Differential seed dispersal systems of endemic junipers in two oceanic Macaronesian archipelagos: the influence of biogeographic and biological characteristics

B. Rumeu · R. B. Elias · D. P. Padilla ·
C. Melo · M. Nogales

Abstract This article evaluates the seed dispersal systems of two congeneric and endemic fleshy-fruited plants in the context of two relatively close oceanic archipelagos. For this purpose, representative populations of the endangered junipers *Juniperus cedrus* in the Canary Islands and Madeira, and *Juniperus brevifolia* in the Azores were studied. Despite both species sharing the same biogeographic region, we set out to test whether different conditions of the islands and biological characteristics of each juniper species determine the distinctive guilds of seed dispersers involved. We assessed the quantitative and qualitative role of the potential frugivores, showing that the wintering *Turdus torquatus* and the native *Turdus merula* were the main seed dispersers for *J. cedrus* and *J. brevifolia*, respectively (Frequency of occurrence: 74.9%, 80.2%; germination increase with respect to controls: 11.6%, 15.5%; for *J. cedrus* and *J. brevifolia*, respectively). The endemic lizard *Gallotia galloti* was quantitatively outstanding as seed disperser of *J. cedrus*, although its qualitative effect does not appear to be beneficial. The introduced rabbit *Oryctolagus cuniculus* acts as a disruptor in both natural seed dispersal systems, as inferred from the high percentage of damaged seeds found in their droppings. Our results indicate that *J. cedrus* and *J. brevifolia* are primarily adapted to ornithochory processes, *T. torquatus* and *T. merula* being their respective legitimate long-distance dispersers. Although these birds should be playing a key role in the connectivity of fragmented populations, the dependence of *J. cedrus* on a migrant bird involves a notable fragility of the system.

B. Rumeu (✉) · D. P. Padilla · M. Nogales
Island Ecology and Evolution Research Group
(IPNA-CSIC), La Laguna, Tenerife, Canary Islands,
Spain
e-mail: brumeu@ipna.csic.es

R. B. Elias
Grupo da Biodiversidade dos Açores (CITA-A),
Departamento de Ciências Agrárias, Universidade dos
Açores, Angra do Heroísmo, Azores, Portugal

C. Melo
Centro do Clima, Meteorología e Mudanças Globais
(C-CMMG), Departamento de Ciências Agrárias,
Universidade dos Açores, Angra do Heroísmo, Azores,
Portugal

Introduction

Plant–animal interactions have been the focus of numerous studies, demonstrating the importance of frugivores in the seed dispersal system of many plant species (Jordano 2000). They determine the seed

shadow patterns, i.e. the spatial distribution of dispersed propagules with respect to their source plant and conspecifics (*sensu* Schupp 1993) and so they can have a significant effect on both the demography and genetic make-up of animal-dispersed plants (Jordano and Godoy 2002). The disperser contribution is determined by its effectiveness, which depends on the quantity of seeds dispersed and the quality of dispersal each seed is submitted to (Schupp 1993). The seed treatment in the disperser digestive tract may have a marked effect on the subsequent germinability of seeds, since both morphological and physiological traits affect the state of the seeds after their ingestion (Nogales et al. 2005). Thereby, the role of seed dispersers as modifiers of germination patterns becomes crucial to the effectiveness of dispersal.

As far as we know, this contribution assesses for the first time, in the context of oceanic archipelagos, the influence of different chronology, biogeography and biological characteristics in the seed dispersal systems of two congeneric fleshy-fruited plant species. We present data on the seed dispersal system of two juniper species endemic to the Macaronesian islands: (1) *Juniperus cedrus* (Webb and Berth.) distributed over the Canary Islands and Madeira; and (2) *Juniperus brevifolia* (Seub.) Antoine, restricted to the Azores. These archipelagos differ in latitude, distance from mainland, geological age, area and altitude of islands, habitat diversity and climate. Hence, the species studied have evolved under distinct ecological conditions; in particular, they vary substantially in the degree of fragmentation of their populations, phenology and main characteristics of the female cones, and groups of potential disperser guilds. In the case of *J. cedrus*, previous information points to the raven *Corvus corax* (nowadays in serious decline in the Canaries) as its long-distance seed disperser in the Canary Islands (Nogales et al. 1999), together with the endemic lizard *Gallotia galloti*, at least on Tenerife (Valido 1999), as short-distance disperser. Nevertheless, recent findings have demonstrated the interaction with the wintering *Turdus torquatus*, a thrush species that actively consumes *J. cedrus* female cones during its stay in the high mountain of Tenerife (92.5% of the total biomass ingested; Rumeu et al. 2009a). However, ravens, wintering thrushes and native lizards are absent in the Azores, where to our knowledge, there

is only one study in which authors report the presence of *J. brevifolia* plant material in the digestive tract of one blackcap *Sylvia atricapilla* (Neves et al. 2004). Therefore, at least *S. atricapilla* and *Turdus merula* (R. B. E., pers. obs.) may be the dispersers of *J. brevifolia* in this archipelago. Lastly, rabbits (*Oryctolagus cuniculus*; probably introduced during the fifteenth century in both archipelagos) may consume female cones of both juniper species, as happens with other junipers (Schupp et al. 1997a, b; Santos et al. 1999). Many studies in continental ecosystems reveal that birds and mammals are the agents that primarily disperse juniper seeds (Schupp et al. 1997a; Santos et al. 1999), thrushes (g. *Turdus*) playing a key role (Livingstone 1972; Zamora 1990; Jordano 1993; García 2001). However, little information is available about the seed dispersal systems of junipers on oceanic islands, although the effectiveness of these processes is crucial for the persistence of their populations (Schupp 1993).

Two representative populations of the Macaronesian endemic junipers were selected for this study, in which the main goals were (1) to identify the main dispersers acting in the seed dispersal systems of both endemic junipers; (2) to assess the quantitative contribution of each frugivore to the seed dispersal system; (3) to compare the qualitative component of the seed dispersal, with special emphasis on morphological damage to seeds; (4) to test, when possible, the seasonal variation in the seed dispersal process; and (5) to evaluate the effect of seed passage through disperser guts by assessing percentages of germination and emergence rates.

In general, we would expect to find the Canary juniper has a more complex seed dispersal system, as due to biogeographical factors (mainly the short distance from the mainland and the great diversity of habitats), the Canary Islands have a more diverse range of potential dispersal agents than the Azores. Beside this, variation in female cone size is significantly grater in the case of *J. cedrus* (Rumeu et al. 2009b), presumably attracting larger seed dispersers in the Canary Islands system. We expect to find differences among the guild of dispersers in their qualitative effect on seed dispersal, although major damage due to seed passage through the digestive tract would not be likely, as juniper seeds have a very hard coat (Chambers et al. 1999; Adams 2008). However, as lizards present longer gut passage time

(hereafter GPT) in comparison to birds (see Traveset 1998 and references therein), they could facilitate germination by producing deeper seed scarification. At least in the case of ectothermic lizards, we expect a greater contribution to the dispersal system during the warmer months, when they are most active.

Materials and methods

Study species

Juniperus cedrus natural populations are very rare and fragmented (IUCN 2009). In the Canary Islands, it grows on La Palma, La Gomera, Tenerife and Gran Canaria (Adams 2008), and nowadays it is mainly restricted to craggy and inaccessible areas. *J. brevifolia*, which is endemic to the Azores archipelago, is distributed throughout all the islands except Graciosa (Adams 2008; Elias 2007), where it is currently extinct. Natural populations on most of the Azores are also scarce and/or fragmented, but there are some islands (Terceira and Flores) where it is still possible to find extensive natural areas occupied by communities dominated by *J. brevifolia* (Elias 2007; Elias and Dias 2009). Both species are considered as endangered (IUCN 2009).

These junipers develop globose female cones with contrasting traits (see Rumeu et al. 2009b for further details). It is worth noting here the marked differences in cone size (*J. cedrus* average diameter: 9.94 ± 1.29 mm; *J. brevifolia*: 7.81 ± 1.06 mm) and phenology. Female cones of both Macaronesian species mature in the second year (Adams 2008) but, while in the case of *J. cedrus* they are available to dispersers throughout the four seasons, *J. brevifolia* presents mature female cones only during summer and autumn (Rumeu et al. 2009b).

Sites

The Canary Archipelago consists of seven main volcanic islands located between 27–29°N and 13–18°W, and only 96 km off the Atlantic coast of northwest Africa. The study of the *J. cedrus* seed dispersal system was carried out on Tenerife, which emerged 12 Ma ago and is the largest of the islands, 2058 km^2 in size. We selected one of the most important natural population*s*, at *Riscos de La*

Fortaleza (2170 m a.s.l.), a craggy geological formation included in *El Teide* National Park. This timberline area is subjected to wide thermal fluctuations throughout the year (about 10°C between maximum and minimum monthly average temperatures), and presents an annual mean temperature of 10.7°C. Annual rainfall is about 368 mm and most of it falls during the winter months (Bustos and Delgado 2004).

Located in the North Atlantic between 36–40°N and 24–32°W, the Azores Archipelago consists of nine main islands of volcanic origin. The distance between them (São Miguel) and the most westerly point of the European continent (Cabo da Roca) is about 1584 km. The population selected to study the seed dispersal system of *J. brevifolia* was located at *Malha Grande* (505 m a.s.l.), on the island of Terceira (402 km^2). The mean annual temperature is 14.0°C and total annual rainfall is 2168 mm, which occurs mainly in autumn and winter (Elias 2007).

Seed collection

Fieldwork was conducted from 2004 to 2009. To identify the main seed dispersers for *J. cedrus*, droppings from the potential frugivores were collected. Faeces and regurgitations from birds were sampled monthly (November 2006–November 2007) by trapping them with five mist nets (117.5 m^2), set up at the only population site where there was a concentration of junipers. Nets were left open for 10.2 h per month (total number: 133 h) and birds captured were ringed and kept in individual ringing bags until they defecated (≈ 30–40 min). Later, they were released in the same place where captured. We also placed plastic films under five female plants in that area to collect droppings and regurgitations from undetermined birds and increase the number of samples. Unfortunately, in late July 2007, a fire swept the netted area, and although the procedure was continued there to complete the year, we replaced the nets the following year (2008) in another nearby population (*Siete Cañadas*) from August to October. As *T. torquatus* was confirmed as a regular wintering bird (Rumeu et al. 2009a), droppings of this species were also collected from January to April of 2008 from the rocks surrounding *J. cedrus* plants, which are commonly used by thrushes as surveillance and resting perches (Livingstone 1972; Zamora 1990).

We considered that practically all these samples corresponded to *T. torquatus* because, although *T. merula* was also present in the area, the latter was scarce and when captured (*n* = 7), no *J. cedrus* seeds were found in its droppings.

As described above, natural populations of *C. corax* are in drastic decline in the archipelago and extinct in the study area. However, to test the role that they could play as seed dispersers of *J. cedrus*, we carried out a captivity experiment. Mature cones from six female plants of *J. cedrus* were collected separately. Two *C. corax* kept in captivity at two recovery centres for wild animals on different islands (Tenerife and Gran Canaria) were fed with female cones from each individual plant. Cages were inspected every day to gather pellets and recover a minimum of 30 seeds per plant. To control mother plant effects and avoid mixing seeds of different plants, after the last female cones were consumed from a given plant, we waited 2 days in case any other seeds were recovered from droppings or pellets.

In the field, we also collected 758 droppings from the native lizard *G. galloti* during the summer (when lizards have a higher metabolic activity) of 2004, at 17 different sites in the areas with *J. cedrus* mother-plants. Moreover, 3001 droppings from *O. cuniculus* were collected in 15 different sites of the population during the same period. In addition, to establish the role of lizards throughout the year, we collected droppings seasonally (spring 2008–winter 2009) by setting a radius of 2 m around each of 13 randomly selected female plants. To ensure that only fresh droppings were sampled, all faecal material was removed before the beginning of the sample collection process. When possible, the diameter of all droppings collected was measured to relate it with lizard body size (Valido and Nogales 2003).

In contrast to *J. cedrus*, which maintains mature cones throughout the year, *J. brevifolia* mature cones are only present during the summer and autumn (Rumeu et al. 2009b). For this reason, fieldwork in the Azores was carried out from August to October of 2008. Faeces and regurgitations from birds were collected by trapping them with 3–5 mist nets (67.5–117.5 m^2) located in four zones ($\approx$630 m apart), which were evenly distributed within the study site. Due to the sampling being seasonally restricted, we tried to trap birds whenever weather conditions permitted fieldwork. Nets were left open

for 6.2 h per day (total number: 136.5 h). To increase the number of samples, droppings from *T. merula* were also collected from the surface of rocks around *J. brevifolia* plants. Droppings from *O. cuniculus* (*n* = 2500) were collected at 27 different sites of the juniper population.

For both juniper species, control seeds were extracted directly from female cones on the plants. Whenever an individual plant could be associated with seeds recovered (as in pellets from ravens in captivity), we used seeds from those plants as controls, and the identity of the source mother plant was followed up throughout the seed germination assessment.

Seed procedures

To assess the quantitative role of each seed disperser, droppings and pellets were stored independently and seeds were manually extracted and counted. Then, to compare the qualitative effect of the different dispersers or treatments, we use a stereomicroscope (10×) and noted the external state of the seeds, classifying them into two categories (damaged and undamaged). To evaluate the effect of seed passage through the disperser guts, different germination experiments were performed in a greenhouse. For further germination details, see recommendations by Traveset and Verdú (2002), and Nogales et al. (2005, 2006).

Juniperus cedrus seeds from lizard and rabbit droppings were sown in October 2004 and monitored for three consecutive years (until March 2007). Since the highest percentage of germination (14.5%) was recorded in the first year (compared to 2.8% in the second year and 0% in the third), we decided to carry out the remaining experiments for only 1 year. As reported by Rodríguez-Pérez et al. (2005), seed emergence patterns in germination experiments can be contradictory in some cases when comparing field versus greenhouse-garden conditions. For this reason, to examine the quality of dispersal, two in situ germination experiments were also performed at both sites during the rainy period (November 2008–March 2009 in *Riscos de La Fortaleza*; October 2008–June 2009 in *Malha Grande*). Seeds were planted independently using meshes of grades: 5.5 cm^2 or 3.5 cm^2 for *J. cedrus* and *J. brevifolia*, respectively. These experiments were protected by covering them

with another finer grade mesh (1.2 cm^2) to avoid predation of seeds and seedlings. In the case of *J. cedrus*, the tested disperser effects were those of *G. galloti*, *T. torquatus*, and control seeds. For *J. brevifolia* in Malha Grande, disperser effects tested were *T. merula* and control seeds ($n = 200$ seeds in all treatments).

Statistical analyses

Categorical analyses (Likelihood ratio tests) were performed to compare the number of seeds per dropping from *G. galloti* over the four different seasons and also the number of germinated seeds after each treatment. In those cases where the use of the same data set was required, we applied the more conservative sequential Bonferroni technique to assess statistical significance. An ANOVA test was used to compare the sizes of *G. galloti* droppings between seasons, and Kolmogorov–Smirnov tests were employed to evaluate differences in germination rates between treatments. To avoid possible bias in these latter analyses, caused by the differential percentages of seed germination from one treatment to another, the only data considered were those from the period when the first seedling emerged until the germination curve was established (Nogales et al. 2006). All analyses were performed using the SPSS statistical package (version 15.0).

Results

Seed–disperser interactions

The relative contribution of each potential frugivore to seed dispersal differed among species (Table 1). In the case of *J. cedrus*, *T. torquatus* showed the highest values of seeds per dropping, frequency of occurrence: 74.9% and percentage of undamaged seeds: 99.7%. The number of seeds was significantly lower for the other dispersers (likelihood ratio test; $P < 0.001$ for all comparisons); interaction with *Erithacus rubecula* was rare, with only one undamaged seed having been recovered from its droppings. On the other hand, in the few samples analysed from *T. merula*, no seeds were found. The endemic lizard *G. galloti* was next in the number of seeds dispersed, the frequency of occurrence of seeds in its droppings being significantly higher than those found for *O. cuniculus* and *E. rubecula* ($G_1 = 1728.11$, $P < 0.001$; $G_1 = 21.91$, $P < 0.001$; respectively). Furthermore, this lizard also presented a lower number of damaged seeds in comparison to *O. cuniculus* ($G_1 = 147.88$, $P < 0.001$). Thus, the lowest values of seeds per dropping, frequency of occurrence and percentage of undamaged seeds corresponded to the alien rabbit *O. cuniculus*.

Turdus merula was the main disperser for *J. brevifolia*, showing the highest numbers of seeds per dropping and frequency of occurrence (81.1%). This

Table 1 Relative contribution of each potential frugivore to *Juniperus cedrus* and *Juniperus brevifolia* seed dispersal systems in the respective study areas (*Riscos de La Fortaleza*, Tenerife, Canary Islands; and *Malha Grande*, Terceira, Azores)

Juniper species	Potential frugivores	No. of seeds per dropping (mean ± SD)	FO (%)	Undamaged seeds (%)	No. of seeds found analysed	No. of droppings analysed
J. cedrus	*Turdus torquatus*	1.48 ± 1.41	74.9	99.7	739	498
J. cedrus	*Turdus merula*	0.00 ± 0.00	0	0	0	6
J. cedrus	*Erithacus rubecula*	0.06 ± 0.24	5.9	100	1	17
J. cedrus	*Fringilla teydea*	0.00 ± 0.00	0	0	0	11
J. cedrus	*Gallotia galloti*	1.15 ± 1.36	59.2	95.3	1669	1444
J. cedrus	*Oryctolagus cuniculus*	0.04 ± 0.24	3.9	56.3	118	3001
J. brevifolia	*Turdus merula*	2.32 ± 2.08	81.1	98.9	761	328
J. brevifolia	*Sylvia atricapilla*	0.11 ± 0.47	6.1	100	7	66
J. brevifolia	*Erithacus rubecula*	0.00 ± 0.00	0	0	0	17
J. brevifolia	*Fringilla coelebs*	0.00 ± 0.00	0	0	0	30
J. brevifolia	*Oryctolagus cuniculus*	0.07 ± 0.31	5.9	41.2	177	2500

FO frequency of occurrence of juniper seeds in the droppings analysed

latter measure was significantly higher than that of *O. cuniculus* and *S. atricapilla* ($G_1 = 896.16$, $P < 0.001$; $G_1 = 138.58$, $P < 0.001$; respectively). Seeds defecated by *S. atricapilla* were scarce but it was the second disperser in importance found for the Azorean juniper system. Lastly, as was the case in the Canaries, the introduced rabbit *O. cuniculus* presented fewer seeds per dropping, lower frequency of occurrence and percentage of undamaged seeds.

Seasonal patterns of seed dispersal

Seasonal variation in seed dispersal agents and their quantitative contribution show that dispersal of *J. cedrus* seeds does not occur equally through the year. No frugivorous birds were captured during the summer (Fig. 1), and lizard droppings at *Riscos de La Fortaleza* ($n = 1444$) were more abundant during the summer season (41.9% of total droppings found) (Table 2). The frequency of occurrence of *J. cedrus* seeds in *G. galloti* droppings, and the number of seeds per dropping were clearly different between seasons ($G_3 = 65.88$, $P < 0.001$; $\chi_3^2 = 18.52$, $P < 0.001$, respectively), with droppings containing seeds and number of seeds per dropping being more frequent during the summer than in the other seasons ($P < 0.05$ for all comparisons). Diameter of *G. galloti* faeces

varied significantly through the year (ANOVA I test; $F_3 = 12.85$, $P < 0.001$); those found in summer were larger than those collected during the other seasons ($P < 0.001$ for all comparisons), indicating that seed dispersal mainly relies on bigger lizards during the warmer period. While *T. torquatus* dispersed 60.5% of seeds during the winter months, *G. galloti* spread the seeds mainly in the warmest season (56.4%). Therefore, a seasonal replacement pattern of the main seed disperser agents allows *J. cedrus* seeds to be dispersed throughout the year (Fig. 2).

Seed germination

Frugivores affected the percentages and germination rates of *J. cedrus* seeds tested in different ways (Fig. 3). Both *C. corax* and *T. torquatus* significantly increased the percentage of seeds germinated ($G_1 = 7.70$, $P = 0.006$; $G_1 = 8.33$, $P = 0.004$, respectively). While 22.5% of control seeds emerged from the soil surface, the figures were 34.1 and 34.5% after gut passage through *C. corax* and *T. torquatus*, respectively. The effect of lizards was different; the endemic *G. galloti* significantly reduced the number of germinated seeds with respect to control ($G_1 = 13.29$, $P = 0.001$), and slowed down their germination (Kolmogorov–Smirnov test; $Z = 1.79$, $P = 0.003$)

Fig. 1 Frugivorous birds trapped in *Riscos de La Fortaleza* over 1 year (November 2006–October 2007; total mist-netting effort: 133 h). Data from August to October were obtained in a nearby population (*Siete Cañadas*) during 2008 (after the fire that affected the original population)
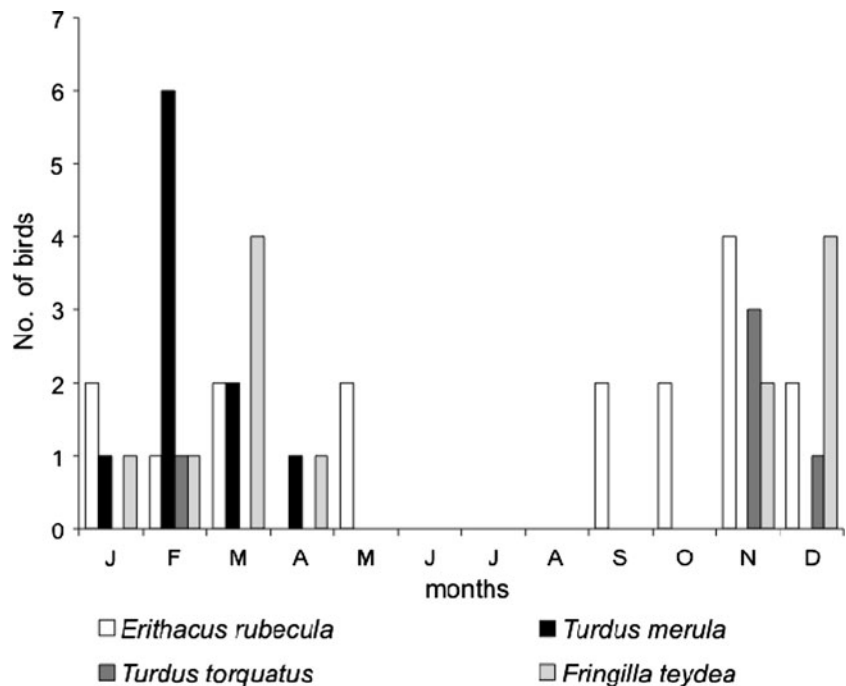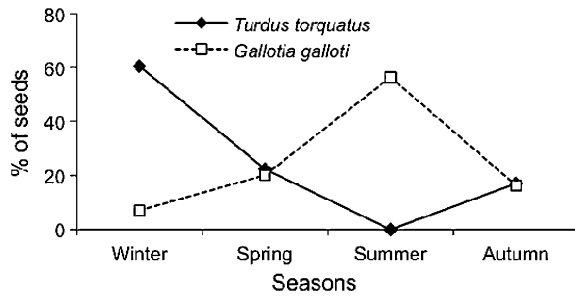
Table 2 Traits of *Gallotia galloti* droppings collected at *Riscos de La Fortaleza* (Tenerife, Canary Islands) over 1 year

Season	No. of droppings found	Dropping diameter (mean ± SD) (mm)	No. of seeds per dropping (mean ± SD)	FO (%)	Damaged seeds (%)	Total no. of seeds found
Winter	118	6.03 ± 1.23 ($n = 83$)	1.06 ± 1.42 ($n = 118$)	54.24	9.60	125
Spring	413	6.04 ± 1.03 ($n = 100$)	0.85 ± 1.06 ($n = 120$)	49.39	5.03	338
Summer	605	6.85 ± 1.23 ($n = 100$)	1.66 ± 1.68 ($n = 120$)	71.24	2.82	923
Autumn	308	5.98 ± 1.16 ($n = 100$)	1.03 ± 1.35 ($n = 120$)	50.65	8.13	283

Fig. 2 Percentage of *J. cedrus* seeds dispersed by the main frugivores present in *Riscos de La Fortaleza* over 1 year

(Fig. 3). Unfortunately, because of the low number of juniper seeds found in *O. cuniculus* faeces, and a high proportion of externally well-developed but empty seeds (see Chambers et al. 1999), we could not present any data about germination success after the *O. cuniculus* gut treatment. We did not obtain conclusive results in the in situ germination experiment with *J. cedrus* seeds in any of the treatments. In all the three treatments, only two control seeds (1% of the control seeds sown) were able to germinate at *Riscos de La Fortaleza*.

In the case of *J. brevifolia*, germination results presented are those derived from the field experiment, since no seeds germinated in the greenhouse. In the in situ test, a higher proportion of those seeds ingested by the thrush species *T. merula* germinated, compared to controls (20.0% and 4.5%, respectively; $G_1 = 23.93$, $P < 0.001$), but they did not emerge faster ($Z = 1.34$, $P = 0.056$) (Fig. 3).
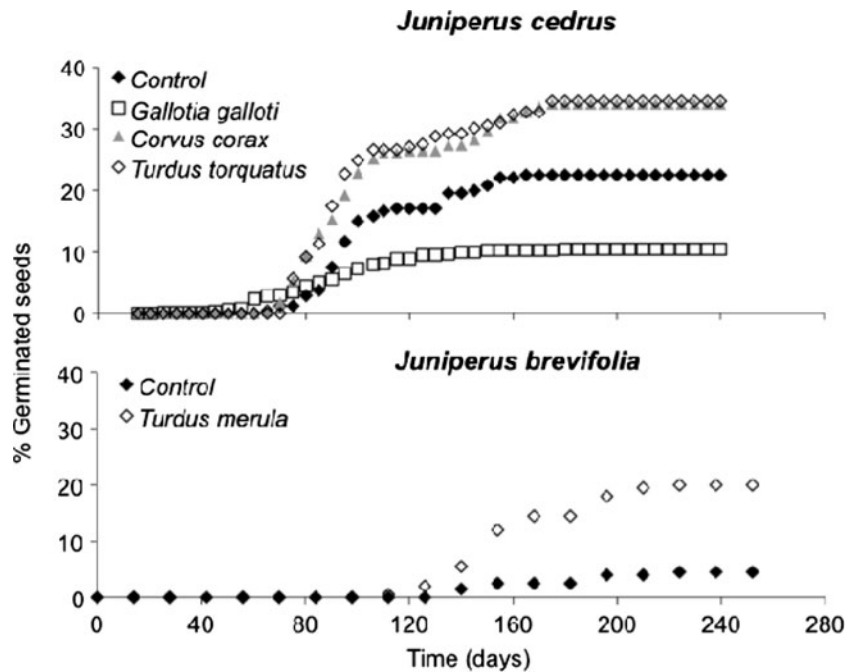
Discussion

Seed dispersal by frugivores

The largest number of *J. cedrus* seeds was found in droppings of the wintering *T. torquatus* and the native lizard *G. galloti*. Frugivore interactions in continental ecosystems between thrushes and different juniper species are well described (García 2001; Jordano 1993; Livingstone 1972; Santos et al. 1999; Zamora 1990). However, after the extinction of *C. corax* in the range of this juniper population, the wintering *T. torquatus* is now the sole long-distance disperser for *J. cedrus* seeds. Hence, its regular annual arrival in the high mountain zone of Tenerife is crucial in the population dynamics of this juniper, enabling distant population nuclei to be linked and contributing to the maintenance of its genetic diversity. An interesting finding revealed during this work, is that although the endemic finch *Fringilla teydea* does not act as *J. cedrus* seed disperser, during the winter months they leave their optimal habitat (pine forest) and take advantage of the timberline resources, actively consuming *J. cedrus* seeds (pers. obs.). In addition, saurochory is mainly an insular phenomenon (Olesen and Valido 2003), and the large number of seeds moved by *G. galloti* confirms that the seed-dispersing role of lizards on islands is more important than previously thought (Cooper and Vitt 2002; Olesen and Valido 2003; Rodríguez et al. 2008). In fact, this high consumption of *J. cedrus* female cones by *G. galloti* becomes relatively important to the dispersal system, given the high density of these lizards in all habitats of the Canary Islands (Olesen and Valido 2003). However, unlike *T. torquatus*, lizards are considered as short-distance dispersers (home range areas reported for *G. galloti* <100 m² ; Molina-Borja 1985).

With respect to *J. brevifolia* on Terceira, the native *T. merula* was the main seed disperser, showing the highest values of seeds per dropping and frequency of occurrence. This case, as described above, is in concordance with the predominant pattern described in continental ecosystems. Nevertheless, to our knowledge and despite its opportunistic frugivore

Fig. 3 Germination
percentages and rates of
J. cedrus and *J. brevifolia*
seeds obtained from
droppings and
regurgitations of the main
seed dispersers. Data from
J. cedrus derive from the
greenhouse experiments,
while those for *J. brevifolia*
are from the in situ
experiment

behaviour, the interaction between *S. atricapilla* and
junipers is not common in continental environments
(see Jordano and Herrera 1981; Jordano 1987).
Average fruit size consumed is strongly correlated
with gape-width of warblers (Jordano 1987), since
fruit size impedes ingestion by those relatively small-
sized dispersers that swallow them whole (Howe and
Westley 1990; Herrera 2002). Hence, the small
female cone size of *J. brevifolia* (7.81 ± 1.06 mm;
Rumeu et al. 2009b) facilitates this interaction.

The introduced rabbit *O. cuniculus* had a negative
effect on the seed dispersal systems of the two
Macaronesian junipers, due to the high percentage of
damaged seeds (43.7 and 58.8% for *J. cedrus* and
J. brevifolia, respectively). Lagomorphs can disperse
seeds of fleshy-fruited plants, including juniper
species (Schupp et al. 1997a, b; Santos et al. 1999).
However, some studies have shown that rabbits break
seeds and therefore reduce seed survival and germi-
nation when feeding on fleshy fruits, in continental
systems (Muñoz-Reinoso 1993) and also in insular
environments like the Canary Islands (Nogales et al.
2005). Taking into account the recent introduction
date of rabbits in both archipelagos (in that the
endemic junipers have not been able to evolve in
contact with them) and the low quantitative and
qualitative effectiveness of seed dispersal, *O. cuniculus*

represents another example of the impact that alien
species can have on native mutualisms (e.g. Nogales
et al. 2005).

Replacement of seed dispersers

In *J. cedrus*, a seasonal variation in frugivorous
interactions was detected. While no frugivorous bird
species were captured during the summer months,
their role in seed dispersal becomes very significant
during the winter, when the migrant *T. torquatus*
disperses a high quantity of *J. cedrus* seeds. However,
its return to breeding sites in March–April coincides
with the time when the temperature starts to rise in the
timberline zone and lizards become more active.
Thus, these short-distance dispersers reach their peak
of seed dispersal activity during the summer months,
when larger droppings were found. According to
Valido and Nogales (2003), there is a positive
relationship between diameter of faecal pellets and
G. galloti body size, and so our results show that
during the summer, bigger lizards actively consume *J.
cedrus* female cones. In general, recorded schedules
of fruit production and depletion suggest adaptation to
dispersal opportunities (Howe and Smallwood 1982).
In this case study, the endemic Macaronesian junipers
show contrasting phenology. While *J. brevifolia*

seed dispersal is restricted to summer and autumn, *J. cedrus* presents mature female cones throughout the year (Rumeu et al. 2009b), allowing year-round dispersal of their seeds by different frugivores.

Effect of disperser gut treatments on seed germination

External damage on *J. cedrus* and *J. brevifolia* seeds was low in the case of birds and reptiles, contrasting with the higher values reported for *O. cuniculus*. For the two juniper species studied, seeds ingested by birds germinated in greater proportions than controls. These results agree with those found in *J. virginiana* (Holthuijzen and Sharik 1985). Nevertheless, they contrast with other studies on junipers, in which passage through bird digestive tracts did not increase germination percentages with respect to controls (Livingstone 1972; Salomonson 1978). After recording the positive effect of *C. corax* in the seed dispersal system of *J. cedrus*, it is striking that without the presence of *T. torquatus* during the winter months, the extinction of this native corvid could have negative consequences on the fitness of *J. cedrus*. However, it is probable that the interaction between *J. cedrus* and the wintering *T. torquatus* has been occurring for a long time, but has passed unnoticed (Rumeu et al. 2009a).

When saurochory has an effect on percentage germination, it is often positive (Traveset 1998). However, despite the interaction between *G. galloti* and *J. cedrus* occurring for much longer period on an evolutionary time scale, the effect of this endemic lizard on germination percentage and rate was negative. Consequences of asynchronous germination are complex, but the effect of lizards on *J. cedrus* germination rate could guarantee that seedling mortality is spread over a longer period, increasing the likelihood of success of undamaged seeds (Harper 1977). Similar results were previously reported when assessing the effect of *G. galloti* on the seed germination of *Rubia fruticosa* (Padilla and Nogales 2009). As this latter study reflects, the reduction in seed viability could be due to the enzymatic effects in the long gut (mean snout-vent length of *G. galloti*: 106.4 ± 12.1 mm) and because herbivorous lizards have long GPT (*G. galloti* mean GPT: 6.9 ± 3.8 days; Valido and Nogales 2003) compared to passerine birds (5–20 min for

regurgitated seeds; 0.3–1.5 h for defecated seeds) (see Traveset 1998 and references therein). Nevertheless, taking into account the important effect of the *J. cedrus* mother plant on seed viability (Rumeu et al. 2009b), further germination experiments with lizards kept in captivity (which permit the control of this mother effect) are essential to clarify the relationship between native lizards and endemic junipers in the Canary Islands.

Concluding remarks

Our results show that the seed dispersal systems of the two endemic Macaronesian junipers differ in some important quantitative and qualitative aspects, like the dispersal agents that are involved and the seasons in which seed dispersal occurs. As expected, *J. cedrus* presented a more complex seed dispersal system than *J. brevifolia* (in which only *T. merula* is quantitatively and qualitatively important), and the ensemble of legitimate known seed dispersers is in concordance with the size of female cones. Therefore, while *J. cedrus* has evolved with large seed dispersers (like *C. corax* and probably giant lizards of the endemic genus *Gallotia* that were abundant in the past), the female cones of *J. brevifolia* are mostly consumed by small and medium size birds such as *S. atricapilla* and *T. merula*. Despite the biogeographic peculiarities of the island systems these junipers inhabit, they are in both cases well adapted to ornithochory, which coincides with the patterns described in continental species. *J. brevifolia* presents a solid seed dispersal system, where the main frugivore involved is a native, ubiquitous and abundant thrush, capable of the maintenance of seed gene flow among populations. However, even though the *J. cedrus* seed dispersal system is more complex than that of *J. brevifolia*, the dependence of *J. cedrus* on the wintering of *T. torquatus* for the long-distance dispersal of its seeds implies great fragility in the system. Moreover, although *T. torquatus* is not globally threatened (IUCN 2009), there has been a decrease in numbers and a reduction in its range in Britain (Burfield and Brooke 2005), where it has been listed as a species deserving high conservation concern (see Sim et al. 2007). Thus, the conservation of this migrant bird species could be the key in the persistence of *J. cedrus* in Tenerife.

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