Seed dispersal by common ravens *Corvus corax* among island habitats (Canarian Archipelago)¹

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Abstract: The role of the common raven (*Corvus corax*; Corvidae) as a seed dispersal agent for plants in the Canary Islands was studied by analysing 2672 pellets collected from all islands of the archipelago. Seeds of 16 species of phanerogams were found (four endemic to the Canaries, three endemic to the Macaronesian islands, six not endemic, and three introduced by man). Vegetation in this archipelago is highly structured according to altitude creating different types of macrohabitats. The quality of the transport of seeds between habitats was evaluated in a preliminary way by making use of the very high fidelity of the plant species to particular macrohabitats. Of the 102 580 potentially fertile seeds (excluding the other 51 061 infertile *Ficus carica* seeds) transported by common ravens, 76.5% were regurgitated in theoretically suitable habitat while the remaining 23.5% were taken to habitats that were not appropriate for the establishment. Common ravens improved germination of six species, whereas an opposite effect was observed for three others. The percentage of viable seeds did not differ for any species between pellet seeds and seeds collected directly from the plants. Considering results from germination and viability experiments and macrohabitat patterns of dispersal, the common raven seems to be an important disperser for nine plant species: *Lycium intricatum* (Solanaceae), *Opuntia ficus-indica* (Cactaceae), *Rubia fruticosa* and *Plocama pendula* (Rubiaceae), *Juniperus turbinata* and *J. cedrus* (Cupressaceae), *Phoenix canariensis* (Arecaceae), *Asparagus pastorianus* (Liliaceae), and *Myrica faya* (Myricaceae).

Keywords: *Corvus corax*, seed dispersal, viability, germination, endemic and native Canarian plants, insular habitats.

Résumé: Nous avons étudié le rôle du grand corbeau, *Corvus corax* (Corvidae), comme agent de dissémination des graines des espèces de la flore des Îles Canaries. Pour ce faire, 2 672 pelotes de régurgitation récoltées sur les îles de l'archipel ont été analysées. Les graines de 16 espèces de phanérogames ont été identifiées, soit quatre espèces endémiques des îles Canaries, trois espèces endémiques des îles de la Macaronésie, six espèces non endémiques et trois espèces introduites. La végétation de l'archipel est principalement structurée en fonction de l'altitude, ce qui résulte en différents types de macrohabitats. La qualité du transport des graines entre les habitats a été évaluée de façon préliminaire en considérant la très haute fidélité des espèces végétales à certains macro-habitats. Des 102 580 graines potentiellement fertiles transportées par les corbeaux (excluant 51 061 graines non fertiles de *Ficus carica*), 76,5 % ont été régurgitées dans des habitats théoriquement favorables, alors que les autres 23,5 % ont été transportées vers des habitats inappropriés. Les corbeaux augmentent la germination des graines de six espèces, alors qu'ils inhibent celle de trois autres. Le pourcentage de viabilité n'est pas significativement différent entre les graines provenant des pelotes de régurgitation et celles récoltées directement sur les plantes, pour quelque espèce que ce soit. Si on prend en considération les résultats des tests de germination et de viabilité, de même que les patrons de dissémination au niveau des macro-habitats, le grand corbeau semble être un agent de dissémination important pour neuf espèces de plantes : *Lycium intricatum* (Solanaceae), *Opuntia ficus-indica* (Cactaceae), *Rubia fruticosa* et *Plocama pendula* (Rubiaceae), *Juniperus turbinata* et *J. cedrus* (Cupressaceae), *Phoenix canariensis* (Arecaceae), *Asparagus pastorianus* (Liliaceae) et *Myrica faya* (Myricaceae).

Mots-clés: *Corvus corax*, dissémination de graines, germination, habitats insulaires, plantes endémiques et plantes indigènes des îles Canaries, viabilité.

Introduction

The common raven (*Corvus corax* L.; Corvidae) is markedly omnivorous through most of its range (Heinrich, 1989; Nogales & Hernández, 1997), and birds from different areas show qualitatively similar diets, although there are considerable quantitative differences (Nogales & Hernández, 1997). While diets in continental environments are dominated by vertebrates throughout the year, common ravens on certain subtropical oceanic islands (e.g., Canary Islands) include much wild fruit in their diet (Nogales & Hernández, 1994). This apparent broadening of trophic niche is a well-documented phenomenon in island birds (Grant, 1965; McArthur, Diamond & Karr, 1972).

The role of common ravens as seed dispersers in island ecosystems has been mentioned anecdotally (Holmboe, 1914; Ridley 1930; Barquín, Nogales & Wildpret, 1986), but little quantitative data exist. A study of seed dispersal by common ravens in island ecosystems can provide valuable new insight into dispersal for several reasons. On islands with important altitudinal differences, such as the Canaries, the vegetation is highly structured, creating different types of macrohabitats (Ceballos & Ortuño, 1951; Figure 1), and ravens readily move between these macrohabitats, allowing a study of large-scale seed movement. In contrast, most studies address dispersal effectiveness at the microhabitat level (Murray, 1988; Schupp, 1993; Ellison *et al.*, 1993). Additionally, the common raven is a generalist

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species of large size (weight *ca.* 800 to 1000 g), whereas most previous studies have dealt with small or medium-sized birds (see Moermond & Denslow, 1985; Snow & Snow, 1988).

Common Ravens inhabit all the islands with an estimated population of around 600 breeding pairs (Nogales, 1992). According to palentological records, it has been present and abundant in the Canaries for at least 2000 years (Alcover & Florit, 1989).

The present study attempts to show: *i*) the importance of seed dispersal by common ravens in the Canaries, *ii*) the effects of common raven gut passage on the viability and germination of seeds, *iii*) the reliability of delivering seeds to a macrohabitat appropriate for plant establishment.

Study area

The Canary Archipelago is of volcanic origin and lies in the Atlantic Ocean about 100 km (at its nearest point) from the African continent. The highest point is on Tenerife (Pico Teide: 3718 m a.s.l.), while the lowest island, Lanzarote, reaches only 671 m a.s.l. The largest island, Tenerife, is 2036 km² and the smallest, El Hierro, is 278 km². The climate on the Canaries varies distinctly with altitude. Mean temperature and annual precipitation range from about 21°C and 100 to 300 mm, respectively, in the coastal zone to about 9°C and 500 to 800 mm, respectively, in the mountain zone. Longitude also plays an important role in climate variation. The eastern islands closest to Africa (Lanzarote and Fuerteventura) are low in altitude and highly influenced by dry winds from the Sahara Desert. Here vegetation is characterized by xerophytic shrubs that only occur in lowlands of the higher central and western islands of the Canaries (Gran Canaria, Tenerife, La Gomera, La Palma, and El Hierro). These larger islands, however, have highly structured forest zones distributed basically as a function of altitude and orientation (Figure 1).

In the upper part of the xerophytic shrub, there are remains of a transition forest that was altitudinally located between the xerophytic shrub and the laurel forest (Figure 1). This macrohabitat, composed of species such as *Juniperus turbinata* L. and *Phoenix canariensis* Chab., has been drastically reduced due to human activities. The dense evergreen laurel forest found on the northern sides of larger islands consists of nearly 20 species of trees and shrubs. Above the laurel forest and xerophytic shrub is a monospecific pine forest of the endemic *Pinus canariensis* Chr. Sm. ex DC. in Buch forming an open, dry woodland. The vegetation of the highest parts is characterized by a sparse shrub of leguminous plants.

The flora of the Canaries has affinities with those of the archipelagoes of the Azores, Madeira, Salvages, and Cape Verde, and all these have been grouped into the so-called Macaronesian Islands. A large proportion of the floristic elements seem to have their origin in the Tertiary flora (especially that of the Pliocene and Miocene) which occupied the regions surrounding the Tethys Sea, primarily in the Mediterranean basin and North Africa (Bramwell, 1974).

Material and methods

Seeds were obtained from 2672 common raven regurgitation pellets collected on the seven main islands (Lanzarote: 248, Fuerteventura: 296, Gran Canaria: 491, Tenerife: 69, La Gomera: 352, La Palma: 13, El Hierro: 1032) and islets (Lobos: 40, La Graciosa: 69, Alegranza: 30, Montaña Clara: 28, Roque del Este: 4). Sample size of pellets are clearly biased among islands due to the fact that we stayed about a week on most of the different islands (total: 62 days) during the summer (July, August, and September) of 1986 and 1987, except El Hierro. On this island we spent 209 days of fieldwork during 1986 and 1987. Furthermore, El Hierro harbors a high population of common ravens, which has been estimated at 99 to 120 breeding pairs, the second highest known density in the species' entire distributional range (Nogales, 1994). Judging by the rapid disintegration of pellets over winter, the material collected during summer visits was probably produced in spring and summer, coinciding with fruiting of most plant species that the common raven eats in the Canaries (Nogales & Hernández, 1994).

In order to test the effect of regurgitation from the digestive tract of the common raven on seed germination, regurgitated seeds were sown in a standard substrate (lapilli, turf, and forest soil). This experiment was performed in a greenhouse every day for three months (90 days), until no further germination was detected. The seeds were watered every two days and the night-day light period condition was that which is naturally found in the study area. There was no influence of germinated seeds on subsequent germination because each seed was planted in an independent compartment. Germination was compared to that of control seeds of the same species which were randomly collected from about 20 plants in one locality. Sample sizes were 70 seeds in most cases (see Valido & Nogales [1994] for more information on the germination method). Since germination of seeds from pellets varied extremely, we also performed a comparison of viability of randomly selected seeds from pellets and seeds from plants ($N = 70$) with the 2, 3, 5 triphenyl tetrazolium test (Scharpf, 1970). We applied G-tests for studying possible statistical differences of both seed treatments (ravens and plants) in the germination and viability experiments.

The effect of transport of seeds by the common raven between macrohabitats was evaluated by comparing the potential ecological possibilities for establishment provided by the habitats where the seeds were regurgitated with those of the most probable typical habitat. All the plant species consumed by common ravens show high fidelity to particular macrohabitats (Rivas-Martínez, 1983; Bramwell & Bramwell, 1990). We recorded the habitat and the site where the pellets were collected and calculated the number of seeds deposited in adequate *versus* inadequate macrohabitats. The establishment of new plants also depends on factors such as seed predation, differential germination and microclimate, (Van der Pijl, 1982) that have not been considered in the present study. We can, however, assess a measure of effectiveness of dispersal (*sensu* Schupp 1993) at a large geographic scale: the proportion of a population's seeds that are dispersed into an unsuitable macrohabitat.

FIGURE 1. Altitudinal distribution of the main macrohabitats of the Canary Islands, and ecological implications of seed dispersal by common ravens in the various islands. (+): 'horizontal' dispersal in which the seeds remain in the same habitat. (-): 'vertical' dispersal in which propagules are displaced into different habitats. Central and western islands: Gran Canaria, Tenerife, La Gomera, La Palma, and El Hierro. Eastern islands: Lanzarote and Fuerteventura.

Results

A total of 153 641 seeds of 16 species were recovered from regurgitated pellets and 73.4% contained at least one seed. Of the 16 species of phanerogams represented in the pellets, seven (43.8%) were endemic to the Canaries or the Macaronesian islands (four and three, respectively), six species (37.4%) were native but not endemic, and another three species (18.8%) have been introduced by humans (Table I). The fruits consumed were highly diverse in form and size, with mean diameters varying from 49.6 mm (*Opuntia ficus-indica*) to 3.5 mm (*Plocama pendula*).

The most common seed was *Opuntia ficus-indica* which has been introduced (Table II). *Ficus carica* had the second largest number of seeds in the pellets ($N = 51\ 061$).

Because it is infertile in the Canaries, it is not considered further. Among the native plants, *Rubia fruticosa* showed the largest representation. The species with the highest number of seeds in a single pellet ($N = 980$) was *F. carica*.

Common ravens significantly improved germination of six species (Table II). However, an opposite effect was observed for three others and there were no significant differences in the other four. These germination results were obtained by performing 13 independent tests, but this method may increase the probability of finding a difference by chance. In order to reduce this effect, we used a more conservative sequential Bonferroni technique proposed by Rice (1989). In this case, only three species (*Phoenix canariensis*, *Opuntia dillenii*, and *O. ficus-indica*) showed improved germination and two species showed a reduced

TABLE I. Characteristics of the fruits of the main species dispersed by common ravens in the Canaries. Biogeography range = CE: Canary endemic taxon, ME: Macaronesian endemic taxon, NNE: native, non-endemic taxon, TIH: taxon introduced by humans; Typical habitats = XS: Xerophytic shrub, LF: Laurel forest, PF: Pine forest, HM: High mountain. Plant species = Apas: *Asparagus pastorianus* Webb et Berth. (Liliaceae), Lint: *Lycium intricatum* Boiss. (Solanaceae), Ppen: *Plocama pendula* Ait. (Rubiaceae), Rfru: *Rubia fruticosa* Ait. (Rubiaceae), Jced: *Juniperus cedrus* Webb et Berth. (Cupressaceae), Jtur: *Juniperus turbinata* L. (Cupressaceae), Phocan: *Phoenix canariensis* Chab. (Arecaceae), Fcar: *Ficus carica* L. (Moraceae), Odill: *Opuntia dillenii* (Ker-Gawl.) Haw. (Cactaceae), Ofic: *Opuntia ficus-indica* (L.) Mill. (Cactaceae), Vmoc: *Visnea mocanera* L. fil. (Theaceae), Mfay: *Myrica faya* Ait. (Myricaceae), Ican: *Ilex canariensis* Poir. (Aquifoliaceae), Lazo: *Laurus azorica* (Seub.) Franco (Lauraceae), and Pincan: *Pinus canariensis* Chr. Sm. ex DC. in Buch (Pinaceae)

Species	Color	Fruit type	Bioge. range	Length (mm)	Diameter (mm)	Fresh weight (g)	Dry weight (g)	% Water	Mean number of seeds/fruit	Individual seed weight (mg)	Number of fruits studied	Typical habitat
Apas	translucent	berry	NNE	20.0	7.1	0.185	0.076	58.92	1.00	32.70	40	XS
Lint	red	berry	NNE	7.4	4.9	-	-	-	6.50	3.10	20	XS
Ppen	translucent	berry	CE	3.2	3.5	0.027	0.008	70.24	2.40	0.70	47	XS
Rfru	translucent	berry	ME	7.5	5.6	0.200	0.037	81.50	1.40	8.20	40	XS
Jced	brown	berry	CE	10.5	11.7	0.650	0.480	26.15	1.10	90.0	40	HM
Jtur	brown	berry	NNE	11.9	12.6	0.960	0.880	8.33	6.40	57.00	40	XS
Phocan	yellow	drupe	CE	18.7	11.8	1.017	0.598	40.20	1.00	340.0	24	XS
Fcar	black	siconium	TIH	33.2	38.0	28.74	6.520	77.31	243.60	1.10	15	XS
Odill	purple	berry	TIH	45.6	34.6	30.37	6.250	80.00	89.60	36.90	19	XS
Ofic	red	berry	TIH	65.2	49.6	71.10	13.90	80.40	184.20	18.00	5	XS
Vmoc	black	capsule	ME	9.6	7.9	0.260	0.160	38.46	1.00	37.00	51	LF
Mfay	black	drupe	NNE	8.6	8.7	0.400	0.100	74.75	1.00	29.00	30	LF
Ican	red	drupe	ME	12.6	13.0	1.420	0.530	62.67	4.70	35.00	30	LF
Lazo	black	drupe	NNE	17.0	12.8	1.611	0.916	43.47	1.00	611.90	40	LF
Pincan	black	-	CE	12.3	6.8	0.130	0.110	9.78	-	-	30	PF

TABLE II. Germination, viability and number of seeds observed in the pellets of common ravens in the Canary Islands. See abbreviations of plant species in Table I, Rine: *Rubus inermis* Pourr. (Rosaceae). Islands = F: Fuerteventura, T: Tenerife, C: Gran Canaria, G: La Gomera, P: La Palma, H: El Hierro. *Ficus carica* seeds are excluded from this table because they are infertile. Seeds of this species are not included in the calculations presented here

Species	Number of seeds dispersed	% seeds dispersed	% seeds moved to suitable habitats	Maximum % of seeds of each plant species dispersed in the context of one island	% of germination			P	% viable seeds from raven pellets
					Raven	Plant	G-test		
Apas	1 336	1.30	100.0	50.5 (F)	67.1	94.0	14.1	<< 0.001	100.0
Lint	1 504	1.47	96.9	39.7 (F)	44.3	44.0	0.019	0.97	90.0
Ppen	541	0.53	92.1	6.0 (C)	52.0	26.0	7.20	0.007	96.4
Rfru	17 947	17.50	100.0	22.1 (H)	52.9	60.0	0.72	0.39	100.0
Jced	79	0.077	69.6	29.6 (P)	16.0	4.3	4.79	0.029	0.0
Jtur	1 765	1.72	89.0	2.2 (H)	10.1	0.0	9.37	0.014	50.0
Phocan	262	0.26	100.0	6.7 (G)	54.9	2.6	36.31	<< 0.001	90.2
Odill	6 556	6.39	35.3	44.5 (T)	12.9	0.0	13.09	<< 0.001	96.6
Ofic	68 886	67.15	72.5	90.1 (G)	30.0	8.6	10.82	0.001	100.0
Vmoc	538	0.52	97.0	0.7 (H)	0.0	5.7	5.43	0.020	
Mfay	2 919	2.84	83.9	3.7 (H)	35.7	28.6	0.82	0.36	90.0
Ican	61	0.059	100.0	0.075 (H)	0.0	0.0			
Lazo	14	0.013	100.0	5.2 (P)	0.0	0.0			
Rine	13	0.012	100.0	0.4 (G)	0.0	38.0	10.73	0.001	
Pincan	159	0.16	42.8	0.5 (C)	44.1	35.7	0.82	0.41	25.0

tendency (*Asparagus pastorianus* and *Rubus inermis*). However, this method is somewhat controversial among researchers, and has not been satisfactorily resolved (Schupp, pers. comm.). Our own inclination is to use the results obtained by the independent tests. The percentage of viable seeds did not differ significantly for any species between pellet seeds and seeds obtained directly from the plants (G-test, $df = 1$, $P > 0.05$ for each species and treatment respectively).

Table II summarizes the number of seeds potentially dispersed to habitats that appear to be ecologically suitable for the establishment and growth of each species. Without taking into account the infertile seeds from *F. carica*, 76.5% of the 102 580 seeds transported by the common ravens in all the islands were regurgitated in their original habitat types, and the remaining 23.5% were moved into habitats inadequate for establishment. Due to the fact that the eastern islands have only one macrohabitat type (xerophytic shrub), the information given on the percentage of seeds carried to appropriate macrohabitats may be misleading. Therefore, the calculations only take into account the data from islands high enough to have more than one macrohabitat (central and western islands). The results obtained this analysis are rather similar, and 72.4% of the 93 551 seeds were deposited in suitable habitats.

Considering all the data from the islands, more than 90% of the seeds of nine species were moved to suitable macrohabitats and only two species had less than 50% dispersed to an appropriate macrohabitat. Most pellets (85%, $N = 2 268$) were collected in the xerophytic shrub while the remaining 15% corresponded to laurel forest ($N = 15$), pine forest ($N = 250$), and high mountain ($N = 139$). Despite thorough prospecting of all types of macrohabitats in the different islands, these data confirm the tendency of the common raven to prefer the open shrub habitat of the lower zones (Nogales, 1994).

Data on viability, germination and seed delivery to appropriate habitats suggest that common ravens act as an

important seed disperser for eight species (*L. intricatum*, *O. ficus-indica*, *R. fruticosus*, *J. turbinata*, *J. cedrus*, *Phoenix canariensis*, *M. faya*, and *P. pendula*) (Table II). Even if the effect of the bird significantly reduces germination for *A. pastorianus*, the other results (seed viability and habitat suitability) suggest that dispersal may be important. Nevertheless, some other species do not seem to benefit. For instance, most seeds of *O. dillenii* and *Pinus canariensis* are moved into unfavourable habitats, although common ravens improve germination in *O. dillenii*. Species typical of the laurel forest (*V. mocanera*, *L. azorica*, *I. canariensis*, and *R. inermis*) were consumed only rarely and no seed germination was observed after passing through the gut of the common raven.

Discussion

Although it is not easy to determine the significance of dispersal simply by observing birds eating or transporting fruits, Herrera & Jordano (1981) and Schupp (1993) cite some of the basic requirements. From the quantitative point of view, seed dispersal depends on *i*) the number of visits made to the plant by a disperser, and *ii*) the number of seeds dispersed per visit. From the qualitative point of view, seed dispersal depends on *i*) the quality of treatment given to a seed in the mouth and gut, and *ii*) the quality of seed deposition as determined by the probability that a deposited seed will survive and develop.

In our case, the quantitative requirements mentioned above seem to be satisfied (see Table II and III, and Nogales & Hernández, 1994). Common ravens in the Canaries cast at least three pellets per day, and they regurgitate seeds all year (Nogales & Hernández, 1997). The number of seeds transported in each visit to a plant is positively correlated with the size of the birds (Howe & Steven, 1979). The large common raven can ingest many fruits, showing a large capacity of seed delivery. Given the large interspecific variation in the size of seeds obtained from the pellets, it

TABLE III. Number of seeds per pellet of the different species consumed by the common raven in the Canaries. See Table I and II for abbreviations of plant species

Species	Frequency of occurrence in all pellets (%)	Mean number of seeds/pellet	SD	Number of seeds/pellet minimum maximum	
Apas	1.9	27	29.4	1	99
Lint	4.1	25	40.7	1	344
Ppen	1.1	19	17.1	1	93
Rfru	16.2	42	61.7	1	467
Jced	0.34	10	7.0	1	18
Jtur	2.8	25	29.3	1	120
Phocan	1.9	6	5.7	1	21
Fcar	22.6	115	144.8	1	980
Odill	2.7	63	49.7	1	357
Ofic	13.1	114	92.8	1	587
Vmoc	2.0	11	12.0	1	48
Mfay	2.7	46	37.1	1	137
Ican	0.11	30	38.2	3	57
Lazo	0.04	14	0	14	14
Rine	0.04	11	0	11	11
Pincan	3.4	2	2.2	1	13

seems likely that common ravens do not have great problems with the burden imposed by different-sized fruit, although this factor is very important in the selection of fruit by small and medium-sized birds (Herrera, 1981; Snow & Snow, 1988). This low level of selection by size conforms with that described by Moermond and Denslow (1985) for dispersal by large birds.

With respect to the qualitative requirements, the effect of the common raven on the seeds, either through manipulation or regurgitation, does not produce large losses in most plant species, as demonstrated by the viability tests. This may be partly due to the lack of strongly developed musculature in the gizzard of the common raven (Oelhafen-Gandolla & Ziswiler, 1981). Furthermore, the treatment provided by the digestive tract of this corvid improved seed germination in six species, had a negligible effect in four species, and reduced germination in three species. Few studies on birds have compared the germination of seeds eaten with controls collected directly from the plants, despite the potential importance of this research field (Howe, Schupp & Westley, 1985; Katusic-Malmberg & Wilson, 1988; Schupp, 1993; Ellison *et al.*, 1993). The results obtained in these studies vary and depend to a large extent on the plant and animal species involved (Lieberman & Lieberman, 1986; Izhaki & Safriel, 1990; Ellison *et al.*, 1993).

With respect to the second requirement for the quality of seed dispersal, an important factor determining the importance of dispersal are the movements of the birds after eating the fruit (Howe & Primack, 1975). The dispersal path followed by the seeds in the mountainous islands of the Canaries, described in the present paper, shows that the majority of seeds dispersed by common ravens are not displaced out of their native habitats. Another important requirement of dispersal quality is based on the number of seeds being dispersed together (Schupp, 1993). If only a few seeds are dispersed in a pellet they may be more likely to survive than if there are hundreds in one pellet and thus suffer from density-dependent seed predation and/or competition. In our case, the majority of pellets were mostly composed of a single species, although a few seeds from

other plants were often present. Mean number of seeds per pellet was variable but high for most plant species (Table III). This particular aspect of seed dispersal by common raven does not seem advantageous according to the optimal dispersal pattern deposition mentioned by Murray (1988).

Common ravens seem to play an important role in the dispersal of certain endemic plants in the Canaries. For the endemic *J. cedrus*, a species considered "endangered" by the IUCN, no other dispersal agent is known at the moment in the islands. For this reason, the future of the species could partially depend on the number of common ravens, whose populations are gradually declining in the Canarian Archipelago (Nogales, 1992). Our results provide additional evidence that effective dispersal does not necessarily depend on specialist frugivores as has been indicated by some authors (Moermond & Denslow, 1985). A particularly case of the importance of a non-specific dispersal agent concerns *O. ficus-indica*, a species introduced by humans into the Canaries in the nineteenth century. This cactus has now become a characteristic feature of some today's Canary Island landscapes in dry areas.

The phenomenon presented in this paper could be relevant and extended to those areas where small habitat surfaces are highly differentiated altitudinally, such as the high oceanic islands and even elevated mountain zones of continental areas.

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