubas et al., 2019). In addition, the importance of top-down control relative to plant defences in driving observed herbivory patterns should be tested. This would require manipulating predator presence on islands and compare herbivory levels on focal insular taxa with similar defence levels, or by contrasting predation and herbivory levels for plant taxa with high versus low defences to test for the relative effects of bottom- versus top-down forcing.

Unlike mammalian herbivory, we found no overall effect of insularity on herbivory by insects or molluscs. The notion that insularity effects on invertebrate herbivory, particularly by arthropods, are more variable and less strong compared to effects on vertebrate herbivory has been discussed previously (e.g. Terborgh, 2010). Patterns of arthropod dispersal to insular systems are thought to be highly stochastic (e.g. relative to vertebrate taxa) and in many instances occur independently of dispersal events by their host plants (Terborgh, 2010). This results in mismatches between herbivore and plant species, and ultimately leads to under-exploitation of insular (non-host) plant species by colonizing herbivores. Based on this, one would predict weaker pressure by herbivorous arthropods on insular plants compared to mainland (e.g. Allan et al., 1973; Janzen, 1973). However, rather than reduced attack on islands, we found no overall effect of insularity on invertebrate herbivory (including insects). Despite stochasticity in dispersal, it is possible that for some groups of flying insects (not so for non-flying insects or other taxa such as terrestrial molluscs) reasonably high rates of colonization to islands result in little or no difference in herbivory between mainland and islands. It is also important to consider that there are many insular systems in which native herbivorous arthropods are highly abundant and exert overwhelming pressure on insular plants (more so than herbivores on mainland; e.g. land crabs; Cubas et al., 2018; Terborgh, 2010), which could counteract other processes (e.g. plant-insect mismatches) which

would otherwise lead to reductions in invertebrate herbivory on islands relative to mainland. In some cases, these native herbivores could even lead to greater herbivory on islands. Work comparing herbivory by endemic and non-endemic invertebrate guilds or species with contrasting life histories (e.g. dispersal ability, diet breadth, body size) is required to assess the range of invertebrate responses to insularity and its causes, as well as determine the relative contributions of different insect taxa or guilds to differences in herbivory between islands and mainland.

4.2 | Insularity effects on plant defences

Although we found no significant island-mainland difference for either type of plant trait, physical defences exhibited a trend for a greater mean value on islands. Physical defences such as spines, thorns and toughness are thought to have evolved primarily as defences against mammalian herbivores (Barton, 2016; Burns, 2019). Following from our herbivory results, we would expect higher damage by introduced mammals on islands (see above) to select for increased physical defences on such plants (Barton, 2016; Burns, 2019), a plausible scenario given enough time for selection to act since mammals were introduced in the last several centuries. It is also possible that observed patterns reflect to some extent plasticity responses to increased vertebrate herbivory on islands, though defence inducibility could also be selected for provided genetic variation in plasticity (Pigliucci, 2005). Common garden experiments where herbivore presence is manipulated on insular plant taxa originating from sites or islands with historically contrasting levels of vertebrate herbivory are needed to tease a part these possibilities (e.g. Skainin & Arcese, 2020), including genetically controlled measurements of constitutive defences and their inducibility. On the other hand, it is also important to consider that in numerous insular systems plants have evolved in the presence of highly abundant avian and reptilian herbivore species that are native to islands (see above), and that some of these species are absent or much less abundant on mainland (Burns, 2019). These insular herbivores would exert strong effects and select for increased plant defences, which would also lead to the observed increase in physical defences on islands. Although this possibility is less likely than the former because of the exclusive focus on introduced herbivores in the analysed studies, it nonetheless deserves to be evaluated in systems where native herbivores exert strong effects on insular plants.

We found no evidence of an overall island to mainland difference in plant chemical defences. Greater variability across studies in insularity patterns for these traits could result from some classes of compounds (e.g. phenolics, terpenes and alkaloids) being selected (albeit not exclusively) by invertebrate herbivores showing inconsistent patterns of abundance or diversity in islands vs. mainland sites. Accordingly, the variability in insularity effects on invertebrate herbivory would be expected to produce concomitant variation in insularity effects to the extent that these chemical compounds mediate interactions with phytophagous arthropods. In addition, different types of compounds could be selected by different species or guilds of invertebrate herbivores (Wise & Rausher, 2013). If these herbivores vary in their responses to insularity, then this may also lead to idiosyncratic



patterns which, when averaged, result in no overall difference. Future work that separates measurements of damage by herbivore species or guilds is necessary to tease apart these responses and their association with metabolite-specific patterns.

In considering the above plant chemical and physical defence patterns, it is important to point out that present-day insular floras might represent a biased sample consisting of highly defended taxa that have survived herbivore introductions (e.g. Leppard & Piilar, 2016). In contrast, less defended species (including endemics) may have been driven to extinction centuries or millennia ago or are currently found in very low abundances (i.e. narrowly distributed endemics) such that they are usually not considered in studies. This scenario could lead to an overestimation of defence levels for insular taxa and ultimately produce a false impression that insular taxa are equally (or even more) defended than mainland plants. Palaeoecological approaches would be required to assess this possibility.

4.3 | Future work

While the number of studies systematically comparing island versus mainland sites is currently low, studies measuring plant traits are more common than those measuring herbivory. This stresses the need for more studies that measure herbivory as well as efforts to simultaneously and candidate plant traits as a basic requirement to assess shifts in plant–herbivore interactions due to insularity. In addition, further work should consider multiple plant species simultaneously in a phylogenetically controlled manner. This can be done either by comparing mainland–island differences for several focal plant species occurring in both environments, or by comparing insular endemics to mainland congeners. Replicated comparison of species with different life forms (herbaceous versus woody plants) would also yield insight into how shifts in plant–herbivore interactions are contingent on (or have shaped) plant life histories. In addition, assessing insularity effects on predation and parasitism is a crucial task that is long overdue and could illuminate the processes behind plant–herbivore patterns. Several authors have discussed the possibility that top-down effects of natural enemies on herbivores are weaker on islands than on the mainland (Holt, 2010; Kay & Wratten, 2006; Terborgh, 2010), and extensions of island biogeography theory to predict changes in food web structure have been put forward (Gravel et al., 2011; Holt, 2010), but empirical (and manipulative) research is largely lacking.

Finally, inserting focal plant–herbivore interactions into a biogeographical and macroecological context is necessary to explicitly investigate how historical and large-scale factors such as geological age, history of colonization, island size, physical heterogeneity, and geographical isolation (Craven et al., 2019; Losos & Ricklefs, 2009; Valente et al., 2014) shape insularity effects on herbivory and plant defences. The influence of climate (Weigelt et al., 2016), invasive species (Craven et al., 2019) and local abiotic factors such as productivity and soil type (Pillon et al., 2010) is also highly relevant for disentangling the ways in which insularity affects plant–herbivore interactions via local and regional changes in diversity or species composition of plant–herbivore communities.

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DATA AVAILABILITY STATEMENT

The data used in this study are archived at <https://doi.org/10.5061/dryad.5hqbk46>.

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**BIOSKETCH**

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

Author contributions: Formulated the idea of the manuscript: XM. Designed the searching protocol: XM, BC, CGV, LAR. Searched the literature and collected data: XM. Contributed materials/analysis tools: XM. Analysed the data: BC. Wrote the manuscript: XM. Contributed critically to the writing: LAR, CGV, BC.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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