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REGULAR PAPER

Foxes provide a direct dispersal service to Phoenician junipers in Mediterranean coastal environments: ecological and evolutionary implications

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Background and aims – Exploring the role of mammalian carnivores as seed dispersers in Mediterranean environments is crucial for understanding biotic interactions and preserving mutualistic networks in areas with high biodiversity. We examine the potential role of the Sardinian fox (*Vulpes vulpes* subsp. *ichnusae*) as a seed-disperser of two juniper species (*Juniperus phoenicea* subsp. *turbinata* and *J. oxycedrus* subsp. *macrocarpa*) in Mediterranean coastal environments.
Methods – Observational and manipulative experiments were conducted in five coastal sites in north-western Sardinia (Italy) between 2010 and 2013.
Key results – We found that Sardinian fox actively disperses seeds of *J. phoenicea* subsp. *turbinata*, whereas no evidence was obtained for the fox dispersing seeds of *J. oxycedrus* subsp. *macrocarpa*. Fox scat contained, on average, 73–86 *J. phoenicea* subsp. *turbinata* seeds, accounting 16.3–17.8 % of the average dung weight. The role of Sardinian fox as a primary disperser of *J. phoenicea* subsp. *turbinata* is by directly dispersing juniper seeds (via defecation) to a specific microhabitat (i.e. 80–90 % of dung was released on dwarf plants, mainly *Helichrysum italicum* subsp. *microphyllum*), which positively affected the survival of emerged seedlings). We quantified that fox dispersed 30 to 100 seeds per day per hectare (3 500–10 500 seeds per hectare in one winter season).
Conclusions – We reported that Sardinian fox is a direct disperser of *J. phoenicea* subsp. *turbinata*, thus playing a major role in secondary successional dynamics in Mediterranean coastal environments. Evolutionary implications are discussed, in that the positive interaction between Sardinian fox and *J. phoenicea* subsp. *turbinata* could be recent, following the introduction of fox to the Tyrrhenian islands during the 7th–6th millennium BC.

Key words – Endozoochory, facilitation, frugivory, *Juniperus oxycedrus* subsp. *macrocarpa*, *Juniperus phoenicea* subsp. *turbinata*, plant-animal interactions, plant-plant interactions, secondary succession, *Vulpes vulpes ichnusae*.

INTRODUCTION

Biodiversity is one of the most extraordinary features of life (Cardinale et al. 2012) and its effects on ecosystem functioning represent major topics in ecology (Wittebolle et al. 2009). It is now recognized that functional approaches to ecosystem processes, which identify functional units of species based on their use of resources and interactions (Thuiller et al. 2013), are essential for understanding the nature and the strengths of relationship between species diversity and ecological functions (Stuart-Smith et al. 2013).

There is growing evidence, especially over the last twenty years, that some positive interactions between plants, and between plants and animals, play a pivotal role in ecosys-

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tem functioning, especially in harsh habitats characterized by high levels of environmental stress (Bertness & Callaway 1994, He & Bertness 2014). Mutualistic networks, characterised by the exchange of mutual benefits, such as pollination and seed dispersal (Song & Feldman 2013) between two groups of species (Suweis et al. 2013), play a fundamental role in maintaining biological diversity (Traveset 1999). Animals dispersing seeds (e.g. birds, mammals, ants) play a major role not only at the population/species level (Emer et al. 2013), but also in influencing the structure of plant communities (Matías et al. 2010). As a consequence, a worldwide decline of animal dispersers (Christian 2001) could trigger a cascade of additional extinctions (LaBar et al. 2013) in a variety of ecosystems.

Frugivorous animals are attracted by fruits of plants whose seeds are embedded in fleshy pulp and then disperse those seeds through defecation (endozoochory) (Howe & Smallwood 1982, Herrera 1985, Howe 1986, Lovisetto et al. 2012, Zhou et al. 2013). Several studies have underlined the roles that various groups of vertebrates play as seed dispersers of fleshy-fruited plants (Herrera 1985). For example, mid-size birds disperse plant species that produce small-sized, fleshy fruits, such as berries (Kelly et al. 2010, Snow & Snow 2010). Likewise, monkeys (Beaune et al. 2013) and bats play a major role in tropical forests (Muscarella & Fleming 2007). Carnivores (Herrera 1989, Fedriani et al. 1999, Traba et al. 2006, Koike et al. 2008, Grünewald et al. 2010, Rosalino et al. 2010, D'hondt et al. 2011, López-Bao & González-Varo 2011) and reptiles (Rodríguez-Pérez et al. 2005, Traveset & Riera 2005) are also important seed dispersers.

Among carnivores, the red fox [*Vulpes vulpes* (Linnaeus, 1758)] has been repeatedly identified as a main seed disperser of several tree species, including some juniper species (Santos et al. 1999, Traba et al. 2006, Fedriani & Delibes 2009, Escribano-Ávila et al. 2012, 2013, 2014, Suárez-Esteban et al. 2013), although the red fox has also often been described as a generalist (rather than specialist) seed disperser (Trewhella et al. 1988, Calisti et al. 1990, Lovari et al. 1994, Goldyn et al. 2003, Dell'Arte & Leonardi 2005, D'hondt et al. 2011, Rico-Guzmán et al. 2012, Díaz-Ruiz et al. 2013, Meisner et al. 2014).

Recent studies reveal that complex dispersal networks exist among fleshy-fruited plants and frugivorous animals (i.e. different groups of frugivores disperse seeds of fleshy-fruited plants at different distances and into different microhabitats; Jordano et al. 2007). Furthermore, short- and long-distance dispersals of the seeds of the same plant species to different microhabitats are guaranteed by complementary assemblages of disperser species (Escribano-Ávila et al. 2012, 2013, 2014). Despite the increasing number of scientific papers examining animal-mediated seed dispersal, there is still a need to confirm and quantify the effects of seed deposition on seedling establishment and survival in order to close the "seed dispersal loop" described by Wang & Smith (2002).

In this paper we try to verify and quantify whether the Sardinian fox (*Vulpes vulpes ichnusae* Miller, 1907) establishes biotic interactions with two juniper species (*Juniperus phoenicea* L. subsp. *turbinata* (Guss.) Nym. and *J. oxycedrus* L. subsp. *macrocarpa* (Sibth. & Sm.) Neilr.) in coastal ecosystems of a Mediterranean island (Sardinia) where the Sardinian fox was introduced about the end of the 7th–6th millennium BC (Masseti 2009). The two juniper species examined in this study are Tertiary relicts that have experienced a contraction in their distributional ranges during the Quaternary (Mao et al. 2010) and perhaps have evolved a novel mutualism for seed dispersion within the last millennia.

The potential role of the Sardinian fox as a disperser organism for the two juniper species was investigated using both observational and experimental approaches. Our hypothesis was that the fox can direct the spatial distribution of juniper trees by directional seed dispersal to specific microhabitats and by enhancing seed germination through endozoochory. In Sardinian coastal habitats, we investigated: (1) if the spatial distribution of seedling junipers and Sardinian fox dung is random or aggregated in specific microhabitats; (2) if juniper seed germination and survival of emerged seedlings is conditioned by seed origin (mother plants vs. fox dung), microhabitat (chamaephytes vs. bare soil), or the interaction between these factors.

MATERIALS AND METHODS

Study species

Junipers belong to the family Cupressaceae, having mainly a Mediterranean to Micronesian distribution (Adams 2014). The Phoenician juniper *Juniperus phoenicea* subsp. *turbinata* (hereafter, called *J. turbinata*) is a mainly-dioecious, slow-growing and long-lived small tree or bush, 1–6 m tall. Strobili are produced between February and March. Pollination is anemophilous, cones are berry-like, with 3–8 seeds surrounded by a fleshy pulp (pseudo fruit) reaching maturity after 18–24 months, and seeds are disseminated by endozoochory and barochory. *J. turbinata* most frequently grows in coastal habitats, along both sandy and rocky coasts (Gianguzzi et al. 2012).

The Large-fruited juniper (*Juniperus oxycedrus* subsp. *macrocarpa*) hereafter called *J. macrocarpa*, is also a mainly-dioecious, slow-growing and long-lived, small tree or bush, 1–5 m tall. Females require two years to develop berry-like, orange-brown mature cones, 12–15 mm in diameter. It is possible to find cones at different stages of maturity on the same plant simultaneously (Juan et al. 2006). Pollination and seed dispersal are similar to *J. turbinata*, but *J. macrocarpa* is a heliophilic, xerophilic, halo-tolerant, and moderately thermophilic plant, growing most frequent in sandy coastal habitats (Díez-Garretas & Asensi 2014).

The natural regeneration of *Juniperus* species is complicated by several factors, including slow growth rate, low seed viability, and/or difficulty in germinating (Juan et al. 2006). Reproductive constraints, together with a long history of range contraction and expansion, have lead to a fragmented genetic structure for both taxa (Dzialuk et al. 2011, Juan et al. 2012).

The red fox belongs to the Order Carnivora and the Family Canidae. It has one of the largest geographical and ecological distributions of any land animal, which demonstrates its high adaptability (Trewhella et al. 1988). Island populations

Table 1 – Characteristics of the study sites.

Site	Cala Barca	La Frana	Coscia di Donna	Porto Ferro	Platamona
Code	site 1	site 2	site 3	site 4	site 5
Coordinates	40°36′17″N 8°8′58″E	40°45′32″N 8°9′42″E	40°54′3″N 8°13′10″E	40°41′11″N 8°12′20″E	40°49′29″N 8°32′9″E
Geology	limestone	sandstone	schist	sand	sand
Elevation (m a.s.l.)	24–30	10–28	5–10	2–5	1–4
Sampled area (m²)	17 625	29 160	6 300	7 020	7 866
Municipality	Alghero	Sassari	Stintino	Sassari	Sorso
Dominant woody species	*Juniperus phoenicea* subsp. *turbinata*	*Pistacia lentiscus* and *Calicotome villosa*	*Juniperus phoenicea* subsp. *turbinata*	*Juniperus oxycedrus* subsp. *macrocarpa*	*Juniperus oxycedrus* subsp. *macrocarpa*
Natura 2000 site	ITB010042	no	ITB010043	ITB011155	ITB010003
Effective management	Porto Conte Regional Park	none	none	none	none

of foxes living in Sardinia and Corsica have been described as being an exclusive subspecies (i.e. *V. vulpes ichnusae*), hereafter referred to as *V. ichnusae* (Sardinian fox), even though its origin still remains uncertain (Frati et al. 1998). *Vulpes vulpes* is an opportunistic carnivore, whose dietary flexibility is due as much to its generalist nature as it is to the heterogeneity of its environment, and seasonal and distributional variations in the availability of its food (Goldyn et al. 2003, Lavin et al. 2003, Dell'Arte & Leonardi 2005, Díaz-Ruiz et al. 2013, Meisner et al. 2014), which makes it an occasional seed disperser (Traba et al. 2006, D'hondt et al. 2011).

Study area

Sardinia, the second-largest island (24 089 km^2) in the Mediterranean Basin, has a 1 897 km coastline. Our study area included 830 km^2 in NW Sardinia, along 130 km of this coastline.

In this study, we searched sites having wide, relatively open areas of dwarf vegetation (garrigue) adjacent to mature juniper groves. Dwarf vegetation was dominated by *Helichrysum italicum* (Roth) G.Don subsp. *microphyllum* (Willd.) Nyman at all sites, whereas associated species varied, depending on whether the site was rocky (co-dominated by *Astragalus terraccianoi* Vals., *Centaurea horrida* Bad., *Euphorbia pithyusa* L., *Limonium* sp.) or sandy (co-dominated by *Armeria pungens* (Link) Hoffmanns. & Link, *Crucianella maritima* L., *Ephedra distachya* L.).

Five study sites were selected (table 1). Cala Barca (site 1) and Coscia di Donna (site 3) were rocky habitats dominated by *J. turbinata*, Porto Ferro (site 4) and Platamona (site 5) were sandy habitats dominated by *J. macrocarpa*, and La Frana (site 2) was sandstone habitat, dominated by dense shrubs of *Pistacia lentiscus* L. and *Calicotome villosa* (Poir.) Link, vegetated with only a few scattered *J. turbinata* trees. The sandstone habitat was studied to determine whether it differed from the other four sites relative to seedling junipers and fox dung, because it had no adult junipers able to produce large amounts of pseudo-fruits.

In order to ensure that our study sites represented independent samples, we selected sites located several kilometres from one another, from a minimum distance of 8.9 km (from site 2 to site 4) to a maximum distance of 40.8 km (from site 1 to site 5). This distance was deemed sufficient for ensuring independent samples because Jordano et al. (2007) had demonstrated that mammals mainly disperse seeds more than 495 m from where they consume them, and mostly into open microhabitats. The location of our study sites was also established by considering the known area of fox home ranges: 5 to 12 km^2 (when environmental conditions are suitable) and 20 to 50 km^2 (when conditions are less favourable; Trewhella et al. 1988). All sites were close to the coast and all had an Oceanic Pluviseasonal Mediterranean bioclimate that consists of prolonged summer drought and mild winters (average annual temperature 16 °C, average temperature of the coldest month > 8 °C, annual rainfall 500–600 mm), falling within a dry thermo-Mediterranean phytoclimatic belt (Canu et al. 2015).

First observational experiment: census of juniper juveniles

The census of juniper juveniles (definition below) was obtained from total counts (*sensu* Bullock 1996) made between November 2011 and March 2012. Three to four people walked along parallel transects to make sure we did not miss or double-count individuals. Each juniper was tagged and recorded with an alphanumeric identification code that indicated site, life stage, microhabitat, and date of monitoring. Juvenile was defined as individuals with cotyledons, often with some acicular juvenile leaves but without stalk, or with a stalk and mature leaves, but a trunk diameter not exceeding 0.5 cm at the base. Microhabitat was characterized by cover type at each sampled point (*sensu* Jordano et al. 2007): (1) bare soil; (2) dwarf vegetation (plant cover dominated by chamaephytes); (3) shrub vegetation (plant cover dominated by phanerophytes); (4) perennial herb vegetation (plant cover dominated by hemicryptophytes and/or geophytes).

Vegetation structure was described as the prevalence (%) of each microhabitat at each site, and was determined from data collected at points sampled along five, 100 m-long transects randomly located at each site (*sensu* Bullock 1996). At each meter along a transect, microhabitat-type was qualitatively recorded, so that for each site, a total of 500 sample points were recorded.

Second observational experiment: distribution pattern and content of fox dung

At the end of October 2011, before counting and collecting fox dung, we removed fox scat already present at the study sites, because otherwise we would not have known over what time span the scat had been deposited. We studied dung deposition every two weeks from November 2011 to March 2012, counting and collecting all scat deposits present at each study site (table 1). The method for censusing Sardinian fox dung was the same method used to census juniper: three to four people walked along parallel transects to make sure we did not miss or double-count scat. During our field census, each scat was assigned to one of the previously mentioned microhabitats (bare soil, dwarf vegetation, shrub vegetation, or perennial herb vegetation), applying the same procedure used for the juvenile juniper census (previous section).

Each scat was put into a small plastic bag, in which we recorded an identifying alphanumeric code, site, and the date of census. After collection, samples were brought to the Plant Ecology lab of the Department of Science for Nature and Environmental Resources at the University of Sassari, where each sample was weighed with a Sartorius precision balance (Model AY612) to the nearest ± 0.01 g. Following the weighing, each sample was manually cleaned to count seeds from junipers and other plant species. Remains of animals (arthropods, small mammals, and birds) were also reported, but not counted or weighed.

Finally, the juniper seed stock extracted from each sample was weighed and preserved in a small paper bag, on which the census identification code was recorded.

Manipulative experiment: germination and survival rates of *J. turbinata* seedlings in relation to their origin and microhabitat

A manipulative experiment was carried out in order to discriminate the effects of the origin and microhabitat on the seed emergence and survival of *J. turbinata* seedlings. To evaluate the effect of seed origin on growth and account for any effects related to site specific conditions, we compared juniper seeds collected from fox dung and seeds collected from mother plants at the same site (sites 1 and 3). To simulate the various microhabitats in our study, we compared planted pots with bare soil only with pots planted with *Helichrysum italicum* subsp. *microphyllum*. We used this chamaephyte because it was the most common plant at the study sites.

To prepare the planting experiment, mature cones of 30–50 *J. turbinata* individuals were randomly collected from sites 1 and 3 (rocky habitat) at the end of January 2012. The manipulative experiment did not include intact fruits; therefore, in this experiment we only evaluated the scarification effect, not the "disinhibition" effect (Samuels & Levey 2005, Robertson et al. 2006).

We used 18 replicates for each combination of origin × microhabitat. Each replicate consisted of one pot with a diameter of 20 cm, a height of 20 cm, and a volume of 5 L. Each pot was filled with soil collected at study site 2 (sandstone habitat), to avoid the potential for introducing seeds from a *J. turbinata* seed bank. To simulate saline air in coastal conditions, each pot was watered with 0.6 g NaCl / 1 L H_2O once per week. To each pot we attached an alphanumeric identification code, which indicated the species from which the seed was obtained (J = *Juniperus* or V = *Vulpes*), the microhabitat (H1 = bare soil and H2 = *Helichrysum italicum* subsp. *microphyllum*), and a number from 1 to 18 to uniquely identify each replicate.

In total, we had of 72 experimental pots, 36 pots planted with seeds from Sardinian fox dung and 36 pots planted with seeds from adult *J. turbinata* cones. In each pot, we planted 10 seeds; therefore, we planted 360 seeds from *V. ichnusae* dung and 360 seeds from adult *J. turbinata* cones. The pots were placed outdoors for one year, from July 2012 to July 2013. This experimental site (40°43′17.91″N 8°32′58.25″E) was located 36.0 km from site 1 and 33.6 km from site 3.

The response variables, monitored every two weeks, were germination frequency of planted seeds (no. of emerged seedlings/10 planted seeds) and survival of seedlings (days of survival/total no. of days of the experiment).

Statistical analyses

In order to verify if the distribution of juniper juveniles and Sardinian fox dung was proportional to microhabitat availability, a χ^2 test was carried out to compare, for each study site, the observed distribution of individuals and scat with their expected distribution. The expected distribution was assumed to represent a random distribution, wherein the occurrence of individuals and dung is proportional to microhabitat availability (in terms of percentage cover). The χ^2 values were compared with the significant level ($P < 0.05$) for the degrees of freedom (df) calculated as:
(no. lines – 1) × (no. columns – 1) (Fowler et al. 1998).

Moreover, the relationship between number of seeds found in fox dung and the set of four microhabitats (bare soil, dwarf vegetation, shrub vegetation, perennial herb vegetation) was investigated using the predictive linear mixed-effects model. All "microhabitat" variables were included as fixed factors, and only "site" was considered as random factor (there were two sites, Cala Barca and Coscia di Donna). The model was simplified using an automated AIC-based (Akaike's Information Criterion) stepwise (backwards) approach (function "stepAIC" in package MASS) after fitting with ML (maximum likelihood) to find the most parsimonious model. Effects were extracted from final models refitted with REML (restricted maximum likelihood) (Zuur et al. 2009). The response variable (number of seeds found in each fox scat) was normalized by a Box-Cox Transformation (Box & Cox 1964), and a Gaussian error distribution with identity link function was selected (Engler et al. 2004). F statistics were used to test the significance of each variable retained in the reduced model.

We used the packages vegan (Oksanen et al. 2015), nlme (Pinheiro et al. 2015) and MASS (Venables & Ripley 2002) for the linear mixed modelling procedure in R (R Core Team 2015).

In the manipulative experiment, two-way ANOVA was used to test if there were significant differences in the number of germinated seeds and the time of survival of the emerged seedlings (one year after sowing), between the two origins of the seeds (mother plant vs. fox dung) and two microhabitats (chamaephytes vs. bare soil). Both analysed factors (origin of the seeds and microhabitats) were considered orthogonal and fixed.

Prior to our analyses, the homogeneity of variances was tested with a Cochran's *C*-test and, whenever necessary, data were appropriately transformed. Post-hoc Student Newman-Keuls tests (SNK, $P < 0.05$) were run to compare means of significant factors (Underwood 1997). ANOVAs were performed using the GMAV5 software package (University of Sydney).

RESULTS

First observational experiment: census of juniper juveniles

A total of 334 juveniles of juniper were censused: 175 at site 1, 9 at site 2, 43 at site 3, 90 at site 4, and 17 at site 5. The highest density of juveniles was found at site 4 (128.6 juveniles ha^{-1}).

Even though dwarf vegetation and bare soil showed similar average cover values (27.1 and 27.6 %, respectively), the highest percentages of juniper juveniles were detected in the dwarf vegetation (garrigue) microhabitat at all sites (average 60 %), ranging from 42.9 % at site 1 to 86 % at site 3. In contrast, the average percent juniper juveniles for the bare soil microhabitat was 30.3 %. The herbaceous microhabitat (not found at site 1) was the microhabitat with the highest average cover (38.6 %), but with the lowest average percent of juniper juveniles (3.4 %). In contrast, the shrubby microhabitat showed the lowest average cover (6.6 %), but hosted an average percent of juveniles that was similar to the herbaceous microhabitat (6.3 %, fig. 1).

The χ^2 test was performed for four sites. The exception was site 2, due to its low values of expected frequencies. The χ^2 test resulted in very significant probabilities at all sites for the garrigue microhabitat (i.e. we recorded more juniper juveniles than expected) (table 2). Bare soil and the shrub microhabitats usually showed χ^2 values that were not significant, with a few exceptions. In contrast to results from other microhabitats, the herbaceous microhabitat contained significantly fewer juveniles than expected.

Second observational experiment: distribution pattern and composition of fox dung

The count of Sardinian fox dung produced useful results only at study sites 1 and 3 (rocky habitat), where 87 and 76 dung were collected, respectively; only three dung were found at site 2 (sandstone habitat), while none were found at sites 4 and 5 (sandy habitat).

At the rocky habitat, the highest percentage of dung was detected in the dwarf vegetation (garrigue) microhabitat, which hosted > 80 % of the total sampled dung (fig. 2).

The χ^2 test resulted in very significant results for the rocky habitat, wherein the garrigue (dwarf vegetation) microhabitat contained much more dung than expected, almost four times what was expected for site 1 (table 3). In contrast to results from the dwarf vegetation microhabitat, the other microhabitats hosted fewer or same number of dung than expected.

At the study site 1, which was monitored over 131 days, we collected 87 fox scats, composed as follows: 63 % with only seeds of *J. turbinata*, 18 % with seeds of *J. turbinata*

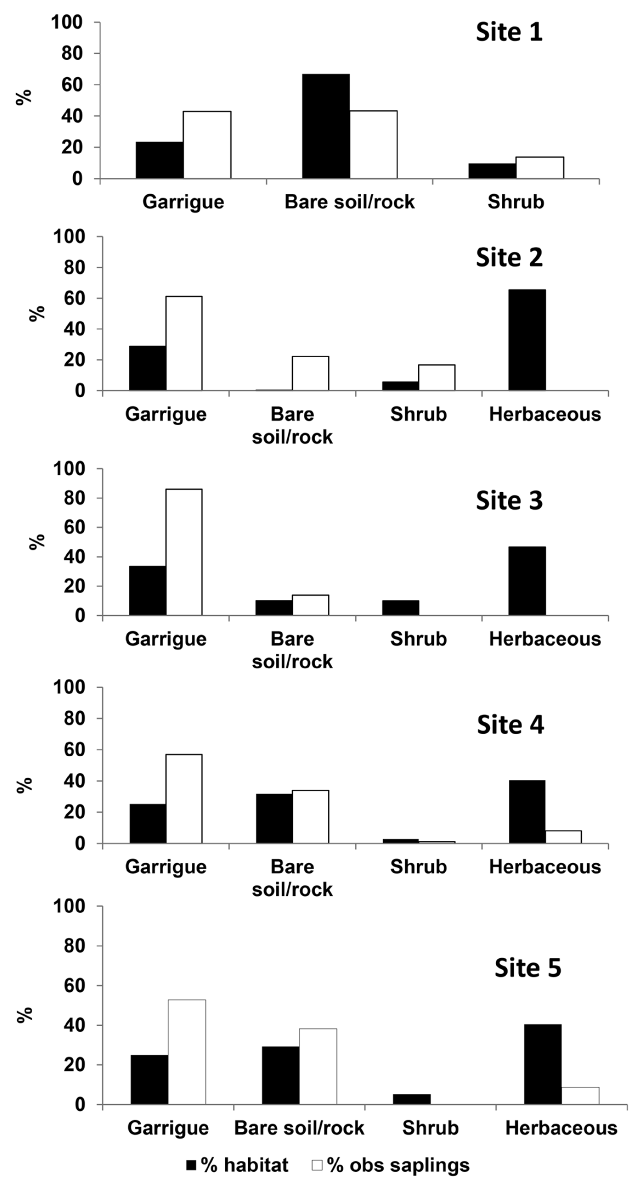

Figure 1 – Percentage of Phoenician juniper (*Juniperus phoenicea* subsp. *turbinata*) juveniles relative to the cover of each microhabitat type, by site.

Table 2 – Percentages of *J. turbinata* juveniles in various microhabitats and cover of each microhabitat at the five study sites. The values and levels of significance of partial χ^2 test are given. Juv. % = percentage of juveniles; df = 1; n.d. = not determined; n.s. = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$.

Microhabitat	Site 1 (N = 175)			Site 2 (N = 9)			Site 3 (N = 43)			Site 4 (N = 90)			Site 5 (N = 17)		
	Cover %	Juv. %	χ^2	Cover %	Juv. %	χ^2	Cover %	Juv. %	χ^2	Cover %	Juv. %	χ^2	Cover %	Juv. %	χ^2
Bare soil	66.8	43.4	40.9**	0.4	22.2	n.d.	10.0	13.9	0.7 n.s.	31.7	33.9	0.1 n.s.	29.3	38.2	0.5 n.s.
Dwarf vegetation	23.5	42.9	27.9**	28.7	61.1	n.d.	33.5	86.0	35.5**	25.1	56.9	36.2**	24.9	52.9	18.5**
Shrub vegetation	9.7	13.7	2.9 n.s.	5.6	16.7	n.d.	9.9	0.0	4.3*	2.7	1.1	0.8 n.s.	5.3	0.0	0.9 n.s.
Perennial herb	not present at this site			65.3	0.0	n.d.	46.6	0.0	20.0**	40.5	8.1	29.1**	40.5	8.8	4.2*

Table 3 – Percentages of Sardinian fox dung in various microhabitats and cover of each microhabitat in two study sites. The values and levels of significance of partial χ^2 test are given. df = 2 at site 1; df = 3 at site 3; n.s. = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$).

Microhabitat	Site 1 (N = 87)			Site 3 (N = 76)		
	Cover %	Dung %	χ^2	Cover %	Dung %	χ^2
Bare soil	66.8	11.5	39.8**	10.0	14.5	1.5 n.s.
Dwarf vegetation	23.5	88.5	156.5**	33.5	80.3	49.6**
Shrub vegetation	9.7	0.0	8.4*	9.9	1.3	5.6 n.s.
Perennial herb	not present at this site			46.6	3.9	29.7**

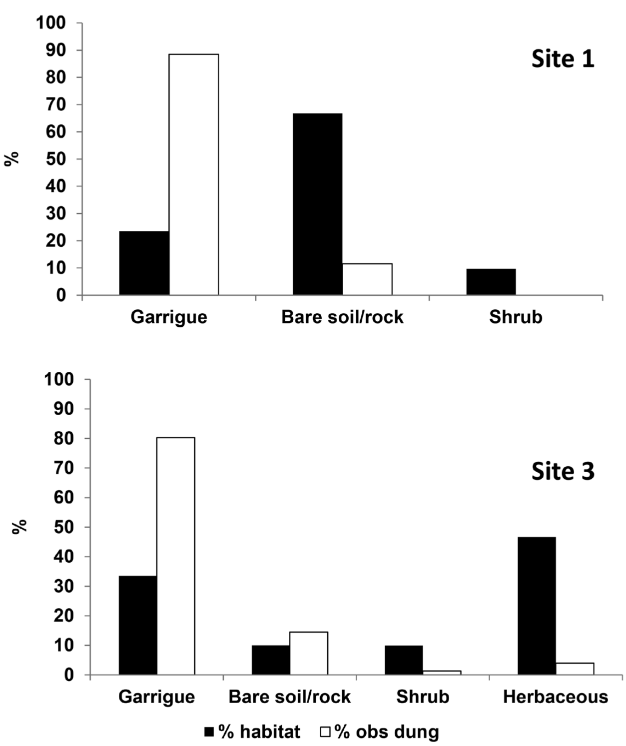

Figure 2 – Percentages of Sardinian fox (*Vulpes vulpes ichnusae*) dung and cover of each microhabitat type, at two sites.

and remains of vertebrates, 5 % with seeds of *J. turbinata* and remains of invertebrates, and 4 % with seeds of *J. turbinata*, dwarf palm (*Chamaerops humilis* L.), and other seeds. The remaining 10 % was constituted by other composition categories. At the study site 3, which was monitored over 107 days, we collected 76 fox scats, composed as follows: 70 % with only seeds of *J. turbinata*, 15 % with seeds of *J. turbinata* and remains of invertebrates, 10 % with seeds of *J. turbinata* and remains of vertebrates. The remaining 10 % of scat consisted of other categories of remains. A higher number of dung and combination of contents were found at site 1 than at site 3 (fig. 3).

We calculated that during the study period, *V. ichnusae* released 3 564 seeds of *J. turbinata* per hectare at site 1 and 10 457 seeds of *J. turbinata* per hectare at site 3. The mean daily release per hectare was 27.2 seeds d^{-1} at site 1 and 97.7 seeds d^{-1} at site 3 (table 4).

On average, the number of seeds found in fox dung was higher in the bare soil (116.5 seeds per fox dung) than the other microhabitats (84.9 seeds per fox dung in dwarf vegetation): predictive models verified that the number of seeds found in fox dung is slightly correlated with bare soil. It is the only response variable that is included in the reduced model and it is more closely related (F-value = 3.53, $P < 0.06$).

Table 4 – **Data on Sardinian fox dung and *Juniperus turbinata* seeds released at two study sites.**

	Site 1 (N = 87)	Site 3 (N = 76)
Average dung weight (g)	8.74 ± 0.58	9.13 ± 0.63
Average seed weight in one dung (g)	1.56 ± 0.18	1.49 ± 0.11
Average no. seeds per dung	73.74 ± 7.53	86.69 ± 6.44
No. total seeds	6415	6588
Hectares surveyed	1.8	0.63
No. days of survey	131	107
seeds ha^{-1}	3564	10457
seeds ha^{-1} day^{-1}	27.2	97.7

Manipulative experiment: germination and survival rates of *J. turbinata* seedlings in relation to their origin and microhabitat

The first seedling emerged on 16 Nov. 2012, four and half months after sowing to pots. Overall, 31 seedlings emerged from the 720 seeds planted, providing a percent germination of 4.3 % for *J. turbinata*. We observed a peak of seedling emergence between 5.5 and 7.5 months after sowing; this is between one and three months after first emergence.

Germination was not observed in 48 pots, of which 27 pots contained seeds from Sardinian fox dung. The maximum rate of seed germination (0.061 ± 0.016 seedlings per pot) was from *J. turbinata* seeds not ingested by fox, planted in bare soil. Seeds collected from mother plants germinated nearly two times more than seeds from dung of Sardinian fox (0.05 vs. 0.03 seedlings per pot, respectively). This result was due mainly to the very low germination rate of seeds collected from fox dung when planted in bare soil (H1, fig. 4A). The ANOVA test did not determine any significant effect of the analyzed factors (origin and microhabitat) nor for the interaction effect between the two factors on the germination of *J. turbinata* seeds (table 5).

The maximum survival time (24.43 ± 5.8 days), was recorded in the pots where seeds derived from Sardinian fox dung were sown under the canopy of *Helichrysum italicum*

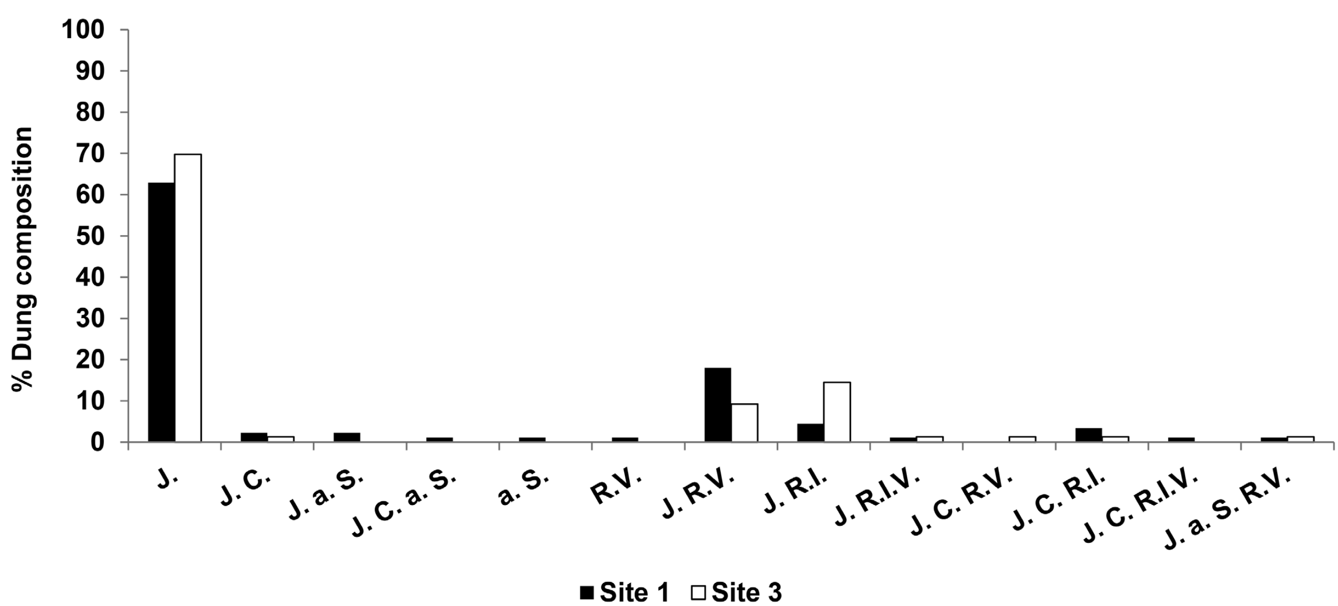

Figure 3 – Composition (%) of Sardinian fox (*Vulpes vulpes ichnusae*) dung at two study sites (site 1, N = 87; site 3, N = 76). Codes are as follows: J. = *J. turbinata*; J.C. = *J. turbinata* + dwarf palm; J.a.S. = *J. turbinata* + other seeds; J.C.a.S. = *J. turbinata* + dwarf palm + other seeds; a.S. = other seeds; R.V. = vertebrate remains; J.R.V. = *J. turbinata* + vertebrate remains; J.R.I. = *J. turbinata* + invertebrate remains; J.R.I.V. = *J. turbinata* + invertebrate/vertebrate remains; J.C.R.V. = *J. turbinata* + dwarf palm + vertebrate remains; J.C.R.I = *J. turbinata* + dwarf palm + invertebrate remains; J.C.R.I.V. = *J. turbinata* + dwarf palm + invertebrate remains + vertebrate remains; J.a.S.R.V. = *J. turbinata* + other seeds + invertebrate remains + vertebrate remains.

Table 5 – Two-way ANOVA, testing the differences between two origins of seeds (Sardinian fox dung vs. *Juniperus turbinata* mother plants) and two microhabitats (bare soil vs. chamaephyte) relative to the probability of germination and survival (in days) of *J. turbinata* seedlings.
N = 18 replicates per each treatment; 10 seeds were sown per replicate.

Source of variation	df	Germination			Survival		
		MS	*F*	*P*	MS	*F*	*P*
Origin	1	0.0095	2.42	0.1243	1.1449	0.47	0.4943
Microhabitat	1	0.0009	0.23	0.6337	16.4898	6.80	**0.0112**
Origin × Microhabitat	1	0.0062	1.57	0.2140	0.2997	0.12	0.7262
Residual	68	0.0039	–	–	2.4248	–	–
Transformation	–	Ln (×+1)	–	–	Ln (×+1)	–	–
Cochran's *C*-test	–	0.3778 n.s.	–	–	0.4204 n.s.	–	–

subsp. *microphyllum* (H2 in fig. 4B). Although the average survival rate of seedlings originating from the two seed stocks was very similar (13.1 days for seeds from fox dung and 12.1 days for seeds from mother plants), we observed dramatic differences in seedling survival for seeds obtained from fox dung, depending on the microhabitat in which they had been sown (fig. 4B): 1.8 days if sown in bare soil and 24.4 days if sown under the canopy of chamaephytes. The survival of seeds collected from mother plants was rather more uniform (9.3 days in bare soil and 14.9 days in *H. italicum* subsp. *microphyllum*).

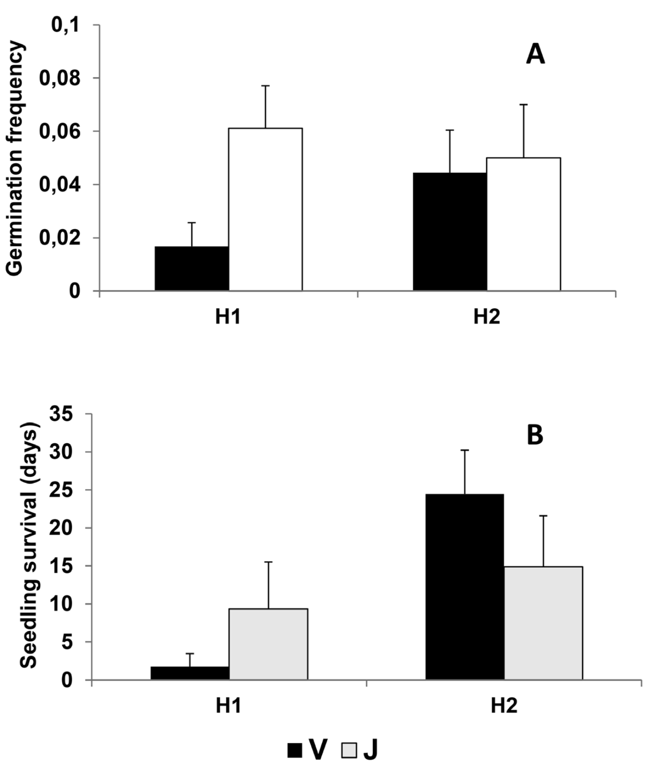

Figure 4 – Germination frequency of *J. turbinata* seeds (A) and time of survival of the emerged seedlings (B) between two origins of seeds (V = Sardinian fox dung vs. J = mother plants) and two microhabitat types (H1 = bare soil vs. H2 = chamaephyte). N = 18 replicates per each treatment; 10 seeds were sown per replicate.

The ANOVA test underscored a significant effect that microhabitat has on the survival of *J. turbinata* seedlings after emergence (table 5), but any significant effect of seed origin or for the interaction between the two analysed factors. The SNK test, related to the factor microhabitat (S.E. = 0.2595), revealed that H1 < H2 (i.e. the survival of *J. turbinata* seedlings after emergence was significantly higher in microhabitat 2-chamaephytes, than in microhabitat 1-bare soil).

DISCUSSION

We found that *V. ichnusae* is an important disperser for *J. turbinata* seeds in rocky, coastal habitats, where 63 % to 70 % of fox scat contained only juniper seeds, accounting for 16.3–17.8 % of total dung weight: each fox scat contained on average 73–86 *J. turbinata* seeds. As a consequence, we measured that foxes released, during autumn-winter months, 20–100 juniper seeds per hectare every day, and a total of 3 500–10 500 seeds per hectare over one winter season (table 4). Having measured a germination rate of 4.3 %, we can therefore estimate that *V. ichnusae* contribution to *J. turbinata* recruitment at Sardinian rocky sites was of 150–450 seedlings ha^{-1} yr^{-1}. Although active dispersal of both *J. macrocarpa* and *J. turbinata* seeds by carnivore mammals (including fox) has been described for continental Europe (Suárez-Esteban et al. 2013), detailed quantitative data about seed dispersal of *Juniperus* species by fox have only been reported for *J. thurifera* by Escribano-Ávila et al. (2012), who found 50–80 (maximum 143) juniper seeds per fox scat. This resulted in a seed rain of > 4 000 seeds ha^{-1} in one study site in Spain during one dispersal season (December–March). Thus, red fox contribution to *J. thurifera* recruitment was estimated to be 159 seedlings ha^{-1} yr^{-1} (Escribano-Ávila et al. 2014). These data help to close the so called "seed dispersal loop" (Wang & Smith 2002), because we not only measure the seed dispersal realized by frugivore mammals, but we also estimate dispersers contribution to the recruitment of fleshy-fruit plants.

Most studies have shown that the primary dispersers of juniper seeds are birds (Tellería et al. 2014), and only rarely do avian dispersers play a secondary role in juniper seeds dispersal (Otto et al. 2010). Even in cases where carnivore mammals have been detected as dispersers of juniper seeds, juniper seeds were usually very scarce in the mammal's faeces (Santos et al. 1999). However, in some areas, especially (but not exclusively) on some islands, mammals (Calisti et al. 1990, Lovari et al. 1994, Santos et al. 1999, Escribano-Ávila et al. 2013) and even reptiles (Otto et al. 2010, Rumeu et al. 2011) can be the primary disperser of juniper seeds. Nonetheless, the frequency and number of *J. turbinata* seeds we found in *V. ichnusae* dung were remarkable and can be probably explained by the absence (or rarity) of other edible, fleshy fruits ripening during the same time period as *J. turbinata*. In Mediterranean coastal environments, choices of edible fruit are probably limited for foxes if compared to the diversity of fruits available in temperate continental areas (D'hondt et al. 2011). The only other fleshy-fruited shrubs ripening during the autumn and winter seasons in our study sites were *Pistacia lentiscus* L. and *Phillyrea angustifolia* L., whose seeds were not found in the examined fox scat, and *Chamaerops humilis* whose seeds were found in low numbers.

The territorial behaviour of fox drives its choice of places to defecate (Trewhella et al. 1988). Foxes mark territories with urine and dung, which are deposited in visible places, such as on soil, stones, and dwarf vegetation, that might also be good olfactory spots. We demonstrated that in our study sites, fox preferentially defecates in a specific microhabitat (dwarf vegetation dominated by the cushion-forming chamaephytes), which, in turn influences the spatial dispersal of juniper seeds and seedlings survival. Other studies have also found that the red fox preferentially selects shrub-type microhabitats for defecation (Escribano-Ávila et al. 2013) and that such defecation patterns may positively influence juniper recruitment, especially in early successional habitats, thus leading to range expansion of juniper populations (Escribano-Ávila et al. 2014).

We found also that seed passage through a fox's gut did not improve (nor decrease) seeds germination rates due to scarification (via partial digestion). However, it is reasonable to expect that a fox's gut improves germination of intact fruit (Samuels & Levey 2005, Robertson et al. 2006). We found that germination rate was low (4.3 %), that in the wild only the 10–15 % of dung is deposited on the bare soil, whereas 80–90 % is released on dwarf vegetation (even if, inexplicably, scat deposited on the bare soil contained on average more juniper seeds than those released on dwarf plants), and that dwarf plants positively affect the survival of the emerged seedlings.

The role of *V. ichnusae* in the recruitment of *J. turbinata* in Sardinian coastal environments is not due to an enhancement of juniper seed germination or survival of juniper seedlings, but is due to the directional dispersal of seeds, through endozoochory, to a microhabitat that is most favourable to seedling survival. We can therefore consider the interaction between *J. turbinata* juveniles and chamaephytes as a case of facilitation (*sensu* Bruno et al. 2003) wherein *V. ichnusae* facilitates the directional dispersal of seeds. In a previous study some of us demonstrated secondary succession led to the expansion of the juniper vegetation over 88.5 % of site 1 within 50 years (Farris et al. 2009). Considering that we detected a germination percentage of 4.3 % in this study, we can estimate that the seed rain of 3 564 seeds ha^{-1} released in 131 days at site 1 produced 153 seedlings, of which 88.5 % emerged in the 23.5 % of the area, occupied by the garrigue microhabitat. On the basis of these data, we can now suggest *V. ichnusae* as the main driver of secondary succession, through a direct dispersal service, in the coastal environments where *J. turbinata* represents the potential natural vegetation (*sensu* Farris et al. 2010).

Despite fox's current role as a disperser of fleshy-fruit seeds of many plants from Mediterranean and temperate areas of Europe and Asia (Traba et al. 2006, Koike et al. 2008, D'hondt et al. 2011, Rico-Guzmán et al. 2012), fox only recently arrived on Mediterranean islands (Frati et al. 1998), In fact, fox was only introduced to Sardinia around the end of the 7th–6th millennium BC (Masseti 2009). The geographic distribution of the juniper species has changed dramatically during the last 11 500 years (Mao et al. 2010). During the Pleistocene (> 1 500 B.P.), species distributions were shifted far to the south of their current ranges and were limited to climatically-protected or lower-elevation areas (Petit et al. 2005, Jiménez-Moreno et al. 2013). During this time, the extinction of animals, including large birds able to disperse fleshy fruits, advanced with shifts in major vegetation belts and habitats (Blondel & Mourer-Chauviré 1998). Climatic-mediated vegetation changes, together with increasing human alterations that led to massive introduction of continental generalist mammals (Masseti 2009), disrupted many plant-animal interactions. Plant species that persisted after extinctions of their seed dispersers, had to evolve new interactions or develop other dispersal strategies (Hampe 2003, Calleja et al. 2009). The interaction between *V. ichnusae* and *J. turbinata* described in this paper can be considered a possible example of a recently-evolved mutualism in an insular setting under human influence (Pires et al. 2014). The biotic interaction here described can contribute to the genetic isolation of Sardinian populations of *J. turbinata*, as highlighted by Meloni et al. (2006).

Our data add quantitative experimental evidence to the relevant role of foxes as long-distance generalist dispersers of fleshy-fruited plants, particularly in human-shaped environments (López-Bao & González-Varo 2011, Suárez-Esteban et al. 2013, García et al. 2014). Conservation and management implications range from the maintenance and restoration of secondary succession processes at the landscape scale, because carnivore mammals with long-distance movements promote seed arrival to open habitats (Escribano-Ávila et al. 2014), to the conservation of single plant species strongly linked to fox for their dispersal and survival (Cancio et al. 2016).

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