



# Exaptation and vulnerability to introduced mammal herbivores on Balearic endemic flora

Miquel Capó<sup>1,2</sup>  | Rocío Pérez-Barrales<sup>3,4</sup> | Joana Cursach<sup>1</sup> | Jaume Garrido<sup>1</sup> |  
Elena Baraza<sup>1</sup> | Juan Rita<sup>1</sup>

<sup>1</sup>Research Group on Plant Biology under Mediterranean Conditions, Biology Department, University of Balearic Islands, Palma, Spain

<sup>2</sup>Departamento de Sistemas y Recursos Naturales, Universidad Politécnica de Madrid, Madrid, Spain

<sup>3</sup>School of Biological Sciences, King Henry Building, University of Portsmouth, Portsmouth, UK

<sup>4</sup>Botany Department, University of Granada, Granada, Spain

## Correspondence

Miquel Capó, Departamento de Sistemas y Recursos Naturales, Universidad Politécnica de Madrid, Madrid, Spain.  
Email: [miquel.capo@uib.es](mailto:miquel.capo@uib.es)

## Funding information

Direcció General de Política Universitària i Recerca (Govern de les Illes Balears), Grant/Award Number: FPI/1925/2016; Ministerio de Economía, Industria y Competitividad, Gobierno de España, Grant/Award Number: CGL2015-70449-R; European Union (NextGenerationEU)

**Handling Editor:** Sandra Nogue

## Abstract

**Aim:** Introduced mammal herbivores are predicted to negatively affect insular flora. However, disentangling which particular traits (1) developed from exaptations and (2) are functional to avoid herbivory remains mainly unknown. This study aims to assess if the flora of continental islands with historic native herbivores are exapted to the introduction of new mammal herbivores and to predict the potential vulnerability of endemic species from islands where mammal herbivores have not been introduced.

**Location:** Balearic Islands.

**Taxon:** 96 Balearic endemic plant species.

**Methods:** We investigated whether the endemic flora on continental islands maintains functional traits that resist introduced mammal herbivores by analysing the chemical and morphological traits related to plant resistance of five individuals for each of 98 species. Also, we measured plant-size variables to assess plant escape strategies. Overall, we combined these traits with the accessibility to goats. Predictive models were generated for species that inhabit islands where goats have not been introduced to assess their potential vulnerability.

**Results:** Endemic species may defend against new herbivores (e.g. goats) if they contain highly toxic compounds (alkaloids, glycosides, coumarins), spinescent and urticating structures, or specific plant architecture (low plant size, high specific leaf area). If such traits are absent, the species may become extinct—unless they inhabit areas inaccessible to goats. On continental islands, some endemic species are expected to resist the introduction of herbivores, while others may be significantly affected.

**Main Conclusions:** From the ancient connection with the mainland, exaptations may allow the plants to resist the presence of introduced herbivores. However, non-exapted species could be threatened by the introduction of non-native ungulates.

## KEYWORDS

defence, escape, exaptation, insularity, plant-herbivore interactions, resistance

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *Journal of Biogeography* published by John Wiley & Sons Ltd.

## 1 | INTRODUCTION

Plant-herbivore interactions represent an important ecological driver for the evolution of defence strategies to prevent, ameliorate and survive herbivory (Agrawal & Fishbein, 2006). Plant defence strategies against herbivory can be classified into three main groups: resistance, tolerance and escape (Mauricio, 2000; Strauss & Agrawal, 1999). Resistance strategies include the production of toxic compounds that make plants unpalatable, namely phenolic compounds (Baraza et al., 2004), condensed tannins (Cooper & Owen-Smith, 1985), flavonoids (Pellissier, 2013), saponins (Ishaaya et al., 1969), triterpenoids (Zwenger & Basu, 2008), glycosides (Diner et al., 2009), alkaloids (Coley, 1987) and coumarins (Howery et al., 2016). Anatomical structures, including spines and high pilosity, provide another layer of defence against herbivory, primarily against mammals (Mauricio, 2000; Milton, 1991). Tolerance includes a wide variety of physiological mechanisms that act to rapidly compensate for the loss of biomass caused by predation (Agrawal, 1998; Rasmann et al., 2009). Finally, the escape strategy consists of avoidance of herbivory, for example, by reducing plant size (Alonso & Herrera, 1996; Gange & Brown, 1989) or inhabiting areas inaccessible to herbivores, such as cliffs or mountain walls (Pisanu et al., 2012).

When herbivory disappears, either herbivores become extinct or plants colonize new environments free of herbivores, the selective pressure linked to resistance may also decrease or disappear, and allow plants to reallocate resources to other functions such as growth, competitiveness or reproductive output (Hull-Sanders et al., 2007; Keane & Crawley, 2002; Pardo et al., 2004). Alternatively, resistance traits can remain in herbivore-free environments if the traits confer a complementary function or appear genetically fixed within the taxonomic group (Wink, 2008), as occurs for structural anti-herbivore traits (Hanley et al., 2007). The hypothesis that resistance traits could disappear in herbivore-free environments has been tested in oceanic island ecosystems, where plant species might lack adaptive defensive traits due to the absence of mammalian herbivores, as exemplified by the flora on volcanic islands such as the Hawaii archipelago (Barton, 2016) or the Canary Islands (Cubas et al., 2019; Nogales et al., 2006). The introduction of exotic herbivores onto oceanic islands leads to severe perturbation to plant communities (Cubas et al., 2019; Nogales et al., 2006) and drives their extinction, and is currently one of the major threats to endemic species (Bowen & Van Vuren, 1997; Campbell et al., 2004; Médail, 2017). In contrast, less is known about the impact of herbivory on the flora of continental islands (Gizicki et al., 2018; Moreira et al., 2021). The plant communities on continental islands are mostly derived from the original flora present on the mainland to which the islands were previously connected. Hence, the flora of continental islands can possess defence traits that evolved in the context of the plant-herbivore interactions present within the original continental flora. While the presence of herbivory defence traits may intuitively imply that plant communities should be resilient to herbivory, evidence of the negative impacts associated with the introduction of invasive mammals, such as goats, on continental islands worldwide

is increasing (Carrion et al., 2011; Moreira et al., 2021), and eradication of introduced herbivores have been performed on several continental islands (Capizzi, 2020). More generally, biological invasions are one of the main causes of biodiversity loss worldwide (De Vos et al., 1956; McNeely et al., 2001; Médail, 2017), with exotic herbivores responsible for the extinction of endemic flora on island ecosystems (Bowen & Van Vuren, 1997; Campbell et al., 2004; Médail, 2017).

The Balearic Islands Archipelago, located in the Western Mediterranean Basin, originated by fragmentation of the eastern coast of the Iberian Peninsula during the Oligocene, 25 Mya (Rosenbaum & Lister, 2002), and provides an example of continental islands inhabited by ancient mammal herbivores that evolved under insular conditions. The most recent connection between the islands and the Iberian Peninsula occurred during the Messinian Salt Crisis 5.9–5.3 Mya when the last terrestrial vertebrate paleofauna arrived at Mallorca. During the first Quaternary glaciations, about 1–2 Mya, the endemic bovid *Myotragus* present in Mallorca colonized the neighbouring island of Menorca (collectively known as the Gymnesic Islands). This bovid evolved under insular conditions, giving rise to the species *Myotragus balearicus* (Bover et al., 2008; Palombo et al., 2013; Winkler et al., 2013). However, there is no evidence of the presence of *Myotragus* in the archaeological records of Eivissa and Formentera (collectively known as the Pityusic Islands), although the fossil records show the presence of the Neogene bovid *Ebusia moralesi* until the Quaternary, when it disappeared and has not been detected during this period (Moyà-Solà et al., 2022).

The extinction of the native mammalian herbivore on the Gymnesic Islands coincided with the colonization by humans (Palombo et al., 2013) and the introduction of new fauna of mammalian herbivores, such as goats, rats and rabbits (4300–4050 years BP; Muñoz et al., 2019; Seguí et al., 2005). The available data suggests that the introduced goats were managed and remained under human control through hunting or breeding purposes (Mayol et al., 2017). More recently, coinciding with land-use abandonment in the last five decades, the feral goat populations have exploded exponentially. Feral goat populations are mainly distributed across the mountains of Mallorca and represent a serious threat to the maintenance and conservation of native vegetation (Capó, Engelbrecht, et al., 2021; Mayol et al., 2017). Thus, the environmental authorities have carried out several programmes to fence areas to protect the flora threatened by goats (Moragues et al., 2015). The number of herds of feral goats on Menorca has also increased in the last decade, although their impact on the native vegetation is less harmful than on Mallorca (Menorca Insular Council, pers. com.). Fortunately, feral goats are not found freely in natural areas of Eivissa and Formentera and only managed individuals are found in farms or private properties (Capó et al., 2022).

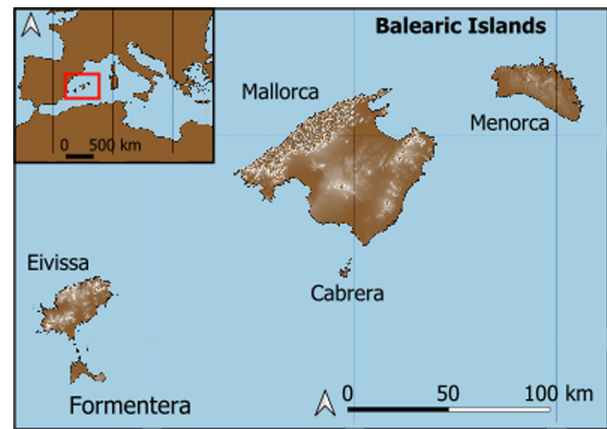
The paleontological history, introduction of feral goats and recent abandonment of the countryside of the Balearic Archipelago represent a unique opportunity to disentangle the interplay between the ecology and evolution of resistance traits to herbivory based on the knowledge already acquired about the endemic flora (Rita &

Payeras, 2006; Roselló & Sáez, 2000, 2008, 2017; Sáez et al., 2011, 2017) and the exhaustive archaeological work to describe the native paleofauna of the entire archipelago (Bover et al., 2008, 2016, 2019; Palombo et al., 2013). Overall, the Balearic Archipelago represents an excellent study case because (i) it is a hotspot of insular endemic flora, (ii) the fossil record confirms the evolution of native mammalian herbivores after the formation of the archipelago, and (iii) the large population of feral goats is currently threatening the native flora within the natural landscapes on some of the islands. Considering this scenario, the objectives of the present study are to (i) evaluate if the flora of this archipelago, which has an evolutionary history with mammal herbivores, are exapted to the introduction of new herbivores—or whether it could be endangered—as reported for endemic species on other islands and (ii) use the data generated to establish a predictive model to evaluate the potential vulnerability of endemic species from islands without introduced ungulates. Our hypotheses are: (i) endemic species inhabiting areas accessible to feral goats will exhibit resistance traits against herbivory, (ii) resistance traits can be predicted based on the phylogenetic and ecological context, and (iii) islands not invaded by introduced ungulates might present flora without resistance traits against herbivory in areas potentially accessible to feral goats. Overall, by using the Balearic Archipelago as a representative case study, we hope to define a methodological and analytical approach to identify the levels to which the endemic flora of continental islands harbour mechanisms that may protect against new herbivores, and this information may help to inform the design of conservation and management strategies for natural resources.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

The Balearic Archipelago (Spain) is located in the central part of the Western Mediterranean Basin (Figure 1). The Archipelago is formed of four main islands with varied topographical and geological characteristics, covering areas from 3640 km<sup>2</sup> (Mallorca) to 83 km<sup>2</sup> (Formentera) and altitude ranges from 0 to 1445 m a.s.l. (Mallorca). The climate is typically Mediterranean, characterized by a dry summer season and rainfall events in spring and autumn (Homar et al., 2009). Owing to the variability in the geography and Mediterranean climate, the Archipelago contains a wide diversity of environments, from salt marshes or temporary ponds to woodlands and mountain gullies, and is home to 1551 plant species, of which 20 are endemic to the Tyrrhenian Islands (including Corsica and Sardinia) and 140 are exclusive to the Balearic Archipelago (Rita & Payeras, 2006; Sáez et al., 2013). The present study assessed 96 Tyrrhenian or Balearic endemic taxa present in the Balearic Archipelago, representing 76 genera and 29 families that occur in various habitats (Table S1). For each endemic taxa, samples from five individuals ( $n = 480$  samples in total) were collected during the springs of 2017 and 2018 to generate phenotypic data on herbivory resistance and escape traits (see below). To assess the variation of



**FIGURE 1** Map of the Balearic Islands archipelago. The islands are Mallorca and Menorca (Gymnesians), Eivissa and Formentera (Pityuses). Projection used: ETRS89/UTM zone 31N. Raster altitudinal layer MDT200 has been acquired from the national institute of geographic information (CNIG) from Spanish Government by free licence obtained in [www.centrodedescargas.cnig.es/](http://www.centrodedescargas.cnig.es/).

herbivory impact on endemic species depending on their ecological distribution, the potential accessibility of herbivores was described based on the environment that the endemic flora occupies. Specifically, plant species that inhabit cliffs and rocky mountain environments (rupicolous communities) were considered inaccessible, whereas species from shrublands and caespitose communities were considered accessible to mammalian herbivores.

### 2.2 | Resistance and escape traits against herbivory in endemic flora

Two types of putative defence traits were assessed: chemical compounds and anatomic structures. We quantified the concentrations of chemical compounds commonly known to provide chemical protection against herbivory; specifically, total phenolic compounds, condensed tannins, triterpenoids, saponins, flavonoids, alkaloids, glycosides and coumarins. The chemical analyses are described in Supporting Information S1. Briefly, mature leaves were collected (up to 2g dry weight), except for taxa with small plant sizes or those under threat, for which up to 100mg dry weight was sampled. The leaf materials of all sampled accessions were stored at 40°C for 1 month to inhibit enzyme activity and avoid the high-temperature volatilization of polyphenolic compounds (Baraza et al., 2009). Samples were ground to a particle size of less than 1mm and conserved in airtight tubes for chemical analysis. Total phenolic compounds were analysed following the Folin–Ciocalteu method (Baraza et al., 2009) with some modifications, and the final readings were performed using a Multiscan Sky Microplate Spectrophotometer (ThermoFisher Scientific Inc.). Tannic acid was used as a standard reference for total phenolic compounds and all readings were relativized to tannic acid equivalents. Tannins were quantified using the

proanthocyanidin assay (Tomás-Barberán, 1995) using cyanidin as a standard for condensed tannins; all readings are presented as cyanidin equivalents (CE). Saponins, flavonoids and triterpenoids were quantified using protocols obtained from AbdulAzeez et al. (2018), Sharma and Janmeda (2017) and Liang et al. (2014), respectively. As sufficient plant material was not available to carry out exhaustive quantification for all species, because most endemic species are small shrubs or herbs, the presence of defence compounds that are usually phylogenetically fixed—such as glycosides, alkaloids and coumarins—were determined using the literature on the presence of these compounds in closely related taxa (Table S2).

The anatomical structures assessed included spinescence and pilosity. Spinescence was classified as spines covering the entire individual (e.g. as for *Astragalus balearicus*, Figure S1A); less abundant, but evident spines (i.e. *Rhamnus bourgeana*, Figure S1B); or as hairs with urticating properties (i.e. *Urtica bianorii*, Figure S1C). Pilosity was defined as a high density of hairs covering the leaves (i.e. *Helichrysum crassifolium*, Figure S1D). The plant-size escape traits assessed included average plant size, total leaf area and specific leaf area (SLA). The average plant size of each species was obtained from the literature (Castroviejo, 1986), total leaf area was determined from images of fully expanded leaves of the sampled individuals using ImageJ software (Abràmoff et al., 2004) and SLA ( $\text{cm}^2/\text{mg}$ ) was calculated by dividing the total leaf area by the dry weight of the same sample.

### 2.3 | Phylogenetic relationships between resistance-escape traits and the effects of goat herbivory

As some resistance and escape traits were described using data from closely related species and some plant families appear overrepresented in the endemic flora, we analysed the raw data and phylogenetically independent contrasted data using pairwise comparisons between traits, according to the methods described by Agrawal and Fishbein (2006). We used the sequences of internally transcribed spacers and rDNA 5.8S from the GenBank® library at the genus level (Supporting Information S2). Once the phylogenetic reconstruction was complete, phylogenetic independent contrasts (PICs) were calculated using the Felsenstein's method (Felsenstein, 1985), as implemented in the ape v5.3 package (Paradis & Schliep, 2019) of R software v3.6.1 (R Core Team, 2022). Pearson correlation indexes were subsequently obtained using the 'cor' and 'cor.mtest' functions of the 'corrgram' package (Wright, 2018) for the raw and PIC data.

A generalized linear model (GLM) was generated to investigate the potential functions of putative resistance and escape traits assessed as strategies to protect against herbivory. The accessibility of herbivores (1/0) was included as a response variable and modelled with a binomial distribution against all other previously described chemical and morphological traits as predictor variables. The analyses were conducted using data derived from the Gymnesic Islands (Mallorca and Menorca), where feral goats are present. Then, model

selection was implemented to determine which traits best predict the accessibility of goats, and the best-fitting model was selected by applying the Akaike information criterion (AIC) using the 'dredge' function of the 'MuMIn' R package (Barton, 2020). The significance of the differences between resistance and escape traits depending on accessibility to goats were assessed in the selected model using the 'Anova' function of the R software package 'car'. Resistance-escape traits were included in the best-fitting model as predictor variables. Traits that correlated significantly with resistance-escape traits in the PIC analysis were included in the principal component analysis (PCA), in which the accessibility of the plants to goats was assessed as a qualitative variable. PCA was performed using the 'PCA' function of the 'FactoMineR' package in R (Le et al., 2008).

To evaluate the overall resistance-escape complex, we calculated trait diversity by considering Shannon's diversity ( $H'$ ) to assess the balance between the richness and abundance of each trait, as described in Morris et al. (2014) for chemical diversity. Calculations were performed using the 'vegan' package v2.5-6 in R (Oksanen et al., 2008).

### 2.4 | Estimation of the potential vulnerability of plant species endemic to islands unaffected by herbivory

Based on the best-fitting model obtained in the previous section, we analysed the potential vulnerability of endemic species to Eivissa and Formentera, where feral goats are not present. We extracted the regression equation of the model constructed for endemic species to Mallorca and Menorca. The model was adjusted to a binomial response variable to distinguish the probability of coexisting with goats. This equation was then implemented for endemic species to Eivissa and Formentera to evaluate the vulnerability of each species to the putative introduction of feral goats. Then, the output was compared with the actual distribution of the species on the islands at present.

## 3 | RESULTS

### 3.1 | Resistance and escape traits against herbivory among endemic flora

Eighty-four species (87.5%) were collected from the Gymnesians and 12 species (12.5%) from the Pityuses. Of the species sampled on the Gymnesic Islands—where feral goats are present—62 occur in areas accessible to goats and 22 were only located in inaccessible habitats. In the whole archipelago, the distribution of endemic species in the three main habitats was not equal: 47% of species are based in shrublands, 30% in caespitose communities and 23% in rupicolous communities.

Of 96 endemic species, 95—all except *Primula acaulis* subsp. *balearica*—were found to contain phenolic compounds at

concentrations ranging from 0.01 to 2.25 ng/mg and 92 species contained condensed tannins at concentrations that varied from 0.01 to 3.87 ng/mg. Quantitative analysis showed that 28.1% (27/96) of the species sampled contained saponins, 52.1% (50/96) contained flavonoids, and 26% (25/96) contained triterpenoids. The literature indicated that 17.7% (17/96) of endemic plants have closely related species with alkaloids; 18.7% (18/96) have glycosides; and 6.2% (6/96) have coumarins. In terms of anatomical traits, 10.4% (10/96) of the endemic species are spinescent or stinging and 18.7% (18/96) exhibited pilosity. The foliar areas ranged from 0.00001 to 648.23 cm<sup>2</sup>, SLA varied from 0.00001 to 1543.80 cm<sup>2</sup>/g and plant size ranged from 3 to 150 cm.

### 3.2 | Phylogenetic relationships between effects of goat herbivory and resistance-escape traits

In PIC analysis (Table S3), the presence of alkaloids was positively correlated with the presence of glycosides ( $r = 0.48$ ,  $p < 0.001$ ), and both the presence of alkaloids and glycosides correlated with the absence of coumarins ( $r = -0.46$ ,  $p < 0.001$  and  $r = -0.39$ ,  $p < 0.001$  respectively). Additionally, the presence of alkaloids and glycosides both correlated positively with the foliar area ( $r = 0.42$ ,  $p < 0.001$  for both). Plant size correlated significantly with SLA in both the raw ( $r = -0.40$ ,  $p < 0.001$ ) and corrected data ( $r = -0.49$ ), and also with the leaf area after applying PIC ( $r = 0.61$ ,  $p < 0.001$ ). While significant correlations between flavonoids and pilosity and between SLA and plant size were observed in the raw data, these correlations disappeared after correcting the species using PIC.

Overall, 25% of endemic species from the Gymnesic Islands exhibited resistance to herbivory through chemical compounds and only 13.10% were spinescent (Capó et al., 2023). After fitting a model that included all the measured putative resistance and escape traits (setting coexistence with goats as the response variable) and using model selection, the variables selected for the best-fitting model were glycosides, coumarins, spinescence and plant size (Table 1). Moreover, although there were no significant differences in either alkaloids or SLA between species that inhabit areas accessible or inaccessible to goats, these factors were considered in the subsequent analysis as they are correlated with glycosides and plant size, respectively, as reported in Table S3.

Principal component analysis was used to infer how the combination of traits explains the development of resistance-escape

strategies among endemic species. The principal components separated groups of species based on the presence of resistance traits—as well as plant size and SLA, which are both measures of escape strategies (Figure 2). PC1 separated species that present resistance traits from species with escape traits, whereas PC2 separated the plants that exhibit resistance traits into species with anatomical resistance traits (spines) and chemical resistance traits (alkaloids, glycosides and/or coumarins). Species that lacked resistance traits were accessible to herbivores if the plant size was small and negatively correlated with high SLA, indicating a plant-size escape strategy. In contrast, species that inhabit areas inaccessible to herbivores exhibited an absence of chemical and anatomic structures and had medium plant size and SLA (Table 1).

### 3.3 | Estimating the potential vulnerability of endemic plant species to islands without introduced herbivores

Principal component analysis separated the sampled species into four major groups, two of which corresponded to shrublands (chemical and anatomical resistance), one to caespitose communities (plant-size escape) and one to rupicolous communities (ecological inaccessibility). Overall, the flora of islands without feral goats showed lower trait diversity than the species from islands where goats are present (Figure 3). However, endemic species that occurred in accessible habitats on islands with goats had a larger plant size and displayed higher trait diversity than the groups of endemic species to islands without feral goats. Interestingly, the endemic flora to islands without feral goats lacked spines and coumarins.

After considering all studied parameters and selecting the best-fitting model (Table 2), we extracted the regression equation obtained using the estimates of the model adjusted to a binomial response variable. Thus, the regression equation was:

$$\text{Coexistence} = \text{inv. logit}(2.908 + 26.987 \times \text{gly} + 22.276 \times \text{cou} + 27.517 \text{spi} - 0.085 \text{size}),$$

where gly = glycosides, cou = coumarins, spi = spinescence and size = plant size.

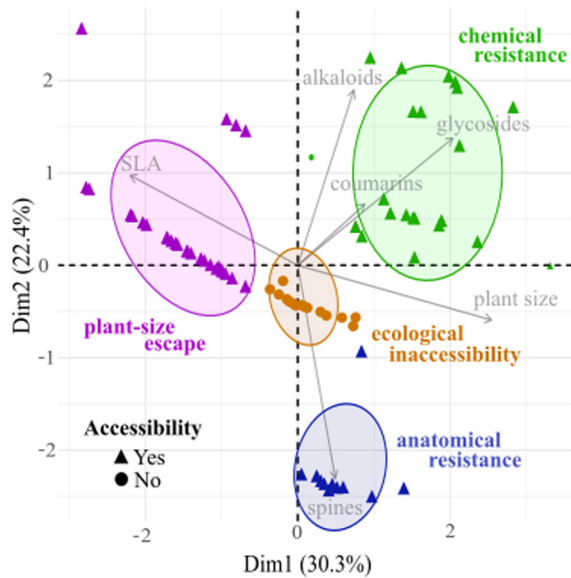
Assuming a future scenario of the introduction of goats, this regression equation was used to predict their coexistence with endemic species to islands where goats are currently absent (Table 3). Based

TABLE 1 Species included in each group and proportions and values of resistance traits obtained by principal component analysis (PCA).

PCA group	Species included (%)	Alkaloids (%)	Glycosides (%)	Coumarins (%)	Spines (%)	Plant size (cm)	Specific leaf area (cm <sup>2</sup> /g)
Chemical resistance	25.00	57.14	100.00	100.00	0.00	67.10	141.65
Anatomical resistance	13.10	7.14	0.00	0.00	100.00	57.27	133.63
Plant-size escape	34.52	28.57	0.00	0.00	0.00	5.00	564.48
Noresistance-escape	27.38	7.14	0.00	0.00	0.00	51.52	134.46



on the regression model and according to their presence of herbivory resistance traits, *Santolina vedranensis* and *Teucrium cossonii* subsp. *punicum* were predicted to be able to coexist with herbivores as these genera of plants contain chemical protective compounds, such as glycosides or coumarins (De Marino et al., 2012; Oganeyan et al., 1991; Silván et al., 1996). Species that were predicted to not be



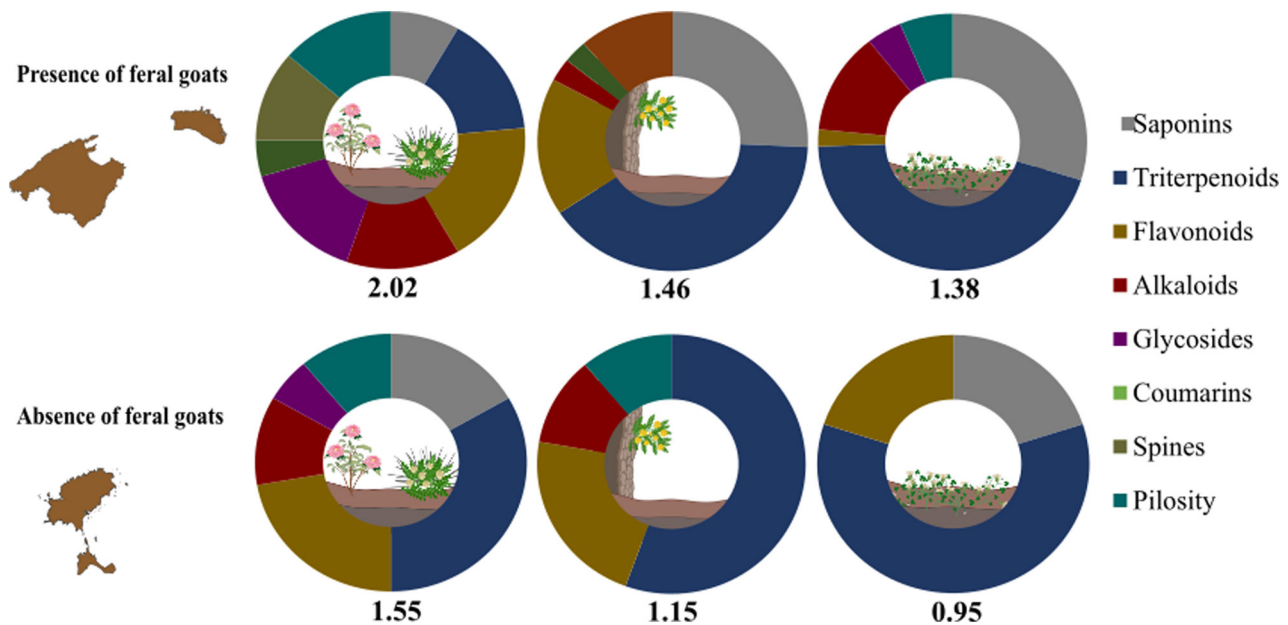
**FIGURE 2** Principal component analysis of the resistance and escape traits of species endemic to the Gymnesic Islands selected in the best-fitting model of putative resistance traits and other correlated parameters after PIC correction. PC1 was mainly constructed of glycosides (24%), specific leaf area (28%) and plant size (38%), while PC2 was mainly constructed of alkaloids (29%), glycosides (15%) and spines (42%).

able to coexist with introduced goats include *Genista dorycnifolia* and *Biscutella ebusitana*, which lack any resistance traits against herbivory and exhibit a large plant size. Additionally, *Thymus richardii* ssp. *ebusitanus*, which has a small plant size and high SLA, was predicted to have a high probability of coexisting with herbivores through an escape strategy. However, overall, 72.7% of species studied on the Pityuses have a 25% or lower probability of coexisting with feral goats. However, despite having resistance traits to facing herbivory, whether anatomical or chemical, other ecological factors can influence the risk of being predated by ungulates. For instance, in herbivore high-density scenarios or in scarce-resources environment, goats can feed on defended plants, as observed in *Euphorbia dendroides* (Capó, Engelbrecht, et al., 2021) and can be a serious threat to endemic species, as observed in previous studies on islets of the Balearic Islands (Capó et al., 2022).

## 4 | DISCUSSION

### 4.1 | Resistance-escape traits and their relationships based on phylogenetic-independent contrasts

The endemic flora of the Balearic Archipelago contains a remarkable proportion of species with resistance and escape traits, with varied structures and chemical compounds that protect against herbivory. The endemic flora of the Gymnesic Islands (Mallorca and Menorca) exhibit two main functional strategies against herbivory: resistance, through highly toxic compounds or anatomic structures, and escape, through small plant size. Species without these traits would probably have otherwise become extinct, or their distribution reduced



**FIGURE 3** Proportions of chemical compounds and anatomical defences present in species endemic to islands with feral goats (upper) and islands without feral goats (lower) separated by community type: shrublands (left), rupicolous (middle) and caespitose (right). Binary traits were relativized to 100%, with each trait represented in a different colour. Numbers indicate Shannon's diversity index.

**TABLE 2** Selection of the five best-fit models for the analysis. Variables included in each model are marked with a cross. The variables were phenolic compounds (TAE), condensed tannins (CE), saponins (Sap), flavonoids (Fla), triterpenoids (Tri), alkaloids (Alk), glycosides (Gly), coumarins (Cou), specific leaf area (SLA), spinescence (Spi), pilosity (Pil) and plant size (size). The Akaike information criterion (AIC) value and its delta ( $\Delta$ ) against the first model are shown in the last two columns.

Model	TAE	CE	Sap.	Fla.	Tri.	Alk	Gly	Cou	SLA	Spi	Pil	Size	AIC	$\Delta$ AIC
M01							X	X		X		X	10.8	0
M02							X	X	X	X		X	13.1	2.32
M03				X			X	X		X		X	13.1	2.32
M04							X	X		X	X	X	13.1	2.32
M05						X	X	X		X		X	13.1	2.32

**TABLE 3** Threatened status and probability of coexisting with introduced herbivores based on a binomial response variable in the model for species endemic to islands without herbivores. Eivissa (Ei), Formentera (Fo) and the surrounding islets (Is). Threatened status is according to the IUCN criteria (Sáez et al., 2017).

Endemic species	Distribution	Threatened	Coexistence B(0,1)
<i>Asperula pau</i>	Ei, Fo, Is	No	0.23
<i>Beta maritima</i> ssp. <i>marcosii</i>	Ei, Fo, Is	Yes	0.20
<i>Biscutella ebusitana</i>	Ei, Fo, Is	No	0.10
<i>Diplotaxis ibicensis</i>	Ei, Fo, Is	No	0.02
<i>Euphorbia marginaliana</i>	Is	Yes	0.003
<i>Galium friedrichii</i>	Ei, Fo, Is	No	0.10
<i>Genista dorycnifolia</i>	Ei	Yes	>0.001
<i>Hippocrepis grosii</i>	Ei	No	0.02
<i>Santolina vedranensis</i>	Is	Yes	1
<i>Teucrium cossonii</i> ssp. <i>punicum</i>	Ei, Is	Yes	1
<i>Thymus richardii</i> ssp. <i>ebusitanus</i>	Ei	Yes	0.58

to islands where herbivores are absent or restricted to habitats inaccessible to goats. The endemic species that inhabit areas inaccessible to goats exhibit some putative resistance traits, such as phenolic compounds, tannins, saponins, triterpenoids, flavonoids or pilosity, but lack other traits such as glycosides, coumarins and spines, and their plant size is similar to other species from Gymnesians unable to coexist with goats. These putative resistance traits may confer additional functions, such as protection against insect herbivory (Hamilton et al., 2001; Waterman et al., 1984) or adaptation to high exposure to light radiation on cliffs (Pereira-Dias & Santos, 2015). Interestingly, some examples of endemic rupicolous species have been detected in accessible communities in areas from which goats have been excluded for long periods (e.g. 10 years after exclusion fencing, on mountains isolated from goat populations)—as represented by some Fabaceae species (i.e. *Hippocrepis balearica*) or Brassicaceae species (*Brassica balearica*), both of which exhibit a low capacity for resistance based on the traits analysed in this study (pers. obs.; data not shown). Also, endemic species from other islands of the Mediterranean with rupicolous habitats have been severely damaged by introduced mammal herbivores when they are in areas accessible to goats, as is the case of *Centaurea horrida* in the island of Sardinia (Pisanu et al., 2012).

As a general trend, few biogeographical studies about plant-herbivore interactions in insular conditions consider PICs (Moreira et al., 2021) and this study proves the importance of incorporating phylogenetic relationships in order to provide clearer results. When

PIC corrections were considered, a strong positive correlation was observed between the presence of alkaloids and glycosides, while a negative correlation was detected between coumarins and alkaloids, and coumarins and glycosides. Alkaloids and glycosides are recognized to be more efficient toxic compounds against ungulate herbivory than other compounds (Majak, 1991; Mattocks, 1968), with the exception of coumarins (Lake, 1999). The presence of alkaloids and glycosides correlated positively with the foliar area, indicating that plants protected by these compounds exhibit wider leaves. Indeed, glycosides and alkaloids efficiently protect plants against mammalian herbivores (Burney & Jacobs, 2013; McNaughton, 1983), although the production of these compounds imposes a high resource cost (Vrieling & van Wijk, 1994; Zangerl & Berenbaum, 1997). Furthermore, the concentrations of phenolic compounds and flavonoids correlated negatively with the foliar area. Plants with low foliar areas were mainly distributed in caespitose communities, which allowed these plants to escape herbivores. Phenolic and flavonoid compounds are known to protect against invertebrate herbivory, but low concentrations of these compounds provide minimal protection against mammal herbivory (Summers & Felton, 1994; Treutter, 2006).

Plant size was a good predictor of protection against mammal herbivory in the best-fitting model. Low plant size values correlated with low foliar area and high SLA, consistent with the hypothesis that plant architecture enables species to escape herbivory by ungulates (Boege & Marquis, 2005; Brown & Lawton, 1991). With regards to other anatomical traits, spines did

not correlate significantly with chemical or anatomical traits in either the raw data or after PIC, which suggests the absence of a relationship between spinescence and chemical protection. Spines may confer other functions, for example, avoidance of water loss in arid environments (Bagella et al., 2019); therefore, the presence of this trait may have been driven as a response to other abiotic factors, such as climate.

Contrary to oceanic islands, the endemic flora of continental islands is derived from the flora present when the connection with the mainland was severed. Hence, it is not surprising to detect that the variation in the phenotypic traits is influenced by phylogenetic relationships and ancestry. If the continental flora evolved in the context of herbivores, and there is a strong phylogenetic signal for highly toxic compounds, it could be expected that the endemic flora of continental islands may be exapted to the introduction of feral goats or other herbivores. Examples of this hypothesis are given by species of the genera *Paeonia* (Wu et al., 2010), *Phlomis* (Amor et al., 2009), *Digitalis* (Ganapaty et al., 2003) and *Helleborus* (Colombo et al., 1990), which all include species that contain toxic compounds that are phylogenetically fixed and evolved over a long time scale, when the Balearic Islands were still connected with Iberian Peninsula.

#### 4.2 | Estimation of the potential vulnerability of endemic plant species to islands without feral goats

Endemic species to the Balearic Islands, where feral goats are absent, displayed fewer resistance and escape traits than similar species on islands invaded by feral goats. Plants of a large size from accessible areas on islands without feral goats exhibited fewer resistance traits than communities on islands where feral goats are present. Moreover, when considering the resistance and escape traits that enable plants to coexist with introduced ungulates, we found that a large proportion of endemic species on the non-invaded islands have a low probability of coexisting with herbivores, in agreement with a previous study (Moreira et al., 2021). This suggests that the plant species on islands without goats would be extremely vulnerable to potential introduction of ungulate herbivores, even those of continental origin, the introduction of herbivores in these islands would probably result on a reduction of the distribution of the flora, leaving inaccessible habitats as the only potential habitats to avoid herbivory. Differences in resistance-escape traits of endemic plants between invaded and non-invaded islands indicate that spatial distribution of endemic flora in Gymnesic Islands might be conditioned by the goat's accessibility and plant capacity to resist or escape.

#### 4.3 | Endemic flora from continental islands do not always lack defences

It has been argued that insular endemic species do not have defences against mammal herbivores (Bowen & Van Vuren, 1997)

and lack tolerance to herbivory (Barton, 2016). However, as presented in this study, this might not be always true, and some species can exapt to herbivory. This exaptation depends on the historical and ecological context in which the endemic species evolved (Capó, Roig-Oliver, et al., 2021) and probably on other ecological factors, such as herbivory pressure by invertebrates or other plant stresses (Moreira et al., 2021). Plant defences are usually assembled through multiple traits of different origins. This co-adapted complex must function by itself, otherwise trade-offs may eventually compromise the evolutionary maintenance and stability of those traits, and the species may reinvest the resources into other ecological functions (Agrawal & Fishbein, 2006; Dobzhansky, 1970). The phylogenetic context supports the hypothesis that the ancient Balearic flora displayed traits to cope with ancient native herbivores, and in turn, these traits function as an exaptation to herbivory in the present-day endemic flora. As observed in other ecological contexts (Kursar & Coley, 2003), the endemic flora to the two Balearic Islands affected by feral goats is structured by resistance-escape strategies. In this case, adaptation of the shrubland species on Majorcan mountains to ancient herbivores or exaptation in response to other evolutionary drivers (i.e. wind or high radiation exposure) that also function against herbivores, would determine the ecological distribution of the toxic and spinescent/stinging endemic species.

The precise functions of individual chemical compounds in protection against ungulate herbivory are unclear, though synergistic effects may occur (Agrawal & Fishbein, 2006). Overall, a general pattern of exaptation was observed in the endemic flora of the Balearic Islands (Figure 4), namely resistance strategies based on (i) chemical resistance, that is, large species that produce highly toxic compounds and grow in habitats accessible to feral goats; (ii) anatomic resistance, that is, plants accessible to feral goats with leaves and flowers surrounded by spines or urticating hairs; (iii) plant-size escape strategies, that is, species accessible to feral goats that grow at ground level with small leaves and high SLA; and (iv) ecological inaccessibility, that is, species that lack any resistance traits to herbivory and have a large plant size, but live in areas inaccessible to herbivores. In areas where ungulate herbivores have not been introduced, species in the ecological inaccessibility category can be found in areas that are potentially accessible to goats. In fact, Moreira et al. (2021) found that island floras tend to present higher physical defences than continental relatives, which agrees with our findings that islands with high ungulate herbivory pressure present higher spinescent or stinging endemic species than those without ungulate herbivores. The insular effect on this plant-herbivore interaction could also be linked to the variation found in that study, but further studies are needed to disentangle the real relationship between anatomical resistance.

## 5 | CONCLUSIONS

The endemic flora to continental islands may be exapted to introduced herbivores, maintaining their traits by (i) pressure



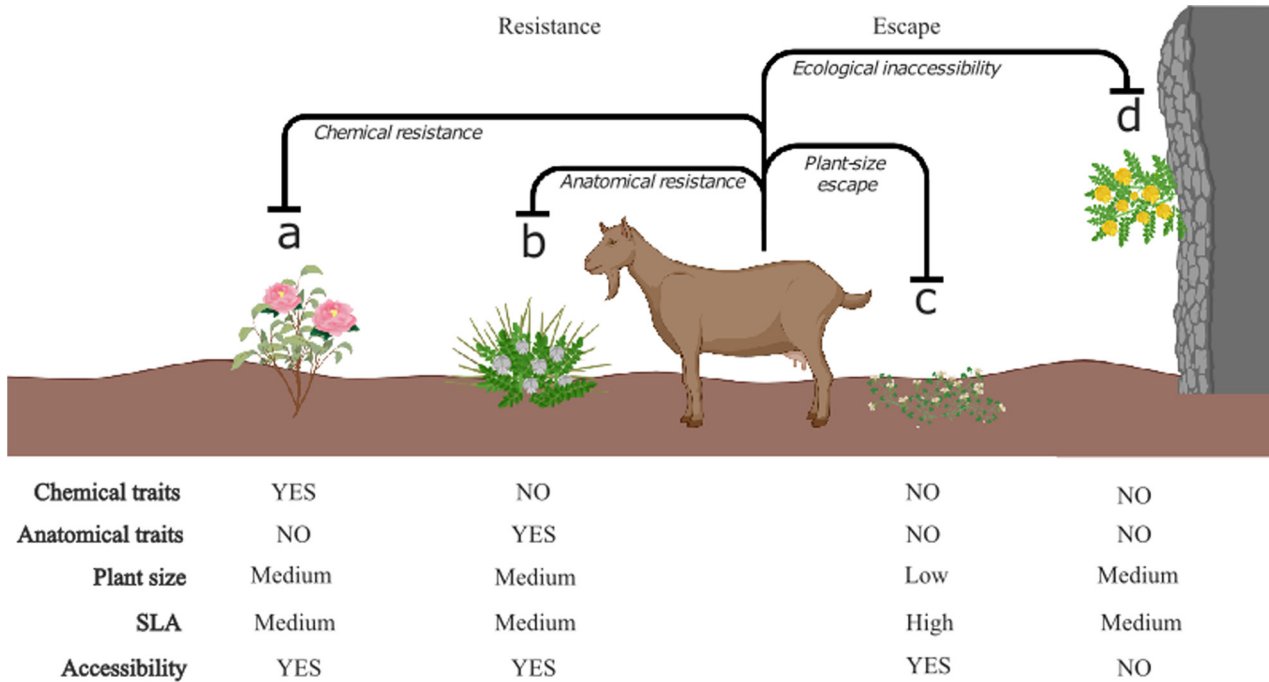


FIGURE 4 Endemic flora complexes based on chemical and anatomical protection against herbivores and their accessibility to introduced herbivores. SLA, specific leaf area.

generated by other herbivores, (ii) a weak trade-off of relocating these resources to face other ecological pressures, (iii) use for a secondary function or (iv) genetic fixation, regardless of ecological context. Exaptation to introduced herbivores is more likely to occur in lineages with a particular phylogenetic history where resistance traits are genetically fixed across evolution of the clade. However, other functional structures such as spinescence seem to be paraphyletic, and these traits may originate from both ancient herbivory pressure or other ecological features (i.e. high wind exposition or protection against radiation). As observed in this study, endemic plant species on islands non-invaded by feral goats are mainly located in accessible areas for ungulates and mostly not defended against herbivory than those occurring on invaded islands, which suggests that their flora is extremely vulnerable to future introductions of non-native ungulates. The present study highlights that knowledge of the functional traits present in the endemic flora is essential to predict potential vulnerability and even estimate which taxa may be more likely to reduce their habitats and even become extinct in the event of the introduction of new herbivores. In turn, this information can be used as a tool to design optimal management strategies to protect endemic flora against introduced herbivores.

#### ACKNOWLEDGEMENTS

The authors are grateful to the Servei de Protecció d'Espècies (Govern de les Illes Balears) for their authorization to sample endemic and threatened species in their natural populations. The authors appreciate the valuable help of Joshua Borràs during the chemical analyses, Carles Cardona of the Centre Forestal de les

Illes Balears (CEFOR) for his help sampling during the fieldwork and Beatrice Landoni for her help with statistical procedures. This work was funded by Project CGL2015-70449-R (Ministerio de Economía y Competitividad, Gobierno de España). M.C. was funded by PhD fellowship FPI/1925/2016 (Direcció General de Política Universitària i Recerca, Govern de les Illes Balears and the European Social Fund) and Margarita Salas postdoctoral fellowship (Ministerio de Universidades, Gobierno de España) through the Recovery, Transformation and Resilience Plan funded by the European Union (NextGenerationEU). Andrea Devlin from Science Editing Experts proofread the manuscript.

#### CONFLICT OF INTEREST STATEMENT

The authors declare they do not have any potential conflicts of interest.

#### DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository (Capó et al., 2023) <https://doi.org/10.5061/dryad.gxd2547r4>.

#### ORCID

Miquel Capó  <https://orcid.org/0000-0002-4394-7080>

#### REFERENCES

- AbdulAzeez, I., Sulaiman Ayodeji, A., & Danjuma, B. (2018). Phytochemical and antimicrobial screening of the leaves of *Crotalaria lachnosa* against *Staphylococcus aureus*, *Salmonella typhi*, *Escherichia coli* and *Klebsiella pneumoniae*. *Archives of Organic and Inorganic Chemical Sciences*, 3(5), 421–425. <https://doi.org/10.32474/aocs.2018.03.000173>

- Abramoff, M. D., Magalhães, P. J., & Ram, S. J. (2004). Image processing with imageJ. *Biophotonics International*, 11(7), 36–41.
- Agrawal, A. A. (1998). Induced responses to herbivory and increased plant performance. *Science*, 279(5354), 1201–1202. <https://doi.org/10.1126/science.279.5354.1201>
- Agrawal, A. A., & Fishbein, M. (2006). Plant defense syndromes. *Ecology*, 87(7), 132–149.
- Alonso, C., & Herrera, C. M. (1996). Variation in herbivory within and among plants of *Daphne laureola* (Thymelaeaceae): Correlation with plant size and architecture. *The Journal of Ecology*, 84(4), 495. <https://doi.org/10.2307/2261472>
- Amor, I. L. B., Boubaker, J., Sgaier, M. B., Skandrani, I., Bhour, W., Neffati, A., Kilani, S., Bouhrel, I., Ghedira, K., & Chekir-Ghedira, L. (2009). Phytochemistry and biological activities of *Phlomis* species. *Journal of Ethnopharmacology*, 125(2), 183–202. <https://doi.org/10.1016/j.jep.2009.06.022>
- Bagella, S., Filigheddu, R., Benesperi, R., Giordani, P., Minuto, L., Viciani, D., Caria, M. C., Pisanu, S., & Casazza, G. (2019). Thorn, spine and prickle patterns in the Italian flora. *Plant Biosystems*, 153(1), 118–133. <https://doi.org/10.1080/11263504.2018.1474961>
- Baraza, E., Gómez, J. M., Hódar, J. A., & Zamora, R. (2004). Herbivory has a greater impact in shade than in sun: Response of *Quercus pyrenaica* seedlings to multifactorial environmental variation. *Canadian Journal of Botany*, 82(3), 357–364. <https://doi.org/10.1139/b04-004>
- Baraza, E., Hódar, J. A., & Zamora, R. (2009). Species, site and seasonal variation in leaf-chemistry diversity of woody mediterranean plants. *Revue d'Ecologie (la Terre et la Vie)*, 64(2), 135–144.
- Barton, K. (2020). *MuMIn: Multi-model inference*. R package version 1.43.17.
- Barton, K. E. (2016). Low tolerance to simulated herbivory in Hawaiian seedlings despite induced changes in photosynthesis and biomass allocation. *Annals of Botany*, 117(6), 1053–1062. <https://doi.org/10.1093/aob/mcw021>
- Boege, K., & Marquis, R. J. (2005). Facing herbivory as you grow up: The ontogeny of resistance in plants. *Trends in Ecology and Evolution*, 20(8), 441–448. <https://doi.org/10.1016/j.tree.2005.05.001>
- Bover, P., Llamas, B., Mitchell, K. J., Thomson, V. A., Alcover, J. A., Lalueza-Fox, C., Cooper, A., & Pons, J. (2019). Unraveling the phylogenetic relationships of the extinct bovid *Myotragus balearicus* bate 1909 from the Balearic Islands. *Quaternary Science Reviews*, 215, 185–195. <https://doi.org/10.1016/j.quascirev.2019.05.005>
- Bover, P., Quintana, J., & Alcover, J. A. (2008). Three islands, three worlds: Paleogeography and evolution of the vertebrate fauna from the Balearic Islands. *Quaternary International*, 182(1), 135–144. <https://doi.org/10.1016/j.quaint.2007.06.039>
- Bover, P., Valenzuela, A., Torres, E., Cooper, A., Pons, J., & Alcover, J. A. (2016). Closing the gap: New data on the last documented *Myotragus* and the first human evidence on Mallorca (Balearic Islands, Western Mediterranean Sea). *Holocene*, 26(11), 1887–1891. <https://doi.org/10.1177/0959683616645945>
- Bowen, L., & Van Vuren, D. (1997). Insular endemic plants lack defenses against herbivores. *Conservation Biology*, 11(5), 1249–1254. <https://doi.org/10.1046/j.1523-1739.1997.96368.x>
- Brown, V. K., & Lawton, J. H. (1991). Herbivory and the evolution of leaf size and shape. *Philosophical Transactions Royal Society of London B*, 333(1267), 265–272. <https://doi.org/10.1098/rstb.1991.0076>
- Burney, O. T., & Jacobs, D. F. (2013). Ungulate herbivory of boreal and temperate forest regeneration in relation to seedling mineral nutrition and secondary metabolites. *New Forests*, 44(5), 753–768. <https://doi.org/10.1007/s11056-013-9381-9>
- Campbell, K., Donlan, C. J., Cruz, F., & Carrion, V. (2004). Eradication of feral goats *Capra hircus* from Pinta Island, Galápagos, Ecuador. *Oryx*, 38(3), 328–333. <https://doi.org/10.1038/nrg1358>
- Capizzi, D. (2020). A review of mammal eradications on Mediterranean islands. *Mammal Review*, 50(2), 124–135. <https://doi.org/10.1111/mam.12190>
- Capó, M., Cursach, J., Picorelli, V., Baraza, E., & Rita, J. (2022). Eradication of feral goats, not population control, as a strategy to conserve plant communities on Mediterranean islets. *Journal for Nature Conservation*, 65, 126108. <https://doi.org/10.1016/j.jnc.2021.126108>
- Capó, M., Engelbrecht, C., Cardona, C., Castells, E., Bartolomé, J., Ramoneda, M., & Baraza, E. (2021). Mildly toxic shrubs as indicators of goats herbivory gives information for the management of natural landscapes on Mediterranean islands. *Science of the Total Environment*, 786, 147391. <https://doi.org/10.1016/j.scitotenv.2021.147391>
- Capó, M., Pérez-Barrales, R., Cursach, J., Garrido, J., & Baraza, E. R. (2023). Dataset from: Exaptation and vulnerability to introduced mammal herbivores on Balearic endemic flora. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.gxd2547r4>
- Capó, M., Roig-Oliver, M., Cardona, C., Cursach, J., Bartolomé, J., Rita, J., & Baraza, E. (2021). Historic exposure to herbivores, not constitutive traits, explains plant tolerance to herbivory in the case of *Medicago* sp. (Fabaceae). *Plant Science*, 307, 110890. <https://doi.org/10.1016/j.plantsci.2021.110890>
- Carrion, V., Donlan, C. J., Campbell, K. J., Lavoie, C., & Cruz, F. (2011). Archipelago-wide Island restoration in the galápagos islands: Reducing costs of invasive mammal eradication programs and reinvasion risk. *PLoS One*, 6(5), e18835. <https://doi.org/10.1371/journal.pone.0018835>
- Castroviejo, S. (1986). *Flora ibérica: plantas vasculares de la Península Ibérica e Islas Baleares*. CSIC Press.
- Coley, P. D. (1987). Interspecific variation in plant anti-herbivore properties: The role of habitat quality and rate of disturbance. *New Phytologist*, 106, 251–263. <https://doi.org/10.1111/j.1469-8137.1987.tb04693.x>
- Colombo, M. L., Tome, F., Servettaz, O., & Bugatti, C. (1990). Phytochemical evaluation of *Helleborus* species growing in northern Italy. *Pharmaceutical Biology*, 28(3), 219–223. <https://doi.org/10.3109/13880209009082817>
- Cooper, S. M., & Owen-Smith, N. (1985). Condensed tannins deter feeding by browsing ruminants in a south African savanna. *Oecologia*, 67(1), 142–146.
- Cubas, J., Irl, S. D. H., Villafuerte, R., Bello-Rodríguez, V., Rodríguez-Luengo, J. L., Del Arco, M., Martín-Esquível, J. L., & González-Mancebo, J. M. (2019). Endemic plant species are more palatable to introduced herbivores than non-endemics. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20190136. <https://doi.org/10.1098/rspb.2019.0136>
- De Marino, S., Festa, C., Zollo, F., Incollingo, F., Raimo, G., Evangelista, G., & Iorizzi, M. (2012). Antioxidant activity of phenolic and phenylethanoid glycosides from *Teucrium polium* L. *Food Chemistry*, 133(1), 21–28. <https://doi.org/10.1016/j.foodchem.2011.12.054>
- De Vos, A., Manville, R. H., & Van Gelder, R. G. (1956). Introduced mammals and their influence on native biota. *Zoologica*, 41(1), 163–194.
- Diner, B., Berteaux, D., Fyles, J., & Lindroth, R. L. (2009). Behavioral archives link the chemistry and clonal structure of trembling aspen to the food choice of north American porcupine. *Oecologia*, 160(4), 687–695. <https://doi.org/10.1007/s00442-009-1340-y>
- Dobzhansky, T. (1970). *Genetics of the evolutionary process*. Columbia University Press.
- Felsenstein, J. (1985). Confidence limits on phylogenetics: An approach using the bootstrap. *Evolution*, 39(4), 783–791.
- Ganapaty, S., Mallika, B. N., Balaji, S., Lakshmi, S. V. V. N. S. M., Thomas, P. S., & Ramana, K. V. (2003). A review of phytochemical studies of *Digitalis* species. *Journal of Natural Remedies*, 3(2), 104–128.
- Gange, A. C., & Brown, V. K. (1989). Insect herbivory affects size variability in plant populations. *Oikos*, 56(3), 351. <https://doi.org/10.2307/3565620>
- Gizicki, Z. S., Tamez, V., Galanopoulou, A. P., Avramidis, P., & Foufopoulos, J. (2018). Long-term effects of feral goats (*Capra hircus*) on

- Mediterranean Island communities: Results from whole Island manipulations. *Biological Invasions*, 20(6), 1537–1552. <https://doi.org/10.1007/s10530-017-1645-4>
- Hamilton, J. G., Zangerl, A. R., DeLucia, E. H., & Berenbaum, M. R. (2001). The carbon-nutrient balance hypothesis: Its rise and fall. *Ecology Letters*, 4(1), 86–95. <https://doi.org/10.1046/j.1461-0248.2001.00192.x>
- Hanley, M. E., Lamont, B. B., Fairbanks, M. M., & Rafferty, C. M. (2007). Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics*, 8(4), 157–178. <https://doi.org/10.1016/j.ppees.2007.01.001>
- Homar, V., Ramis, C., Romero, R., & Alonso, S. (2009). Recent trends in temperature and precipitation over the Balearic Islands (Spain). *Climatic Change*, 98(1–2), 199–211. <https://doi.org/10.1007/s10584-009-9664-5>
- Howery, L. D., Provenza, F. D., & Ruyle, G. B. (2016). *How do domestic herbivores select nutritious diets on rangelands?* <http://hdl.handle.net/10150/625544>
- Hull-Sanders, H. M., Clare, R., Johnson, R. H., & Meyer, G. A. (2007). Evaluation of the evolution of increased competitive ability (EICA) hypothesis: Loss of defense against generalist but not specialist herbivores. *Journal of Chemical Ecology*, 33(4), 781–799. <https://doi.org/10.1007/s10886-007-9252-y>
- Ishaaya, I., Birk, Y., Bondi, A., & Tencer, Y. (1969). Soyabean saponins IX.—Studies of their effect on birds, mammals and cold-blooded organisms. *Journal of the Science of Food and Agriculture*, 20(7), 433–436. <https://doi.org/10.1002/jsfa.2740200716>
- Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, 17(4), 164–170. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0)
- Kursar, T. A., & Coley, P. D. (2003). Convergence in defense syndromes of young leaves in tropical rainforests. *Biochemical Systematics and Ecology*, 31(8), 929–949. [https://doi.org/10.1016/S0305-1978\(03\)00087-5](https://doi.org/10.1016/S0305-1978(03)00087-5)
- Lake, B. G. (1999). Coumarin metabolism, toxicity and carcinogenicity: Relevance for human risk assessment. *Food and Chemical Toxicology*, 37(4), 423–453. [https://doi.org/10.1016/S0278-6915\(99\)00010-1](https://doi.org/10.1016/S0278-6915(99)00010-1)
- Le, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software*, 25(1), 1–18.
- Liang, C., Liu, Z., Liu, X., Geng, Y., Song, H., Ding, S., Lei, X., Feng, Z., Liu, J., & Deng, Y. (2014). The extract optimization and identification study of bioactive total triterpenoids from the rare traditional Chinese medicine Qinling *Polyporus umbellatus*. *Journal of Chemical and Pharmaceutical Research*, 6(6), 1283–1289.
- Majak, W. (1991). Metabolism and, absorption of toxic glycosides by ruminants. *Journal of Range Management*, 45, 67–71. <https://journals.uair.arizona.edu/index.php/jrm/article/download/8686/8298>
- Mattocks, A. R. (1968). Toxicity of pyrrolizidine alkaloids. *Nature*, 217(5130), 723–728. <https://doi.org/10.1038/217723a0>
- Mauricio, R. (2000). Natural selection and the joint evolution of tolerance and resistance as plant defenses. *Evolutionary Ecology*, 14, 491–507.
- Mayol, J., Alcover, J. A., Domènech, O., Moragues, E., & Rita, J. (2017). *La cabra, espècie invasora a les Balears*. Editorial Lleopard Muntaner.
- McNaughton, S. J. (1983). Physiological and ecological implications of herbivory. In *Physiological plant ecology III* (pp. 657–677). Springer. [https://doi.org/10.1007/978-3-642-68153-0\\_18](https://doi.org/10.1007/978-3-642-68153-0_18)
- McNeely, J. A., Mooney, H. A., Neville, L. E., Schei, P. J., & Waage, J. K. (2001). *Global strategy on invasive Alien species published by IUCN*. Global Invasive Species Programme. <http://planet.uwc.ac.za/nisl/Biodiversity/pdf/globalstrategy.pdf>
- Médail, F. (2017). The specific vulnerability of plant biodiversity and vegetation on Mediterranean islands in the face of global change. *Regional Environmental Change*, 17(6), 1775–1790. <https://doi.org/10.1007/s10113-017-1123-7>
- Milton, S. J. (1991). Plant spinescence in arid southern Africa: Does moisture mediate selection by mammals? *Oecologia*, 87(2), 279–287.
- Moragues, E., Manzano, X., & Sáez, L. (2015). Una illa al cim, el cim d'una illa: Singularitat i conservació de la flora vascular del Puig Major. *Monografies de La Societat d'Historia Natural de les Balears*, 20, 69–82.
- Moreira, X., Castagneyrol, B., García-Verdugo, C., & Abdala-Roberts, L. (2021). A meta-analysis of insularity effects on herbivory and plant defences. *Journal of Biogeography*, 48(2), 386–393. <https://doi.org/10.1111/jbi.14003>
- Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S. A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., & Rillig, M. C. (2014). Choosing and using diversity indices: Insights for ecological applications from the German biodiversity Exploratories. *Ecology and Evolution*, 4(18), 3514–3524. <https://doi.org/10.1002/ece3.1155>
- Moyà-Solà, S., Quintana-Cardona, J., & Köhler, M. (2022). *Ebusia moralesi* n. gen. nov. sp, a new endemic caprine (Bovidae, Mammalia) from the Neogene of Eivissa Island (Balearic Islands, Western Mediterranean): Evolutionary implications. *Historical Biology*, 1–18. <https://doi.org/10.1080/08912963.2022.2060099>
- Muñoz, M., Barceló, A., Rayó, C., Bernat, M., Barceló, J. M., Castillo, V., Castro, F., Vaquerizas, P. H., Blanco-Aguiar, J. A., Aparicio, F., Seguí, B., & Villafuerte, R. (2019). Seguimiento y recuperación de las poblaciones de conejo europeo (*Oryctolagus cuniculus cuniculus*) en Mallorca (Illes Balears) (2016–2019). In G.X. Pons, A. Barceló, M. Muñoz, L. del Valle & B. Seguí (Eds.), *Recerca i gestió dins l'àmbit cinegètic*. *Monografies de la Societat d'Historia Natural de les Balears* (Vol. 28, pp. 21–40).
- Nogales, M., Rodríguez-Luengo, J. L., & Marrero, P. (2006). Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Review*, 36(1), 49–65. <https://doi.org/10.1111/j.1365-2907.2006.00077.x>
- Oganesyan, G. B., Galstyan, A. M., Mnatsakanyan, V. A., Shashkov, A. S., & Agababyan, P. V. (1991). Phenylpropanoid glycosides of *Teucrium polium*. *Chemistry of Natural Compounds*, 27(5), 556–559. <https://doi.org/10.1007/BF00630353>
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M., Henry, H., & Wagner, H. (2008). *vegan: Community ecology package*. Version 2.5-6. <http://cran.r-project.org/>
- Palombo, M. R., Rozzi, R., & Bover, P. (2013). The endemic bovids from Sardinia and the Balearic Islands: State of the art. *Geobios*, 46(1–2), 127–142. <https://doi.org/10.1016/j.geobios.2012.10.011>
- Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Pardo, C., Cubas, P., & Tahiri, H. (2004). Molecular phylogeny and systematics of *Genista* (Leguminosae) and related genera based on nucleotide sequences of nrDNA (ITS region) and cpDNA (trnL-trnF intergenic spacer). *Plant Systematics and Evolution*, 244(1–2), 93–119. <https://doi.org/10.1007/s00606-003-0091-1>
- Pellissier, F. (2013). Early physiological responses of *Abies alba* and *Rubus fruticosus* to ungulate herbivory. *Plant Ecology*, 214(1), 127–138. <https://doi.org/10.1007/s11258-012-0151-0>
- Pereira-Dias, F., & Santos, M. (2015). Adaptive strategies against water stress: A study comparing leaf morphoanatomy of rupicolous and epiphytic species of Gesneriaceae. *Revista Brasileira de Botânica*, 38(4), 911–919. <https://doi.org/10.1007/s40415-015-0180-8>
- Pisanu, S., Farris, E., Filigheddu, R., & García, M. B. (2012). Demographic effects of large, introduced herbivores on a long-lived endemic plant. *Plant Ecology*, 213(10), 1543–1553. <https://doi.org/10.1007/s11258-012-0110-9>
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rasmann, S., Johnson, M. D., & Agrawal, A. A. (2009). Induced responses to herbivory and jasmonate in three milkweed species. *Journal of Chemical Ecology*, 35(11), 1326–1334. <https://doi.org/10.1007/s10886-009-9719-0>

- Rita, J., & Payeras, T. (2006). Biodiversidad de las plantas vasculares de las Islas Baleares. *Orsis: Organismes i Sistemes*, 21, 41–58.
- Roselló, J. A., & Sáez, L. (2000). Index Balearicum: An annotated check-list of the vascular plants described from the Balearic Islands. *Collectanea Botanica*, 25(1), 3–203.
- Roselló, J. A., & Sáez, L. (2008). Index Balearicum (II): An annotated check-list of the vascular plants described from the Balearic Islands. Additions (2002–2007) and corrections. *Flora Montiberica*, 39, 58–64. <https://doi.org/10.3989/collectbot.2000.v25.42>
- Roselló, J. A., & Sáez, L. (2017). Index Balearicum (III): An annotated check-list of the vascular plants described from the Balearic Islands. Additions (2008–2016) and corrections. *Orsis: Organismes i Sistemes*, 31, 65–78. <https://doi.org/10.3989/collectbot.2000.v25.42>
- Rosenbaum, G., & Lister, G. S. (2002). Rewlative mortiosn of Frica, Iberia and Europe during Alpine orogeny. *Tectonophysics*, 359, 117–129.
- Sáez, L., Fraga Arguimbau, P., & López-Alvarado, J. (2011). *The flora of the Balearic Islands*. Islands and Plants: Preservation and Understanding of Flora on Mediterranean Islands, September 2014, 91–103 <https://doi.org/10.13140/2.1.2289.6000>
- Sáez, L., Fraga, P., & López-Alvarado, J. (2013). The flora of the Balearic Islands. In E. Cardona, I. Estaún, M. Comas, & P. Fraga (Eds.), *Islands and plants: Preservation and understanding of flora on Mediterranean Islands* (pp. 91–103). Consell Insular de Menorca.
- Sáez, L., Roselló, J. A., & Fraga, P. (2017). *Llibre vermell de la flora vascular de les Illes Balears: Vol. XIX. Direcció General Espais Naturals i Biodiversitat*. Govern de les Illes Balears.
- Seguí, B., Payeras, L., Ramis, D., Martínez, A., Delgado, J. V., & Quiroz, J. (2005). La cabra salvaje mallorquina: Origen, genética, morfología, notas ecológicas e implicaciones taxonómicas. *Bolleti de La Societat d'Historia Natural de Les Balears*, 48, 121–151.
- Sharma, V., & Janmeda, P. (2017). Extraction, isolation and identification of flavonoid from *Euphorbia nerifolia* leaves. *Arabian Journal of Chemistry*, 10(4), 509–514. <https://doi.org/10.1016/j.arabjc.2014.08.019>
- Silván, A. M., Abad, M. J., Bermejo, P., Sollhuber, M., & Villar, A. (1996). Antiinflammatory activity of coumarins from *Santolina oblongifolia*. *Journal of Natural Products*, 59(12), 1183–1185. <https://doi.org/10.1021/np960422f>
- Strauss, S. Y., & Agrawal, A. A. (1999). The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution*, 14(5), 179–185.
- Summers, C. B., & Felton, G. W. (1994). Prooxidant effects of phenolic acids on the generalist herbivore *Helicoverpa zea* (Lepidoptera: Noctuidae): Potential mode of action for phenolic compounds in plant anti-herbivore chemistry. *Insect Biochemistry and Molecular Biology*, 24(9), 943–953. [https://doi.org/10.1016/0965-1748\(94\)90023-X](https://doi.org/10.1016/0965-1748(94)90023-X)
- Tomás-Barberán, F. A. (1995). Analysis of phenolic plant metabolites. *Phytochemistry*, 38(4), 1064. [https://doi.org/10.1016/0031-9422\(95\)90191-4](https://doi.org/10.1016/0031-9422(95)90191-4)
- Treutter, D. (2006). Significance of flavonoids in plant resistance: A review. *Environmental Chemistry Letters*, 4(3), 147–157. <https://doi.org/10.1007/s10311-006-0068-8>
- Vrieling, K., & van Wijk, C. A. M. (1994). Cost assessment of the production of pyrrolizidine alkaloids in ragwort (*Senecio jacobaea* L.). *Oecologia*, 97(4), 541–546. <https://doi.org/10.1007/BF00325894>
- Waterman, P. G., Ross, J. A. M., & Mckey, D. B. (1984). Factors affecting levels of some phenolic compounds, digestibility, and nitrogen content of the mature leaves of *Barteria fistulosa* (Passifloraceae). *Journal of Chemical Ecology*, 10(3), 387–401. <https://doi.org/10.1007/BF00988087>
- Wink, M. (2008). Plant secondary metabolism: Diversity, function and its evolution. *Natural Product Communications*, 3(8), 1205–1216.
- Winkler, D. E., Schulz, E., Calandra, I., Gailer, J. P., Landwehr, C., & Kaiser, T. M. (2013). Indications for a dietary change in the extinct bovid genus *Myotragus* (Plio-Holocene, Mallorca, Spain). *Geobios*, 46(1–2), 143–150. <https://doi.org/10.1016/j.geobios.2012.10.010>
- Wright, K. (2018). *corrgram: Plot a correlogram*. R package version 1.13.
- Wu, S. H., Wu, D. G., & Chen, Y. W. (2010). Chemical constituents and bioactivities of plants from the genus *Paeonia*. *Chemistry and Biodiversity*, 7(1), 90–104. <https://doi.org/10.1002/cbdv.20080148>
- Zangerl, A. R., & Berenbaum, M. R. (1997). Cost of chemically defending seeds: Furanocoumarins and *Pastinaca sativa*. *American Naturalist*, 150(4), 491–504. <https://doi.org/10.1086/286077>
- Zwenger, S., & Basu, C. (2008). Plant terpenoids. Applications and future potentials. *Biotechnology and Molecular Biology Reviews*, 3(1), 1–7. <http://digscholarship.unco.edu/biofacpubhttp://digscholarship.unco.edu/biofacpub/4http://www.academicjournals.org/BMBR>

### BIOSKETCH

**Miquel Capó** is working on the impact of herbivores on plant communities, especially those from Mediterranean and insular ecosystems. He is interested in producing useful information to design conservation actions to palliate the impact of introduced species on natural landscapes.

**Author contributions** Miquel Capó, Rocío Pérez-Barrales, Elena Baraza and Juan Rita formulated the hypothesis, conceived the experiment and designed the analysis. Miquel Capó, Joana Cursach, Jaume Garrido carried out the sampling and the analysis of the chemical compounds. Miquel Capó and Rocío Pérez-Barrales analysed the data and wrote the first draft of the manuscript. All authors contributed with the writing of the final version of the paper.

### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Capó, M., Pérez-Barrales, R., Cursach, J., Garrido, J., Baraza, E., & Rita, J. (2023). Exaptation and vulnerability to introduced mammal herbivores on Balearic endemic flora. *Journal of Biogeography*, 00, 1–12. <https://doi.org/10.1111/jbi.14602>