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Xoaquín Moreira ·  
Luis Abdala-Roberts *Editors*

# Ecology and Evolution of Plant-Herbivore Interactions on Islands

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

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

## Abstract

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

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## 4.1 Phenotypic Syndromes in Macaronesian Plants: Biogeographical Framework

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

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

In this chapter, we review the available evidence on putatively defensive traits for a particular island-mainland system: the Macaronesian islands and their Mediterranean continental source area. The Macaronesian islands are composed of four volcanic archipelagos (Azores, Madeira, Canary Islands and Cape Verde) lying on the North Atlantic Ocean, of which the Canary Islands harbour the highest plant diversity (c. 600 taxa). From a climatic point of view, Late Pleistocene shifts from tropical to Mediterranean-type conditions within some island areas likely promoted active reciprocal biodiversity exchange between Macaronesian and mainland settings (Fernández-Palacios et al. 2011; García-Verdugo et al. 2019a; Caujapé-Castells et al. 2022). Up to five vegetation belts can be currently differentiated within each island, with Mediterranean-like thermophilous shrublands occupying lowland zones (Fernández-Palacios et al. 2011). Mediterranean-type habitats in Macaronesia are, however, characterized by particular features associated with the latitudinal location of the archipelagos. For instance, lowland zones experience subtropical conditions (i.e. narrow annual temperature range) and high exposure to UV radiation all year round (Utrillas et al. 2013; García-Verdugo 2014; see also Weigelt et al. 2013). Importantly, the Macaronesian flora has evolved in the absence of large herbivores until the arrival of human colonists (Gangoso et al. 2006; De Nascimento et al. 2020). In this regard, we could expect island endemic lineages to

show clear phenotypic responses depicting herbivore release with respect to ungulate browsers (e.g. Bowen and Van Vuren 1997). Comparisons of insect diversity between both settings have been studied in less detail, but herbivore guilds such as beetles (Coleoptera) appear to exhibit low diversity (Becker 1992), which would also support the idea of reduced insect herbivore pressure on the island setting. Studies on Macaronesian plant lineages have comprised traits related to defence against browsers (i.e. spines) or chemical traits that could affect both browsing mammals and insect herbivores (i.e. secondary compounds) (e.g. Shmida and Werger 1992; Monroy and García-Verdugo 2019; Moreira et al. 2022). Even though levels of insect herbivore pressure are difficult to assess, browsing pressure by ungulates is generally shown as a major driving force in the evolution of insular plant defence (Bowen and Van Vuren 1997; Vourc'h et al. 2001), and hence we would expect Macaronesian endemics to have lost (or lowered, at least) traits related to anti-herbivory defence.

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

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

### **4.2.1 Spinescence**

Researchers have recurrently noticed that some island plant species do not display spinescence (i.e. the physical defences in the form of spines, thorns or prickles), while their mainland relatives do (Carlquist 1980; Bowen and Van Vuren 1997; Burns 2014; reviewed in Burns 2019). If spinescence plays a role as a browsing



deterrent, an intuitive explanation for this pattern is that evolution in the absence of browsers may have resulted in the loss or reduction of such mechanical defences.

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

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

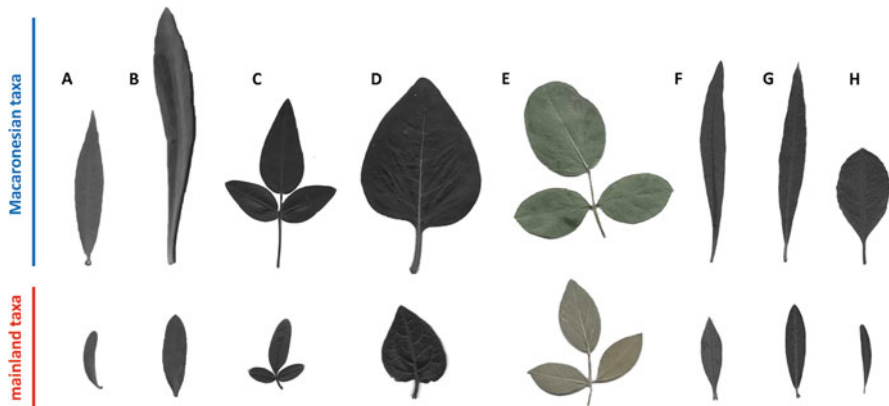
In conclusion, loss of spinescence does not seem to be a generalized feature of island plants. Studies conducted to date indicate similar levels of spinescence on islands versus mainland areas, and in some cases even higher trait values for insular plants. Differences between Macaronesian and Mediterranean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

### 4.2.2 Leaf Size

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

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

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



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

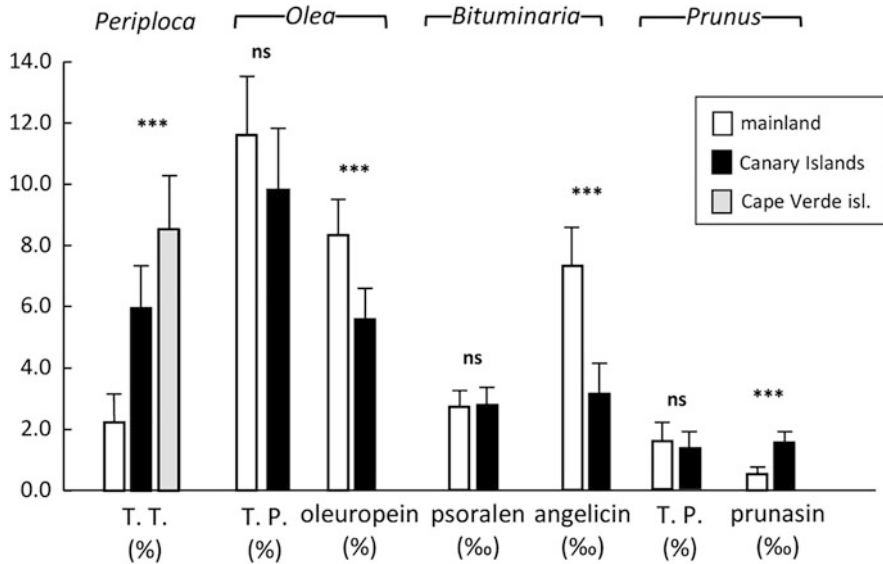
Macaronesia and the Mediterranean mainland area is the much narrower temperature range of the islands (García-Verdugo 2014). Thus, climatic conditions could favour convergent patterns towards large leaf sizes across island taxa, whereas selection towards smaller leaf sizes would prevail in continental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

### 4.2.3 Secondary Metabolites

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

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

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



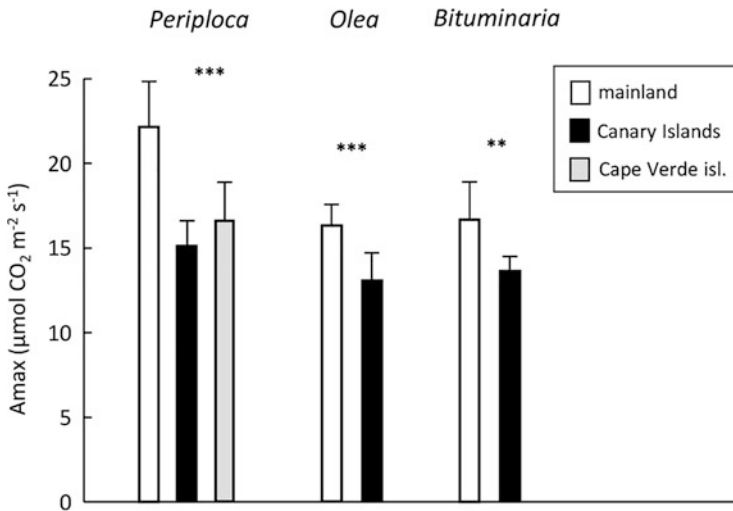
**Fig. 4.2** Levels of putatively defence compounds in species pairs grown under common garden conditions. Statistical differences ( $***p < 0.001$ ) are based on the results provided in each study. Data are extracted from: Monroy and García-Verdugo (2019) for *Periploca*, García-Verdugo et al. (2023)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

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

#### 4.2.4 Photosynthetic Rates

Photosynthetic performance has never been considered a putative component of the island syndrome (see Burns 2019; Baeckens and Van Damme 2020). However, we believe that this trait could help provide an integrative view on plant defence, since  $\text{CO}_2$  assimilation rates intrinsically lie at the core of defence theories (growth-defence trade-off; Herms and Mattson 1992; Wright et al. 2004) and carbon-based secondary metabolites are strongly related to photosynthetic patterns (Karabourniotis et al. 2014; Menzies et al. 2016).

Estimates of photosynthetic rates under common garden conditions have seldom been assessed in Macaronesian versus Mediterranean lineages. Considering the few studies available, there appears to be a clear tendency towards lower  $\text{CO}_2$  assimilation rates in Macaronesian taxa (Fig. 4.3). Differences in photosynthetic rates suggest alternative resource-use strategies adopted in xeric habitats that differ in seasonality. Because photosynthesis in continental Mediterranean areas is strongly limited both by water availability (prolonged summer drought) and by temperature



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

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

Furthermore, differences in CO<sub>2</sub> assimilation rates could influence defence allocation. For example, a conservative resource-use efficiency in photosynthesis is typically associated with high investment in polyphenolic compounds with a protective role (Karabourniotis et al. 2014), which is in line with the pattern previously discussed for Macaronesian taxa inhabiting lowland habitats (see Sect. 4.2.3—Secondary Metabolites). Apart from implications in herbivore resistance, lower photosynthetic rates on Macaronesian plants could translate into limited herbivory tolerance. Traits such as compensatory growth or resprouting ability following herbivore attack (Fornoni 2011) may be limited on island taxa that display conservative rates of carbon storage and high construction costs for photosynthetic tissues (i.e. investment in large amounts of secondary compounds, large leaf sizes). Limited tolerance to herbivory might thus contribute to explaining why Macaronesian

endemic plants are more negatively impacted by exotic browsing mammals than non-endemics (Cubas et al. 2019).

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### 4.3 Synthesis and Future Considerations: A Syndrome Perspective

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

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

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

In conclusion, there is limited evidence that Macaronesian island lineages have lost their defence traits with regard to mainland counterparts. Emerging leaf phenotypic patterns could be mostly explained by disparate patterns of climate-driven

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

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