

**Introduced rabbits as seed-dispersing frugivores:  
a study case on an environmentally diverse  
oceanic island (Tenerife, Canarias)**

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**Trabajo de Fin de Máster**

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# **MEMORIA DEL TRABAJO DE FIN DE MÁSTER**

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## **Abstract**

Rabbits have travelled with humans to the most remote archipelagos, having been introduced on at least 800 islands worldwide. This herbivore has caused a devastating effect on endemic insular plants, causing changes in species composition, cascading extinctions and disruption of native seed dispersal systems worldwide. However, its ecological impacts as disrupting native seed dispersal systems have not been studied from a holistic perspective in any of the archipelagos where rabbits were introduced. Here, we assess the role of rabbits as frugivores and seed-dispersers on the most extensive and diverse island of the Canary Archipelago, Tenerife, across its five main vegetation zones represented in an altitudinal gradient 0 – 3715 m a.s.l. To this end, 120 transects per vegetation zone were conducted (August 2020–November 2021) to collect fresh faecal samples from a total of 244 latrines. They consisted of 29,538 droppings in which we found seeds from 73 plant species, 29 of which were identified to species level (13 endemic, eight natives and eight introduced by humans). About 70% of the seeds were identified as fleshy-fruited plant species while the remaining nine were dry fruits. Of the former, only nine showed a percentage of intact seeds greater than 75%, another nine species between 50-75%, and three lower than 50%. The digestive effect of rabbits on seedling emergence was generally low, compared to that produced by native seed dispersers. Since fleshy-fruited plants and rabbits have not been linked in their evolutionary history in the Canaries, the former seems to have their own legitimate seed dispersers.

## Introduction

Oceanic islands often harbour unique biodiversity but are highly vulnerable to global change effects (Paulay 1994). Most of the biota of these islands are threatened by the introduction of alien species, one of the major drivers of native biodiversity loss (McNeely et al. 2001; Spatz et al. 2017).

Mammals are one of the main taxonomic vertebrate groups involved in biological invasions (Courchamp et al. 2003). The European rabbit (*Oryctolagus cuniculus*), a native species from southwest Europe and North Africa, has successfully colonised all continents except Antarctica (Thompson and King 1994). It has also been introduced to at least 800 islands around the world, including the Macaronesian islands (Flux and Fullagar 1992). Its great success and wide distribution are often attributed to high population growth rates and reproductive capacity but also depend on climatic conditions, and food and refuge availability (Soriguer 1988; Flux and Fullagar 1992).

Rabbits shape the landscapes and therefore have been considered as important ecosystem engineers in their native areas, due to the important effects of their herbivory and construction of burrows (Delibes-Mateos et al. 2008; Delibes-Mateos and Gálvez-Bravo 2009). In this native area, rabbits also play a role as seed dispersers (Gálvez-Bravo 2008; Dellafiore et al. 2006, 2007, 2010; Larrinaga, 2010; Mancilla-Leytón et al. 2013). However, they cause severe damage to the invaded ecosystems, especially on islands, causing devastating effects on endemic plants and cascading extinctions (Bowen and Vuren 1997; Courchamp et al. 2003; Caujapé-Castells et al. 2010; Carrion et al. 2011). According to the International Union for Conservation of Nature, *O. cuniculus* has been

catalogued as one of the 100 most dangerous invasive species on the planet (Lowe et al. 2000; GISD 2021).

On islands, this herbivore shows preference for seedlings, inhibiting the recruitment of many tree and shrub species (Cooke 2012). It can also disrupt native seed dispersal systems and even promote the spread of invasive plant species, leading to an invasional meltdown effect (sensu Simberloff and Holle, 1999; Nogales et al. 2006; López-Darias and Nogales 2008).

In the Canary Islands, *O. cuniculus* was introduced in the 15th century, during the European conquest (De Abreu Galindo 1977; Nogales et al. 2006). Currently, the rabbit is distributed in all habitats of the main islands of the archipelago and on the islets of Alegranza, La Graciosa and Lobos, except Montaña Clara, where it was successfully eradicated between 2000 and 2001 (Martín et al. 2002). The first detailed studies on the diet of rabbits were carried out on Alegranza, an islet with a dry environment and low diversity of plant species (Marrero and Martín 1999, 2000; Martín et al. 2003). On some islands of the archipelago, seeds from native, endemic and introduced plants were found in rabbit droppings (Nogales et al. 1995, Nogales et al. 2005, López-Darias and Nogales 2008; Arévalo et al. 2010). Recent publications showed however that the endemic flora is browsed more intensely than non-endemic, with up to 67% of endemic species consumed by rabbits (Cubas et al. 2019, 2021; González-Mancebo et al. 2019). Furthermore, they modify the soil chemistry and abundance of the dominant plant species in the high mountain ecosystem (Cubas et al. 2017, 2018). Parada-Díaz et al. (2022) have recently shown that in disturbed laurel forest areas of Garajonay National Park (on La

Gomera), rabbits affect establishment, recruitment and flowering rate, which can lead to a depletion of the seed bank.

Despite the Canary archipelago being one of the most important geographical zones of the Mediterranean biodiversity hotspot (Myers et al. 2000), the role of rabbits as disruptors of the native seed disperser systems in these islands is still poorly known (but see Nogales et al. 1995, 2005; López-Darias and Nogales 2008). Here, we study the ecological role of rabbits as frugivores and seed-dispersers in the five main vegetation zones of Tenerife and throughout its entire altitudinal gradient. Specifically, the main objectives of this work were to: (1) identify the seeds of the plant species consumed by *O. cuniculus*, (2) assess whether habitat type and season influence its frugivory, and (3) evaluate the seedling emergence capacity of the main species consumed, after their passage through the rabbit gut in comparison with other native guilds of dispersers.

As a general hypothesis, we expected that the introduced rabbits could disrupt the seed dispersal systems of many native and endemic plants in the different habitats of Tenerife. However, since these plants have evolved in the absence of terrestrial mammals in the current presence of their native guild dispersers -with which they have evolved- this lagomorph would not be expected to play an important role as seed disperser. We also discuss the potential for an invasional meltdown scenario in the study systems.

## **Materials and Methods**

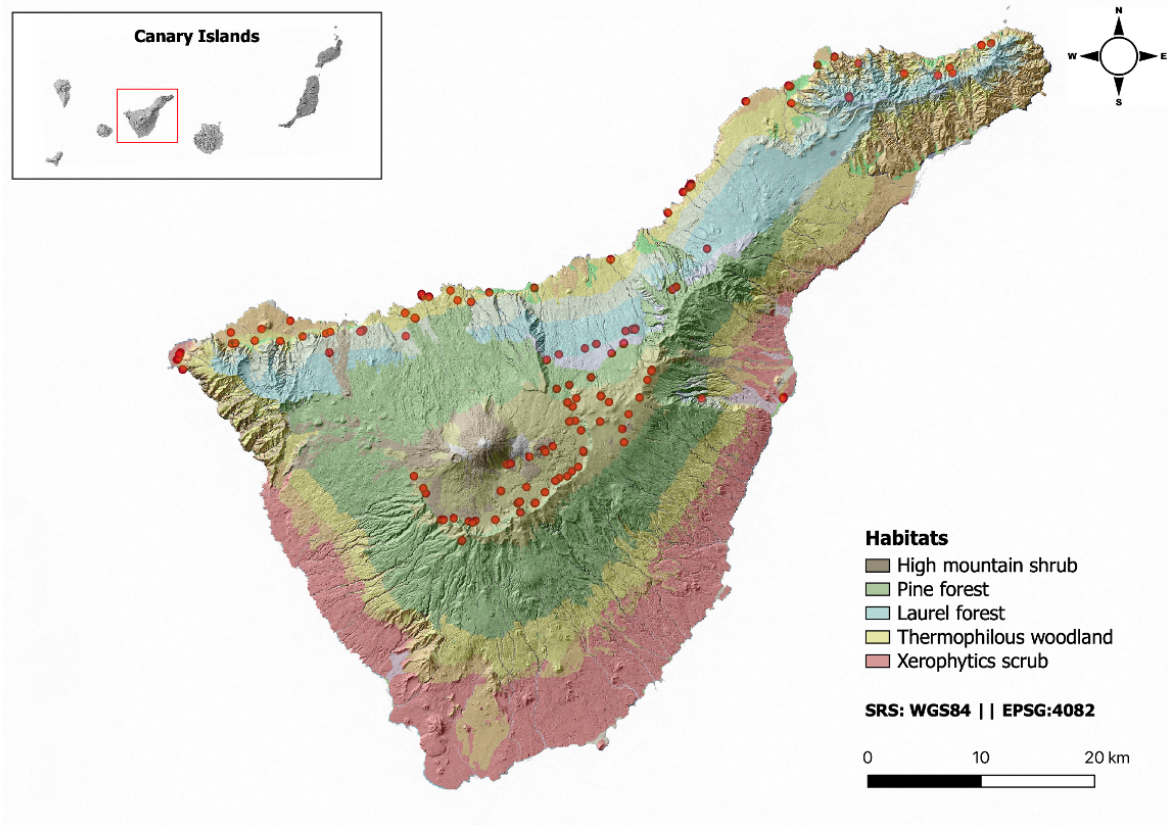
### *Study areas*

This study was carried out on Tenerife (Canary Islands, Spain), a volcanic island located about 300 km from the northwest coast of Africa. It is the largest and highest island in the archipelago, with a surface area of 2036 km<sup>2</sup> and reaching an altitude of 3715 m a.s.l at the peak of Teide stratovolcano. Volcanism on Tenerife spans at least the last 12 Myr (Guillou et al. 2004).

Depending on the winds, there are two contrasting slopes (Northeast and Southwest). The northeast zone receives the trade winds, bringing more precipitation to the environment, while the southeast is warmer and more arid (Marzol Jaén 1988). Orientation and altitude determine the climatic conditions of the Canary Islands. Tenerife is the island with the greatest variability in environmental factors in the archipelago, with five main vegetation zones represented on its the northeast oriented slopes, from the coast to the summit: (1) coastal and xerophytic scrubs ( $\approx$  0-200 m a.s.l., 19-21 °C, 50-200 mm annual rainfall), (2) thermophilous woodlands ( $\approx$  200-400 m a.s.l., 15-19 °C, 250-400 mm), (3) laurel forests ( $\approx$  400-1500 m a.s.l., 13.5-17.7 °C, 450-950 mm), (4) pine forest ( $\approx$  1500-1900 m a.s.l., 11-16 °C, 450-550 mm) and (5) high mountain (alpine or supramediterranean shrubs) (> 1900 m a.s.l., 7-12.7 °C, 350-500 mm) (Marzol Jaén 1988, Del Arco Aguilar and Rodríguez-Delgado 2018, partially modified).

Our study was conducted in all significant environmental gradients, within an altitudinal range between 0 and 3715 m a.s.l. (Fig. 1).





**Fig. 1.** Geographical location of the island of Tenerife with the five main habitats and sites of the latrines collected (red points).

### *Procedures*

A total of 600 transects (120 per vegetation zone), 30x2 m each, were conducted from August 2020 to November 2021. These transects were located on the northern slopes of the island where the main five habitats are well represented. Within each transect, we inspected for latrines of *O. cuniculus*, and whenever we found them, fresh faecal droppings were collected. Our sampling unit consisted of all the fresh droppings per latrine and transect, discarding the old droppings. All samples were labelled individually and georeferenced with a handheld GPS (Photo 1).



**Photo 1.** Collecting samples in one of the latrines during a transect in El Teide National Park.

In the laboratory, faecal samples were analysed under a stereomicroscope (10x magnification) to identify the plant seeds by species using reference collections at the IPNA-CSIC, the germplasm bank of the Teide National Park and the Digital Atlas of Seeds of the Canary Islands (Atlas Digital de Semillas de las Islas Canarias 2021) (Photo 2). We visually classified seeds as damaged or intact and measured their seed diameter with a digital calliper as a proxy of seed size (Photo 3). Taxonomy of animals and plants, and the biogeographical status of each taxa, follows the checklist of the Biota of the Canary Islands (Arechavaleta et al. 2010).



Photo 2. Process of analysis and identification of seeds in the rabbits' droppings.

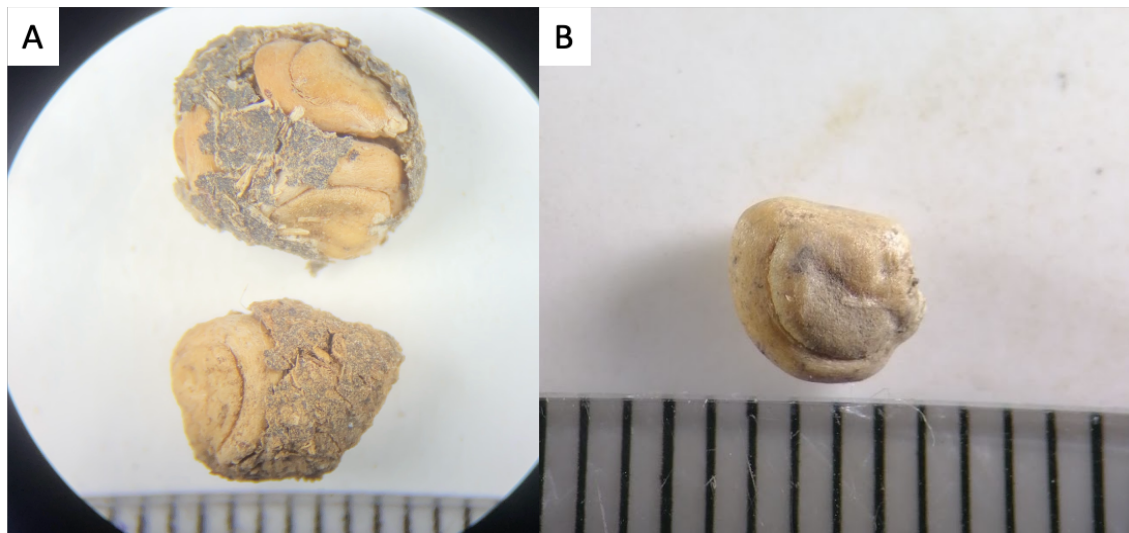
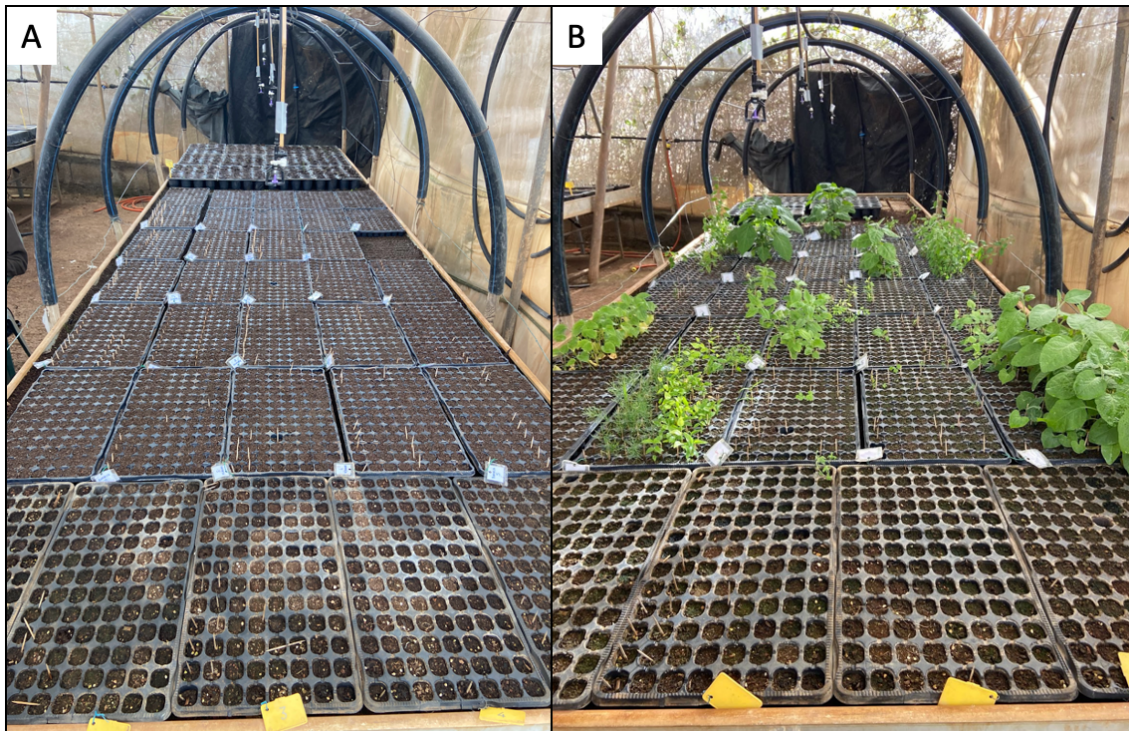


Photo 3. A. *Opuntia dillenii* seeds in two droppings of rabbits. B. Intact seeds of *O. dillenii* measured during the identification process.

To assess the effect of seed passage through rabbit guts, germination experiments were performed for 6 months in a greenhouse belonging to Tagoro MA (Tacoronte, 300 m a.s.l.). We buried each species identified, and those unidentified, in a 4 cm<sup>2</sup> pot (5 mm in depth) containing a standard substrate (25% peat, 25% volcanic sand, and 50% agricultural soil) and watered them every 2 days. Seeds were sown after the summer, following the natural cycle of rains, which fall mostly in autumn in the Canaries (Rodríguez et al. 2007; Photo 4). Seed emergence was considered when any part of the seedling emerged at the soil surface (see Nogales et al. 2005).



**Photo 4.** Germination experiment: (A) at the beginning and (B) six months later.

### *Statistical analyses*

To test whether vegetation zone, season (Winter: months 12,1,2; Spring: months 3,4,5; Summer: months 6,7,8, Autumn: months 9,10,11), plant species, and seed size influence frugivory by rabbits, Generalised Linear Models (GLM) were used with the relative abundance of seeds (both damaged and intact) per latrine as the response variable, adjusting data to a Gamma distribution of errors. Spearman correlation tests were performed between the potential relationships between the frequency of occurrence of seeds in latrines and the seed size of the different plant species. A categorical analysis (Pearson test) was made to compare the number of emerged seeds between native and introduced plant species. All analyses were performed using the ‘stats’ package of the software R 4.1.2 (R Core Team 2022).

## Results

### *Frugivory and digestive treatment*

A total of 244 samples were analysed, distributed over the five main habitats of Tenerife, corresponding to 29,538 droppings (Table 1). Overall, seeds from 73 plant species were recorded, 29 of which were identified to specific levels (13 endemics, 8 natives, and 8 introduced by humans, Fig. 2). Most of the seeds found in droppings were from plants that produce dry fruits ( $n= 53$ ; 73%) and only 20 (27%) of them belonged to fleshy-fruited plants. Of the identified seeds, twenty were those of fleshy-fruited plant species and the others ( $n= 9$ ) to dry fruits (Fig. 3).

**Table 1** Faecal samples collected from latrines and droppings analysed in each vegetation zone per season. Legend: Wt= Winter; Sp= Spring; Sm= Summer; At= Autumn

Vegetation zone	Seasons	Latrines	Droppings
High mountain shrub	Wt	14	1817
	Sp	16	2059
	Sm	17	3036
	At	55	7374
Pine forest	Wt	14	900
	Sp	4	332
	Sm	2	110
	At	11	1018
Laurel forest	Wt	3	306
	Sp	-	-
	Sm	4	151
	At	9	1139
Thermophilous woodland	Wt	6	300
	Sp	9	873
	Sm	12	1869
	At	11	1068
Xerophytic scrub	Wt	8	1053
	Sp	17	1922
	Sm	18	2634
	At	15	1586

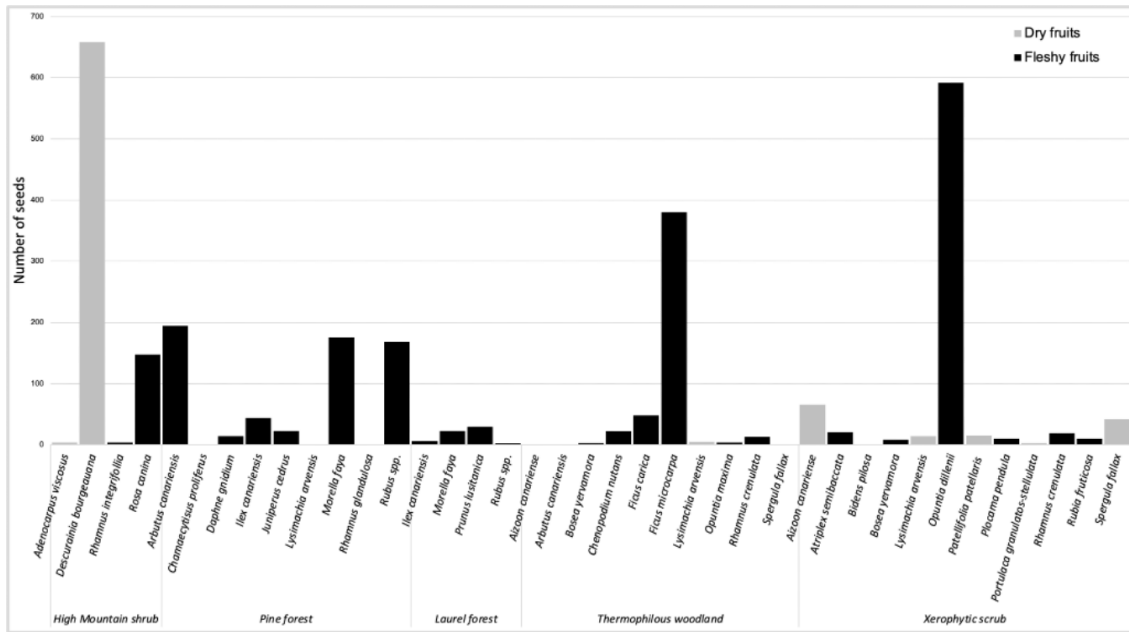
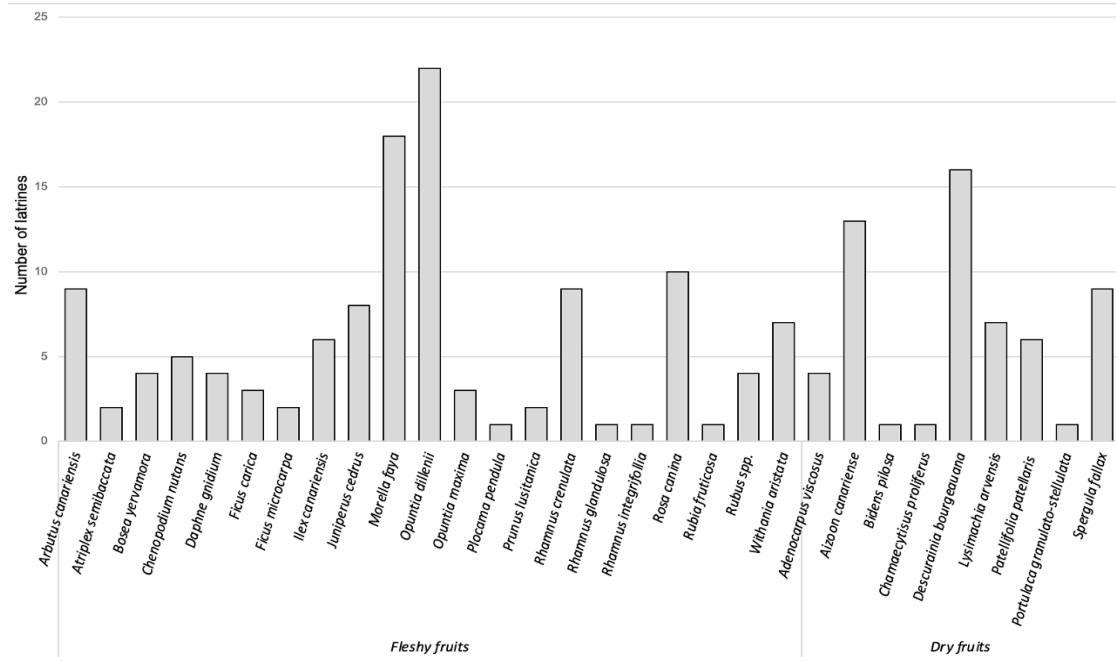


Fig. 2. Number of seeds of plant species identified from the rabbit latrines in each habitat on Tenerife.

Analysing the number of identified seeds per habitat at each altitude. The introduced *Opuntia dillenii* was the most dispersed in the xerophytic scrub, the introduced *Ficus microcarpa* (although locally and in highly disturbed places) and *F. carica* (more widely distributed but linked to anthropic areas) and the native *Rhamnus crenulata* in the thermophilous woodland, *Prunus lusitanica* and *Morella faya* in the laurel forest, *Arbutus canariensis*, *M. faya* and *Rubus spp.* in the pine forest, and *Descurainia bourgeauana* and *Rosa canina* in the high mountain shrub (Fig. 3).



**Fig. 3.** Frequency of occurrence of the identified plant species in latrines of rabbits on Tenerife.

A total of 1973 intact seeds (82.3%) corresponded to those identified species. Considering that seeds from introduced species are apparently more frequent in the two lower habitats in altitude, due to human modification, we can classify the five habitats in two main types: 1) basal (xerophytic scrub and thermophilous woodland) and 2) montane (laurel forest, pine forest and high mountain shrub). If we analyse the number of seeds of endemics and non-endemics, a significant number of non-endemic seeds were recorded in the basal with respect to the montane one ( $\chi^2_1=998.0$ ;  $p<0.001$ ).

Of the total fleshy-fruited plants identified, only 9 species showed a percentage of intact seeds greater than 75% (e.g. *A. canariensis*, *F. carica*, *O. dillenii*, and *P. lusitanica*), 9 species between 50-75% (e.g. *F. microcarpa*, *Ilex canariensis* and *Rubia fruticosa*) and for 3 species it was lower than 50% (e.g. *Atriplex semibaccata* and *Withania aristata*). Analysing the number of intact seeds with respect to the biogeographical range of the identified fleshy-fruited plant species, 38% were from endemic or native while 62% were introduced species (Table 2).



**Table 2** Analysis of fleshy (A) and dry (B) seeds per rabbit dropping and latrine on Tenerife. A= Fleshy fruits and B= Dry fruits. Legend: CE= Canarian endemism; ME= Macaronesian endemism; NA= Native; IN= Introduced; XS= Xerophytic scrub; TW= Thermophilous woodland; LF= Laurel forest; PF= Pine forest; HM= High mountain shrub; Wt= Winter; Sp= Spring; Sm= Summer; At= Autumn

**A**

Species (Fleshy fruits)	Total seeds	Intact seeds (%)	Total seeds/ number of droppings analysed	Total seeds/ number of latrines analysed	Seed diameter (mm)		Biogeographic range	Habitats					Season
					Average	Range		XS	TW	LF	PF	HM	
<i>Arbutus canariensis</i>	195	96.41	0.0066	0.7992	1.38	1.1-1.8	CE				PF		At
<i>Atriplex semibaccata</i>	21	4.76	0.0007	0.0861	1.14	0.4-1.5	IN	XS					Sp
<i>Bosea yervamora</i>	12	91.67	0.0004	0.0492	1.18	1-1.3.0	CE	XS	TW				Sp
<i>Chenopodium nutans</i>	22	59.09	0.0007	0.0902	0.65	0.4-0.8	IN	XS	TW				Sp
<i>Daphne gnidium</i>	14	85.71	0.0005	0.0574	1.22	1.1-1.3	NA				PF		Sm; At
<i>Ficus carica</i>	48	97.92	0.0016	0.1967	1.24	1.1-1.3	IN		TW				Sp
<i>Ficus microcarpa</i>	380	75.00	0.0128	1.5574	0.96	0.7-1.2	IN		TW				Sm
<i>Ilex canariensis</i>	50	74.00	0.0017	0.2049	3.43	3.0-4.4	ME			LF	PF		Sm
<i>Juniperus cedrus</i>	23	78.26	0.0008	0.0943	3.8	3.3-4.9	ME				PF		At
<i>Morella faya</i>	198	58.08	0.0067	0.8115	3.95	3.3-4.9	NA			LF	PF		Sm
<i>Opuntia dillenii</i>	592	95.10	0.0200	2.4262	4.42	4.0-5.5	IN	XS					Sm
<i>Opuntia maxima</i>	4	50	0.0001	0.0164	3.24	2.8-3.7	IN		TW				Sm
<i>Plocama pendula</i>	10	100	0.0003	0.0410	0.86	0.7-1.0	CE	XS					Wt
<i>Prunus lusitanica</i>	30	93.33	0.0010	0.1230	6.07	5.4-6.5	NA			LF			Sm
<i>Rhamnus crenulata</i>	33	57.58	0.0011	0.1352	2.26	1.2-3.5	CE	XS	TW				Sp

<i>Rhamnus glandulosa</i>	1	0	0.0000	0.0041	2.26	1.5-2.8	ME				PF	Sm
<i>Rhamnus integrifolia</i>	4	75	0.0001	0.0164	2.38	1.9-2.8	CE				HM	At
<i>Rosa canina</i>	148	54.73	0.0050	0.6066	2.55	2.3-2.8	NA				HM	Sm
<i>Rubia fruticosa</i>	10	90	0.0003	0.0410	2.16	1.8-2.7	ME	XS	TW			Wt
<i>Rubus</i> spp.	170	64.12	0.0057	0.6967	1.86	1.5-2.1	-			LF	PF	Sm
<i>Withania aristata</i>	13	46.15	0.0004	0.0533	2.97	2.4-3.7	CE	XS	TW			Sp

**B**

Species (Dry fruits)	Total seeds	Intact seeds (%)	Total seeds/ number of droppings analysed	Total seeds/ number of latrines analysed	Biogeographic range	Habitat					Season
						XS	TW	LF	PF	HM	
<i>Adenocarpus viscosus</i>	4	100	0.0001	0.0164	CE					HM	At
<i>Aizoon canariense</i>	67	55	0.0023	0.2746	NA	XS					Sm; At
<i>Bidens pilosa</i>	1	0	0.0000	0.0041	IN	XS					Sm
<i>Chamaecytisus proliferus</i>	1	100	0.0000	0.0041	CE				PF		At
<i>Descurainia bourgeauana</i>	661	65	0.0223	2.7090	CE					HM	At
<i>Lysimachia arvensis</i>	20	100	0.0007	0.0820	NA	XS	TW		PF		Sm
<i>Patellifolia patellaris</i>	15	33	0.0005	0.0615	NA	XS					Wt; Sp
<i>Portulaca granulatostellulata</i>	3	66	0.0001	0.0123	IN	XS					At
<i>Spergularia flaccida</i>	43	60.5	0.0015	0.1762	NA	XS	TW				Sp

Results from the GLM showed that the only statistically significant variable that explains the relative abundance of seeds per latrine was “plant species” ( $\chi^2_{22}= 181.97$ ;  $p < 0.001$ ), and the model explained 99% of the variation in the response variable. Specifically, *O. dillenii* was the most abundant species in the latrines ( $\beta = 0.23$ ;  $p = 0.0057$ ). No relationships were found between the seed size of plant species consumed and frequency of occurrence in the latrines analysed ( $R_s = 0.198$ ;  $p = 0.389$ ).

### *Seedling emergence*

A total of 921 intact seeds of 23 plant species were used in the germination experiment, 13 of which emerged, nine fleshy-fruited and four dry fruited plants (Table 3, Photo 5). More than 10% of seed emergence was recorded in *Bosea yervamora*, *R. crenulata*, *A. canariensis*, *O. dillenii*, *Juniperus cedrus* and *R. fruticosa*. *Chamaecytisus proliferus* and *Adenocarpus viscosus* also emerged although in a smaller percentage. Overall, seed emergence was relatively low ( $n = 49$  seeds; 5.32%). No significant differences were found in seed emergence between native (9.2%) and introduced (8.8%) fleshy-fruited plants ( $\chi^2_1 = 0.011$ ;  $p = 0.91$ ). In this seed germination experiment, we identified the emergence of a seed of cf. *Portulaca oleracea*.

**Table 3** Plant species sown during the germination experiments and percentage of emerged seeds

Species	Planted seeds	Seed emergence (%)	Fruit type
<i>Arbutus canariensis</i>	40	17.5	Fleshy
<i>Atriplex semibaccata</i>	5	0	Fleshy
<i>Bosea yervamora</i>	10	50	Fleshy
<i>Chenopodium nutans</i>	13	0	Fleshy
<i>Daphne gnidium</i>	12	8.3	Fleshy
<i>Ilex canariensis</i>	37	0	Fleshy
<i>Juniperus cedrus</i>	18	11.1	Fleshy
<i>Morella faya</i>	40	7.5	Fleshy
<i>Opuntia dillenii</i>	40	12.5	Fleshy
<i>Opuntia maxima</i>	2	0	Fleshy
<i>Plocama pendula</i>	8	0	Fleshy
<i>Prunus lusitanica</i>	27	0	Fleshy
<i>Rhamnus crenulata</i>	16	37.5	Fleshy
<i>Rosa canina</i>	40	0	Fleshy
<i>Rubia fruticosa</i>	9	11.1	Fleshy
<i>Rubus</i> spp.	41	2.4	Fleshy
<i>Withania aristata</i>	5	0	Fleshy
<i>Adenocarpus viscosus</i>	4	25	Dry
<i>Aizoon canariense</i>	29	3.45	Dry
<i>Chamaecytisus proliferus</i>	1	100	Dry
<i>Descurainia bourgeauana</i>	40	0	Dry
<i>Patellifolia patellaris</i>	5	0	Dry
<i>Spergula fallax</i>	26	3.85	Dry



**Photo 5.** Some of the species germinated during the experiment. A: *Opuntia dillenii*, B: *Rhamnus crenulata*  
C: *Morella faya*, and D: *Juniperus cedrus*.

## **Discussion**

This is the first study in which the ecological impacts of rabbits disrupting native seed dispersal systems are studied from a holistic perspective in any of the archipelagos where they were introduced. Our data indicate that rabbits in Tenerife are, in general, important disruptors of the native seed dispersal systems.

### *The consumption of fruits*

A higher number of seeds from endemic and native plant species were consumed compared to introduced ones (Table 2), coinciding with the pattern observed by Cubas et al. (2019) on the herbivory of this lagomorph in Tenerife. Despite the fact that the majority of seeds (73%) were dry fruits or from them, we could only identify nine species; this group of plants showed a great abundance. In general, dry seeds are smaller in size and more easily damaged due to their softer consistency than those of fleshy-fruited plants. It is generally assumed that large seeds tend to be dispersed by vertebrates, while small seeds tend to be abiotic-dispersed. However, Janzen's (1984) hypothesis: "the foliage is the fruit", suggests that endozoochory is a very important dispersal mechanism for small seeds when large herbivores feed on leaves and accidentally consume them. On the other hand, Larrinaga (2010) showed that the European rabbit actively selects small seeds. Despite the complexity to accurately quantify the number of seeds, due to destruction by rabbits during their mastication and digestion, the same pattern could occur in Tenerife, where rabbits consume mainly small fruits.

In the xerophytic scrub and the thermophilous woodland habitats, rabbits are mostly dispersing seeds from introduced species (*O. dillenii* and *F. carica*, respectively), whereas in the rest of the habitats the majority of the identified seeds dispersed corresponded with native and endemic plant species. This is probably linked to the significant impacts suffered by these two habitats, where the human populations are mostly settled in this archipelago and have introduced many species (Fernández-Palacios et al. 2008). The degraded state of the xerophytic scrub potentially facilitates the spread of exotic plant species, which may lead to a homogenisation of the environment. Therefore, plants such as *O. dillenii* are aggressive invasive species and occupy a large surface area of these dry areas rapidly, producing essential changes in the soil and vegetation (see Eldridge and Myers, 2001; Cubas et al. 2018). On islands where introduced rabbits were eradicated, there was an increase in the groundcover and abundance of native species in subsequent years (Olivera et al. 2010; Rita et al. 2022), but only when the seed banks are in a good conservation state, which is not possible several hundred years after their introduction (González-Mancebo et al. 2022).

In the native range of this lagomorph, such as the coastal dunes of Spain, rabbits disperse at least 10 plant species (5.7% of the species present) (Dellafiore et al. 2007). It has also been shown that in Dehesa (Mediterranean ecosystem type), endozoochory by rabbits and other herbivores plays an important role in the dynamics of plant communities (Malo and Suárez 1995). It has also been found to feed on juniper (*Juniperus phoenicea*

*ssp. turbinata*) in Doñana National Park (Spain), dispersing 38% of the intact seeds found in droppings (Muñoz-Reinoso 1993).

In other areas of the world where they have been introduced, the European rabbit has also been found to disperse plant species. On Robinson Crusoe Island, the endozoochorous dispersal of the exotic Opium poppy (*Papaver somniferum*) contributes to its expansion (Fernández and Sáiz, 2007).

### *The state of seeds after digestion and seedling germination*

Most of the 12 plant seed species identified that showed more than 75% of intact seeds were from fleshy-fruited plants. Damaged seeds found in faeces were related to the mastication and digestion processes (Nogales et al. 1995). Rabbits probably predate even more seeds than those we have found, since many seeds are destroyed and are impossible to quantify.

Among the identified seeds, intact seeds from introduced species were quantitatively higher than native ones. According to the environment, European rabbits deposited viable seeds in all five habitats studied. In mainland ecosystems, interactions between vertebrate dispersers and fleshy-fruited plants are not specialised but rather the sum of interacting species (Herrera, 2002). This network of non-specialised interactions probably benefits the fleshy-fruited plants by improving their germination and diversification, particularly germination timing (Fedriani and Delibes, 2009).



In general, the percentage of seed emergence for the majority of fleshy-fruited plant species in this work decreased when rabbits consumed them, compared to when they were eaten by the native seed dispersers (both lizards and birds) (Table 4). Of the 17 plant species included in the experiment, only the seeds of *B. yervamora* showed high values in their percentage of emergence when consumed by rabbits, but a similar value was also recorded when native birds dispersed the seeds. This negative germination effect and the fact that rabbits also produce a different spatial seed rain with respect to the native dispersers (lizards and birds) could have important ecological implications in the lower recruitment of native plants (Nogales et al. 1995; López-Darias and Nogales 2008; La Mantia et al. 2019).

Rabbits similarly affected the seed emergence of fleshy-fruited plants when comparing native and introduced plant species. In our case, the wide distribution of the invasive *O. dillenii* in the xeric lowland habitats of the Canaries is clearly facilitated by native and introduced vertebrates such as rabbits, since its hard-resistant seeds germinate after being consumed (Padrón et al. 2011). This fact highlights that this lagomorph can facilitate the dissemination of introduced plants and in some cases, this ecological interaction has been crucial in the establishment of exotic plants on some Mediterranean islands (Bourgeois et al. 2005). This is another potential example that introduced herbivores facilitate the settlement of exotic plants, enabling plant invasions and potentially an invasive meltdown effect (Simberloff and Holle 1999; Parker et al. 2006).

**Table 4** Comparison table of the main fleshy-fruited plant species included in the seed emergence experiment (in percentage), including the different frugivores and seed dispersers. Percentages in bold derive from secondary seed dispersal processes (see Padilla et al. 2012). Most data obtained from literature dealing with the Canary Islands

Plant species	Seed emergence (%)				
	Control	Lizard	Birds	Rabbits (Own data)	Reference
<i>Arbutus canariensis</i>	-	-	-	17.5	Own data
<i>Atriplex semibaccata</i>	-	-	-	0.0	Own data
<i>Bosea yerbamora</i>	48.2	14.3	≈57.0*	50	Padilla et al. (2012); González-Castro 2012*
<i>Chenopodium nutans</i>	-	-	<b>10.4</b>	0.0	Padilla et al. (2012)
<i>Daphne gnidium</i>	-	0.0	-	8.3	Own data
<i>Ilex canariensis</i>	0.0	-	2.5*	0.0	Nogales et al. (1999); Own data*
<i>Juniperus cedrus</i>	22.5	10.0	34.5	11.1	Rumeu et al. (2011)
<i>Morella faya</i>	28.6	28.0*	35.7	7.5	Nogales et al. (1999); Own data*
<i>Opuntia dillenii</i>	29.0	≈38.0	12.9*	12.5	Padrón et al. (2011); Nogales et al. (1999)*
<i>Opuntia maxima</i>	8.6	-	30.0	0.0	Nogales et al. (1999)
<i>Plocama pendula</i>	66.5	70.4**	52.0*	34.5	Nogales et al. (1995); Nogales et al. (1999)*; Valido 1999**
<i>Prunus lusitanica</i>	-	-	-	0.0	Own data
<i>Rhamnus crenulata</i>	49.6	43.0	<b>25</b>	37.5	Padilla et al. (2012)

<i>Rosa canina</i>	-	-	-	0.0	Own data
<i>Rubia fruticosa</i>	92.9	67.1	≈34.0	11.1	Valido and Nogales (1994); González-Castro 2012*
<i>Rubus</i> spp.	52.2	38.6	<b>11.1</b>	2.4	Padilla et al. (2012)
<i>Withania aristata</i>	28.6	55.7	≈41.0*	0.0	Valido and Nogales (1994); González-Castro 2012*

### *Concluding remarks and future avenues of research*

Rabbits disperse the seeds of 22 identified native and endemic species, indeed some of them (*B. yervamora*, *R. crenulata*, *A. canariensis*, *J. cedrus* and *R. fruticosa*) showed a seed emergence higher than 10% after being consumed by rabbits. Nevertheless, their recruitment does not depend on this lagomorph because it has not been linked to their evolutionary history, and these plants have their own legitimate (Nogales et al. 2016) and ecologically more efficient seed dispersers (Table 4). Furthermore, its role as an introduced herbivore in the Canary Islands is decisive, limiting the recruitment of native species and altering plant cover and composition, as well as promoting chemical changes in the soil (Cubas et al. 2019).

Our results show the European rabbit's potential for endozoochorous seed dispersal. Understanding this dispersal mechanism is critical when implementing control strategies to avoid introducing exotic fleshy-fruited plants onto oceanic islands (see Sáiz and Fernández 2007). However, it would be desirable that more studies of this type be carried out in other archipelagos where this species has been introduced. Its seed-disperser efficiency and effectiveness should also be compared with the native guilds of dispersers. Furthermore, other aspects such as the spatial seed rain, the fate of seedlings that they probably also consume, and their survival, would come closer to a complete study on their real ecological role.

Lastly, it is important to note that the ecological effects of non-native species combined with climate change on oceanic islands (e.g. the Canaries) compromise the conservation of oceanic islands' endemic biota. It is expected that at least in some insular

areas with high endemicity, rabbit population densities could increase and therefore their impacts on island vegetation (Bello-Rodríguez et al. 2021; Martín-Esquivel et al. 2021).

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