

Biogeographical comparison of terrestrial invertebrates and trophic feeding guilds in the native and invasive ranges of *Carpobrotus edulis*

Jonatan Rodríguez^{1,2,3,4,5}, Ana Novoa^{4,5,6}, Adolfo Cordero-Rivera³,
David M. Richardson⁴, Luís González^{1,2}

1 Plant Ecophysiology Group, Department of Plant Biology and Soil Science, University of Vigo, 36310 Vigo, Spain **2** CITACA, Agri-Food Research and Transfer Cluster, Campus da Auga, University of Vigo, 32004-Ourense, Spain **3** ECOEVO Lab, E. E. Forestal, University of Vigo, 36005 Pontevedra, Spain **4** Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa **5** Department of Invasion Ecology, Institute of Botany of the Czech Academy of Sciences, CZ-252 43, Průhonice, Czech Republic **6** South African National Biodiversity Institute, Kirstenbosch Research Centre, Claremont, South Africa

Corresponding author: Jonatan Rodríguez (jonatan@uvigo.es)

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Abstract

Plant invasions impact on biodiversity by altering the composition of native communities by disrupting taxonomic and functional diversity. Non-native plants are often released from their natural enemies, which might result in a reduction of the attack of primary consumers. However, they can also be exposed to the attack of new herbivores that they might not be able to tolerate. Hence, invertebrate communities can be influenced by invasive non-native plants, which in turn modify interactions and change environmental conditions. In this study, we examined the compositional and trophic diversity of invertebrate species, comparing ecosystems with and without the plant species *Carpobrotus edulis* in coastal areas in its native (South Africa) and introduced (Iberian Peninsula) ranges. Results show that *C. edulis* has a clear impact on invertebrate communities in its non-native range, reducing their abundance in invaded areas, and particularly affecting certain trophic groups. Invasive *C. edulis* also alters the invertebrate diversity by not

only reducing abundance but also by altering species composition. Overall, the physical dominance of *C. edulis* modifies the co-occurrence of invertebrate assemblages, reducing the number of trophic groups and leading to substantial effects on primary consumers. Results suggest that the lack of natural enemies might be an important driver of the expansion of *C. edulis* in its introduced range. Further work is needed to examine long-term changes caused by non-native plants on invertebrate assemblages and the subsequent modification of biological interactions.

Keywords

Alien species, beta-diversity, biological invasions, enemy release hypothesis, insects, invasion ecology, plant-animal interactions, species richness

Introduction

Drivers of change such as globalization, habitat fragmentation, and climate change facilitate the arrival, establishment and proliferation of invasive non-native species (Rossman 2009; Litchman 2010; Early et al. 2016). Biological invasions may induce a wide variety of environmental impacts, such as biodiversity loss (Habel et al. 2019) or functional changes of the invaded ecosystems (Vitousek et al. 1997). Many native organisms, including soil biota and assemblages of plants and animals, can be directly or indirectly threatened by invasive species (McCary et al. 2016; Smith-Ramesh 2017; Wardle and Peltzer 2017). One reason why invasive species can induce such impacts is because they can occupy the functional space of natives (Loiola et al. 2018), leading to novel biotic interactions in resident communities (Prior et al. 2015; van Kleunen et al. 2018). Some authors have pointed this out for invasive plants, highlighting that they can alter invertebrate assemblages through non-trophic mechanisms (McCary et al. 2016; Smith-Ramesh 2017; Rodríguez et al. 2020) resulting in ecosystem-wide cascading effects (Sugiura et al. 2013; López-Núñez et al. 2017). Many studies have explored how plant invasions alter biotic interactions in invaded ecosystems (Traveset and Richardson 2020), but there is little research on the changes in biotic interactions mediated by invasive plants comparing native and introduced ranges (DeWalt et al. 2004; Maron et al. 2004; Callaway et al. 2011). In this regard, biogeographical studies comparing impacts of invasive plants in their native and invasive ranges can help us to elucidate whether the magnitude of impacts is enhanced in the introduced range (Hierro et al. 2005).

Non-native plants are often released from their natural enemies (i.e. Enemy Release Hypothesis; Keane and Crawley 2002) but can also accumulate many native herbivores in the introduced range (Maron and Vilà 2001; Levine et al. 2004), which may affect native invertebrate communities in different ways. While some studies have reported that plant invasions can lead to dramatic declines of native insect diversity, others have shown that diversity does not decrease because the native biota is replaced by other non-native or native invertebrate species (Hejda et al. 2017). Sakai et al. (2001) suggested that functional and taxonomic groups may interact in ways that protect the composition of some communities against invasion more than others. Hence, the im-

pacts of invasive plants on invertebrate assemblages may vary from negative to neutral or positive depending on their role in the community (Litt et al. 2014; Clusella-Trullas and Garcia 2017). Moreover, non-native plants can alter the feeding behaviour of only certain invertebrate assemblages through non-trophic mechanisms (Procheş et al. 2008; Smith-Ramesh 2017). Some authors have reported that non-native plants may induce strong negative effects on primary (McCary et al. 2016) and secondary consumers (Langellotto and Denno 2004; Scherber et al. 2010). Notwithstanding these findings, other authors have reported that predators may benefit from plant invasions (Gomes et al. 2018). For pollinators, effects vary, depending on the studied species (Davis et al. 2018). Increases in the amount of organic matter contributed by invasive plants rarely benefit detritivores (Castro-Díez and Alonso 2017). Hence, to understand the impacts of invasive plants on native invertebrate communities, it is important to consider groups of invertebrates with diverse functional, behavioural and trophic roles. Nonetheless, most studies on the impacts of plant invasions have focused only on particular assemblages of arthropod species (Spafford et al. 2013; Bezemer et al. 2014).

Plant invasions are a major concern in Europe (European Union 2014; European Commission 2017), where the South African mat-forming succulent *Carpobrotus edulis* (L.) N.E. Br. (Aizoaceae) is among the most problematic invasive plant species (Nentwig et al. 2018). This perennial clonal plant (for details see Gonçalves 1990) inhabits cliffs, rocky shorelines and dunes in South Africa, and now threatens a wide range of Mediterranean-climate coastal areas in Australia, California, Chile, France, Italy, Portugal and Spain (D'Antonio and Mahall 1991; Traveset et al. 2008; Vilà et al. 2008; Campoy et al. 2018). *Carpobrotus edulis* was intentionally introduced to Europe for gardening in the 17th century, and it was subsequently deliberately disseminated for sand and dune stabilization (Campoy et al. 2018). Its capacity for clonal propagation allows *C. edulis* to spread horizontally (Roiloa et al. 2010; Fenollosa et al. 2016), and to form dense monospecific stands that can cover the encircling surface in a few years (D'Antonio and Mahall 1991). This can lead to changes in the dynamics of the invaded areas by replacing local flora (Novoa et al. 2012; Novoa et al. 2013) and altering the invertebrate communities (Bartomeus et al. 2008; Rodríguez et al. 2019). *Carpobrotus edulis* represents a severe threat for the conservation of coastal ecosystems in the Iberian Peninsula (Campoy et al. 2018), and the factors influencing its invasion and its impacts are well documented (Novoa and González 2014; Roiloa et al. 2014; Lechuga-Lago et al. 2016; Souza-Alonso and González 2017). However, little attention has been given to its influence on the species composition and trophic groups of native invertebrate communities (Rodríguez et al. 2019). Moreover, most studies of *C. edulis* related to invertebrate communities have only targeted the herbivorous feeding guild (Rodríguez et al. 2018; Vieites-Blanco et al. 2019). Therefore, it is necessary to study the direct and indirect effects of *Carpobrotus* on the trophic and taxonomic groups of native invertebrates in invaded ecosystems (Spafford et al. 2013; Bezemer et al. 2014).

We investigated the composition and trophic feeding guilds of invertebrate species by comparing coastal areas with and without *C. edulis* in the native (South African) and introduced (Iberian Peninsula) range of the species. We hypothesized that (i) areas with

C. edulis will show higher differences in diversity compared with areas where the species is absent in its non-native range, the Iberian Peninsula. We also hypothesized that (ii) the composition of invertebrate species will be altered through reduced beta-diversity in invaded areas due to the lower replacement of species. We also expected (iii) a higher diversity of trophic groups in well-preserved areas in the native range of *C. edulis*.

Methods

Study area

The study was carried out at ten locations, five of them within the native range of *C. edulis* in the Cape Floristic Region (Western Cape, South Africa) and five in the introduced range in the north-western Iberian Peninsula (Galicia, Spain, and Região Norte, Portugal) (Suppl. material 1: Table S1). The study areas share similar characteristics such as the Mediterranean sub-humid climate with Atlantic trend (Beck et al. 2018) and coastal dune vegetation (Allsopp et al. 2014; González et al. 2017). To ensure independence in the invertebrate community, locations in both regions were separated by at least 15 km. In each study area, dominant plant species, vegetation cover and distance to the sea were recorded (Suppl. material 1: Table S1). Sampling was conducted in 2016 during spring, the flowering season for both native and introduced ranges (Campoy et al. 2018), coinciding with the time period of maximum emergence of most invertebrates in nymphal and adult forms (from March to June, in the Iberian Peninsula and from September to December, in South Africa).

Sampling design

We established two different sampling areas at each location: plant communities with and without *C. edulis*, with an area of 200 m² each (20 m × 10 m) and at least 100 m apart ($n = 5$). To compare the invertebrate occurrences between areas by visual spot-checks (i.e. hand collection by inspecting each plant), we randomly dropped a standard quadrat grid (0.5 m × 0.5 m) at 3 m intervals ten times within each plot. To identify and quantify the number of aerial invertebrates we used a total of 100 yellow sticky traps (0.2 m × 0.1 m; two faces) in late spring (June in the Iberian Peninsula and December in South Africa). Five traps were evenly spaced within each plot (between 0.2 m to 0.5 m above ground) (see Fig. 1 for details) and were maintained for a week. All invertebrates in the specific adult life form found in each quadrat and collected by the traps were sorted and assigned to a morphospecies using morphological differences (Oliver and Beattie 1996). Each individual was then identified to a taxon group (order, family, genus and species or morphospecies) using invertebrate field guides (Chinery 1997; McGavin 2002; Barrientos 2004; Picker et al. 2004; Ruiz et al. 2006) and the assistance of expert entomologists (Suppl. material 1: Table S2).

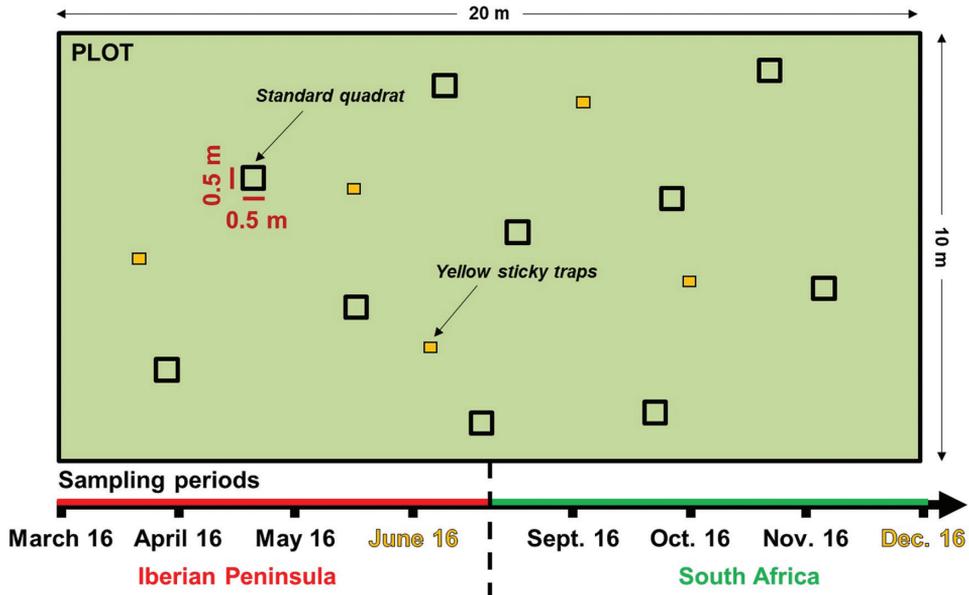


Figure 1. Schematic representation of the experimental design for assessing differences in terrestrial invertebrates and trophic feeding guilds in the native (South Africa) and invasive (Iberian Peninsula) ranges of *Carpobrotus edulis*. Within the plot, standard quadrats (black squares) and yellow sticky traps (yellow rectangles) are represented.

Based on their mouthparts and the predominant feeding behaviour of each identified family/genus/species, we assigned each individual to a trophic feeding guild, roughly corresponding to different trophic levels: detritivores, herbivores, nectar feeders, parasitoids and predators.

Data analysis

We estimated the invertebrate species richness between the coastal areas of South Africa and the Iberian Peninsula that differ in plant community (with and without *C. edulis*) by using the *specpool* function in the ‘vegan’ R package v.2.5–2 (Oksanen et al. 2018). To establish sampling representativeness, we used four non-parametric species estimators (Chao2, Jack 1, Jack 2 and bootstrap), taking into account that invertebrate assemblages usually have rare species (Hortal et al. 2006). Species accumulation curves were used to represent the cumulative species as a function of the number of plots sampled to examine the accumulative and rarefaction number of species (Gotelli and Colwell 2001), and the species diversity was then compared between areas using sample-size-based rarefaction and extrapolation (R/E) curves (Chao et al. 2016). We computed species accumulation curves using the *specaccum* function in ‘vegan’ R package. Sample-size-based (R/E) curves were applied to quantify three measures of species

diversity (Hill numbers) with standardised sample size, including unconditioned 95% CI using the 'iNEXT' R package (Hsieh et al. 2016).

To evaluate the differences in the invertebrate community, we used Generalized Linear Mixed Models (GLMMs) to test the effect of the region (South Africa and Iberian Peninsula) and plant community (with and without *C. edulis*) for differences in invertebrate species abundance, richness and diversity indices (Margalef, Shannon, Simpson and Pielou evenness). We compared invertebrate trophic and taxonomic diversity between areas using GLMMs to test the effect of the region and plant community for differences on abundance and species richness. To establish statistical comparisons between models, we used the *glmer* function in 'lme4' R package v.1.1–19 (Bates et al. 2015). Models were carried out with species nested within the plant community using Wald Chi-square Method and maximum likelihood (Laplace Approximation) using Poisson distribution and link function = log, while comparisons between areas were examined using the 'lsmeans' R package (Lenth 2016).

To examine beta-diversity differences, we used a multivariate test for homogeneity of dispersion analyses (PERMDISP) of differences in invertebrate composition among studied areas. We assessed the species turnover (replacement of one species by others among locations of the same plant community), nestedness (species richness gain or loss among locations where species lists vary across different plant communities) and total beta-diversity (Anderson 2006; Baselga 2010). PERMDISP analyses determined the average distance of observation to the geometric centre (centroid) of each predefined group, e.g. invertebrates associated with *C. edulis* from the Iberian Peninsula (Anderson 2006). Significance tests were carried out based on a Jaccard's dissimilarity matrix and 999 permutations using the *beta.pair* function in 'betapart' R package (Baselga and Orme 2012).

Lastly, the species composition was analysed using a non-metric multidimensional scaling (NMDS) ordination based on a Bray-Curtis similarity matrix of standardised and $\log(x+1)$ transformed data. Differences were tested using a permutational multivariate analysis of variance (PERMANOVA) with the *adonis* function (strata = location) in 'vegan' R package. PERMANOVA was used to test for differences among coastal areas of South Africa ($n = 5$) and the Iberian Peninsula ($n = 5$) for the effect of plant community (with and without *C. edulis*), distance to the sea, vegetation cover, and their interaction. All statistical analyses were performed using the software programme R (R Development Core Team, 2019; v.3.6.1).

Results

Alpha-diversity

A total of 13,785 invertebrate individuals were identified by visual spot-checks and yellow sticky traps; these were assigned to 90 families and 170 morphospecies (Suppl. material 1: Tables S2–S3). Species belonged to 19 distinct orders, of which six orders

(Araneae (12 species), Coleoptera (17), Diptera (61), Hemiptera (32), Hymenoptera (20) and Lepidoptera (9)) and six feeding guilds (detritivores (13), herbivores (58), nectar feeders (15), omnivores (19), parasites (20) and predators (45)) were used for the data analysis. The remaining orders were grouped into a category named “Other taxa” (13); these included Amphipoda, Coccoidea, Collembola, Isopoda, Julida, Mantodea, Neuroptera, Opiliones, Orthoptera, Psocoptera, Stylommatophora, Thysanoptera and Trombidiformes. Relative abundances of invertebrate groups differed between the studied areas (Fig. 2). In South Africa, the relative abundances in areas with *C. edulis* tend to be more balanced among groups, where we found a higher abundance of other taxa and Formicidae than in areas without *C. edulis* (Fig. 2). For the Iberian Peninsula, our results showed a reduction of Diptera and Other taxa at areas with *C. edulis* (Fig. 2). However, we found an increase for Hemiptera and Hymenoptera at areas with *C. edulis*.

Table 1. Number of collected invertebrate species (S_{obs}) and individuals as well as the estimated richness of species (calculated by Chao2, Jack 1, Jack 2 and bootstrap species estimators) from South Africa and Iberian Peninsula at locations that differ in plant community (with and without *Carpobrotus edulis*).

Area	S_{obs}	Individuals	Chao2 (\pm SD)	Jack1 (\pm SD)	Jack2	Bootstrap (\pm SD)
Overall (all combined)	171	13785	210.86 (17.47)	207.63 (7.35)	227.40	187.87 (4.06)
Overall South Africa	104	8283	123.64 (11.32)	124.58 (5.82)	134.39	113.65 (3.29)
<i>Carpobrotus edulis</i>	89	4684	105.28 (9.34)	109.16 (7.08)	117.02	98.66 (3.95)
No <i>Carpobrotus edulis</i>	91	3599	110.53 (10.73)	113.08 (6.20)	122.78	101.26 (3.29)
Overall Iberian Peninsula	94	5502	124.11 (15.87)	119.48 (6.06)	134.09	105.30 (3.23)
<i>Carpobrotus edulis</i>	75	2283	100.13 (13.70)	98.04 (6.86)	110.42	85.32 (3.66)
No <i>Carpobrotus edulis</i>	72	3219	118.46 (29.51)	93.12 (6.28)	108.95	80.87 (3.26)

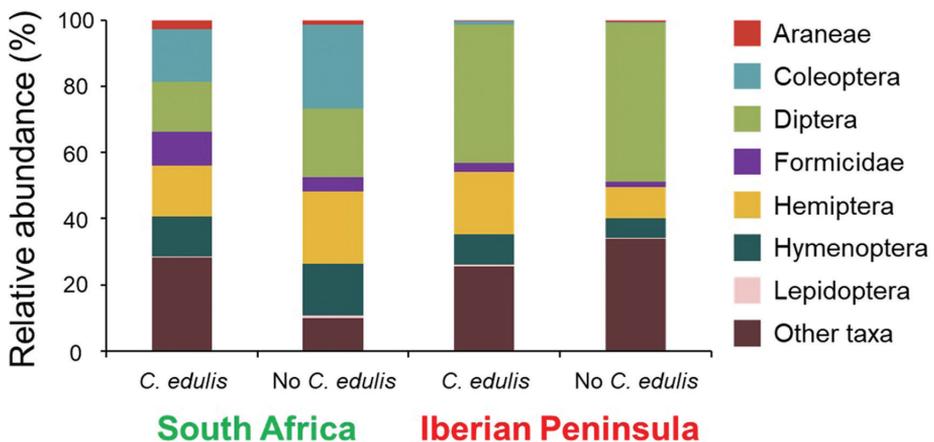


Figure 2. Relative abundances of taxa (order) within each studied area. The abundance of each taxon was calculated as the percentage of sequences per location for a given invertebrate group. The group ‘Other taxa’ encompasses grouped orders with lower abundance.

Species accumulation curves and the estimated number of species in relation to the species observed indicated that the sampling effort was adequate to capture the majority of the species (Suppl. material 1: Fig. S1; Table 1). Overall, species richness estimators showed that the coastal areas of South Africa had the highest quantity of observed and estimated species, despite no large differences having been observed for estimated species between regions (Table 1). Sample-size-based rarefaction and extrapolation (R/E) curves showed differences among the areas (Fig. 3), where we found values close to saturation for the exponential of Shannon's entropy index and the inverse of Simpson's concentration index. Nevertheless, we did not find low slopes towards the end for species richness. For South Africa, our results showed a higher species diversity in areas without *C. edulis* than in areas where the species is present (Fig. 3). The results are different for the Iberian Peninsula, where the invaded areas had generally higher species diversity estimates (Fig. 3). Comparing the two regions showed that areas with *C. edulis* overlapped when using the 95% confidence intervals for diversity estimates for species richness and Shannon diversity, while substantial differences were found in areas without *C. edulis* (Fig. 3).

GLMMs indicated that the levels of abundance and invertebrate diversity indices (species richness, Margalef, Shannon, Simpson, Pielou evenness) tended to be signifi-

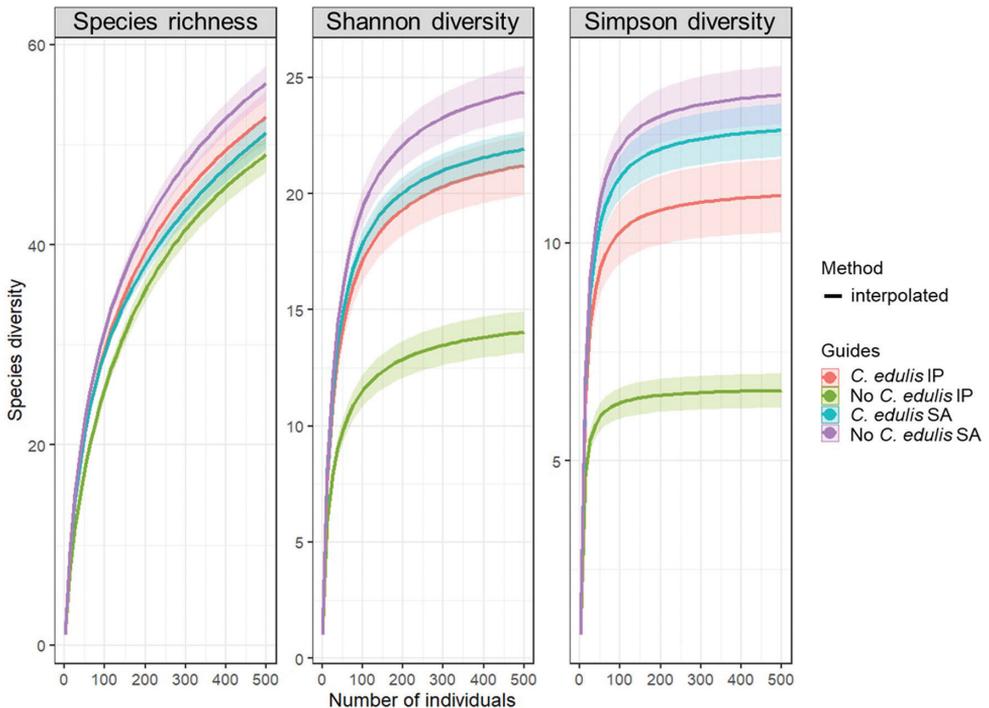


Figure 3. Sample-size-based rarefaction (solid line segment) sampling curves with 95% confidence intervals (shaded areas) for the invertebrate species richness of areas with and without *Carpobrotus edulis* for both regions, South Africa (SA) and Iberian Peninsula (IP), separated by diversity order: species richness (left panel), Shannon diversity (central panel) and Simpson diversity (right panel).

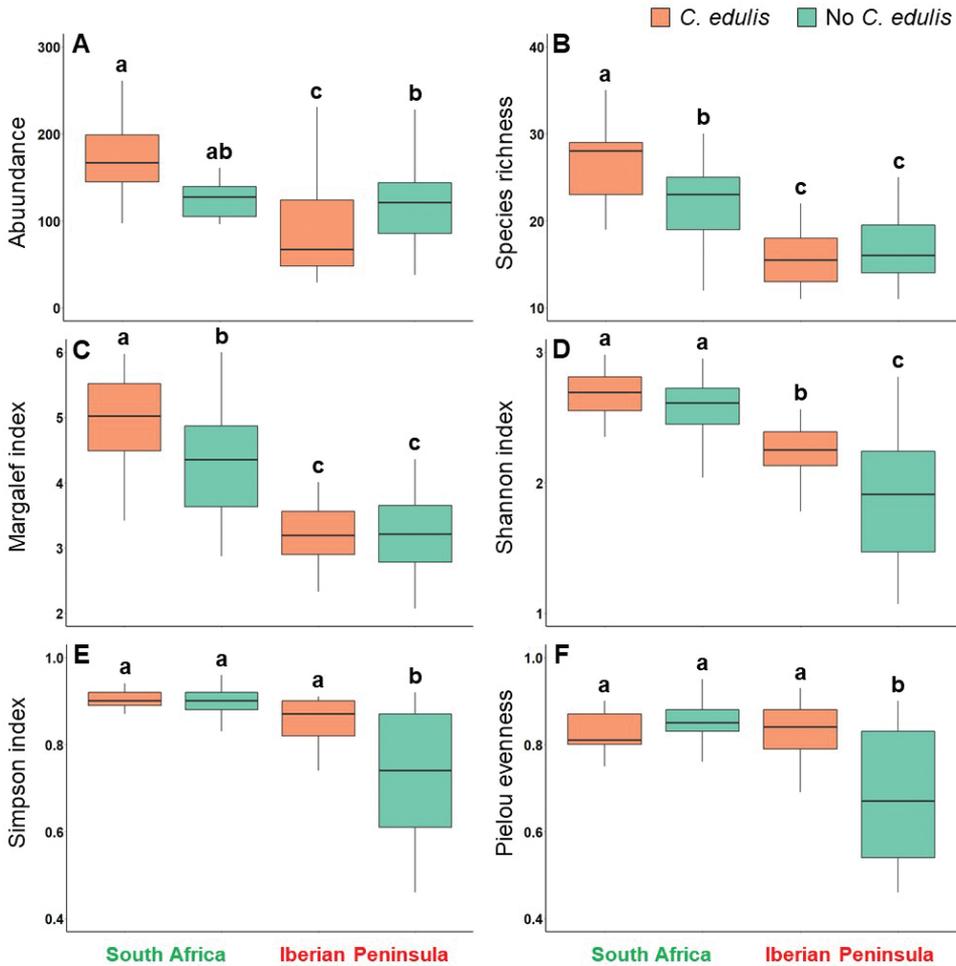


Figure 4. Effect of the plant community (with and without *Carpobrotus edulis*) for differences in **A** abundance **B** species richness **C** Margalef **D** Shannon **E** Simpson and **F** Pielou Evenness recorded among regions of South Africa and Iberian Peninsula. Model-adjusted least square means values \pm SE are shown. Different letters indicate statistical significance at $p \leq 0.05$ level using Generalized Linear Mixed Models.

cantly higher in South Africa than in the Iberian Peninsula (Fig. 4; Table 2). Our results showed significant differences for the interaction of region and plant community, in abundance and diversity indices (Table 2). On average, the areas with *C. edulis* in South Africa had higher values of abundance, species richness, and Margalef and Shannon indices (about 100%, 70%, 50% and 20% more, respectively) than the areas with *C. edulis* in the Iberian Peninsula (Figs 4A–D). However, for the Simpson and Pielou evenness indices, no significantly different values were found between South Africa and the Iberian Peninsula in the areas with *C. edulis*. The values of these indices were, however, significantly lower in areas without *C. edulis* in the Iberian Peninsula than in any of the other studied areas (Figs 4E–F).

Table 2. Results from the Generalized Linear Mixed Models (GLMM) to test the effect of the region (South Africa and Iberian Peninsula) and plant community (with and without *Carpobrotus edulis*) for differences in abundance, species richness and diversity indices (Margalef, Shannon, Simpson and Pielou evenness) between the invertebrate samples collected. Models were carried with species nested within plant community using Wald Chi-square Method and restricted maximum likelihood (REML). Abundance and species richness were fitted by maximum likelihood (Laplace Approximation) using Poisson distribution and link function = log.

Effect	df	χ^2	Pr(>Chisq)
Abundance			
Region (R)	1, 100	4.717	0.029*
Plant community (PC)	1, 100	0.903	0.342
R × PC	1, 100	377.912	0.001***
Species richness			
Region (R)	1, 100	18.851	0.001***
Plant community (PC)	1, 100	4.021	0.044*
R × PC	1, 100	7.661	0.005**
Margalef index			
Region (R)	1, 100	14.824	0.001***
Plant community (PC)	1, 100	11.956	0.001***
R × PC	1, 100	6.085	0.013*
Shannon index (H')			
Region (R)	1, 100	15.014	0.001***
Plant community (PC)	1, 100	13.294	0.001***
R × PC	1, 100	5.587	0.018*
Simpson index (D)			
Region (R)	1, 100	7.618	0.006**
Plant community (PC)	1, 100	18.651	0.001***
R × PC	1, 100	17.924	0.001***
Pielou evenness (J)			
Region (R)	1, 100	3.959	0.046*
Plant community (PC)	1, 100	13.053	0.001***
R × PC	1, 100	32.060	0.001***

df = Degrees of Freedom, *Pr(>Chisq)*- *p*-value. Asterisks indicate statistical differences *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Values in bold indicate significance at $p \leq 0.05$.

Beta-diversity

PERMDISP analyses revealed no dissimilarity for species turnover, nestedness and total beta-diversity, indicating that beta-diversities are very similar among areas with and without *C. edulis* (Fig. 2; Suppl. material 1: Table S4). In South Africa, the invertebrate species composition was only altered by the distance to the sea and its interaction with plant community (Fig. 5A; Table 3A). The NMDS ordination, which fit the data with two axes (Stress = 0.22, Fig. 5A), demonstrated that distance > 500 m is positioned above and distance 0–500 m below on the axis NMDS 2. In addition, the ordination separated the area with *C. edulis* at the left and without *C. edulis* at the right on the axis NMDS 1. Nevertheless, we did not find significant differences that support this representation. In the Iberian Peninsula, the PERMANOVA results showed that the

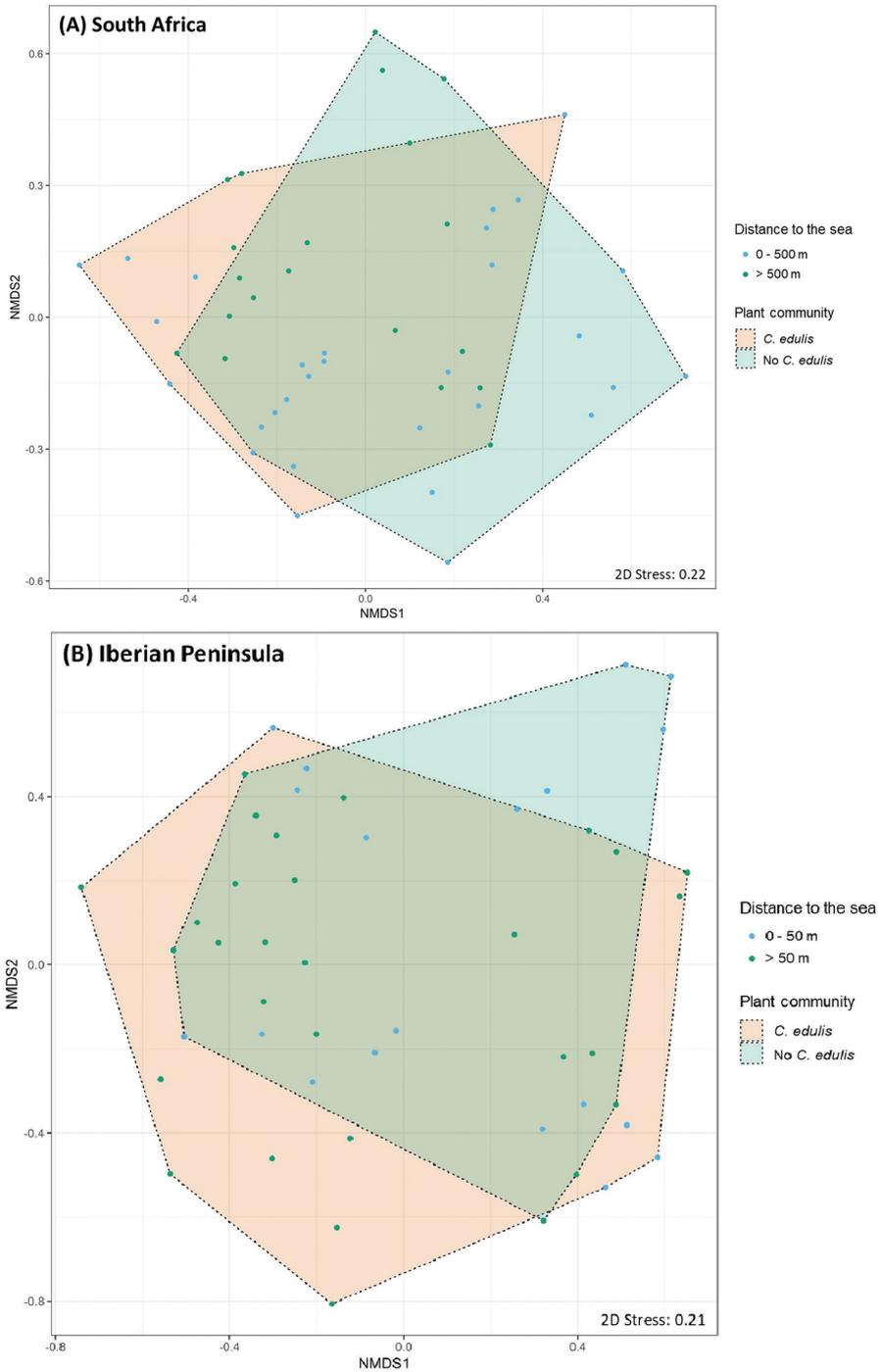


Figure 5. Non-metric multi-dimensional scaling based on a Bray–Curtis matrix of dissimilarities in **A** South Africa and in **B** Iberian Peninsula, showing distances between areas for the species composition and differences in the plant communities (with and without *Carpobrotus edulis*) and distances to the sea.

Table 3. Results from the multivariate permutational analysis (PERMANOVA) of differences for South Africa and Iberian Peninsula at locations that differ in plant community (with and without *Carpobrotus edulis*), distance to the sea and vegetation cover. The PERMANOVA with the *adonis* function (strata = location) in the ‘vegan’ package in R was based on a Bray-Curtis similarity matrix of standardised on $\log(x + 1)$ transformed data.

PERMANOVA	df	SS	MS	<i>Pseudo-F</i>	R^2	<i>Pr(>F)</i>
(A) South Africa						
Plant community (PC)	1	0.095	0.095	0.767	0.014	0.413
Distance to the sea (DS)	1	0.388	0.388	3.121	0.056	0.001***
Vegetation cover (VC)	1	0.227	0.227	1.824	0.032	0.403
PC × DS	1	0.418	0.418	3.365	0.060	0.001***
PC × VC	1	0.140	0.140	1.124	0.020	0.446
DS × VC	1	0.254	0.254	2.040	0.036	0.131
PC × DS × VC	1	0.198	0.198	1.593	0.028	0.190
Residuals	42	5.224	0.114		0.752	
Total	49	6.945			1.000	
(B) Iberian Peninsula						
Plant community (PC)	1	0.300	0.2997	1.744	0.031	0.032*
Distance to the sea (DS)	1	0.248	0.2485	1.445	0.026	0.002**
Vegetation cover (VC)	1	0.284	0.2843	1.654	0.030	0.336
PC × DS	1	0.758	0.7577	4.408	0.080	0.001***
PC × VC	1	0.109	0.1096	0.638	0.011	0.864
DS × VC	1	0.249	0.2491	1.449	0.026	0.343
PC × DS × VC	1	0.338	0.3386	1.970	0.035	0.027*
Residuals	42	7.219	0.1792		0.759	
Total	49	9.507			1.000	

df = Degrees of Freedom, SS = Sum of Squares, MS = Mean Square, *Pseudo-F*- *F*-statistic, *Pr(>F)*- *p*-value. Asterisks indicate statistical differences *, $p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$. Values in bold indicate significance at $p \leq 0.05$.

invertebrate species composition was altered by the presence of *C. edulis* (i.e. plant community), the distance to the sea and their interaction, but not by vegetation cover (Fig. 5B; Table 3A). The NMDS ordination, which fit the data with two axes (Stress = 0.21, Fig. 5B), showed that the areas with *C. edulis* are positioned along the axis NMDS1 and below on the axis NMDS2, while those without *C. edulis* are positioned mainly above on the axis NMDS2. Similar results were found for distance to the sea, where distance > 50 m is below, and distance 0–50 m is above on the axis NMDS 2.

Trophic and taxonomic groups

GLMMs revealed significant differences for almost all the groups (except detritivores), while for species richness significant differences between plant communities and regions were only found for herbivores, nectar feeders, parasites and predators (Suppl. material 1: Table S5). Abundance of almost all trophic groups was significantly higher in areas with and without *C. edulis* in South Africa, while the areas with *C. edulis* in the Iberian Peninsula had the lowest values, except for herbivores (Suppl. material 1: Table S5). Besides, the areas with *C. edulis* in South Africa had the highest values for species

richness, while areas with and without *C. edulis* in the Iberian Peninsula tend to have the lowest values, except for detritivores and omnivores (Suppl. material 1: Table S5).

Within taxonomic groupings, results revealed a significantly higher abundance of almost all groups in areas with and without *C. edulis* in South Africa (except Diptera), while the areas without *C. edulis* in the Iberian Peninsula had the lowest values, except for Araneae, Diptera and Other Taxa (Suppl. material 1: Table S5). Similar results were found for taxonomic species richness, where the areas with *C. edulis* in South Africa had highest values, except for Diptera and Lepidoptera. By contrast, the significantly lowest values were found in the Iberian Peninsula; for Araneae, Formicidae and Hemiptera in areas with *C. edulis* and for Coleoptera, Hymenoptera, Lepidoptera and Other taxa in areas without *C. edulis*. (Suppl. material 1: Table S5).

Discussion

Alpha-diversity

The Cape Floristic Region of South Africa is recognised as a global biodiversity hotspot (Myers et al. 2000). Moreover, it is known that some non-native plants can offer suitable habitat for diverse assemblages of arthropods (Prasad and Hodge 2013; Rodríguez et al. 2019). Nevertheless, non-altered areas without introduced plants tend to support more diversity than invaded areas (Bezemer et al. 2014; van Hengstum et al. 2014). We therefore initially hypothesized that areas with *C. edulis* will show higher differences in diversity compared with areas without it in its non-native range, the Iberian Peninsula. As predicted, our results demonstrate that coastal areas in South Africa had higher values for the abundance and diversity indices (species richness, Margalef, Shannon, Simpson and Pielou evenness) than the areas in the Iberian Peninsula. However, in the Iberian Peninsula, we found that the presence of *C. edulis* significantly reduced only the abundance, while it increased the values of the Shannon, Simpson and Pielou evenness indices. Some authors have noted that introduced plants may induce a negative effect on the arthropod communities (Procheş et al. 2008; Dibble et al. 2013; Van der Colff et al. 2015; Maola et al. 2016). However, this does not seem to be the case for *C. edulis* (Rodríguez et al. 2019). Although *C. edulis* clearly has negative impacts on native ecosystems in the Iberian Peninsula (Novoa et al. 2012; Novoa et al. 2013), our results show an increase in terms of invertebrate diversity indices.

Biodiversity is not always reduced following invasion of non-native plants. Invasive plants can induce the replacement of the native biota by species with similar characteristics (Hejda et al. 2017). Hence, alterations to biodiversity caused by invasive plants can affect native arthropod assemblages and their trophic role in the community in many ways – neutrally, negatively or even positively (Litt et al. 2014; Clusella-Trullas and Garcia 2017). Our results showed that species estimators and rarefaction curves in coastal areas of South Africa had the highest quantity of observed and estimated species, and were higher for areas without *C. edulis*. However, the opposite patterns were found for the Iberian Peninsula. This can be explained by the fact that few rare non-native species can live

exclusively in areas where *C. edulis* is present in the Iberian Peninsula (Rodríguez et al. 2019); this can influence the species estimations due to their low abundance. There is evidence of insect declines in heavily plant-invaded areas (Habel et al. 2019; Richard et al. 2019), and the effects of invasive plants on recipient communities can be predictable and preventable (Buckley and Catford 2016). However, our results showed no decline in local richness of native invertebrates in invaded areas. In some cases, non-native plants can favour the presence of native generalist species, but they can also promote a considerable increase of non-native insects (Wingfield et al. 2011; Crous et al. 2016; Cordero-Rivera et al. 2019). Therefore, these results might be explained by the fact that the invasion does not change alpha diversity over time (Pandolfi and Lovelock 2014), because species gains could compensate species losses (species turnover) due to an increase in beta-diversity (Dornelas et al. 2014). Therefore, the changes can seem small or be otherwise unapparent to date, but disruptive effects of invasive plants sometimes turn out to be important for rare insects (Wagner and Van Driesche 2010).

Beta-diversity

Plant invasions frequently alter the structure of native communities by disrupting their trophic interactions and changing the ecological processes of the invaded areas, which often creates new environmental scenarios (Crous et al. 2016; Rodríguez et al. 2019). It is therefore expected that the presence of *C. edulis* modifies the distribution and presence of invertebrates in its invasive range (i.e. the Iberian Peninsula), but not in its native range (i.e. in South Africa). Hence, our second hypothesis proposes that the composition of invertebrate species will be altered by reducing beta-diversity in invaded areas due to the lower replacement of species. As expected, our results showed that invertebrate species composition was affected by the presence of *C. edulis* in the Iberian Peninsula, while we did not find differences in South Africa. However, contrary to our expectations, we found no differences in beta-diversity for all studied areas. This is probably explained by the fact that *C. edulis* is chemically not so different from the neighbouring plants and is, therefore, “edible”. Another possible explanation relates to the direct effects of decreased plant diversity (Litt et al. 2014). Many plant invasions alter the habitat structure inducing severe impacts on ecosystems (McCary et al. 2016; Smith-Ramesh 2017), but consequences of the invasion process are species- and habitat-specific (Richardson et al. 2007). Studying the effect of introduced plants invading different microhabitats is key to detecting an alteration of the associated native fauna (Harvey et al. 2014). On the other hand, our results showed that the distance to the sea alters the species composition, suggesting that salt spray and/or plant diversity, or even prevalent wind (Wiktelius 1981; Nguyen and Nansen 2018), could mediate the diversity of invertebrate species in areas closer to the sea. This finding agrees with the results of Rodríguez et al. (2019) which showed that the invertebrate species composition varies with distance to the sea, with beta-diversity tending to be higher in areas further from the coastline.

Trophic and taxonomic groups

We expected a higher diversity of trophic groups in well-preserved areas in the native range of *C. edulis*. Accordingly, in the Iberian Peninsula, the abundance and species richness of trophic groups were significantly lower than in South Africa. Moreover, our results show that, in the Iberian Peninsula, the abundance and species richness of feeding guilds tended to be significantly reduced by the presence of *C. edulis*. These results agree with previous research which found that introduced plants can alter the trophic diversity in invaded areas (Procheş et al. 2008; Moroń et al. 2009; Maela et al. 2016; McCary et al. 2016; Rodríguez et al. 2020). The reduction in the abundance of herbivores, omnivores and predators in the areas invaded by *C. edulis* compared with those without *C. edulis* is striking. In agreement with our results, introduced plants can have strong negative effects on primary consumers (McCary et al. 2016). Procheş et al. (2008) also noted that herbivorous insects, but not other insects, are scarce on non-native plants. This agrees with the Enemy Release Hypothesis (ERH) (Elton 1958; Keane and Crawley 2002), which suggests that invasive non-native species are favoured by the loss of their natural enemies in the introduced range, enhancing their vigour by the reduction of pressure from natural enemies (Jeffries and Lawton 1984; Colautti et al. 2004; Ceryngier et al. 2018). Non-native plants can also favour the increase of secondary consumers as predators (Van der Colff et al. 2015; Smith-Ramesh 2017; Gomes et al. 2018). However, our results showed that the invasive plant *C. edulis* can reduce the presence of predators, as also happens with other invasive plants (Langellotto and Denno 2004; Scherber et al. 2010). Nevertheless, the reduction in natural enemies is not necessarily constant over time (Flory and Clay 2013; Crous et al. 2016; Stricker et al. 2016). Invasions are dynamic and invasive non-native species could acquire enemies over the years after their introduction (Hawkes 2007; Schultheis et al. 2015). Thus, monitoring is necessary to confirm that we are not overestimating the alteration of the native invertebrate communities (i.e. long-term sampling intervals).

At the taxonomic level, our results show differences mainly between regions, but also the invasive *C. edulis* in the Iberian Peninsula significantly influences the abundance of Diptera, Hemiptera and other taxa groups. In areas invaded by *C. edulis*, the reduction of secondary consumers as predators could imply a reduction in predation pressure on herbivorous invertebrates (members of Hemiptera and Coleoptera) (Simao et al. 2010), increasing the possibility of herbivore damage to the introduced plant. However, our results also show a reduction in the abundance of Diptera and Other taxa in invaded areas by *C. edulis* in the Iberian Peninsula.

Ecosystem processes and species functional diversity at a local scale can be influenced by the invasion of non-native plants (Simao et al. 2010). Combining the use of trophic and taxonomic diversity is advantageous for improved comprehension of the impacts of invaders on ecological processes (Gomes et al. 2018). An increase in the extent and abundance of non-native plants can result in decreased trophic diversity, even if local native diversity is maintained (Vellend et al. 2013; Dornelas et al. 2014). By contrast, other authors have noted that non-native plants tend to support higher

invertebrate taxonomic diversity than native plants, whereas native assemblages have more specialist species, resulting in higher diversity (Okimura and Mori 2018). Hence, maintaining trophic diversity is key to preserve the link between biodiversity and ecosystem functioning (Isbell et al. 2011; Veen et al. 2018). Our results show that trophic and taxonomic dissimilarity was mainly determined by the replacement of species and functions between regions and the areas with and without *C. edulis*. These findings reinforce the interpretation that the invasion of *C. edulis* in the Iberian Peninsula alters the composition of invertebrate species and trophic groups (Rodríguez et al. 2019).

Conclusion

Overall, coastal areas in South Africa are more diverse and had a greater abundance of invertebrates compared to the Iberian Peninsula. Invertebrate species composition was affected by *C. edulis* in the Iberian Peninsula, while the results did not indicate the same in South Africa (see Fig. 6). Therefore, the invasive non-native plant *C. edulis* alters invertebrate assemblages and trophic groups in invaded areas, which may modify plant-invertebrate interactions. *Carpobrotus edulis* has a strong negative effect on primary consumers, suggesting that the lack of natural enemies might be key to its expansion in its introduced range. Understanding whether non-native species cause ecological harm or benefit over species at different community levels is crucial, especially to provide insights to guide conservation and restoration programmes. To this end, further work is needed to examine long-term changes caused by invasive plants on invertebrate assemblages and the subsequent modification of ecological networks.

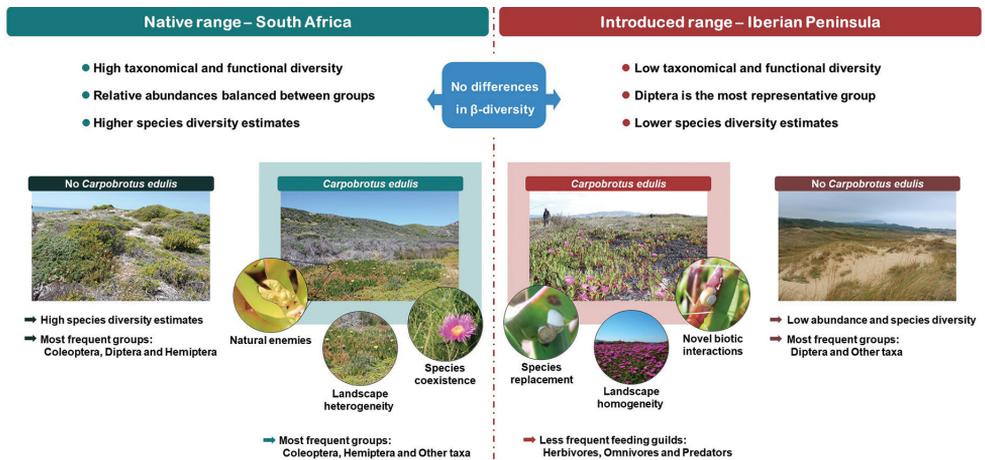


Figure 6. Theoretical diagram describing the main results obtained comparing ecosystems with and without the plant species *Carpobrotus edulis* in coastal areas in its native and introduced ranges. On the left side, the native range is represented (Western Cape, South Africa). On the right, the invasion of *C. edulis* causes changes in the invaded areas (Galicia, Spain).

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Supplementary material I

Biogeographical comparison of terrestrial invertebrates and trophic feeding guilds in the native and invasive ranges of *Carpobrotus edulis*

Authors: Jonatan Rodríguez, Ana Novoa, Adolfo Cordero-Rivera, David M. Richardson and Luís González

Data type: Studied areas, characteristics, occurrences, tables, images

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