

## Covariation in diaspore mass and dispersal patterns in three Mediterranean coastal dunes in southern Spain

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**Abstract:** The coastal dunes of southern Spain are an original Mediterranean ecosystem, insufficiently studied under dispersal. This study explores covariation patterns among diaspore mass, size, morphology, dispersal mode, and spatial dispersal in 78 native coastal dune species. Three coastal dunes under different climates were sampled and differentiated between fixed and mobile dunes. The Pérez-Harguindeguy methodology was applied and ANOVA, Kruskal–Wallis, and Mann–Whitney U tests were used in order to analyze the covariation. Diaspores were essentially small seeds or achenes (2–4 mm, from 10–5 to 1 g). The study revealed that diaspore mass is a key trait in the differentiation among dunes. Diaspore sizes vary between fixed and mobile dunes, and the smallest diaspores were overrepresented in Mediterranean-subdesert and in mobile dunes. The dispersal mode differed between the dunes and between fixed and mobile dunes. Anemochory was greater in Mediterranean-subdesert (50%) compared with Mediterranean-oceanic (8.5%) and Mediterranean-subtropical (9.5%) dunes and with mobile dunes (46.4%). Restricted dispersal is overrepresented in Mediterranean-oceanic dunes whereas developed spatial dispersal is in subdesert dunes. It has been shown how coastal dunes under variations in the Mediterranean climate could show differences of dispersal traits. Mobile dunes show dispersal patterns closer to those found in Mediterranean-subdesert dunes.

**Key words:** Antitelechoric mechanisms, coastal dunes, diaspore mass, dispersal modes, Mediterranean vegetation, spatial dispersal

### 1. Introduction

Seed dispersal and seed mass are critical criteria regulating the spatial and temporal distribution of plants and determine many key aspects in plant life (Weiher et al., 1999) and in ecological conservation (Haddad et al., 2003).

Dispersal involves both fitness costs and benefits that may vary with spatial scale. The cost/benefit evolutionary strategy of dispersal is clearly important in the establishment of a species in critical environmental habitats, such as the coastal dunes. Gadgil (1971) suggested that an organism should disperse over long distances if the gain from the chance of reaching a better habitat exceeds the loss from risk of death during dispersal. Plants producing well-dispersed seeds experience a high risk of landing in unsuitable sites (Bonte et al., 2003). In contrast, plants with poorly dispersed seeds experience a high risk of density stress from abundant neighbor siblings. Such plants reduce the seed number to reduce the competition and at the same time produce bigger seeds that should produce larger, more competitive plants (Watkinson and Harper, 1978). This scenario is applicable for the

Mediterranean oceanic and subtropical coastal vegetation of southern Spain, especially that on stable fixed dunes (Herrera, 1995).

The evolution of diaspore dispersal under progressive heterogeneous habitats of mobile dunes is highly nonlinear and can lead to the coexistence of different dispersal strategies (Baguette et al., 2012). The high costs of dispersal produce divergent pressures by simultaneous selection against dispersal propensity, i.e. the probability to leave a suitable habitat patch selecting for increased dispersal abilities (Poethke and Hovestadt, 2002), or the ability to travel across unsuitable habitats and to locate suitable habitats from a distance (Bonte et al., 2010). Consequently, more specialized dispersal modes are expected for mobile dunes. For example, wind, as a specialized long-distance dispersal mode, is considered as the most efficient agent of dispersal in plants inhabiting mobile dunes (Maun, 2009).

High ecological diversity in terms of environmental heterogeneity and variability of species composition is among the features that distinguish coastal dune vegetation (Van der Maarel, 1993). Plants growing in coastal dunes

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exhibit various morphological and ecophysiological characteristics that depend on the dune types. Dune type is defined on the basis of the distance from the coast (e.g., mobile/semifixed close to the sea and fixed inland dunes) (Liu et al., 1996). Each dune type has a special vegetation structure (Da Silva, 2011). Fixed dunes have more dense vegetation, dominated by shrubs and trees, and represent a mature climax stage. However, mobile dune vegetation is more open and is constituted by more pioneer communities of perennial herbs and small shrubs that are adapted to survive the intense disturbance associated with the proximity of the sea (Costa-Pérez and Valle-Tendero, 2004). Plants growing closer to the coast suffer from low availability of nutrients, salt spray, and substrate mobility.

The coastal Mediterranean dunes are particularly fragile and vulnerable as a result of the dual threat posed by coastal erosion and human impact (Cori, 1999). For example, *Juniperus* sp. communities, which characterize the Mediterranean-oceanic and -subtropical coastal dunes, and *Ziziphus lotus* communities, which characterize the Mediterranean-subdesert dunes, are among the most endangered coastal communities in southern Spain. These communities and their habitats are catalogued as priority for conservation according to Red Natura 2000 (Ministry of Environment and Rural and Marine Affairs, 2009). Although the dimensions of these communities are narrow, their functions are important and irreplaceable (Martinez et al., 2013).

Despite the knowledge of dispersal modes being vital to the study of coastal dune ecology (Poschold and Bonn, 1998; Maun, 2009), limited studies focusing on the assessment of the dispersal traits in the Mediterranean coastal dunes (Costa-Pérez and Valle-Tendero, 2004) have been carried out to date. The objective of this study deals with the exploration, for the first time, of patterns of (co)variation of dispersal mode, diaspore mass, size, morphology, and spatial dispersal in 78 perennial species on coastal dunes in southern Spain with differences within the Mediterranean macroclimate (Mediterranean-oceanic, Mediterranean-subtropical, Mediterranean-subdesert) and between dune sectors (mobile semifixed and fixed dunes). The selection of the study area in southern Spain offers the interesting opportunity to study these ecosystems under different conditions of the Mediterranean macroclimate and different oceanic influences (from transitional dunes between the Atlantic Ocean and the Mediterranean Sea to typical Mediterranean dunes). Consequently, the results obtained in the present work go beyond the regional scope and could be useful at a larger scale.

Antitelechoric mechanisms (Ellner and Schmid, 1981; van Rooyen et al., 1990; van Rheede van Oudtshoorn and van Rooyen, 1999) include bradyspory, myxosperry, and synaptosperry, which protect diaspores from predation

and other dangers and regulate the intra- and interyear timing of dispersal and germination (Gutterman, 2001). At the same time, plant life traits and dispersal modes have been proposed to affect the dispersal phenology (Snow, 1965). This study assesses covariation in dispersal patterns of Mediterranean coastal dunes in southern Spain that follow the same tendency as the lowland Mediterranean scrublands. It also attempts to ascertain how antitelechoric mechanisms are developed in response to the particularity of this coastal habitat.

Although zoochory and secondary dispersal by vertebrates are considered complementary relevant dispersal modes in fixed dunes (Couvreur et al., 2005) and important mechanisms in sand stabilization (Dellafiore et al., 2006; Gallego-Fernández et al., 2015), this is the first attempt to investigate the biotic dispersal in Mediterranean-oceanic and -subtropical dunes where trees and large shrubs are predominant (Costa-Pérez and Valle-Tendero, 2004). Trees and large shrubs tend to produce zoochoric large seeds (Jurado et al., 1991) and play an important functional role in the mature stage of ecosystems (Díaz and Cabido, 1997).

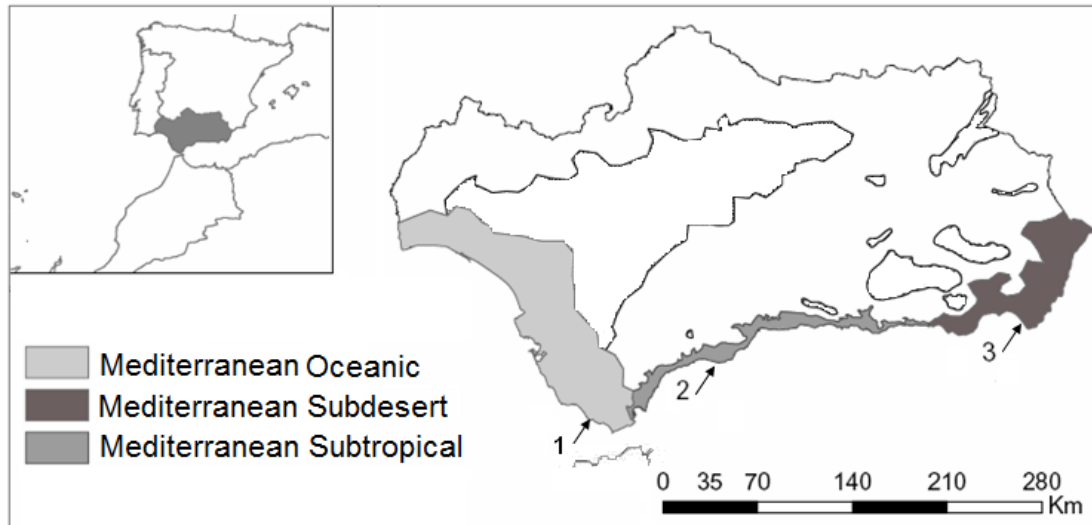
The hypothesis that dispersal patterns in coastal dunes could be affected by climate and sea proximity was tested in order to answer the following question: do dispersal traits and dispersal patterns differ among coastal dunes and dune types with different Mediterranean macroclimates? Moreover, it was tested whether all the studied dunes follow the predominant dispersal trends of other coastal dune ecosystems (e.g., spatial dispersal by the wind; Maun, 2009). Finally, it is expected that in Mediterranean-subdesert dunes, aridity promotes spatial dispersal over restricted areas according to other arid ecosystems (Navarro et al., 2006, 2009; Pueyo et al., 2008).

## 2. Materials and methods

### 2.1. Study area and species set

This study was carried out in three coastal dunes in southern Spain with different Mediterranean climates (DERA, 2013): Parque Natural (P.N.) del Estrecho in Cádiz (Mediterranean-oceanic climate) (52 species), Monumento Natural (M.N.) de Artola-Cabopino in Málaga (Mediterranean-subtropical) (34 species), and Parque Nacional Cabo de Gata-Níjar in Almería (Mediterranean-subdesert) (24 species) (Figure 1).

Climatic data were obtained from Alcaraz and Peinado (1987). In P.N. del Estrecho, the average annual rainfall is 794 mm, with maximum values in November (133 mm) and minimum in August (0 mm). Annual temperatures are milder than in the other two dunes (mean minimum of 13.4 °C in January and mean maximum of 23.5 °C in August). M.N. Artola-Cabopino has an average annual rainfall of 659 mm, with a similar rainy season to P.N. del



**Figure 1.** Climate areas in southern Spain and study areas. Black arrows show the study areas: 1) P.N. del Estrecho, 2) M.N. Artola-Cabopino, 3) P.N. Cabo de Gata-Níjar. Data source: DERA (2013).

Estrecho. P.N. Cabo de Gata-Níjar has the driest dunes (average annual rainfall of 308 mm) and a different rainy season (maximum rainfall values are observed in March and December, 40 mm). Across the climatic data studied and as a mean, January was the coldest month (mean minimum of 12.5 °C) and August the hottest (mean maximum 24.5 °C).

Data samplings were made on 78 major representative perennial species with the highest cover values in the three coastal dunes studied (Van der Maarel, 1993; Costa-Pérez and Valle-Tendero, 2004). Field sampling and phenological observations were carried out in the three dunes studied monthly between December 2010 and November 2014 following the methodology put forward by Orshan (1989). Voucher specimens of the studied species were stored in the MGC Herbarium. Botanical nomenclature follows that of Castroviejo (1986–2007).

## 2.2. Dispersal traits

In this study the term “diaspore” was used to refer to the dispersal unit (Weiher et al., 1999). A diaspore was categorized to either disperse as a seed or an entire fruit. When a fruit is dehiscent, the diaspore was described as seeds. The diaspore disperses as an entire unit when fruits are indehiscent.

The dispersal traits were studied for 20 diaspores from each species. For species with small dispersal units, 100 diaspores were studied from a minimum of 20 individuals and measured following the methodology of Pérez-Harguindeguy et al. (2013). The measurements were taken on the whole diaspore when it had morphological structures (e.g., pappus, hairs) (van Rheede van Oudtshoorn and van Rooyen, 1999).

Dispersal modes were distinguished following van der Pijl (1982). We considered that species with developed spatial dispersal are those whose diaspores are equipped with structures that facilitate spatial dispersal, such as flying structures (dispersed by abiotic vectors) or nutrient structures (dispersed by biotic vectors) (Ellner and Schmid, 1981). Species with restricted dispersal lack dispersal-enhancing characters in their diaspores (Willson, 1993). Seawater dispersal species were determined based on the work of García-Mora et al. (1999). Seasonality of dispersal (diaspore release time) was studied on a minimum of 10 individuals of each species following Orshan (1989).

Species, taxonomic family, growth forms, diaspore mass, size, type and morphology, antitelechoric mechanism, dispersal mode, spatial dispersal, and seasonal diaspore release time are available in the Appendix.

## 2.3. Statistical analysis

Diaspore mass was  $\log_{10}$ -transformed prior to statistical analysis in order to normalize the distribution. The Kolmogorov–Smirnov test confirmed the normality assumptions ( $P > 0.05$ ). Two-way analysis of variance (ANOVA) was applied after verifying the homogeneity of variance by Levene’s test ( $P > 0.05$ ) to assess the significant differences in seed mass (as a dependent factor) using dune type (fixed and mobile) and Mediterranean macroclimate type (M-oceanic, M-subtropical, and M-subdesert) as independent factors (fixed effects). To assess the significant differences of the categorical traits between the three studied coastal dunes and the two dune types, Kruskal–Wallis and Mann–Whitney U tests were used.

Ballistic and ombrohydrochoric species were not used in the analyses due to their low frequencies (Appendix). All statistical analyses were performed with SPSS 15.0 (SPSS Inc.).

### 3. Results

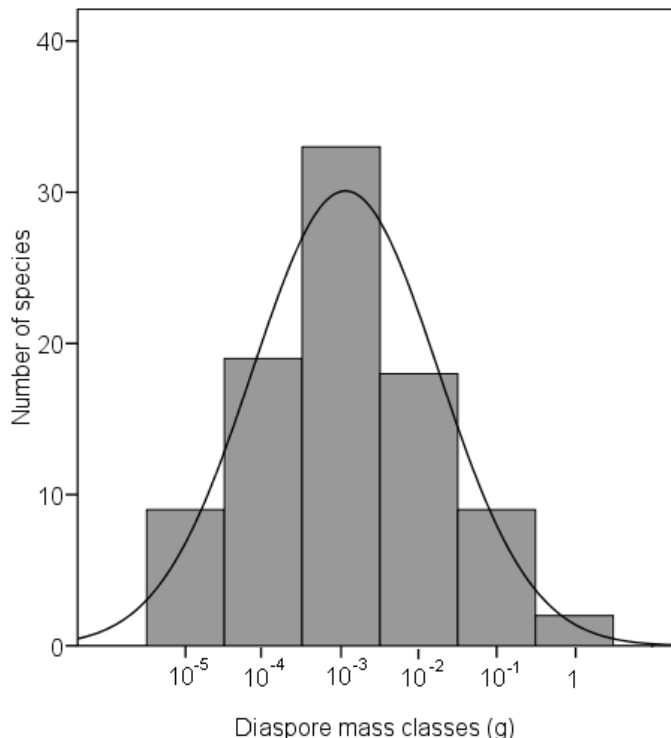
#### 3.1. Variation of diaspore mass, size and type

The diaspore mass ranged from 7492.22 mg in *Quercus coccifera* to 0.02 mg in *Erica scoparia*; both are in M-oceanic fixed dunes (Appendix). The frequency distribution of diaspore mass classes on a logarithmic scale produced an approximately normal distribution between  $10^{-5}$  and 1 g. The class of  $10^{-3}$  was predominant (36.7%) (Figure 2).

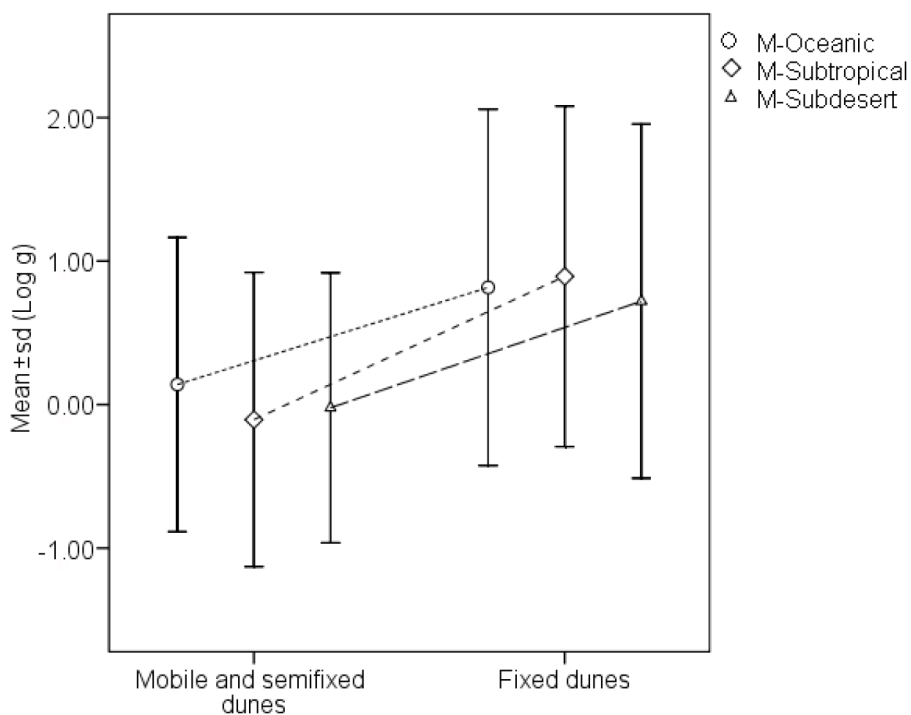
Two-way ANOVA showed that diaspore mass varied significantly between dune types ( $F = 8.32$ ,  $P < 0.01$ ), but not among the three coastal studied dunes ( $F = 0.39$ ,  $P > 0.05$ ). Diaspore mass was greater in fixed compared to mobile dunes (Figure 3). Diaspore mass spanned  $10^5$  ranges in fixed dunes (from  $10^{-5}$  to 1 g), but only spanned  $10^3$  ranges in mobile/semifixed dunes (from  $10^{-5}$  to  $10^{-2}$  g). The heaviest diaspores were in fixed M-subtropical dunes while the lightest were in mobile/semifixed M-subdesert dunes (Appendix).

Kruskal–Wallis tests indicated that differences in diaspore size were significant between the two dune types (fixed vs. mobile/semifixed) ( $K = 5.37$ ,  $P < 0.05$ ), but not among the three coastal studied dunes ( $K = 0.38$ ,  $P < 0.05$ ). In fixed and mobile/semifixed dunes the frequency of species with tiny diaspores was greater than that of species with the largest diaspores. The ratio between species with tiny to those with the largest diaspores was 1.6 in fixed dunes, but it was 5.5 in mobile dunes. Species with small diaspores (2–4 mm) were more represented in all three studied dunes compared to species with the other size categories. Species with larger diaspores were more represented in M-oceanic than in M-subtropical and in M-subdesert dunes (Figure 4a). The ratios between species with tiny (<2 mm) to those with large (>10 mm) diaspores were 2.6, 1.7, and 4 in M-oceanic, M-subtropical, and M-subdesert dunes, respectively.

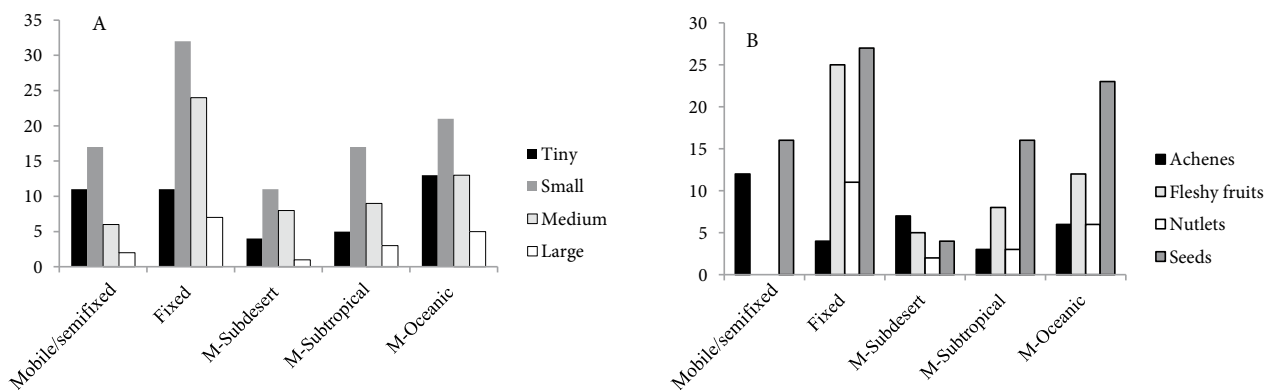
Kruskal–Wallis tests indicated that the difference in diaspore type (seeds vs. fruits) was significant between the three studied coastal dunes ( $K = 6.49$ ,  $P < 0.05$ ), but not for dune types ( $K = 0.64$ ,  $P < 0.05$ ). Fruits are more represented than seeds on the three fixed studied dunes. For M-oceanic and M-subtropical mobile dunes, there were no significant differences between species producing fruits and seeds, but



**Figure 2.** Diaspore mass distribution of studied species in Mediterranean coastal dunes of southern Spain. The Kolmogorov–Smirnov test confirmed the normality assumption.



**Figure 3.** Variation of diaspore mass (mean ± sd) of studied species among studied Mediterranean coastal dunes in southern Spain and dune types.



**Figure 4.** Variation of dispersal traits among studied Mediterranean coastal dunes in southern Spain and dune types. The numbers (y-axis) represent species frequency. A) Diaspore size. B) Diaspore type.

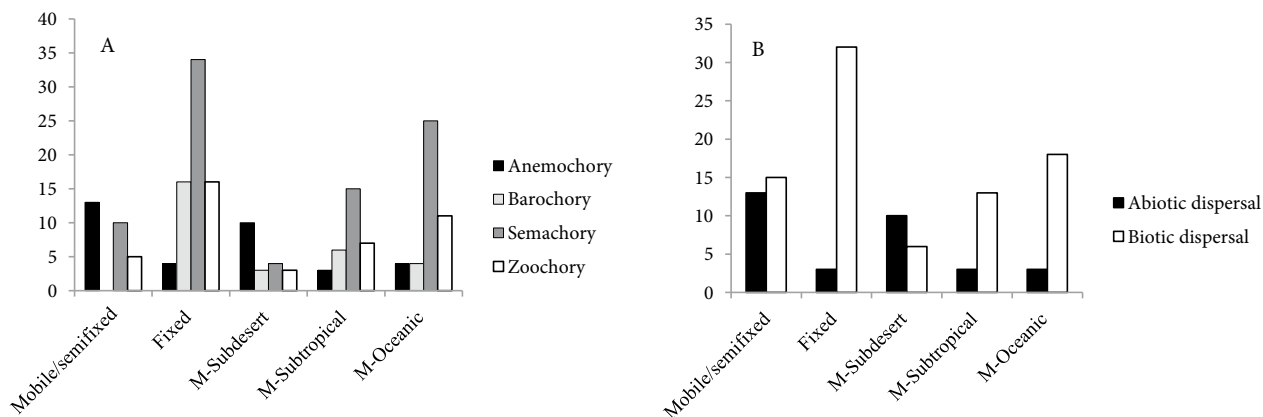
species with fruits were overrepresented in M-subdesert dunes (Table).

Kruskal–Wallis tests showed that the fruit types varied significantly between the three studied coastal dunes ( $K = 7.09, P < 0.05$ ), but not between dune types ( $K = 0.12, P < 0.05$ ). Occurrence of seeds was more frequent in M-oceanic and M-subtropical than in the M-subdesert dunes. However, the reverse was true for occurrence of achenes (Figure 4b). The ratio of species with achenes vs. seeds was 1.8 in M-subdesert and 0.4 and 0.3 in M-oceanic and M-subtropical dunes, respectively.

Regarding the dune types, plants with fleshy fruits and nutlets were represented by 37.3% and 16.4% of total species studied respectively in fixed dunes, but they were not represented in the mobile dunes. In addition, species with achenes were three times greater in mobile than in fixed dunes, but species with seeds were 68% greater in fixed than in mobile/semifixed dunes.

### 3.2. Variation of dispersal mode and spatial dispersal

The dispersal mode differed significantly among the three studied coastal dunes ( $K = 13.17, P < 0.05$ ) and between dune types ( $U = 1.26, P < 0.01$ ). The proportion of species



**Figure 5.** Variation of dispersal traits among studied Mediterranean coastal dunes in southern Spain and dune types. The numbers (y-axis) represent species frequency. A) Dispersal mode. B) Spatial dispersal.

**Table.** Percentages of some important dispersal traits in the studied species in Mediterranean coastal dunes of southern Spain.

Dispersal traits	M-Oceanic		M-Subtropical		M-Subdesert		Fixed		Mobile and semifixed		Total	
	N	%	N	%	N	%	N	%	N	%	N	%
Dispersal unit												
Fruits	30	56.6	17	51.5	21	84.0	44	62.0	24	60.0	68	61.3
Seeds	23	43.4	16	48.5	4	16.0	27	38.0	16	40.0	43	38.7
Total	53	100	33	100	25	100	71	100	40	100	111	100
Diaspore morphology												
Hooked appendages	3	9.1	2	9.5	1	11.1	1	2.4	5	22.7	6	9.5
Without appendages	30	90.9	19	90.5	8	88.9	40	97.6	17	77.3	57	90.5
Nutrient structures	15	78.9	10	76.9	5	45.5	30	90.9	0	0.0	30	75.0
Open balloons	0	0.0	0	0.0	1	9.1	1	3.0	0	0.0	1	2.5
Pappus	3	15.8	2	15.4	4	36.4	2	6.1	5	71.4	7	17.5
Wings	1	5.3	1	7.7	1	9.1	0	0.0	2	28.6	2	5.0
Total	19	100	13	100	11	100	33	100	7	100	40	100
Antitelechory mechanisms												
Bradyspory	24	57.1	19	57.6	10	40.0	43	58.9	10	37.0	53	53.0
Synaptospermy	14	33.3	10	30.3	13	52.0	23	31.5	14	51.9	37	37.0
Myxospermy	4	9.5	4	12.1	2	8.0	7	9.6	3	11.1	10	10.0
Total	42	100	33	100	25	100	73	100	27	100	100	100
Spatial dispersal												
Restricted	31	59.6	18	52.9	8	33.3	39	52.7	18	50.0	57	51.8
Developed	21	40.4	16	47.1	16	66.7	35	47.3	18	50.0	53	48.2
Total	52	100	34	100	24	100	74	100	36	100	110	110

with anemochory was significantly greater in M-subdesert (50%) than in M-oceanic (8.5%) and M-subtropical (9.5%) dunes. Similarly, anemochory was predominant in mobile dunes (46.4%) compared to fixed dunes (5.7%) (Figure 5a). Of the total anemochoric species, 78% were found in M-subdesert mobile dunes. Conversely, semachoric species were overrepresented in M-oceanic (48.1%) and M-subtropical (44.1%) dunes compared to M-subdesert dunes (16.7%). Barochoric species were similarly represented in fixed dunes, but were absent in mobile dunes (Appendix).

Kruskal–Wallis tests showed that the spatial dispersal did not vary significantly among the three studied coastal dunes ( $K = 4.53$ ,  $P > 0.05$ ) or between the two types of dunes ( $K = 0.07$ ,  $P > 0.05$ ). Nevertheless, species with restricted dispersal were more represented in fixed and mobile M-oceanic dunes, while the reverse was true in the M-subdesert dunes. There were no differences between the proportions of species with restricted and developed spatial dispersal in the M-oceanic dunes (Table). The frequency of plants with developed spatial dispersal was twice that of restricted dispersal in M-subdesert dunes, but was only 67% and 89% of restricted dispersal in M-oceanic and M-subtropical respectively (Table).

Spatial dispersal (biotic vs. abiotic) varied significantly between the three studied dunes ( $K = 11.93$ ,  $P < 0.05$ ) and between the dune types ( $U = 114.51$ ,  $P < 0.05$ ). Biotic dispersal was significantly overrepresented, compared to abiotic, in M-oceanic and M-subtropical dunes, but the reverse was true in M-subdesert dunes (Figure 5b). In addition, biotic dispersal was more than 10 times greater than abiotic dispersal in fixed dunes, but abiotic dispersal was only 2.6 times greater than biotic in the mobile dunes. In the M-oceanic and M-subtropical fixed dunes, no abiotic dispersal was recorded, but more than one-third of the species of M-subdesert dunes have abiotic dispersal (Appendix).

### 3.3. Variation of the antitelechoric mechanisms

The presence of antitelechory did not differ significantly between the three studied coastal dunes ( $K = 1.93$ ,  $P > 0.05$ ), but it did vary between the dune types ( $K = 4.54$ ,  $P < 0.05$ ). Species with antitelechoric mechanisms were overrepresented in the three fixed studied coastal dunes (100% in M-subdesert and 69.27% in M-subtropical dunes) (Appendix). Bradispority is the only antitelechoric mechanism with significant differences among the three studied coastal dunes ( $K = 8.84$ ,  $P < 0.05$ ) and between dune types ( $U = 149.52$ ,  $P < 0.01$ ). It was less represented in mobile than in fixed studied dunes (Table).

### 3.4. Seasonal pattern of dispersal

In coastal dunes dispersal occurs all year, except for seawater species (Appendix). Synchrony at the time of diaspore release was more pronounced in June (53.63%). Small shrubs with restricted dispersal, dry seeds, and those without antitelechoric mechanisms had distributed dispersal time in hot, dry months from June to September with a peak in July (80.36% of the total small shrubs studied).

In contrast, large shrubs with spatial dispersal delayed diaspore release, with fleshy fruits showing maximum values of dispersal at the end of summer, between September (89.47%) and October and November (83.33%). These species synchronized the time of diaspore release to the beginning of the rainy months (Appendix).

## 4. Discussion

The present study highlighted, for the first time, differences in dispersal traits among different types of dunes (in terms of climate and mobility). It has been shown how coastal dunes under variations in the Mediterranean climate could show differences of dispersal traits. Mobile dunes show closer dispersal patterns to those found in M-subdesert dunes (P.N. Cabo de Gata-Níjar) according to results found for leaf functional traits (Rodríguez-Gallego et al., 2015) and for phenological plant traits (Rodríguez-Gallego and Navarro, 2015).

The frequency of diaspore mass distribution of the coastal dunes species of southern Spain showed normal distribution (between  $10^{-5}$  and 1 g), which coincided with the distribution of diaspore mass in other dune ecosystems, such as Indiana dunes (Mazer, 1989) and sandy soils in China (Zhao et al., 2011). The approximately normal distribution of seed mass on a log scale means that selection favors relatively small seeds (the class of  $10^{-3}$  g), which are more common, compared to relatively large ones. The dominance of smaller diaspore mass could be explained in light of the harsh, nutrient-limited habitats of the coastal dunes, where the selection of species with small seeds reflects strong competition for resources (Cordazzo, 2006). Comparisons between five temperate floras spanning three continents indicated that seeds above 100 mg tend to be adapted for dispersal by vertebrates, seeds below 0.1 mg tend to be unassisted, and seeds between 0.1 and 100 mg could be dispersed by wide ranges of dispersal modes (Westoby et al., 1996). The seed masses of most species of the dunes of southern Spain are mostly within the third group (0.1–100 mg), indicating the possibility of the occurrence of different dispersal modes.

The results of this study indicated the dominance of the larger and heavier diaspores in M-oceanic and M-subtropical dunes, and the smaller ones in M-subdesert

dunes. Such mass and size variation could be explained in light of the relationship between the resources required for diaspore development and plant growth forms. Fixed M-oceanic and M-subtropical dunes are characterized by greater proportions of larger, heavier seeds and they are dominated by trees and large shrubs (Appendix). Larger seeds require larger species that support them with more resources, help them to disperse, and provide them with more time to mature (Jurado et al., 1991; Navarro et al., 2008). However, species from mobile dunes are smaller shrubs with small diaspores.

Long-distance dispersal in the coastal dunes is crucial to allow successful colonization on newly formed suitable patches, especially those exposed to unpredictable environmental conditions on mobile dunes (Guterman, 2001; Maun, 2009). Under such conditions, wind has been considered as the most efficient agent of dispersal (Maun, 2009). The shorter shrubby vegetation on the mobile dunes adopts wind as a main dispersal agent (Fenner, 2000; Navarro et al., 2008). In our study, wind dispersal was predominant in small shrubs of M-subdesert dunes and in mobile dunes (e.g., *Phagnalon saxatile*, *Launaea* sp., *Salsola* sp., *Crucianella maritima*). These species have synastospemic diaspores mainly dispersed during the harshest months (June and July), but they extend their diaspore dispersal until December–March (Appendix), widening the window of germination and establishment (Navarro et al., 2008). Synastospemy combined with wind dispersal and secondary dispersal by vertebrates has been shown to be an important strategy of protection of seeds during their transport (Navarro et al., 2009).

The results of the study indicated the dominance of the developed spatial dispersal in M-subdesert fixed dunes according to other arid ecosystems (Navarro et al., 2008; Pueyo et al., 2008). The dominance of the developed spatial dispersal could be attributed to efficient utilization of the spatiotemporal variable and to the reduction of competition between offsprings and consequently the increase in overall fecundity.

The results of this study indicate that more than 86% of the species of the mobile dunes are dispersed through abiotic modes, in accordance with Castley et al. (2001). The most common dispersal mode in the mobile dunes is anemochory (36.1%), followed by semachory (27.8%). In both modes, winds are very important in dispersing the seeds. It is interesting to note that species from mobile dunes are dispersed only by pappi (71.4%) and wing structures (28.6%). This further emphasizes the importance of abiotic dispersal by winds and minimizes the importance of biotic dispersal in the mobile dunes.

Diaspore dispersal is restricted and controlled by vegetation density in the fixed dunes (Watkinson and

Harper, 1978; French et al., 2011). The results obtained indicated that diaspore dispersal in the fixed M-oceanic and M-subtropical dunes has an interplay between restricted dispersion, mainly semachory, and more developed dispersal through vertebrate dispersal. Around 90% of the species of fixed dunes produce fruits with nutritive structures. In addition, 78.9% and 76.9% of the species of the M-oceanic and M-subtropical dunes, respectively, produce nutritive diaspores, compared with only 54.5% in M-subdesert dunes. The nutritive structures usually attract animals, directly (zoochory) or secondarily by vertebrates when seeds are dispersed by gravity (barochory). Couvreur et al. (2005) indicated that zoochory is a more developed mechanism in denser coastal dune vegetation and should be important in fixed M-oceanic and M-subtropical dunes. This mechanism was considered as a critical dispersal mode for the maintenance of coastal dunes through the dispersal of climax woody plant species (Castley et al., 2001).

The results also showed that 48% of the species of studied M-oceanic dunes and 44% of species of M-subtropical dunes had semachoric dispersal. This restricted dispersal mode allows more seeds to fall around maternal plants and hence foster the kin competition. Under such conditions, mother plants impose seed dormancy to stagger the germination of offspring to circumvent density-dependent competition (Ellner, 1986). It has been reported that mother plants produce some allelochemicals that regulate dormancy (e.g., prevent germination) until the prevailing of the favorable conditions for germination and seedling establishment (Preston and Baldwin, 1999).

Seawater is an important and occasionally specialized long-distance dispersal mode in four species inhabiting the mobile dunes (*Eryngium maritimum*, *Euphorbia paralias*, *Medicago marina*, and *Otanthus maritimus*). When diaspores of these species swell they can be carried with storms or floods to the sea for long periods (Yang et al., 2012). Nevertheless, they can be carried back to coasts where they might be established (van der Maarel, 1993; Yang et al., 2012). These species develop additional dispersal modes, such as the zoochory (epizoochory) in the case of *Eryngium maritimum* and *Medicago marina*, and ballistic dispersal for *Euphorbia paralias* and semachory dispersal in *Otanthus maritimus*. The presence of multiple dispersal modes in species inhabiting the mobile dunes enables them to survive the spatially and temporally unpredictable conditions of these habitats.

This study includes a detailed characterization of dispersal traits in southern Spain's coastal dunes, which will help to develop our knowledge about these vulnerable ecosystems. Seed collection for restoration projects should be carried out during the months when the



highest number of species is in the dispersal phase (June–September), which coincides with the maximum touristic use of these environments. Species of restricted dispersal and antitelechoric mechanisms should be carefully observed in conservation planning, and in the case that these species are located on mobile/semifixed dunes, they may be protected by fences.

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**Appendix.** Diaspore size (length): tiny, <2 mm; small, 2–4 mm; medium, 4–10 mm; large, >10 mm. Antitelechoric mechanism: B, bradyspory; M, myxosperry; S, synaptosperry. Spatial dispersal: RD, restricted dispersal; DDA, developed spatial dispersal by abiotic vectors; DDB, developed spatial dispersal by biotic vectors.

		Growth forms	Diaspore mass (mg)	Diaspore size	Diaspore type	Diaspore morphology	Antitelechoric mechanism	Dispersal mode	Spatial dispersal	Time of dispersal (diaspore release time)
Mediterranean-oceanic dunes (P.N. del Estrecho)										
Fixed dunes	<i>Adenocarpus telonensis</i>	LS	5.66 ± 0.85	Large	Seed	Nothing	Absent	Semachory	RD	Apr–Jun
	<i>Calamintha nepeta</i> subsp. <i>nepeta</i>	H	1.64 ± 0.04	Medium	Nutlet	Nothing	Absent	Semachory	RD	Jan–Dec
	<i>Calicotome villosa</i>	LS	10.59 ± 1.80	Small	Seed	Nothing	Absent	Semachory	RD	Jun–Aug
	<i>Calluna vulgaris</i>	SS	0.06 ± 0.01	Tiny	Seed	Nothing	Absent	Semachory	RD	Nov–Apr
	<i>Cistus albidus</i>	LS	1.21 ± 0.22	Tiny	Seed	Nothing	B	Semachory	RD	Jun–Jan
	<i>Cistus crispus</i>	SS	0.47 ± 0.15	Tiny	Seed	Nothing	B	Semachory	RD	Aug–Feb
	<i>Cistus ladanifer</i>	LS	0.36 ± 0.02	Tiny	Seed	Nothing	B	Semachory	RD	May–Dec
	<i>Cistus monspeliensis</i>	SS		Small	Seed	Nothing	B	Semachory	RD	Jun–Nov
	<i>Cistus salvifolius</i>	LS	1.27 ± 0.24	Tiny	Seed	Nothing	B	Semachory	RD	Jun–Dec
	<i>Cytisus striatus</i>	LS	3.89 ± 0.32	Small	Seed	Nothing	M	Semachory	RD	Aug–Oct
	<i>Corema album</i>	SS	77.75 ± 13.53	Medium	Berry	Nutrient structures	S, B	Zoochory	DDB	Jul–Oct
	<i>Chamaerops humilis</i>	LS	931.83 ± 164.37	Medium	Drupe	Nutrient structures	B	Barochory	DDB	Sep–Dec
	<i>Daphne gnidium</i>	LS	6.40 ± 1.98	Small	Berry	Nutrient structures	S	Zoochory	DDB	Aug–Mar
	<i>Dianthus broteri</i>	SS		Small	Seed	Nothing	Absent	Semachory	RD	Jul–Sep
	<i>Erica scoparia</i>	SS	0.02 ± 0.01	Tiny	Seed	Nothing	Absent	Semachory	RD	May–Aug
	<i>Fumana thymifolia</i>	SS	1.32 ± 0.13	Small	Seed	Nothing	M	Semachory	RD	Jun–Jul
	<i>Galium tricornutum</i>	SS	6.28 ± 1.57	Small	Achene	Hooked appendages	S, B	Zoochory	DDB	Sep–Dec
	<i>Halimium halimifolium</i>	LS	0.47 ± 0.10	Tiny	Seed	Nothing	M, B	Semachory	RD	Jun–Sep
	<i>Juniperus oxycedrus</i> subsp. <i>macrocarpa</i>	T	986.92 ± 159.89	Large	Galbulus	Nutrient structures	S, B	Barochory	DDB	Jan–Dec
	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	T	475.3 ± 59.03	Medium	Galbulus	Nutrient structures	S, B	Barochory	DDB	Jan–Dec
	<i>Lavandula stoechas</i>	SS	0.61 ± 0.06	Medium	Nutlet	Nothing	B	Semachory	RD	Jun–Nov
	<i>Lonicera implexa</i>	LS	11.56 ± 1.25	Small	Berry	Nutrient structures	S, B	Zoochory	DDB	Sep–Nov
	<i>Marrubium vulgare</i>	SS	0.9 ± 0.22	Medium	Nutlet	Nothing	Absent	Anemochory	RD	Jul–Nov
	<i>Myrtus communis</i>	LS	121.37 ± 17.97	Small	Berry	Nutrient structures	S, B	Zoochory	DDB	Sep–Dec
	<i>Olea europaea</i> var. <i>sylvestris</i>	T		Medium	Drupe	Nutrient structures	B	Barochory	DDB	Jan–Mar
	<i>Osyris alba</i>	LS	167.56 ± 46.77	Small	Drupe	Nutrient structures	B	Zoochory	DDB	Jul–Oct
	<i>Phlomis purpurea</i>	LS	4.09 ± 0.84	Medium	Nutlet	Nothing	B	Semachory	RD	Aug–Nov
	<i>Phyllirea angustifolia</i>	T		Medium	Drupe	Nutrient structures	Absent	Barochory	DDB	Oct–Nov
	<i>Pistacia lentiscus</i>	T	30.09 ± 7.14	Small	Drupe	Nutrient structures	B	Zoochory	DDB	Aug–Feb
	<i>Quercus coccifera</i>	T	7492.22 ± 1394.52	Large	Nutlet	Nutrient structures	B	Barochory	DDB	Sep–Nov
	<i>Rhamnus alaternus</i>	LS	63.23 ± 10.50	Small	Berry	Nutrient structures	S	Zoochory	DDB	Jun–Aug
	<i>Rhamnus lycioides</i>	LS	33.73 ± 5.97	Small	Berry	Nutrient structures	S	Zoochory	DDB	Jun–Sep
	<i>Ruscus aculeatus</i>	LS	366.02 ± 119.98	Large	Drupe	Nutrient structures	B	Zoochory	DDB	Aug–Oct
	<i>Ruta chalepensis</i>	SS	0.22 ± 0.03	Tiny	Seed	Nothing	B	Semachory	RD	Jul–Oct
	<i>Sideritis arborescens</i> subsp. <i>perezlarae</i>	SS	1.95 ± 0.22	Medium	Nutlet	Nothing	B	Semachory	RD	Jun–Oct
	<i>Stauracanthus boivinii</i>	LS	1.84 ± 0.55	Small	Seed	Nothing	Absent	Ballistic dispersal	RD	Apr–Dec
	<i>Teucrium fruticans</i>	LS	3.69 ± 1.80	Medium	Nutlet	Nothing	Absent	Semachory	RD	Jun–Oct
	<i>Ulex australis</i>	LS	2.33 ± 0.63	Small	Seed	Nothing	Absent	Ballistic dispersal	RD	Feb–Apr
	<i>Viola arborescens</i>	SS	2.22 ± 0.77	Small	Seed	Nothing	Absent	Semachory	RD	Jan–Feb
			247.43 ± 1138.11							

Mobile/ semifixed dunes	<i>Asteriscus maritimus</i>	SS	0.22 ± 0.04	Medium	Achene	Pappus	S	Ombrohydrochory	RD	Sep–Nov
	<i>Crucianella maritima</i>	SS	4.81 ± 1.51	Small	Seed	Wings	Absent	Anemochory	DDA	Jun–Jul
	<i>Eryngium maritimum</i>	H	28.94 ± 4.83	Large	Twin-fruit	Hooked appendages	S, B	Zoochory *	DDB	Sep–Nov
	<i>Euphorbia paralias</i>	H	2.03 ± 0.38	Small	Seed	Nothing	Absent	Ballistic dispersal *	RD	Jul–Sep
	<i>Frankenia laevis</i>	SS		Small	Seed	Nothing	Absent	Semachory	RD	Jun–Jul
	<i>Helicrysum picardii</i>	SS		Small	Achene	Pappus	S, B	Anemochory	DDA	Jun–Jul
	<i>Limonium emarginatum</i>	SS		Tiny	Achene	Nothing	Absent	Semachory	RD	Jun–Oct
	<i>Limonium sinuatum</i>	SS		Tiny	Achene	Nothing	Absent	Semachory	RD	Jul–Sep
	<i>Lotus creticus</i>	H	2.33 ± 0.012	Tiny	Seed	Nothing	Absent	Ballistic dispersal	RD	Jun–Sep
	<i>Malcolmia littorea</i>	H	0.07 ± 0.04	Tiny	Seed	Nothing	M	Semachory	RD	Jan–Dec
	<i>Medicago marina</i>	H	33.31 ± 7.08	Medium	Pod	Hooked appendages	S	Zoochory *	DDB	Jun–Sep
	<i>Ononis natrix</i>	SS	1.04 ± 0.37	Small	Seed	Nothing	Absent	Semachory	RD	May–Aug
	<i>Phagnalon saxatile</i>	SS	0.05 ± 0.05	Tiny	Achene	Pappus	S	Anemochory	DDA	May–Jun
			8.09 ± 13.19							
Mediterranean-subtropical dunes (M.N. Artola Cabopino)										
Fixed dunes	<i>Asparagus aphyllus</i>	SS		Medium	Berry	Nutrient structures	S, B	Barochory	DDB	Sep–Feb
	<i>Calicotome villosa</i>	LS	10.55 ± 1.28	Small	Seed	Nothing	Absent	Semachory	RD	Jun–Aug
	<i>Cistus monspeliensis</i>	SS	0.98 ± 0.20	Small	Seed	Nothing	B	Semachory	RD	Jun–Nov
	<i>Cistus salviifolius</i>	LS	0.7 ± 0.17	Small	Seed	Nothing	B	Semachory	RD	Jun–Dec
	<i>Chamaerops humilis</i>	LS	1754.62 ± 193.45	Large	Drupe	Nutrient structures	B	Barochory	DDB	Sep–Dec
	<i>Daphne gnidium</i>	LS		Small	Berry	Nutrient structures	S	Zoochory	DDB	Aug–Mar
	<i>Dianthus broteri</i>	SS		Small	Seed	Nothing	Absent	Semachory	RD	Jul–Sep
	<i>Euphorbia terracina</i>	H	3.76 ± 0.48	Small	Seed	Nothing	Absent	Ballistic dispersal	RD	Mar–Jun
	<i>Rubia peregrina</i>	SS		Medium	Achene	Nothing	S, B	Zoochory	DDB	Jun–Jul
	<i>Genista umbellata</i>	SS	0.63 ± 0.20	Small	Seed	Nothing	Absent	Semachory	RD	Jun–Jul
	<i>Halimium commutatum</i>	LS		Tiny	Seed	Nothing	M, B	Semachory	RD	Jul–Nov
	<i>Halimium halimifolium</i>	LS	0.21 ± 0.04	Tiny	Seed	Nothing	M, B	Semachory	RD	Jun–Sep
	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	T	354.01 ± 48.39	Medium	Galbulus	Nutrient structures	S, B	Barochory	DDB	Jan–Dec
	<i>Lavandula multifida</i>	SS	0.59 ± 0.91	Small	Nutlet	Nothing	M, B	Semachory	RD	Jun–Nov
	<i>Lavandula stoechas</i>	SS	1.16 ± 0.06	Medium	Nutlet	Nothing	B	Semachory	RD	Apr–Aug
	<i>Myrtus communis</i>	LS	90.57 ± 19.15	Medium	Berry	Nutrient structures	S, B	Zoochory	DDB	Sep–Dec
	<i>Olea europaea</i> var. <i>sylvestris</i>	T	494.41 ± 113.54	Medium	Drupe	Nutrient structures	B	Barochory	DDB	Jan–Mar
	<i>Phlomis purpurea</i>	LS	1.49 ± 0.81	Medium	Nutlet	Nothing	B	Semachory	RD	Jul–Oct
	<i>Phyllirea angustifolia</i>	T		Medium	Drupe	Nutrient structures	Absent	Barochory	DDB	Oct–Nov
	<i>Pistacia lentiscus</i>	T	25.34 ± 3.67	Small	Drupe	Nutrient structures	B	Zoochory	DDB	Aug–Feb
<i>Quercus coccifera</i>	T		Large	Nutlet	Nutrient structures	Absent	Barochory	DDB	Sep–Nov	
<i>Rhamnus lycioides</i>	LS	57.4 ± 9.14	Small	Berry	Nutrient structures	S	Zoochory	DDB	Jun–Sep	
<i>Ruta chalepensis</i>	SS	1.1 ± 0.08	Small	Seed	Nothing	B	Semachory	RD	Jul–Oct	
<i>Ulex australis</i>	LS	9.4 ±	Small	Seed	Nothing	Absent	Ballistic dispersal	RD	Feb–Apr	
			165.11 ± 432.82							
Mobile/ semifixed dunes	<i>Crucianella maritima</i>	SS	4.38 ± 0.80	Small	Seed	Wings	Absent	Anemochory	DDA	Jun–Jul
	<i>Eryngium maritimum</i>	H	23.6 ± 8.04	Large	Twin-fruit	Hooked appendages	S, B	Zoochory *	DDB	Sep–Nov
	<i>Helicrysum picardii</i>	SS	0.06 ± 0.01	Small	Achene	Pappus	S, B	Anemochory	DDA	Jun–Jul
	<i>Lotus creticus</i>	H	0.71 ± 0.15	Small	Seed	Nothing	Absent	Ballistic dispersal	RD	Jun–Sep
	<i>Malcolmia littorea</i>	H	0.11 ± 0.18	Tiny	Seed	Nothing	M	Semachory	RD	Jan–Dec
	<i>Medicago marina</i>	H	23.06 ± 9.62	Medium	Pod	Hooked appendages	S	Zoochory *	DDB	Jun–Sep
	<i>Ononis natrix</i>	SS	3.48 ± 0.47	Small	Seed	Nothing	Absent	Semachory	RD	May–Aug
	<i>Phagnalon saxatile</i>	SS	0.04 ± 0.01	Tiny	Achene	Pappus	S, B	Anemochory	DDA	May–Jun
	<i>Scrophularia canina</i>	SS	0.29 ± 0.03	Medium	Seed	Nothing	B	Semachory	RD	May–Nov
	<i>Silene niceensis</i>	H	0.18 ± 0.02	Tiny	Seed	Nothing	Absent	Semachory	RD	Jun–Oct
			5.59 ± 9.47							

Mediterranean-subdesert dunes (P.N. Cabo de Gata-Níjar)										
Fixed dunes	<i>Asparagus albus</i>	SS	10.6 ± 3.7	Medium	Berry	Nutrient structures	S, B	Barochory	DDB	Sep-Feb
	<i>Asparagus horridus</i>	SS		Medium	Berry	Nutrient structures	S, B	Barochory	DDB	Sep-Feb
	<i>Frankenia boissieri</i>	SS	1.98 ± 0.45	Small	Calyx	Nothing	S	Semachory	RD	May-Jun
	<i>Launea arborescens</i>	LS	1.13 ± 0.07	Small	Achene	Pappus	S	Anemochory	DDA	Jan-Dec
	<i>Launea naudicaulis</i>	SS	0.59 ± 0.25	Medium	Achene	Pappus	S	Anemochory	DDA	Jan-Dec
	<i>Lycium intricatum</i>	LS	25.84 ± 12.52	Large	Berry	Nutrient structures	S	Zoochory	DDB	Jan-Dec
	<i>Teucrium hieronymi</i>	SS	2.9 ± 1.41	Small	Calyx	Open balloon	S, B	Anemochory	DDA	Jul-Nov
	<i>Thymelaea hirsuta</i>	SS		Small	Nutlet	Nothing	B	Semachory	RD	Jun-Sep
	<i>Thymus hyemalis</i>	SS	0.05 ± 0.01	Tiny	Nutlet	Nothing	M	Semachory	RD	Jun-Aug
	<i>Withania frutescens</i>	LS	75.72 ± 19.85	Medium	Berry	Nutrient structures	S	Zoochory	DDB	Jun-Oct
	<i>Ziziphus lotus</i>	LS	750 ± 125.35	Medium	Drupe	Nutrient structures	B	Barochory	DDB	Aug-Nov
			96.53 ± 246.26							
Mobile/ semifixed dunes	<i>Asteriscus maritimus</i>	SS		Medium	Achene	Pappus	S	Ombrohydrochory	RD	Sep-Nov
	<i>Crucianella maritima</i>	SS	5.33 ± 2.31	Small	Seed	Wings	Absent	Anemochory	DDA	Jun-Jul
	<i>Helichrysum stoechas</i>	SS	0.04 ± 0.01	Small	Achene	Pappus	S, B	Anemochory	DDA	Jun-Jul
	<i>Limonium lobatum</i>	SS	0.36 ± 0.08	Tiny	Achene	Nothing	Absent	Ombrohydrochory	RD	Jul-Sep
	<i>Lotus creticus</i>	H	0.81 ± 0.12	Tiny	Seed	Nothing	Absent	Ballistic dispersal	RD	Jun-Sep
	<i>Medicago marina</i>	H	39.03 ± 12.20	Medium	Pod	Hooked appendages	S	Zoochory *	DDB	Jun-Sep
	<i>Ononis natrix</i>	SS	1.55 ± 0.13	Small	Seed	Nothing	Absent	Semachory	RD	May-Aug
	<i>Othantus maritimus</i>	SS	1.04 ± 0.34	Medium	Achene	Nothing	Absent	Semachory *	DDA	Jul-Sep
	<i>Phagnalon saxatile</i>	SS	0.06 ± 0.01	Tiny	Achene	Pappus	S	Anemochory	DDA	May-Jun
	<i>Plantago albicans</i>	H		Small	Seed	Nothing	M, B	Ombrohydrochory	RD	Jun-Aug
	<i>Salsola oppositifolia</i>	SS		Small	Samara	Wings	B	Anemochory	DDA	Nov-Mar
	<i>Salsola vermiculata</i>	SS		Small	Samara	Wings	B	Anemochory	DDA	Nov-Apr
	<i>Teucrium dunense</i>	SS	2.98 ± 1.41	Small	Calyx	Open balloon	S, B	Anemochory	DDA	Jul-Nov
			5.69 ± 12.62							