

Weak effects of the exotic invasive *Carpobrotus edulis* on the structure and composition of Portuguese sand-dune communities

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Received: 11 March 2009 / Accepted: 7 October 2009
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Abstract Sand dune ecosystems have a high conservation value worldwide, but they are highly threatened by exotic plant invasion. We investigated the impacts of the exotic invasive species *Carpobrotus edulis* on the composition and structure (spatial pattern, total cover, species diversity and species co-occurrence) of native sand dune communities in the western coast of Portugal. We studied eight sites following a north-south gradient; in each site we established 8–10 transects of 25 contiguous quadrats of one square meter. *C. edulis* had a significantly clumped pattern in five of the study sites, which, however, was not related to the spatial pattern of native species. The effects of climate on the community structure variables were on average three times stronger than those of *C. edulis*. This species also had small effects on the floristic composition of native species. Our results indicate that the success

and impacts of *C. edulis* are habitat-dependent and context-specific. They also provide evidence of a strong resilience to the impacts of invasion in the studied sand dune ecosystems: *C. edulis* did not reach large abundances or exert negative impacts on native communities to the extent expected. These ecosystems provide a unique opportunity to increase our understanding on the origin of impacts by invasive species, and on how particular communities resist the impacts of an invader.

Keywords Abiotic gradients · Ecosystem structure · Species composition · Invasion impacts

Abbreviations

SEM Structural equation modeling
SES Standardized effect sizes

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Introduction

The plant communities of sand-dune ecosystems are adapted to living in the harsh dynamic equilibrium of the sandy substrate, with constant sand movements, salt spray, and intense winds. These ecosystems, and the Mediterranean sand-dunes in particular, are of high biogeographic interest, and hold many threatened species and endemisms (Habitat Directive 92/43EEC). Despite their conservation value, they are

constantly under threat from human constructions and leisure activities, and from biological invasions by exotic plants (e.g., D'Antonio 1993; Conser and Connor 2009). Such invasions have been considered the second most important cause of change in the composition, structure, and functioning of natural ecosystems worldwide—following habitat destruction (Simberloff et al. 2005; Thuiller et al. 2005; Walther et al. 2002).

Successful invasions change the role of native species in communities, disrupt evolutionary processes, and cause radical changes in native species abundance, that may lead to their local extinction (Mack et al. 2000). Ultimately, invasive species lead to the progressive and often irreversible homogenization of plant communities, with a single species dominating and influencing the processes of the entire ecosystem (Mack et al. 2000; Vitousek et al. 1997). Therefore, biological invasions are expected to lead to a long-term loss of biodiversity and a permanent change in ecosystem processes (D'Antonio and Vitousek 1992; Wisser et al. 1998). However, Sax and Gaines (2008) stress that there is a lack of recorded extinctions due to invasions, which does not appear to be related with a lack of knowledge.

In a recent review, Levine et al. (2004) have documented 150 studies on the impacts of exotic plants, and found a roughly equal number of studies on the effects on community structure (species diversity and composition) and the effects on ecosystem processes (nitrogen cycling, hydrology, etc.). In particular, research on biological invasions has focused on aspects like: the invasion process (e.g., D'Antonio 1993; Vilà and D'Antonio 1998), invasive species biology (e.g., Reichard 1997; Suehs et al. 2004), hybridization problems (e.g., Albert et al. 1997; Suehs et al. 2004; Vilà and D'Antonio 1998), the characteristics of invaded ecosystems (e.g., Burke and Grime 1996; Wisser et al. 1998), the role of disturbance in facilitating biological invasions (e.g., D'Antonio et al. 1999; Hobbs and Hobbs 1992), mechanisms of resistance to invasions (Prieur-Richard et al. 2002), factors involved in successful invasions (D'Antonio 1993), and the vulnerability of ecosystems to invasion (Gritti et al. 2006).

The succulent plant *Carpobrotus edulis* (L.) N.E. Br (common iceplant or sea fig) is a perennial mat-forming species native from South Africa (Albert 1995) that invades coastal habitats in many parts of

the world (D'Antonio 2006). Different studies have described the spread of *C. edulis* in sand dune ecosystems of Portugal (Almeida and Freitas 2001; Campelo et al. 1999), and the direct and indirect negative influences of this exotic invasive on native plant communities worldwide: it competes for space and resources, and alters soil chemistry and nutrient cycles (e.g., Albert 1995; D'Antonio and Haubensak 1998). However, most studies on the interactions between this exotic invasive and the native communities it invades have considered only one or a few target native species (e.g., Conser and Connor 2009), or focused on the mechanisms of competition between *C. edulis* and natives (D'Antonio and Mahall 1991; Traveset et al. 2008). Little attention has been given to the effects of *C. edulis* on the structure and composition of invaded communities.

Natural gradients provide an ideal opportunity for ecological studies (Lortie and Cushman 2007), because the relative abundance of native and exotic species in plant communities is largely modified by local abiotic factors. We considered two natural gradients to evaluate the real short-term effects of *C. edulis* on sand dune communities: a climatic North-South gradient along the western coast of Portugal, and the small-scale abiotic stress gradient related to the distance to the shoreline. Our objectives were: (a) to determine the spatial patterns of *C. edulis* in invaded sand dune ecosystems; (b) to evaluate its spatial association with the native species; (c) to investigate the direct effects of *C. edulis* on the species co-occurrence and diversity of native communities, along large- and small- scale abiotic gradients; and (d) to assess how much of the variation in the composition of the native community is explained by the invasive species independently from the environmental and spatial factors.

Methods

Study area and species

We studied eight sites of coastal sand dune communities distributed along the Portuguese coast (Fig. 1a, b). Four sites were located in the northern coast (Fig. 1c; Nazaré, PVieira, Leirosa and Quiaios), with 700 to 1,000 mm mean annual precipitation and mean annual temperature between 13 and 14°C. Another four sites

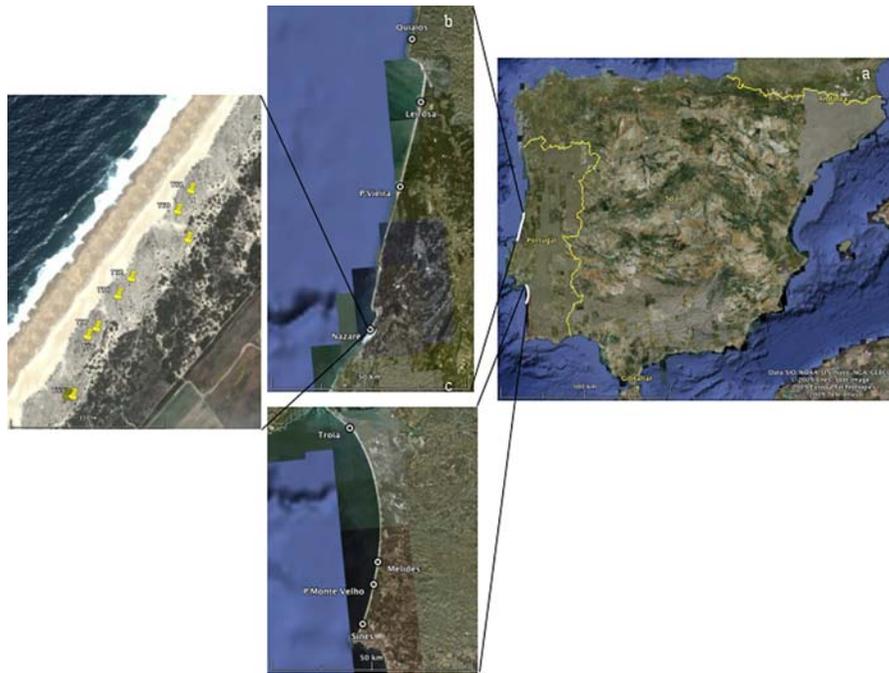


Fig. 1 **a** Study areas in coastal sand dunes of western Portugal; **b** and **c** distribution of the eight study sites; **c** example of the distribution of eight transects in the white dune zone, in a study site (maps adapted from Google Earth 4.3.7204.0836 beta)

were located in the southern coast (Fig. 1d; Sines, PMVelho, Melides, and Troia), and have mean annual precipitation and temperature between 600 and 700 mm, and between 15 and 16°C, respectively.

We considered all the perennial and bi-annual species, including the exotic invasive *C. edulis*. Although re-sampling on different seasons was not made in order to sample all the annual species, those annual species that were present at the time of the field-work were also registered. *C. edulis*, known as “higo marino” in Spanish, “sea fig” in American English, or “chorão-das-praias” in Portuguese, is a perennial mat-forming succulent plant, native to South Africa (Albert 1995). It has been used as an ornamental plant or for erosion control, from which it has spread and invaded disturbed and coastland habitats all round the world. When *C. edulis* becomes established, it forms impenetrable mats with a high vegetative reproductive rate that are barely affected by herbivory or competition from native species. In addition, this exotic species interacts both directly and indirectly with the native plant communities. Previous studies have shown that *C. edulis* competes with native plants for space and resources, suppressing their establishment, growth and reproduction, and that

this species alters soil chemistry, reducing soil pH, changing the nitrogen availability to other species, preventing sand movement and disrupting osmotic levels in the soil (Albert 1995; D’Antonio and Haubensak 1998; Vivrette and Muller 1977).

Sampling of plant communities and environmental variables

In each of the eight study sites, we randomly established 8–10 transects in the white dunes, i.e., after the embryo and the fore—dunes, and before the grey dunes (Fig. 1e). Each transect consisted of 25 contiguous quadrats of one square meter. A total of 72 transects and 1,800 quadrats (observation units) were sampled. All transects were parallel to the coast line and had an upwards exposition. Between April and August of 2008, we registered the percentage cover of each perennial and bi-annual species in each quadrat. Although we aimed to analyze the impact of *C. edulis* on native plant communities, the methodology of establishing close-paired quadrats could not be used because *C. edulis* is highly frequent in the study area, independently of its varying abundance and clone size, and therefore it was almost impossible

to establish a sufficiently large number of quadrats without *C. edulis*.

Climatic variables (mean annual precipitation, temperature and radiation) for each site were obtained from Ninyerola et al. (2005). We calculated the distance to the shoreline from the GPS coordinates of each transect using Google Earth (version 5.0 beta; <http://earth.google.com/>). This distance was employed as a surrogate for abiotic stress, since smaller distances from the shoreline indicate more intense salt spray, sand movement, and soil salinity, and lower soil nutrient availability (Henriques and Hay 1992).

Quantification of community structure

We determined different parameters to characterize the structure of the studied communities: spatial pattern, C-score, species diversity, and total plant cover. We used the Spatial Analysis by Distance Indices (SADIE; Perry 1998; Perry et al. 1999) to calculate the spatial structure of *C. edulis* and the relationships between this pattern and that of the native species density (i.e., number of species per unit area). Details of this approach can be found elsewhere (Perry et al. 1999, 2002). We used SADIE's index of aggregation (I_a) to summarize the spatial pattern of *C. edulis* and native species in the transects; this was clumped if $I_a > 1$, random if I_a is close to 1, and regular if $I_a < 1$ (Perry et al. 1999). An increase in the I_a values suggests an increase in the spatial aggregation of vegetation. Both patterns were related using SADIE's spatial association index (see Winder et al. 2001; and Perry and Dixon 2002 for details). Additionally, we used the χ_i index (Perry and Dixon 2002) to compare the spatial aggregation/segregation of *C. edulis* and native species density. We also performed a χ -test with the null hypothesis of overall spatial association/dissociation between *C. edulis* and native species density occurring by chance in random data.

We performed SADIE analysis separately for each transect by using presence/absence data and SADIE-Shell for Windows software, version 1.22 (SADIE 2001). All the SADIE analyses were performed with 2340 permutations. The t -tests were conducted in Statistica v6.0 (StatSoft 2001).

The C-score index quantifies the co-occurrence patterns in communities (Gotelli 2000). If a community is structured by competitive or facilitative

interactions, the C-score should be significantly larger or smaller than expected by chance, respectively. We selected the C-score among different available indices because it is robust to the presence of noise in the data and has good statistical properties (reviewed by Gotelli 2000). For each transect, the data were organized as a presence-absence matrix, where each row and column represented a different species and sampling quadrat, respectively. The C-score was calculated for each pair of species as $(R_i - S)(R_j - S)$, where R_i and R_j were the matrix row totals for species i and j , and S was the number of squares in which both species occur, and it was then averaged over all possible pairs of species in the matrix. The indices obtained from each matrix were compared to 10,000 randomly assembled 'null' matrices. These matrices were obtained using a fixed-fixed null-model (Gotelli 2000). In this null model, both the species frequencies and the number of species in each sample unit are kept constant in the random matrices, and thus the rareness of each species is retained (Gotelli 2000). Because the values of the C-score are dependent on the number of species and the number of co-occurrences within each transect, and to make the results of different transects comparable, we obtained a standardized effect size (SES) for each transect. It was calculated as $(I_{\text{obs}} - I_{\text{sim}})/S_{\text{sim}}$, where I_{obs} is the observed value of the C-score, and I_{sim} and S_{sim} are the mean and standard deviation, respectively, of this index obtained from the 10,000 null communities (Gotelli and Entsminger 2003). Values of SES larger or smaller than 0 indicated prevailing spatial segregation or aggregation among the species within a community, respectively.

Species diversity was estimated by Shannon's index of diversity, calculated with the software EstimateS (Colwell 1994–2004). This variable was transformed using an exponential function (as $S' = S^4$) to achieve distribution normality. Total plant cover was calculated for each transect as the average value of the total plant cover in the 25 1 m² quadrats of each transect. The percentage cover of *C. edulis* was square-root transformed to achieve distribution normality (Schork and Remington 2000).

Numerical analysis

We used structural equation modeling (SEM) to determine the relative importance of both *C. edulis*

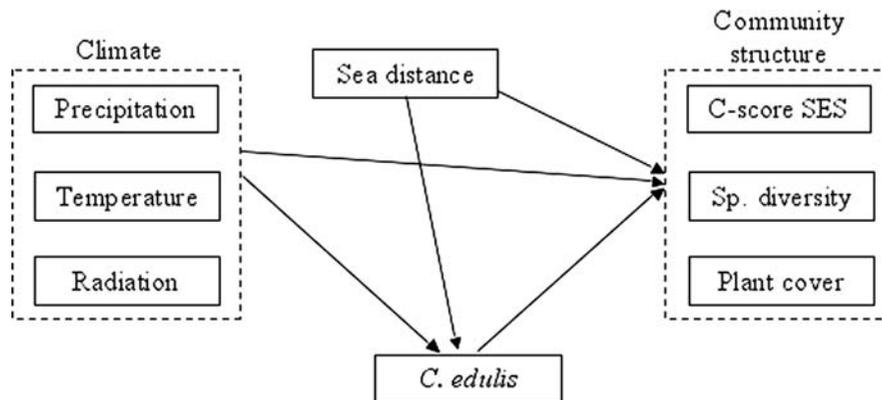


Fig. 2 Hypothetical structural equation model of the causal relationships between the environmental variables (climate and distance to the shoreline), the exotic invasive species *Carpobrotus edulis*, and various parameters defining the structure of the native sand dune community. Arrows indicate

unidirectional causal relationships; rectangles represent exogenous and endogenous variables; dashed boxes represent general concepts (i.e., “climate” and “community structure”) underlying measured variables

and climatic variables as drivers of the native sand-dune communities structure. Our hypothetical model is presented in Fig. 2, where arrows indicate putative causal relationships among the variables. It includes four exogenous variables (precipitation, temperature, radiation, and distance to the sea), of which three were combined in a composite variable (climate). These variables have a direct influence on each of the endogenous variables (i.e., community structure variables): percentage cover of *C. edulis*, SES, species diversity, and percentage cover of native species. Each community structure variable is also hypothetically directly influenced by the cover of *C. edulis*. The model was constructed in AMOS 5.0 (Amos 2003), and was parameterized by the maximum likelihood estimation technique (see Shipley 2002 for details on this estimation). Standardized path coefficients, which are equivalent to standardized partial regression coefficients, were used as indicators of the strength of the causal relationships established in the model. We evaluated the model fit probability with a test statistic asymptotically distributed as a chi-square. A non-significant χ^2 value ($P > 0.05$) indicates that the pattern of covariance predicted by the hypothetical model is not distinguishable from the observed covariance (Iriondo et al. 2003), i.e., there is a good fit between the model and the data (Grace 2006). Other goodness-of-fit tests were also used, considering different rules-of-thumb for each index: Joreskog’s Goodness of Fit index (GFI) > 0.95 ; root mean square error of approximation (RMSEA) close

to zero; and Bentler and Bonett’s normed-fit index (NFI) > 0.95 (Grace 2006; Iriondo et al. 2003). Additionally, the bootstrap procedure was used to estimate the standard errors with resampling methods, and to test the null hypothesis that the model is correct; a non-significant ($P > 0.05$) Bollen-Stine bootstrap index reveals (with $P > 0.05$) a good fit of the model by the data.

Finally, variations in the composition and abundance of native species, and their relations with the percentage cover of *C. edulis*, were examined using multivariate techniques. As proposed by Borcard et al. (1992), the following sequence of complementary analyses was conducted: (1) a correspondence analysis (CA) of the species abundance matrix to identify the main floristic gradients and the total floristic variance; (2) a stepwise canonical correspondence analysis (CCA, ter Braak 1986) of the species data constrained by environmental and spatial variables, to identify how much of the floristic variance is explained by these variables, and to determine the statistical significance of their relationships; (3) a stepwise CCA of the species data constrained by the cover of *C. edulis*; (4) a partial CCA (pCCA; Økland and Eilertsen 1994) of the species data constrained by the best environmental and spatial predictors (previously determined in step 2) and with the cover of *C. edulis* as covariable, to determine the structured floristic variance explained by the former independently of the latter; and (5) a pCCA using the best environmental and spatial predictors as covariables,

to the determine the structured floristic variance explained by *C. edulis* independently from the spatial and environmental variables; these covariables correspond to the predictors. The spatial variables corresponded to an extended matrix with a polynomial function of the geographic coordinates, obtained in SpaceMaker2 (Borcard and Legendre 2004). The amount of variance explained in each step (i.e., the variance partitioning) was calculated as the percentage of total floristic variance, given by the sum of all eigenvalues in the CA (Borcard et al. 1992). Log transformation [$y = \log(y + 1)$] and downweighting of rare species were applied to the species matrix. Manual selection and Monte-Carlo permutation tests (with 9,999 unrestricted permutations) under the reduced model were used. All the ordination analysis and tests were performed in CANOCO for Windows, version 4.5 (ter Braak and Smilauer 2002).

Results

Spatial patterns of *Carpobrotus edulis* and native species

A total of 48 perennial and bi-annual native species were found in the studied sand dune communities (Appendix). The mean species richness in all transects was 14.2, with a standard deviation of 3.7. *Carpobrotus edulis* was present in all transects and in 64% of the quadrats, with a mean percentage cover of

13.9 ± 7.2 (mean \pm SD), and a maximum percentage cover of 42.6% (Appendix). Albeit we have not measured it, we observed during the field measurements that *C. edulis* had small clone sizes in the studied communities.

We found an overall clumped spatial pattern for *C. edulis* ($I_a > 1$), which was significantly different from randomness in five of the study sites (Fig. 3). The native species density was also clumped in all sites, but the null hypothesis of a random distribution was rejected in only one site (Fig. 3). Moreover, *C. edulis* and the density of native species (number of species per quadrat) showed a slight spatial dissociation ($\chi_i < 0$) for all sites except Quiaios (Fig. 4). The exotic invasive species and the native species density were negatively associated in 15% (11/72) of the transects, and positively associated in 7% (5/72) of the transects. However, the results from the one-sample *t*-test showed no significant departures from the null hypothesis of random association (i.e., a reference mean of zero) in any of the sites studied. Also, we could not reject the null hypothesis of spatial associations/dissociations equivalent to those expected by chance in a random sample data (in a χ -test with 7 d.f., $P = 0.6425$).

Effects of *Carpobrotus edulis* on the community structure

Our SEM showed good fit with the data, as indicated by the non-significant χ^2 (0.785, d.f. = 2, $P = 0.675$),

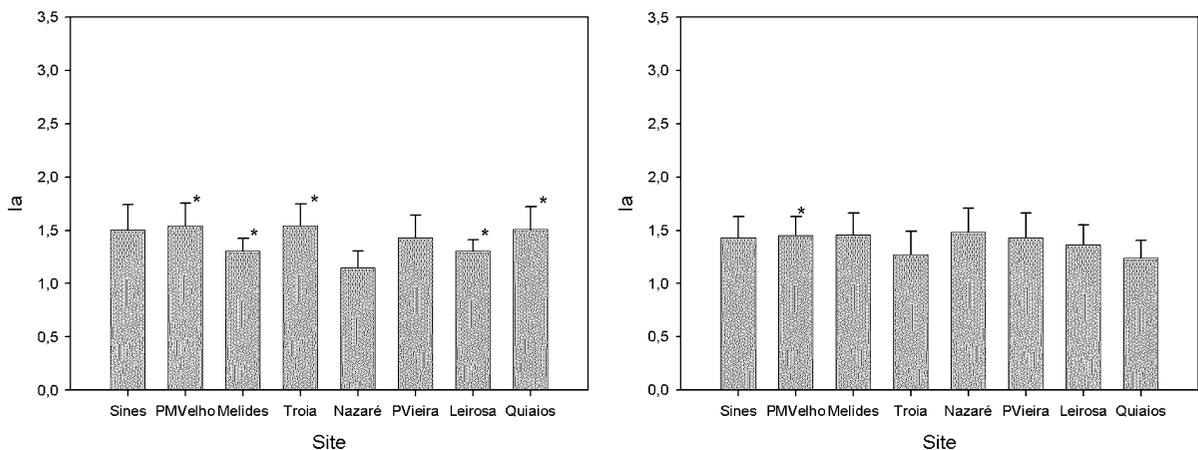


Fig. 3 Spatial aggregation indexes (I_a) of *Carpobrotus edulis* (left) and native species density (right), in each of the studied sites. Data represent mean \pm SE ($n = 8-10$). Asterisks (*)

indicate a significant rejection of the null hypothesis ($P < 0.05$) in a *t*-test comparing the average I_a values with the expected mean for a random spatial pattern (i.e., $I_a = 1$)

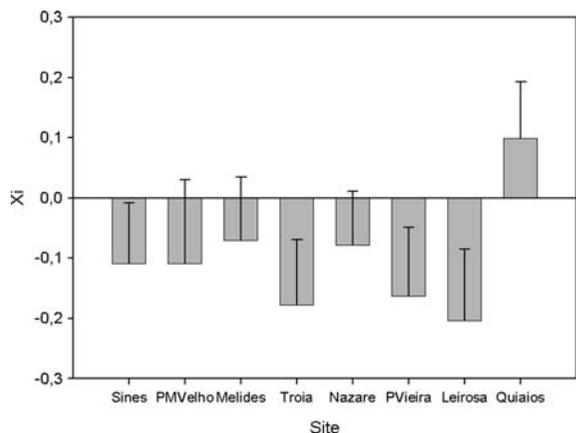


Fig. 4 Mean values and standard error bars for the overall spatial association between the cover of *Carpobrotus edulis* and the density of native species (number of species per quadrat), for each site ($n = 8-10$)

the Bollen-Stine bootstrap tests ($P = 0.514$), and other indices such as GFI (0.997), RMSEA (0.000, $P = 0.719$), and NFI (0.996). This model was able to explain more than 25% of the plant cover ($R^2 = 0.26$), almost 20% of the species co-occurrence patterns ($R^2 = 0.19$), and about 10% of the species diversity ($R^2 = 0.12$; Fig. 5). The direct effects of the composite variable “climate” upon the community structure variables were on average

three times higher than those of *C. edulis*; climate also had a strong influence upon the percentage cover of *C. edulis* (Fig. 5).

Effects of *Carpobrotus edulis* on community composition

Multivariate models used to explore the variations in the composition and abundance of native species revealed that the spatial and environmental variables explained more than 50% of the species variance, even when the effects of *C. edulis* were controlled (Table 1). In contrast, this exotic invader explained only 3% of the variance in native species composition, and this value decreased to 1.4% when the spatial and environmental variables were controlled (Table 1).

Although *C. edulis* explains only 1.4% of the species ordination (Table 1; Fig. 6), it correlates with the positive direction of the first axis (weighted correlation = 0.62). The most relevant results from this ordination were that from the three endemic (and rare or vulnerable) species sampled only one was negatively correlated with *C. edulis*: *Thymus carnosus*, positioned in the negative side of the first pCCA axis. In fact, the presence and abundance of the other two endemic (and vulnerable) species, *Herniaria*

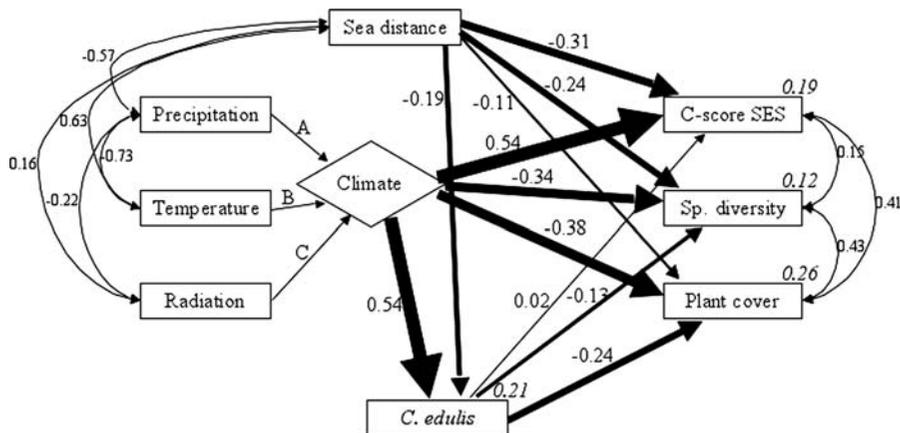


Fig. 5 Results of the structural equation modelling. Standardized path coefficients appear above *unidirectional arrows*, and are equivalent to regression weights or partial correlation coefficients. The width of each unidirectional causal relationship (*one-sided arrows*) is proportional to the path coefficient. *Numbers* at the upper-right corner of endogenous variables are the R^2 values, and represent the explained variance for that variable. Goodness-of-fit test statistics indicate a very strong fit

of the model to the data (see text). *A, B, C, D* correspond to different values of the parameters estimates depending on the response variable; *A* (C-score SES) = 0.13, *A* (Sp. Diversity) = 1.28, *A* (Plant cover) = 1.32, *A* (*C. edulis*) = 0.45; *B* (C-score SES) = 0.93, *B* (Sp. Diversity) = 0.39, *B* (Plant cover) = 1.15, *B* (*C. edulis*) = 1.28; *C* (C-score SES) = 0.57, *C* (Sp. Diversity) = 0.37, *C* (Plant cover) = -0.19

Table 1 Summary results of the analyses of variance partitioning in the composition and abundance of native species: (1) unconstrained correspondence analysis (CA); (2) stepwise canonical correspondence analysis (CCA) for determining the best spatial and environmental predictors; (3) stepwise CCA

Analysis	Data matrix	Constrained by	Covariables	Trace	<i>P</i> (trace)	% of species variance
CA	Species	–	–	2.194	–	100
CCA	Species	Env. and spatial variables	–	1.234	0.001	56.2
CCA	Species	<i>C. edulis</i>	–	0.068	0.007	3.1
CCA	Species	Env. and spatial variables	<i>C. edulis</i>	1.196	0.001	54.5
pCCA	Species	<i>C. edulis</i>	Env. and spatial predictors	0.03	0.011	1.4

For each analysis, the sum of all eigenvalues (trace), the model significance (by Monte Carlo test), and the percentage of the community variance explained, are shown

maritima and *Santolina impressa*, did not seem to be negatively influenced by *C. edulis* (they both appeared at the right side of the ordination diagram).

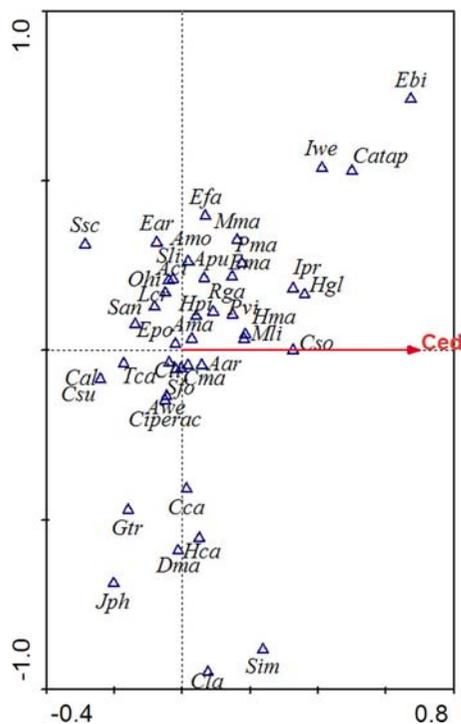


Fig. 6 Biplot of the partial canonical correspondence analysis (pCCA) showing plot scores of plant species and the vector of *Carpobrotus edulis* abundance, which is positively related with the first pCCA axis. For species abbreviations see Appendix. *Thymus carnosus* (Tca) was the only endemic species at the left side of the ordination diagram, and thus negatively correlated with the abundance of *C. edulis*; the other two endemic species—*Herniaria maritima* (Hma) and *Santolina impressa* (Sim)—are at the right side of the ordination diagram

with *Carpobrotus edulis* as explanatory variable; (4) stepwise partial CCA constrained by the best spatial and environmental predictors, and partialing out the effects of *C. edulis*; (5) stepwise partial CCA constrained by *C. edulis* and partialing out the effects of the spatial and environmental predictors

Discussion

It is widely assumed that exotic invasive species generate a complex suite of changes within the system that will have consistently negative impacts on the plant communities they invade (Alvarez and Cushman 2002; Meiners 2007). In particular, it is expected that exotic invasive species: (a) have an invasive potential derived from their ability to evolve to reallocate their resources (Evolution of Increased Competitive Ability—EICA—Hypothesis; Blossey and Notzold 1995); (b) spread rapidly because they are liberated from their co-evolved natural enemies (Enemy Release Hypothesis—ERH; Keane and Crawley 2002; Torchin et al. 2003); (c) are competitively superior to natives and ultimately lead to decreased populations of native species (D’Antonio and Mahall 1991; Gould and Gorchov 2000; Hutchinson and Vankat 1997); (d) alter species composition (Alvarez and Cushman 2002), reducing the native species diversity and dramatically altering the native communities (Simberloff et al. 2005; Thuiller et al. 2005; Williamson 1999); (e) out-compete the natives creating large monospecific stands (D’Antonio and Mahall 1991; Collins and Wein 1993; Hager 2004; Hamilton et al. 1999); and (f) greatly alter ecosystem processes (Ehrenfeld 2003). However, the aforementioned expectations do not always hold true (Alvarez and Cushman 2002), and in our study there was evidence that the effects of *C. edulis* on the structure and composition of sand dune plant communities were not as strong as expected.

Carpobrotus edulis showed a clumped pattern in most of the sites. Once established, it propagates

rapidly by clonal growth (D'Antonio 1993), with the growth rate of shoots reaching up to 40 cm year⁻¹ (Traveset et al. 2008). It has also been described that this species is able to surround and grow over the existing vegetation, creating monospecific stands (D'Antonio and Mahall 1991). However *C. edulis* did not form monospecific stands as large as expected in our study area, probably due to: (1) recent colonization, (2) frequent disturbance events, (3) strong interspecific competition with the natives, and (4) high species richness—since larger clones are usually associated with lower species richness (Traveset et al. 2008). D'Antonio (1993) also showed that the growth of *C. edulis* (even in the absence of herbivores and competitors) was very slow at the backdune sites, compared with other sites such as grasslands and coastal scrubs.

The mats of overlapping stems of *C. edulis* were randomly associated with the native species density, with only a slight (non-significant) spatial dissociation between them. Therefore, this invasive species did not have a negative influence as strong as expected upon the native species density structure (Conser and Connor 2009; D'Antonio 1993), with native species growing under or within the mats of *C. edulis*. Both biotic and abiotic processes influence the success of any exotic species (Lortie and Cushman 2007), and in the backdune habitats the interference by existing vegetation is important in limiting seedling growth of *C. edulis* (D'Antonio 1993), which in turn alters the net impacts of the invader on the natural communities.

The negative relationship between the percentage cover of *C. edulis* and the total cover of native species is related with the kind of vertical arrangement of sand dune communities, which are commonly low-stature and open systems. In such types of communities, i.e., without a complex vertical arrangement of vegetation, plant cover is commonly assumed to be a surrogate of biomass (Dullinger et al. 2007). Therefore, our results suggest that *C. edulis* had a negative influence on the net productivity of the natural sand dune communities. According to Vilà et al. (2006), the magnitude of the impact of *C. edulis* on the reduction in native plant species diversity (and richness) is very variable. In our study sites, this exotic invasive species had a negative influence on the diversity of native species, but this effect was rather weak. There was also a very small influence of

C. edulis upon the co-occurrence patterns of the native communities, which suggested that the communities with more *C. edulis* are more competitive (i.e., with higher values of the C-score SES).

The relative abundance of native and exotic species in plant communities is largely modified by local abiotic factors, and natural gradients provide an ideal opportunity to test this hypothesis (Lortie and Cushman 2007). We considered two natural gradients: one at the larger scale, climate, and other at a smaller scale, the distance to the shoreline. Both the large- and small- scale environmental factors considered were by far (three and two times on average, respectively) much more influential than *C. edulis* in determining the structure of native sand dune communities (Fig. 5). This influence of climate upon the percentage cover of *C. edulis*, contradicts the results from Traveset et al. (2008), who found that this species performed equally well in different environments. In fact, the success of an invasive species depends not only on its intrinsic traits but also on the particular characteristics of the recipient habitat and the abiotic factors (Funk and Vitousek 2007; Going et al. 2009). Also, habitat type is a relevant predictor of clone size for some species (Hobbs and Hobbs 1992; Traveset et al. 2008). The distance to the shoreline was important in explaining the percentage cover of *C. edulis* and the community structure variables: both the exotic and the native species generally performed better or at least were more abundant at smaller distances to the shoreline, i.e., under higher levels of abiotic stress. Lortie and Cushman (2007) also showed that local abiotic gradients have consistent directional effects on plant communities and predict the abundance of exotic species, in a coastal dune system in northern California. The abiotic environment can also affect invasions by influencing the outcome of biotic interactions (e.g., Byers 2002; Reinhart et al. 2006), as revealed in our study by the strong influence of the global and local—scale abiotic factors (climate and shoreline distance) on the co-occurrence patterns of the native communities (see also Dullinger et al. 2007; Maestre et al. 2009).

Regarding the floristic variance of sand dune communities, *C. edulis* did not play a role as important as expected (Alvarez and Cushman 2002; Coleman and Levine 2007; Simberloff et al. 2005; Thuiller et al. 2005; Williamson 1999). It explained

only 1.4% of the species variance, and did not suppress native endemic species. In contrast, the spatial and environmental factors explained almost 55% of the total variance in community composition. Although the dense mats of *C. edulis* may constitute a substantial obstacle to the germination and establishment of native species (Vilà et al. 2006), there is not much evidence of any strong competitive effects of the exotic invasive upon the adult survivorship, growth or reproduction (Thomson 2005). For example, native shrubs can displace their rooting profiles downward and therefore can still overlap with *C. edulis*, and survive within the mats formed by this invasive species (D'Antonio and Mahall 1991).

In our study, the small impacts of *C. edulis* on the native community structure and composition could be explained by the low cover and reduced mat sizes. In fact, although *C. edulis* has a remarkable capacity to cope with both high and low light, in full sunlight it showed reddish and senescing leaves, which corresponds to significantly lower photochemical efficiency and reveals chronic photoinhibition and high light stress (Traveset et al. 2008). In turn, the low performance is usually associated with lower soil impacts (Traveset et al. 2008); for example, there are variable effects of *C. edulis* on C cycling related to habitat, mat age and thickness (Vilà et al. 2006). Our results revealed that somehow the native species are able to cope with *C. edulis*, dealing with the considerable litter layer it produces and the changes it promotes on the soil properties and cycles (Vilà et al. 2006). Hager (2004) also showed that sometimes the invader is not the best response competitor, and thus is not a superior invader of established vegetation. Also, invaders that are already physiologically stressed by the abiotic environment may be particularly vulnerable to negative interactions with the resident community (Alpert et al. 2000; D'Antonio 1993; Levine et al. 2004). The nature of interactions between biotic and abiotic factors depends on the relative tolerances of the residents and the invader to the stresses imposed by their environment (Going et al. 2009). Therefore, although under some circumstances *C. edulis* appears to compete aggressively with native species (D'Antonio and Mahall 1991), there might be a minimum level of invasion that is required before its effects on native

species become apparent (Alvarez and Cushman 2002).

Although we have not evaluated the effects of the native community on the invasibility by *C. edulis*, a meta-analysis from Levine et al. (2004) showed that the species interactions constrain the establishment, spread, performance and impact of invaders, rather than completely repelling them from communities. Also, the dominant paradigm in the literature on invasion ecology is that successful invaders must overcome biotic resistance, and that the resident community reduces the invasion success, through a diversity of biotic processes, such as competition (Levine et al. 2004). Our analyses at multiple sites suggested that there is a strong resistance to the impacts of invasion in the studied sand dune ecosystems, with *C. edulis* exerting weaker negative impacts than expected on native communities

The mechanisms underlying the impacts of exotic plant invasions on native communities are rarely elucidated (Coleman and Levine 2007; Thomson 2005), and the mechanisms and changes might not have proportionate consequences for the community structure (Levine et al. 2004), with invaders having large impacts in some systems but not others. Besides, the success (Funk and Vitousek 2007) and the impact (Vilà et al. 2006) of an invasive species in general, and of *C. edulis* in particular, are habitat-dependent and context-specific (D'Antonio 1993). Here we presented evidence of weak impacts from the exotic invasive *C. edulis* upon the structure and composition of native sand-dune communities, along the large gradient of the western coast of Portugal. These invaded systems (that suffer little impact at the community level) must be considered to fully understand how impacts arise (Levine et al. 2004), and what allows communities to resist the impacts of an invader.

Levine et al. (2004) reported a publication bias by which studies reporting significant invader impacts are more likely to be published than those showing non-significant effects. However, the weak effects of *C. edulis* on native communities are extremely important, and management actions should be implemented to eliminate it from the studied communities before it reaches higher abundances and clone sizes. In this way, it would be possible to eliminate the risks of higher and

irreversible impacts on the studied natural sand-dune ecosystems.

Acknowledgments “We thank Ana Mouro and João Mouro for their help with the field-work, and we thank Matthew A. Bowker and Adrián Escudero for their help with the statistical analyses. We also thank to anonymous referees who helped improve the paper. SMM was supported by grant SFRH/BPD/39744/2007, given by the European Social Funds of the Portuguese Foundation for Science and Technology, Ministry of Sciences and High Education. FTM was supported by a Ramón y Cajal contract from the Spanish Ministerio de Ciencia e Innovación (MCINN), co-funded by the European Social Fund, by the Fundación BBVA (BIOCON06/105 project), by the British Ecological Society (Studentship 231/1975), by the Comunidad de Madrid (grant S-0505/AMB/0335), and by the MCINN (grant CGL2008-00986-E/BOS).”

Appendix

List of all the species sampled in 8 sites of the sand dune systems of the western coast of Portugal. All species except *C. edulis* are native species; the endemisms, legal protection, and cover percentages of each species (mean, standard deviation (Std. Dev.), and minimum and maximum) are also shown. Nomenclature follows Franco (1971–1984), Franco and Afonso (1994–1998). V, vulnerable; R, rare; P, endemism of Portugal; I, endemism of the Iberian Peninsula; a, Decreto-Lei no 140/99 Annex B-II and B-IV; b, Decreto-Lei no 316/89 Annex I; c, Habitats Directive 92/43/CEE, Annex II and IV; d, “Bern convention” (1979 Annex I) (Table 2).

Table 2

Species	Abbreviation	Life form	Endemism	Legal protection	Mean	Std. dev.	Minimum	Maximum
<i>Ammophila arenaria</i>	Aar	Graminoid			0.8	1.3	0.0	8.2
<i>Anagallis moneli</i>	Amo	Forb			0.4	0.8	0.0	3.5
<i>Antirrhinum majus</i> spp. <i>cirrhigerum</i>	Aci	Forb			0.4	0.7	0.0	3.3
<i>Armeria pungens</i>	Apu	Shrub			0.5	0.9	0.0	4.0
<i>Armeria welwitschii</i>	Awe	Shrub			0.4	1.1	0.0	5.2
<i>Artemisia campestris</i> ssp. <i>maritima</i>	Ama	Shrub			1.7	3.5	0.0	19.0
<i>Cachrys libanotis</i>	Cli	Forb			2.4	3.5	0.0	13.3
<i>Calendula suf fruticosa</i>	Csu	Forb			0.3	0.7	0.0	3.1
<i>Calystegia soldanella</i>	Cso	Forb			0.3	0.9	0.0	4.6
<i>Carpobrotus edulis</i>	Ced				13.9	7.2	2.3	42.6
<i>Carthamus lanatus</i> ssp. <i>lanatus</i>	Cla	Graminoid			0.0	0.1	0.0	0.6
<i>Catapodium marinum</i>	Catap	Graminoid			0.0	0.3	0.0	2.4
Cyperaceae	Ciperac	Forb			0.3	0.9	0.0	3.5
<i>Corema album</i>	Cal	Shrub			6.6	10.0	0.0	39.8
<i>Corynephorus canescens</i>	Cca	Graminoid			1.5	2.6	0.0	10.4
<i>Crucianella maritime</i>	Cma	Shrub			3.1	4.2	0.0	15.8
<i>Dactylis marina</i>	Dma	Graminoid			0.2	0.8	0.0	5.2
<i>Echium arenarium</i>	Ear	Forb			0.0	0.1	0.0	0.6
<i>Elymus farctus</i>	Efa	Graminoid			0.4	0.9	0.0	5.0
<i>Erodium cicutarium</i> ssp. <i>bipinnatum</i>	Ebi	Forb			0.0	0.1	0.0	0.8
<i>Erygium maritimum</i>	Ema	Shrub			0.1	0.3	0.0	1.6
<i>Euphorbia paralias</i>	Epa	Forb			0.0	0.0	0.0	0.3
<i>Euphorbia portlandica</i>	Epo	Forb			0.6	0.8	0.0	2.8
<i>Galium tricornutum</i>	Gtr	Liana			0.1	0.3	0.0	1.6
<i>Halimium calycinum</i>	Hca	Shrub			0.0	0.2	0.0	1.8
<i>Helichrysum italicum</i> spp. <i>picardii</i>	Hpi	Shrub			6.0	6.5	0.0	29.8

Table 2 continued

Species	Abbreviation	Life form	Endemism	Legal protection	Mean	Std. dev.	Minimum	Maximum
<i>Herniaria maritima</i>	Hma	Forb	P	V, a, b, c, d	0.3	0.6	0.0	4.0
<i>Hypochaeris glabra</i>	Hgl	Forb			0.1	0.2	0.0	1.1
<i>Iberis ciliata</i> ssp. <i>welwitschii</i>	Iwe	Forb			0.1	0.4	0.0	2.4
<i>Iberis procumbens</i> ssp. <i>procumbens</i>	Ipr	Forb			0.3	0.7	0.0	3.4
<i>Juniperus phoenicea</i>	Jph	Small tree			2.3	6.8	0.0	31.4
<i>Lagurus ovatus</i>	Lov	Graminoid			0.0	0.0	0.0	0.3
<i>Linaria lamarckii</i>	Lla	Forb			0.0	0.1	0.0	0.4
<i>Lotus creticus</i>	Lcr	Forb			1.1	2.3	0.0	12.9
<i>Malcolmia littorea</i>	Mli	Forb			0.6	2.0	0.0	9.6
<i>Medicago marina</i>	Mma	Forb			0.8	1.7	0.0	8.9
<i>Ononis natrix</i> ssp. <i>hispanica</i>	Ohi	Forb			0.4	1.4	0.0	8.0
<i>Otanthus maritimus</i>	Oma	Forb			0.0	0.3	0.0	2.2
<i>Pancratium maritimum</i>	Pma	Forb			0.8	1.3	0.0	6.0
<i>Pimpinella villosa</i>	Pvi	Forb			0.2	0.8	0.0	5.1
<i>Plantago coronopus</i>	Pco	Forb			0.0	0.0	0.0	0.2
<i>Reichardia gaditana</i>	Rga	Forb			0.1	0.2	0.0	1.2
<i>Santolina impressa</i>	Sim	Shrub	P	V, a, c	0.2	1.1	0.0	8.2
<i>Sedum anglicum</i>	San	Forb			0.0	0.2	0.0	1.9
<i>Sedum foresteranum</i>	Sfo	Forb			3.8	1.7	0.0	9.2
<i>Silene littorea</i>	Sli	Forb			0.3	0.5	0.0	2.6
<i>Silene scabriflora</i>	Ssc	Forb			0.0	0.2	0.0	1.3
<i>Thymus carnosus</i>	Tca	Shrub	I	R, a, b, c, d	3.0	4.2	0.0	16.3
<i>Verbascum litigiosum</i>	Vli	Forb			0.0	0.0	0.0	0.3

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