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Assembly of species' climatic niches of coastal communities does not shift after invasion

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Abstract

Question: Do invasions by invasive plant species with contrasting trait profiles (*Arctotheca calendula*, *Carpobrotus* spp., *Conyza bonariensis*, and *Opuntia dillenii*) change the climatic niche of coastal plant communities?

Location: Atlantic coastal habitats in Huelva (Spain).

Methods: We identified the species composition of 216 paired (non-invaded and invaded) 10 × 10 m plots along the coast. For each species, we calculated its climatic niche based on the two main axis of a PCA constructed with nine climatic variables. We defined the community ensemble niche by the union of the overall climate niches of co-occurring species within a plot. We compared niche overlap metrics between non-invaded and invaded paired communities.

Results: There was an almost complete overlap in the community ensemble niches between non-invaded and invaded plots for the four invaders. Plots invaded by *Carpobrotus* spp. presented the lowest niche stability and those invaded by *A. calendula* had the highest. Plots invaded by *Carpobrotus* spp. showed the highest values of niche unfilling and expansion. In contrast, plots invaded by *O. dillenii* exhibited the lowest niche unfilling. Species similarity between non-invaded and invaded plots was on average 58%. The community ensemble niches differed depending on the invasive species and were related to differences in community species similarity between non-invaded and invaded plots. Overall, there was a positive correlation between community species similarity and climatic niche stability, and a negative correlation between community difference in taxonomic richness and climatic niche stability.

Conclusions: Species assemblages in coastal vegetation did not change their community ensemble climatic niches after invasion by plants with contrasted life forms. This pattern is likely the result of invasion which did not trigger major changes in species richness and composition, or alternatively, because the species that were locally displaced by invasion have been substituted by others with similar climatic requirements.

KEYWORDS
biological invasions, climatic niche, community assembly, ordination techniques, Raup-Crick similarity index, Sørensen similarity index, Spanish coastal vegetation, species composition, stability

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1 | INTRODUCTION

Biological invasions are one component of global change with multiple environmental impacts on ecosystem services and human well-being (Vilà & Hulme, 2017). Invasive plant species can cause these impacts at different levels of ecological complexity, ranging from individuals to whole ecosystems (Vilà et al., 2006, 2011). At the community level, invasive plants can alter the structure of plant communities in many ways, mostly by modulating the abundance or extirpating certain native species, and reducing native species richness and diversity, therefore modifying community composition (Fairfax & Fensham, 2000; Vilà et al., 2011).

The reduction in native species diversity, together with the removal of key species and the replacement by others, can also strongly influence the functional structure of the community and, in turn, how the invaded community copes with resource acquisition and environmental conditions (Jucker et al., 2013). One aspect that remains to be explored is the extent to which these community changes can modify how the community can cope with long-term changes such as climate change (Tilman & Downing, 1994; Chapin et al., 1997; Kühsel & Blüthgen, 2015). For instance, invasion could filter out a group of species less adapted to certain conditions associated with climate change (i.e., with poorer capacity either to resist extreme climatic events or to recover afterwards) which would lead to a contraction of the community ensemble niche. On the other hand, invasion could facilitate or be concurrent with an enlargement of the community ensemble niche because of the arrival of species with a broader environmental tolerance (e.g. cosmopolitan species). Ultimately, this process might facilitate the resistance of the community to changes.

Despite the impressive advances in species distribution modeling of single species with climate change (Parmesan & Yohe, 2003; McMahon et al., 2011), including invasive species (Benning et al., 2002; Bellard et al., 2018), one aspect that has been poorly explored is whether there is a synergistic effect of invasions and climate change scaling up from particular species to plant community. An approach to understand the consequences of invasion and climate change for the recipient communities is to describe how invasion can modify the assemblage of the climate niches of co-occurring species in the invaded community (community ensemble niche hereafter). If changes occur, they might affect the functioning of the community, changing its vulnerability to long-term drivers such as climate change. Given that the species in the community might differ in their tolerance to climatic factors (niche breadth; Herrera et al., 2018) and optima (i.e., niche complementarity; Gross et al., 2007), the assemblage of the climatic niche of the community can be characterized by the variability and overlap of the climatic niche of all species belonging to that community (Kühsel & Blüthgen, 2015). Community climatic shifts will be relevant for ecosystem resistance or adaptation particularly in a climate change context. For instance, in a Mediterranean context, if after invasion the climatic community niche shifts toward a species assemblage less able to cope with the xeric conditions of coastal habitats, then the non-invaded community might be better suited to the projected warmer and drier conditions than the invaded community. To the best of our knowledge, changes in the community ensemble niche after invasion have never been explored.

Community ensemble niche could be studied using standard ordination methods widely used to estimate niche shifts for single species. For example, Broennimann et al. (2012) developed a statistical framework that allows comparing environmental niches based on species occurrence and spatial environmental data between native and introduced ranges. Similarly, Hernández-Lambrano et al. (2017) used this method to analyze niche changes of two invasive species in different geographical areas and time periods. Here we take a novel approach to assess the community ensemble niche by considering the occurrences of all species in that community. In other words, we consider the potential climatic niche of a community as the ensemble of the climatic conditions where all the species in the community occur.

In this study, we used an extensive field survey of paired (non-invaded and invaded) coastal plant communities to examine changes in the community ensemble niche after invasion. We separately compared communities invaded by four different invasive species with contrasting life strategies: two annual species and two perennials. Our questions were: (a) does the community ensemble niche of the non-invaded plant community change with invasion; and (b) do changes in the community ensemble niche match species composition changes (i.e., richness and similarity) in the community with invasion? We hypothesized that changes in the community after invasion would lead to a contraction in the community ensemble niche because some species at the edge of their environmental niche will disappear. Those species at the margin of their environmental niche are more vulnerable to perturbations such as invasions but they also contribute to enlarge the community ensemble niche toward wider environmental conditions. Furthermore, we expected higher community changes and thus higher ensemble niche differences in the communities invaded by the perennial species compared to annual invaders. In fact, previous research highlighted that perennial invaders drive changes in the taxonomic structure of the invaded community (Vilà et al., 2006; Castro-Díez et al., 2016; de la Riva et al., 2019).

2 | METHODS

2.1 | The study area

The study area was located in sparse foredune vegetation along the southwestern coast of Spain (province of Huelva, Andalusia), ranging from Isla Cristina (37°11′40″ N, 7°19′50″ W) to Sanlúcar de Barrameda (36°48′10.5″ N, 6°20′56.28″ W; Figure 1a). The climate of the study region is typically Mediterranean, with warm and dry summers and mild winters (mean temperature of the warmest month 25.8°C, mean temperature of the coldest month 11°C, and an annual precipitation of 525 mm; AEMET, 2019). The coast is characterized by large sandy areas (dunes) fragmented by several large wetland systems (Guadalquivir and Odiel marshlands), urban areas (mainly summer residential homes), harbors, and industrial zones (González-Moreno et al., 2017; Gutiérrez-Cánovas et al., 2020).

2.2 | Study species

Our study focused on the most common exotic species in the study area, all of them considered invasive in Spain (Sanz-Elorza et al., 2004).

Arctotheca calendula (capeweed) is a rosette-forming annual plant native to South Africa which can be found in warm areas of the world, mainly in disturbed, urban, and coastal habitats (CABI Int., 2019). This plant needs sunlight and high temperatures to grow. It can reproduce sexually and asexually, and spreads rapidly by wind and by developing stolons. It arrived in Europe (Portugal) as an ornamental in the 18th century and was reported in Spain for the first time (province of Cádiz, close to the study area) at the beginning of the 20th century (Sanz-Elorza et al., 2004). It infests turf and pasture and can compete with crops that have an economic value, also generating a negative effect on stock production (less palatable forage). Besides, it is a source of allergies and dermatitis for sensitive individuals (CABI Int., 2019).

Carpobrotus spp. (hottentot fig) includes the chamaephytes *Carpobrotus acinaciformis* and *Carpobrotus edulis*, species that are not always distinguished and share many functional traits (Castro-Díez et al., 2016). They are perennial succulent plants also native to South Africa, used as ornamental and for erosion control. The first record in northern Spain is from 1900 (Sanz-Elorza et al., 2004). They reproduce vegetatively by rooting fragments and sexually by producing abundant small seeds. Their dispersal depends mainly on frugivorous mammals and gulls (CABI Int., 2019). They are widespread on cliffs and sand dunes, salt marshes, and coastal scrubs, mainly in Europe. They form dense mats that displace and inhibit the growth of native vegetation and reduce soil pH (Vilà et al., 2006; CABI Int., 2019). They require well-drained soils and full sun and are relatively tolerant to salinity and drought (Sanz-Elorza et al., 2004).

Conyza bonariensis (hairy fleabane) is an annual herbaceous plant native to temperate zones of South America, which has been introduced in many parts of the world as a seed contaminant. Seeds are efficiently dispersed by wind thanks to its pappus. It arrived in Europe at the beginning of the 18th century and in Spain it has been known since the 19th century (Sanz-Elorza et al., 2004). It is a nitrophilous and thermophilous plant with a basal rosette, which appears in disturbed and ruderal sites, being a problem in low-tillage systems but also in some agricultural crops (Sanz-Elorza et al., 2004; CABI Int., 2019).

Opuntia dillenii (erect prickly pear) is a succulent shrub native to Central America, from southeast USA to Ecuador. It reproduces

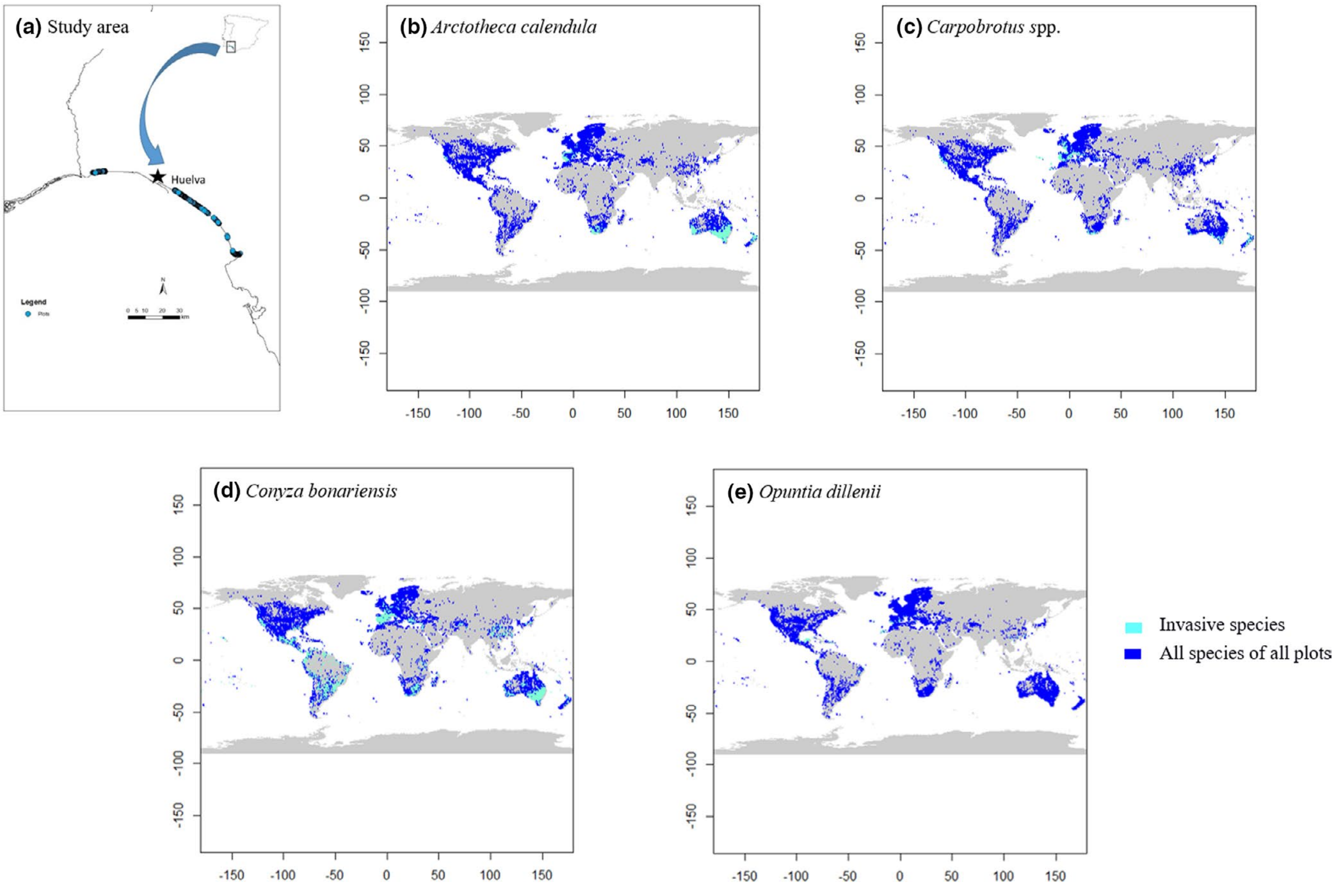

FIGURE 1 (a) Location of the plots in the study area. (b) Global occurrences of the species in these plots for each invader (data source: GBIF, Global Biodiversity Information Facility)

sexually and asexually. Animals that consume its fruits contribute to its spread (Padrón et al., 2011). It arrived in Europe in the 16th century following the colonization of America, mainly for use as an ornamental and as green fence. In Spain, it was reported in 1874 (Sanz-Elorza et al., 2004) and since then, it has invaded abandoned orchards (Vilà et al., 2003). It has a high tolerance to drought conditions and it is the source of important socioeconomic and environmental impacts (CABI Int., 2019).

2.3 | Floristic occurrence survey

An intensive floristic survey was carried out between 2010 and 2011 along a coastal strip of 125 km to record the occurrence of exotic species. The four study species were identified and georeferenced by walking parallel to the shoreline along the coastal vegetation at 50 m from the shoreline; in this way, the influence of the highest tides was avoided. When the strip of coastal vegetation was wide enough, an additional parallel walk was placed at 50 m inwards from the previous one. Although the survey intended to cover the entire coast between the two mentioned localities, only 70 km out of the 125 km total coastal line were finally sampled due to accessibility problems or lack of coastal vegetation in urbanized or afforested land.

The plant community in the area is rather heterogeneous (e.g. forbs, graminoids, and trees). Therefore, for each target invasive species occurrence, pairs of 10 m × 10 m plots were set up. One plot included the invasive species (hereafter, invaded plot) which had an average cover of 23% for *Arctotheca calendula*, 32% for *Carpobrotus* spp., 14% for *Conyza bonariensis*, and 28% for *Opuntia dillenii* (Gutiérrez-Cánovas et al., 2020). We avoided plots with two or more co-occurring invaders and plots totally dominated by the invader. The other plot contained only native species and it was located nearby (<20 m) to ensure that each pair of plots was subjected to the same environmental conditions. In total, 216 pairs of plots were sampled (54 for *Arctotheca calendula*, 67 for *Carpobrotus* spp., 61 for *Conyza bonariensis*, and 34 for *Opuntia dillenii*) where 106 native species were identified (Appendix S1), *Vulpia myuros*, *Lotus creticus*, and *Ammophila arenaria* being the most common taxa. Figures 1b–e show that the species in the community under analysis are found in all continents, i.e., cosmopolitan species are present in the community and they occupy a variety of habitats. Species identification followed Valdés et al. (1987) and taxon names were also checked with The Plant List (http://www.theplantlist.org/).

2.4 | Climatic niche analysis

2.4.1 | Plant data

For each species found in the floristic survey, including the four invasive species, we characterized its global climatic niche. For this

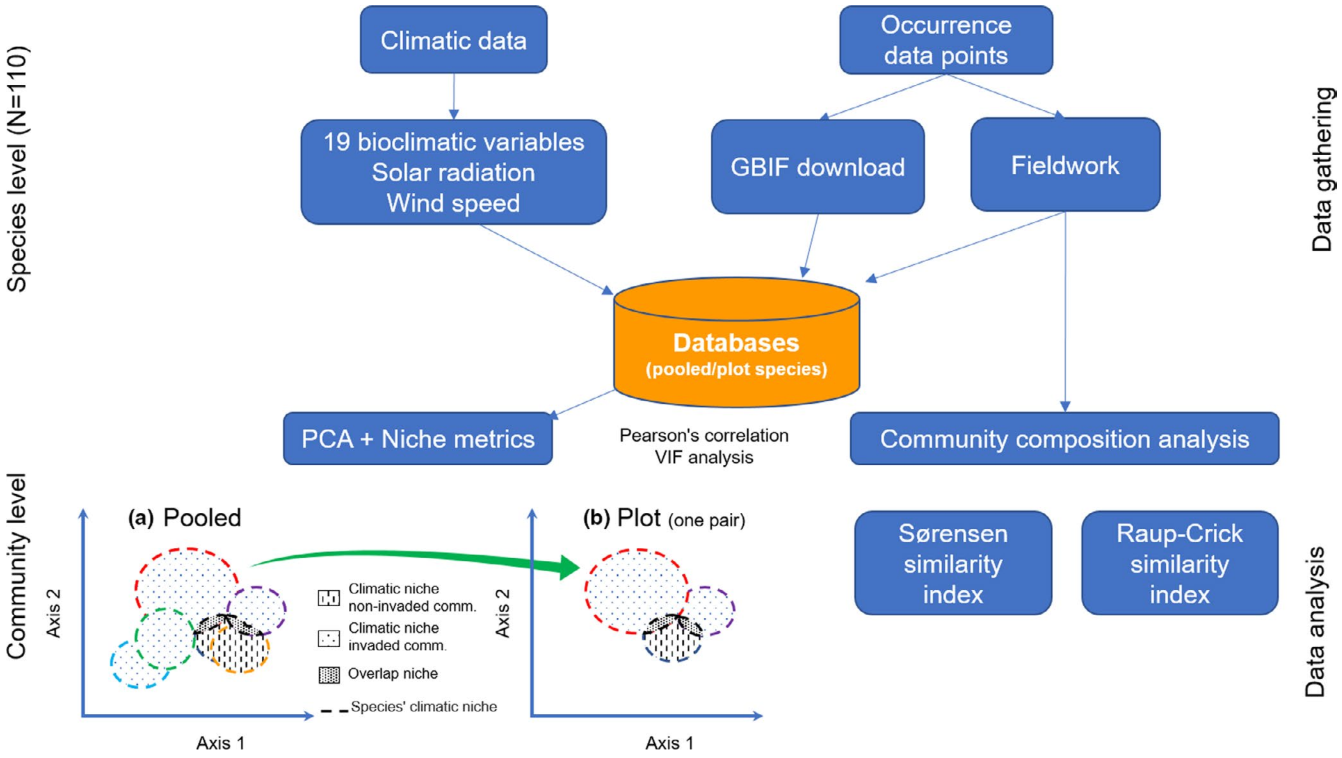

FIGURE 2 Flowchart summarizing the steps in our analysis. Plot (a), pooled species, considers all the species in the non-invaded plots vs all the species in the invaded plots. Plot (b), plot species, shows an example of one pair of non-invaded (one species) and invaded plots (two species). GBIF, Global Biodiversity Information Facility; PCA, Principal Component Analysis; VIF, variation inflation factor

TABLE 1 WorldClim variables used in the analysis after correlation test and VIF (variation inflation factor) analysis

Variable (units)	Code	Calculation
Mean diurnal range (°C)	*bio02*	Mean of monthly temperature range (max–min)
Temperature seasonality (°C)	*bio04*	Standard deviation × 100
Mean temperature of wettest quarter (°C)	*bio08*	
Mean temperature of driest quarter (°C)	*bio09*	
Precipitation seasonality (mm)	*bio15*	Coefficient of variation
Precipitation of warmest quarter (mm)	*bio18*	
Precipitation of coldest quarter (mm)	*bio19*	
Mean annual solar radiation rad (kJ m^{-2} day^{-1})	*meanrad*	
Mean annual wind speed (m/s)	*meanwind*	

purpose, we first compiled all available occurrence data per species from the Global Biodiversity Information Facility (GBIF, www.gbif.org; Figure 2; Appendix S2). The database was filtered considering only data with valid coordinates and we excluded records preserved in museums, botanical gardens, and other ex-situ facilities. Sampling bias per species was corrected filtering one occurrence per 10 arc-min resolution (circa 349 km^2) and using a smooth kernel density function (Broennimann et al., 2012). In total, the plant database resulted in 359,962 occurrences of 110 species, with 22 of them being present in only one plot (either non-invaded or invaded).

2.4.2 | Climate data

The initial set of climatic predictors was composed of 19 bioclimatic variables plus solar radiation and wind speed that were downloaded from the WorldClim 2.0 climate database for the period 1970–2000 at a 10 arc-min spatial resolution (c. 19 km at the equator; Fick & Hijmans, 2017). These climatic variables were extracted for the occurrence database of the pooled species (i.e., the database had 359,962 observations × 21 variables; Figure 2). To avoid multi-collinearity among variables, a correlation test (variables with a Pearson's coefficient higher than 0.7 were excluded) and a variation inflation factor (VIF) analysis (threshold of 5) were carried out. As a result, nine variables related to temperature and precipitation seasonality, interactions between extreme temperature and precipitation, together with solar radiation and wind speed were retained for analysis (Table 1). All these variables summarize the seasonal regime of the Mediterranean climate (Thompson, 2005).

2.4.3 | Measurement of shifts in the community ensemble climatic niche

To describe the climatic niche of each species we adapted the widely used ordination method proposed by Broennimann et al. (2012). According to Kühsel and Blüthgen (2015), we considered the community ensemble niche as the union of the climatic niche of all co-occurring species. Therefore, we performed a Principal Component Analysis (PCA) based on the selected climatic variables of the global data set (Table 1), and used its first two axes (explaining 60% of the variation; Appendix S3) to characterize the whole climatic space of the entire set of species (i.e., pooled species; Figure 2). Then, following Broennimann et al. (2012) and González-Moreno et al. (2015), first, we divided this environmental space into a grid of 100 × 100 cells and, second, we used a kernel density function to convert occurrences into densities. This procedure allows correction for sampling bias and environmental availability, respectively, and ensures that the results are independent of the grid resolution. Hence, we used this PCA as the reference system to compare the climatic niches of the non-invaded and invaded communities for:

- Pooled species. We estimated the overlap between the community ensemble niche for all the species found in the whole set of non-invaded plots vs those in all invaded plots for all, irrespective of the invasive species. This analysis provides an estimation of the overall niche overlap resulting from invasion across the study area, considering the effect of all invasive species and irrespective of local extirpations.
- Plot species. We analyzed the climatic niche overlap for all co-occurring species in each pair of non-invaded vs invaded plots; then we aggregated niche overlap metrics (mean and standard error of all plots) for each invasive species. This approach allowed a better analysis given that the niche breadth of widely distributed species (i.e., cosmopolitan species) is generally overestimated when using coarse-grained data (Kirchheimer et al., 2016).

All occurrences of the four invasive species were excluded from the corresponding calculation in both analyses since we focused only on native species. In all cases, several niche overlap metrics were calculated. First, following Petitpierre et al. (2012), we measured the difference between non-invaded and invaded community ensemble niches with the following three metrics: (a) niche stability (i.e., proportion of the space occupied by the non-invaded community that overlaps with the space of the invaded community); (b) niche unfilling (i.e., proportion of the climatic space occupied by the non-invaded community not overlapping with the space of the invaded community); and (c) niche expansion (i.e., proportion of the climatic space occupied by the invaded community not overlapping with the space of the non-invaded community). In addition, we used the similarity index Schoener's *D* to calculate the niche overlap between non-invaded and invaded species assemblages. This metric varies from 0 (when the climatic niches of the communities are totally dissimilar) to 1 (when there is a complete overlap; Warren et al., 2008; Broennimann et al., 2012). Finally, we calculated the median of the distribution density and the median of the available climatic space in both non-invaded and invaded communities to assess the overall direction of the shifts (Broennimann et al., 2012; Petitpierre et al., 2012; González-Moreno et al., 2015). All analyses were carried out in R using the *ecospat* package (R Development, 2019).

2.5 | Community species composition

Given that only presence data were available, community ensemble niche shifts were analyzed by comparing two composition indices: richness and similarity. For each plot, we calculated the species richness and for each pair of non-invaded and invaded plots, we calculated the Sørensen similarity index (SI):

$$\mathrm{SI} = \frac{2j}{(a+b)}$$

where j is the number of species found in both plots, a the number of species in non-invaded plots, and b the number of species in invaded plots (Magurran, 1988). These values were then averaged across all pairs of plots of the same invasive species. Finally, we used the Raup–Crick similarity metric to compare the communities of pairs of plots (presence/absence data of non-invaded and invaded plots) and test how different they were from those obtained under a null model. In this way, this metric can help detect the structure in the community. We used only pairs of plots with richness higher than five species for this calculation (67% of the plots) to take into consideration the limitations of this metric (i.e., a low number of species for comparison is a problem when attempting to detect deviations from the null model), as highlighted by Chase et al. (2011).

We also quantified to what extent changes in the climatic niche assemblage between non-invaded and invaded communities were related to compositional changes. Therefore, we computed Spearman's rank correlation between the climatic niche stability and the Sørensen similarity index of non-invaded and invaded plots, as well as between the climatic niche stability and the difference in the taxonomic richness of plots (i.e., between non-invaded and invaded plots), for each invasive species. All analyses were carried out in R (R Development, 2019).

3 | RESULTS

3.1 | Community ensemble niches

The climatic space of the community can be summarized by the first two PCA axes (Appendix S3). PCA1 is related to the mean temperature of the driest quarter (*bio09*) and the mean diurnal range (*bio02*) (35.95% of the variance); PCA2 is related to temperature seasonality (*bio04*), precipitation of the coldest quarter (*bio19*), and wind speed (24.06% of the variance). The measurements of the climatic niche shift due to invasion for the pooled species for the pooled species, irrespective of the invasive species, show an almost complete overlap between non-invaded and invaded plots (unfilling = 0.0; expansion = 0.0008; stability = 1; Figure 3).

Analysis of the paired plots also reveals an almost complete overlap of the community ensemble niche between non-invaded and invaded plots for the four invasive species (Table 2; Appendix S4). Several plots denote a contraction of the community ensemble niche after invasion (Table 2; see for example, the green color of plots nr. 279 and 342 in Appendix S4, Figure A; or plots nr. 20 and 133 in Appendix S4, Figure B). In contrast, only few plots show an expansion of the community ensemble niche after invasion (see for example, the orange color of plot 375 in Appendix S4, Figure A; plots 119 and 137 in Appendix S4, Figure B; or plot 240 in Appendix S4, Figure D).

Plots invaded by *Carpobrotus* spp. and *Opuntia dillenii* are, relatively, the least stable (Table 2). In addition, plots invaded by *Carpobrotus* spp. show the lowest Schoener's *D*, with the highest values of unfilling and expansion (Table 2; Appendix S4, Figure B). In contrast, plots invaded by *Opuntia dillenii* exhibit the highest Schoener's *D* and the lowest unfilling. Plots invaded by *Arctotheca calendula* and *Conyza bonariensis* are the most stable. Besides, the range of Schoener's *D* is smaller for *Carpobrotus* spp. and *Arctotheca calendula*. This means that the community niche of plots both non-invaded and invaded by these species, are the least similar for these two species.

3.2 | Community species composition

The number of species ranged between 1 and 12 species for non-invaded plots, and between 2 and 16 species for invaded plots. Most of the native species (88 out of the 106 species) were found in both non-invaded and invaded plots (Appendix S1), while 12 native species were found only in invaded plots. The most widespread native species were found in paired plots invaded by *Carpobrotus* spp. (i.e., *Lotus creticus* was present in 44 non-invaded plots and in 30 invaded plots; *Vulpia myuros* was found in 39 non-invaded plots and in 32 invaded plots), and by *Conyza bonariensis* (i.e., *Ammophila arenaria* was reported in 29 non-invaded plots and in 25 invaded plots). For three out of the four exotic species studied here, invaded plots exhibited a higher number of species than non-invaded ones (Table 3); 69%, 75%, 89%, and 91% of the plots invaded by *Arctotheca calendula*, *Carpobrotus* spp., *Conyza bonariensis*, and *Opuntia dillenii*, respectively, showed the same or higher taxonomic richness than their corresponding non-invaded plots. According to the Sørensen similarity index of the paired plots, those invaded by *Opuntia dillenii* maintained the highest similarity, while invasion by *Carpobrotus* spp. resulted in the lowest similarity (Table 3). The Raup–Crick index gave a value of 0 for 69% of the paired plots; only 10% of them had an index value higher than 0.5, indicating a random allocation of the species in most plots.

FIGURE 3 Overlap between the community ensemble niche of the species in non-invaded and invaded plots for pooled species, irrespective of the invasive species. Dark shading shows the density of the occurrences of the species by cell. Colored areas are the portion of these conditions actually occupied by the community. The tiny red arrow shows the environmental distance between the median of the distribution density for each community

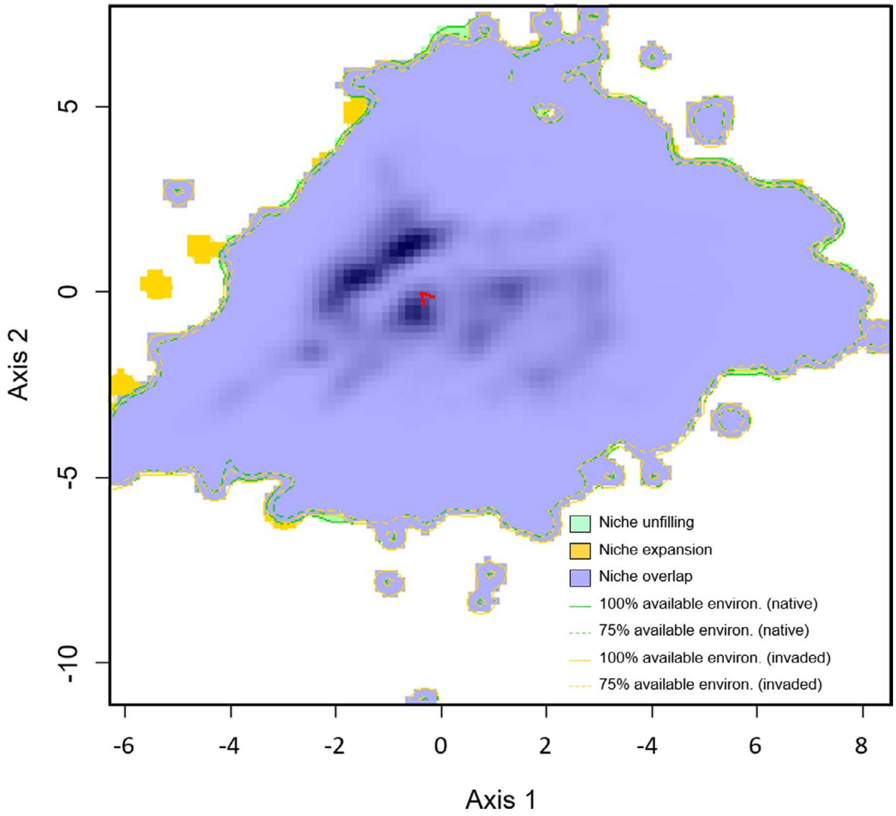

TABLE 2 Climatic niche metrics (mean ± *SE*) comparing non-invaded and invaded communities of every paired plot

Metrics	*Arctotheca calendula*	*Carpobrotus* spp.	*Conyza bonariensis*	*Opuntia dillenii*
Stability	0.995 ± 0.00	0.976 ± 0.01	0.989 ± 0.01	0.985 ± 0.01
Unfilling	0.008 ± 0.00	0.074 ± 0.02	0.016 ± 0.01	0.003 ± 0.00
Expansion	0.005 ± 0.00	0.024 ± 0.01	0.011 ± 0.01	0.015 ± 0.01
Schoener's *D*	0.655 ± 0.03	0.580 ± 0.03	0.780 ± 0.03	0.797 ± 0.04

TABLE 3 Average (mean ± *SE*) taxonomic richness (number of native species) and Sørensen similarity index for non-invaded (C) and invaded (I) plots. *N* = total number of paired plots

Invasive	*N*	Richness C	Richness I	Sørensen
Arctotheca calendula	54	7.00 ± 0.22	7.31 ± 0.22	0.501 ± 0.04
Carpobrotus spp.	67	5.82 ± 0.24	6.84 ± 0.31	0.439 ± 0.03
Conyza bonariensis	61	6.62 ± 0.28	8.2 ± 0.34[a]	0.631 ± 0.03
Opuntia dillenii	34	7.59 ± 0.37	8.79 ± 0.46	0.753 ± 0.32

[a] Comparison statistically significant according to Gutiérrez-Cánovas et al. (2020).

Spearman's rank correlation coefficients between the Sørensen similarity index and the community ensemble niche stability were significantly positive for all invasive species except for *Conyza bonariensis*, the highest correlation being for *Opuntia dillenii* and *Arctotheca calendula* plots. The difference in taxonomic richness between non-invaded and invaded plots was negatively correlated with the community ensemble niche stability, and it was statistically significant for *Carpobrotus* spp. and *Opuntia dillenii* (Table 4).

4 | DISCUSSION

4.1 | Analysis of the community ensemble niche

There is evidence that biological invasions modify the structure of plant communities (Fairfax & Fensham, 2000; Vilà et al., 2011) but no information about their influence on other characteristics of the community such as the ecological niche is available. We analyzed the effects of invasion by four exotic species with different

TABLE 4 Spearman's rank correlation coefficients between community ensemble niche stability and Sørensen species similarity and difference in taxonomic richness between non-invaded and invaded plots

Species	Niche stability vs Sørensen	Niche stability vs dif. taxonomic richness
Arctotheca calendula	0.542 (***)	−0.199 (n.s.)
Carpobrotus spp.	0.288 (*)	−0.303 (*)
Conyza bonariensis	0.196 (n.s.)	−0.117 (n.s.)
Opuntia dillenii	0.621 (***)	−0.444 (**)

In parentheses *p*-values: *, $p \leq .05$; **, $p \leq .01$; ***, $p \leq .001$.

life strategies on the climatic niche of a plant community located in a coastal area of southwestern Spain. We expected that invasion would lead to a shift or contraction in the community ensemble niche. However, the species assemblage in coastal vegetation did not change its community ensemble niche after invasion. In fact, average measurements of niche overlap indicated that there is almost no change between the climatic niches of the non-invaded and invaded communities (i.e., niche stability > 95%), even when the invaders exhibit different functional traits. This overall small change in the community ensemble niche after invasion may be explained because the niche estimation arises from pooling the different niche spaces of many species (Kühsel & Blüthgen, 2015) that likely overlap in their global distribution. In addition, several cosmopolitan species (e.g. *Dactylis glomerata*, *Geranium molle*, *Plantago coronopus*, *Rumex crispus*, *Sonchus oleraceus*) with a broad climatic niche are found in the community and do not seem to be negatively affected by the invasion (i.e., they were found in both non-invaded and invaded plots). This pattern may diminish the impact of the invaders on the community ensemble niche. Nevertheless, the effect of invasion can be locally important, as shown by some pairs of plots displaying large differences in climatic niche (2% of paired plots had stability values below 0.5 or unfilling values above 0.6%).

Across the studied species, *Carpobrotus* spp. show a relatively large effect on the community ensemble niche and on the community composition as indicated by the different measures used in this study. In fact, they produced the lowest climatic niche stability, Schoener's *D*, and Sørensen similarity index but also led to the greatest expansion, although the new set of species would not have filled the community ensemble niche (i.e., highest niche unfilling). This could be explained because the invasion could promote the arrival of other cosmopolitan species related to disturbed habitats, but belonging to the native community and with similar climatic requirements. The remarkable influence of *Carpobrotus* spp. on plant communities of coastal areas regarding community composition and climatic niche, agrees with previous literature. For example, Castro-Díez et al. (2016) found that *Carpobrotus* spp. invasion on two Mediterranean islands led to a reduction in species richness, functional diversity, and redundancy of the recipient communities. Also de la Riva et al. (2019) reported that *Carpobrotus* spp., together with *Arctotheca calendula*, had a great impact on the non-invaded community due to their functional profile, which makes *Carpobrotus* spp. better competitors in terms of acquisitive traits (e.g. leaf nitrogen concentration and leaf area per unit of leaf dry mass). Eventually, *Carpobrotus* spp. can create favorable conditions for the establishment of ruderal plants, as reported by Santoro et al. (2012) in the coastal dunes of Central Italy. Human activities along the coast and sand movement opening gaps together with some of the traits of *Carpobrotus* spp. such as dispersal and transport mechanisms (including a high capacity of seeds and plant fragments to tolerate seawater immersion for long periods), clone viability several months after fragmentation, clonal growth, low moisture requirements for germination, early growth not affected by low moisture levels, and great phenotypic plasticity (Novoa et al., 2012; González-Campoy et al., 2017, 2018, 2019; Roiloa et al., 2017; Podda et al., 2018; Portela et al., 2019; Souza-Alonso et al., 2019, 2020), explain the successful establishment of this taxonomic complex in the region, and its eventual impact on native communities.

Contrary to expectations, *Opuntia dillenii* did not have an important effect on the community ensemble niche nor on the community composition. This result agrees with those of other authors. For example, de la Riva et al. (2019) worked in the same area and found that this species was the most functionally dissimilar invader. However, it did not cause many differences in the native species' trait profiles, e.g. they exhibited higher values of seed mass and lower leaf carbon concentration, trait related to drought resistance in invaded plots. On the other hand, *Opuntia dillenii* has the longest residence time since its historical introduction in the region, which could explain a certain homogenization of the community composition. This is supported by the highest Sørensen similarity index and the highest correlation between niche stability and the difference in taxonomic richness.

Invasion by annuals, i.e., *Arctotheca calendula* and *Conyza bonariensis*, led to the most stable communities but with disparate results regarding the climatic niche analysis. In relative terms, Schoener's *D* was higher for *Conyza bonariensis*, indicating that the native species in the invaded plots cover a similar climatic niche as the species in the non-invaded plots. This result suits the higher Sørensen similarity index for *Conyza bonariensis*, although the difference in taxonomic richness is the highest. De la Riva et al. (2019) found that this species was the invader functionally most similar to the native community and also that *Arctotheca calendula*, with its acquisitive strategy, had an important impact on the community, triggering changes in trait composition (e.g. higher specific leaf area and specific root length) in addition to a reduction of the functional and phylogenetic diversity.

4.2 | The effect of species composition on the community ensemble niche

Overall, the absence of a clear shift in climatic community niche is associated with a negligible change in species richness and composition after invasion. This rationale is supported by the lack of a clear pattern or association of species with non-invaded or invaded plots, as indicated by the analysis of the Raup–Crick similarity index. Furthermore, the stability of the community ensemble niche increased with higher similarity in the composition between both types of plots. This finding reinforces the interlink between compositional and climatic niche differences. *Carpobrotus* spp. and *Conyza bonariensis* were the species with a weaker correlation between these two aspects. Particularly, taxonomic similarity between non-invaded and invaded plots was the highest when *Opuntia dillenii* was the focal plant, a result that relates to the higher and significant correlation between similarity and community stability for this species. Consistently, the highest value of Schoener's *D* indicated that the climatic niche was rather similar after invasion by this species. This connects with the low effect of this species on the species' trait profiles of the native community (de la Riva et al., 2019).

Coastal areas impose strong limitations to plants (Wilson & Sykes, 1999; Santoro et al., 2012). This habitat can be extremely harsh, with soils poor in nutrients and moisture due to their high permeability, strong winds, salt spray, and high dynamism. Therefore, it is likely that species in these communities are controlled by other limiting factors rather than climate. Such environmental conditions control species composition leading to low species richness and vegetation cover (Del Vecchio et al., 2015), with no clear association of native species with any of them in this case. Although the average number of species in the study area was low, it was higher than in the plant community from the Cape coast of South Africa described by Hertling and Lubke (1999), who reported five to six species per stand in native plots and in plots invaded by *Ammophila arenaria*. Several considerations could explain the relatively low species richness. Limited vegetation coverage in dune areas could result in little biotic resistance to the arrival of invasive species with suitable characteristics. In addition, areas regularly modified, such as dunes, would remain chronically at an initial phase of colonization, thus not being dominated by any species. More studies would be necessary to improve our understanding of this point given that plots completely dominated by any of the four invaders were excluded from our study. Another issue to be taken into consideration is that richness is not the only measurement of diversity, and sometimes it does not match diversity trends in a community after invasion. For example, Hertling and Lubke (1999) found no significant difference in richness in the coastal dune vegetation of the Cape coast, but Simpson's diversity was lower in invaded stands. Unfortunately, data of species relative abundance were not available in our database to explore these diversity metrics.

4.3 | Implications for understanding plant communities invaded by exotic species with different life strategies

This study contributes to the analysis of biological invasions dealing with a plant community invaded by exotic species with different life strategies. Nevertheless, it highlights that several issues should be considered in further research to improve the interpretation of the potential effect of invasion on the community assembly. The study covered a homogeneous environment and more contrasting climatic gradients (e.g. mountains) will likely provide better insights into the effect of invasions on the community ensemble niche, particularly in the face of climate change. Thus, the inclusion of species with dissimilar climatic niches and stronger competitive interactions will improve this analysis. Besides, the addition of variables regarding abiotic stress (e.g. salinity) or human influence conditions would help understand if there are changes in the community ensemble niche after invasion (e.g. González-Moreno et al., 2013; Cabra-Rivas et al., 2016; Hernández-Lambrano et al., 2017). In addition, the use of abundance data would help improve our understanding of the cause and effect relationship between invasion and diversity (Wilsey et al., 2005; Mattingly et al., 2007).

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AUTHOR CONTRIBUTIONS

ASL, PGM, and MV designed the research. ASL, PGM, and FL contributed to data analysis. ASL with contributions from PGM wrote the original draft and all authors discussed the results and contributed to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Part of the data and the program source code used in this study are available in the repository Consorcio Madroño (https://doi.org/10.21950/BWFV9U).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Species present in the community and type of plot where they are found

Appendix S2. Occurrence downloads from GBIF

Appendix S3. PCA biplot of the worldwide climatic space for all species in the community

Appendix S4. Overlap between the climatic community niche of the species found in non-invaded and invaded pairs of plots

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