





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

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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 and 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.

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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; Global Invasive Species Database 2021). The European rabbit (*Oryctolagus cuniculus* L.), 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 (Soriquer 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; Delafiore 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 (IUCN), *O. cuniculus* has been catalogued as one of the 100 most dangerous invasive species on the planet (Lowe et al. 2004; GISD 2021).

On islands, this herbivore shows preference for seedlings, inhibiting the recruitment of many tree and shrub species (Cooke 2012; Irl et al. 2012; Cubas et al. 2018). 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; López-Darias and Nogales 2008).

In the Canary Islands, *O. cuniculus* was introduced in the fifteenth century, during the European conquest (De Abreu Galindo 1977). 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 (Nogales et al. 2006), 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, 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 (La Gomera Island), 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

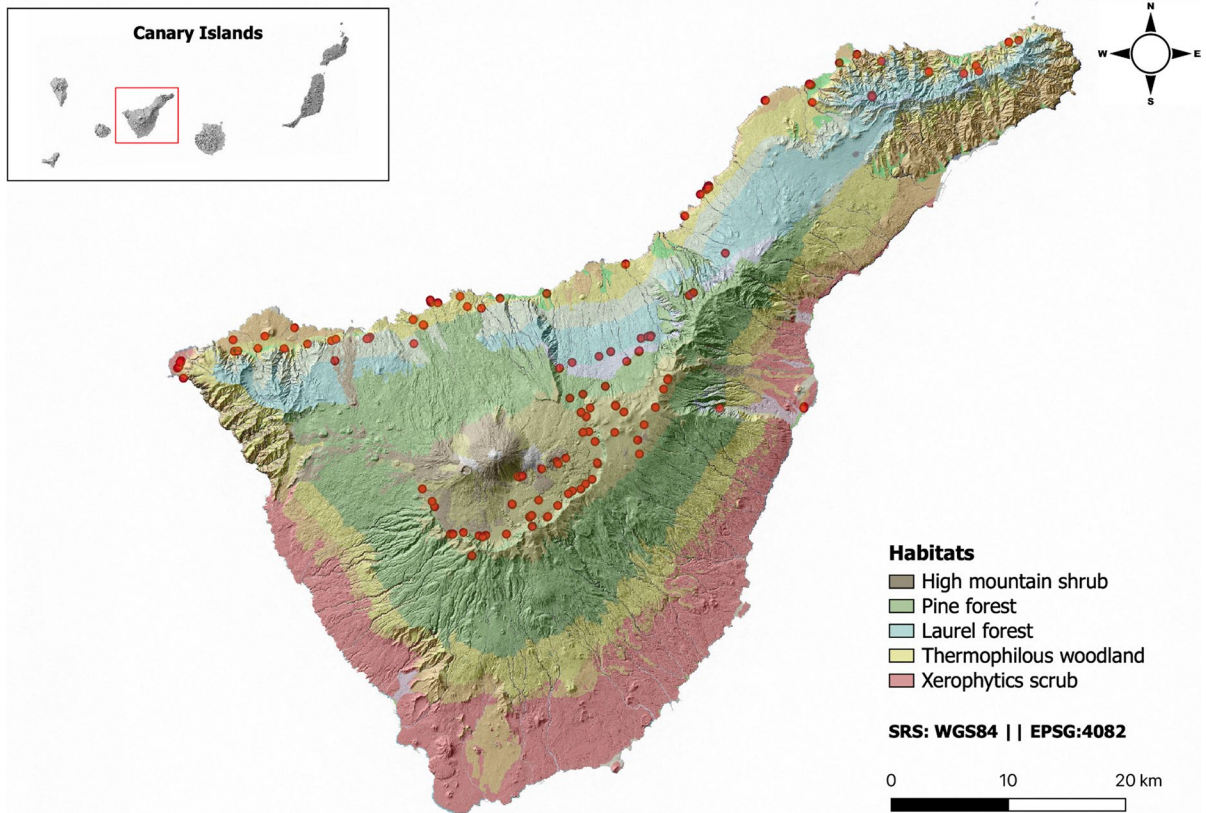


Fig. 1 Geographical location of the island of Tenerife with the five main habitats and sites of the transects with latrines of rabbits where droppings were collected (red points)

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 km² 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 north-east oriented slopes, from the coast to the summit: (1) coastal and xerophytic scrubs (≈ 0–200 m a.s.l., 19–21 °C, 50–200 mm annual rainfall), (2) thermophilous woodlands (≈ 200–400 m a.s.l., 15–19 °C, 250–400 mm), (3) laurel forests (≈ 400–1500 m a.s.l., 13.5–17.7 °C, 450–950 mm), (4) pine forest (≈ 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).

Procedures

A total of 600 random transects (120 per vegetation zone), 30×2 m each, were conducted from August 2020 to November 2021. These transects were located mostly 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 (darker colour) per latrine and transect, discarding the old droppings. All samples were labelled individually and georeferenced with a handheld GPS.

In the laboratory, faecal samples were analysed under a stereomicroscope (10× 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). We visually classified seeds as damaged or intact and measured their seed diameter with a digital calliper as a proxy of seed size. Taxonomy of plants, and the biogeographical status of each taxa, follows the checklist of the Biota of the Canary Islands (Arechavaleta et al. 2010; Gobierno de Canarias 2022).

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 also those unidentified, in a 4 cm² 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). Seed emergence was considered when any part of the seedling emerged at the soil surface (see Nogales et al. 2005).

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

Table 1 Faecal samples collected from latrines and droppings analysed in each vegetation zone per season

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

Wt Winter, Sp Spring, Sm Summer, At Autumn

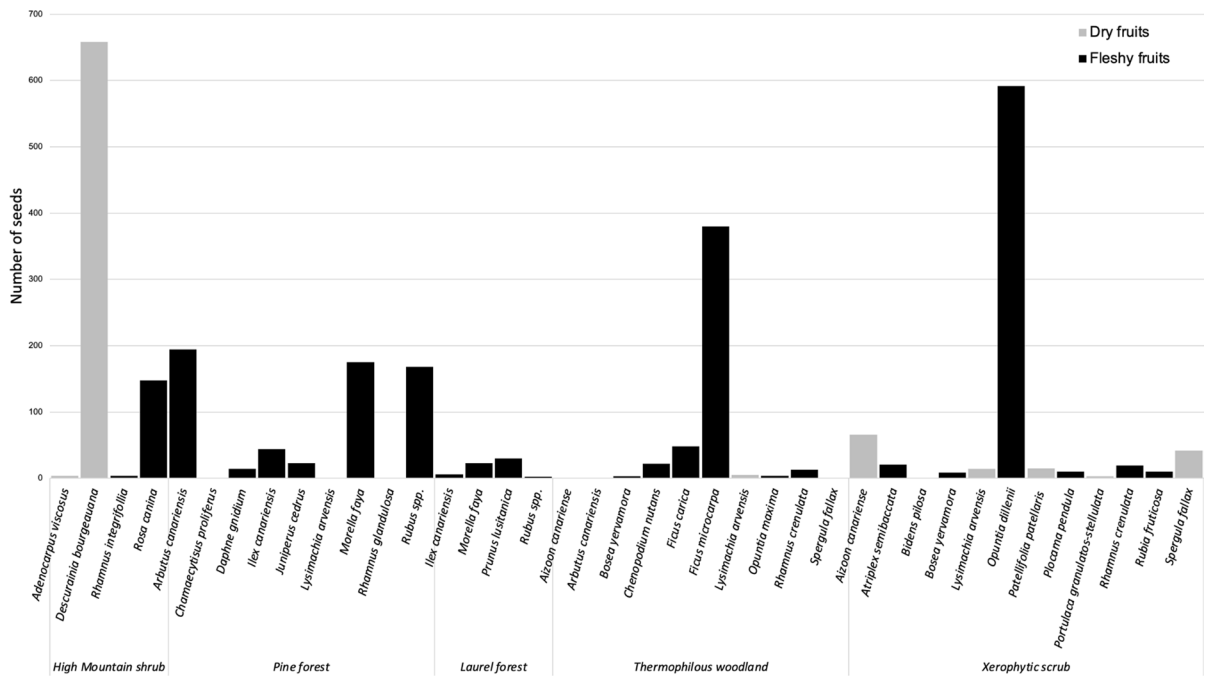


Fig. 2 Number of seeds of plant species identified from the rabbit latrines in each habitat on Tenerife

identified to specific levels (13 endemics, 8 natives, and 8 introduced by humans, Fig. 2). Most of the seed-types found in droppings were from plants that produce dry fruits ($n=49$; 67%) and only 24 (33%) of them belonged to fleshy-fruited plants. Of the identified seeds to species level, twenty were those of fleshy-fruited plants and the others ($n=9$) to dry fruits (Fig. 3). 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). A total of 1973 intact seeds (82.3%) corresponded to those identified species (1448 seeds-73% of fleshy fruited plants and 525 seeds-27% of dry fruits). 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). Moreover, if we analyse the number of seeds of endemics and non-endemic plants, 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 and 75% (e.g. *F. microcarpa*, *Ilex canariensis* and *Rubia fruticososa*) 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).

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 ($\beta = 0.23$; $p = 0.0057$).

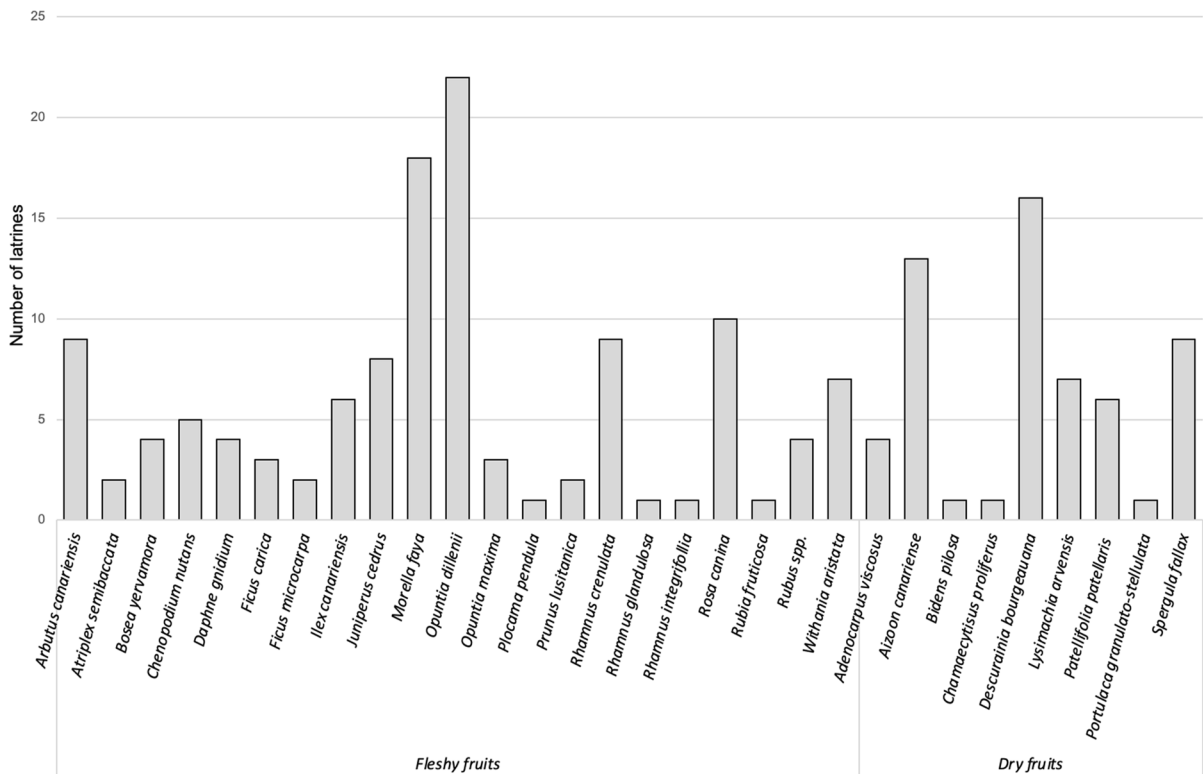


Fig. 3 Frequency of occurrence of the identified plant species in latrines of rabbits on Tenerife

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, 9 fleshy-fruited and 4 dry fruited plants (Table 3). 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 ($\chi^2_1 = 0.011$; $p = 0.91$).

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 that most of the seed-types found in droppings were from plants that produce dry fruits ($n = 49$; 67%), we could only identify 9 species. 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

Table 2 Analysis of fleshy (A) and dry (B) seeds per rabbit dropping and latrine on Tenerife

Species (Fleshy fruits)	Total seeds	Intact seeds (%)	Total seeds/number of droppings analysed	Total seeds/number of latrines analysed	Seed diameter (mm)	Biogeographical range		Habitats				Season	
						Average	Range	XS	TW	LF	PF		HM
A													
<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	3.80	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 fruticososa</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	Bio-geographic 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		

Table 2 (continued)

Species (Dry fruits)	Total seeds	Intact seeds (%)	Total seeds/ number of droppings analysed	Total seeds/ number of latrines analysed	Bio-geographic range	Habitat				Season
						XS	TW	LF	PF	
<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 granulatosetellulata</i>	3	66	0.0001	0.0123	IN	XS				At
<i>Spergula fallax</i>	43	60.5	0.0015	0.1762	NA	XS	TW			Sp

A = Fleshy fruits and B = Dry fruits

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

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

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).

In other insular 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). 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 in prep).

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).

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

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

Plant species	Seed emergence (%)				
	Control	Lizard	Birds	Rabbits (Own data)	References
<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>	–	–	10.4	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	25	37.5	Padilla et al. (2012)
<i>Rosa canina</i>	–	–	–	0.0	Own data
<i>Rubia fruticosus</i>	92.9	67.1	≈34.0	11.1	Valido and Nogales (1994), González-Castro (2012)*
<i>Rubus</i> spp.	52.2	38.6	11.1	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)*

Percentages in bold derive from secondary seed dispersal processes (see Padilla et al. 2012). Most data obtained from literature dealing with the Canary Islands

Data with asterisks correspond to the article in the same line from which the information was obtained

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 (for more information about these habitats, see Del Arco Aguilar and Rodríguez Delgado 2018). 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).

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 Fernández and Sáiz 2007). However, it would be desirable that more studies of this type be carried out in other archipelagos where this species has been introduced.

Concluding remarks

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. fruticososa*) showed a seed emergence higher than 10% after being consumed. 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). 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 endemism, 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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References

- Archavaleta M, Rodríguez S, Zurita N, García A (coord.) 2010 Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009. Gobierno de Canarias
- Arévalo JR, Afonso L, Naranjo A, Salas M (2010) Invasion of the Gran Canaria ravines ecosystems (Canary Islands) by the exotic species *Acacia farnesiana*. *Plant Ecol* 206:185–193
- Atlas Digital de Semillas de las Islas Canarias (2021) Atlas Digital de Semillas de las Islas Canarias. <https://www.atlasdesemillasdec Canarias.org/>. Accessed 20 April 22
- Bello-Rodríguez V, Mateo RG, Pellissier L, Cubas J, Cooke B, González-Mancebo JM (2021) Forecast increase in invasive rabbit spread into ecosystems of an oceanic island (Tenerife) under climate change. *Ecol Appl* 31:e02206
- Bourgeois K, Suehs CM, Vidal E, Médail F (2005) Invasional meltdown potential: facilitation between introduced plants and mammals on French Mediterranean islands. *Écoscience* 12:248–256
- Bowen L, Vuren DV (1997) Insular endemic plants lack defenses against herbivores. *Conserv Biol* 11:1249–1254
- Carrion V, Donlan CJ, Campbell KJ, 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:e18835
- Caujapé-Castells J, Tye A, Crawford DJ, Santos-Guerra A, Sakai A, Beaver K, Lobin W, Florens FBV, Moura M, Jardim R, Gómes I, Kueffer C (2010) Conservation of oceanic island floras: present and future global challenges. *Perspect Plant Ecol Evol Syst* 12:107–129
- Cooke BD (2012) Rabbits: Manageable environmental pests or participants in new Australian ecosystems? *Wildl Res* 39:279–289
- Courchamp F, Chapuis JL, Pascal M (2003) Mammal invaders on islands: Impact, control and control impact. *Biol Rev* 78:347–383
- Cubas J, Martín-Esquivel JL, Del Arco M, González Mancebo JM (2017) El conejo europeo como ingeniero del paisaje en la alta montaña canaria. *Conserv Veg* 21:14–17
- Cubas J, Martín-Esquivel JL, Nogales M, Irl SDH, Hernández-Hernández R, López-Darías M, Marrero-Gómez M, Del Arco M, González-Mancebo JM (2018) Contrasting effects of invasive rabbits on endemic plants driving vegetation change in a subtropical alpine insular environment. *Biol Invas* 20:793–807
- Cubas J, Irl SDH, Villafuerte R, Bello-Rodríguez V, Rodríguez-Luengo JL, Del Arco M, Martín-Esquivel JL, González-Mancebo JM (2019) Endemic plant species are more palatable to introduced herbivores than non-endemics. *Proc R Soc Biol Sci* 286:20190136
- Cubas J, Kluge J, Bello-Rodríguez V, Del Arco M, Cooke B, González-Mancebo JM (2021) Can habitat type predict the abundance of the European rabbits on oceanic islands? *Commun Ecol* 22:93–105
- De Abreu Galindo J (1977) Historia de la conquista de las siete islas de Canarias. Goya Ediciones. Santa Cruz de Tenerife, España
- Del Arco Aguilar M, Rodríguez Delgado O (2018) Vegetation of the Canary Islands. *Plant and vegetation*, vol. 16. Springer International Publishing, Cham
- Delibes-Mateos M, Delibes M, Ferreras P, Villafuerte R (2008) Key role of European rabbits in the conservation of the Western Mediterranean basin hotspot. *Conserv Biol* 22:1106–1117
- Delibes-Mateos M, Gálvez-Bravo L (2009) El papel del conejo como especie clave multifuncional en el ecosistema mediterráneo de la Península Ibérica. *Ecosistemas* 18:14–25
- Dellafiore CM, Muñoz-Vallés S, Gallego-Fernández JB (2006) Rabbits (*Oryctolagus cuniculus*) as dispersers of *Retama monosperma* (L.) Bois seeds in a Coastal Dune System. *Écoscience* 13:5–10
- Dellafiore CM, Gallego-Fernández JB, Muñoz-Vallés S (2007) The contribution of endozoochory to the colonization and vegetation composition of recently formed sand coastal dunes. *Res Lett Ecol* 1:1–3
- Dellafiore CM, Gallego-Fernández JB, Muñoz-Vallés S (2010) The rabbit (*Oryctolagus cuniculus*) as a seed disperser in a coastal dune system. *Plant Ecol* 206:251–261
- Eldridge DJ, Myers CA (2001) The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. *J Arid Environ* 47:325–337
- Fedriani JM, Delibes M (2009) Functional diversity in fruit-frugivore interactions: a field experiment with Mediterranean mammals. *Ecography* 32:983–992

- Fernández A, Sáiz F (2007) The European rabbit (*Oryctolagus cuniculus* L.) as seed disperser of the invasive opium poppy (*Papaver somniferum* L.) in Robinson Crusoe Island. Chile Mastozool Neotrop 14:19–27
- Fernández-Palacios JM, Otto R, Delgado JD, Arévalo JR, Naranjo A, González-Artiles F, Morici C, Barone R (2008) Los bosques termófilos de Canarias. Cabildo Insular de Tenerife. Santa Cruz de Tenerife
- Flux JC, Fullagar P (1992) World distribution of the rabbit *Oryctolagus cuniculus* on islands. Mamm Rev 22:151–205
- Gálvez-Bravo L (2008) El conejo europeo (*Oryctolagus cuniculus*) como especie ingeniera de ecosistemas. PhD Thesis. Universidad de Alcalá de Henares
- Global Invasive Species Database (2021) *Species profile: Oryctolagus cuniculus* <http://www.iucngisd.org/gisd/speciesname/Oryctolagus+cuniculus>. Accessed 24 Nov 2021
- Gobierno de Canarias (2022) Banco de datos de biodiversidad de Canarias. www.biodiversidadcanarias.es. Accessed 05 July 2022
- González-Castro A (2012) Estructura y funcionamiento de sistemas de dispersión de semillas en un ecosistema mediterráneo en condiciones de insularidad: el bosque termófilo de Canarias. PhD Thesis. Universidad de La Laguna
- González-Mancebo JM, Cubas J, Bello-Rodríguez B, Del Arco M (2019) Cinco siglos de invasión del conejo europeo (*Oryctolagus cuniculus* L.) en ecosistemas árido-secos de Tenerife. Vieraea 46:597–624
- Guillou H, Carracedo JC, Paris R, Pérez Torrado JP (2004) Implications for the early shield-stage evolution of Tenerife from K/Ar ages and magnetic stratigraphy. Earth Planet Sci Lett 222:599–614
- Herrera CM (2002) Seed dispersal by vertebrates. In: Herrera CM, Pellmyr O (eds) Plant-animal interactions: an evolutionary approach. Blackwell, Oxford, pp 186–208
- Irl SDH, Steinbauer MJ, Babel W, Beierkuhnlein C, Blume-Werry G, Messinger J, Palomares Martínez Á, Strohmeyer S, Jentsch A (2012) An 11-yr enclosure experiment in a high-elevation island ecosystem: introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics. J Vegetation Sci 23:1114–1125
- Janzen DH (1984) Dispersal of small seeds by big herbivores: foliage is the fruit. Am Nat 123:338–353
- La Mantia T, Rühl J, Massa B, Pipitone S, Lo Verde G, Bueno RS (2019) Vertebrate-mediated seed rain and artificial perches contribute to overcome seed dispersal limitation in a Mediterranean old field. Restor Ecol 27:1393–1400
- Larrinaga AR (2010) Rabbits (*Oryctolagus cuniculus*) select small seeds when feeding on the fruits of *Corema album*. Ecol Res 25:245–249
- López-Darias M, Nogales M (2008) Effects of the invasive Barbary ground squirrel (*Atlantoxerus getulus*) on seed dispersal systems of insular xeric environments. J Arid Environ 72:926–939
- Lowe S, Browne M, Boudjelas S, De Poorter M (Eds.) (2004) 100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database. In: The Invasive Species Specialist Group (ISSG) a specialist group of the species Survival Commission (SSC) of the World Conservation Union (IUCN). New Zealand: 12
- Malo JE, Suárez F (1995) Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia 104:246–255
- Mancilla-Leytón JM, González-Redondo P, Martín Vicente A (2013) Effects of rabbit gut passage on seed retrieval and germination of three shrub species. Basic Appl Ecol 14:585–592
- Marrero P, Martín C (1999) Dieta primaveral del conejo (*Oryctolagus cuniculus* L.) en Alegranza, Islas Canarias (Lagomorpha Leporidae). Vieraea 27:105–113
- Marrero P, Martín C (2000) Spring food preferences of rabbits (*Oryctolagus cuniculus* L., 1758) on the Islet of Alegranza (Canarian Archipelago). Z Säugetier 65:246–250
- Martín A, Nogales M, Alonso M, Rodríguez B, De León L (2002) Restauración de los Islotes y del Risco de Famara (Lanzarote). Universidad de La Laguna, Departamento de Biología Animal (Zoología)
- Martín C, Marrero P, Nogales M (2003) Seasonal variation in the diet of wild rabbits *Oryctolagus cuniculus* on a semi-arid Atlantic island (Alegranza, Canarian Archipelago). Acta Theriol 48:399–410
- Martín-Esquível JL, Marrero-Gómez MV, González Mancebo JM (2021) Efectos del cambio climático en la vegetación de la alta montaña de Tenerife. Ecosistemas 30:2189
- Marzol Jaén, MV (1988) La lluvia, un recurso natural para Canarias. Caja General de Ahorros de Canarias. Santa Cruz de Tenerife
- McNeely JA, Mooney HA, Neville LE, Schei P, Waage LK (2001) Global strategy on invasive alien species. IUCN, Gland, Switzerland and Cambridge
- Muñoz-Reinoso JC, (1993) Consumo de gálbulos de sabinia (*Juniperus phoenicea* ssp. *turbinata* Guss, 1891) y dispersión de semillas por el conejo (*Oryctolagus cuniculus* L.) en el Parque Nacional de Doñana. Doñ Act Vert 20:49–58
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858
- Nogales M, Valido A, Medina F (1995) Frugivory of *Plocama pendula* (Rubiaceae) by the Rabbit (*Oryctolagus cuniculus*) in xerophytic zones of Tenerife (Canary Islands). Acta Ecol 16:585–591
- Nogales M, Hernández EC, Valdés F (1999) Seed dispersal by Common Ravens *Corvus corax* among island habitats (Canarian Archipelago). Écoscience 6:56–61
- Nogales M, Nieves C, Illera JC, Padilla DP, Traveset A (2005) Effect of native and alien vertebrate frugivores on seed viability and germination patterns of *Rubia fruticosa* (Rubiaceae) in the eastern Canary Islands. Funct Ecol 19:429–436
- Nogales M, Rodríguez-Luengo JL, Marrero P (2006) Ecological effects and distribution of invasive non-native mammals on the Canary Islands. Mammal Rev 36:49–65
- Nogales M, Heleno RH, Rumeu B, González-Castro A, Traveset A, Vargas P, Olesen JM (2016) Seed-dispersal networks on the Canaries and the Galápagos archipelagos: interaction modules as biogeographical entities. Glob Ecol Biogeogr 25:912–922
- Olivera P, Menezes D, Trout R, Buckle A, Geraldine P, Jesus J (2010) Successful eradication of the European rabbit (*Oryctolagus cuniculus*) and house mouse (*Mus musculus*) from the island of Selvagem Grande

- (Macaronesian archipelago), in the Eastern Atlantic. *Integr Zool* 5:70–83
- Padilla DP, González-Castro A, Nogales M (2012) Significance and extent of secondary seed dispersal by predatory birds on oceanic islands: the case of the Canary archipelago. *J Ecol* 100:416–427
- Padrón B, Nogales M, Traveset A, Vilà M, Martínez-Abraín A, Padilla DP, Marrero P (2011) Integration of invasive *Opuntia* spp. by native and exotic seed dispersers in the Mediterranean area and the Canary Islands. *Biol Invas* 13:831–844
- Parada-Díaz J, Cubas J, Del Arco M, Fernández-López Á, González-Mancebo JM (2022) Changing the landscape: Short-term disruption of recruitment, height growth and flowering of endemic plants on Macaronesian heathlands by invasive alien rabbits. *Biol Conserv* 272:109596
- Parker JD, Burkepille DE, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459–1461
- Paulay G (1994) Biodiversity on oceanic islands: Its origin and extinction. *Amer Zool* 34:134–144
- R Core Team (2022) R: a language and environment for statistical computing. Vienna, Austria. <https://www.R-project.org/>
- Rita J, Capó M, Cursach J (2022) Eradication of rabbits from islets is essential for conservation of microinsular vegetation and narrow endangered flora: the case of *Medicago citrina* (Fabaceae) in s'Espartar islet (Balearic Islands, Western Mediterranean Basin). *Biod Conserv* 31:779–796
- Rodríguez A, Nogales M, Nieves C (2007) Germination responses of the *Rubia fruticosa* Ait. Seed dispersal system in different experimental seasons. *Afr J Ecol* 45:361–364
- Rumeu B, Elias RB, Padilla DP, Melo C, Nogales M (2011) Differential seed dispersal systems of endemic junipers in two oceanic Macaronesian archipelagos: the influence of biogeographic and biological characteristics. *Plant Ecol* 212:911–921
- Simberloff D, Holle BV (1999) Positive interactions of non-indigenous species: Invasional meltdown? *Biol Invas* 1:21–23
- Soriguer RC (1988) Alimentación del conejo (*Oryctolagus cuniculus* L. 1758) en Doñana, SO. España Doñana Acta Vert 15:145–150
- Spatz DR, Zilliacus KM, Holmes ND, Butchart SH, Genovesi P, Ceballos G, Tershy BR, Croll DA (2017) Globally threatened vertebrates on islands with invasive species. *Sci Adv* 3:e1603080
- Thompson HV, King CM (1994) The European rabbit: the history and biology of a successful colonizer. Oxford University Press, Oxford
- Valido A (1999) Ecología de la dispersión de semillas por los lagartos endémicos canarios (g. *Gallotia*, Lacertidae). PhD Thesis, University of La Laguna
- Valido A, Nogales M (1994) Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70:403–411

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