



The endemic shrubland community of Teide National park under threat from the invasive European rabbit: a microhistological approach using faecal samples

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Abstract

Alien herbivores can have various deleterious impacts on plant communities, especially on oceanic islands where the flora tends to be dominated by endemic species. The European rabbit (*Oryctolagus cuniculus* L.), a polyphagous herbivore, alters plant communities through overgrazing in the areas it has invaded. In Teide National Park, a protected natural area on Tenerife (Canary Islands), rabbit herbivory is one of the main threats to the conservation of its wild flora. A microhistological study of rabbit pellets was carried out, identifying plant tissues based on cellular parameters to characterize its diet for a year in the National Park. A total of 12 plant species, mostly Canary endemics, were detected in the rabbit pellets. Despite this diversity, the diet mainly consists of three plant species: *Spartocytisus supranubius*, *Pterocephalus lasiospermus* and *Descurainia bourgeauana*, respectively. The latter two plant species represent a larger proportion of the diet than their coverage would suggest, potentially indicating selective foraging. This study clarifies the diet and food preferences in Teide National Park. It reveals that these rabbits consume plants previously thought to be too unpalatable, like *P. lasiospermus* or *Adenocarpus viscosus*. The data confirm the detrimental impact of rabbits on the flora of the Park and support the need to reduce the populations of this invasive herbivore, to mitigate the damage it causes. Furthermore, these results will surely contribute to designing management plans as precisely as possible, to re-establish potential plant communities and conserve existing diversity.

Keywords Alien species · Herbivores · Conservation · Protected area · Diet · Canary islands

Introduction

The invasion of ecosystems by exotic species, originally facilitated by human activities, is considered the primary cause of biodiversity loss on islands (e.g. Vitousek et al.

1997; McNeely et al. 2001). Invasive vertebrates, in particular, are the main cause of extinctions and remain a critical threat to island species today (Courchamp et al. 2003). Alien herbivores have wide-ranging impacts on invaded ecosystems, notably affecting plant communities, their associated fauna and soil dynamics (Donlan et al. 2002; Courchamp et al. 2003; Kossoff et al. 2024). Their effects are magnified on oceanic islands (Donlan et al. 2002; Cubas et al. 2018) where many plant species have evolved in the absence of native herbivores. Such plants thus lack defences against herbivory (Carlquist 1974; Bowen and Van Vuren 1997; Traveset and Santamaría 2004; Kavanagh 2014; Cubas et al. 2019), being more susceptible to extinction (Bowen & Van Vuren 1997).

The European wild rabbit (*Oryctolagus cuniculus*, L.), probably native to the Iberian Peninsula and Mediterranean France, was introduced by humans into many areas of Europe, South America, Australia (Monnerot et al. 1994)

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and more than 800 islands around the world (Flux and Fulagar 1992). It is considered a keystone species in Iberian ecosystems, where it causes significant changes in the composition and structure of plant communities through grazing (Delibes-Mateos and Gálvez-Bravo 2009). Furthermore, in their natural ecosystem, rabbits contribute to the maintenance of plant species diversity, modifying soil fertility, and providing trophic resources for many invertebrate species through their excreta, breeding sites or shelters (Delibes-Mateos et al. 2008; Gálvez-Bravo et al. 2011).

Rabbits have been described as a polyphagous grazer due to its consumption of many different plants, but has a hierarchical diet, often selecting certain taxa regardless of their density (Lees and Bell 2008). Rabbit grazing alters the abundance of specific plants. In its natural distribution range this reduces interspecific competition (Delibes-Mateos et al. 2008), decreasing the cover of more palatable species and increasing that of less consumed plants (García-Fuentes et al. 2006). However, in regions where *O. cuniculus* is introduced, non-adapted plant communities become impoverished through overgrazing, which alters plant community dynamics and structure (Lees and Bell 2008). In fact, there are numerous examples of island endemisms threatened with extinction by introduced rabbits (Donlan et al. 2002; Bañares et al. 2004; Simensen and Eichhorn 2012). In the Canary Islands, this species feeds on at least 47 plant species listed as threatened (Rodríguez-Piñero and Rodríguez-Luengo 1993).

Oryctolagus cuniculus is present on the Canary Islands, except for Montaña Clara islet where it was eradicated (Martín et al. 2002). Since the gradual conquest of the archipelago by Spain during the 15th century, the European rabbit has occupied all available habitats (Nogales et al. 2006). Despite significant damage to the native vegetation, rabbit diet in the archipelago is poorly studied, except in the xeric habitats of the islet of Alegranza. There, *O. cuniculus* was found to consume more than 20 different plant species, clearly selecting two of them (*Salsola vermiculata* L. and *Chenoleoides tomentosa* (Lowe) Maire & Weiller) regardless of their density (Martín and Marrero 1999; Marrero and Martín 2000). This diet has seasonal variations depending on the plant species to be found with green vegetative parts (Martín et al. 2003). Although dietary studies have not been carried out in the rest of the archipelago, many articles show the negative impact of the European rabbit on native vegetation (Garzón-Machado et al. 2010; Irl et al. 2012, 2014; Cubas et al. 2019; González-Mancebo et al. 2019). Although they feed on a great number of fruits of some endemic plants, the effectiveness of rabbits as a disperser is clearly lower than native vertebrates, acting rather as a disruptor of natural seed dispersal systems (Nogales et al. 1995, 2005; Rumeu et al. 2011;

Guerrero-Campos et al. 2023). At the same time, European rabbits are a potential disperser of invasive plant species like *Acacia farnesiana* (L.) Willd. (Arévalo et al. 2010; Salas et al. 2009) and *Opuntia* spp. (Padrón et al. 2011). However, the worst effect of *O. cuniculus* is loss of diversity due to grazing pressure, as observed in several of the Canary Islands (Garzón-Machado et al. 2010; Martín-Esquivel et al. 2020; Parada-Díaz et al. 2022). For example, on La Palma, *O. cuniculus* has a negative impact on the distribution and abundance of some endemic legumes (Garzón-Machado et al. 2010), promoting a mono-dominant vegetation in sub-summit shrub areas through its selective grazing. This favours the spread of the poorly palatable *Adenocarpus viscosus* subsp. *spartioides* versus more intensely consumed species, some of which are highly endangered (Irl et al. 2012, 2014).

The European wild rabbit is the most abundant herbivorous mammal in Teide National Park and one of the main threats to conservation of wild Canarian flora (Cubas et al. 2017). Rabbit density in the summit zone of Tenerife can range between 5.9–0.61 rabbits/ha (Bello-Rodríguez et al. 2021). In this protected natural area the harmful effect of this invasive herbivore has also been well described. In fact, the summit shrubland there presented the highest rabbit damage in all the ecosystems on Tenerife (Cubas et al. 2019). Exclosure plots show that overgrazing by *O. cuniculus* is linked to the decreasing population of the keystone plant species *Spartocytisus supranubius* (L.f.) Christ ex G. Kunkel and the expansion of *Pteroccephalus lasiospermus* Link ex Buch (Cubas et al. 2018). This impact is attributable to the different palatability of these two species. Rabbit pressure, along with that from another introduced herbivore, the mouflon (*Ovis aries musimon* Pallas, 1811), affect some local endemic endangered species like *Rhaponticum canariense* DC. (Bañares et al. 2004; Carqué et al. 2004), *Viola cheiranthifolia* Humb. & Bonpl. (Seguí et al. 2017), *Echium auberianum* Webb & Berthel. (Cabrera-Pérez 2004) and *Juniperus cedrus* Webb & Berthel. subsp. *cedrus* (Rumeu et al. 2011).

The Teide National Park has been implementing science-based management for some time now (Durbán and Martín-Esquivel 2021). To this end, they have promoted and financed applied studies to solve or help understand problems that affect this protected natural area. Studies have been carried out on the vegetation present on Teide and its surroundings, including its phytosanitary status, pollination, climate change, and herbivory, aiming at its conservation. Results from exclusion plots reveal the potential composition of plants that should be present in certain areas of the National Park in the absence of herbivores (Cubas et al. 2018). However, the specific plant species rabbits consume were unknown; to date only observations of plants browsed

by rabbits had been recorded in the National Park (Cubas et al. 2019). Knowing which species they feed on year-round and in what amounts allows us to make much more accurate damage estimates, strengthening the strategy of controlling their populations. This will in turn allow us to improve conservation plans for threatened plants when rabbit consumption is detected and improve management of summit plant communities, for instance, by including species not previously thought to be eaten by rabbits. To determine rabbit diet in the National Park directly, we carried out a microhistological study of excreted pellets in different areas of the territory throughout the year. Based on the identification of plant cell structures, this method has been widely and satisfactorily used in herbivorous species and is one of the best options to determine quantitative diet composition at plant species level (Garnick et al. 2018).

Methodology

Study area

The Canary Islands are a volcanic archipelago comprising seven major islands off the south-west Atlantic coast of NW Africa. Near their centre is Tenerife, the largest and highest island in the Canaries, forming the base of the Teide stratovolcano. Specifically, this study focused on the Teide National Park, which is located between 2000 and 3716 m above sea level (a.s.l.) approximately. Its climatic conditions are determined mainly by altitude and orientation (Del Arco et al. 2006). Precipitation is scarce, varying between 349 mm in the south and 460 mm in the north. Temperatures are generally mild throughout the day and descend during the night, especially at ground level (Del Arco et al. 2006). Teide National Park vegetation is configured mainly by an arid alpine shrubland formation *Spartocytisetum supranubii*, dominated by *Spartocytisus supranubius* (L. f.) Christ ex G. Kunkel (Fabaceae), *Adenocarpus viscosus* (Willd.) Webb & Berthel. subsp. *viscosus* (Fabaceae) and *Descurainia bourgeauana* (E. Fourn.) O. E. Schulz (Brassicaceae), and in which *Pterocephalus lasiospermus* Link ex Buch (Dipsacaceae) is common (Arco & Rodríguez-Delgado, 2018). Double isolation from other territories due to insularity and ecological differences has shaped a unique flora with high rates of endemism (Bañares et al. 2011). The vascular flora consists of 220 taxa, of which 73 are endemic to the archipelago, 33 to the island and 16 to the National Park (González et al. 2009). Currently, three species are in danger of extinction and five are vulnerable, according to the National and Canary Island catalogues of threatened species (Gobierno de Canarias 2023).

Sampling sites and methods

We sampled fourteen localities in the National Park (Fig. 1; Table 1) every two months (six periods) in 2017. Within each locality, 24 circular 1 m² plots were selected along line transects at approximately 20 m intervals, from which all rabbit pellets (droppings) were removed before beginning the first sample period (2017 January). In each subsequent sampling all pellets excreted during each of the previous two months were collected.

Diet study and plant availability

Diet composition was determined by microhistological analyses of pellets using a light microscope. This methodology has already been applied successfully for many herbivores, reptiles (Valido and Nogales 1994; Pérez-Cembranos et al. 2016; Qasim et al. 2018), birds (Pulido and Díaz 1994; Marrero et al. 2004), and mammals (Holisova et al. 1986; Alfayate and Rodríguez-Luengo 1991; Mohammad et al. 1995), including the rabbit (Marques and Mathias 2001; Martín et al. 2003).

Only intact uniform droppings were analysed; fragmented, disaggregated or misshapen ones were excluded. Ten pellets from different plots in each locality (14) and sampling period (6) were analysed whenever possible, to a total of 810 pellets from Teide National Park (Table S1). Each pellet was diluted in water before placement on slides. Fifteen optical fields were randomly examined at 20× magnification for each pellet sample. Plant tissues in the pellets were identified based on cellular characteristics (epidermal cells, stomata, trichomes, etc.), using a reference collection that included most of the plant species present at these localities, along with a previous one (Alfayate 1990). The microhistological reference collection with 28 species belonging to 15 families was deposited at the IPNA-CSIC research institute, La Laguna (Table S2).

Plant composition of the habitat was examined to explore the relationship between diet composition and plant availability. At each locality, a 25 m² grid was selected and coverage of each plant species estimated visually as a percentage, taking into account stratification or multiple layers of existing vegetation (Kent 2012).

Statistical analysis

The variable used for diet characterisation was the percentage of optical fields containing each plant item (%OF). A likelihood ratio test (*G*) (SPSS Statistics, version 26) was applied to compare the number of plant species in each pellet sample (i.e. dietary diversity at different localities).

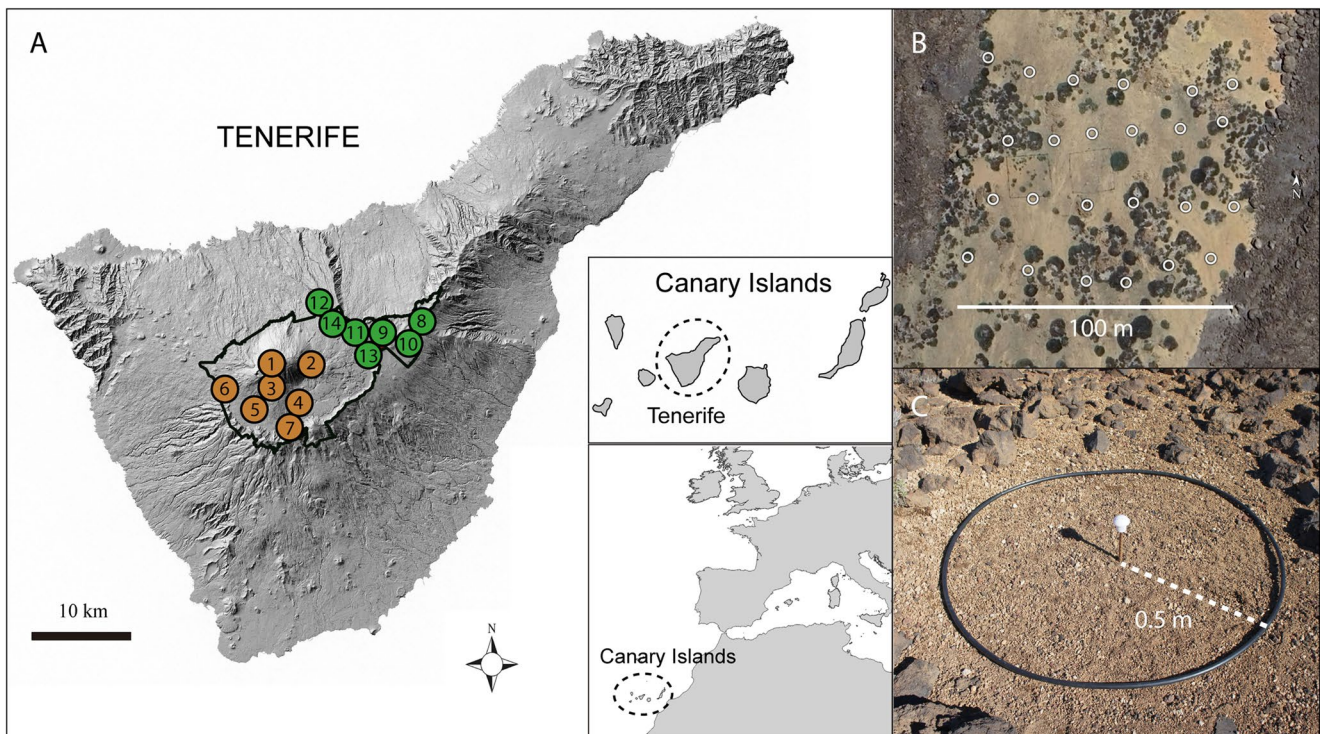


Fig. 1 Sampling sites on Tenerife. A: Northeast localities indicated with green circles and southwest localities with brown circles. Locality numbers as in Table 1. Limit of Teide National Park is indicated by a continuous black line. B: Example of a locality, Mancha Ruana

(1-brown), with 24 plots (white circles) along four line transects., C: Sampling plot where pellets are collected, the white stake marks the centre. Map credit: Gobierno de Canarias

Levin's niche breadth index (B_i) indicated whether these rabbits had a specialised (values close to 0) or generalist diet (close to 1) (Krebs 1999). Diet selection was quantified using the Savage index, S_i (Savage 1931), which takes into account the consumption (diet) with respect to food availability (vegetation cover), and the significance of selection evaluated by χ^2 test (Manly et al. 1993).

To assess the variables that affect each plant species abundance in rabbit droppings, a general linear model (GLM) with a Gaussian distribution was applied to the dataset. Thus, a total of twelve GLMs were carried out. For each model, plant species abundance was the dependent variable, and sampling area (localities) and sampling season were independent variables.

To investigate the effect of rabbit intraspecific competition on rabbit trophic niche breadth, a Spearman correlation test was performed on the variables rabbit density and Levin index on the total data set. Additional Spearman tests were conducted by categorising the data by location or date to determine if there was a correlation between rabbit density and the number of plants consumed at specific locations or dates. Rabbit density data were obtained from Teide National Park estimates, which were calculated by counting pellets in one-meter-diameter areas previously cleaned (MITECO 2017).

GLM analyses were conducted in R version 3.3.1. In addition, multiple Tukey comparisons evaluated, two by two, which localities and dates presented significantly different means.

Results

Plant epidermis remains belonging to a total of 12 taxa were recognized in 810 pellets, 11 of which were identified at species level and 1 at genus level. The main components of *O. cuniculus* diet were *S. supranubius* (41.30% OF), *P. lasiospermus* (22.78% OF) and *D. bourgeauana* (20.13% OF). Lesser amounts of *A. viscosus* (8.24% OF), *Arrhenatherum calderae* A. Hansen (3.98% OF) and *Erysimum scoparium* (Brouss. ex Willd.) Wettst. (2.11% OF) were found in the pellets analysed. Finally, six other species were present in a proportion under 1% OF: *Micromeria* sp., *Bromus* sp., *Andryala pinnatifida* Aiton, *Carlina xeranthemoides* L.f., *Nepeta teydea* Webb & Berthel. and *Argyranthemum tenerifae* Humphries (Table 2). All are Canary Island endemics with the probable exception of *Bromus*, a genus with endemic and non-endemic species in the National Park. Consumption/excretion of plant species varied according to locality and time of year (Table 2, S3 and Fig. S1).

Table 1 Sampling localities with geographical coordinates, elevation (m a.s.l.) and plant cover (%)

Locality	LC	m a.s.l.	Plant cover (%)												
			S.sp	P.la	D.bo	A.vi	E.au	P.spp	E.sc	A.te	N.te	T.we	P.ca	E.wi	C.xe
Southwest loc.															
Mancha Ruana	1	2959	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Montaña Blanca	2	2728	25.00	0.00	15.00	0.00	50.00	0.00	5.00	5.00	0.00	0.00	0.00	0.00	0.00
El Valle	3	2680	58.82	0.00	19.61	14.71	0.00	0.98	0.00	4.90	0.98	0.00	0.00	0.00	0.00
Cañada Blanca	4	2165	50.00	30.00	15.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chafarí	5	2145	35.00	10.00	0.00	20.00	0.00	30.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00
Montaña Negra	6	2086	50.00	40.00	0.00	5.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ucanca	7	2015	70.00	30.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Northeast loc.															
Izaña	8	2366	58.25	9.71	29.13	0.97	0.00	0.00	0.00	0.00	0.97	0.00	0.00	0.97	0.00
Maja	9	2287	38.83	24.27	33.98	0.00	0.97	0.00	0.00	0.00	0.97	0.00	0.00	0.00	0.00
Fasnía	10	2197	38.46	38.46	19.23	0.00	0.00	0.00	0.00	0.00	0.96	0.96	0.00	0.96	0.96
El Portillo	11	2112	52.08	31.25	5.21	10.42	0.00	0.00	0.00	0.00	0.00	1.04	0.00	0.00	0.00
La Fortaleza	12	2110	50.00	10.00	5.00	25.00	0.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00	0.00
Chiqueros	13	2096	75.00	10.00	10.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Guancheros	14	2050	50.00	25.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Plant cover was estimated in June 2017

LC: locality codes; m a.s.l.: m above sea level, elevation; S.sp: *Spartocytisus supranubius*; P.la: *pterocephalus lasiospermus*; D.bo: *descurainia bourgeauana*; A.vi: *adenocarpus viscosus*; E.au: *echium aubertianum*; P.spp: *Poaceae* spp.; E.sc: *erysimum scoparium*; A.te: *argyranthemum tenerifae*; N.te: *Nepeta teydea*; T.we: *Tolpis webbii*; P.ca: *Pinus canariensis*; E.wi: *echium wildpretii*; R.ca: *rhaponticum canariense*; C.xe: *Carlina xeranthemoides*

Table 2 Abundance (OF) of rabbit diet items detected in pellets during the different time periods in all sampled localities in the Teide National Park. % OF: percentage of optical fields in which each plant item appeared after analysing the pellet content

Plant Species	Dec-Feb	Feb-Apr	Apr-Jun	Jun-Aug	Aug-Oct	Oct-Dec	Total
	%OF	%OF	%OF	%OF	%OF	%OF	%OF
<i>Spartocytisus supranubius</i>	40.04	40.99	43.46	40.20	43.50	39.76	41.30
<i>Pterocephalus lasiospermus</i>	28.85	25.75	20.97	19.77	21.68	19.44	22.78
<i>Descurainia bourgeauana</i>	21.00	23.08	18.70	13.69	17.63	27.35	20.13
<i>Adenocarpus viscosus</i>	4.82	2.91	3.86	19.27	11.27	7.06	8.24
<i>Arrhenatherum calderae</i>	1.61	2.97	8.83	3.97	3.19	3.14	3.98
<i>Erysimum scoparium</i>	2.26	2.44	2.33	1.92	1.93	1.72	2.11
<i>Micromeria</i> sp.	1.04	0.76	0.82	0.42	0.30	1.10	0.74
<i>Bromus</i> sp.	0.00	0.82	0.56	0.62	0.40	0.13	0.43
<i>Andryala pinnatifida</i>	0.39	0.00	0.35	0.14	0.07	0.26	0.20
<i>Carlina xeranthemoides</i>	0.00	0.23	0.12	0.00	0.00	0.00	0.06
<i>Nepeta tetradlea</i>	0.00	0.03	0.00	0.00	0.03	0.00	0.01
<i>Argyranthemum tenerifae</i>	0.00	0.03	0.00	0.00	0.00	0.03	0.01

Levin's niche breadth index was low ($Bi=0.24$), since the rabbits' diet mainly comprises three plant species: *S. supranubius*, *P. lasiospermus* and *D. bourgeauana*, despite feeding on at least 12 plant species. Furthermore, this parameter yielded the highest values (broadest niche) in summer between June and August ($Bi=0.36$) and the lowest in February-April ($Bi=0.24$) (Table S4). Populations with a higher Levin's index were situated in El Portillo and on Montaña Blanca, while those located in Mancha Ruana and El Valle showed a narrower niche (Table S3).

Dietary diversity (number of species detected in each pellet) was significantly different between localities ($G_{65}=1730.701$, $p=0.000$). Between one and six plant species were found in each pellet, with a mean of 2.81 (Table S5). This diversity was higher in the northeastern localities than in the southwestern ($G_5=540.877$, $p=0.000$).

Regarding detection of plant species through the year, that of the most important diet component -*S. supranubius*- was practically constant. Statistical differences between time periods were detected ($LR=54.26$; $df=5$; $p<0.001$), however in the two by two comparison only differences between Oct-Dec/Apr-Jun and Oct-Dec/Aug-Oct were confirmed. The amount of *P. lasiospermus* identified varied through the year ($LR=168.75$; $df=5$; $p<0.001$), being more intensely grazed in winter (Dec-Apr). Comparisons between the different periods revealed significant differences, especially between seasons. The proportion of *D. bourgeauana* remnants varied greatly, depending on the sampling months. It showed significant differences ($LR=165.7$; $df=5$; $p<0.001$), being greater in winter (Dec-Apr). Significant differences in intake during the respective periods were detectable, except in some contiguous periods. Detection of *A. viscosus* was higher for summer (Jun-Oct), with statistical differences around the year ($LR=597.58$; $df=5$; $p<0.001$). A higher apparent intake of *A. calderae* was

detected in spring (Apr-Jun) ($LR=229.89$; $df=5$; $p<0.001$) (Table 2 and Fig. S1).

Remnant abundance of the main feeding plants in pellets was different according to locality (*S. supranubius* ($LR=1165.06$; $df=13$; $p<0.001$), *P. lasiospermus* ($LR=2257.24$; $df=13$; $p<0.001$), *D. bourgeauana* ($LR=3924.2$; $df=13$; $p<0.001$), *A. viscosus* ($LR=537.76$; $df=13$; $p<0.001$) and *A. calderae* ($LR=1609.54$; $df=13$; $p<0.001$)). *Spartocytisus supranubius* was always among the most detected, in some localities almost exclusively (Mancha Ruana and El Valle), while in others it was the least, as in El Portillo. *Pterocephalus lasiospermus* was also detected in the droppings from all localities, from 30 to 40% in Ucanca, El Portillo and La Fortaleza to 1–2% in Mancha Ruana and El Valle. *Descurainia bourgeauana* made up 50–40% of identified remnants in some localities (Maja, Montaña Blanca and Cañada Blanca) and in others very low percentages, even zero (Chafarí). *Adenocarpus viscosus* was found in relatively low percentages; around 20% in El Portillo and almost none in Mancha Ruana and El Valle. *Arrhenatherum calderae* consumption was apparently highly variable, with percentages between 25% and 15% in two localities (Chafarí and Montaña Negra) and very low or zero in the rest (Table S3). The proportion of *S. supranubius* was significantly higher with altitude ($z=0.663$, $p<0.01$). The opposite trend was found for *P. lasiospermus* ($z=-0.731$, $p<0.01$) and *A. viscosus* ($z=-0.648$, $p<0.05$).

In each locality the numbers of components of *O. cuniculus* diet varied between six and ten (Mancha Ruana and La Fortaleza, respectively), as did the remnant percentage of each. In some localities, usually a single plant species was grazed and the rest in very low proportions (Mancha Ruana and El Valle). Results from other places were more varied, such as Chiqueros with three species detected about 30% each, or others with four species above 10% (Montaña Negra, Izaña, Fasnía and El Portillo) (Table S3).

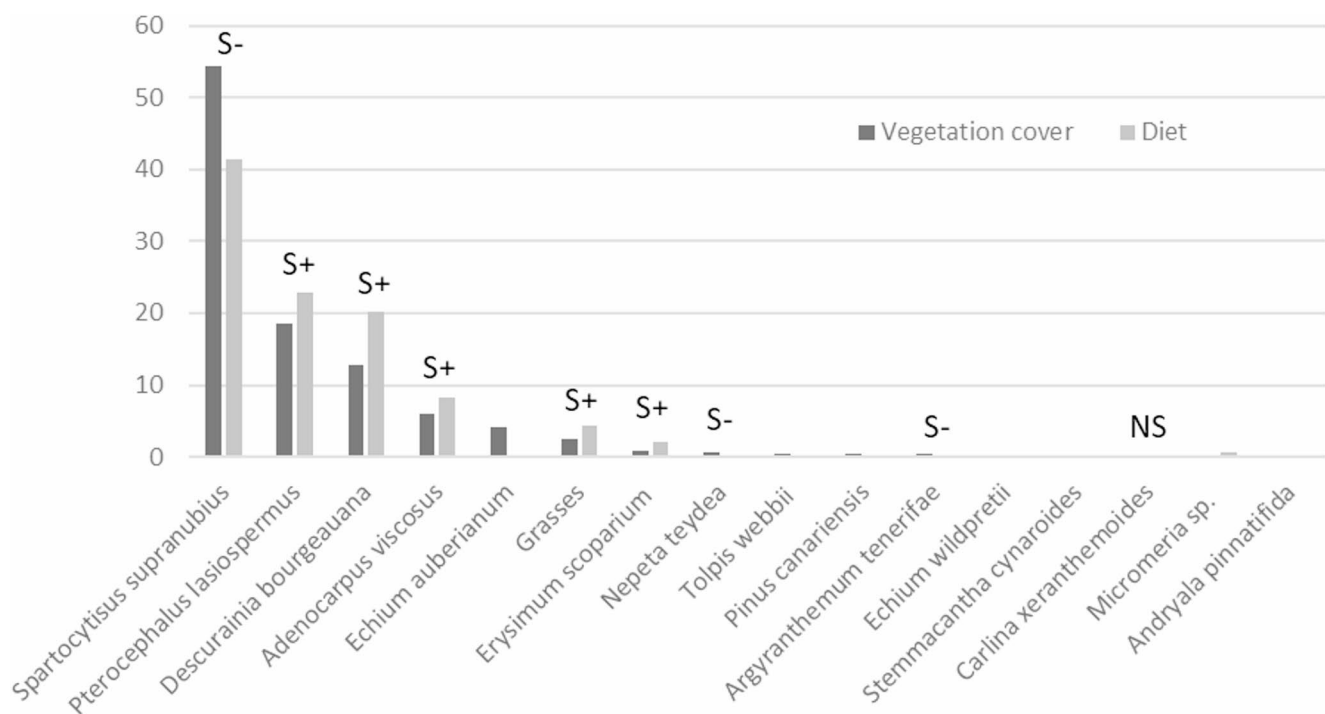


Fig. 2 Relationship between food availability (vegetation cover) and consumption (diet). Values in %. NS, no selection; S+, positive selection; S-, negative selection. The x-axis shows the plants detected in

the pellet analyses and the y-axis the percentage of each plant in the study plots (vegetation cover) and in the diet

With regard to food selection, the most abundant plant remnants found in *O. cuniculus* faeces should reflect plant availability in the habitats they occupied. However, *P. lasiospermus* (Savage index, $Sav=1.23$), *D. bourgeauana* ($Sav=1.57$), *A. viscosus* ($Sav=1.38$), *E. scoparium* ($Sav=2.66$) and grasses ($Sav=1.75$) were apparently more frequently selected than expected from their respective availability in this habitat (Fig. 2). In contrast, there was a negative selection of *S. supranubius*, the most abundant plant and main diet component ($Sav=0.76$) (Fig. 2). Another two plant species appear as negatively selected: *N. teydea* ($Sav=0.02$) and *A. tenerifae* ($Sav=0.03$) (Fig. 2). Selection of *S. supranubius* was significantly less in the localities where rabbits had a more generalist diet (higher Levin index) ($z=-0.926$, $p<0.001$). In contrast, *P. lasiospermus* ($z=0.611$, $p<0.05$) and *A. viscosus* ($z=0.622$, $p<0.05$) were probably more intensely grazed in such localities with high Levin indices.

Selection of the main plant species in the diet varied between localities. Against the general trend, *S. supranubius* was positively selected in two localities, non-selected in five, and negatively selected in seven of them. *Pteroccephalus lasiospermus* was less frequently detected in pellets than expected from its availability in four localities, non-selected in five and positively selected in another five. *Descurainia bourgeauana* was positively selected in seven localities, non-selected in five and negatively in only one (Table S6).

Rabbit densities in the studied localities of the Teide National Park ranged from 3.9 (± 1.8) to 0.1 rabbits/ha in 2017 (MITECO 2017; Table S7). Cañada Blanca (3.23), Izaña (2.88), Mancha Ruana (2.72) and El Portillo (2.42) are the localities with the highest density of rabbits in 2017, while Montaña Blanca has the lowest density (0.18) (Table S7, Fig. S2). The periods with the highest rabbit densities were April-June and August-October, and the lowest were June-August (Table S7). No correlation was found between rabbit density and the Levin index ($R=0.12$, $p=0.29$) except for El Portillo, which was the only locality showing a correlation (negative) between these two variables ($R=-0.94$, $p=0.017$). Only the August-October time period showed a correlation, which was positive ($R=0.8$, $p<0.01$).

Discussion

Microhistological analysis is extensively employed to investigate herbivore diets (Pareja et al. 2021; Kamla et al. 2021; Espunyes et al. 2019; Hernández-Teixidor et al. 2014; Simensen and Eichhorn 2012; Martínez-García et al. 2012; Marrero and Nogales 2005; Martín et al. 2003; Marques and Mathias 2001; Mátrai et al. 1998). This technique may have certain limitations, such as potential underestimation of some plant species, due to their varied digestibility or not detecting several minor species during analysis (McInnis et

al. 1983). Nevertheless, the use of microhistology is recommended to obtain quantitative diet composition at the plant species level (Garnick et al. 2018).

Our results describe diet composition in relation to overall plant cover, though inferences about true dietary selection are constrained by our availability metric not fully representing accessible biomass, particularly for taller shrubs. Plant remnants in rabbit faecal pellets from Teide National Park were derived from twelve plant species in total. *Oryctolagus cuniculus* has been described as a polyphagous grazer because it consumes many different plant species (Lees and Bell 2008), as observed in Portugal, where rabbits are native and fed on at least 151 species belonging to 39 families. Similarly, on the Aegean island of Lemnos, introduced rabbits apparently consume at least 150 plant taxa (Kontsiotis et al. 2015). In Australia, rabbits grazed on more than 67 plant species (Martin et al. 2007), and 45 plant species in Argentina (Bobadilla et al. 2023). Contrastingly, in Teide National Park the number of plant species consumed was lower (only 12). A predominant consumption of a few plant species was also reported by Martín and Marrero (1999) on the Canary islet of Alegranza, and by Laspina et al. (2013) in Argentina, places where rabbits are non-native. Dietary diversity of rabbits in Teide National Park, with 1–6 species per dropping (mean, 2.81) was lower than in Australia at 2–11 (mean, 5.4) (Martin et al. 2007).

Although rabbits consume up to 12 plant species in this national park, their hierarchical diet mostly consisted of only *S. supranubius*, *P. lasiospermus* and *D. bourgeauana*. The reason for this may be that these species make up more than 80% of the vegetation cover. Rabbit diets mainly composed of the most abundant plants in their feeding area have been described previously (Martín and Marrero 1999; Donlan et al. 2002; Lees and Bell 2008; Simensen and Eichhorn 2012). Despite consuming mainly the most abundant plants present in the feeding area, they are able to select from those with the greatest vegetation cover. Indeed, *P. lasiospermus* and *D. bourgeauana* were selected above their density and *S. supranubius* below it (Fig. 2). This is in accordance with previous data (Martín and Marrero 1999; Donlan et al. 2002; Lees and Bell 2008; Simensen and Eichhorn 2012).

Spartocytisus supranubius is the most common plant species found in these rabbits' diet, but with declining populations since approximately 1995 (Kyncl et al. 2006; Cubas et al. 2022). Individual bushes of this species show inhibited rejuvenation, probably due to the joint effects of climate change (Perera-Castro et al. 2018), displacement of native pollinators by introduced honeybees (Valido et al. 2014) and rabbit predation of shoots and juvenile shrublets (Irl et al. 2012; Cubas et al. 2018). Large aggregations of their droppings (latrines) also affect the symbiosis of soil rhizobia (nitrogen-fixing) populations beneath or near this

plant (Pulido-Suárez et al. 2021). This species is considered highly palatable for rabbits (Cubas et al. 2017), similar to other Fabaceae in native rabbit habitats (Delibes-Mateos et al. 2008). Visual signs of browsing damage to vegetation had previously pointed to the high consumption of *S. supranubius* and *D. bourgeauana* (Cubas et al. 2017), the latter being the third most consumed plant in introduced rabbit diet. *Pterocephalus lasiospermus* was however the second most-consumed, despite being described as “poorly palatable for rabbits” according to previous visual samplings (Cubas et al. 2017, 2018). A similar case arises with their feeding on *Adenocarpus viscosus*, which has a variety of alkaloids that potentially act as a defence mechanism against mammalian herbivory (Cheeke 1988; Greinwald et al. 1992). However, wild rabbit diet can include substantial quantities of some alkaloids without showing signs of toxicity (Pierson et al. 1977; Swick et al. 1982). *Arrhenatherum calderae* (%OF 3.98) and *Bromus* sp. (%OF 0.43), as monocots, possess lower levels of secondary metabolites (tannins and terpenes) compared to the rest of the plants (dicotyledons) consumed by rabbits in the National Park (Bozinovich 2003). These latter plants were scarcely consumed, but might be useful in diluting the intake of secondary metabolites, as described for the mara (*Dolichotis patagonum*) in Argentina (Rodríguez and Dacar 2008). Furthermore, rabbits exhibit specialist feeding behaviour when food is abundant and generalist behaviour when food resources are limited in the feeding area (Chapuis 1990). A higher detection % of *P. lasiospermus* and *A. viscosus* linked to greater niche breadth could indicate that these species are consumed when other resources are scarce, or that these species are preferred by rabbits and consumed when available. Instead, when food supply does not enable a more selective diet, ingestion of *S. supranubius* would increase. The relative preference for a specific plant species is closely associated with the rest of species in the environment, their availability and phenology (Wildpret and Martín-Osorio 2004; Fernández-Olalla and San Miguel-Ayán 2007).

Differences in the consumption of certain plant species throughout the year were revealed (Fig. S1). The Levin index showed a wider niche breadth in the dry months, which indicates the need to widen the range of their trophic resources. Consumption of *A. viscosus* apparently increased in summer. Food plant selection patterns might also be influenced by the presence of defensive plant-produced allelochemicals (Raubenheimer and Simpson 2003), and differences in the alkaloid profile in flowers and leaves have been found in it. Its leaves are rich in the bipiperidyl alkaloid adenocarpine, while flowers store high amounts of tyramine (Greinwald et al. 1992). Increased *A. viscosus* consumption coincides temporarily with flowering (Wildpret and Martín-Osorio 2004). The preference for this plant in summer, as well as

the absence of damage observed in previous visual surveys (Cubas et al. 2017, 2018), could be explained by consumption of the flowers of this species during this period. However, further research is needed to confirm this hypothesis. When high-quality food becomes less available during the dry season, generally less palatable (Ferreira and Alves 2009; Martins et al. 2002) and even toxic taxa (Kontsiotis et al. 2015) are consumed in the struggle for survival. Consumption of *Arrhenatherum calderae* is also linked to seasonality. It is a perennial grass (Wildpret and Martín-Orsorio 2004), so its year-round availability would explain its greatest intake in the dry months. This indicates that rabbits in the Teide National Park are opportunists, changing their diet according to the temporary resources or phenological state of plants, as in other habitats around the world (Donlan et al. 2002; Martins et al. 2002; Martín et al. 2003; Martín et al. 2007). This pattern also aligns with the opportunistic foraging behaviour documented in other lagomorphs in Mediterranean systems (Rizzardini et al. 2019; Freschi et al. 2025).

Through overgrazing, *Oryctolagus cuniculus* is changing the dynamics and structure of the plant community in Tenerife's summit shrubland (Kyncl et al. 2006). *Spartocytisus supranubius* populations are declining and *P. lasiospermus* is strongly expanding its distribution (Kyncl et al. 2006), due to the combined action of climatic change (Perera-Castro et al. 2018) and rabbit activity (Cubas et al. 2018), as previously mentioned. However, rabbits usually consumed more *D. bourgeauana*, *P. lasiospermus* and *A. viscosus* but less *S. supranubius* than expected from the respective plant cover in this habitat, according to our results. To interpret the availability of large plant species, it is necessary to consider the accessibility of biomass to herbivores (Fernández-Olalla and San Miguel-Ayán 2007). Rabbits typically consume foliage below 40–50 cm in height (Cooke and McPhee 2007; Cooke et al. 2008), so most mature *S. supranubius* plants are out of reach, resulting in overestimation of the availability of this resource and underestimating the others. In fact, visual sampling of browsing damage has revealed that nearly 100% of *S. supranubius* individuals and only around 20% of *P. lasiospermus* show rabbit damage (Cubas et al. 2018). In any case, feeding preferences need not accurately reflect the quantitative damage to vegetation (O'Reilly and McArthur 2000). Rabbits can exhibit a markedly high preference for seedlings that constitute a very small proportion of available plant biomass (Lange and Graham 1983), but contributing to long-term total biomass reduction through the effect on recruitment and regeneration (Irl et al. 2012; Cubas et al. 2018). Some researchers have proposed that rabbit impact on the vegetation of summit Tenerife vegetation has increased in the last few decades due to rising temperatures (Cubas et al. 2018), which have led to an increase in rabbit populations, even

expanding their altitudinal distribution above 3000 m a.s.l. (Cubas et al. 2019). Rabbit populations may exhibit dietary changes in response to fluctuations in intraspecific competition throughout the year (Somers et al. 2008). Our findings indicate that temporal and spatial variations in population density do not significantly affect their trophic niche breadth in Teide National Park. However, in the period August–October, niche breadth and rabbit density showed a positive and strong correlation, which may be because rabbits became more generalist as their populations increased during these months. Increased consumption of *S. supranubius* at higher altitudes could be explained by its better status/condition, due to lower predatory pressure from rabbits until recent times. At lower altitudes, lack of juveniles (Cubas et al. 2018) and biomass of this broom species below rabbit height due to overgrazing can explain the apparent descent in its intake. Scarcity of this resource (abundant in cover, but now out of reach) could be forcing rabbits to consume more of the less palatable *P. lasiospermus* and *A. viscosus*. This could be the case for the El Portillo locality, where rabbits consumed more of these two plants than *S. supranubius*. However, when the rabbit population increases in this locality, rabbits tend to narrow their trophic niche, maybe due to a greater reduction in plant availability.

Climate change is accelerating the decline of the Teide white broom (Cubas et al. 2022). This is even more pronounced on the southern slope of the National Park, due to warmer temperatures and lower precipitation (Martín-Esquivel et al. 2020; Pulido-Suárez et al. 2021; Cubas et al. 2022). As this legume fixes nitrogen in the soil, its population decline is expected to impoverish plant communities, affecting the total productivity and carrying capacity of the summit shrub habitat (Cubas et al. 2018; Martín-Esquivel et al. 2020). Rabbits are able to switch to any other palatable forage species, permitting an abundant rabbit population despite a decrease in preferred plant food (Donlan et al. 2002). As strong invader, the rabbits will probably increase the consumption of the other two main components of their diet in this national park or select other available plant species.

Climate change and herbivores have driven changes in the diversity of alpine communities in Tenerife, altering the abundance of some plant species (Martín-Esquivel et al. 2020). These factors affect endangered species, the maintenance of essential ecological interactions, and, therefore, National Park management (Durbán and Martín-Esquivel 2021). One of the primary measures managers take to reduce herbivore pressure is to erect large exclosures and also to reduce of rabbit populations through the implementation of effective control measures, mainly hunting with dogs and ferrets (MITECO 2017; Martín-Esquivel et al. 2020). Knowing which plants the rabbit consumes in each

area of the national park and in what proportions can inform restoration of degraded areas by identifying key species for revegetation and protection. The study of rabbit diet can also aid in detecting the presence of less common species that are not easily observed in areas where rabbits are abundant due to intensive browsing. Such information can be valuable where it is considered necessary to include the planting of this scarce species missing from communities in exclusion plots, or at higher altitudes to safeguard against the upward moving effects of climate change. Furthermore, the adoption of innovative methods, such as near-infrared reflectance spectroscopy (NIRS), could more accurately quantify nutritional intake in studies on the diet of herbivores (Rossa et al. 2025).

Conclusion

Microhistological analysis of faeces has shown to be a useful method to study rabbit diet in Teide National Park, even demonstrating the cryptic consumption of some plants unrevealed by earlier visual samplings of browsing damage. These data are particularly valuable for management of flora in the Park and comparable protected areas. With increasing pressure from herbivores and climate change, understanding the rabbit damage revealed by dietary evidence is critical to designing exclusion plots that favour and conserve existing diversity. The generalist and opportunistic feeding behavior documented in this study underscores the necessity of population control to mitigate impacts on this vulnerable ecosystem.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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