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A phylogenetically controlled test does not support the prediction of lower putative anti-herbivore leaf traits for insular woody species

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Abstract

Aim: It is predicted that insular plant taxa have evolved reduced defences in response to lower herbivore pressure on islands. However, the few studies testing this hypothesis have addressed variation in individual defensive traits, without paying attention to patterns of correlated trait expression (i.e. defence syndromes).

Location: Balearic and Canary Islands.

Taxon: Ninety-one woody plant species.

Methods: We tested whether plant species with contrasting histories of insularity (namely, endemics, non-endemic natives and exotics) differed in their defensive syndromes using a suite of morphological, physical, and chemical traits putatively associated with herbivory. For this, we measured eight leaf traits of 42 endemic, 29 native non-endemic and 20 introduced species for which specimens were sourced from botanical gardens found in two archipelagos: the Balearic and Canary Islands.

Results: We conducted phylogenetic-controlled analyses which showed that, contrary to predictions, insular taxa (endemics and non-endemic natives) across both archipelagos were more defended (thicker, smaller leaves with less nutrients) than exotic species. There were no differences in chemical defence (phenolic compounds) between endemics, non-endemic natives and exotics. Finally, we also found different defence syndromes between archipelagos: whereas species from the Balearic Islands were more physically defended, on average, those from the Canary Islands had higher chemical defences.

Main conclusions: Overall, these results point to a defence syndrome based on low-nutrient and physically defended leaves characteristic of insular plant taxa that is indistinct for endemic and non-endemic taxa, relative to introduced species, as well as quantitative and qualitative differences in defences between archipelagos owing to changes in species composition and likely also to different histories of biotic or abiotic pressure.

KEYWORDS
Balearic Islands, Canary Islands, chemical defences, defence syndromes, endemic plants, herbivory, nutrients, physical defences

1 | INTRODUCTION

Despite covering merely 5% of the planet's land surface, islands sustain 30% of the species found in biodiversity hotspots and exhibit remarkably high endemism levels (Myers et al., 2000). Such outstanding features are thought to be the result of evolutionary processes acting under long-term isolation which promote high levels of in-situ species diversification (Whittaker et al., 2017). In the case of plants, insular endemic floras comprise nearly 20% of the diversity of vascular plant species described to date (Tershy et al., 2015; Veron et al., 2019). A high proportion of these species are under threat of extinction due to human impacts such as deforestation, land-use change and introduction of exotic plant and animal species (Caujapé-Castells et al., 2010; Harter et al., 2015). Ecological and evolutionary research aimed at insular floras, particularly endemics, is thus needed to inform about conservation and restoration practices in the face of past and ongoing human-driven disturbances (Borges, 2018).

One of the key topics at the intersection of insular species evolution and conservation concerns how past and present biotic (e.g. herbivory) or abiotic (e.g. climate) forcing on islands shape variation within and among species in plant anti-herbivore defences (reviewed in Burns, 2019; Moreira & Abdala-Roberts, 2021). Relative to their mainland counterparts, insular plant taxa have presumably evolved reduced defences since geographical isolation also brings about low abundance and diversity of mammalian and insect herbivores (Bowen & Van Buren, 1997; Carlquist, 1974; Vourc'h et al., 2001). The assumed reduction of herbivore pressure and the consequent reduction of plant defences on islands are expected to be greater for island endemics relative to non-endemic natives, as the insularity histories of the former have progressed entirely in isolation under low herbivory, whereas the latter have likely experienced higher herbivory at some point during their evolutionary history on mainland (reviewed in Burns, 2019; Moreira et al., 2021). Following the same logic, exotic plant species would be expected to be more defended than either insular endemic or non-endemic native taxa (Carpenter & Capuccino, 2005), as they have a more recent history (prior to introduction) of exposure to presumably higher herbivory on mainland. That said, exotics represent non-random subsets of species for which particular traits conferring an adaptive advantage in a new environment, including high growth and reproductive or dispersal capacity (Brandenburger et al., 2020; van Kleunen et al., 2010), but not necessarily high defences (e.g. defences might not play a major role on colonization success of exotics on islands; see Lloret et al., 2005). In this sense, exotics may even be a priori less defended, on average, than the mainland species pool, if, for example, defences trade off with high competitive or reproductive capacity (Funk & Throop, 2010). In addition, introduced taxa may quickly evolve reduced defences in the absence of enemies (Enemy Release; Keane & Crawley, 2002) such that differences relative to native and endemic insular taxa may be weak or absent. To date, however, no systematic comparisons of defensive traits across taxa representing different evolutionary origins (insular or non-insular) and histories of island colonization have been conducted to test these hypotheses.

Empirical work focusing on exotic mammalian herbivores has provided indirect support for the expectation of lowered plant defences and increased susceptibility to herbivores for insular plants. For example, Cubas et al. (2019) found that endemic plant taxa on Tenerife (Canary Islands) were more heavily browsed by introduced rabbits than either non-endemic natives or introduced exotics, suggesting lower resistance and higher palatability for endemics. Previous work has also reported that endemics are highly susceptible to introduced herbivorous mammals (e.g. rabbits, feral goats or deer; Bowen & Van Buren, 1997; Cubas et al., 2018, 2019), and a recent meta-analysis found that non-endemic plant taxa native to islands were more heavily attacked by introduced mammals on islands than on mainland areas (Moreira et al., 2021). Having said this, other studies have reported no differences or lower levels of herbivory on insular plants (e.g. Gorman et al., 2014), and it has been pointed out that some insular systems have especially abundant native vertebrate or invertebrate herbivores which can result in higher herbivore pressure (and thus possibly also higher plant defences) on islands than on mainland sites (Terborgh, 2010).

A key shortcoming of available studies is that plant defensive traits have seldom been measured, evidently leading to an incomplete assessment and understanding of the consequences of insularity effects for plant–herbivore interactions and plant defences. Instead, studies involving plant trait measurements have usually focused on other functional traits, showing that island endemics exhibit greater resource-use efficiency than non-endemic counterparts (Gorman et al., 2014; Gulias et al., 2003; Lavergne et al., 2004). Although some of these traits may correlate with herbivory patterns (e.g. nutrient levels or physical/structural traits; Carmona et al., 2011; Marquis et al., 2012), assessments of putative defensive traits are ultimately needed to gain insights into the effect of insularity on the evolution of plant defences.

The few studies comparing plant defences on islands and mainland thus far have addressed focal traits individually (e.g. Monroy & García-Verdugo, 2019; Moreira et al., 2019; Vourc'h et al., 2001). Nonetheless, plant species frequently express several defensive traits simultaneously leading to patterns of correlated trait expression or the so-called defence syndromes. These syndromes are expected to emerge when plant species are attacked by multiple herbivore species (as is often the case) which select for different traits or trait combinations (Agrawal & Fishbein, 2006; Defossez et al., 2018; Moreira et al., 2020), or when traits are genetically or metabolically linked (Osbourn, 2010). Evidence gathered thus far suggests that patterns of correlated expression in multiple defences are common and taxonomically widespread, thus raising the question as to whether plants on islands have evolved distinct defensive syndromes relative to their mainland counterparts. For example, *Eucalyptus* species endemic to islands converge towards lower specific leaf area (SLA; thicker leaves), shorter internodes and slower growth rates than non-endemics (Gorman et al., 2014), indicating that insularity shapes suites of functional traits. Nonetheless, an explicit analysis of trait co-expression patterns in search of functional syndromes was not conducted, and, to our knowledge, no study

to date has done so in the case of putative defensive traits against herbivory.

In this study, we investigated whether plant species with contrasting evolutionary and colonization histories on islands differ in their univariate and multivariate (syndromes) patterns of variation for traits putatively associated with herbivory. Specifically, we measured leaf phenotypic traits in 42 endemics, 29 non-endemic natives and 20 introduced species using specimens sourced from botanical gardens located in two archipelagos, namely Balearic and Canary Islands. Interestingly, these insular systems exhibit contrasting histories of herbivore pressure: some Balearic Islands were previously home to currently extinct native ungulates (Bover et al., 2008, 2014) and thus the traditional assumption of reduced herbivore pressure on islands may not hold in this case, whereas Canary Island species have historically evolved in the absence of large native herbivores. The inclusion of both systems based on prior knowledge on their histories can inform causes behind similarities/differences in patterns of trait variation between systems, as well as enrich our analyses (e.g. setting up a priori contrasts) and interpretations of plausible underlying causes. Overall, this study complements previous insularity tests for functional traits and herbivory and, to our knowledge, represents the first evaluation of insularity effects on plant defensive traits and syndromes within a broad phylogenetic context, thus furthering our understanding of the evolution of plant defences on islands.

2 | MATERIALS AND METHODS

2.1 | Study system

Our study focused on two island floras with contrasting biogeographical features. Off the coast of NW Africa (Figure 1), the Canary Island flora is composed of c. 600 plant endemic taxa (26% of the total) that evolved in the absence of large herbivores until the introduction of domesticated ungulates in the last five centuries (Fernández-Palacios & Whittaker, 2008). Biogeographical analyses suggest that most lineages of the Canarian flora have a Mediterranean origin (García-Verdugo et al., 2019), although the latitude at which the islands are found results in a subtropical climate (Dorta, 1991). On the other hand, the Balearic Island flora displays a smaller number of endemics (c. 120 species; 7% of the total; Sáez et al., 2013). Unlike the Canarian archipelago, some Balearic Islands (Figure 1) such as Majorca, Menorca and Cabrera were previously home to a number of native ungulates that went extinct shortly after the arrival of human colonists (Bover et al., 2014). The flora of this system is composed of pre- and post-Mediterranean taxa that occur under a Mediterranean-type climate (Sáez et al., 2013). While this poses some difficulties for comparing across systems and deriving generalities, at the same time differences across systems or islands are likely commonplace and offer an opportunity to test for commonalities and differences among islands within a region or among regions. In addition, differences between systems set up a scenario
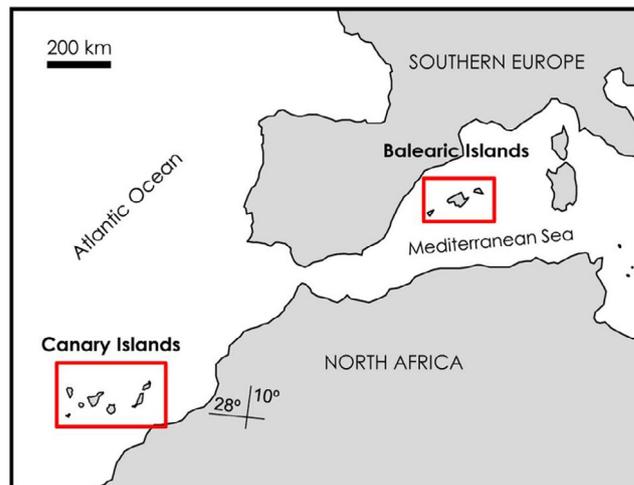
FIGURE 1 Map showing the location of the two insular systems used for this study (Canary Islands and Balearic Islands)

that provides insight into how contrasting histories of herbivore pressure or climatic conditions shape insularity effects on plant traits.

2.2 | Sampling design

We took advantage of the specimens found within the most representative botanical gardens of each archipelago and performed therein all plant sampling, namely, the 'Viera y Clavijo' Botanical Garden—Unidad Asociada a CSIC (island of Gran Canaria, Canary Islands) and the Jardí Botànic de Sóller (island of Majorca, Balearic Islands). These institutions display the most representative living collections of endemic and non-endemic island species of each flora. The specimens found at both gardens in all cases originated from seed material sourced from natural habitats and collected over the last 40 years. By sampling all species and individuals under similar abiotic conditions (e.g. soil, weather) within each garden, we were able to minimize effects of environmental variation on plant traits (i.e. sensu common garden experiments). Accordingly, previous work has made use of plants growing in botanical gardens to compare species traits and herbivory (e.g. Pearse & Hipp, 2014), proving to be a useful tool.

Because the number of endemic species present in each system is sharply unbalanced, we stratified taxa representation in our study. First, we built a list of species of interest for the purposes of this study from the database of the living collections available at each institution. Specifically, we focused on long-lived, woody taxa (i.e. shrubs and small trees) as these represent the most common life-form among endemics from both island systems. In addition, focal species were only eligible if a minimum of three mature individuals were available. Second, we sought to control for phylogenetic effects by prioritizing congeneric species across systems (e.g. *Globularia cambessedesii* Willk. in the Balearic Islands and *Globularia*

salicina Lam. in the Canary Islands), while also maximizing phylogenetic diversity by including taxa from as many families as possible (Figure 2). These selection criteria resulted in 20–22 focal endemic species from each botanical garden, representing 32 families (Table S1). On the other hand, we also sampled a set of non-endemic native and introduced woody species commonly distributed within the archipelagos (Table S1). Thus, we selected 19 and 13 non-endemic native species for the Balearic and Canary Islands, respectively, which were also sourced from seed at each botanical garden and in most cases were closely related to the endemics previously chosen (e.g. *Globularia alypum* L.; Table S1). Finally, we sampled 10 introduced species included in international and/or regional checklists of exotic

species (Table S1). These species originate from different continents and regions, including Europe (two species), South America (eight species), North America (two species), Asia (two species), Oceania (two species) and Africa (four species), therefore precluding biases due to geographical origin. In addition, most of these species are of recent introduction (<100 years in both archipelagos), and have therefore likely not evolved substantial differences in traits under novel conditions of insularity (i.e. they would conserve trait values similar to their regions of origin).

To ensure that summer-deciduous species included in the study were bearing mature foliage, we sampled all plants in both botanical gardens several weeks after the first autumn rains (from 15 to

FIGURE 2 Phylogenetic tree of the studied plant species using Smith and Brown's (2018) GBOTB megatree generated based on molecular data from GenBank release 2018 and incorporating data from the Open Tree of Life synthetic tree release 9.1. White dots are plant species from Balearic Islands (BAL), whereas black dots are plant species from Canary Islands (CAN) . Our analysis is based on phylogenetic megatree that has been published by Smith and Brown (2018, HYPERLINK https://doi.org/10.1002/ajb2.1019)

30 November 2019). We sampled three to five individuals of each species displaying above reproductive size threshold, from which we collected three fully exposed twigs from their outer canopy layers using pruning shears. From each twig, we collected two to four fully expanded undamaged leaves (typically sampled from the second to the fourth internodes) for leaf trait measurements.

2.3 | Estimation of physical and chemical defences and nutritional traits

We measured leaf trichomes, spinescence, SLA and leaf size as putative physical defences. Trichomes and spinescence reduce herbivory by physically inhibiting feeding or movement (Burns, 2019; Fordyce & Agrawal, 2001; Valverde et al., 2001), whereas SLA is correlated with leaf toughness and can therefore act as a proxy of structural defence against herbivory (Hanley et al., 2007; Pearse & Hipp, 2009). In addition, smaller leaves frequently reduce recognition by herbivores and thus tend to exhibit lower levels of herbivore damage (Brown et al., 1991; Zhang et al., 2017). To measure these traits, we scanned five undamaged leaves per plant, and then dried them at 45°C for 48 h before weighing them using a precision balance (AB54; Mettler-Toledo AG). We estimated leaf size (in cm^2), leaf trichomes and spinescence (binary variable: 1 = presence, 0 = absence) from scanned images using IMAGEJ 1.51j8 software. This latter variable was scored at the whole-plant level and encompassed stems, petioles and leaves (i.e. spines, thorns and prickles) commonly associated with herbivore defence (Burns, 2016). We obtained SLA (in $cm^2 g^{-1}$) by dividing leaf size by its corresponding dry mass.

We chose to measure total phenolic compounds and condensed tannins in leaves as putative chemical defences. These compounds are toxic and deterrent to a broad range of phytophagous insects and mammalian herbivores across a number of plant taxa (Levin, 1971; Mithöfer & Boland, 2012; Salminen & Karonen, 2011), and have been previously measured to quantify chemical defences in island plants (Monroy & García-Verdugo, 2019; Moreira et al., 2019). To estimate the concentration of these compounds, we finely ground c. 2 g of oven-dried plant material (45°C to constant weight) in liquid nitrogen. We extracted phenolic compounds from 20 mg of plant tissue with 70% methanol in an ultrasonic bath for 15 min, followed by centrifugation and subsequent dilution of the methanolic extract (Moreira et al., 2014). We colorimetrically determined total phenolic content by the Folin–Ciocalteu method in a Biorad 650 microplate reader (Bio-Rad Laboratories) at 740 nm, using tannic acid as standard. We determined leaf condensed tannins in the aqueous methanol extracts by the procyanidine method (Sampedro et al., 2011). We mixed the methanolic extract with acidified butanol and a ferric ammonium sulphate solution, allowed to react it in a boiling water bath for 50 min and then rapidly cooled it on ice. We colorimetrically determined condensed tannin content in this solution in a Biorad 650 microplate reader at 550 nm, using purified condensed tannins of 'quebracho' (*Schinopsis balansae* Engl.; Droguería Moderna, Vigo, Spain) as standard. We expressed phenolic compound concentrations in mg g^{-1} tissue on a dry weight basis. Because a large number of plant species did not have condensed tannins in their leaves, we used a binary variable (1 = presence, 0 = absence) for statistical analyses.

In addition, we measured phosphorus and nitrogen in leaves as nutritional traits, as they are typically found in low concentrations in plant tissues and can therefore act as limiting resources for herbivore growth and development (Huberty & Denno, 2004; Mattson, 1980). To quantify these macronutrients, we digested approximately 0.3 g of ground dried leaf material in a mixture of selenous sulphuric acid and hydrogen peroxide (Moreira et al., 2012). Diluted aliquots of the digestion were analysed by colorimetry for quantification of nitrogen (indophenol blue method) and phosphorus (molybdenum blue method) concentration using a Biorad 650 microplate reader (Bio-Rad Laboratories) at 650 and 700 nm, respectively (Walinga et al., 1995). We expressed nitrogen and phosphorus concentrations in mg g^{-1} tissue on a dry weight basis.

2.4 | Statistical analyses

2.4.1 | Phylogenetic signal in plant traits

First, we used *The Plant List* database to standardize nomenclature (www.theplantlist.org/) and combined intraspecific taxa (e.g. subspecies and variety) with their parent species. We split the five species that were sampled at both archipelagos (i.e. *Cistus monspeliensis*, *Phillyrea angustifolia*, *Bituminaria bituminosa*, *Pistacia lentiscus* and *Olea europaea*) as sister Canarian-Balearic species with an arbitrary 0.1 Myrs distance to their common ancestor. Then, we automatically generated a phylogenetic tree using Smith and Brown's (2018) GBOTB megatree, which we accessed through the *phylo.maker* function in the 'V.PhyloMaker' package of R (Jin & Qian, 2019). Then, we estimated the phylogenetic signal (lambda value, λ) for all traits using mean values at the species level with the function *phylosig* of the package 'phytools' in R (Revell, 2012). A λ of 1 indicates phylogenetic conservatism consistent with the tree topology and a random walk model (i.e. trait similarity is directly proportional to the extent of shared evolutionary history). A λ of 0 indicates no influence of shared ancestry on plant traits (i.e. phylogenetic independence).

2.4.2 | Effect of insularity history on individual plant traits

First, we decoupled traits from the phylogeny using phylogenetic eigenvalues as described in de Bello et al. (2017). Briefly, we summarized phylogenetic information by calculating eigenvectors from a principal coordinate analysis on pairwise genetic distances among plant species. We regressed traits over phylogenetic eigenvectors using Generalized Linear Model with Gaussian (for normally distributed traits) or binomial (for binary traits) error distributions and used a stepwise model selection to identity the minimum adequate subset of predictors among eigenvectors. For each trait, we extracted the residuals of the minimum adequate model which represent

phylogenetic-independent variability in traits. Then, we tested for the effect of species insularity history (three levels: endemic, non-endemic native and introduced), insular system (two levels: Balearic Islands and Canary Islands) and their interaction (to test for differential patterns across archipelagos) individually for each phylogenetically independent trait using ordinary least square models. For all these analyses, we used species-level means.

2.4.3 | Effect of insularity history on defence syndromes

To test for defence syndromes, we summarized all plant traits by conducting a principal component analysis (PCA) using the 'FactorMineR' package in R (Lê et al., 2008). From this analysis, we extracted the standardized z-scores of the first two components (PC1 and PC2, respectively), and tested for the effect of species insularity history, insular system and their interaction on such values using the same approach described above for individual plant traits.

3 | RESULTS

3.1 | Effect of species insularity history on individual defensive traits

3.1.1 | Physical traits and nutrients

We found a significant phylogenetic signal for most traits, except for spinescence (Table 1). In addition, species insularity history significantly predicted several traits (Table 2), whereby endemic and non-endemic native species did not differ and had, on average, lower mean values of SLA, leaf size, nitrogen and phosphorus than introduced species (Table 2; Figure 3c–f). All other traits were not significantly affected by species insularity history (Table 2; Figure 3a,b). In addition, insular system significantly predicted some traits (Table 2), whereby species from the Balearic Islands exhibited a greater mean value of spinescence (0.20 ± 0.05 vs. 0.11 ± 0.05 score) and a lower mean value of leaf size (15.10 ± 3.19 vs. 25.08 ± 3.36 cm^2) than those from the Canary Islands. In addition, we found no significant species insularity history by system interaction in any case (Table 2; Figure S1a–f).

3.1.2 | Chemical defences

We found a significant phylogenetic signal for both total phenolics and condensed tannins (Table 1). There was no significant effect of species insularity history on either total phenolics or condensed tannins (Table 2; Figure 3g,h). Insular system significantly predicted leaf total phenolics (Table 2), whereby species from the Canary Islands exhibited a greater mean value (62.15 ± 5.16 vs. 37.42 ± 4.89 mg g^{-1} d.w.) than those from the Balearic Islands. In addition, we found no

TABLE 1 Analysis of the phylogenetic signal (λ = lambda) in allocation to constitutive physical defences (trichomes, spinescence, specific leaf area [SLA], and leaf size), nutritional traits (nitrogen and phosphorus) and chemical defences (total phenolics and condensed tannins) in leaves of 91 woody plant species. The maximum-likelihood estimate of λ (lambda, an estimate of the phylogenetic signal) and its associated log-likelihood values ('ln lik') are shown, as well as when λ is forced to $\lambda = 0$. Lambda varies between 0 and 1, where a value of 1 indicates phylogenetic conservatism consistent with the tree topology and a random walk model (i.e. trait similarity is directly proportional to the extent of shared evolutionary history), whereas a value of 0 indicates no influence of shared ancestry on traits (i.e. phylogenetic independence). Cases where the λ value differed significantly from 0 according to the log-likelihood ratio test are shown in bold type

Variable	λ_x	ln lik ($\lambda = x$)	ln lik ($\lambda = 0$)	p-value
Trichomes	0.42	−55.22	−57.47	**0.034**
Spinescence	0.23	−37.65	−38.80	0.131
Leaf size	0.73	−523.03	−528.58	**0.001**
SLA	1.00	−400.50	−411.26	**<0.001**
Nitrogen	0.70	−352.76	−358.86	**<0.001**
Phosphorus	0.42	−163.17	−166.28	**0.013**
Total phenolics	0.78	−428.51	−436.42	**<0.001**
Condensed tannins	0.75	−49.25	−59.85	**<0.001**

significant species insularity history by insular system interaction in either case (Table 2; Figure S1g,h).

3.2 | Effect of species insularity history on defence syndromes

The first two axes from the PCA together explained 51% (34% and 17%, respectively) of the variance across species for the eight traits measured. Specifically, we found that PC1 was positively related to SLA, nitrogen and phosphorus (Figure S2), whereas PC2 was negatively related to spinescence and positively related to leaf size (Figure S2).

The GLM on z-scores indicated that species insularity history significantly predicted variation in both PCs (Table 2), whereby endemic and non-endemic natives did not differ and exhibited a lower mean value for PC1 (i.e. thicker leaves with less macronutrients) than introduced species (Table 2; Figure 4a). In addition, endemics and non-endemic natives did not differ and exhibited a lower mean value for PC2 (i.e. smaller leaves, spinier plants) than introduced species (Table 2; Figure 4b). Insular system significantly predicted PC2 but not PC1 (Table 2), whereby plant species from the Canary Islands exhibited a greater mean for z-values for this axis (i.e. larger leaves, less spiny plants) than species from the Balearic Islands (0.277 ± 0.072 vs. 0.097 ± 0.055). Finally, there was no significant interaction between species insularity history and insular system for either PC1 or PC2 (Table 2).

Trait	Study factor	$df_{num,den}$	F-value	p-value
Trichomes	Insularity history (IH)	2, 87	2.24	0.113
	Insular system (IS)	1, 87	0.46	0.499
	IH × IS	2, 87	1.60	0.208
Spinescence	IH	2, 87	1.50	0.229
	IS	1, 87	8.49	**0.005**
	IH × IS	2, 87	1.18	0.312
SLA	IH	2, 87	3.34	**0.040**
	IS	1, 87	0.79	0.377
	IH × IS	2, 87	0.92	0.403
Leaf size	IH	2, 87	14.19	**<0.001**
	IS	1, 87	4.21	**0.043**
	IH × IS	2, 87	2.71	0.072
Nitrogen	IH	2, 87	6.24	**0.003**
	IS	1, 87	3.92	0.051
	IH × IS	2, 87	1.94	0.150
Phosphorus	IH	2, 87	3.94	**0.023**
	IS	1, 87	2.16	0.145
	IH × IS	2, 87	0.64	0.531
Phenolics	IH	2, 87	0.81	0.448
	IS	1, 87	5.37	**0.023**
	IH × IS	2, 87	0.08	0.920
Tannins	IH	2, 87	1.15	0.319
	IS	1, 87	0.24	0.625
	IH × IS	2, 87	2.67	0.075
PC1	IH	2, 87	4.21	**0.018**
	IS	1, 87	0.11	0.744
	IH × IS	2, 87	2.11	0.128
PC2	IH	2, 87	3.50	**0.034**
	IS	1, 87	16.66	**<0.001**
	IH × IS	2, 87	1.20	0.307

TABLE 2 Results from the ordinary least square models testing for the effects of species insularity history (endemic, non-endemic native or introduced species), insular system (Balearic or Canary Islands) and their interaction on leaf physical (trichomes, spinescence, specific leaf area [SLA], and leaf size), nutritional (nitrogen and phosphorus), and chemical (total phenolics and condensed tannins) traits putatively associated with herbivory for 91 woody plant species (see Section 2 for sample sizes by species insularity histories). We analysed each trait individually and also tested effects on the z-values from the first two axes (accounting 51% of variation in traits) from a Principal Components Analysis to test for effects on patterns of trait correlated expression. Principal component (PC) 1 was positively associated with SLA and nutrients, whereas PC2 was negatively associated with spinescence and leaf size. F-values, degrees of freedom and significance levels (p) are shown. Significant effects ($p < 0.05$) are in bold

4 | DISCUSSION

Our results show that, on average, insular endemics had similar trait values compared to non-endemic natives, and differed from exotics in several of the physical and nutritional traits studied. Counter to predictions, we found no evidence that insular taxa were less defended than introduced species; instead, they exhibited trait values indicative of higher physical defence (especially Balearic species) and lower nutritional quality, and we found no effect of insular species status on chemical defences. The multivariate analyses were consistent by showing trait combinations distinctive of insular (endemics and native non-endemics) relative to exotic taxa whereby the former had smaller, thicker and spinier leaves with less nutrients and the latter exhibited trait values indicative of low physical defences, high nutrients and overall a resource-acquisitive strategy. Overall, these results point to a functional-physical defence syndrome based on low-nutrient and physically defended leaves for insular plant taxa that is indistinct for endemic and non-endemic taxa, relative to introduced species.

Our analysis based on a taxonomically broad subset of plant species from two biogeographically distinct insular systems revealed unexpected patterns of allocation to defensive traits among groups of species with contrasting histories. Contrary to findings from early work (Bowen & Van Buren, 1997; Carlquist, 1974; Vourc'h et al., 2001), we found no evidence that endemic taxa were poorly defended compared to non-endemic natives or introduced species co-occurring in the same insular setting. Instead, we found that insular endemics and non-endemic natives had thicker, smaller and low nutrient leaves relative to introduced species, a pattern consistent across archipelagos despite their contrasting features. These results point to a more conservative strategy by insular taxa, in agreement with a study by Gorman et al. (2014) comparing endemic versus non-endemic *Eucalyptus* species. In contrast, introduced species, many of which are invasive, exhibited a resource-acquisitive strategy reflected by higher SLA values and nutrient concentrations suggestive of high growth capacity typical of invasive taxa (Leishman et al., 2010; van Kleunen et al., 2010).
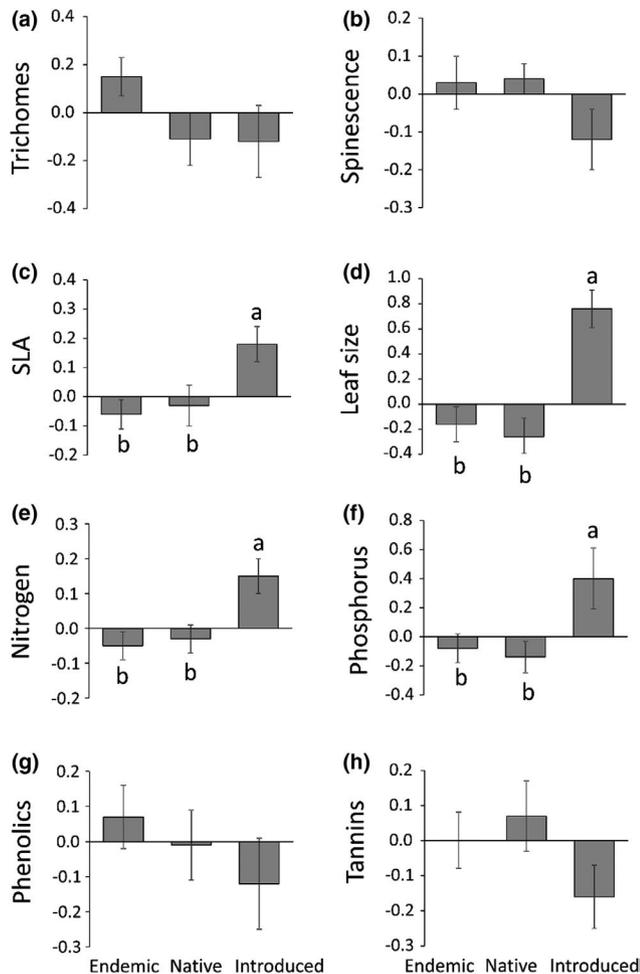
FIGURE 3 Allocation to (a) trichomes (0/1), (b) spinescence (0/1), (c) specific leaf area (SLA, cm^2 g^{-1}), (d) size (cm^2), (e) nitrogen concentration (mg g^{-1} d.w.), (f) phosphorus concentration (mg g^{-1} d.w.), (g) total phenolic concentration (mg g^{-1} d.w.) and (h) condensed tannins (0/1) in leaves of 91 woody plant species corresponding to three species insularity histories (endemics, non-endemic natives and introduced) in two insular systems (Balearic Islands and Canary Islands). Bars are residuals from the general linear models ± standard error (N = 20–42 plant species). Statistics are shown in Table 2. Different letters indicate significant ($p < 0.05$) differences between species insularity histories

In addition, insular taxa exhibited greater leaf thickness (correlated with toughness) and spine presence (particularly for Balearic species which correlate with resistance against herbivory (Carmona et al., 2011; Marquis et al., 2012), particularly by browsers. This pattern could be explained by different histories of vertebrate herbivory, either a historical legacy in the case of native ungulates (now extinct) in the Balearic Islands (i.e. defensive anachronism) or a recent history of herbivory by introduced mammals in the Canary Islands. Relatedly, Cubas et al. (2019) found that endemics from Canary Islands were more attacked by an introduced European rabbit than non-endemics and exotic species, a pattern which could implicate defences in both ways, that is, greater pressure induces higher defences for endemics (consistent with our interpretation), or that lower defences result in higher susceptibility. In addition,

consistent with our findings, a recent meta-analysis by our group addressing both herbivory and plant defences (including Balearic and Canary Islands, as well as other Mediterranean systems) found greater herbivory by introduced mammals and a trend for higher plant physical defences for insular relative to mainland populations of species native to islands, that is, non-endemic natives (Moreira et al., 2021). It should also be noted that physical traits such as leaf toughness and trichome density can mediate resistance against extreme abiotic events (e.g. drought, salinity, radiation, low resource levels; He et al., 2018), and therefore may represent a response to island conditions other than herbivore pressure. Taken together, the observed patterns of variation in physical traits and nutrients suggest a more conservative resource use strategy due to abiotic forcing and/or a history of high browsing pressure (native or introduced vertebrates) for insular taxa, whereas exotics showed lower physical defences and a bias towards resource-acquisitive strategy.

Chemical defences, on the other hand, did not significantly differ between insular and introduced plant taxa, a pattern that was qualitatively consistent across archipelagos. This finding agrees with our meta-analysis showing no difference in plant chemical defences between plant species with disjunct island–mainland distributions (Moreira et al., 2021), suggesting that insularity effects on different components of plant secondary chemistry are highly variable. Previous studies showed that phenolic groups such as tannins and flavonoids are usually correlated with both insect and vertebrate herbivory (Levin, 1971; Roslin & Salminen, 2008), and could be under selection by different herbivore species and insect guilds with varying feeding modes and degrees of specialization. If different groups of secondary metabolites have evolved in response to interactions with different herbivore species or guilds, then efforts are needed to assess both univariate and multivariate variation for more types of compounds as well as conduct chemical analyses with a greater resolution within each class of metabolites, combined with finer assessments of herbivory levels by different herbivore taxa. These more detailed analyses (i.e. variation within specific, targeted classes of compounds informed by plant–herbivore natural history) following from broad information obtained from comprehensive assessments (e.g. metabolomics), could help uncover evolutionarily meaningful patterns of variation in secondary chemistry. In addition, as mentioned above for physical traits, phenolic compounds can also play a role in abiotic resistance (e.g. thermal tolerance, photoprotection; Close & McArthur, 2002), whereby differences in abiotic conditions between insular systems and mainland (Weigelt et al., 2013) could select for differences in compound concentrations. An explicit assessment of abiotic factors (e.g. climate, soil, light levels) is therefore also warranted.

Our comparison of insular systems indicated higher spinescence and smaller leaves for taxa from the Balearic Islands, whereas those from the Canary Islands exhibited higher chemical defences and larger and thinner leaves. Small and physically defended leaves are common in Balearic species (e.g. endemics), where the characteristic xerocanthic vegetation is dominated by small shrubs that frequently bear spines (Tébar et al., 2004; Terradas, 1991). In addition to species composition differences (e.g. due to environmental filters), these trait
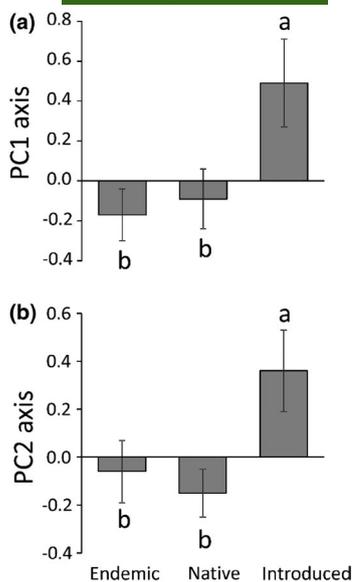
FIGURE 4 Comparison of z-values from the (a) first (PC1) and (b) second (PC2) axes of a principal component analysis summarizing variation in eight plant traits, namely trichomes, spinescence, specific leaf area (SLA), size, nitrogen concentration, phosphorus concentration, total phenolic concentration and condensed tannins across 91 woody plant species with contrasting insularity histories (endemics, non-endemic natives and introduced). Species were sampled from two insular systems, namely the Balearic Islands and Canary Islands. PC1 was positively related to SLA, nitrogen and phosphorus, whereas PC2 was negatively related to spinescence and positively to leaf size. Bars are residuals from the general linear models ± standard error (N = 20–42 plant species). Statistics are shown in Table 2. Different letters indicate significant (p < 0.05) differences between species insularity histories

differences could have also evolved in response to past selection by extinct native ungulates in Balearic Islands (Burns, 2019), possibly representing a defensive anachronism in physical traits. Likewise, abiotic factors such as more intense wind exposure (Terradas, 1991) as well as the aridity characteristic of the Meditarranean-type climate could have shaped higher levels of physical traits relative to the Canary Islands. Nonetheless, it is not possible to test these hypotheses and determine their plausibility based on the data at hand; further detailed studies correlating abiotic factors with physical traits across species, experimental manipulation of herbivory (e.g. using mechanical damage) and herbivore bioassays to test resistance, and replicated comparisons of islands with contrasting histories of ungulate herbivory would provide robust approaches to this end. On the other hand, it is worth also noting that we found that five species sampled in both archipelagos displayed higher levels of total phenolics (55% on average) coupled with larger leaf size (77% on average) in the Canary Islands compared to those sampled in the Balearic Islands. The same pattern was observed in 8 out of 10 congeneric Canarian-Balearic endemics, suggesting different underlying explanations relative to physical defences (e.g. recent history of high herbivory levels by introduced herbivores in the Canary Islands). This finding is coupled with larger leaves for Canary Island species which builds on the hypothesis that transitions from

Mediterranean to subtropical island conditions select for plant trait combinations associated with longer leaf and plant life spans (García-Verdugo et al., 2020; Lens et al., 2013).

While the above patterns of trait variation controlled for phylogeny, it is important to also point out that we found a phylogenetic signal for almost all the traits measured, showing that shared evolutionary history is an important factor explaining variation in functional traits and defences across the studied plant taxa in these archipelagos (Ackerly, 2009). These findings included functional traits (e.g. SLA, nutrient levels) which frequently exhibit evolutionary labile patterns under insular plant radiations (e.g. woodiness, growth and photosynthetic rates; García-Verdugo et al., 2014; Herben et al., 2014; Santiago & Kim, 2009). Our findings thus highlight that insular floras can exhibit phylogenetic conservatism despite tendencies of functional trait convergence observed in other insular systems (García-Verdugo et al., 2014). Interestingly, the only exception to these findings was spinescence. This trait was more frequently observed in Balearic endemic species and suggests a possible case of evolutionary convergence in response to herbivore pressure exerted by extinct native browsers or to abiotic factors, as previously discussed (Burns, 2019).

4.1 | Limitations and future directions

There are some aspects of our study that point to limitations to be addressed in future investigations on insularity effects on plant–herbivore interactions and plant defences. For example, measuring levels of herbivory in addition to defences (e.g. by insects or introduced mammals) is necessary for a robust test of insularity effects that link plant putative defences and herbivore pressure (Moreira et al., 2021). Endemics and native non-endemics could experience higher levels of herbivory, thus explaining higher physical defences. Within this context, two additional features stand out. To the extent that is possible, measurements of herbivory that separate damage by different vertebrates and invertebrate guilds (or species) is needed, as pooling data across groups can sometimes mask important patterns. In addition, joint tests of herbivory and plant defences should also consider controlled assessments (common garden, greenhouse) separating constitutive from induced defences to better understand how plant defensive strategies have evolved under insularity.

Another important point to make is that our assessment of chemical defences was not comprehensive. Our approach revealed no clear patterns of chemical defence across a broad phylogenetic sample of the insular floras considered, but species-specific mechanisms of chemical defence cannot be ruled out. Indeed, an assessment of other types of secondary compounds would provide a more robust characterization of variation in secondary chemistry underlying plant defence and defence syndromes. Likewise, a more detailed study on particular classes of compounds (relevant to specific plant–herbivore taxa) would be warranted, pending information on the natural history of key interactions.

Additional study design features, which complement or build on the approach used here, are also recommended. Specifically, this

would include an increase in the number of species that achieves a balanced representation of taxa of different life-forms (e.g. we did not include herbs) as well as a better representation of endemic species. In addition, while there are advantages to sourcing plants from botanical gardens, this may lead to biases and reduced variation in the genetic pools sampled as well as to plasticity-based variatoin in response to garden conditions that is not representative of natural (in situ) variation. Accordingly, in-situ measurements based on natural levels of variation combined with common garden or greenhouse experiments (e.g. to reduce environmental effects in plant trait measurement) to inform observed patterns in the field represent a robust way forward.

Finally, as a side note to studies including exotic species, we note that although the species sampled in this group did not exhibit biases in their geographical origin and were of recent introduction (preventing evolved trait values under insularity that confounded the comparison with native species), they belonged to genera that are not represented by any other (native) species on the studied islands. As a result, taxonomy and evolutionary history may have been confounded in our comparison of exotics to island natives. While this limitation is likely common in other systems due to idiosyncratic introduction patterns and a high chance that native and introduced species are taxonomically distant, careful examination in some systems may allow to at least partially account for these biases (e.g. when available, a priori selection of focal genera that include island native and non-native species).

CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data used in this study are archived at https://doi.org/10.5061/dryad.qbzkh18jf.

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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 experiment: XM, CGV, LAR. Performed the field sampling: CGV, JCC, JCG, MVF. Performed plant measurements: BLN, XM, CGV. Contributed reagents/materials/analysis tools: XM, CGV. Analysed the data: BC, XM. Wrote the first draft of the manuscript: XM. Contributed critically to the writing: CGV, LAR, BC.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.