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

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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; Rodriguez 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-
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Impacts 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 (Prochêș 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-Diez 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).
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 richness: species richness, species evenness, and species diversity.

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.
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, Pscoptera, 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 (±SD)    | Jack1 (±SD)   | Jack2    | Bootstrap (±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)   |
| *Carpobrotus edulis*  | 89          | 4684        | 105.28 (9.34)  | 109.16 (7.08) | 117.02   | 98.66 (3.95)    |
| No *Carpobrotus edulis* | 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)   |
| *Carpobrotus edulis*  | 75          | 2283        | 100.13 (13.70) | 98.04 (6.86)  | 110.42   | 85.32 (3.66)    |
| No *Carpobrotus edulis* | 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).](image-url)
Carpobrotus edulis alters invertebrate diversity significantly 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).

**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 ± SE are shown. Different letters indicate statistical significance at p ≤ 0.05 level using Generalized Linear Mixed Models.
**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

### 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    |  \( \chi^2 \) | 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 \( p \leq 0.05 \).
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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.
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

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**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   | Pseudo-F | $R^2$ | Pr(>F)   |
|------------------|----|------|------|----------|------|----------|
| **(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 $p \leq 0.05$. 
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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 (Procheș et al. 2008; Dibble et al. 2013; Van der Colff et al. 2015; Maoela 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 (Wikrelius 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 (Procheș et al. 2008; Moroń et al. 2009; Maoela 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). Procheș 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](image-url) 

**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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References

Allsopp N, Colville JF, Verboom GA (2014) Fynbos: Ecology, evolution, and conservation of a megadiverse Region. Oxford University Press, New York, United States of America. https://doi.org/10.1093/acprof:oso/9780199679584.001.0001

Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62: 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x

Barrientos JA (2004) Curso práctico de Entomología. Asociación Española de Entomología, CIBIO-Centro Iberoamericano de Biodiversidad and Universitat Autònoma de Barcelona, Barcelona.

Bartomeus I, Vilà M, Santamaría L (2008) Contrasting effects of invasive plants in plant-pollinator networks. Oecologia 155: 761–770. https://doi.org/10.1007/s00442-007-0946-1

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19: 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga A, Orme CDL (2012) Betapart: an R package for the study of beta diversity. Methods in Ecology and Evolution 3: 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x
Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical Software 67: 1–48. https://doi.org/10.18637/jss.v067.i01

Beck HE, Zimmermann NE, McVicar TR, et al. (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific Data 5: 1–12. https://doi.org/10.1038/sdata.2018.214

Bezemer TM, Harvey JA, Cronin JT (2014) Response of native insect communities to invasive plants. Annual Review of Entomology 59: 119–141. https://doi.org/10.1146/annurev-ento-011613-162104

Buckley YM, Catford J (2016) Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. Journal of Ecology 104: 4–17. https://doi.org/10.1111/1365-2745.12501

Callaway RM, Bedmar EJ, Reinhart KO, et al. (2011) Effects of soil biota from different ranges on Robinia invasion: acquiring mutualists and escaping pathogens. Ecology 92: 1027–1035. https://doi.org/10.1890/10-0089.1

Campoy JG, Acosta ATR, Affre L, et al. (2018) Monographs of invasive plants in Europe: Carpobrotus. Bot Lett 165: 440–475. https://doi.org/10.1080/23818107.2018.1487884

Castro-Díez P, Alonso Á (2017) Effects of non-native riparian plants in riparian and fluvial ecosystems: A review for the Iberian Peninsula. Limnetica 36: 525–541.

Ceryngier P, Nedvěd O, Grez AA, et al. (2018) Predators and parasitoids of the harlequin ladybird, Harmonia axyridis, in its native range and invaded areas. Biological Invasions 20: 1009–1031. https://doi.org/10.1007/s10530-017-1608-9

Chao A, Chiu CH, Jost L (2016) Statistical challenges of evaluating diversity patterns across environmental gradients in mega-diverse communities. Journal of Vegetation Science 27: 437–438. https://doi.org/10.1111/jvs.12420

Chinery M (1997) Guía de los Insectos de Europa. Ediciones Omega, Barcelona.

Clusella-Trullas S, Garcia RA (2017) Impacts of invasive plants on animal diversity in South Africa: A synthesis. Bothalia 47: 1–12. https://doi.org/10.4102/abc.v47i2.2166

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721–733. https://doi.org/10.1111/j.1461-0248.2004.00616.x

Cordero-Rivera A, Calviño-Canella M, Rodríguez J, et al. (2019) Invertebrados exóticos invasores en Galicia: situación e problemática. In: Ramil-rego P, Vales C (Eds) Especies Exóticas Invasoras: situación y propuestas de mitigación. Monografías do Ibader, Serie Biodiversidade, Lugo, 9–20.

Crous CJ, Burgess TI, Le Roux JJ, et al. (2016) Ecological disequilibrium drives insect pest and pathogen accumulation in non-native trees. Annals of Botany 9: plw081. https://doi.org/10.1093/aobpla/plw081

D’Antonio CM, Mahall BE (1991) Root profiles and competition between the invasive, exotic perennial, Carpobrotus edulis, and two native shrub species in California coastal scrub. American Journal of Botany 78: 885–894. https://doi.org/10.1002/j.1537-2197.1991.tb14492.x

Davis ES, Kelly R, Maggs CA, Stout JC (2018) Contrasting impacts of highly invasive plant species on flower-visiting insect communities. Biodiversity and Conservation 27: 2069–2085. https://doi.org/10.1007/s10531-018-1525-y
Carpobrotus edulis alters invertebrate diversity

DeWalt SJ, Denslow JS, Ickes K (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85: 471–483. https://doi.org/10.1890/02-0728

Dibble KL, Pooler PS, Meyerson LA (2013) Impacts of plant invasions can be reversed through restoration: a regional meta-analysis of faunal communities. Biological Invasions 15: 1725–1737. https://doi.org/10.1007/s10530-012-0404-9

Dornelas M, Gotelli NJ, McGill B, et al. (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science (80-) 344: 296–299. https://doi.org/10.1126/science.1248484

Early R, Bradley BA, Dukes JS, et al. (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. Nature Communications 7: 12485. https://doi.org/10.1038/ncomms12485

Elton CS (1958) The ecology of invasions by animals and plants, Methuen. Chapman and Hall, London. https://doi.org/10.1007/978-1-4899-7214-9

European Commission (2017) Commission implementing regulation (EU) 2017/1263 of 12 July 2017 updating the list of invasive alien species of Union concern established by implementing regulation (EU) 2016/1141 pursuant to regulation (EU) No 1143/2014 of the European Parliament and of the European Union 182: 37–39.

European Union (2014) Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species. Official Journal of the European Union 317: 35–55.

Fenollosa E, Roach DA, Munné-Bosch S (2016) Death and plasticity in clones influence invasion success. Trends in Plant Science 21: 551–553. https://doi.org/10.1016/j.tplants.2016.05.002

Flory SL, Clay K (2013) Pathogen accumulation and long-term dynamics of plant invasions. Journal of Ecology 101: 607–613. https://doi.org/10.1111/1365-2745.12078

Gomes M, Carvalho JC, Gomes P (2018) Invasive plants induce the taxonomic and functional replacement of dune spiders. Biological Invasions 20: 533–545. https://doi.org/10.1007/s10530-017-1555-5

Gonçalves ML (1990) *Carpobrotus* N.E. Br. In: Castroviejo S, Laínz M, López González G, et al. (Eds) Flora Iberica, II vols. M., 82–85.

González L, Rubido-Bará M, Lechuga-Lago Y, Rodríguez J (2017) Una amenaza perseverante y silenciosa: Flora exótica invasora en los ecosistemas costeros de Galicia. Quercus 376: 18–25.

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Habel JC, Samways MJ, Schmitt T (2019) Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. Biodiversity and Conservation 28: 1343–1360. https://doi.org/10.1007/s10531-019-01741-8

Harvey KJ, Britton DR, Minchinton TE (2014) Detecting impacts of non-native species on associated invertebrate assemblages depends on microhabitat. Austral Ecology 39: 511–521. https://doi.org/10.1111/ace.12111
Hawkes CV (2007) Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. The American Naturalist 170: 832–843. https://doi.org/10.1086/522842

Hejda M, Hanzelka J, Kadlec T, et al. (2017) Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species’ traits. Diversity and Distributions 23: 997–1007. https://doi.org/10.1111/ddi.12596

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range. Journal of Ecology 93: 5–15. https://doi.org/10.1111/j.0022-0477.2004.00953.x

Hortal J, Borges PAV, Gaspar C (2006) Evaluating the performance of species richness estimators: Sensitivity to sample grain size. Journal of Animal Ecology 75: 274–287. https://doi.org/10.1111/j.1365-2656.2006.01048.x

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7: 1451–1456. https://doi.org/10.1111/2041-210X.12613

Isbell F, Calcagno V, Hector A, et al. (2011) High plant diversity is needed to maintain ecosystem services. Nature 477: 199–202. https://doi.org/10.1038/nature10282

Jeffries MJ, Lawton JH (1984) Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23: 269–286. https://doi.org/10.1111/j.1095-8312.1984.tb00145.x

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17: 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. Oecologia 139: 1–10. https://doi.org/10.1007/s00442-004-1497-3

Lechuga-Lago Y, Sixto-Ruiz M, Roiloa SR, González L (2016) Clonal integration facilitates the colonization of drought environments by plant invaders. AoB Plants 8: plw023. https://doi.org/10.1093/aobpla/plw023

Lenth RV (2016) Least-Squares Means: The R Package lsmeans. Journal of Statistical Software 69: 1–33. https://doi.org/10.18637/jss.v069.i01

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7: 975–989. https://doi.org/10.1111/j.1461-0248.2004.00657.x

Litchman E (2010) Invisible invaders: non-pathogenic invasive microbes in aquatic and terrestrial ecosystems. Ecology Letters 13: 1560–1572. https://doi.org/10.1111/j.1461-0248.2010.01544.x

Litt AR, Cord EE, Fulbright TE, Schuster GL (2014) Effects of invasive plants on arthropods. Conservation Biology 28: 1532–1549. https://doi.org/10.1111/cobi.12350

Loiola PP, de Bello F, Chytrý M, et al (2018) Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. Journal of Ecology 106: 2230–2241. https://doi.org/10.1111/1365-2745.12986

López-Núñez FA, Heleno RH, Ribeiro S, et al. (2017) Four-trophic level food webs reveal the cascading impacts of an invasive plant targeted for biocontrol. Ecology 98: 782–793. https://doi.org/10.1002/ecy.1701
Carpobrotus edulis alters invertebrate diversity

Maoela MA, Roets F, Jacobs SM, Esler KJ (2016) Restoration of invaded Cape Floristic Region riparian systems leads to a recovery in foliage-active arthropod alpha- and beta-diversity. Journal of Insect Conservation 20: 85–97. https://doi.org/10.1007/s10841-015-9842-x

Maron JL, Vilà M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95: 361–373. https://doi.org/10.1034/j.1600-0706.2001.950301.x

Maron JL, Vilà M, Arnason J (2004) Loss of enemy resistance among introduced populations of St. John’s Wort (Hypericum perforatum). Ecology 85: 3243–3253. https://doi.org/10.1890/04-0297

McCary MA, Mores R, Farfan MA, Wise DH (2016) Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: A meta-analysis. Ecology Letters 19: 328–335. https://doi.org/10.1111/ele.12562

McGavin GC (2002) Smithsonian handbooks: Insects – spiders and other terrestrial arthropods. Dorling Kindersley, DK Publishing, London.

Moroń D, Lenda M, Skórka P, et al. (2009) Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. Biological Conservation 142: 1322–1332. https://doi.org/10.1016/j.biocon.2008.12.036

Myers N, Mittermeier RA, Mittermeier CG, et al. (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853: 853–858. https://doi.org/10.1038/35002501

Nentwig W, Bacher S, Kumschick S, et al. (2018) More than "100 worst" alien species in Europe. Biological Invasions 20: 1611–1621. https://doi.org/10.1007/s10530-017-1651-6

Nguyen HDD, Nansen C (2018) Edge-biased distributions of insects. A review. Agronomy for Sustainable Development 38: 11. https://doi.org/10.1007/s13593-018-0488-4

Novoa A, González L (2014) Impacts of Carpobrotus edulis (L.) N.E.Br. on the germination, establishment and survival of native plants: A clue for assessing its competitive strength. PLoS One 9: 1–12. https://doi.org/10.1371/journal.pone.0107557

Novoa A, González L, Moravcová L, Pyšek P (2012) Effects of soil characteristics, allelopathy and frugivory on establishment of the invasive plant Carpobrotus edulis and a co-occurring native, Malcolmia littorea. PLoS One 7: e53166. https://doi.org/10.1371/journal.pone.0053166

Novoa A, González L, Moravcová L, Pyšek P (2013) Constraints to native plant species establishment in coastal dune communities invaded by Carpobrotus edulis: Implications for restoration. Biological Conservation 164: 1–9. https://doi.org/10.1016/j.biocon.2013.04.008

Okimura T, Mori AS (2018) Functional and taxonomic perspectives for understanding the underlying mechanisms of native and alien plant distributions. Biodiversity and Conservation 27: 1453–1469. https://doi.org/10.1007/s10531-018-1503-4

Oksanen AJ, Blanchet FG, Friendly M, et al. (2018) Package ‘vegan.’ Community Ecol. Package. https://CRAN.R-project.org/package=vegan

Oliver I, Beattie AJ (1996) Designing a cost-effective invertebrate survey: A test of methods for rapid assessment of Biodiversity. Ecological Applications 6: 594–607. https://doi.org/10.2307/2269394

Pandolfi JM, Lovelock CE (2014) Novelty trumps loss in global Biodiversity. Science (80- ) 344: 266–267. https://doi.org/10.1126/science.1252963

Picker M, Griffiths CL, Weaving A (2004) Field guide to insects of southern Africa. Struik Publishers, Cape Town, South Africa.
Prasad AV, Hodge S (2013) The diversity of arthropods associated with the exotic creeping daisy (Sphagneticola trilobata) in Suva, Fiji Islands. Entomologist’s Monthly Magazine 149: 155–161.

Prior KM, Robinson JM, Meadley Dunphy SA, Frederickson ME (2015) Mutualism between co-introduced species facilitates invasion and alters plant community structure. Proceedings of the Royal Society B: Biological Sciences 282: 20142846. https://doi.org/10.1098/rspb.2014.2846

Procheș Ş, Wilson JRU, Richardson DM, Chown SL (2008) Herbivores, but not other insects, are scarce on alien plants. Austral Ecology 33: 691–700. https://doi.org/10.1111/j.1442-9993.2008.01836.x

R Development Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Richard M, Tallamy DW, Mitchell AB (2019) Introduced plants reduce species interactions. Biological Invasions 21: 983–992. https://doi.org/10.1007/s10530-018-1876-z

Richardson DM, Holmes PM, Esler KJ, et al. (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Diversity and Distributions 13: 126–139. https://doi.org/10.1111/j.1366-9516.2006.00314.x

Rodríguez J, Calbi M, Roiloa SR, González L (2018) Herbivory induced non-local responses of the clonal invader Carpobrotus edulis are not mediated by clonal integration. Science of the Total Environment 633: 1041–1050. https://doi.org/10.1016/j.scitotenv.2018.03.264

Rodríguez J, Cordero-Rivera A, González L (2020) Characterizing arthropod communities and trophic diversity in areas invaded by Australian acacias. Arthropod Plant Interact. https://doi.org/10.1007/s11829-020-09758-5

Rodríguez J, Thompson V, Rubido-Bará M, et al. (2019) Herbivore accumulation on invasive alien plants increases the distribution range of generalist herbivorous insects and supports proliferation of non-native insect pests. Biological Invasions 21: 1511–1527. https://doi.org/10.1007/s10530-019-01913-1

Roiloa SR, Rodríguez-Echeverría S, de la Peña E, Freitas H (2010) Physiological integration increases the survival and growth of the clonal invader Carpobrotus edulis. Biological Invasions 12: 1815–1823. https://doi.org/10.1007/s10530-009-9592-3

Roiloa SR, Rodríguez-Echeverría S, López-Otero A, et al. (2014) Adaptive plasticity to heterogeneous environments increases capacity for division of labor in the clonal invader Carpobrotus edulis (Aizoaceae). American Journal of Botany 101: 1301–1308. https://doi.org/10.3732/ajb.1400173

Rossman AY (2009) The impact of invasive fungi on agricultural ecosystems in the United States. Biological Invasions 11: 97–107. https://doi.org/10.1007/s10530-008-9322-2

Ruiz A, Cárcaba Á, Porras AI, Arrébola JR (2006) Caracoles terrestres de Andalucía. Guía y manual de identificación. Fundación Gypaetus, Consejería de Medio Ambiente de la Junta de Andalucía.

Sakai AK, Allendorf FW, Holt JS, et al. (2001) The population biology of invasive species. Annual Review of Ecology, Evolution, and Systematics 32: 305–332. https://doi.org/10.1146/annurev.ecolsys.32.081501.114037
Carpobrotus edulis alters invertebrate diversity

Scherber C, Eisenhauer N, Weisser WW, et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468: 553–556. https://doi.org/10.1038/nature09492

Schultheis EH, Berardi AE, Lau JA (2015) No release for the wicked: enemy release is dynamic and not associated with invasiveness. Ecology 96: 2446–2457. https://doi.org/10.1890/14-2158.1

Simao MCM, Flory SL, Rudgers JA (2010) Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. Oikos 119: 1553–1562. https://doi.org/10.1111/j.1600-0706.2010.18382.x

Smith-Ramesh LM (2017) Invasive plant alters community and ecosystem dynamics by promoting native predators. Ecology 98: 751–761. https://doi.org/10.1002/ecy.1688

Souza-Alonso P, González L (2017) Don’t leave me behind: viability of vegetative propagules of the clonal invasive Carpobrotus edulis and implications for plant management. Biological Invasions 19: 2171–2183. https://doi.org/10.1007/s10530-017-1429-x

Spafford R, Lortie C, Butterfield B (2013) A systematic review of arthropod community diversity in association with invasive plants. NeoBiota 16: 81–102. https://doi.org/10.3897/neobiota.16.4190

Stricker KB, Harmon PF, Goss EM, et al. (2016) Emergence and accumulation of novel pathogens suppress an invasive species. Ecology Letters 19: 469–477. https://doi.org/10.1111/ele.12583

Sugiura S, Tsuru T, Yamaura Y (2013) Effects of an invasive alien tree on the diversity and temporal dynamics of an insect assemblage on an oceanic island. Biological Invasions 15: 157–169. https://doi.org/10.1007/s10530-012-0275-0

Traveset A, Moragues E, Valladares F (2008) Spreading of the invasive Carpobrotus aff. acinaciformis in Mediterranean ecosystems: The advantage of performing in different light environments. Applied Vegetation Science 11: 45–54. https://doi.org/10.1111/j.1654-109X.2008.tb00203.x

Traveset A, Richardson DM (2020) Plant invasions: the role of biotic interactions. CABI, Wallingford, UK (in press).

Van der Colff D, Dreyer LL, Valentine A, Roets F (2015) Invasive plant species may serve as a biological corridor for the invertebrate fauna of naturally isolated hosts. Journal of Insect Conservation 19: 863–875. https://doi.org/10.1007/s10841-015-9804-3

van Hengstum T, Hooftman DAP, Oostermeijer JGB, van Tienderen PH (2014) Impact of plant invasions on local arthropod communities: A meta-analysis. Journal of Ecology 102: 4–11. https://doi.org/10.1111/1365-2745.12176

van Kleunen M, Bossdorf O, Dawson W (2018) The ecology and evolution of alien plants. Annual Review of Ecology, Evolution, and Systematics 49: 25–47. https://doi.org/10.1146/annurev-ecolsys-110617-062654

Veen GF, van der Putten WH, Bezemer TM (2018) Biodiversity-ecosystem functioning relationships in a long-term non-weeded field experiment. Ecology 99: 1836–1846. https://doi.org/10.1002/ecy.2400

Vellend M, Baeten L, Myers-Smith IH, et al. (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proceedings of the National Academy of Sciences of the United States of America 110: 19456–19459. https://doi.org/10.1073/pnas.1312779110
Vieites-Blanco C, Retuerto R, Lema M (2019) Effects of the fungus *Sclerotinia sclerotiorum* and the scale insect *Pulvinariella mesembryanthemi* on the ice plant *Carpobrotus edulis* from native and non-native areas: evaluation of the biocontrol potential. Biological Invasions 21: 2159–2176. https://doi.org/10.1007/s10530-019-01964-4

Vilà M, Siamantziouras ASD, Brundu G, et al. (2008) Widespread resistance of Mediterranean island ecosystems to the establishment of three alien species. Diversity and Distributions 14:839–851. https://doi.org/10.1111/j.1472-4642.2008.00503.x

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth’s ecosystems. Science (80-) 277: 494–499. https://doi.org/10.1126/science.277.5325.494

Wagner DL, Van Driesche RG (2010) Threats posed to rare or endangered insects by invasions of nonnative species. Annual Review of Entomology 55: 547–568. https://doi.org/10.1146/annurev-ento-112408-085516

Wardle DA, Peltzer DA (2017) Impacts of invasive biota in forest ecosystems in an aboveground-belowground context. Biological Invasions 19: 3301–3316. https://doi.org/10.1007/s10530-017-1372-x

Wiktelius S (1981) Wind dispersal of insects. Grana 20: 205–207. https://doi.org/10.1080/00173138109427667

Wingfield MJ, Roux J, Wingfield BD (2011) Insect pests and pathogens of Australian acacias grown as non-natives – an experiment in biogeography with far-reaching consequences. Diversity and Distributions 17: 968–977. https://doi.org/10.1111/j.1472-4642.2011.00786.x

**Supplementary material I**

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

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

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