



Long-term spatio-temporal expansion of the native-invasive *Retama monosperma* on coastal dunes: Importance of land-use and natural dispersal vectors

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ABSTRACT

Expansion of invasive species inducing sands stabilization is becoming an important ecological problem in coastal dunes in some parts of the world. *Retama monosperma*, an endemic to coasts of SE Spain and NE of Morocco, late-colonizing shrub occurring in sandy coastal areas, was planted along the coast of SW Spain during the 20th century to stabilize dunes. In recent decades, the species has spread rapidly, becoming invasive, and sometimes incurring notable changes in its environment and plant community. The expansion patterns of *R. monosperma* from 1956 to 2001 were described and quantified at the landscape scale within a protected dune system, using GIS. The differential effects on expansion patterns of the main factor controlling the population spread, grazing by domestic livestock and the abundance of wild rabbits, were analyzed comparatively. *R. monosperma* displays an exponential, invasive-type expansion trend, presenting a mean annual coverage increase of 15% and a mean lateral spread rate of 65.5 m yr⁻¹ from the original population nucleus to the Western and Eastern ends of the study area. The dispersal activity primarily of rabbits and the absence of competing woody species contribute to this rapid expansion. The highest local increases in plant coverage could be related to increased rabbit abundance and to the improved germination rates of seeds which have passed through the rabbit gut. In contrast, areas highly grazed by livestock present the lowest increases, and an open-type plant community is maintained there for a longer time.

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Introduction

The process of coastal dune stabilization consists of the progressive reduction of sand movement, closely related to an increase in vegetation coverage, and following a positive feedback mechanism (Yizhaq et al., 2007). The process involves significant changes in dune geomorphology and other environmental characteristics, such as lower incidence of wind and salt spray and increases in soil organic matter and nutrients (El-Bana et al., 2002; Muñoz Vallés et al., 2011) as well as in the type of flora and fauna supported by the dunes (Lichter, 1998; Levin and Ben-Dor, 2004; Plassmann et al., 2010). In different parts of the world, dune stabilization is having a negative impact on the richness and diversity of dune plant and animal species of high conservation value, and is becoming an important environmental problem (Avis, 1995; Alvarez and Cushman, 2002; Conser and Connor, 2009; Isermann et al., 2007; Isermann, 2008; Kutiel et al., 2004a; Marchante et al., 2008; Wiedemann and Pickart, 1996). At present, fixation and

stabilization of coastal dunes are identified by several authors as one of the main threats to these ecosystems (Isermann et al., 2007; Jørgensen and Kollmann, 2008; Kutiel et al., 2004a).

The recent increase in stability of coastal dunes has been caused, in certain cases, by factors such as global or local climatic change (Panario and Piñeiro, 1997; Tsoar, 2005; Tsoar et al., 2009) and changes in agricultural and livestock uses (Isermann et al., 2007; Levin and Ben-Dor, 2004; Plassmann et al., 2010); or as a result of a decrease in herbivory by domestic livestock or wild grazers such as rabbits (Hodgkin, 1984; Levin and Ben-Dor, 2004; Ranwell, 1960, 1972; Thomas, 1963). In many cases, however, dune stabilization has been directly anthropogenic and is the product of attempts to prevent dune erosion and to stabilize blowing transgressive sand sheets (Pye, 1983). Since the late 18th century, various countries have implemented dune fixation and stabilization techniques that include planting rapid-growth herbaceous and/or woody species tolerant to environmentally stressful dune conditions, such as e.g. *Ammophila arenaria*, *Hippophae rhamnoides*, *Rosa rugosa*, several species of the genus *Carpobrotus*, *Acacia*, *Eucalyptus*, *Pinus* and *Retama*, among others, with no regard to their exotic character in terms of the ecosystem in which they were planted (Avis, 1989; Buell et al., 1995; Isermann, 2008; Kith-y-Tassara, 1946; Kollmann et al., 2009; Kutiel et al., 2004a,b; Wiedemann and Pickart, 1996).

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Over time, many of these species have spread beyond their initial plantation areas, further stabilizing the surrounding dune systems, and sometimes exhibiting invasive behaviour and causing serious problems for the conservation of the coastal dune ecosystems (Avis, 1995; Conser and Connor, 2009; Marchante et al., 2008; Zunzunegui et al., 2012).

Coastal dune areas are susceptible to plant invasion because of the open nature of the plant communities and existence of micro-sites suitable for species establishment, as well as typically low levels of plant–plant competition (Jørgensen and Kollmann, 2008). In recent years, the importance of the expansion of exotic species in coastal dunes and their potential to induce changes in the structure and functioning of resident communities, have been recognized (Sakai et al., 2001; Valéry et al., 2009). A limited number of studies deal with the invasive expansion of native species within their natural area of distribution (Peters et al., 2006; Van Auken, 2000). Such studies are particularly scarce in the case of coastal dunes (Isermann et al., 2007; Isermann, 2008; Nielsen et al., 2011), where the rapid expansion and increase in coverage of some species, particularly shrubs, significantly contributes to the dune stabilization process, altering the functioning of the entire ecosystem. An analysis of historical invasions, spread rates and patterns, conducted at the landscape scale, can be linked to proximate causes and can contribute to an understanding of how changes in structure and functioning of dune ecosystems occur (Valéry et al., 2009; Vilà and Ibáñez, 2011). Such analyses can also be used to model future spread (Kollmann et al., 2009), as well as help to determine the effectiveness of different management practices (Ansley et al., 2001).

Along the coast of SW Spain, *Retama monosperma* (L.) Boiss. (Talavera, 1999), a N-fixing leguminous native shrub, was sown in coastal dunes during the 20th century, either alone or together with other species like *Pinus pinea* and *Ammophila arenaria*, in order to stabilize the dunes (Kith-y-Tassara, 1946). In most of the locations where it was planted without other species, *R. monosperma* has displayed invasive behaviour and has rapidly expanded beyond the plantation areas (Valdés et al., 2007). It has caused 'retamar' formations in high densities that have led to sand stabilization in open, semi-stabilized dunes and induced substantial changes in dune soil and plant community, as well as at the landscape level (Muñoz Vallés et al., 2011; Zunzunegui et al., 2012). In addition, the species is presently considered to be a non-native invasive plant in other countries around the world such as USA (California: Cal-IPC, 2006; Randall, 1997; Rejmanek and Randall, 1994) and Australia (Randall, 2007).

The expansion of a plant species is dependent on its life history characteristics, including the production and dispersal of propagules, the characteristics of the resident ecosystem and the

prevailing environmental conditions (Peters et al., 2006). In this regard, conservation and management approaches, as well as disturbances, can affect population trends in vegetation.

In coastal dunes, wild rabbits, hares and livestock are the main potential dispersal agents of *R. monosperma* (Dellafiore et al., 2006). On the other hand, the traditional use of dunes as livestock grazing areas, or the presence of wild grazers, have often controlled the excessive growth of plant coverage and encroachment, becoming an important factor in the maintenance of low vegetation coverage in semi-stabilized dunes and their characteristic open-type communities (Kooijman and Van der Meulen, 1996; Levin and Ben-Dor, 2004; Manzano and Návar, 2000; Zhao et al., 2005). Land use type and policies for nature conservation and management could therefore play an important role in controlling trends of *R. monosperma* expansion in the coastal dunes where the species grows.

This study presents a detailed reconstruction of the historical expansion of *R. monosperma* on a dune landscape by using aerial photography and GIS analysis. Specific objectives were: (1) to model the expansion of *R. monosperma* over the dune landscape, (2) to find out variations in expansion rates and spatio-temporal trends, and (3) to test how the presence of livestock and abundance of wild rabbits, conditioned by the policies of natural areas conservation, could act to influence the invasion process.

Materials and methods

Study area

The study was conducted on the El Rompido spit, a semi-isolated and protected dune system located in the Piedras river estuary, in the central coastal region of the Gulf of Cadiz, SW Spain (37°12' N, 7°07' W), and included in the natural range of *R. monosperma* (Fig. 1). The spit stretches eastwards for approximately 12 km running parallel to the coastline, is between 300 and 700 m in width and currently covers an area of 534.7 ha (Gallego-Fernández et al., 2006). The spit actively grows eastward at a mean annual rate of around 42 m over the last 50 years, adding about 1.5 ha of new surface area to the system every year (Muñoz Vallés, unpub. data). The climate is Mediterranean, with an influence from the Atlantic Ocean. Mean annual temperature is 18.2 °C and mean annual rainfall is 583 mm, with a pronounced drought period from May to September (29 yr. record, 1974–2003; Gibrleón Meteorological Station, Huelva). The spit supports different vegetation communities, largely dependent on geomorphology and sedimentary traits. They range from high beach and active dune communities to interior semi-stabilized and stabilized dunes, inter-dune wet depressions or 'slacks', salt marshes and tidal swales (Gallego-Fernández et al., 2006). At the beginning of the twentieth

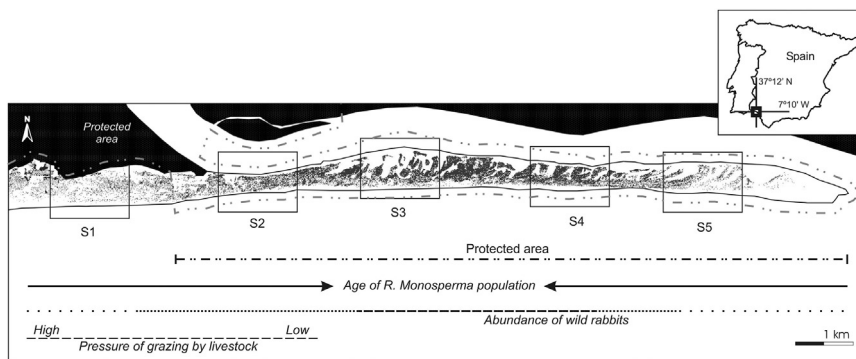


Fig. 1. The El Rompido spit study area on the coast of SW Spain. Limits of Protected Area, gradient of age of *R. monosperma* population, estimated abundance of wild rabbits and pressure of grazing by livestock are indicated. The location of 5 homogeneous sectors selected for further comparisons is also shown. *R. monosperma* coverage on the spit in 2001 is represented by black shading.

century, highly mobile sands with scarce vegetation, dominated by the psammophilous *Ammophila arenaria*, existed in the area (San Miguel de la Cámara, 1913). In the forties decade, a small *R. monosperma* population located in the central sector of the spit is detectable, and it is presumable that it was planted there in the 1920–30s decades (Gallego-Fernández et al., 2006). At present, the species is widely distributed in almost all the inland dunes.

Most of the spit surface (73%) has been included in the protected natural area 'Paraje Natural Marismas del Río Piedras y Flecha del Rompido' since 1989 (Fig. 1), and integrated into the European NATURA 2000 network (ES6150006). Nine habitat types, included in Annex I of the European Habitat Directive (Anonymous, 1992) are represented on the spit. This includes semi-stabilized dune habitats (European Communities protected habitats 2130 and 2250) where *R. monosperma* grows. In addition, eleven endangered dune species and subspecies (two of them protected under law) growing on these dune habitats have been recorded in the area (Muñoz Vallés et al., 2009). The spit is subject to low tourist pressure. Grazing by domestic livestock is prohibited within the protected area; nevertheless, low grazing levels still occur within a reduced zone close to the limits of the protected area. Benefitting from the protection policies and low accessibility of the area, an important population of wild rabbits exists in the spit: warrens are estimated to number 444 ± 161 (mean \pm S.E.), and are mainly concentrated in the central and central-eastern sectors (Dellafiore et al., 2008) – Fig. 1.

Study species

Retama monosperma is a mid-successional, N-fixing woody species found in coastal sandy areas, endemic to SW Spain and NW Morocco. Nevertheless, it successfully establishes in other areas under Mediterranean climate around the world (Muñoz Vallés et al., in press). Adult plants attain heights of 3–4.5 m, canopy diameters of up to 10 m and individual mean coverage of up to 70 m². Through monitoring individuals by means of historical aerial photography (Muñoz Vallés et al., 2005), it has been estimated that a lifespan of 55–80 years is possible. Clonal growth has not been documented in this species, however, it can produce from ~335 to ~2800 fruits per m² of canopy in the study area, from late May to September. The fruits lack evident dispersal adaptations, and merely fall to the ground where they remain available for dispersers until the next fruiting season (Muñoz Vallés et al., in press). The rapid expansion of the species has been mainly enhanced by the dispersing activities of the wild rabbit (*Oryctolagus cuniculus*), as well as an improvement in seed germination rates which occurs after the passage of seeds through the rabbit gut (from 13% to 24%; Dellafiore et al., 2006, 2010). The species is at present widely distributed in the study area, and is the dominant species in the semi-stabilized dunes, which represent the main habitat on the spit (57% of the total spit surface; Gallego-Fernández et al., 2006).

Mapping *R. monosperma* coverage

This study was based upon a temporal sequence of aerial orthophotographs, corresponding to the dates 1956 (B/W, scale 1:33,000), 1977 (B/W, scale 1:18,000), 1989 (colour, scale 1:5000) and 2001 (colour, scale 1:5000). Photographs were scanned at high resolution of 1200 dpi, and the central zone of each one was selected in order to avoid edge distortion. They were further geo-rectified using Ground Control Points taken in the field by GPS. Using these, a digital orthophoto mosaic was created for each date and added to a GIS (ArcView 3.2). An additional aerial photograph from 1946 (B/W, scale 1:45,000) was examined. It was not added to the GIS due to low image quality but it was used to delimit the original population of the species in the central sector of the spit.

Individual or groups cover of *R. monosperma* canopies was digitalized into the GIS at an approximate scale of 1:500. It was first mapped on the basis of the most recent date mosaic (2001), with the highest resolution and image quality, and subsequently on the orthophoto mosaics from the dates 1989, 1977 and 1956. The work on each date and map was successively supported in the previously built maps. Due to the availability of photographs, analysis of 90% of the current total surface of the spit was possible. This excluded a scarce area of 53.47 ha located at the western extreme. Adult individuals of *R. monosperma* were easily recognizable in the photographs due to their texture and tone, their characteristic circular or ellipsoidal shape and their size, significantly larger than adults of the other woody species present, such as *Artemisia campestris* subsp. *crithmifolia*, *Crucianella maritima* *Helichrysum italicum* subsp. *picardii* and *Thymus carnosus*, even from a young age.

Analysis of total coverage and temporal change

Total analyzed surface, semi-stabilized dune surface (suitable for the establishment of *R. monosperma*; this excludes the beach, embryo dunes and salt marshes), total coverage of the species and percentage of coverage per semi-stabilized dune surface were obtained from the GIS for every studied date. Rate of increase in coverage was subsequently calculated as the regression of the square root of the area covered by the species as a function of time, in accordance with previous models in biological invasion theory (Buell et al., 1995; Skellam, 1951). In addition, the main directions of the populations lateral spread were identified and maximum rates of lateral spread were subsequently calculated as the differences in the population' limits between dates. Spread towards the coastline was estimated only in the 3 km long central frame of the spit, corresponding to the original population nucleus.

Analysis of spatio-temporal patterns of expansion

All digital maps of dune surface and *R. monosperma* coverage were divided within the GIS into contiguous 50 m \times 50 m cells using a grid (Brown and Carter, 1998; Middleton et al., 2008). Both dune surface and coverage of *R. monosperma* per dune surface (%) within each cell were calculated. Due to the heterogeneity of the area, e.g. dune and salt marshes, only those cells in which >75% of the surface was dune surface were considered valid cells, and were used in the analyses. This appropriate cell size for change detection was determined after testing it in comparison with another two sizes of cells, 100 m \times 100 m and 25 m \times 25 m. The amount of 100 m \times 100 m cells was limited by the heterogeneity of the area, and covered a smaller surface than the 50 m \times 50 m ones did. On the other hand, 25 m \times 25 m cells were too small in size and rapidly reached high percentages of *R. monosperma* coverage. For these reasons, analyses were finally carried out using 50 m \times 50 m cells only.

Cells were classified into five categories according to the coverage of *R. monosperma* per dune surface, as follows: C0: cov. = 0%; C1: 0% < cov. \leq 25%; C2: 25% < cov. \leq 50%; C3: 50% < cov. \leq 75%; C4: 75% < cov. \leq 100%. The total number of valid cells per category and date was calculated, and maps of the distribution of cell categories on each date were produced.

Analysis of spatio-temporal change in relation to grazing by domestic livestock and wild rabbit abundance

Five homogeneous sectors of 1 km in length each were selected throughout the study area, according to livestock grazing intensity and abundance of wild rabbit. Characteristics of these sectors are indicated in Table 1, and their location is shown in Fig. 1.

Table 1

Characteristics of sectors (S1–S5) selected for analysis of spatio-temporal change in relation to land use and conservation level.

	S1	S2	S3	S4	S5
Included in the protected area	No	Yes	Yes	Yes	Yes
Intensity of livestock grazing ^a	High	Low	None	None	None
Abundance of wild rabbit ^b	Very low(0.0)	Low(1.3)	High(2.1)	The highest(3.0)	Very low(0.5)
Distance from the oldest population nucleous (km) ^c	5.3	2.4	0	2.9	5.2

^a According to Zunzunegui et al. (2012).^b Mean number of warrens per ha, according to Dellafiore et al. (2008).^c Measured from the centre of the sectors.**Table 2**Descriptive data about semi-stabilized dune area, *R. monosperma* covering and valid cells used for further analyses, from the analysis on GIS on four study dates between 1956 and 2001.

	1956	1977	1989	2001
Semi-stabilized dune surface (ha)	271.53	288.94	295.51	296.84
<i>R. monosperma</i> total coverage (ha)	15.03	44.24	75.10	116.19
<i>R. monosperma</i> coverage per semi-stabilized dune surface (%)	5.53	15.31	25.41	39.14
Number of valid cells (50 m × 50 m)	823	877	882	884
Semi-stabilized dune surface included in the valid cells (%)	68.95	71.80	71.40	71.22
<i>R. monosperma</i> coverage included in the valid cells (%)	66.99	67.19	69.01	76.99

Livestock grazing intensity was estimated as mean number of droppings per m² and mean number of fruits per m² found below *R. monosperma* canopies, according to Zunzunegui et al. (2012). High intensity corresponded to approximately 16 droppings and less than 5 fruits per m²; low intensity corresponded to approximately 6 droppings and 167 fruits per m²; non-intensity corresponded to 0 droppings and approximately 1158 fruits per m². Abundance of wild rabbits was estimated as warren density, according to Dellafiore et al. (2008) (Table 1).

For each sector, *R. monosperma* coverage (% of suitable surface) per useful cell and date was calculated. Mean coverage per cell was compared in the five sectors for each date using one-way ANOVA and the post hoc Tukey test. The rate of increase in coverage was calculated within each sector, over the course of the 45 years studied, as the regression of the square root of the area covered by the species as a function of time (Buell et al., 1995; Skellam, 1951). Data were transformed (arcsine x) prior to analysis in order to comply with the assumption of homogeneity. For statistical analysis, the statistical software package STATISTICA 6.0 was used.

Results

Total coverage of *R. monosperma* and temporal change

Due to growth dynamics of the spit, both the area of the spit in total as well as the area of dunes increased over time (Table 2, Fig. 2). The total area covered by *R. monosperma* substantially increased during the 45 years analyzed; from 15.0 ha occupied in 1956 (5.5% of dune surface) to 116.2 ha (39.1% of dune surface) in 2001. Assuming a linear increase, there was an annual mean increase in the area covered by the species of almost 15%. The mean annual increase in coverage was higher between 1956 and 1977 (9.3%), but coverage increase in relation to population size was lower between 1977 and 1989 (5.8%), and between 1989 and 2001 (4.6%): Table 3. The annual rate of increase in total shrub coverage was found to fit an exponential curve (Fig. 3).

Retama monosperma reached the western limit of the digital maps during the first period (1956–1977), and reached the western end of the spit in 1989. Westward lateral spread was the most rapid during the first studied period, advancing more than 120 m yr⁻¹

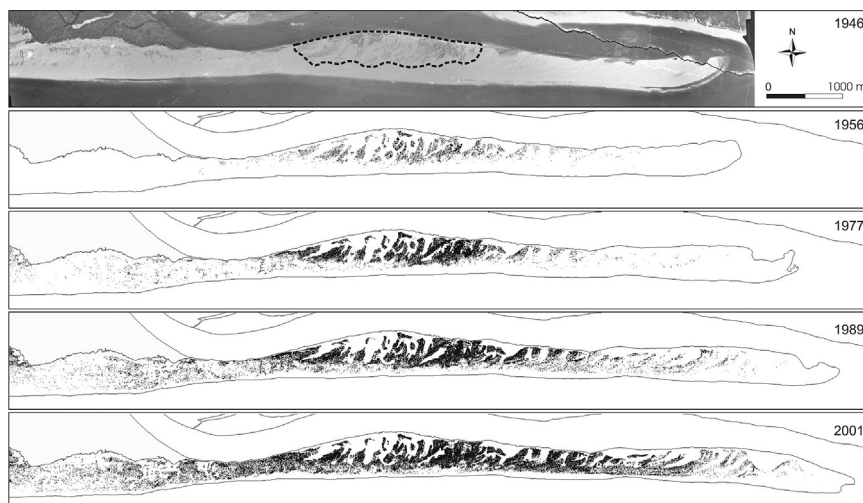


Fig. 2. Distribution of *R. monosperma* coverage on each of four different dates on the El Rompido spit, SW Spain. Above, the location of the original population core is marked by discontinuous line over an aerial photograph from 1946.

Table 3

Rates of *R. monosperma* coverage increase and lateral spread of the population limits in each of the three distinguished periods and over the total of 45 years. Since the population reached the western end of the spit at some time between 1977 and 1989, westward lateral spread during the period 1977–1989 was not calculated, but this advance was certainly inexistent between 1989 and 2001.

	1956–1977	1977–1989	1989–2001	1956–2001
Total increase of <i>R. monosperma</i> coverage (%)	194.45	69.74	54.71	673.23
Annual rate of increase in <i>R. monosperma</i> coverage (%)	9.26	5.81	4.56	14.96
Annual rate of westward lateral spread (m yr ⁻¹)	55.76	77.17	17.00	51.13
Annual rate of eastward lateral spread (m yr ⁻¹)	>120.00	–	0.00	79.78
Annual rate of lateral spread towards the coastline (m yr ⁻¹)	1.57	–1.00	1.50	0.87

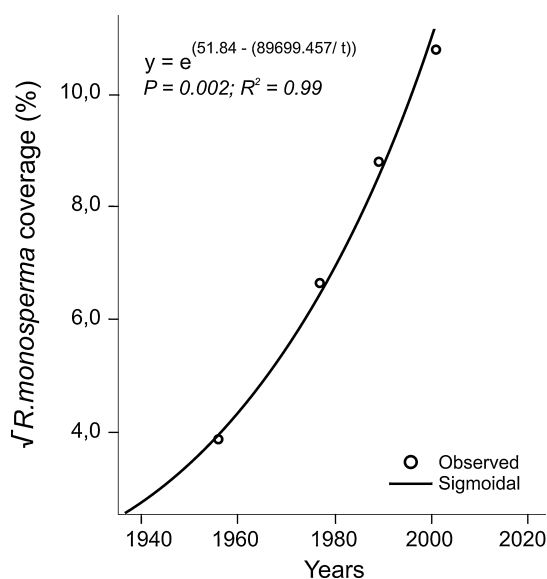


Fig. 3. Increase in *R. monosperma* coverage on the El Rompido spit, SW Spain, as function of time.

(Table 3). In this case, we were not able to calculate the westwards advance of the population during the period 1977–1989, but we can say that this advance was null between 1989 and 2001 (Table 3). The eastward advance was slower in comparison with the westwards advance. A maximum speed of 77.2 m yr⁻¹ was achieved between 1977 and 1989, and decreased afterwards (Table 3). By 1977, the population had reached an area very close to the eastern extreme of the spit. Nevertheless, the eastern end of the spit had still not been reached by 2001 (Fig. 2).

Lateral spread towards the coastline was between one and two orders of magnitude slower than spread along the length of the spit, at around 0.9 m yr⁻¹ between 1956 and 2001, and in fact showed a retreat between 1977 and 1989 (Table 3).

Patterns of *R. monosperma* expansion

The spit growth dynamics produced an increase in the number of valid cells from 823 to 884 over the studied period. Valid cells

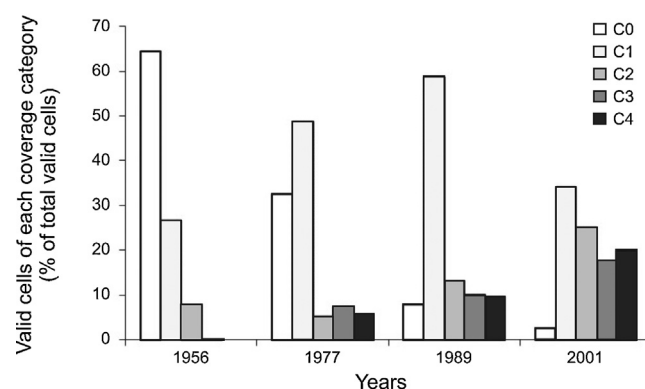


Fig. 5. Relative abundance of valid 50 m × 50 m cells belonging to each of five coverage categories, as percentage of the total number of valid cells, on each of four analyzed dates.

covered between 69% and 72% of the semi-stabilized dune surface and between 67% and 77% of the digitalized coverage of *R. monosperma*.

Categorized values of *R. monosperma* coverage were in 2001 higher at the inner, older colonized cells (coverage categories C3 and C4), which were located in the central area of the spit, and lower (C0 and C1) in the more recently colonized cells, which were located more to the exterior parts of the spit (Fig. 4). The percentage of empty cells (C0) was higher at the first date analyzed, 1956, but rapidly decreased over time as the population expanded (Fig. 5).

From 1956 to 1977, the population preferentially expanded eastward, and generally maintained a low coverage (below 25%) outside the central nucleus area. At every date, apart from 1956, the C1 cells, associated with colonization events, were found to be the most abundant coverage category. The percentage of C1 cells increased until 1989, when C0 were below 8%, and decreased thereafter. This indicates a change from a predominantly colonization of new cells to a pattern in the final period when the population became more dense. Cells from categories C2, C3 and C4 were generally less abundant than C0 or C1, and followed a general increasing trend over time (Fig. 5). The central nucleus area showed moderate or null increases in coverage from 1977 to 2001, while coverage losses were registered in somewhat more than 1% of cells

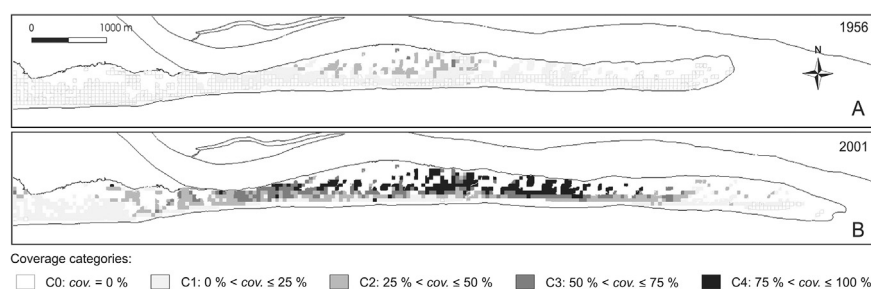


Fig. 4. Distribution of categories of *R. monosperma* coverage (C0–C4) in 50 m × 50 m cells in 1956 (A) and 2001 (B).

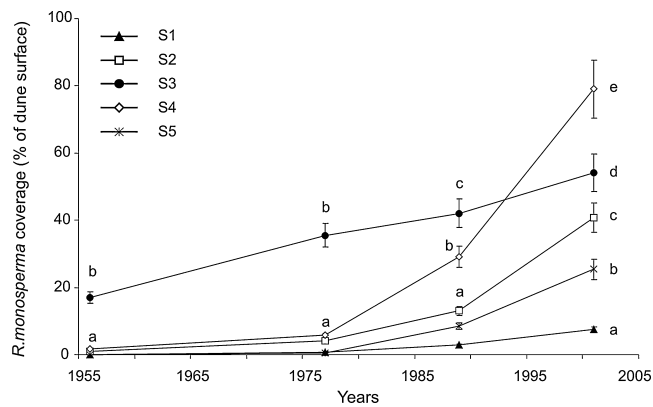


Fig. 6. Increases in *R. monosperma* coverage in 5 selected sectors of the El Rompido spit, on each of four analyzed dates. S1: outside the protected area, high intensity of livestock grazing, very low rabbit abundance; S2: protected, low intensity of livestock grazing, low rabbit abundance; S3: protected, no grazing by livestock, high rabbit abundance; S4: protected, no grazing by livestock, the highest abundance of rabbits; S5: protected, no grazing by livestock, very low rabbit abundance. Asterisks indicate significant differences found by ANOVA; different letters indicate significant differences.

from 1977 to 1989 and 1.8% from 1989 to 2001. Over time, although *R. monosperma* colonized westward more quickly than eastward, the occurrences became denser towards the east. This pattern can be related with the differential effect of grazing by domestic livestock and wild rabbits (Fig. 4).

Patterns of *R. monosperma* expansion in relation to grazing by domestic livestock and wild rabbit abundance

Grid cells corresponding to the C1 coverage category, associated with colonization events, increased until 1977 in sectors S2 and S4, and until 1989 in S5, and decreased afterwards. The maximum number of C1 cells in S3 was reached in 1956, decreasing afterwards, while in S1 the maximum was reached in 2001 (data not presented). This indicates a change in dynamics, mainly from colonization of new cells (majority of C1) to population densification (C1 decrease), which varied between sectors studied.

ANOVA revealed significantly higher mean values of *R. monosperma* coverage per cell in S3, the population core, during 1959 and 1977 (1956: $F=65.10$; $P<0.001$; 1977: $F=71.64$; $P<0.001$), while the remaining sectors maintained similar and lower values (Fig. 6). Mean coverage per cell continued to be significantly higher in S3 in 1989, while values in S4 significantly increased in comparison with S1, S2 and S5 ($F=59.73$; $P<0.001$). In 2001, mean coverage per cell showed significantly different values in every sector ($F=144.34$; $P<0.001$). In this year, the highest coverage values were obtained in S4, exceeding those of the population core (S3), while progressively lower values were obtained in S3, S2, S5 and S1 (Fig. 6). The annual rate of increase in coverage fitted an exponential curve in sectors S1 ($P=0.002$; $R^2=0.99$), S2 ($P=0.004$; $R^2=0.99$), S4 ($P=0.016$; $R^2=0.97$) and S5 ($P=0.023$; $R^2=0.96$), but it fitted a lineal curve in sector S3 ($P=0.007$; $R^2=0.99$).

Discussion

Our study shows that *Retama monosperma* has rapidly expanded in the open, semi-stabilized dunes over the 45 year period covered by the data, from an original central nucleus estimated to have been founded in the 1920s to 1930s (Gallego-Fernández et al., 2006). Speed of lateral spread exceeded 108 m yr^{-1} , and still the population is actively colonizing dune surfaces that newly become available. A substantial increase in coverage of 673% occurred during those 45 years, and at present a predominant dynamic of

population densification can be registered. The stand have the potential for further encroachment. This expansion has in turn contributed to the stabilization of much of the dune system, inducing substantial changes in the dune flora and vegetation structure (Muñoz Vallés et al., 2011; Zunzunegui et al., 2012).

According to Alpert et al. (2000), in ecosystems characterized by stressful environmental conditions, certain regionally native species may display more acutely invasive expansion as compared to alien species, as a result of being better adapted to those conditions. The annual growth rate in coverage of *R. monosperma* (15%) was significantly higher than the 2.9% found for the alien *Acacia saligna* in an analysis of data over 34 years by Kutiel et al. (2004b) in coastal dunes of Israel. It was similar to values registered by Kollmann et al. (2009) for the alien *Rosa rugosa* (16.4%; 18 years analyzed) in coastal dunes of Denmark. The annual rate of lateral expansion of the *R. monosperma* population (65.5 m yr^{-1}) was also significantly higher than the lateral expansion rate of other woody species in coastal dunes of England reported by Fuller and Boorman (1977; 5 m yr^{-1} for the shrubs *Rhododendron ponticum* and *Hippophæ rhamnoides*). The observed trend of expansion of *R. monosperma* in coastal dunes of southern Spain is therefore comparable to the invasive-type expansion exhibited by allochthonous invasive species (see also Buell et al., 1995). The linear trend of increase in population density shown in the central sector of the spit could be related to the simultaneous growth of a majority of individuals of the same age, deliberately introduced to fix dunes near to the tunny fishery that was active in this sector during the first half of 20th century. This fact must be taken into account when interpreting the results, as the historical mass plantation of *R. monosperma* that occurred there, means that the natural slow introduction and establishment phases of invasion dynamics did not occur in this case. Judging about the invasive potential of *R. monosperma* it must be taken into account generally, that this species is also used as an ornamental plant, a fact which facilitates its introduction into new areas (Talavera, 1999). Resulting from such introductions, *R. monosperma* is presently considered to be a non-native invasive plant of coastal shrublands, grasslands, and the chaparral in California, USA (Cal-IPC, 2006; Randall, 1997; Rejmanek and Randall, 1994), and an invasive, noxious weed on the coasts of SW Australia (Randall, 2007).

The recorded annual growth rate of *R. monosperma* coverage on the investigated spit was found to be 9.8 times that which Kutiel et al. (2004a) found for the total vegetation coverage (1.8%; 34 yr.) in plant-colonized coastal dunes under Mediterranean climate of southern Israel. In that study, the expansion of vegetation was found to be related to the dune stabilization process and to a decrease in the abundance of sand-dwelling organisms. The expansion of *R. monosperma*, and in consequence the progressive stabilization of dunes, in the El Rompido spit and other dune systems in SW Spain, have negative consequences for the conservation of semi-stabilized dunes (European Communities protected habitat 2130 and 2250; Anonymous, 1992). In addition to the rapid expansion, the species could induce significant changes in the local environment that may facilitate the recruitment of species less tolerant to environmental stress (mainly nitrophilous, ruderal and/or weed species, such as *Anagallis arvensis*, *Erigeron sumatrensis*, *Paronychia argentea*, *Solanum alatum* and *Urtica membranacea*, among others). Further, it may negatively affect the dune flora beneath the canopy, increasingly with higher *R. monosperma* age and coverage (Muñoz Vallés et al., 2011; Zunzunegui et al., 2012). This significant alters the vegetation abundance, composition and structure, with negative effects upon other dune plant species the vitality of which will suffer from the decline of open, semi-stabilized dunes (Muñoz Vallés et al., 2009, 2011). In this way, *R. monosperma* behaves as a native-invasive species, and shows a

high potential for inducing significant functional changes within the dune ecosystem.

In agreement with Valéry et al. (2009), this study supports the idea that the expansion of native-invasive species may have negative effects on ecosystem diversity and stability. In addition, it may have great relevance for the conservation of properties and processes within the ecosystems under *R. monosperma* invasion, likewise as it would be the case of an invasive spread of alien species.

Excessive coverage of *R. monosperma* should therefore be controlled and managed in some locations of SW Spain and S Portugal, in order to preserve the existing plant communities and the persistence and functioning of semi-stabilized dune habitats. In this regard, it has been observed that seawater inundation by high tides causes obvious physiological damage to this native-invasive species, and sand burial and saltwater intrusion appear to limit its establishment (Muñoz Vallés et al., in press). It has been also observed that *R. monosperma* seedlings and young stands develop successfully in open areas, but recruitment under adult canopies of the species is very limited. Rey Benayas et al. (2002) found significant competition between weeds and *R. sphaerocarpa* seedlings when growing together, but shading (e.g. provided by *Retama* adults) improved performance of the seedlings. These latter seemed to be in a competition for water resources with weeds. This same interaction could occur between *Retama* adults and seedlings, so adults could control the population recruitment under its canopies through competition – but this should not solve the expansion problem. In this regard, further studies are required in order to assess the factors that limit seedling establishment and survival.

Previous studies have identified wild rabbits as important dispersers of *R. monosperma* in coastal dunes (Dellafiore et al., 2006, 2010). It is estimated that each rabbit could disperse between 2484 and 4041 seeds yr^{-1} , at both short and long distances (up to 335 m from the nearest mature plant of *R. monosperma*), contributing to the development of the species seed bank. In addition, passage through the rabbit gut improves seed germination rates, from 13% to 24%, (Dellafiore et al., 2006). These processes certainly have facilitated – and continue doing so – the rapid lateral expansion of the *R. monosperma* population over the continuous dune surface. They contribute also to overcome obstacles in the dune surface represented by salt marshes and tidal swales (Gallego-Fernández et al., 2006). As in previous studies found, the interaction between wild rabbits and *R. monosperma* works as a feed-back system, where the rabbit acts as seed disperser over short and long distances and improves seed germination rates (Dellafiore et al., 2006), while *R. monosperma* in turn provides rabbits with refuge space and food (Dellafiore et al., 2008). Our results show a long-term net increase of the extent and coverage of the shrub population in areas where rabbits are distributed, without the concurrence of another type of disturbance, a situation which leads to the stabilization of the dune system. This clearly contrasts with previous studies of grazing in European coastal dunes, where rabbits play an important role in maintaining low levels of vegetation coverage and increasing sand dune mobility (Burggraaf-van Nierop and van der Meijden, 1984; Hodgkin, 1984; Ranwell, 1960).

In contrast, sectors subjected to grazing by livestock showed significantly lower increases in *R. monosperma* coverage over time, which was even lower in the area subjected to higher pressure (S1). This led to maintenance of an open type of plant community for a longer period of time. This retarding effect on expansion and densification of the *R. monosperma* population probably results from high consumption rates of the *Retama* fruits by goats and sheep (Zunzunegui et al., 2012), as well as by a poor capacity of these animals for dispersal. Castro et al. (2005) found that passage of

Retama sphaerocarpa seeds through the gut of livestock did not significantly increase germination rates, except where the seed had been damaged during mastication. However, we found that passage through goat digestive systems (where the seed remained inside the gut from 1 to 5 days), increased subsequent germination rates from 5% (in non-consumed seeds) to 48% (Muñoz Vallés, unpublished data). Over a five days observation period we found a final 32% seed recovery from excrements of the experimentally studied goats. This, together with the final germination rate data (weighted to mean daily recovery), resulted in a final effective germination percentage of 16%, which was similar to the rates in control seeds (13%) reported by Dellafiore et al. (2006). In this comparison, it is important to take into account the loss of seeds due to consumption and subsequent defecation by goats outside the dune system. This does not occur to the same extent in the case of seed consumption by rabbits, as they are resident within the dune system. In addition, predation on seedlings of *R. monosperma* by domestic livestock has been not quantified. Our results concur with those of other studies where livestock grazing contributes to the maintenance of open-type plant communities as well as to the mobility of sands, due to the decrease in vegetation coverage (Kooijman and Van der Meulen, 1996; Levin and Ben-Dor, 2004; Manzano and Nívar, 2000; Zhao et al., 2005). In this way, the observed coverage increase in sector S2 from 1989 to 2001 could be related to the reduction in intensity of pasture activities that followed the declaration of the site as a protected area (1989). According to the results reported by other authors, such effects of livestock activity on dune vegetation can change, depending on factors such as soil characteristics (Kohyani et al., 2008; Van Dijk, 1992; Zuo et al., 2008), intensity of grazing (Carter, 1988), or also the monitoring scale (Kohyani et al., 2008). In some cases, decreasing competitive interactions caused by high grazing pressure have resulted in the loss of grasslands and the further development of shrub formations (Isermann et al., 2007; Roth et al., 2009). However, other negative effects of livestock pasture activities there, like trampling, soil compaction and eutrophication or dispersion of adventitious species from outside the system have not yet been quantified. Low to medium coverage of *R. monosperma* would be positive for the survival of the endangered reptile *Chamaeleo chamaeleon*, that is present on the study area, but intensive grazing and trampling by domestic livestock would be very harmful for the reproduction of this species, since they lay their eggs on the soil.

Implementation of grazing by livestock may appear to be a suitable management tool for the control of excessive coverage of *R. monosperma* in these coastal dunes, and it has been advocated, indeed, by Plassmann et al. (2010). However, the potential consequences of adopting such a management strategy in a fragile dune ecosystem need to be understood more fully (Raffaele et al., 2007). Zunzunegui et al. (2012) in a study at the El Rompido spit investigating the effects of different herbivory intensity and density of *R. monosperma* on an endangered shrub species, *Thymus carnosus*, discourage the management with livestock. They anticipate the future extinction of *T. carnosus* in the dunes because it suffers from the competition with *R. monosperma*, although the speed of this process would be conditioned by the livestock pressure intensity. This latter study proposes, in terms of *T. carnosus* population conservation, a clear-cutting management of *R. monosperma* plants, reducing by this way their number in order to maintain open dunes spaces.

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