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Functional and phylogenetic consequences of plant invasion for coastal native communities

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Abstract

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

Location: Atlantic coastal habitats in Huelva (Spain).

Methods: We identified species diversity and composition in 220 paired (invaded and non-invaded) plots along the coast (440 plots in total). We measured nine functional traits for every native and invader species, namely, specific leaf area (SLA), specific root length (SRL), leaf and root dry mass content (LDMC and RDMC) and carbon isotope fraction ($\delta^{13}C$). We calculated, at the plot scale, community means (CMs) for each trait, functional richness, Faith's phylogenetic diversity and functional and phylogenetic mean pairwise dissimilarities.

Results: Three out the four species showed rather extreme trait values compared to the native flora with greater impact on invaded communities. In plots invaded by *A. calendula* the values of the native communities of SLA and SRL increased, while LDMC, RDMC and $\delta^{13}C$ decreased showing CMs more similar to its functional profile. Besides, these plots showed lower functional and phylogenetic diversity in the native component of the community. In plots invaded by *Carpobrotus* spp. and *O. dillenii* the CMs values for LDMC and $\delta^{13}C$ increased, but have little effect on the functional and phylogenetic structure of the native communities, while no differences were observed for the communities invaded by *C. bonariensis* (the most functionally similar to the native species).

Conclusions: Our study highlights that inferring community assembly rules from the exploration of functional and phylogenetic differences between invaded and non-invaded plots is not straightforward. By considering invaders with different functional profiles, we have shown that species with different mechanisms of invasion have contrasting impacts on the community. Consequently, the effect of plant invaders differs depending on their functional distinction from the recipient community, rather than their phylogenetic origin.

KEYWORDS

alien species, functional richness, functional structure, non-native plants, phylogenetic diversity, seed mass, specific leaf area, specific root length

1 | INTRODUCTION

Human activities are responsible for the worldwide introduction of thousands of non-native species, some of which might become invasive and cause environmental impacts (Simberloff et al., 2013). Non-native invasive plants can cause the local loss of native species, shifts in community dominance and consequently alterations of ecosystem processes (Gordon, 1998; Vieites-Blanco & González-Prieto, 2018; Vilà et al., 2011). There is a myriad of non-exclusive mechanisms by which invasive plant species modify recipient communities, including a combination of the ability to exploit empty niches, greater competitive ability, and lower susceptibility to natural enemies compared to native species (Catford, Jansson, & Nilsson, 2009).

The evaluation of the effects of invasive plant species on the community assembly has traditionally relied on descriptors of taxonomic diversity and species composition (Arianoutsou et al., 2013; Thomas & Palmer, 2015; Vilà et al., 2006). However, there is growing recognition that descriptors of the functional and phylogenetic structure of communities can give better insights into community assembly processes in invaded communities (Jucker, Carboni, & Acosta, 2013) and the impact on ecosystem functioning (Finerty et al., 2016). In general, descriptors of functional and phylogenetic structure can inform on the nature and strength of species interactions, and they can help predict community responses to global change (Gagic et al., 2015; Hulme & Bernard-Verdier, 2018a; Villéger, Grenouillet, & Brosse, 2014).

Previous studies on this subject have shown divergent impacts of invasive species on the functional and phylogenetic structure of the invaded community. For instance, Castro-Díez, Pauchard, Traveset, and Vilà (2016) and Lapiedra, Sol, Traveset, and Vilà (2015) reported lower phylogenetic and functional diversity in response to *Carpobrotus* spp. invasion on Mediterranean islands, but Jucker et al. (2013) documented changes in functional (but not phylogenetic) diversity on the west coast of Italy. Such context dependency suggests that the invader's effects on the functional and phylogenetic structure of a native plant community will depend on: (1) the phylogenetic and functional features of the native species that are more susceptible to being outcompeted by the invader, which could lead to decreased functional and/or phylogenetic diversity of the recipient community; and (2) the dissimilarity of the functional traits and the phylogenetic relatedness of the invader with respect to the recipient community, which might increase the functional and/or phylogenetic diversity by providing a novel subset of traits and/or evolutionary origins to the recipient communities (Castro-Díez et al., 2016; Hulme & Bernard-Verdier, 2018b; Lapiedra et al., 2015). These two complementary sources of variation could explain the contrasting patterns that have been reported regarding the impact of invasive plant species on native communities. Ecological theory predicts that exotic species can establish themselves in native communities by being somehow different in resource use from the resident species, meaning that they will tend to occupy a different niche. Conversely, they can be functionally and/or phylogenetically similar, in which case the invasive species would occupy a similar niche and probably compete more strongly with the resident species (limiting similarity; MacArthur & Levins, 1967). Both processes can result in complex changes in the functional and phylogenetic structure of the native community (MacDougall, Gilbert, & Levine, 2009).

The phylogenetic structure of a community is usually used as a proxy for the functional structure, because trait divergence can be ideally traced back through a phylogenetic tree (Gerhold et al., 2011; Lapiedra et al., 2015). However, phylogenetically related species may differ in certain traits as a consequence of niche divergence (e.g., sympatric speciation), or distant species may show similar traits due to ecological convergence (Losos, 2008, 2011). Therefore, considering both functional and phylogenetic approaches can provide complementary insights into the ecological and evolutionary processes involved in the species assembly of invaded communities (Hulme & Bernard-Verdier, 2018a). While the functional structure of plant communities is closely related to the different ecological strategies used to cope with abiotic filters and to establish species interactions, the phylogenetic structure can provide insights into the role of the different evolutionary histories of the species in the community assembly (Xu et al., 2017; references therein). However, few articles have simultaneously investigated differences in both functional traits and phylogenetic patterns between invaded and non-invaded plant communities (but see Jucker et al., 2013; Loiola et al., 2018).

Here, we aim to study the effects of four invasive plant species with contrasting functional and phylogenetic features — *Arctotheca calendula* (L.) Levyns, *Carpobrotus* N.E.Br. spp., *Conyza bonariensis* (L.) Cronquist and *Opuntia dillenii* (Ker Gawl.) Haw. — on the taxonomic, functional and phylogenetic structure of plant communities on the Atlantic coast of Southwest Spain. We first quantified the differences in functional composition (community mean [CM] values for each trait) between invaded and reference non-invaded communities for each invasive species, in order to assess both the successful functional strategies of the native species after invasion and the functional strategies of the invaders. Second, we compared the taxonomic, functional and phylogenetic diversity of the invaded and non-invaded communities. Differences between the invaded and non-invaded communities could have been caused only by the contribution of the invader species, and/or by the observed changes among the native species (Loiola et al., 2018). To clarify these possible sources of variation, we first compared the invaded and non-invaded communities, including only the native species, and secondly we developed the same analysis but with inclusion of the invaders.

2 | METHODS

2.1 | Study area and field sampling

We conducted a vegetation sampling in coastal dunes along a 125-km strip of the Atlantic coast in Southwest Spain (Appendix S1). The climate is Mediterranean with an oceanic influence; the mean annual rainfall is 560 mm, albeit with considerable inter-annual variation,

since it ranges from <300 mm in dry years to 1,000 mm in extremely wet years (Lloret et al., 2016). The mean annual temperature is 16.5°C, with mean temperatures of 24.7°C in the hottest month (July) and 10.0°C in the coldest month (January). The most common and abundant invasive plant species in the area are *A. calendula*, *Carpobrotus* spp., *C. bonariensis* and *O. dillenii* (González-Moreno, Pino, Cózar, García-de-Lomas, & Vilà, 2017), all of which are widespread on coastal rocks, cliffs and sand dunes in Spain (Sanz-Elorza, Dana, & Sobrino, 2004). "*Carpobrotus* spp." includes both *C. acinaciformis* (L.) L.Bolus and *C. edulis* (L.) N.E.Br. (Wisura & Glen, 1993), given that their hybrids are widely naturalised on coastal rocks, cliffs and sand dunes (Suehs, Affre, & Médail, 2004; Traveset et al., 2008). In addition, the two species are ecologically and functionally similar and difficult to distinguish in the field.

The vegetation survey was carried out, in collaboration with the Andalusian Environmental Administration (in spring of 2010 and 2011), by walking transects parallel to the coast and 50 m from the shoreline (for more details, see González-Moreno et al., 2017). When any of the target invasive species was detected, we set up a 10 m × 10 m plot (hereafter, invaded plot). Another plot, containing only native species, was chosen as the control in close vicinity (ca. 20 m), in the same habitat to ensure that each pair of plots was subjected to similar conditions (Vilà et al., 2006). All the plant species present in each plot were noted. In total, we sampled 220 paired plots: 57 for *A. calendula*, 68 for *Carpobrotus* spp., 61 for *C. bonariensis* and 34 for *O. dillenii*. In total, our database has 110 species.

2.2 | Plant traits

In spring 2017, during the peak of plant growth, healthy adults of each of the 110 species were selected randomly from the study area for the measurement of seven above-ground and two below-ground functional traits. For each species, the individuals sampled were selected from within the core of the distribution range of the species in the study area; that is, avoiding edge populations that may present extreme trait values within the species. All trait measurements were carried out according to the criteria and methodology defined by Pérez-Harguindeguy et al. (2013).

Leaves from six individuals per species were collected to measure specific leaf area (SLA, leaf area per unit of leaf dry mass; m^2/kg), leaf dry matter content (LDMC, leaf dry mass per unit of leaf water-saturated fresh mass; mg/g), leaf nitrogen concentration (LN; %), leaf carbon concentration (LC; %) and the carbon isotopic ratio ($\delta^{13}C$; ‰).

Fine roots (<2 mm diameter) were sampled in four individuals per species by excavating the first 20–30 cm of the soil depth close to the plant basal stem. They were kept in ice and taken to the laboratory for root trait measurements. We measured specific root length (SRL, root length per unit of root dry mass; m/kg) and root dry matter content (RDMC, root dry mass per unit of water-saturated fresh mass; mg/g). The root length data were obtained by analysing the scanned root samples with WinRHIZO 2009 (Regent Instruments, Quebec City, QC, Canada).

Plant height (P_{height}; m) and seed mass (S_{mass}; mg) were compiled from the published literature (Castroviejo et al., 1986) and from seed databases available in 2017 (Semillas Cantueso, http://www.semillascantueso.com, Banco de Germoplasma Vegetal Andaluz –BGVA–, Goethe University Frankfurt, http://www.seed-dispersal.info, and the Royal Botanic Gardens, http://data.kew.org/sid/). For five species (*Artemisia crithmifolia*, *Centaurea pullata*, *Rumex tingitanus*, *Silene littorea* and *Spergularia nicaeensis*) we did not find seed mass values; however, because seed mass is strongly conserved through the phylogeny (Lord, Westoby, & Leishman, 1995), we estimated the seed mass of each of these species from the average value of the species of the same genus that were registered.

Given the multidimensionality of plant functions, we chose these nine traits because of their importance in providing information about different independent axes of ecological strategies (see de la Riva, et al., 2018; Díaz et al., 2016; Funk, et al., 2017). Specifically, we selected traits associated with resource acquisition (SLA, SRL, LN), drought resistance (LDMC, RDMC, LC) and water use efficiency (ʒ13C) (see Appendix S2 for specific functional roles), which are expected to be good indicators of competition in arid environments (Hulme & Bernard-Verdier, 2018a) or in environments with water shortage, such as our study system (dunes). In addition, we selected two traits that represent different dimensions of trait variation related to reproduction and competition for light (P_{height} and S_{mass}).

2.3 | Data analysis

To account for phylogenetic diversity, we constructed phylogenies by using the comprehensive Angiosperm species-level phylogeny from Zanne et al. (2014), as updated by Qian and Jin (2016), which is included in the R package "S. PhyloMaker" (Qian & Jin, 2016). The distance of the few species (17) that were not found in PhytoPhylo was supplanted by the distance of the closest species of the same genus found in the mega-phylogeny tree (see the phylogenetic tree in Appendix S3 for further information).

The trait data were log-transformed prior to the analyses, to reduce distribution skewness. For each plot, we estimated taxonomic richness, CM traits and measures of functional and phylogenetic diversity. For the invaded plots all indices were calculated with (+i) and without (–i) the invasive species, to separate the impacts on the community due to the invader's presence from those due to the exclusion of native species by the invader (Castro-Díez et al., 2016).

We calculated the averaged CMs for each trait as the mean value of each trait across the species present in the plot. To characterize the functional dissimilarity between each invasive species and all the native species, and to quantify the functional richness of the native community, we computed a matrix containing the pairwise functional dissimilarity across species, using the Euclidean distance (hereafter, Euclidean trait matrix) after standardizing traits (mean = 0, *SD* = 1). We built a functional space through a Principal Coordinates Analysis (PCoA), to examine the dissimilarity between species (Laliberté &

Legendre, 2010) and to visualize the functional differences between the native species and the invader species. To identify which traits were correlated with each axis, we used Pearson correlation coefficients (see Appendix S4). We kept three dimensions because they represented a substantial part of the original Euclidean trait matrix (63.5%; mean squared deviation = 0.80, see Maire, Grenouillet, Brosse, & Villéger, 2015), and the functional spaces of higher dimensions contained axes with no clear ecological meaning.

Then, we calculated for each plot the taxonomic richness (the total number of species per plot), the functional richness (F_{rich}, the amount of the functional space — where each trait is a dimension — occupied by all the species present; Laliberté & Legendre, 2010; Villéger, Mason, & Mouillot, 2008) and Faith's phylogenetic diversity index (PD, calculated with the R package "PICANTE"; Kembel et al., 2010), which is the minimum total length of all the phylogenetic branches required to span a given set of taxa on the phylogenetic tree (Faith, 1992). F_{rich} represents the change in functional space caused by the change in the community structure, while PD quantifies the total independent evolutionary history of a subset of taxa (Veron, Davies, Cadotte, Clergeau, & Pavoine, 2017; Villéger et al., 2008) and both indices are positively correlated to species richness. In addition, to have a comparable index for both functional and phylogenetic diversity, we calculated the mean pairwise dissimilarity (MPD) index, based either on the species pairwise phylogenetic distances or on the Euclidean trait matrix (Swenson, 2014). The MPD is the mean distance between all pairs of species in a plot, and summarises the distance between all species combinations in a community (Loiola et al., 2018) and it does not increase with species richness. We calculated the functional and phylogenetic MPD indices (*F*MPD and *P*MPD, respectively) based on existing algorithms (de Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016). The selected indices integrate the main components of community structure enclosed by other related indices.

For each invader's dataset, we compared the CM trait values and taxonomic, functional and phylogenetic indices of the invaded (both with and without the invader) and control plots by means of paired *t* tests. In addition, to check whether the differences between the control and the invaded plots were caused by the invader and not by spatial variability, we compared each control plot with the nearest control plot in the paired *t* tests (significant differences among the control plots could indicate that the natural variability of these communities is similar to or higher than that of the patterns associated with the invasion process). We used null models to check if the functional and phylogenetic diversity patterns were a trivial consequence of species richness variation. We randomised the traits combinations across species, while fixing the number of species of each plot (999 runs) and estimating the same functional and phylogenetic indices. For each index, we estimated whether the differences observed between invaded and non-invaded plots were significantly different from those obtained between randomised communities (null differences). Such divergence was considered the Standardised Effect Size [SES, = (observed difference − mean null difference) / *SD* null differences].

3 | RESULTS

3.1 | Invasive plant traits and their effects on the community functional composition

The mean trait values of the plots invaded by *A. calendula*, *Carpobrotus* spp. and *O. dillenii* were significantly different from their control counterparts when the invaders were included in the statistical analyses (I + i). These results reflect the distinctive functional profiles of the invasive species. The invasion by *A. calendula*, an invasive species with a clear acquisitive strategy, increased the community values of SLA and SRL, while it reduced the values of $\delta^{13}C$ and dry tissue density spp. (Figure 1 and Appendix S5). In turn, plots invaded by *Carpobrotus* spp. and *O. dillenii* showed higher CM values for $\delta^{13}C$ and lower values for SLA, LDMC, LN and LC, with respect to control plots. *O. dillenii* also showed lower values of RDMC and higher values of S_{mass} and P_{height} than native species. By contrast, plots invaded by *C. bonariensis* had a higher CM value for LN than the controls (Figure 1 and Appendix S5).

When the invasive species were not considered in the calculation of the CM values of invaded plots (I − i), we found fewer differences between invaded and control plots. Plots invaded by *A. calendula* (I − i) showed lower LN, plant height, SLA and $\delta^{13}C$ values (the differences for the last two being marginally significant, $p < 0.07$) in comparison with control plots, indicating that native species with high LN and plant height were more prone to being displaced by *A. calendula*. The native species in the plots invaded by *Carpobrotus* spp. (I − i) showed lower CM values for SRL and higher ones for LDMC, RDMC and seed mass, with respect to control plots. This indicates that *Carpobrotus* spp. displaced species with high SRL, low leaf and root density and low S_{mass}. The native component in the plots invaded by *C. bonariensis* (I − i) showed a higher CM value only for $\delta^{13}C$, relative to control plots, while the native component of the plots invaded by *O. dillenii* had higher S_{mass} and lower LC (Figure 1 and Appendix S5).

Finally, we checked whether the significant differences found between control and invaded plots were promoted mostly by the presence of the invasive plant and not by differences in the spatial plot location or by chance. We did not find any significant trait differences when comparing pairs of nearest control plots ($p > 0.1$ in all cases; Appendix S6).

The PCoA analyses mirrored well the differences observed in the previous analysis. In agreement with the disparate functional strategies displayed by the invasive species, *A. calendula* was located at the negative extreme of the first PC axis. This axis represents a trade-off between acquisition and conservation strategies (Figure 2 and Appendix S4). *Carpobrotus* spp. and *O. dillenii*, the two succulent invaders, were located at the negative extreme of the second PCoA axis. This axis sorts species along a change from high LDMC and $\delta^{13}C$ values to high LN and LC values. It is worth noting that *O. dillenii* was clearly the invader that was functionally most dissimilar, as shown by its isolated position at the extreme of the second PCoA axis. As expected, *C. bonariensis* was the invader most similar to the native

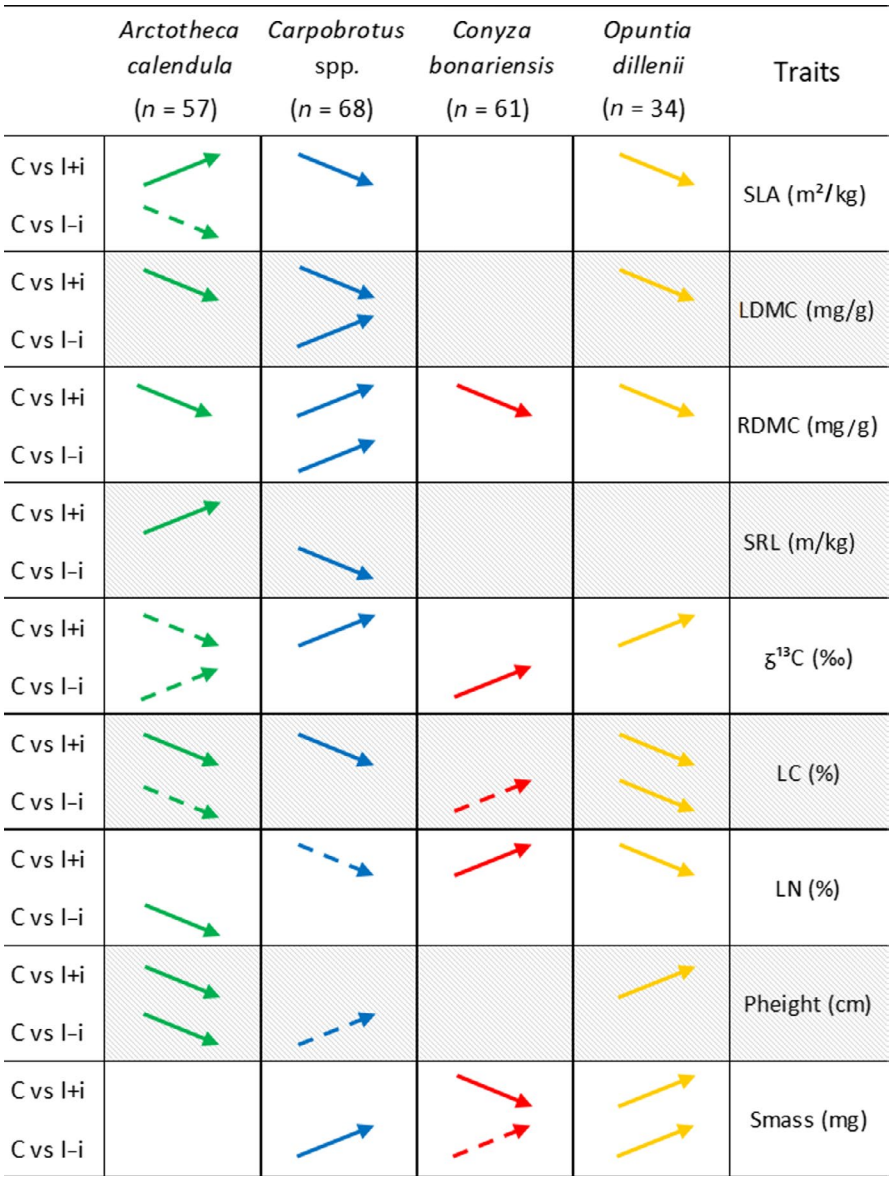

FIGURE 1 Effect of invasion on community trait means for the nine functional traits. Each trait was compared between the control plots (C) and the invaded plots (including [I + i] or excluding [I − i] the invader plant). Solid lines indicate significant differences ($p < 0.05$) obtained with paired *t* tests, while dashed lines indicate marginally significant differences ($p < 0.10$). Arrows pointing up or down mean that there were lower or higher values, respectively, in the invaded plot [Colour figure can be viewed at wileyonlinelibrary.com]

species, and the PCoA analyses did not place this invader in any peripheric region.

3.2 | Differences in taxonomic richness and in functional and phylogenetic diversity between invaded and non-invaded communities

Most of the functional and phylogenetic diversity indices showed significant differences between the observed invaded and control plots. In the case of *A. calendula*, we found lower values of taxonomic richness and of the functional and phylogenetic diversity indices in the invaded plots when the invader was excluded from the analysis (I − i) (Figure 3 and Appendix S7). However, when *A. calendula* was included in the analysis, there was an increase in the value of FMPD, but not of PMPD, which suggests that *A. calendula* is extending the functional space of the community, but not the phylogenetic diversity. Plots invaded by *Carpobrotus* spp. and *O. dillenii* showed higher values of species richness, F_{rich}, and PD when the invaders were included in the analysis (I + i), highlighting the functional and phylogenetic uniqueness of both invaders. Moreover, the plots invaded by *Carpobrotus* spp. and, particularly, by *O. dillenii* showed increases in FMPD, without PMPD variations (Figure 3), suggesting that this significant increase in functional over-dispersion was not associated with higher phylogenetic divergence. In plots invaded by *Carpobrotus*, the native community (I − i) showed FMPD values similar to those in control

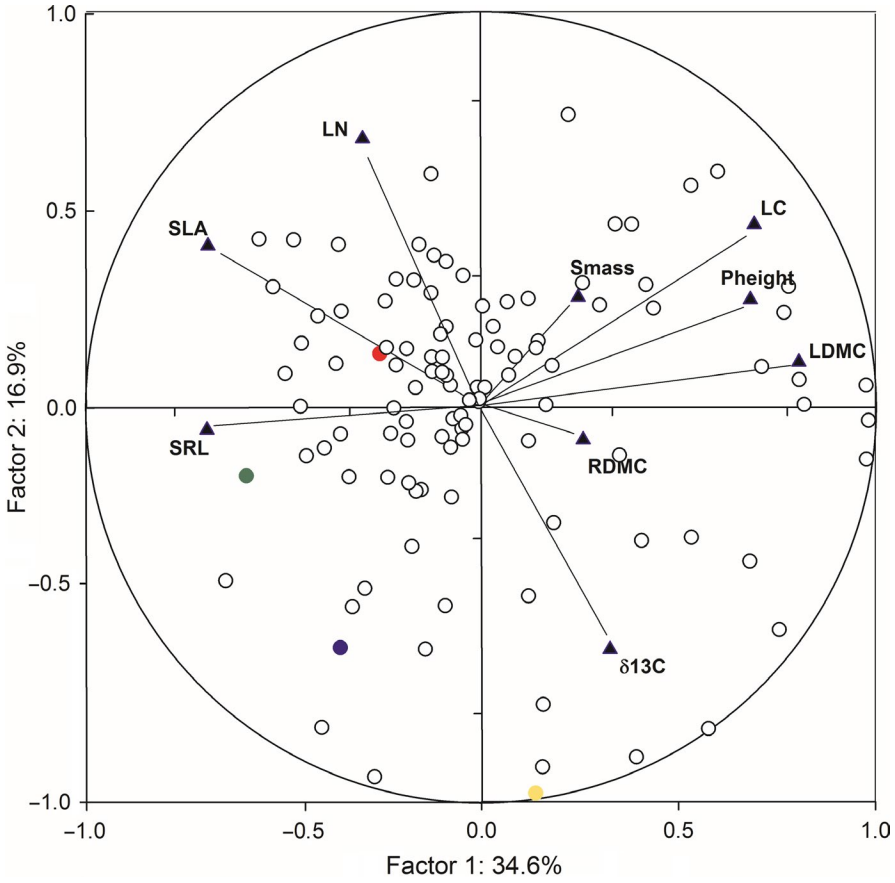

FIGURE 2 Principal Coordinates Analysis (PCoA) for the nine traits and the 110 species. The positions of the native and invasive species are shown by empty and colored circles, respectively: *Arctotheca calendula* (green), *Carpobrotus* spp. (blue), *Conyza bonariensis* (red), and *Opuntia dillenii* (yellow). The position of each trait in the space defined by the two main principal components is represented with a blue triangle [Colour figure can be viewed at wileyonlinelibrary.com]

plots, indicating that the native taxa remaining after the invasion were functionally closer to each other. Finally, the plots invaded by *C. bonariensis* represent a mixed case. Regardless of the inclusion or not of *C. bonariensis* in the calculations, the number of species was significantly increased, both locally (taxonomic richness; Appendix S7) and globally (when pooling all the species occurring in invaded and control plots, plots invaded by *C. bonariensis* showed a clear increase in species richness; Appendix S8). This local enrichment translated into a slightly higher F_{rich} (including or excluding *C. bonariensis* from the calculations) than in control plots, but produced no notable differences in *P*MPD or *F*MPD. The results of these paired *t* tests were not consistent when applying the null model (SES). Thus, the null model suggests that changes in functional and phylogenetic diversity were the reflection of the variations in species richness (Appendix S9).

4 | DISCUSSION

Documenting how invasive species alter natural communities from a functional and phylogenetic point of view is a critical approximation to understanding the mechanisms driving species assembly (see Castro-Díez et al., 2016; Jucker et al., 2013; Loiola et al., 2018). By selecting four invasive species with contrasting traits, we showed that changes in the functional and phylogenetic composition after invasion are dependent on the functional profile of the invader. Three out of the four species showed rather extreme trait values compared to the native flora, which seem to have greater impact on invaded communities. The impact ranged from a decline in functional and phylogenetic diversity in the *A. calendula* invasion to a small increase in the functional and phylogenetic diversity of the invaded communities after invasion by the two species with the most dissimilar functional profiles, *Carpobrotus* spp. and *O. dillenii*, and by *C. bonariensis*, the invader that is the most similar, functionally, to the native community. Overall, it seems that the phylogenetic and functional patterns responded more to the taxonomic richness variations than to trait-based assembly processes.

4.1 | Invasive plant traits and their effects on the community functional composition

As a consequence of the differences among the functional profiles of the invasive species evaluated, the dimensions and the direction of the community functional composition changed with the invader's identity, according to its similarity with respect to the native community. For instance, the *A. calendula* trait profile is consistent with the "fast return on investment" end of the leaf economic spectrum (Wright et al., 2004); this might partially explain the successful establishment of *A. calendula* in these low-resource ecosystems (i.e., dunes) (Funk, Nguyen, Standish, Stock, & Valladares, 2017; Funk & Vitousek, 2007). Thus, the presence of *A. calendula* in the community increased the assimilation rate per unit of mass and nutrient

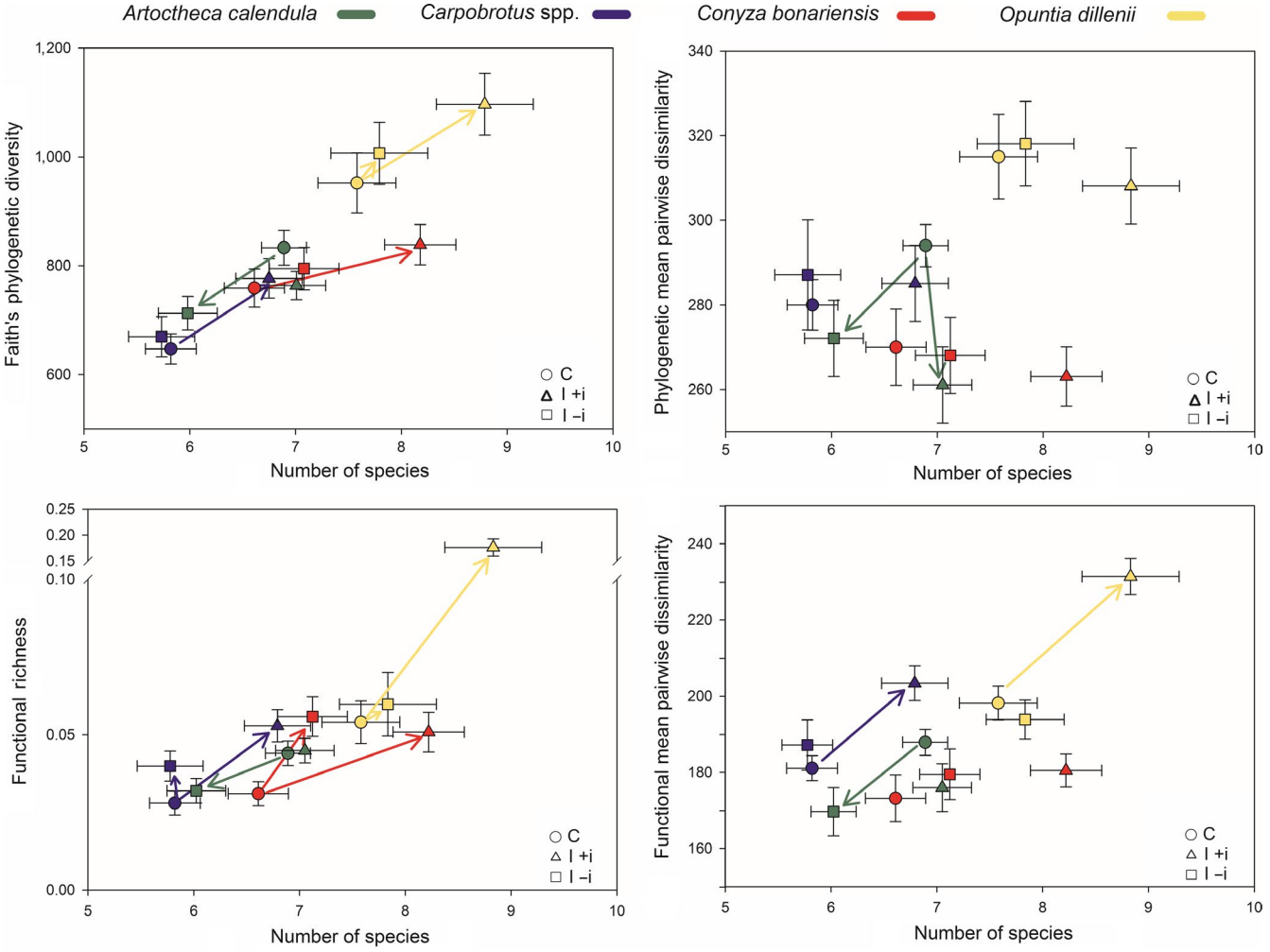

FIGURE 3 Changes (mean and standard error) in phylogenetic structure indices (Faith's phylogenetic diversity and mean pairwise dissimilarity) and functional structure indices (functional richness and mean pairwise dissimilarity) between the invaded (including [I + i] or excluding [I − i] the invader) and control (C) plots. Significant differences in the indices between invaded plots and the controls (paired *t* test; see Appendix S7) are indicated with arrows. The indices were calculated independently for each invader: *Arctotheca calendula*, *Carpobrotus* spp., *Conyza bonariensis*, and *Opuntia dillenii* [Colour figure can be viewed at wileyonlinelibrary.com]

acquisition and lowered the water-use efficiency (i.e., higher mean values of SLA and SRL and lower $\delta^{13}C$; de la Riva, et al., 2018; Reich, Tjoelker, Walters, Vanderklein, & Buschena, 1998). Moreover, *A. calendula* seems to suppress native species with acquisitive traits similar to its own (in I − i plots the CM value of LN was lower and SLA and $\delta^{13}C$ were marginally lower and higher, respectively, than in control plots), suggesting that the mechanism explaining the success of *A. calendula* is competitive exclusion.

Similarly, the native species found in plots invaded by *Carpobrotus* spp. showed on average traits associated with a conservative use of resources, as reflected by the higher community values of RDMC and LDMC and the lower SRL value (de la Riva, et al., 2018; de la Riva et al., 2016). This could be the consequence of the reduction of the soil water availability caused by the clonal growth of *Carpobrotus* sspp. and its root overlap with native plants (Andreu, Manzano-Piedras, Bartomeus, Dana, & Vilà, 2010; D'Antonio & Mahall, 1991).

We acknowledge that our study is observational and, therefore, we cannot demonstrate if the results are a consequence of invasion or of pre-existing patterns in the species assemblage, which have facilitated invasive plant establishment. However, the fact that some native species with acquisitive traits disappeared from communities invaded by *A. calendula* and *Carpobrotus* spp. suggests that these invaders possess functional profiles that make them competitively superior to native acquisitive species. This mechanism creates a competitive hierarchy that excludes some of the native species after invasion (Mayfield & Levine, 2010). By contrast, the plots invaded by *C. bonariensis* and *O. dillenii* did not show many variations in the species' trait profiles of the native species, except for the mean value of seed mass. In both cases, the mean value of the seed mass of the native species was higher in invaded plots. Large-seeded species might produce plants with deeper and more extensive roots, able to explore other parts of the soil profile, as compared to seedlings from species that are small seeded. This may create a mechanism

whereby niche differences exist when resources are scarce (Kraft, Godoy, & Levine, 2015; Quero, Villar, Marañon, Zamora, & Poorter, 2007; Westoby, Falster, Moles, Vesk, & Wright, 2002). We should highlight that while *C. bonariensis* possesses traits similar to those of the native community, *O. dillenii* shows the greatest functional difference from the native species due to its CAM metabolism, which has been observed to be facultative in *Carpobrotus* spp. (Herrera, 2009). This fact makes these latter invaders very efficient when water is limiting (Ehleringer & Monson, 1993; Maiquetía, Cáceres, & Herrera, 2009). Hence, our results show that invasion can be context-dependent even in the same ecosystem (i.e., coastal dunes). This is because contrasting functional strategies allow exotic species to invade native communities, and result in different functional impacts (Funk, et al., 2017).

4.2 | Differences in taxonomic, functional and phylogenetic diversity between invaded and non-invaded communities

When invasive species have traits very different to those of the native species in the recipient community, it is likely that they will occupy at least one different functional dimension that allows them to establish themselves in the community but with limited impact (Castro-Díez et al., 2016; Godoy & Levine, 2014; Ordoñez, Wright, & Olff, 2010). Yet, functional differences can also promote the fitness differences that cause the competitive displacement of certain functional groups of native species (MacDougall et al., 2009). Given that the invasive species had little effect on the functional composition of the native communities, it is likely that the observed traits were associated more with niche differences than with fitness differences, except in the case of *A. calendula*. This invasive species was the only one that tended to reduce the taxonomic, functional and phylogenetic richness/diversity, as well as promoting functional and phylogenetic clustering in the recipient community. The fact that the functional diversity of plots invaded by *A. calendula* was lower that of control plots only when the invader was excluded from the calculation suggests that *A. calendula* might be occupying the functional space of the excluded native species. Hence, the risk of local species extinction as a result of the presence of *A. calendula* seems to be higher for functionally closer native species with greater competitive ability (Naeem, 1998; Walker, Kinzig, & Langridge, 1999). However, this does not seem to be the case for the phylogenetic distance, which declines when *A. calendula* is excluded. This result suggests that *A. calendula* can fill empty gaps or occupy the existing functional niche space of the displaced species, rather than expanding the portion of the phylogenetic and trait space occupied by native species (Loiola et al., 2018). Indeed, the loss of phylogenetic variability in the invaded plots when *A. calendula* is excluded supports the prediction that competition can eliminate species with similar trait-based ecological strategies from phylogenetically less related taxa (Mayfield & Levine, 2010). Conversely, when the invasive species has a functional profile at the edges of the functional spectrum of the resident native species (e.g., *Carpobrotus* spp. and *O. dillenii*), the invader seems to exploit an empty niche without substantially altering the functional and phylogenetic structure of the native community. Therefore, these invaders may coexist with the native flora as a result of weak competition or niche complementarity (MacDougall et al., 2009; van Kleunen, Dawson, & Maurel, 2015). However, the suggestion that invaders with contrasting functional profiles take advantage of niche differences should be taken with caution. For instance, prior research has shown that *Carpobrotus* spp. are very dominant in coastal communities and strongly decrease the functional diversity of invaded communities (Castro-Díez et al., 2016; Jucker et al., 2013). Probably, we found a result different from that of previous work because we did not include information regarding the time since invasion or the abundance of the invaders, related factors that promote fitness differences and create an extinction debt mediated by plant invasions.

In contrast with the other invasive species evaluated, *C. bonariensis* was the only one whose presence was associated with an increase in species and functional richness but did not cause a shift in the phylogenetic structure or the functional relatedness (similar PD, *P*MPD and *F*MPD). This pattern suggests that the invaded plots showed higher functional richness due to the trivial increase in the taxonomic richness, as indicated by the null models. A likely explanation for this pattern is that areas with *C. bonariensis* are usually ruderal. Disturbed habitats might facilitate the establishment of species with similar traits, because environmental filtering might play a greater role than biotic competition (Cornwell, Schwilk, & Ackerly, 2006; Grime, 2006). For instance, Mediterranean old-fields invaded by *C. bonariensis* showed an increase in other Asteraceae species (Prieur-Richard et al., 2002), which could explain the low functional over-dispersion of the "new" species without phylogenetic variations (Blomberg, Garland, & Ives, 2001).

One aspect of our study that warrants further comment is the differences in the trends of functional and phylogenetic variability, especially for those indices independent of species richness (*P*MPD and *F*MPD). Hence, although it is frequently assumed that the phylogenetic diversity is a proxy for functional diversity in invasion studies (Gerhold et al., 2011; Lapiedra et al., 2015; Lososová et al., 2015; but see, for example, Lososová et al., 2016), our results indicate that the phylogenetic structure can be complementary to, but not a substitute for, the functional trait structure (Hulme & Bernard-Verdier, 2018a).

5 | CONCLUSIONS

Our study highlights that trying to infer community assembly rules from the exploration of functional and phylogenetic differences between invaded and non-invaded plots is not straightforward. By including invaders with different functional profiles, this study has shown that different mechanisms of invasion might operate, with contrasting impacts on the structure of the recipient community. Changes in the community functional structure upon invasion can

be explained by the functional profile of the invasive plant species. Consequently, in this work, the effect of the invasive plant species differed depending on its functional distance from the recipient community. For instance, while *A. calendula* promoted changes in the native community trait composition and reduced the functional and phylogenetic diversity, *Carpobrotus* spp., *O. dillenii* and *C. bonariensis* had little effect on the functional and phylogenetic diversity of the invaded community. In light of the species dependency of our results, we advise caution when evaluating the mechanisms of community assembly, in an invasion context, based on changes in functional composition. Moreover, the lack of agreement between the functional and phylogenetic diversity indices supports previous suggestions that investigating the phylogenetic structure of communities is complementary to, but not a substitute for, determining changes in the functional composition.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Study area along the Atlantic coast in Huelva province

Appendix S2. List of the nine functional traits considered in this study

Appendix S3. The phylogenetic tree of the studied species

Appendix S4. Results of the first three axes from the PCoA

Appendix S5. Comparison of community trait means between the control and the invaded plots

Appendix S6. Comparison of community trait means with the nearest control plot

Appendix S7. Differences in taxonomic richness and in functional and phylogenetic structure between control and invaded plots

Appendix S8. Total number of native species recorded across all plots for control and invaded plots

Appendix S9. Standard Effect Size estimations based on paired *t* tests between control plots and invaded plots

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