

Vertebrate-mediated seed rain and artificial perches contribute to overcome seed dispersal limitation in a Mediterranean old field

Running head: Vertebrate-mediated seed rain in Mediterranean

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**Author contributions:** JR, TL, BM conceived and designed the research; TL, JR collected the data; SP, JR analyzed the seeds; RSB, GLV analyzed the data; RSB, TL wrote the manuscript and all authors revised and contributed to the final version

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/rec.13009

## ABSTRACT

Natural regeneration of vegetation is a frequent outcome of land abandonment, although the rate and diversity of such regeneration may be severely restricted by seed dispersal limitation, amongst other factors. In spite of this, studies aiming to quantify seed rain and test methods to enhance it, such as artificial perches, are still underrepresented in the Mediterranean. In our study, we quantified seed rain density and richness and tested the effects of artificial perches on such rain over a distance gradient on seven Mediterranean island old fields. In each of the seven sites, we positioned three sampling stations, each consisting of one seed trap under an artificial perch and one as a control on the ground, distributed at 30, 60 and 90 m from natural vegetation remnant. All traps received seeds, suggesting no overall dispersal limitation. Of the eleven seed species found, ten were fleshy-fruited and dispersed by vertebrates. Seed traps under perches received significantly higher seed rain of fleshy-fruited species dispersed by birds, while ground traps received significantly more seeds of the species also dispersed by mammals, especially *Rubus ulmifolius*. The distance from the seed source was non-significant in all cases. Our study demonstrate the key role of vertebrate-mediated seed dispersal services to overcome dispersal limitation in old fields, as well as the effective contribution of even small artificial perches in contrasting such limitation. The lack of differences over the distance gradient reveal that the upper spatial limit of dispersal limitation was not achieved.

Keywords: artificial perch, birds, fleshy-fruited species, natural regeneration, seed dispersal limitation

### Implications for practice

- Restoration programs should consider the seed rain provided by vertebrates as an indicator to evaluate the occurrence and magnitude of seed dispersal limitation.
- Unlike taller perches, the smaller ones used in our study are cheap and easy to install and transport, and actually increased the level of seed rain falling in old fields, proving to be a cost-effective restoration tool.
- The relatively homogeneous seed rain along the distance gradient indicates the minimum range where seed dispersal still active, useful to optimize the spatial design of mixed passive and active restoration.

## INTRODUCTION

Agriculture actually covers around 40% of the terrestrial ice-free surface, in most cases replacing the previous natural vegetation cover (Meli et al. 2017; Levers et al. 2018). On the other side, the abandonment of agricultural fields is growing in the last decades, especially in developed countries, already producing millions of hectares of old fields (Cramer et al. 2008; Pausas & Millán 2019). The restoration of at least a part of these old fields is necessary to re-equilibrate biodiversity, reestablish ecosystem services (e.g. carbon storage and hydrological control) as well as to achieve key international commitments such as Aichi targets in the Convention on Biological Diversity (Massa & La Mantia 2007; Ceausu et al. 2015; Butchart et al. 2016).

Active restoration (e.g. seeding and planting seedlings) has been widely employed and greatly contributes to vegetation recovery, although it may become unaffordable (e.g. lack of post-planting maintenance) or unsuccessful (e.g. lack of natural regeneration), especially in vast or harsh areas (Pausas et al. 2004; Pasta et al. 2012; Meli et al. 2017). Therefore, natural regeneration (i.e. passive restoration) is essential to improve vegetation recovery, and understand the mechanisms limiting or enhancing such regeneration is of great interest in restoration ecology (Meli et al. 2017; Badalamenti et al. 2018; Ssekuubwa et al. 2019).

Many old fields were cultivated and managed thoroughly over decades, centuries or even millennia, limiting or extinguishing seed bank and vegetative growth capacity (e.g. resprout) while increasing dispersal limitation dependency (Nathan & Muller-Landau 2000; Turnbull et al. 2000; Török et al. 2018). Assuming the presence of some natural vegetation remnants (seed source), seeds may fail to arrive in suitable sites due to the lack of dispersers or seed dispersal interactions, and such limitation generally increases as distance from the seed source increases (Clark et al. 1998; Saavedra et al. 2015; Valiente-Banuet et al. 2015).

In the Mediterranean region, woody, fleshy-fruited species are key components of the vegetation (Jordano 2000); consequently, animals, especially bird and mammals, play a decisive role in natural regeneration by dispersing their seeds (Herrera 1995; Ne'eman & Izhaki 1996; Escribano-Avila et al. 2014). Nonetheless, different animals may play different seed dispersal roles, as for example, mammals have a higher gut-retention time and are expected to deposit seeds more independently of vegetation structure, while birds have lower gut-retention time but may quickly cover longer distances, although they usually defecate or regurgitate seeds when perched on shrubs or trees (Pausas et al. 2006; Jordano et al. 2007; Escribano-Avila et al. 2014; García et al. 2016). Therefore, the availability of perching structures, such as trees and shrubs, help overcome dispersal limitation, and, at the same time, help promote differential contribution to the seed rain by accumulating more bird-dispersed species (Holl 1998; Pausas et al. 2006; Rost et al. 2009; Cavallero et al. 2013; Parejo et al. 2014). However, due to the common practice of removal of woody species in croplands, perches are usually absent (La Mantia et al. 2008; Pausas & Millán 2019). In cases such as these, artificial structures, like branch piles or artificial perches, may be useful in order to induce seed rain (Shiels & Walker 2003; Vogel et al. 2016; Castillo-Escrivà et al. 2019). Accordingly to a recent review, artificial perches did enhance seed rain richness and density and promoted higher recruitment (Guidetti et al. 2016 and references therein), despite some drawbacks such as poor seedling establishment have also been found (Graham & Page 2012; Heelemann et al. 2012). Additionally, tall perches may be costly and hard to transport and install, limiting their large-scale application (Graham & Page 2012), whereas no direct comparisons using small and tall artificial perches are available (Guidetti et al. 2016). Dispersal limitation has been detected as a barrier for regeneration also in the Mediterranean, and the use of artificial perches has been proposed to reduce such limitation (Vallejo et al. 2012). However, the majority of the studies with artificial perches were carried out in the tropics, whereas their effectiveness to

help the restoration of European and Mediterranean old fields remains largely unknown (Guidetti et al. 2016).

In Pantelleria, the intensive agriculture has a long history, but, in the last 80 years, the cultivated surface was gradually reduced from 80% to around 20% (La Mantia et al. 2007). Recruitment patterns of its typical Mediterranean vegetation have been evaluated in old fields terraces (La Mantia et al. 2008; Rühl & Schnittler 2011; Novara et al. 2013), although no details about the main process generating this recruitment (i.e. seed rain) are available so far. Here we aim to assess (1) the patterns of overall seed rain (2) the extent to which artificial perches enhance abundance and richness in the seed rain and (3) the extent to which this seed rain may be limited by distance from the seed source.

## METHODS

### Study site

Our study was carried out on Pantelleria, the largest of the Sicilian smaller islands (83 km<sup>2</sup>), located approx. 95 km from the mainland of Sicily and 67 km from the Tunisian coast (lat 36°48' N, long 11°59' E) (Fig.1). This volcanic island is characterized by mixed-relief terrain with a number of plain areas close to the coast, becoming hillier towards the center; the highest elevation is reached on Montagna Grande (836 m a.s.l.). Rock substrates are mostly acid, silicic volcanites (pantellerites and trachytes) (Civetta et al. 1984) and soils on the island are mainly Lithosols, Regosols and Andic brown soils. The climate is typically Mediterranean with an average annual rainfall of 409 mm and mean monthly temperatures ranging between 11.7 to 25.6°C (Gianguzzi 1999). The woody vegetation on Pantelleria is characterized by typical Mediterranean maquis, composed in total by 49 species, but with high dominance of *Quercus ilex* (holm oak) and fleshy-fruited shrubs and small trees such as *Phillyrea latifolia* (Mock privet), *Arbutus unedo* (Strawberry tree), *Pistacia lentiscus* (Lentisk), *Myrtus communis* (Common myrtle),

*Daphne gnidium* (Lax-leaved daphne), *Lonicera implexa* (Evergreen honeysuckle) and *Rubus ulmifolius* (Elmleaf blackberry) (Gianguzzi 1999). The vegetation and the geomorphology of the island have been intensively modified by humans for many centuries, mainly to supply the need for wood and to create more suitable conditions for agriculture, especially with the construction of terraces to increase farmland (Pasta & La Mantia 2003).

At the beginning of the 20<sup>th</sup> century, more than 80% of the island was used for agriculture, mostly viticulture; however, nowadays, for a number of socio-environmental reasons, cultivated land has fallen to less than 20%, with caper monocultures being the main crop (Rühl et al. 2005; La Mantia et al. 2008). On those abandoned lands, secondary succession is taking place and formerly cultivated areas are being recolonized by spontaneous vegetation (La Mantia et al. 2008; Novara et al. 2013). In Pantelleria, potentially frugivorous animals are mostly rats (*Rattus sp.*), rabbits (*Oryctolagus cuniculus*), nesting, migrant and wintering birds (e.g. Blackbird *Turdus merula*, Song Thrush *T. philomelos*, European Robin *Erithacus rubecula*, Sardinian Warbler *Sylvia melanocephala*, Eurasian Blackcap *S. atricapilla*, Garden Warbler *S. borin*, Common Redstart *Phoenicurus phoenicurus* and Black Redstart *P. ochrurus*), and lizards (Massa et al. 2015).

### **Seed rain on the old fields**

We assessed the cumulative seed rain in two consecutive fruiting seasons (September – April) in the years 2011-2012 and 2012-2013 in seven different sites located in the south-east of Pantelleria (Fig. 1, Table S1). All selected sites were abandoned ( $\pm 10$  years) grapes and caper orchards, that have never been burned or used as pasture, with actual vegetation composed mostly by grasses and forbs, with woody cover limited to small ( $< 1$  m tall) scattered shrubs covering no more than 15% of the surface (Rühl et al. 2005; La Mantia et al. 2008; Rühl & Schnittler 2011). All seven sites have a common border with a patch of

relatively homogeneous Mediterranean maquis, belonging to the *A. unedo* and *Erica arborea* (Tree heath) maquis physiognomy (Gianguzzi 1999), and share the same geological substrate (acid silicic vulcanites) (Civetta et al. 1988; Di Figlia et al. 2007) and the same Thermo-Mediterranean Upper Arid bioclimate (Gianguzzi 1999).

At each of the seven sites we set three sampling stations, each comprising a pair of seed traps, made of a round plastic tray 60 cm in diameter (0,17 m<sup>2</sup>), installed along a distance gradient of 30, 60 and 90 m from the maquis patch (Fig. 2). At each sampling station, one trap was located underneath a 1.5 m high wooden perch with a 20 cm wooden stick on the top. The seed trap was elevated at around 100 cm in order to assess exclusively bird seed rain and the perch effect. The other seed trap was located on the ground, in order to include terrestrial seed dispersers, at a distance of 10 m from the seed trap under the perch (Fig. 3). The cost of each artificial perches was around 4 euros and they were obtained in a local market. In total we installed 21 seed traps under perches and 21 seed traps on the ground. All seed traps had small holes covered with a plastic sheet to permit water drainage but capture the seeds; they were also covered with wire mesh (1x1cm) to prevent secondary seed removal or predation. Seed traps were never placed under or close to woody vegetation cover (vine or caper plants, isolated small shrubs).

### **Seed collection and processing**

The traps were verified four times each season and all feces and seeds present were collected in tagged plastic bags indicating the date, site, type and distance of the seed trap. In the laboratory, the feces were dried at 30°C for three days, carefully broken apart, and all seeds were identified and counted with the aid of metal sieves (2 mm) and magnifying lenses. Wind-dispersed seeds were discarded as the aim of the study only concerned vertebrate-mediated seed dispersal.

To facilitate identification, we collected a sample of fruits of each species of fleshy-fruited plants present on the maquis patches and cleaned the seeds to make a reference collection. The species were assigned to a seed dispersal type based on the main types of animals recorded as dispersing seeds (birds or mixed birds and mammals), according to classifications by Jordano (1995) and Ne'eman & Izhaki (1996) as well as one species (*Genista sp.*) with dry fruit was classified as gravity seed dispersal (barochory).

### **Data analyses**

Our analysis was performed in two steps. First to test the effects of season, tray type (perch or ground), distance and their interaction on overall seed rain density and richness we used a two-way ANOVA. Subsequently, we pooled data from the two seasons, excluded the gravity dispersed species (*Genista sp.*) due to low sample size in perches ( $n = 3$ ) and performed separated two-way ANOVA to focus on bird and mixed-dispersed seeds. We included the interaction of tray type and distance based on the assumption that seed traps under perches would receive a lower seed rain density and richness as distance from the seed source increased, since comparative studies reported that bird seed dispersal should be more constrained by distance than mammals seed dispersers (e.g. Jordano et al. 2007). Due to the low sampling size of perch and ground seed traps per distance class per site, we did not include site as an effect in the models, but we checked for overall seed-rain density and richness differences between sites using a one-way ANOVA and a Tukey HSD test. Seed density data were not normally or Poisson distributed ( $p < 0.001$ ), thus to meet ANOVA assumptions, seed density was log-transformed before each analysis and richness data were analyzed within a GLM after verifying the Poisson distribution of data. In all cases, we considered  $p < 0.05$  as being statistically significant. All analyses were performed with R version 3.5.1 (R Core Team 2018).

## RESULTS

### Seed rain density and richness

During the two sampling seasons, we collected 5,857 seeds in the seed traps, belonging to 11 families from 11 species, nine from native species present on the maquis and two from cultivated species (Common grape vine *Vitis vinifera* and Caper bush *Capparis spinosa*) present in the surrounding old fields (Table 1). Three species accounted for 88% of seeds, headed by *R. ulmifolius* with 3,312 (56.7%), while *C. spinosa* and *D. gnidium* had the lowest occurrence with 41 (0.68%) and 37 (0.63%) seeds, respectively (Table 1).

All traps received at least one seed, with an average density of 801.3 ( $\pm$  1,027.3 SD) seeds/m<sup>2</sup>. The average seed richness in the traps was five species ( $\pm$  1.7 SD), ranging from one to as many as nine on a single trap. Shrubs were the predominant life form in the dispersed seeds with five species, followed by trees with three, vines with two and one herbaceous plant (Table 1). *P. lentiscus* presented the most widely distributed seed rain, reaching 93% of the seed traps, while *C. spinosa* and *Genista* sp. were recorded in only 7% of the traps.

Ten species found in the traps have fleshy fruits that are dispersed by vertebrates: six species being dispersed by birds and four by mixed bird and mammals, while one species (*Genista* sp.) has dry fruits, probably carried on by the wind or accidentally by animals (Table 1). We recorded no significant effect of seasons on overall seed-rain density ( $F = 1.85$ ,  $p = 0.18$ ) and richness ( $X^2 = 0.65$ ,  $p = 0.62$ ), and data of the two seasons was pooled in the subsequent results. Overall seed-rain density differed between sites ( $F = 3.47$ ,  $p = 0.008$ ), although the Tukey test showed that just site D differed from sites A and B (Supporting information Fig. S1). Richness in turn varied marginally ( $X^2 = 12.6$ ,  $p = 0.05$ ).

### Artificial perches versus ground seed traps over the distance gradient

We found no significant differences in the overall seed rain richness ( $X^2 = 0.69$ ,  $p = 0.41$ ) and density ( $F = 1.27$ ,  $p = 0.26$ ) in the traps located under perches or on the ground, with all 11 species found in both trap types (Table 1, Table S2). However, when comparing the density of the different dispersal types, perches received more bird-dispersed seeds ( $F = 4.86$ ,  $p = 0.03$ ) while plants with mixed-dispersal type had a higher density on ground traps ( $F = 10.13$ ,  $p = 0.003$ ; Table S2; Fig. 4). Richness, in turn, did not vary among seed traps under perches or at the ground in both bird and mixed dispersal plants ( $p > 0.05$ ; Table S2). Of the 2,985 seeds found in the ground seed traps, 39% were extracted from rats and rabbits feces, whilst for the remaining seeds, the disperser was not clearly identifiable. However, bird feces were also found in ground seed traps, demonstrating that birds also contributed to seed rain on the ground. The plant species with the clearest pattern were *C. spinosa* and *Prasium majus* (White hedge-nettle) with only 2.5% and 6.8% of seeds found under perches, respectively. The opposite was observed for *D. gnidium*, with only 2.7% of seeds found in the ground seed traps.

As regards the distance gradient, we found no significant differences in all comparisons (Table S2; Fig. 5). Furthermore, the interaction of tray type and distance was also not significant for overall, bird and mixed-dispersal models (Table S2).

## DISCUSSION

### Dispersal limitation and seed rain

Dispersal limitation has been found to be a constraint for Mediterranean old fields restoration (Pausas et al. 2006; Rost et al. 2009). In our study, despite the disproportionate contribution of each plant species, 16% of the traps received from two to eight seeds, and 84% received more than 17 seeds. This finding suggests that, in the studied period and distance scale, Pantelleria old fields seems to be not suffering from dispersal limitation of the most abundant fleshy-fruited species present in the maquis. Nonetheless, *Olea*

*europaea* var. *sylvestris* (Wild olive), *L. implexa* and *Smilax aspera* (Common smilax), were absent in the traps but present in the maquis and recruited in the old fields, as well as the very high seed rain of *Rubus ulmifolius* seems uncoupled with their lower cover values (La Mantia et al. 2008; Rühl & Schnittler 2011). On the other side, the high seed rain density of the typical maquis species (*A. unedo*, *D. gnidium*, *P. lentiscus*, *P. latifolia* and *M. communis*) seems to reflect the recruitment patterns found on those studies. Considering the complexity and spatio-temporal fluctuations on the way from seed dispersal to effective establishment, such consistent and inconsistent patterns may be expected (Jordano & Herrera 1995; Rey & Alcántara 2000). In our study, the observed seed rain was generated by birds, rats, rabbits, but probably also lizards. Despite being unable to identify the bird species dropping the seeds, probably *T. merula*, *T. philomelos*, *E. rubecula* and members of *Sylvia* genus are among the main dispersers, as they are the most abundant frugivorous birds on Pantelleria (Massa et al. 2015). Furthermore, the three most abundant dispersed plants, *R. ulmifolius*, *R. peregrina*, and *P. lentiscus*, are known to be highly consumed, and consequently dispersed, by those birds (Herrera 1995; Nogales et al. 2013; González-Varo et al. 2014); a relationship also verified elsewhere in Sicily (R. S. Bueno, unpublished data). In Pantelleria, all the most common frugivorous mammals found in the Mediterranean, such as foxes, badgers, and martens, are absent, whereas rats and rabbits are highly abundant (Vari 2008). These two species are reported to act as both seed dispersers and seed predators (Delibes-Mateos et al. 2008; Shiels 2011); however, judging by the number of intact seeds collected from their feces, their seed dispersal role, at least for the small-seeded species, is certainly significant in Pantelleria. On the Mediterranean islands, lizards are important components of seed dispersal networks (Rodríguez-Pérez et al. 2005; González-Castro et al. 2012). In Pantelleria, we can assume this also to be true. The local species (*Podarcis siculus*) may be contributing to seed dispersal of different species (Rodríguez-Pérez et al. 2005; Nogales et al. 2013) and particularly regarding the

dissemination of *C. spinosa*. On a neighboring volcanic island (Linosa), lizards are reported to be the main dispersers of this species (Fici & Lo Valvo 2004).

### **Effectiveness of artificial perches**

Considering all eleven species found in the seed traps (overall seed rain), we found no significant differences between seed density and richness under perches or at ground level (Table S2). This result was unexpected, considering that, usually, perches receive greater seed rain (Guidetti et al. 2016) and that usually, birds tend to avoid open areas such as those where our perches were installed (González-Varo et al. 2014; García et al. 2016). Other studies, for example, found consistent seed rain under perches, whereas seed limitation was detected outside perches (Shiels & Walker 2003; Graham & Page 2012). Our sampling design, with seed traps located on the ground, contributed to such lack of difference, once we were able to detect the strong influence of ground seed dispersers (e.g. rabbits and rats). For example, ground traps received more than twice the quantity of *R. ulmifolius* seeds than perches, many retrieved from their feces. Additionally, all six species typically dispersed by birds were also found in the ground seed traps. However, considering only bird-dispersed species, perches indeed received a higher seed rain (Figure 4). The height of our perches (1.5 m) is below the average height ( $\pm 3$  m) of perches used in other studies (Guidetti et al. 2016), and is much smaller, and consequently cheaper and easier to be installed, than some similarly designed artificial perches (e.g. Holl 1998; Graham & Page 2012). Despite direct comparisons of artificial perches with different heights are lacking, the small one used in our study indeed demonstrated to be a valuable tool in increasing seed rain in abandoned areas also in typical Mediterranean communities (Vallejo et al. 2012). For a more in-depth analysis of the actual role of perches in restoration from a community-wide perspective, however, it is important to consider seed

fate, given that higher seed rain is not always associated with higher recruitment (Graham & Page 2012; Heelemann et al. 2012; de Almeida et al. 2016).

### **Influence of distance**

Distance to the source of seeds has been identified as a key factor in determining seed rain intensity, with most seeds falling close to the source (Cubiña & Aide 2001; Parejo et al. 2014; Oliveira et al. 2018). However, in our study, distance neither influenced seed rain density nor richness. Other studies would seem to corroborate our results, finding limited or no distance effects on seed-rain density, even over greater distances (up to 2500 m), although some changes in species composition were observed (Rost et al. 2009; Graham & Page 2012; Zwiener et al. 2014; Guidetti et al. 2016). Seed-disperser identity and behavior matters in this case, as for example, Holl (1998) observed the higher frequency of birds using perches located far from the forest than closer ones, although only a small subset of the bird-species pool used those perches. Another potential explanation for this lack of distance influence is that our distance gradient maybe not far enough to detect distance limitations, as even mobility-restricted birds, such as warblers, can fly up to 100 m (Jordano et al. 2007). Furthermore, considering the geographical position of Pantelleria, we cannot exclude the potential contribution of highly mobile migrant birds, such as thrushes (Viana et al. 2016).

Variations in the fruiting landscape are also known to influence bird habitat use and seed rain, where a fruit rich matrix can attract frugivorous animals in a disproportionate way (Escribano-Avila et al. 2014; Martínez & García 2015). However, this is not the case for our sites, given that all old fields were deprived of such fruits, causing no ulterior attraction effect. In any case, further studies covering a wider distance gradient and applying novel techniques, such as DNA barcoding (González-Varo et al. 2017), must be made in order to verify the degree of functional and spatial redundancy or complementarity of seed dispersal services provided by each species (Bueno et al. 2013).

In Sicily, the role played by vertebrates in the spread of seeds has been observed in the past (Pistone 1890), although its application in restoration ecology has been widely underestimated throughout the Mediterranean (Méndez et al. 2008). In Pantelleria, almost all past reforestations were carried out using mainly pines and eucalyptus, without the use of native fleshy-fruited plants; a pattern found also in many other Mediterranean reforestations (Pausas et al. 2004; Vallejo et al. 2012). These homogeneous reforestations are easily subject to degradation and show almost no positive increase in biodiversity over time (La Mantia & Pasta 2001; Pasta et al. 2012). In contrast, the few examples available of restoration using native species have given excellent results (La Mantia et al. 2012). This effective but costly option, however, may be unnecessary on those areas where seed rain is not a limiting factor. Despite the fact that even a single tree can trigger re-naturalization processes (La Mantia & Bueno 2016), conserving and recreating diversified seed source patches across the landscape (e.g. adopting a mosaic configuration) is key in order to guarantee the natural regeneration potential via seed dispersal.

In conclusion, our results demonstrated the importance of seed dispersal by vertebrates in generating the intense seed rain arriving in Pantelleria old fields, suggesting that dispersal limitation may not be a constraint for vegetation recovery even up to 90 m from the natural vegetation remnant. Despite the relevant seed rain on the ground traps, the artificial perches greatly enhanced seed rain of bird-dispersed species, bringing with it a different species composition and demonstrating to be a valid tool for restoration also in the Mediterranean.

### **Acknowledgements**

This paper is dedicated to the memory of Vincenzo Gabriele, known as Vincenzo Spata who said to Tommaso La Mantia: “The Sardinian warbler is the worst enemy of farmers

because it feeds on berries and distributes seeds everywhere”. We dedicate also to all farmers of Pantelleria that respected the seeds traps and work hard the field. Special thanks to Salvatore Pasta for the help in many phases of research, Giovanni Bonomo for the logistic support and for his fantastic “passito” and Broni Hornsby for the English review. This work was financially supported by the MIUR-PRIN project “Climate change mitigation strategies in tree crops and forestry in Italy” (CARBOTREES) and for recent bird observations we thank the Site d’Etude en Ecologie Global, Pantelleria - CNRS as well as BioDivMex Mistrals program.

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Table 1. Species of seed collected in the seed traps in Pantelleria with presence (x) or absence at the seven sites (A to G), percentage of the total abundance (%), mean density (seeds/m<sup>2</sup>) and standard deviation (SD) of seeds. Mixed main disperser represents dispersal by both birds and mammals.

Family	Specie	Life form	Main dispersers	Fruit type	A	B	C	D	E	F	G	%	Mean density ( $\pm$ SD)
<b>Native</b>													
Rosaceae	<i>Rubus ulmifolius</i>	Shrub	Mixed	Berry	x	x	x	x	x	x	x	56.7	463 ( $\pm$ 802)
Rubiaceae	<i>Rubia peregrina</i>	Vine	Bird	Berry	x	x	x	x	x	x	x	13.2	108 ( $\pm$ 225)
Anacardiaceae	<i>Pistacia lentiscus</i>	Tree	Bird	Drupe	x	x	x	x	x	x	x	13.1	105 ( $\pm$ 219)
Ericaceae	<i>Arbutus unedo</i>	Tree	Mixed	Berry	x	x	x	x	x	x	x	5.7	46 ( $\pm$ 93)
Oleaceae	<i>Phillyrea latifolia</i>	Tree	Bird	Drupe	x	x	x	x	x	x	x	2.9	18 ( $\pm$ 26)
Fabaceae	<i>Genista</i> sp.	Shrub	Gravity	Dry		x			x			2.2	11 ( $\pm$ 52)
Myrtaceae	<i>Myrtus communis</i>	Shrub	Bird	Drupe	x				x	x	x	0.9	7 ( $\pm$ 21)
Lamiaceae	<i>Prasium majus</i>	Herb	Bird	Drupe				x	x	x	x	0.8	6 ( $\pm$ 34)
Thymeliaceae	<i>Daphne gnidium</i>	Shrub	Bird	Drupe	x	x	x			x	x	0.6	5 ( $\pm$ 14)
<b>Cultivated</b>													
Vitaceae	<i>Vitis vinifera</i>	Shrub	Mixed	Berry	x	x	x		x	x	x	3.0	24 ( $\pm$ 48)
Capparidaceae	<i>Capparis spinosa</i>	Vine	Mixed	Berry			x				x	0.7	5 ( $\pm$ 35)

## Figure captions

Figure. 1 – Location of Pantelleria Island and the seven study sites (A – G). See table S1 for further site details.

Figure 2. Sampling design with three sampling stations composed of paired seed traps, one under a perch and one on the ground distributed over the distance gradient in each of the seven study sites in Pantelleria.

Figure 3. Example of the seed trap under the artificial perch and seed trap on the ground located in the old fields in Pantelleria.

Figure 4. Boxplots indicating the median (horizontal line), 25–75% quartiles (box) and 5–95% centiles (whiskers) of the seed density (log) in the perch and ground seed traps between birds and mixed seed dispersal types.

Figure 5. Boxplots indicating the median (horizontal line), 25–75% quartiles (box) 5–95% centiles (whiskers) and extreme values of the seed density in the ground and perch seed traps over the distance gradient. All comparisons were non-significant ( $p > 0.05$ ).

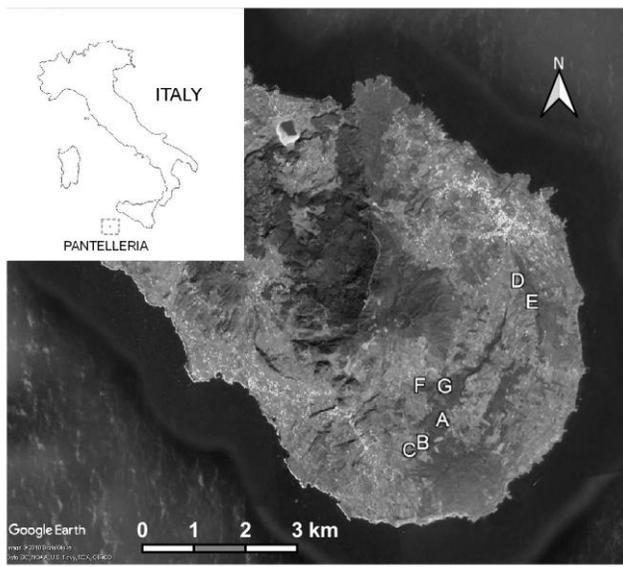


Figure. 1

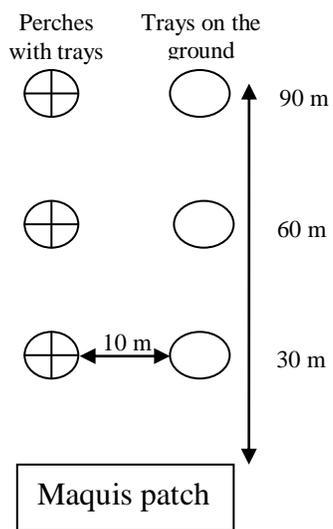


Figure 2



Figure 3

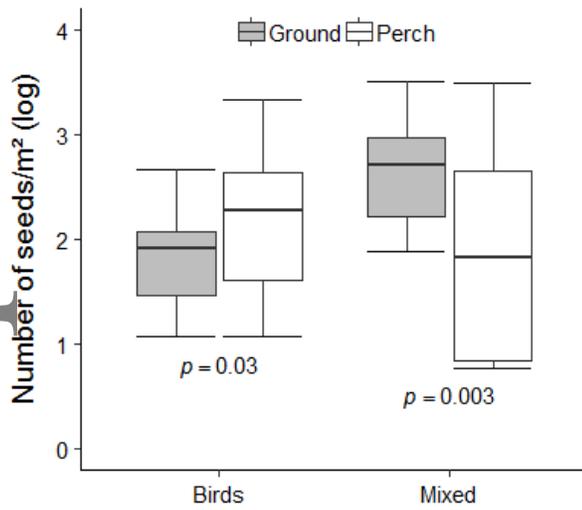


Figure 4.

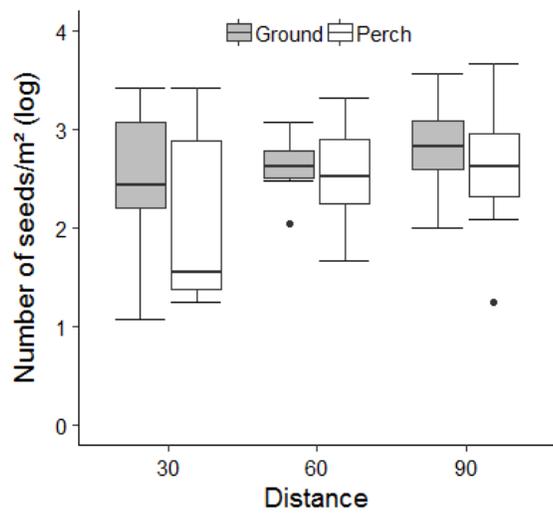


Figure 5.