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The impact on plant communities of an invasive alien herb, *Oenothera drummondii*, varies along the beach-coastal dune gradient

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Abstract

One of the major threats to the diversity of coastal dunes is the expansion of invasive species, such as *Oenothera drummondii* subsp. *drummondii* (Onagraceae). In southwestern Spain, we studied the impact of this American invasive on community structure and composition along a beach-dune gradient (beach, foredune, and inland dunes). Differences in density, biomass, and the cover of *O. drummondii*, the cover of perennial and annuals/biennials species, and Shannon diversity index H' and dominance λ were compared between invaded and uninvaded sectors. We observed that the intensity and impact of the invasion by *O. drummondii* varies along the beach-dune gradient. The abundance of the invasive plant increased inland and in consequence, its impact on species richness and composition was highest in inland dunes. Here, plant cover of *O. drummondii* represented 57.9% of total plant cover; species richness was reduced (with 3.3 fewer species per 2 x 2 plot), diversity H' was lower while dominance λ was higher. At a broader scale, species richness in the invaded sector was 25% larger than in the uninvaded sector, because of the presence of ruderal species. Species composition also was modified after the invasion. The abundance of a keystone native species was largely reduced (*Ammophila arenaria*), and some natives became locally extinct (*Otanthus maritimus, Eryngium maritimum, Medicago marina* and *Elymus farctus*). We conclude that the high environmental severity of the beach and foredunes results in a reduced invasion and impact of *O. drummondii*, whereas the milder conditions of inland dunes promote its expansion. The shift in community structure and composition can have an increasing domino effect and thus monitoring, and mitigation actions are necessary. When doing so,

the environmental heterogeneity of the beach-dune gradient should be considered, given its relevance in the invasion process.

Keywords: Plant biomass; coastal dunes; gradient analysis; plant invasion; Species richness

Highlights

- We studied the impact of the invasive *O. drummondii* on Spanish coastal dunes.
- The intensity and impact of the invasion increased along the beach-dune gradient.
- The abundance of native species decreased, and some became locally extinct.
- High environmental severity of the beach and foredunes attenuates invasion.
- Milder conditions of inland dunes facilitate invasion and promote ruderals.

Nomenclature and taxonomic reference: Valdés, B., S. Talavera and E. Fernández Galiano (eds.) (1987). Flora Vascular de Andalucía Occidental 1-3. Ketres Editora S.A., Barcelona.

1. Introduction

The negative impact of exotic invasive species on the integrity of plant communities and ecosystems, as well as on the existence of rare and endangered species, has been observed and demonstrated worldwide (Vilá et al., 2011; Pysek et al., 2012). Such impacts increase over time and are usually irreversible or extremely difficult to deal with, and hence, are acknowledged as one of the major threats to biodiversity worldwide (EEA, 2012; Joppa et al., 2016). Studies aimed at understanding the ecological processes that lead to biological invasions are ample (van Kleunen et al., 2010; Vilá et al., 2011), and have mostly focused on species invasiveness (functional attributes, increments in abundance and their differences with native resident species) (Stanisci et al., 2010) and habitat invasibility (vulnerability to invasion) (Carboni et al., 2010; Santoro et al., 2012a; Ledger et al., 2015). Nevertheless, both approaches oftentimes do not consider community dynamics and environmental heterogeneity. In consequence, an increasing number of studies have recently demonstrated that the invasion process is affected by temporal changes in the abiotic environment, the invaded community, and in the invasive species themselves (del Vecchio et al., 2015). Furthermore, the spatial scale at which biological invasions are monitored (large areas -countries vs. small areas -vegetation plots) and the environmental heterogeneity in which they occur have proved to be relevant in understanding and assessing the invasion phenomena (Santoro et al., 2012a; del Vecchio et al., 2015). However, although there is a growing number of studies that report the impacts of invasive species on different communities, the role of environmental heterogeneity remains mostly unknown (but see Santoro et al., 2012a).

Among the ecosystems and habitats that have been most affected by invasive species, coastal dunes are outstanding and have been regarded as an “extreme case of species invasion” (Castillo and Moreno-Casasola, 1996). Indeed, they are threatened by invasive species owing to habitat heterogeneity and the frequent occurrence of intense disturbance events (Acosta et al., 2008; Santoro et al., 2012a), which provide the opportunity for the colonization by invasive species. The problem of species invasions on coastal dunes is relevant because of the potential loss of the high biodiversity of very specialized flora and fauna (van der Maarel, 2003), which includes species that are tolerant to the extreme abiotic conditions of coastal dunes (García-Mora et al., 1999; Maun, 1998). Furthermore, coastal dunes provide a host of ecosystem services to society, including water quality, scenic beauty, recreation, and shoreline protection from storms and sea-level rise through flood and erosion control (Everard et al., 2010; Salgado and Martínez, 2017; Feagin et al., 2019). Thus, the relevance of preserving these ecosystems is heightened because these ecosystem services rely on the integrity of coastal dune communities.

Previous studies show that invasive species on coastal dunes are diverse, with multiple origins and destinations. These earlier findings have demonstrated that several species (i.e., *Carpobrotus acinaciformis, C. edulis, Ammophila arenaria, Acacia longifolia, Rosa rugosa,* among others) are aggressively invasive and result in species decline through different invasive processes (Marcantonio et al., 2014; Sarmati et al., 2019). Frequently, native coastal dune plants are replaced by exotic invasives, and this species turnover becomes more intense with invasion time. This pattern holds for invasives such as *Acacia* *longifolia* (Marchante et al., 2015), *Ammophila arenaria* (Pickart, 2013) and *Carpobrotus aff. acinaciformis* (Santoro et al., 2012b). Some relevant findings in this regard highlight the biogeographic origin of the invasive species, which affects their impact in native vegetation (Ledger et al., 2015). Other studies show that the expansion of invasive species leads to the artificial stabilization of sand movement (Wiedemann and Pickart, 2004) as well as changes in shoreline dynamics (Masterman and Ellison, 2018). Furthermore, del Vecchio et al. (2015) also observed that the severity of the impact of the invasive species might be associated with human disturbances, which facilitate dispersal and colonization of invasive species.

Environmental sea-inland gradients are also relevant for the process and impact of species invasions (Lortie and Cushman, 2007). The beach-dune gradients are characterized by a variety of habitats, with pioneer communities on the beach, followed by embryo dunes, foredunes, and inland dunes further away from the coastline. Different environmental factors change along this gradient: wave impact, salinity (marine flooding and salt spray), wind intensity, and sand burial decrease inland, while nutrient availability and soil development increase. The above leads to a dynamic, but fragile, ecological and vegetation gradients along this narrow strip that is determined by the tolerance to these limiting factors. In this sense, Santoro et al. (2012a) observed that the increasing population of an invasive alien species, *Carpobortus* aff. *acinaciformis*, resulted in the collapse of the community structure. In this case, the invasive species became overly abundant, while the natural vegetation zonation along the beach-dune gradient was eliminated. Also, native plant assemblages are affected by invasive species in more subtle ways through the disruption of species interactions which result in changes in community structure (Trasevet and Richardson, 2014).

Oenothera drummondii subsp. *drummondii* Hook, native to Mexico and southern USA, is an invasive species that has colonized many dune systems worldwide during the last century. Studies on the impact of *O. drummondii* have focused on estimating the degree of invasion (Campos et al., 2004; García-de-Lomas et al., 2015), its occurrence on coastal plant communities of the Iberian Peninsula (Galán de Mera et al., 1997); its physiological attributes that enable the species to be an effective invader (Zunzunegui et al., 2014) and eradication actions (García-de-Lomas et al., 2016). Nevertheless, the invasion patterns along the beach-dune gradient and the impact of *O. drummondii* in the plant community has not been studied yet.

Within this framework, this paper reports the analysis of how the beach-dune environmental gradient affects the invasion of *O. drummondii* on coastal dune plant communities in Southern Spain, in terms of changes in community structure and the loss of biodiversity. In detail, this paper addresses the following questions:

- Does the beach-dune gradient modify species invasion?
- Are there microsites along the beach-dune gradient (dune types or zones) that are more prone to being invaded by alien plant species?
- How do community structure and composition change after the arrival and expansion of the invasive alien species?

2. Materials and methods

2.1 Study species

The beach evening primrose, *Oenothera drummondii* subsp. *drummondii* (Onagraceae) is, native to the coastal dunes in Eastern Mexico and South-eastern USA (Dietrich and Wagner, 1988; Dietrich, 1997;). In its native range, *O. drummondii* is relatively scarce (Moreno-Casasola, 1988; Gallego-Fernández and Martínez, 2011) but it is abundant in invaded locations. It is considered invasive in Australia (ALA, 2014), China (Xu et al., 2012) and Spain (García-de-Lomas et al., 2015) and naturalized in Egypt (Shaltout et al., 2016), South Africa (Frean et al., 1997), Israel (Dufour-Dror, 2012), and New Zealand (Heenan et al., 2002). In Spain, it was first recorded in the Gulf of Viscay (N Spain) in 1915 (Campos and Herrera, 2009) and near the town Rota (Gulf of Cadiz, SW Spain) in 1957 (Silvestre, 1980) and now it is considered invasive (García-de-Lomas et al., 2015).

The main stems of this short-lived perennial herb are erect to procumbent, and the basal side-stems are prostrate or ascending to about 50 cm tall with a strong taproot. The plant is self-compatible, outcrossing and pollinated by hawkmoths in its native habitats (Wagner et al., 2007). The species reproduces and spreads by small and numerous seeds which have a high germination rate.

2.2 Study site

The study was carried out in a coastal dune system of Huelva, Spain (37° 9’ 20’’ N, 6° 54’ 40’’ W). These dunes are very recent, formed after the construction of the jetty *Juan Carlos I* in 1981 (Rodríguez-Ramírez et al., 2008). The dune system stretches for 7 km running parallel to the jetty and is between 200 to 400 m width. The area is included in the protected natural area "Marismas del Odiel" since 1989 and integrated into the European NATURA 2000 network (ES0000025).

Ever since this dune system was formed, the mobile dunes became colonized by native coastal dune species, which slowly increased plant cover and increased biodiversity. Four habitat types included in Annex I of the European Habitat Directive 92/43/EEC (2013) occur in the study site: (1) Embryo dune, characterized by *Cakile maritima* and *Polygonum maritimum* (habitat type 1210 and 2010; Royo and Traveset, 2009; Gracia et al., 2009), (2) foredune, characterized by the dominance of *Ammophila arenaria* (habitat type 2120; Gracia, 2009), (3) Fixed coastal dunes with herbaceous vegetation dominated by *Crucianella maritima* (habitat type 2130 and 2230; Gracia and Muñoz, 2009; Gómez-Serrano and Sanjaume, 2009).

The climate is Mediterranean with winter rains and summer droughts, a mean annual temperature of 17.8 °C and a mean annual rainfall of 467 mm. The dune system and beach cover 110 ha, of which ca. 70 ha are invaded by *O. drummondii*, mostly along the 4 km of the western margin. The eastbound dunes have not been invaded yet (Fig. 1). The first records of *O. drummondii* in the southwest of the Iberian Peninsula date from 1957 (Silvestre, 1980), and in the study area it was registered for the first time in 1996 (M.R. García-Mora personal communication).

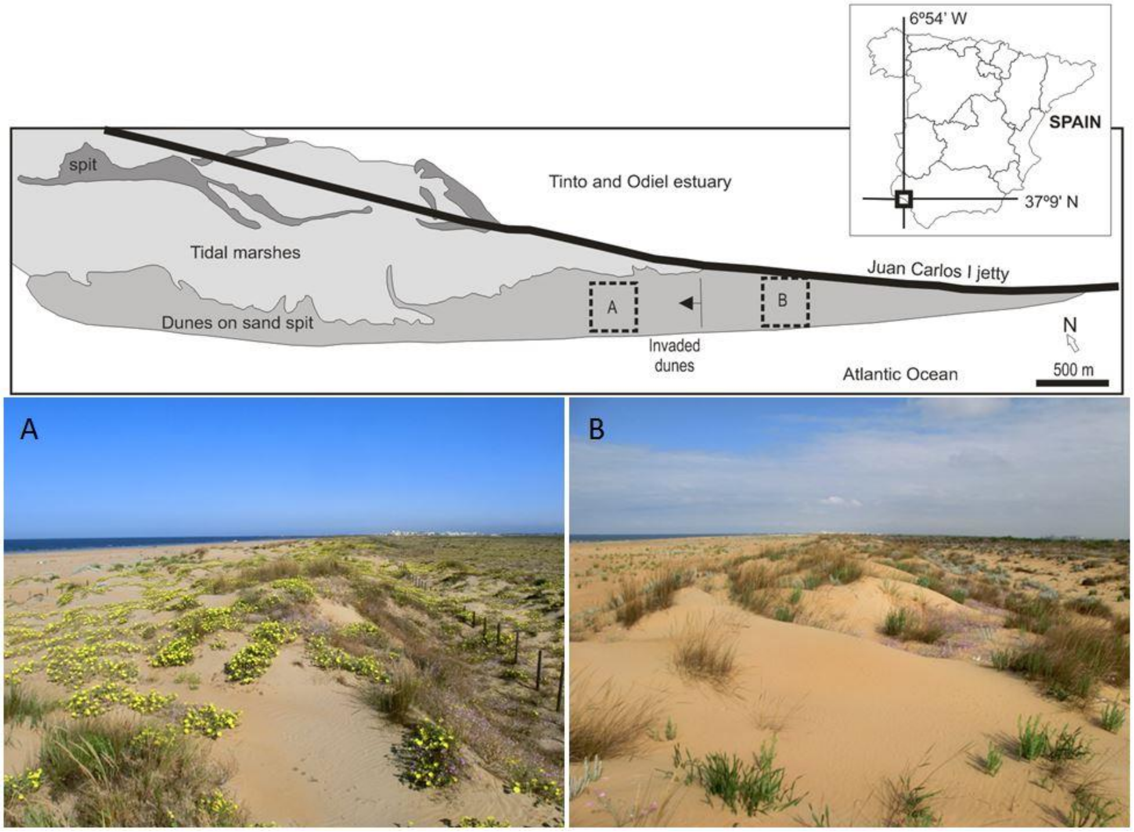

Fig. 1. Geographic location of the study area. Boxes and photographs show the invaded (A) and uninvaded (B) sectors.

2.3 Vegetation sampling

To address the critical issue of how environmental gradients, affect biological invasions we undertook a comparative study of dune plant communities in an uninvaded area (control) and an adjacent location that has been invaded by *O. drummondii*. These comparisons were performed based on the premise that, before the invasion by *Oenothera*, community structure and composition of invaded and uninvaded communities were similar (field observations by J.B. Gallego-Fernández, since 1990; personal communication from M.R. García-Mora). Fieldwork took place in April 2013. Sampling plots were located based on a restricted random method using GIS.

We chose two sectors (invaded and uninvaded) to measure the impact of the invasive plant. The sectors were 200 m wide (parallel to the shoreline) and 300 m inland each. The two sectors were 1 km apart from each other, and both included the beach, foredune and inland dunes. Then, to select the sampling plots, each sector was subdivided into a grid of 10 x 10 m quadrats which were numbered separately, depending on their location (beach, foredune, inland dunes). The quadrats to be sampled were later selected with random numbers until we had a total of 95 quadrats per sector. The only conditions were that the quadrats to be sampled should not be adjacent to each other and that the total number of quadrats should be proportional to the entire area of each habitat because the relative surface covered by each was different. Once the quadrats to be sampled were located in the GIS system, UTM coordinates at the center of each quadrat were collected and then they were used to find the quadrats in the field, with a GPS. Finally, at the center of each quadrat, we established 2 x 2 m plots in which vegetation was sampled, adding a total of 190 sampled plots. Plot size was selected based on similar studies carried out with coastal dune vegetation (Carboni et al., 2011; Gallego-Fernández and Martínez, 2011).

We generated a list with the identity of all species found in each sampling plot to characterize the abundance/dominance structure of the invaded and uninvaded communities. Also, plant cover per species and the percentage of bare sand were visually estimated using a 5% interval on the rank scale. Further, above-ground biomass of *O. drummondii* was collected by cutting all individuals at the sand surface level. Samples were oven-dried at 60° C for 48 h and then weighed on a precision balance. For all plots, distance to the shoreline was recorded.

2.4 Data analyses

Two-way fixed-factor ANOVA was used to test whether total plant cover, *O. drummondii* cover, the cover of annual, biannual and perennial species (excluding *O. drummondii* data) and bare sand was different between invaded and uninvaded sectors and across the beach, foredune, and inland dune zones. Pair-wise *a posteriori* comparison was based on the Tukey procedure (Underwood, 1997). An Arc-cosine transformation was applied to plant cover data before performing statistical analyses (Zar, 1999). Differences in the number of *O. drummondii* individuals and biomass per plot were tested by paired Mann-Whitney test between the three zones (beach, foredune, and inland dune) in the invaded sector.

PRIMER v.6.1.10 (PRIMER-E, Plymouth, UK) was used to calculate species richness (S), Shannon's diversity index (H'), and Simpson's index of dominance (λ) based on species cover. Differences of these indexes between invaded and uninvaded plots across the three zones were used to measure the effect of invasion on community structure and composition using paired t-tests (IBM SPSS Statistics for Windows, version 25; Armonk, NY, USA). Before performing the statistical analyses, a logarithmic transformation was applied to H' and λ, and a square rooted transformation was applied. S. *O. drummondii* was excluded from the diversity analyses because this species was the main factor distinguishing between invaded and uninvaded plots (Hejda and Pysek, 2006).

To assess the response of plant communities of the three zones (beach, foredune, and inland dune) to plant invasion we used repeated measures permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001; McArdle and Anderson, 2001), and post-hoc pairwise comparisons. PERMANOVA, a non-parametric multivariate technique, calculates an F-statistic from pseudo-F ratios. These analyses were performed excluding *O. drummondii*. Since PERMANOVA does not require multivariate normality, the data were not transformed. The analyses were based on Bray-Curtis dissimilarity values of species abundances standardized to species' maxima. The analyses were performed using 9999 permutations, with the permutation of residuals under a reduced model, fixed effects sum set to zero and type III sums of squares. A PERMDISP analysis was used for quantifying differences in variability of plant communities' composition (Clarke, 1993). Finally, SIMPER analysis was used to determine the contribution of each species to the average Bray-Curtis dissimilarity index between invaded and uninvaded vegetation of beach, foredune, and inland dune. The above enabled us to distinguish the species that contribute most to the differences observed between the two sectors. Multivariate analyses of community composition and relative frequency data were carried out in PRIMER v.6.1.10 with the PERMANOVA+ add in (PRIMER-E, Plymouth, UK).

Changes in plant diversity were visualized using relative importance curves (Gallego-Fernández and Martínez, 2011). For this purpose, species were ranked in decreasing order of importance, based on plant abundance. Relative Importance values were calculated by adding relative frequency (proportion of plots where a species occurred) and relative cover (proportional cover per species, relative to total plant cover [all species] per plot). These curves were calculated including *O. drummondii* values to assess whether dominance in invaded communities differed from that of uninvaded ones.

3. Results

3.1 Abundance of O. drummondii

In each sector, total plant cover was not significantly different between foredunes, and inland dunes, but the cover at the beach was significantly lower (Uninvaded: $F_{2,92} = 10.8$, $P < 0.0001$; Invaded: $F_{2,92} = 16.468$, $P < 0.001$). Comparisons between sectors only yielded significant differences on the beach, where total plant cover was significantly larger in the invaded sector (Table 1). The percentage of bare sand decreased inland, but it did not differ significantly between invaded and uninvaded sites (in any of the zones that we studied) ($P > 0.05$).

As expected, *O. drummondii* was very abundant in the invaded sector, but it varied between zones (Table 1). In the invaded sector, the invasive was found in 31% of the beach plots; 65% of the foredune plots, and in all plots of the inland dunes. *O. drummondii* also was present in the uninvaded sector, but only in 6% of the plots located on the inland dunes. In the invaded sector, plant density, dry biomass, and plant cover per plot of *O. drummondii* were significantly higher in the inland dunes and lower on the beach (Cover: $F_{2,92} = 10.80$, $P < 0.0001$; density: H = 58.354, $P < 0.0001$; biomass: H = 56.898, $P < 0.001$). The maximum density of *O. drummondii* plants growing on inland dunes was 9.3 individuals per square meter, with 35% plant cover and 213.9 g/m2 of dry biomass.

Table 1. Changes in community composition and structure in three zones (beach, foredunes and inland dunes) studied in sectors that were invaded and uninvaded by the exotic herb *Oenothera drummondii*. Statistical comparisons refer to invaded vs. uninvaded sectors in each of the monitored zones. n.s., not significant; nt, not tested. Significant levels of Mann-Whitney tests are: * < 0.05; ** = 0.01; *** = 0.001.

	Beach			Foredune			Inland dune		
	Invaded	Uninvaded	P	Invaded	Uninvaded	P	Invaded	Uninvaded	P
Number of sampling plots	13	13		17	16		65	66	
Total plant cover per plot (%)	13.0 ± 8.9	5.6 ± 3.6	*	21.0 ± 12.4	25.6 ± 16.4	ns	28.8 ± 13.9	29.6 ± 17.1	ns
Bare sand (mean % per plot)	83.5 ± 12.2	92.0 ± 6.3	ns	75.5 ± 16.7	71.8 ± 16.7	ns	66.4 ± 16.6	68.1 ±16.4	ns
Total number of species	10	7		19	13		46	35	
Oenothera drummondii data									
Frequency (No. plots present)	4	0	nt	11	0	nt	65	4	nt
Number of individuals/plot	0.08 ± 0.12	0	nt	1.0 ± 0.8	0	nt	4.5 ± 1.9	0.03 ± 0.1	***
Biomass (dry g/m2)	3.4 ± 7.2	0	nt	16.4 ± 15.1	0	nt	82.6 ± 40.3	1.1 ± 6.8	***
Cover / plot (%)	3.6 ± 7.7	0	nt	6.3 ± 5.7	0	nt	15.2 ± 8.2	0.1 ± 0.7	***
O. drummondii (relative cover %)	13.9 ± 27.9	0	nt	37.1 ± 32.8	0	nt	57.9 ± 26.0	0.6 ±3.3	***

3.2 Species composition

A total of 55 vascular plant species from 21 families were recorded (Appendix 1). From these, 7.3% of the species are exotics: *O. drummondii*, *O. laciniata*, *Arctotheca calendula*, and *Conyza canadensis*. Furthermore, 41.8% are considered typical dune species. Invaded and uninvaded sectors had a total of 49 and 35 species, respectively, and this trend was also observed in the three zones, with a higher number of species in the invaded sites (Table 1). From the total number of species, 29 were observed in both sectors, invaded and uninvaded, 20 were only found in the invaded sector, and 6 were exclusive to the uninvaded site (Appendix 1). The local distribution of species revealed that a relatively large number 37 (65%) of species only grew on inland stabilized dunes. The only species that were observed growing in all zones considered were *Pancratium maritimum*, *Ammophila arenaria*, *Polygonum maritimum, Euphorbia paralias*, and *Otanthus maritimus*.

Most of the species (92.7%) were herbaceous, and only 7.3 % were woody. Life cycles of the species found were diverse: el 34.5% are perennials, 58.2 % annuals, and 7.3 % biennials. In both sectors, species richness of annual and biennial species increased inland. However, differences between sectors only were significant on inland dunes. In contrast, species richness of perennials decreased inland. Again, the number of perennial species (excluding *O. drummondii*) was significantly larger in inland dunes in the uninvaded sector (Figure 2).

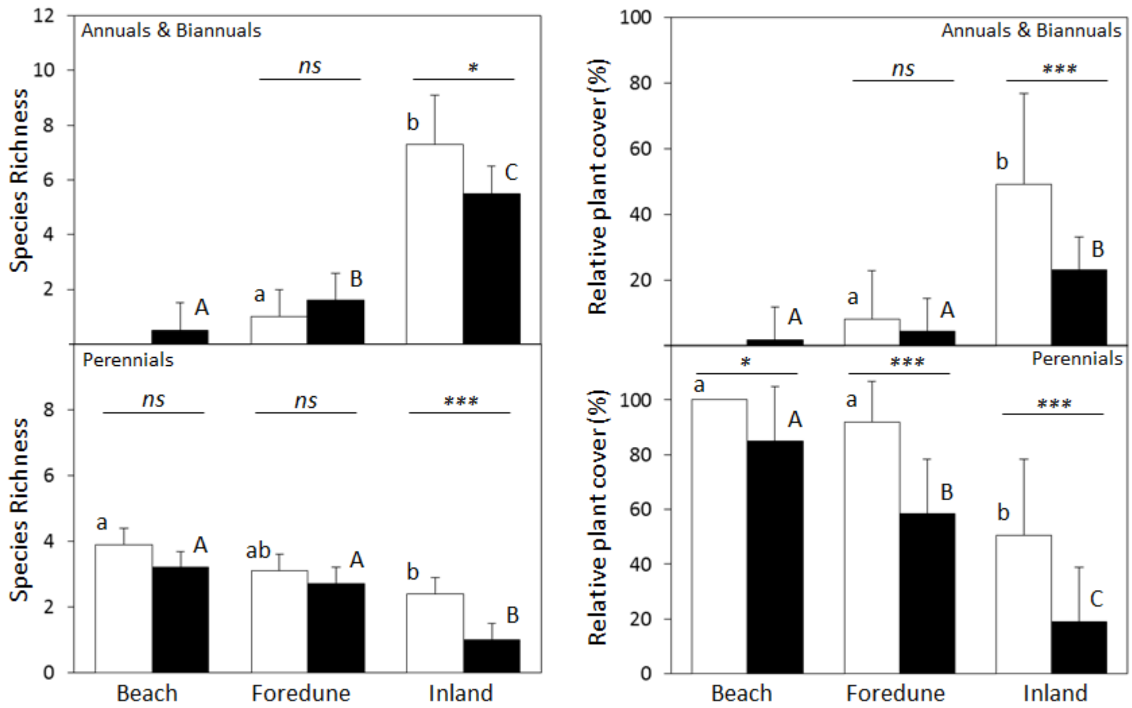

Fig. 2. Species richness and relative plant cover (mean ± se) of annual and biannual and perennial (not *O. drummondii*) species of coastal dune communities surveyed at three zones (beach, foredune, and inland dunes) in sectors that were invaded (black) and uninvaded (white) by the exotic herb *Oenothera drummondii*. Comparisons between zones (invaded vs. uninvaded) are indicated by the lines above each pair of bars (Mann-Whitney tests; ns = not significant; *** = $P < 0.001$). Comparison between zones of the invaded sector is indicated by capital letters. Comparisons between zones of the uninvaded sector are shown in small letters. Both analyses with ANOVA and Tukey comparisons; same letters indicate non-significant differences.

3.3 Changes in plant cover

To determine the impact of *O. drummondii* on species abundance according to their life cycles, we compared relative plant cover of annuals, biennials, and perennials but did not consider *O. drummondii*. The plant cover of annual and biennial species increased inland in both sectors. However, the only significant difference was observed in inland dunes, where plant cover was significantly larger in the uninvaded sector. Unlike annuals and biennials, plant cover of perennials decreased inland and, in all cases, it was significantly larger in the uninvaded sector (Figure 2).

3.4 Diversity

In both sectors, species richness and Shannon´s diversity were significantly larger on inland dunes than on the beach and foredunes (Figure 3). Furthermore, species richness and Shannon´s diversity were significantly smaller in the invaded sector, but this was not so on the beach and foredunes (t = 5.259, $P < 0.001$ and t = 7.544, $P < 0.001$, respectively). In contrast with the above, dominance (Simpson Index) was significantly smaller in inland dunes, but it was in inland dunes where we found significant differences between sectors (Figure 3). In this case, dominance was significantly larger in the invaded sector than in the uninvaded sector. The comparisons of the Simpson Index between invaded and uninvaded sectors showed that differences were only significant in inland dunes, where the invaded sector had larger values (t = 4.353, $P < 0.001$).

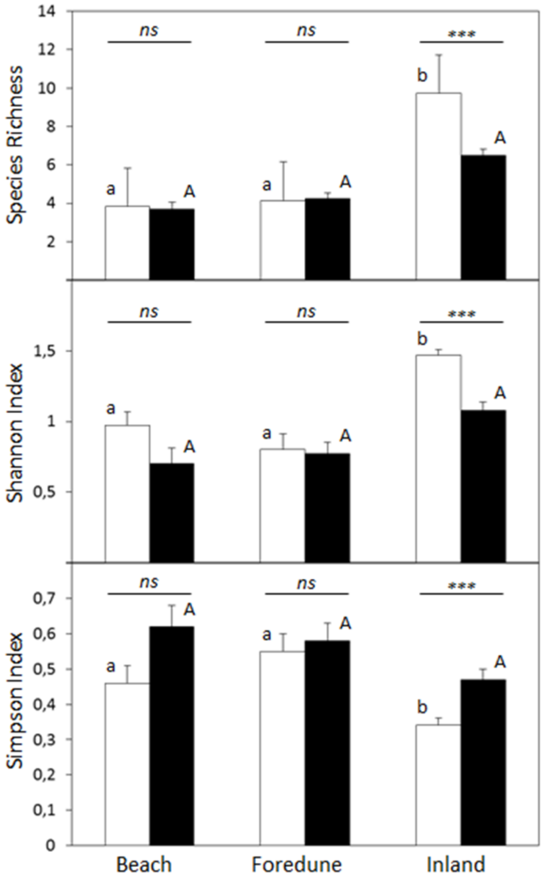

Fig. 3. Diversity indices (mean ± se) of coastal dune communities surveyed at three zones (beach, foredune, and inland dunes) in sectors that were invaded (black) and uninvaded (white) by the exotic herb *Oenothera drummondii*. Comparisons between zones (invaded vs. uninvaded) are indicated by the lines above each pair of bars (ns = not significant; *** = $P < 0.001$). Comparison between zones of the invaded sector is indicated by capital letters. Comparison between zones of the uninvaded sector is shown in small letters. Both analyses with ANOVA and Tukey comparisons; same letters indicate non-significant differences. Cover of *O. drummondii* was omitted when the indices were calculated.

Rank abundance curves show that *O. drummondii* was the dominant species, especially on inland dunes in the invaded sector (Figure 4). In turn, plant communities in the uninvaded sector were more equitable, with a larger number of species with intermediate values, and the absence of extremely dominant species. This trend was more marked on inland dunes. The dominant species in the uninvaded sectors varied between zones: *Polygonum maritimum* was the dominant species on the beach, *Ammophila arenaria* in the foredune, and *Malcolmia littorea* in inland dunes.

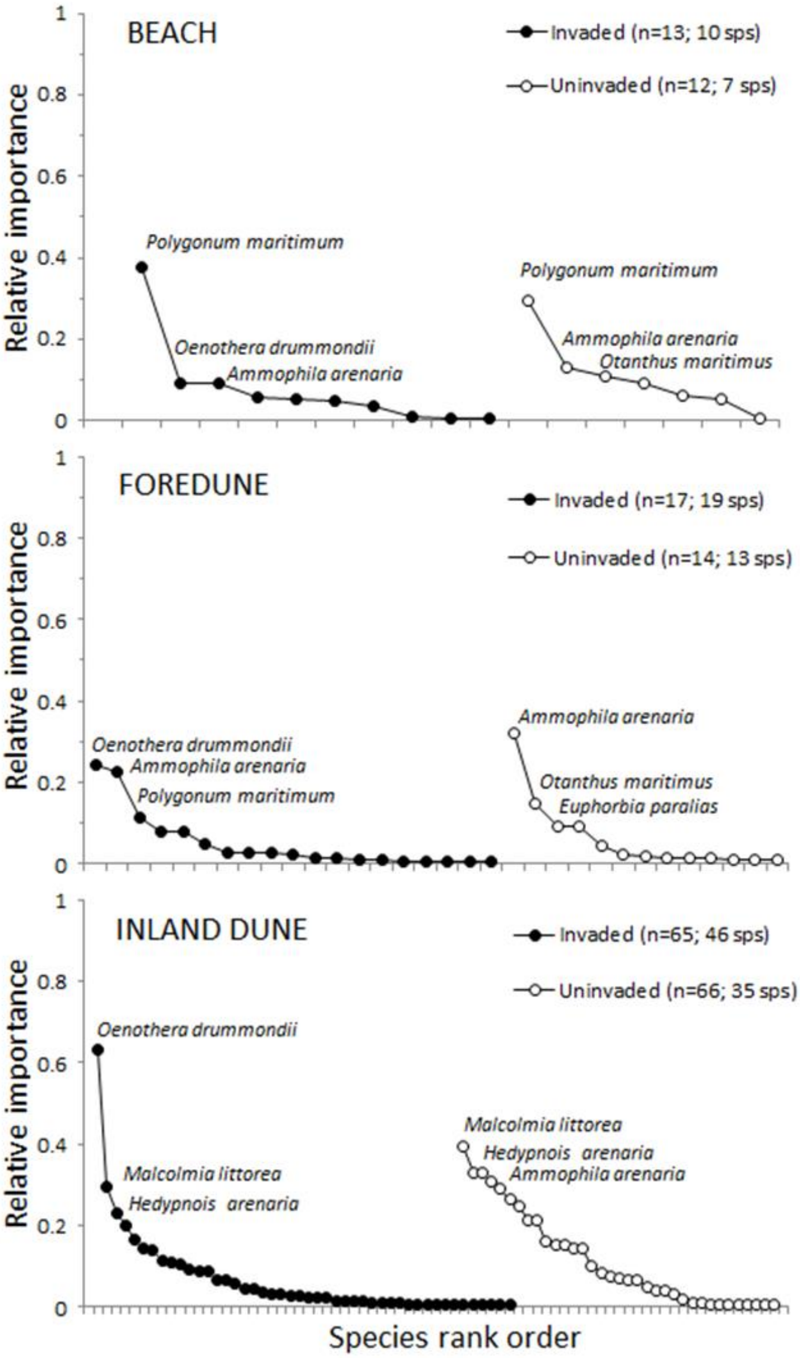

Fig. 4. Rank-abundance curves of plant communities on the beach, foredunes, and inland dunes in sectors that were invaded and uninvaded by the exotic herb *Oenothera drummondii.*

3.5 Community changes in invaded and uninvaded dunes.

We observed that the cover of native species was negatively correlated with the cover of *O. drummondii*. Also, the cover of native plants was larger in the uninvaded sector. Nevertheless, these trends were not statistically different. Additionally, PERMANOVA tests performed with species frequency and plant cover showed that differences between sectors (invaded and uninvaded plant communities) and between zones (beach, foredunes and inland dunes) were highly significant (Table 2). Pair-wise *a posteriori* comparisons indicated that such differences were significant for the beach and inland dunes but not so in the foredunes (Table 2). PERMDISP tests showed that multivariate dispersion was significantly greater within uninvaded communities in inland dunes (Table 2).

Table 2. Results of two way fixed factor PERMANOVA tests on vegetation community data for invaded and uninvaded sectors of three zones: beach, foredune, and inland dunes. Results of PERMDISP tests on vegetation community data for invaded and uninvaded sectors in three zones: beach, foredune, and inland dunes, and analysis testing the variability between zones.

	PERMANOVA test					PERMDISP test	
Source of variation	*df*	SS	MS	F	P	F	P
Sector	1	12337	12337	4.3612	0.0003	6.7208	0.0001
Zone	2	118500	59252	20.945	0.0001	53.535	0.001
Sector x Zone	2	6148.9	3074.5	1.0868	0.3478		
Residual	182	514850	2828.9				
Total	187	662520					

PERMDISP tests					
Invaded vs. Uninvaded	t	P	Pair-wise test	t	P
Beach	1.7737	0.0212	Beach – Foredune	3.9923	0.002
Foredune	1.4463	0.0671	Beach – Inland dune	11.317	0.003
Inland dunes	2.5093	0.0001	Foredune – Inland dune	4.0724	0.001

SIMPER analyses showed that the average dissimilarity between invaded and uninvaded communities was lowest at the beach (46.92) and highest (81.43) in inland dunes (Table 3). The species that mostly discriminated between invaded and uninvaded plant communities were *Ammophila arenaria* and *Othantus maritimus*, both perennials and with a reduced cover on invaded dunes. *Polygonum maritimum* grows exclusively on the beach, and the beach was not largely colonized by the invasive plant. Consequently, this species contributed to the dissimilarity between invaded and uninvaded communities, because colonization by the invasive on the beach was reduced. Also, in inland dunes, annual species such as *Polycarpon alsinifolium*, *Hedypnois arenaria*, and *Erodium cicutarium* contributed significantly to the dissimilarity between invaded and uninvaded areas.

Table 3. Discriminating species for dissimilarity between zones invaded and non-invaded zones by *Oenothera drummondii* identified by the dissimilarity percentage procedure analyses (SIMPER). The list includes the cumulative species contribution, up to 90%, to the average dissimilarity. Data are untransformed.

Species	Average Abundance Invaded sector	Average Abundance Uninvaded sector	Average dissimilarity	Dissimilarity /SD	Contribution (%)	Cumulative contribution (%)
Beach. Average dissimilarity between Invaded and Uninvaded sectors: 46.92						
Polygonum maritimum	73.14	46.47	16.30	1.45	34.74	34.74
Ammophila arenaria	7.78	16.13	8.26	0.74	17.60	52.34
Otanthus maritimus	5.12	14.17	6.98	1.04	14.87	67.21
Euphorbia paralias	4.76	11.75	6.58	0.87	14.03	81.24
Elymus farctus	6.08	4.29	3.97	0.86	8.46	89.70
Eryngium maritimum	0.99	6.95	3.64	0.66	7.77	97.47
Foredune. Average dissimilarity between Invaded and Uninvaded sectors: 66.83						
Ammophila arenaria	42.02	51.55	20.51	1.42	30.69	30.69
Otanthus maritimus	8.91	20.97	11.89	0.92	17.79	48.48
Euphorbia paralias	11.96	10.14	8.57	0.87	12.83	61.32
Polygonum maritimum	12.75	0.41	6.30	0.75	9.43	70.75
Elymus farctus	0.49	6.77	3.35	0.76	5.02	75.77
Pancratium maritimum	4.62	1.21	2.85	0.31	4.26	80.03
Malcolmia littorea	2.54	3.35	2.53	0.61	3.79	83.81
Lotus creticus	4.86	0.00	2.43	0.25	3.64	87.45
Erodium cicutarium	1.68	2.56	2.00	0.38	2.99	90.44
Inland dune. Average dissimilarity between Invaded and Uninvaded sectors: 81.43						
Ammophila arenaria	14.48	22.55	13.49	1.05	16.56	16.56
Malcolmia littorea	14.25	12.93	8.68	0.84	10.67	27.23
Otanthus maritimus	4.62	15.05	8.53	0.80	10.48	37.71
Polycarpon alsinifolium	11.93	6.73	7.37	0.71	9.05	46.76
Hedypnois arenaria	7.20	7.96	5.32	0.76	6.54	53.30
Erodium cicutarium	4.23	6.59	4.40	0.72	5.41	58.71
Pancratium maritimum	4.80	4.24	4.20	0.41	5.16	63.87
Cyperus capitatus	4.97	1.04	2.90	0.34	3.57	67.44
Silene nicaeensis	3.17	2.55	2.53	0.44	3.10	70.54

Hypochaeris glabra	4.67	0.70	2.52	0.50	3.09	73.63
Pseudorlaya pumila	1.61	2.87	1.86	0.65	2.28	75.91
Anthemis maritima	3.49	0.00	1.74	0.22	2.14	78.05
Reichardia gaditana	3.12	0.56	1.70	0.26	2.09	80.14
Medicago littoralis	0.21	2.95	1.55	0.31	1.91	82.05
Eryngium maritimum	0.00	3.06	1.53	0.44	1.88	83.93
Linaria pedunculata	2.56	0.44	1.40	0.39	1.72	85.64
Lotus creticus	1.96	0.35	1.14	0.23	1.40	87.04
Conyza canadensis	1.15	1.53	1.14	0.55	1.40	88.44
Echium gaditanum	0.23	1.71	0.94	0.26	1.16	89.60
Andryala arenaria	0.97	1.05	0.88	0.50	1.09	90.69

As expected, the species that contributed to similarities within zones of invaded and uninvaded sectors were unlike those that contributed to dissimilarities. *Polygonum maritimum* contributed the most to the similarity between invaded and uninvaded beaches. In the foredunes, *Ammophila arenaria* was the species that most contributed to the similarity between invaded and uninvaded sectors (more than 67%). In inland dunes, *Ammophila arenaria* and *Malcolmia littorea* explained over the 47% within uninvaded communities (Table 4). In invaded inland dunes, *Malcolmia littorea* and *Polycarpon alsinifolium* explained over the 55% of the overall similarity.

Table 4. Species contributing to similarities within invaded and uninvaded zones by *Oenothera drummondii*, identified by similarity percentage analyses (**SIMPER**). The list includes the cumulative species contributing up to 90% of the average similarity. The average abundance (cover percentage per plot) is calculated across three sites. Data are untransformed.

Species	Average abundance	Average similarity	Similarity /SD	Contribution (%)	Cumulative contribution (%)
Beach					
Group Invaded. Average similarity: 67.85					
Polygonum maritimum	73.14	61.77	3.36	91.03	91.03
Group Uninvaded Average similarity: 47.89					
Polygonum maritimum	46.47	33.06	1.78	69.04	69.04
Otanthus maritimus	14.17	5.07	0.58	10.59	79.64
Ammophila arenaria	16.13	4.22	0.57	8.81	88.44
Euphorbia paralias	11.75	3.11	0.37	6.50	94.94
Foredune					
Group Invaded. Average similarity: 21.41					
Ammophila arenaria	35.61	14.52	0.57	67.80	67.80
Polygonum maritimum	9.88	1.96	0.30	9.16	76.96
Euphorbia paralias	7.26	0.98	0.16	4.57	81.53

Hedypnois arenaria	7.89	0.83	0.18	3.89	85.42
Otanthus maritimus	8.65	0.81	0.15	3.76	89.18
Silene nicaeensis	6.67	0.71	0.20	3.31	92.49
Group Uninvaded. Average similarity: 42.92					
Ammophila arenaria	51.55	32.35	1.21	75.37	75.37
Otanthus maritimus	20.97	6.45	0.45	15.03	90.40
Inland dune					
Group Invaded. Average similarity: 17.02					
Malcolmia littorea	16.07	5.82	0.66	34.17	34.17
Polycarpon alsinifolium	14.36	3.55	0.38	20.85	55.01
Ammophila arenaria	12.20	1.99	0.22	11.70	66.72
Hedypnois arenaria	4.89	1.33	0.48	7.80	74.51
Hypochaeris glabra	5.12	0.95	0.31	5.57	80.08
Erodium cicutarium	5.10	0.63	0.21	3.69	83.77
Linaria pedunculata	3.02	0.43	0.27	2.52	86.29
Pancratium maritimum	5.78	0.42	0.09	2.49	88.78
Cyperus capitatus	5.98	0.40	0.10	2.36	91.14
Group Uninvaded. Average similarity: 29.50					
Ammophila arenaria	22.55	8.99	0.59	30.47	30.47
Malcolmia littorea	12.93	4.98	0.76	16.87	47.34
Otanthus maritimus	15.05	4.67	0.45	15.84	63.18
Hedypnois arenaria	7.96	3.11	0.72	10.54	73.72
Erodium cicutarium	6.59	2.34	0.60	7.93	81.65
Polycarpon alsinifolium	6.73	1.82	0.49	6.16	87.81
Pseudorlaya pumila	2.87	0.79	0.48	2.68	90.49
Silene nicaeensis	2.55	0.64	0.42	2.18	92.66

4. Discussion

4.1 Does the beach-dune gradient modify species invasion? Are there microsites along the beach-dune gradient (dune types) that are more prone to being invaded by alien plant species?

We detected a modest number of aliens, which represented 7.3% of a total of 55 vascular plant species from 21 families that were recorded. This finding was slightly larger than reports from similar studies. For example, Carboni et al. (2010) found that alien species represented 7% of total species richness. However, and like the findings by Carboni et al. (2010), alien spread in our study area was correlated with changes in community structure and composition. Our results showed that, indeed, the invasion by *O. drummondii* increased inland and differed along the beach-dune gradient. This trend was observed in terms of frequency, density, biomass and plant cover of the invasive plant. The least invaded zones were the beach and foredunes, whereas inland dunes were invaded the most. Similar studies have shown that the changing environmental conditions along the beach-dune gradient largely affect the successful expansion and impact of exotic invasive species, although the results are divergent. In coincidence with our results, Kolb et al. (2002) and Acosta et al. (2008) found that in Californian coastal ecosystems, and on Italian coastal dunes, respectively, greater invasion occurred in less harsh sites. These authors concluded that the beach and embryo dunes had limited alien invasions because the environmental stress reduces the ability of invasives to thrive and use the available resources (Davis et al., 2000). On the contrary, Lortie and Cushman (2007) observed higher levels of invasion when environmental conditions were extreme, while Carboni et al. (2011) found that intermediate levels of disturbance and stress offered the best conditions for colonization and spread of invasive species (*Carpobrotus* *acinaciformis* and *Xanthium orientale*). That is, Carboni et al. (2011) showed that at intermediate levels of moisture, salt spray and organic matter, found on the upper beach, in between the beach-dune gradient, had the highest cover of alien species. The diverse and inconclusive trends in this regard clearly show that patterns of species invasions depend on the environmental conditions and the species involved.

Indeed, in our case, the environmental conditions along the beach-dune gradient are probably affecting the ability of *O. drummondii* to become equally invasive along the beach-dune gradient. The extreme stress conditions of the beach and foredunes, with high salinity and sand movement, make it difficult for new species, not adapted, to survive under such selective pressures imposed by the environment (García Mora et al., 1999; Maun, 2004; Gallego-Fernández and Martínez, 2011). However, in more benign conditions, such as inland dunes, *O. drummondii* can successfully colonize, get established and become dominant. These inland conditions mostly resemble those from the native habitats of *O. drummondii* which mostly grow on vegetated foredunes and inland dunes, where exposure to salinity and sand movement is reduced (Moreno-Casasola and Espejel, 1986).

In consequence with the above, the most significant impact of *O. drummondii* was observed on inland dunes, where the invasive plant reached the highest plant cover. Such extensive growth is probably due to the massive growth of the roots and efficient use and assimilation of water which was greater than that observed for native species such as *Otanthus maritimus* (Zunzunegui et al., 2014). Furthermore, the successful invasion of *O. drummondii* on inland dunes is also the result of a large number of seeds and their effective dispersal through barochory and zoochory through native hares, which then form a seed bank that lasts longer than four years (Gallego-Fernández et al., Unpublished results).

4.2 How does community structure and composition change after the arrival and expansion of the invasive alien species?

Like in many studies on the impact of invasive species (Hejda et al., 2009, Vilà et al., 2011), our results confirm that indeed, the abundance of *O. drummondii* is associated with changes in community diversity and composition. In our study sites, we observed that species richness and species diversity, *H'*, increased inland in both invaded and uninvaded sectors but this increment was lower in the invaded sectors. The dominant species varied depending on the zone and if the area was invaded or not. Dominant native species in the uninvaded sectors retained smaller relative importance values. In turn, *O. drummondii* was the most dominant species in all zones on invaded sector, but mostly so on inland dunes, monopolizing space and resources and thus, reducing frequency and abundance and ultimately diversity of native species (see for instance Hejda et al., 2009; Carboni et al., 2010; del Vecchio et al., 2015 among others). Interestingly, invasion by *O. drummondii* did not result in larger plant cover on inland dunes, which was similar to uninvaded dunes, because the increment in plant cover of the invasive increased at the expense of the natives. This is probably the result of limited resources (water and nutrients) which constraint vegetation growth (Levinsh, 2006).

The impact of *O. drummondii* also varied depending on the life cycle of native species. For example, plant cover of native perennials such as *Ammophila arenaria* and

Otanthus maritimus was largely reduced by *O. drummondii* (a reduction of 66 and 91% respectively). This is especially relevant because *A. arenaria* can be considered as a keystone species in the community, because it is a dune builder, and regulates sand movement. Thus, a reduction in its cover will likely modify dune morphology and the environmental heterogeneity and functioning of uninvaded coastal dunes. Other perennials were locally eliminated from invaded dunes (*Eryngium maritimum, Medicago marina,* and *Elymus farctus)*. In turn, the abundance of annual and biennial species either decreased or remained relatively scarce in invaded sectors. Similar species turn-over have been recorded in similar coastal dunes (Acosta et al., 2008; Carboni et al., 2010; Vila et al., 2011; Asensi, 2016).

Finally, the impact of *O. drummondii* is scale dependent. At a local level, in our 2 x 2 plots, species invasion corresponded with a reduction in species richness. However, on a larger scale (the 200 x 300 m sectors) species richness was 24% larger in invaded inland dunes, in comparison with those from the uninvaded sector. Most of these new species are ruderal annual and biennial species, not typical from the dunes. Nevertheless, the area covered by these species is reduced (0.5%), and they are not very frequent either (1-6% of the sampling plots), although it is possible that they may expand over time and exacerbate changes in the original plant community (Davies, 2011).

In addition to the above, our results also reveal a high dissimilarity between invaded and uninvaded sectors which is evidence of the impact that the species invasion has had on community structure and composition. These findings are in accordance with previous studies. For example, Hejda et al. (2009) demonstrated that even when biological invasions have a limited impact on species richness, species composition may also be altered with a notorious increment in ruderal species in invaded communities (Hejda and Pysek, 2006). Additionally, community structure may also be changed after the invasion. For example, Santoro et al. (2012a) showed how ice plant invasion modified community assemblage by eliminating facilitative interactions which are of concern for biodiversity conservation. Like community responses to disturbances such as wildfires, community assemblage became random instead of aggregated, which means that community assembly patterns changed. In our case, the decreased relative cover of native species is changing community structure and assembly patterns, which will lead to a different community.

4.3 Study caveats

Our sampling design enabled us to measure the impact of *O. drummondii* on native plant communities by comparing invaded and uninvaded sites, by considering different habitats (dune types) along the beach-dune gradient. Such an approach is useful because it compares large data sets over a wide range of environments. Nevertheless, there is some uncertainty regarding the status of invaded plots before the invasion. Thus, it is reasonable to wonder if invaded, and uninvaded plots are comparable, since they may differ owing to factors other than invasion (Levine et al., 2003; Hejda et al., 2009). In our case, invaded and uninvaded sectors are comparable because they are exposed to similar environmental conditions since they are located relatively close together, and comprise similar habitats along the beach-dune gradient. The topography in the dune system of the Juan Carlos I jetty is relatively simple so prior to the invasion by *O. drummondii*, the invaded and uninvaded sectors were similar.

This study focused on the impact of *O. drummondii* on a recently formed dune system, with reduced species richness and intense sand movement. Thus, the invasion process took place during primary succession, when, indeed, the frequent and intense disturbance events and relatively low plant density, provide an opportunity for the colonization of invasive species (Acosta et al., 2008; Santoro et al., 2012a). It would be interesting to explore if the invasion process would have been as intense and rapid if the community were mature. Probably, this would not be the case, because high plant density and diversity of mature communities are likely to out-compete the expansion of *O. drummondii*. This is in coincidence with field observations in the native habitats along the coasts of Mexico.

Our experimental design, with two large sectors, can be considered as lacking adequate replicates of the invaded and uninvaded conditions. However, similar sampling methods with one single large study area, and an immersed grid of plots, have been performed in different long-term studies focused on plants (*i.e.* Schnitzer et al., 2012; Condit, 2017) and animals (Palacios et al., 2018). This method has proved to be useful because it allows plants to be mapped and located easily and guarantees that the area remains undisturbed for a long time. Furthermore, the large number of quadrats (95 per sector) was sufficient to include the environmental heterogeneity within each sector. Thus, we think that our sampling method yielded results that are valid and useful.

4.4 Future expansion of O. drummondii and control strategies

It was interesting to note that, even though the plant cover of *O. drummondii* per plot may be considered to be relatively low (3.6% on the beach, 6.9 on the foredune and 15.2 on inland dunes) the impact on the abundance and cover of native species was significant. Ongoing studies have revealed that this species uses water nutrients and light more efficiently than native plants (such as *O. maritima*), and thus, hydric stress in the Mediterranean coastal dunes is lower for the invasive (Zunzunegui et al., unpublished data). Furthermore, the leaves of *O. drummondii* contain allelopathic substances (ursolic acid and β-sitosterol) (Zunzunegui et al., unpublished results) which inhibit the germination of native plants (Pereira et al., 2007).

The colonization and expansion of *O. drummondii* have occurred at a relatively fast rate since it was first observed at the study site in 1996 (ca. 4 ha per year). Such invasiveness may be the result of anthropogenic disturbances which open space for colonization, and to the efficient seed dispersal of *O. drummondii*. Locally, seed dispersal occurs through barochory and endozoochory (native hares). In a geographical scale, seed dispersal probable takes place through ocean currents (Gallego-Fernández et al., unpublished results). More recent samplings (2018) in the same sites have revealed that the invaded and uninvaded sectors have remained without significant changes (personal observation). The above suggests that *O. drummondii* has probably formed a stable population. Nevertheless, the changes in community structure and composition and the following modification in community dynamics may include loss of species interactions (see, for example, Santoro et al., 2012; Trasevet and Richardson, 2014). This could lead to a domino effect on coastal dune biodiversity and functioning that is of conservation concern, especially when highly specialized species become threatened. Thus, the invasion of *O. drummondii* should be carefully monitored, and control strategies need to be implemented so that the dispersion is limited, and the effects are mitigated (Hobbs and Huenneke, 1992; Gurevitch et al., 2011; Santoro et al., 2012a). Finally, the differences observed between zones in terms of the impact of invasion should be considered in management and conservation targets.

5. Conclusions

This study showed that the invasion of *O. drummondii* in the coastal dunes of southwestern Spain is associated with changes in community structure and composition and, that these depend on local conditions. The differences in invasiveness and impact of the invasive species along the beach-dune environmental gradient can help predict where the impact will be more intense, and thus, where mitigation actions are most necessary. In zones with high environmental severity such as the beach and foredunes, the invasive species was less abundant, and thus, changes in native vegetation were less drastic. The contrary was observed on inland dunes, which are exposed to milder conditions. Additionally, the abundance of native dune builder species such as *Ammophila arenaria* and *Otanthus maritimus* was significantly reduced in the presence of *O. drummondii*, while other native species were locally eliminated in the invaded sector. Thus, the shift in community structure and composition could have a domino effect on coastal dune biodiversity and needs to be carefully monitored and mitigated as much as possible. When doing so, the environmental heterogeneity of the beach-dune gradient should also be considered, given its relevance in the invasion process.

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