

Beetle assemblage dynamics after invasive ice plant (Carpobrotus) removal on a small Mediterranean island

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Title: Beetle assemblage dynamics after invasive ice plant (*Carpobrotus*) removal on a small Mediterranean island.

Running Head: *Carpobrotus* removal effects on beetle assemblages

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Abstract

Invasive plant species, such as *Carpobrotus* species, threaten the biodiversity of Mediterranean islands. Ecological restoration can include the control of invasive plants, but the effect of *Carpobrotus* removal on arthropods is understudied. Here, we evaluated the influence of *Carpobrotus* removal on beetle assemblages, on a Mediterranean island. Between November 2011 and February 2012, we manually removed *Carpobrotus* and its litter. A site composed of native shrubland vegetation located in the vicinity was studied to estimate the beetle assemblage natural variations. Two years before removal (2010-2011), and every two years following removal (2013, 2015, 2017, 2019), we sampled beetles with pitfall traps. Vegetation did not change at the shrubland site and beetle assemblages stayed relatively stable. After the removal of *Carpobrotus* at the *Carpobrotus* site, a diverse halophilic grassland vegetation colonized as well as some chamaephytes. The taxonomic and functional richness of beetle species increased significantly following removal. Assemblage composition changed significantly between pre- and post-removal years with a high taxonomic turnover rate. Predators (e.g. Staphylinidae, Carabidae) and detritivores (Tenebrionidae) most likely benefited from the vegetation opening, while the diversification of microhabitats led to the availability of a wider variety of prey. Large floricolous beetles (Scarabaeidae) were the most reduced by *Carpobrotus* removal along with small non-flying beetles. This rapid change in beetle assemblages occurred within seven years. Future studies should be carried out in areas where reference ecosystems are available to meet the requirements of a Before-After-Control-Impact approach.

Keywords: Alien plant eradication, Coleoptera, Conservation management, Insular native biodiversity, Mediterranean type ecosystems, Restoration processes.

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Implications for practice:

- Restored native plant communities provide a wider range of plant diversity, heights, litter quality and availability, and flowering phenology than *Carpobrotus* mats.
- *Carpobrotus* removal created a diversified plant community, providing more microhabitats for beetles and induced the diversification of beetle assemblages in restored area.
- *Carpobrotus* removal opened up the habitat allowing large beetles dependent on such habitat for moving or hunting to colonize.
- Further studies will have to define an adequate reference ecosystem and be carried out on larger patches of *Carpobrotus* as they are common on Mediterranean coastlines.

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Introduction

Invasive species have considerable impacts on ecosystems worldwide (Pyšek et al. 2020). Invasive plants may impact the amount of nutrients and water in soils, plant community productivity, the abundance, diversity and survival of native species, including that of soil biota, animal activities, as well as fire patterns (Pyšek et al. 2012). Mediterranean Basin islands are frequently invaded by non-native plant species (Hulme et al. 2008; Vila et al. 2010), threatening their original plant communities which include many endangered or endemic species (Celesti-Grapow et al. 2016). Islands are also known to be more vulnerable to invasions due to vacant niches and naïve species (Whittaker et al. 2017).

Carpobrotus acinaciformis (L.) L.Bolus and *Carpobrotus edulis* (L.) N.E. Br. ("ice plant", Aizoaceae) are succulent plants native to South Africa. They were introduced in many coastal regions of the world for ornamental or soil stabilization purposes (Campoy et al. 2018). These two species and their introgressed hybrids are particularly noxious invasive plants. They have significant negative impacts on biodiversity on both a local and global scale (Vilà et al. 2006; Hulme et al. 2008; Celesti-Grapow et al. 2016). They grow in dense mats competing with native species, reducing the number of microhabitats and thus homogenizing the landscape, altering soil properties and producing allelopathic substances then decreasing native plant germination (Conser & Connor 2009; Santoro et al. 2011; Novoa et al. 2012; Novoa & González 2014; Badalamenti et al. 2016; Campoy et al. 2018; Vieites-Blanco & González-Prieto 2018).

The control of invasive plants can be a valuable management tool for invaded areas (Pyšek et al. 2020), although restoration success is not always confirmed, due to inadequate monitoring (Kettenring & Adams 2011). Before and after invasive plant control, monitoring should be carried out on various taxa representing various trophic levels to better guide their

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management (Blossey 1999). In many areas of the world, *Carpobrotus* species are the targets of management plans (Campoy et al. 2018), and while plant community dynamics have been monitored in a few cases (Andreu et al. 2010; Magnoli et al. 2013; Krebs et al. 2015; Chenot et al. 2018; Buisson, Braschi, et al. 2020; Lazzaro et al. 2020), advanced multiple taxa studies are needed.

Litt et al. (2014), in a review of arthropod communities and functional group responses to non-native invasive plants, reported that the total abundance of arthropods decreased in 62% of studies and taxonomic richness decreased in 48% of studies. The effects of *Carpobrotus* presence on arthropod assemblages (Palmer et al. 2004; Orgeas et al. 2007; Rodríguez et al. 2020) and on pollinators (Moragues & Traveset 2005; Bartomeus et al. 2008) have been studied by comparing areas with and without *Carpobrotus*. *Carpobrotus* has an extremely negative effect on both the average species richness and the abundance of Coleoptera, Formicidae and Heteroptera populations (Orgeas et al. 2007). On the other hand, *Carpobrotus* can favor populations of ubiquitous herbivore species, such as some Cicadellidae and Aphidae (Homoptera) (Rodríguez et al. 2019). However, *Carpobrotus* control effects on arthropods are poorly documented (Knapp 2014; Braschi et al. 2021).

Amid arthropods, beetles are excellent indicator organisms (McGeoch 1998; Kotze et al. 2011) and can be particularly useful to observe the effects of environmental management and restoration (Longcore 2003; Gerlach et al. 2013; Buchholz et al. 2013; Borchard et al. 2014; Bowie et al. 2019). Indeed, beetles are taxonomically well documented, abundant and live a wide range of temporal and spatial niches (Kremen et al. 1993); (ii) their ecology has also been well documented, and beetle composition changes significantly with the variation of abiotic and biotic parameters, and with management and disturbances, including on small scales (Lövei & Sunderland 1996; Rainio & Niemelä 2003) and (iii) beetles can be sampled efficiently and standardized sampling methods are available (Samways et al. 2009).

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The aim of our study was to assess how *Carpobrotus* removal influenced beetle assemblages. We studied beetle assemblages two years before (2010-2011) and seven years after *Carpobrotus* removal (2013, 2015, 2017, 2019) at a site invaded by *Carpobrotus*. In parallel, we studied a site composed of native shrubland vegetation where no management was applied. We did not choose the shrubland site as a restoration target, but as a local reference for natural variations in beetle assemblages. We hypothesize that the taxonomic and functional diversity of beetle assemblages increase after *Carpobrotus* removal, following native vegetation colonization (Buisson, Braschi, et al. 2020).

Methods

Study sites

Bagaud island (43°00'N 6°21'E), the study area, is fully described in Ruffino et al. 2015; Buisson, Braschi, et al. 2020 and Braschi et al. 2021. It is a 59-hectare strict biological reserve of the Port-Cros National Park, located in the Mediterranean Sea in Southern France.

We chose two study sites with comparable soil type, slope and elevation roughly located 400 m away from each other:

(i) The *Carpobrotus* removal site was the biggest patch of *Carpobrotus* found on the island (0.5 ha), and was surrounded by native shrubland. *Carpobrotus* was introduced on Bagaud Island around 1850 and covered ca. 2 ha of the island in various patches before removal. It was manually removed between November 2011 and February 2012 (Buisson, Braschi, et al. 2020) and left to decompose in piles on site at least 5 meters away from the monitoring transects (we chose not to export it from the island to avoid disseminating the fruits; Chenot et

al. 2018). Follow-up controls were regularly carried out to remove germinations and resprouts every year after 2013 (Buisson, Braschi, et al. 2020).

(ii) The shrubland site is a low matorral non-invaded plant community, composed of *Cistus monspeliensis* L., 1753, *Cistus salviifolius* L., 1753, *Erica arborea* L., 1753, *Pistacia lentiscus* L., 1753, *Phillyrea angustifolia* L., 1753, and *Smilax aspera* L., 1753. At this site, Buisson, Braschi, et al. 2020 have shown that vegetation dynamics is slow, and the plant community remained unchanged over the study period. Given enough time, vegetation of the *Carpobrotus* removal site may develop towards the community structure of this shrubland site, as it is surrounded by this vegetation type, but this was not expected to happen within the timeframe of this study (seven years after removal). This site is, therefore, not a restoration reference for the *Carpobrotus* removal site at the timescale of this study. For this study, it is a site where no management was applied and where only natural variations of arthropod assemblages occur. If we do not observe any variation in the arthropod community at this site, then the variations observed at the *Carpobrotus* removal site could more readily be attributed to the removal.

Sampling design

To sample beetles, we used pitfall traps, made of 10-cm deep, 5-cm diameter plastic jars, filled with ethylene-glycol and a few drops of detergent. Each sampling year, we placed the pitfall traps for four 3-week periods starting in mid-April, early May, end of May/early June and mid-September. For beta-diversity analyses and the relationship between plant and beetle species richness, pitfall trap catches in each trap over the four sampling periods were averaged. In the center of each site, we placed a 45-m transect on which ten traps were placed every 5 meters. Traps were sampled two years before the removal of *Carpobrotus* (2010, 2011), and every two years thereafter (2013, 2015, 2017, 2019). Beetles were first sorted by morphospecies (Oliver & Beattie 1996) then identified to the species level by taxonomic

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experts using TAXREF v13.0 as a taxonomic reference (Gargominy et al. 2019). We pooled some taxa when we could not reach the species level (it was a necessity to study male specimens in many cases): by family (Mordellidae), sub-family (Aleocharinae) or genus (*Anaspis*, *Arthrolips*, *Corticaria*, *Corticarina*, *Longitarsus* and *Melanophtalma*) (Table S1).

Environmental variables

We retrieved the weather data from the weather station in Porquerolles: daily rainfall and minimum and maximum daily temperatures and we calculated an average daily temperature (Table S2).

We visually estimated the total percent cover of vegetation, bare ground, litter and *Carpobrotus*, as well as the percent cover of each species in 100-m² plots (5.64 m diameter circles). We placed three plots: one at each end of each transect and one in the middle of each transect. We described each plot using cover classes (5: > 76%, 4: 51-75%, 3: 26-50%, 2: 11-25%, 1: 1-10%, i < 1%,) and sampled plots each sampling year in late April. For the statistical tests, we then used the middle of each cover class (5 = 87.5%, 4 = 62.5%, 3 = 37.5%, 2 = 17.5%, 1 = 5.5%, i = 0.5%). Plant species lists were generated according to TAXREF v13.0 (Gargominy et al. 2019) and plant species richness calculated for each plot and year. In order to describe the vegetation structure, plant species were then classified following Raunkiær plant life forms (chamaephytes, geophytes, hemicryptophytes, phanerophytes, therophytes: Raunkiaer 1934) using Tison et al. (2014). The proportion of each plant type in each plot was adjusted so that the sums were equal to 100%.

Functional traits

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We selected seven functional traits of beetles based on the literature (Koch 1989-1992): i) average body size in five classes (class 1: < 2mm, class 2: 2-5 mm, class 3: 5-10 mm, class 4: 10-20 mm, class 5: > 20 mm). ii) and iii) four preferred habitats for larvae and for adults (soil, litter, plant and flower), iv) and v) three foraging habits for larvae and for adults (detritivore, herbivore and predator), vi) whether a species is able to fly or not (binary) at the adult stage and vii) two circadian activity rhythms (diurnal, crepuscular / nocturnal) at the adult stage (Table S3).

Data analysis

All data analyses were run on the free statistical software R-3.6.2 (R Core Team 2020).

Environmental variables

We tested potential differences in vegetation variables (bare ground, litter or specific plant percent cover, plant life forms, some dominant species cover and species richness) between years independently for the two sites. We thus run ten Generalized Linear Mixed Models (GLMM; package glmmTMB: Brooks et al. 2017), one for each site and each variable. Sampling years were integrated in the model as a fixed factor while plots were integrated as a random factor, to consider repeated measures in the same plots. We then ran pairwise contrast comparisons with a Tukey adjustment (package emmeans: Lenth et al. 2020). We fitted the models with a beta error distribution except for species richness for which we chose a Poisson error distribution.

Taxonomic diversity and species abundances

We tested potential differences in beetle diversity (species richness, Simpson index 1/D, Shannon Evenness H/log(S)) between years independently for the two sites. We used

GLMMs, one for each site and each variable. Sampling years were integrated in the model as a fixed factor and traps and sampling periods nested in sampling year as random factors. These analyses were followed by pairwise contrast comparisons with a Tukey adjustment. We fitted the models with a Poisson error distribution.

We tested potential variations in beetle species abundance between years using a Generalized Linear Model (GLM) for Multivariate Abundance Data (mvabund package: Wang et al. 2020) integrating sampling year as a fixed effect. We fitted the model with a negative binomial distribution, followed by pairwise contrast comparisons.

To explore the relationship between plant species diversity and beetle diversity at the *Carpobrotus* removal site, we associated the first three traps, of which species richness was summed, to the first plot on the transect. We did the same for the last three traps associated with the last plot on the transect and the rest of the traps associated with the plot in the middle of the transect. We fitted a linear model as the residuals were normal.

Functional diversity

We calculated functional evenness (FEve) and functional species richness (FRic) using the Distance-Based Functional Diversity Indices (FD package: Laliberté et al. 2014) based on two matrices: an abundance matrix of species that occurred at least three times at each site and a functional traits matrix of the same species. We then tested for differences in FEve and FRic between years with a GLMM as described above with traps as a random effect with a beta error distribution for FEve and a Poisson error distribution for FRic.

Taxonomic beta diversity

For each year, using mean annual species abundances, we separated beta diversity in two components: turnover (replacement of some species by others between sampling events) and

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nestedness (loss or gain of species between sampling events) (package betapart: Baselga 2010).

Trait response to environmental gradient

To identify the beetle species most impacted by *Carpobrotus* removal, RLQ followed by fourth-corner analyses were run (ade4: Dray et al. 2012). The statistic measures the link between three tables: the table L ($n \times p$, Table S1) containing the abundances of p species with three minimum occurrences at n sites, a second table R ($n \times m$, Table S2) with the measurements of m environmental variables for the n sites, and a third table Q ($p \times s$, Table S3 after removing the habitat and trophism for larvae) describing s species traits of adult for the p species.

Results

Environmental variables

Over the six years of the study, the mean rainfall from September to April, thus preceding sampling, was 725 mm (Table S2) (Braschi et al. 2021). Rainfall from September to April was ca. 40% higher in 2015 (1045 mm), and ca. 40% lower in 2017 (390 mm). The mean rainfall during sampling was 91 mm in spring-summer and 42 mm in autumn. Spring-summer rainfall was high in 2010 (245 mm), close to average in 2013 and 2015, and rather low in the three other years. Autumn rainfall was high in 2019 (101 mm), close to average in 2010, 2013 and 2015, and very low in 2011 and 2017. The mean temperature in autumn and spring before sampling was slightly lower in 2011 and 2013, while the mean temperature during sampling was slightly lower in 2010 and 2013.

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Most of the vegetation variables measured at the shrubland site were not significantly different between years (Fig. S1A). Bare ground increased slightly, but significantly, from 1.3% on average from 2010 to 2017 to 13.5% in 2019 (Fig. S1B).

As shown by Braschi et al. 2021, plant species richness significantly increased after *Carpobrotus* removal from 11.7 to 22.4 species / 100 m² plot in the *Carpobrotus* removal site (Fig. S1A). Also, *Carpobrotus* and litter cover significantly declined in 2013. While *Carpobrotus* cover remained low, litter cover significantly increased (Fig. S1B)(Braschi et al. 2021). Bare ground cover peaked in 2013, just after removal (Fig. S1B). Geophyte cover increased significantly in 2013 ($\chi^2 = 25.5$, $p < 0.001$), hemicryptophyte cover was significantly higher in 2015 and 2017 ($\chi^2 = 86.1$, $p < 0.001$) and therophyte cover increased steadily after *Carpobrotus* removal ($\chi^2 = 94.2$, $p < 0.001$; Fig. 1). Chamaephyte excluding *Carpobrotus* and phanerophyte cover did not vary significantly with time. *Lotus cytisoides* L., 1753 and *Sonchus asper* subsp. *glaucescens* (Jord.) P.W.Ball, 1878 covers peaked in 2015 and/or 2017 to decrease again in 2019 while various *Anisatha* species cover increased (Fig. S1B).

Beetle diversity and variations in beetle abundances

In total, we captured 2418 beetle specimens distributed in 129 taxa (Table S1). Fewer beetles were found at the shrubland site (N = 918, 85 taxa) than at the *Carpobrotus* removal site (N = 1500, 89 taxa). At the shrubland site, the most frequent species in 2010-2011 were *Ptinus bidens* (32.4%) and *Baromiamima concinna* (29.8%). Between 2015 and 2019, the most frequent species were *Ptinus bidens* (15.2%), *Dendarus coarcticollis* (14.6%) and *Baromiamima concinna* (9.0%). At the *Carpobrotus* site, the most frequent species were *Ptinus bidens* (38.3%) and *Trachyphloeus laticollis* (14.7%) before removal (2010-2011).

After removal (2015-2019), the most frequent taxa were *Arthrolips* spp. (15.0%) and *Asida dejeanii* (11.7%).

At the shrubland site, species richness, Simpson diversity index (1/D) and Shannon Evenness (e^H) did not vary ($\chi^2 = 6.92$, $p = 0.226$, $df = 5$; $\chi^2 = 6.25$, $p = 0.282$, $df = 5$; $\chi^2 = 9.09$, $p = 0.105$, $df = 5$ respectively; Fig. 2). At the *Carpobrotus* removal site, species richness and Simpson diversity index increased significantly after *Carpobrotus* removal ($\chi^2 = 36.93$, $p < 0.001$, $df = 5$; $\chi^2 = 32.27$, $p < 0.001$, $df = 5$; respectively; Fig. 2) while Shannon Evenness remained stable ($\chi^2 = 2.55$, $p = 0.767$, $df = 5$). Detritivore and predator beetle species richness increased significantly ($\chi^2 = 17.45$, $p = 0.004$, $df = 5$; $\chi^2 = 32.77$, $p < 0.001$, $df = 5$ respectively) while herbivore beetle richness remained stable ($\chi^2 = 12.33$, $p = 0.030$, $df = 5$; Fig. 3). Beetle species richness was positively correlated to the plant species richness ($r^2 = 35\%$, $p = 0.006$; Fig. 4).

Only *Ptinus bidens* varied significantly between year (LRT = 64.52, $p = 0.001$) at the shrubland site (LRT = 683.6, $p < 0.001$, $df = 5$; Table 1), with the highest abundance in 2013 and the lowest abundance in 2015-2019. Beetle abundances significantly differed between years at the *Carpobrotus* removal site (LRT = 1068, $p = 0.001$, $df = 5$; Table 1): *Arthrolips* spp (LRT = 65.37, $p = 0.001$), *Asida dejeanii* (LRT = 60.56, $p = 0.001$), *Oligota muensteri* (LRT = 63.50, $p = 0.001$), *Harpalus attenuatus* (LRT = 33.77, $p = 0.001$), *Longitarsus* spp (LRT = 56.64, $p = 0.001$), *Corticarina* spp (LRT = 47.39, $p = 0.001$) increased after restoration. *Coccinella septempunctata* (LRT = 42.02, $p = 0.001$) was more abundant in 2013.

Assemblage functional diversity

At the shrubland site, we did not detect any difference in functional richness or evenness between years ($\chi^2 = 4.24$, $p = 0.514$, $df = 5$ and $\chi^2 = 10.34$, $p = 0.065$, $df = 5$ respectively; Fig. 5).

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At the *Carpobrotus* removal site, functional richness (FRic) was significantly lower before *Carpobrotus* removal ($\chi^2 = 36.64$ $p < 0.001$, $df = 5$) and increased steadily following removal (Fig. 6). Functional evenness (FEve) peaked in 2013 and was lowest in 2017 ($\chi^2 = 12.16$, $p < 0.032$, $df = 5$; Fig. 5).

Assemblage composition response to restoration treatment

At the shrubland site, composition variation in beetle assemblages was highest between 2017 and other years (Table 2a) and this was more due to species turnover across years (range: 21.6 to 71.4%) than nestedness (range: 0.2 to 7.7%).

Compositional variation was highest between pre- and post-*Carpobrotus* removal (range: 53.6 to 67.6%) (Table 2B) at the restoration site, and this was more due to species turnover (range: 17.7 to 67.6%) than nestedness (range: 0.6 to 16.3%).

Trait response to environmental variables

At the shrubland site, the RLQ analysis (projected inertia: axis 1 = 51.10%, axis 2 = 42.01%) did not separate the years the groups clearly (see also Supplement S1).

At the *Carpobrotus* removal site, the RLQ analysis (Fig. 6) sorted the sites into three groups: years 2010 and 2011, preceding *Carpobrotus* removal; 2013; and years 2015 to 2019, after the removal (see also Supplement S1). The first axis (46.15%) is significantly associated with plant richness and mean temperatures before sampling periods (September to April) on one hand, and by *Carpobrotus* and litter covers on the other hand. Years preceding the removal were correlated with high covers of *Carpobrotus* and litter while post-removal were correlated with a high plant richness, 2013 being intermediate. Mean temperatures before sampling periods (September to April) were also hotter during the post-removal years, 2013

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being intermediate. The second axis (31.27%) is significantly associated with total vegetation cover and bare ground cover. Year 2013 was correlated with a high bare ground cover, while the post-removal years gradually reached the high level of total vegetation cover that characterized the years preceding the removal. Functionally, the years preceding the removal were characterized by nocturnal and detritivorous beetles that dwell on the litter, such as *Dienerella parilis*, *Ptinus bidens* and *Trachyphloeus laticollis*. The intermediate year (2013) was characterized by diurnal beetles that dwell on flowers, such as *Coccinella septempunctata* and *Netocia* spp. The post-removal years were associated with ground-dwelling predators, such as *Harpalus attenuates*, *Oligota muenstri* and *Ocypus* spp.

Discussion

As shown by Braschi et al. (2021), the variability of precipitation between years was high during the study period which is characteristic of Mediterranean climates (Deitch et al. 2017). On the other hand, vegetation parameters remained relatively unchanged at the shrubland site (Buisson, Braschi, et al. 2020; Braschi et al. 2021), as it has been demonstrated with other shrubland types under normal Mediterranean climatic variation (Rodriguez-Ramirez et al. 2017). Many indices of beetle alpha-diversity (beetle richness, Simpson, Shannon, FRic, FEve) therefore did not vary either at the shrubland site during the study. As there was no invasive species removal at this site, the observed stability of vegetation and beetles is relatively normal although there was a strong rainfall variability normal. Beetle assemblages can vary with habitat conditions, vegetation structure and succession stages (Lassau et al. 2005), but stable habitats without disturbance, such as shrublands, have more stable assemblages over time.

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The taxonomic composition of assemblages however varied significantly between 2017, which had low rainfall in both the winter preceding sampling and during sampling, and the three years with the highest rainfall both the winter preceding sampling and during sampling (i.e. 2010, 2013 and 2015). Precipitation and therefore humidity (Nève 1994; Lövei & Sunderland 1996; Dajoz 2002) as well as temperature (Mazia et al. 2006; Saska et al. 2013), are major factors that influence the distribution of beetle populations, especially Carabidae and Tenebrionidae. These abiotic parameters potentially explain the inter-annual variation in for *Dendarus coarcticollis*, *Ptinus bidens* and *Baromiamima concinna*, as well as the significantly different composition in 2017.

The *Carpobrotus* removal site underwent drastic changes in environmental parameters and vegetation following *Carpobrotus* removal (Buisson, Braschi, et al. 2020; Braschi et al. 2021). *Carpobrotus* was reduced by two-third in 2013 and bare ground was more than a third higher. Native vegetation which recolonized the site was mainly composed of herbaceous species (geophytes, hemicryptophytes, therophytes), and more than twice as riche in species (Buisson, Braschi, et al. 2020). The vegetation thus became not only richer in species, but also in structure compared to the *Carpobrotus* mat, providing arthropods with a diverse range of plant heights and microhabitats (with increased bare ground and a wider range of litters). The landscape at the beetle scale therefore transformed from quasi-solid *Carpobrotus* i) first, to a halophilic grassland with some chamaephytes, such as *Jacobaea maritima* (L.) Pelser & Meijden, 2005, *Lotus cytisoides* L., 1753, *Euphorbia pithyusa* L., 1753, *Sonchus bulbosus* (L.) N.Kilian & Greuter, 2003 and *Anisantha diandra* (Roth) Tutin ex Tzvelev, 1963 and then, ii) in 2019, to a halophilic grassland with less chamaephytes and more Poaceae (Buisson, Braschi, et al. 2020).

Beetle assemblages do vary with vegetation composition (Perner et al. 2005; Schaffers et al. 2008) and structure (Morris 2000; Ponel et al. 2003), which may explain why beetle

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species richness increased, species composition changed and species turnover was high between the year preceding removal and after. On Californian coastal dunes, Knapp (2014) used an experimental restoration approach removing *Carpobrotus edulis* and showed that arthropod abundance decreased exponentially with increasing *Carpobrotus* cover for most arthropod taxa. The development of a *Carpobrotus* monospecific mat with dense roots and litter can constitute a limiting factor for the diversity of species by physically limiting beetle movement and reducing habitat diversity. *Carpobrotus* also replaces the food resources of natural habitats by resources that are not palatable or hardly exploitable by local insect fauna (leathery and fleshy tissues of *Carpobrotus*, secondary substances, etc.) (Campoy et al. 2018; Rodríguez et al. 2019). Even though *Carpobrotus* has a relatively long flowering time, a habitat composed of a single plant species reduces the time at which flowers are available for flower-dwelling species. In diverse plant communities, flowering phenology is spread-out over a longer period and therefore resources are available for a longer period of time (Wolf et al. 2017). However, plant species richness was never correlated with arthropods after *Gypsophila paniculata* (Baby's breath) removal from sand dune systems (Emery & Doran 2013), maybe due to the relatively low diversity characteristic of these habitats.

One of the species the most affected by *Carpobrotus* removal was *Asida dejeanii*, a large omnivorous darkling beetle (Tenebrionidae), that dwells on the ground or under stones and is characterized by an affinity for open and xeric areas (Soldati 2006). *Asida* sp. are drastically reduced by grazing exclusion that induces a higher plant cover (Blight et al. 2011). *Bioplanes meridionalis* and *Dichillus minutus*, two other ground darkling beetles, also increased after *Carpobrotus* removal. These three species were likely favored by the large increase in bare ground after 2013, as variation in soil habitats have long been known to affect ground-dwelling beetle species richness and composition (Perner & Malt 2003; Mazia et al. 2006). The opening up of the environment facilitates their circulation on the soil, as well as

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their capture in the pitfall traps (Woodcock 2005; Brown & Matthews 2016). *Carpobrotus* removal also triggered a boom in ant abundances during our experiment (Buisson et al. 2019), and may have secondarily favored the myrmecophilous species *Dichillus minutus* (Parker 2016).

Ground and litter predators, such as *Oligota muensteri*, *Ocypus ophthalmicus* and *Harpalus attenuatus* also depend on vegetation with patches of bare ground that allow for running on the ground and catching prey. Vegetation diversification also increases the diversity of prey: for example, mites constitute the main component of the diet of *Oligota* sp. (Shimoda et al. 2015) and both were simultaneously found in higher abundance after 2015 in our study (Buisson, Boucheraki, et al. 2020). Higher numbers of microhabitats and plant species also led to increased arthropod species richness, notably good disperser beetles, such as *Arthrolips* and *Longitarsus* genera.

Several flying species responded rapidly following *Carpobrotus* removal in 2013, such as *Netocia morio* and *Netocia oblonga*. The accumulation of fresh *Carpobrotus* litter left in piles in 2012 may have favored the emergence of their larvae from the litter. Subsequently, the removal of large *Carpobrotus* flowers constituting a potential habitat for the flower-dwelling adults (Tauzin 2009) may have caused the collapse of *Netocia* spp. The accumulation of decaying *Carpobrotus* nearby also likely benefited detritivorous beetles, such as *Hirticollis hispidus* or *Berginus tamarisci*, and favored the arrival of other detritivorous arthropods, such as diplopods (Buisson, Boucheraki, et al. 2020). Then two predators, *Coccinella septempunctata* and Aleocharinae exploded in 2013, probably related to the development of the new herbaceous flora and the proliferation of herbivore preys including Aphids (Buisson, Boucheraki, et al. 2020).

On the contrary, *Dienerella parilis* seems negatively affected by *Carpobrotus* removal. This non-flying Latridiidae (Rücker 2018) dwelling in the litter was severely impacted by the

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elimination of its habitat and was replaced after 2015 by another Latridiidae genus, *Corticarina*, which possesses similar functional traits except the capacity to fly. Another non-flying plant-dwelling beetle, *Trachyphloeus laticollis*, was also impacted by *Carpobrotus* removal and began to slowly stabilize with the vegetation recolonization following removal.

Carpobrotus litter is present throughout the year while in the restored habitat, litter is more variable between seasons and also between years due to annual plants dying and perennial plants drying out in summer. This may explain the fluctuations in litter beetle abundances, such as *Ptinus bidens*. Litter-dweller detritivore and predator taxa were similarly most negatively affected with increasing *Carpobrotus* cover in Knapp (2014).

Arthropod communities can converge to natural configurations within a few years after *Carpobrotus* is removed and replaced with native vegetation on Californian coastal dunes (Knapp 2014). Similar rapid changes in beetle assemblages after the removal of invasive species were observed: a few years after the removal of *Ligustrum chinensis* (Chinese privet, Ulyshen et al. 2010), *Lonicera maackii* (Amur honeysuckle, Masters et al. 2017), *Salix cinerea* (Gray sallow, Watts et al. 2015), five years after the removal of *Phragmites australis* (Common Reed, Gratton & Denno 2005) and six years after the removal of planted *Pinus* spp. (Eckert et al. 2019).

This project monitored beetle populations before and after the removal of a quasi-solid *Carpobrotus* mat with a thick, slowly decomposing litter. Native vegetation recolonized the site well (Buisson, Braschi, et al. 2020) and created a range of microhabitats more diverse between seasons than *Carpobrotus* inducing higher taxonomic and functional diversity in the beetle assemblages. Detailed monitoring, not only of vegetation dynamics but also of arthropod assemblages, was important for understanding how changes in the abundance of species influenced their interactions and ecosystem processes. The *Carpobrotus* removal site

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was relatively small (half a hectare) and native vegetation from which beetles could colonize on the ground or by flying was close by (Braschi et al. 2021). Such a study will have to be implemented where *Carpobrotus* patches are larger to assess beetle ability to recolonize at a larger scale. Future studies also need to be carried out elsewhere in the Mediterranean to check if these findings can be replicated. Long-term study, from before (two years) to after restoration (seven years), proved essential to assess the restoration success of this invasive plant removal.

Establishing an adequate control treatment is necessary to perform Before-After-Control-Impact analyses (i.e. BACI, BACIPS or RCT study designs; Thiault et al. 2017; Pardini et al. 2018; Chevalier et al. 2019). There was no reference ecosystem on Bagaud Island that was adequate for the duration of the study. Running such an experiment elsewhere, where such a reference ecosystem is available, would allow a BACI approach and allow for more accurate estimates of biodiversity responses to restoration (Christie et al. 2019).

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Tables

Table 1. Beetle species for which the abundance varied significantly ($p < 0.001$) between years (A) at the shrubland site and (B) at the *Carpobrotus* removal site.

(A)

Taxa	**LRT**	***p***	**significance**
Ptinus bidens	0.001	64.523	***

(B)

Taxa	**LRT**	***p***	**significance**
Arthrolips spp.	65.37	0.001	***
Oligota muensteri	63.50	0.001	***
Asida dejeanii	60.26	0.001	***
Longitarsus spp.	56.64	0.001	***
Corticarina spp.	47.39	0.001	***
Coccinella septempunctata	42.02	0.001	***
Harpalus attenuatus	33.77	0.001	***

Table 2. Taxonomic turnover (replacement of some species by others between two years –in dark grey) and taxonomic nestedness (loss or gain of species between two years –in light grey) - resultant components of taxonomic diversity on abundance data (A) on the shrubland site and (B) on the *Carpobrotus* removal site.

(A)	2010	2011	2013	2015	2017	2019
2010		5.26%	0.72%	0.24%	1.50%	5.14%
2011	21.57%		4.89%	4.95%	0.51%	7.75%
2013	48.57%	39.71%		0.66%	2.06%	2.21%
2015	44.62%	30.77%	31.86%		2.11%	3.24%
2017	71.43%	64.71%	69.05%	63.00%		6.60%
2019	22.86%	41.83%	57.99%	47.93%	44.44%	

(B)	2010	2011	2013	2015	2017	2019
2010		4.11%	14.46%	6.43%	9.75%	4.11%
2011	17.76%		15.92%	7.49%	11.90%	6.79%
2013	53.57%	55.26%		4.53%	0.57%	9.80%
2015	67.86%	69.74%	61.90%		6.49%	7.84%
2017	66.23%	64.35%	77.06%	31.06%		16.32%
2019	56.63%	52.82%	56.12%	27.00%	18.18%	

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Figures

Figure 1. Mean percent cover ± SE of plant types varying significantly between years (2010 to 2019) at the *Carpobrotus* removal site. The mean is calculated on three plots / year, located at each end of the pitfall transect and in the middle. Raunkiær plant life forms (geophytes, hemicryptophytes, therophytes: Raunkiær 1934) using Tison et al. (2014). The proportion of each plant type in each plot was adjusted so that the sums were equal to 100%.

Figure 2. Annual beetle species richness (S) and species diversity (Simpson diversity index 1-D and Shannon evenness H/log(S) (mean values + SE) / trap for the shrubland site (black circles) and the *Carpobrotus* removal site (green triangles). The red dotted line represents the *Carpobrotus* removal period (winter 2011-12). Bars not sharing letters were significantly different between years ($p < 0.05$).

Figure 3. Annual beetle species richness (S) for the detritivores (black circles), herbivores (green triangles) and predators (red crosses) at the *Carpobrotus* removal site. The red dotted line represents the *Carpobrotus* removal period (winter 2011-12). Bars not sharing letters were significantly different between years ($p < 0.05$).

Figure 4. Regression ($r^2 = 35\%$, $y = 0.76x + 0.07$, $p = 0.006$) between beetle and plant species richness during the study (2010-2019) at the *Carpobrotus* removal site. Pitfall trap catches in each trap were averaged over the four sampling periods; the first three traps, of which species richness was summed, were associated to the first plot on the transect, the last three traps were associated with the last plot on the transect and the rest of the traps were associated with the plot in the middle of the transect.

Figure 5. Annual beetle species functional richness (FRic ± SE) and functional evenness (FEve ± SE) for the shrubland site (black circles) and the *Carpobrotus* removal site (green triangles). The red dotted line represents the *Carpobrotus* removal period (winter 2011-12). Bars not sharing letters were significantly different between years ($p < 0.05$).

Figure 6. RLQ analysis (package: ade4, Dray et al. 2012) at the *Carpobrotus* removal site. The statistic measures the link between three tables: L (species abundance with more than three occurrences across samples, Table S1), R (environmental variables of samples, Table S2) and Q (species traits on adult, Table S3). Because presenting all variables on the same plot would be illegible, we draw two stacking plots defined by the two first axes of the RLQ analysis (projected inertia: axis 1 = 46.15%, axis 2 = 31.27%): A) beetle species associated to years and B) environmental variables and species traits. Significant associations (framed) identified by the fourth corner analysis are represented in blue for the variables associated with the first axis and in orange for the variables associated with the second axis (variables with no significant association are in black).

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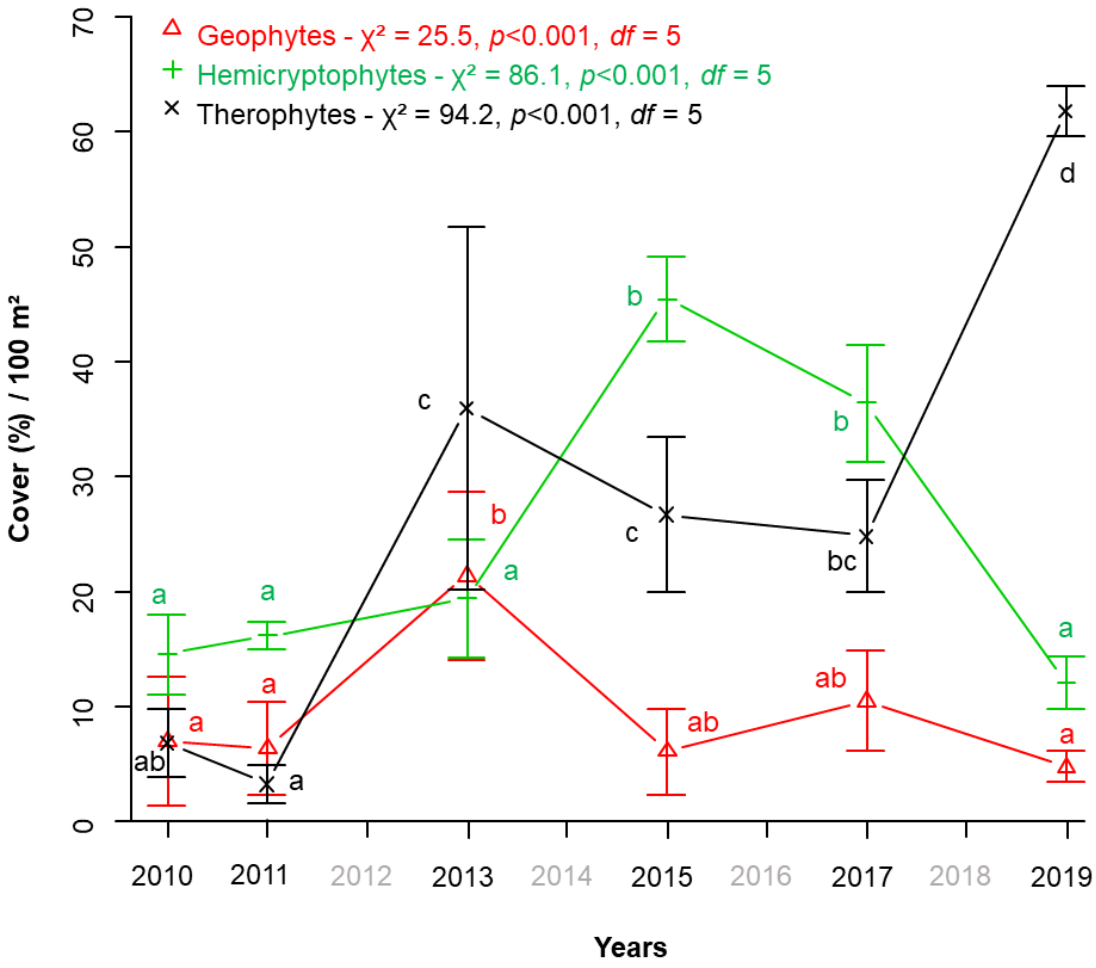
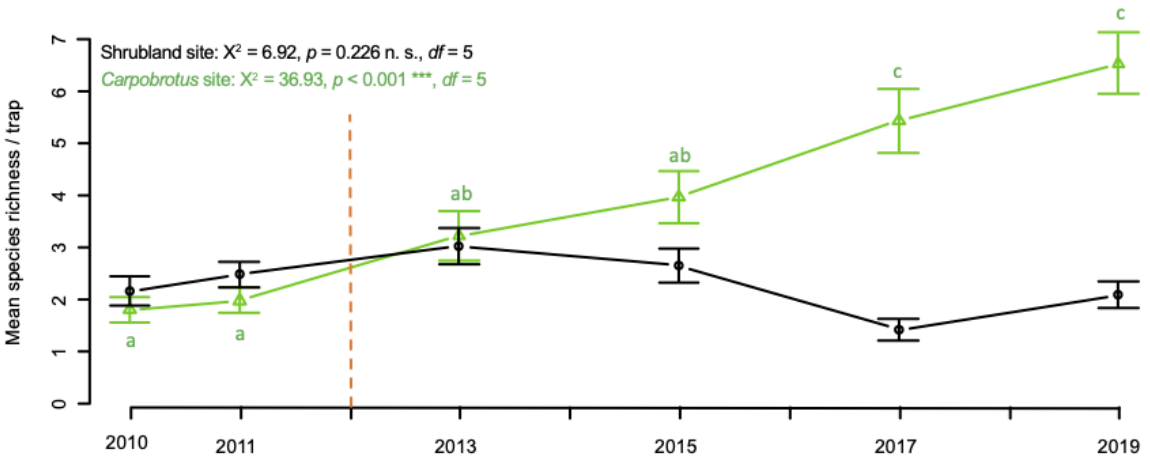
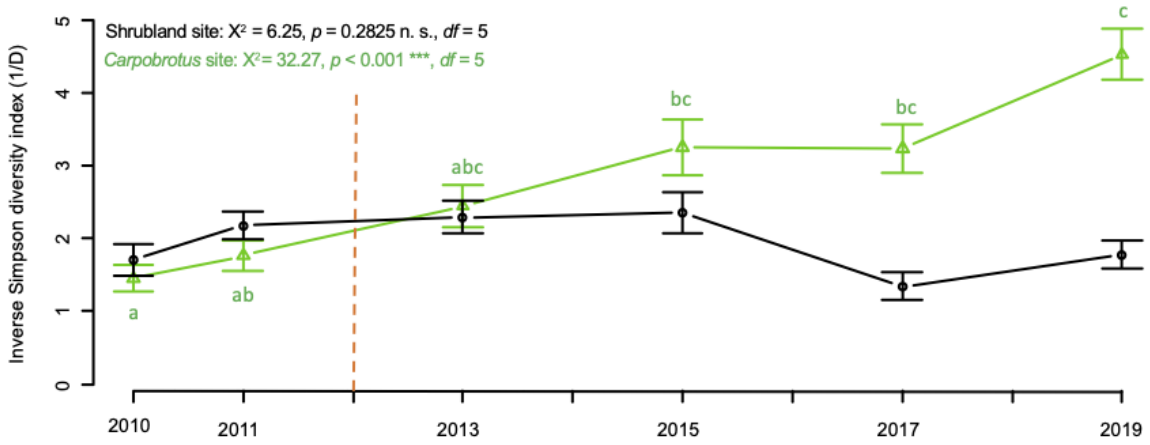


Figure 1. Mean percent cover ± SE of plant types varying significantly between years (2010 to 2019) at the *Carpobrotus* removal site. The mean was calculated on three plots / year, located at each end and the middle of the pitfall transect. Raunkiær plant life forms includegeophytes, hemicryptophytes, therophytes (Raunkiær 1934) using Tison et al. (2014). The proportion of each plant type in each plot was adjusted so that the sums were equal to 100%.

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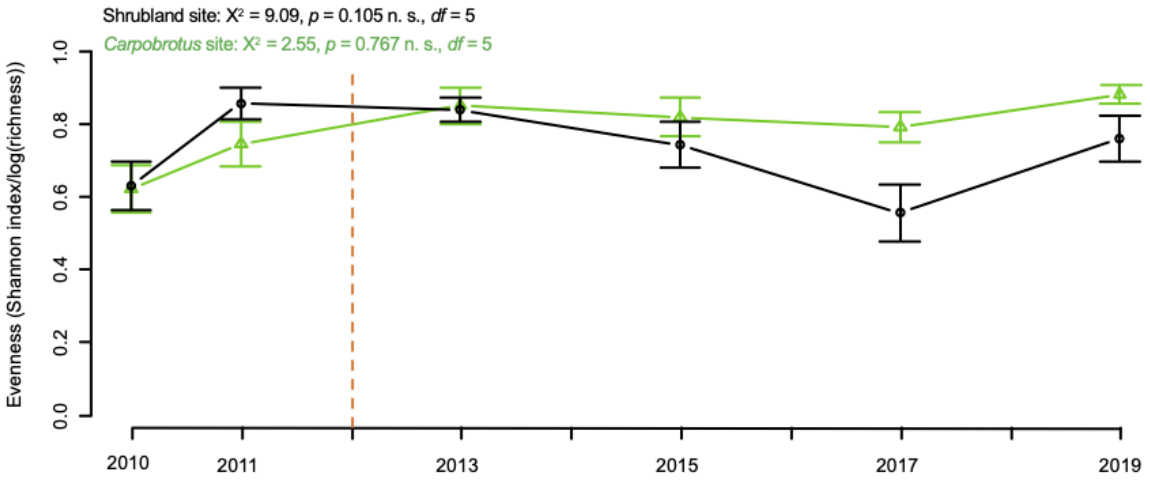


Figure 2. Annual beetle species richness (S) and species diversity (Simpson diversity index 1-D and Shannon evenness H/log(S) (mean values + SE) / trap for the shrubland site (black circles) and the *Carpobrotus* removal site (green triangles). The red dotted line represents the *Carpobrotus* removal period (winter 2011-12). Bars not sharing letters were significantly different between years ($p < 0.05$).

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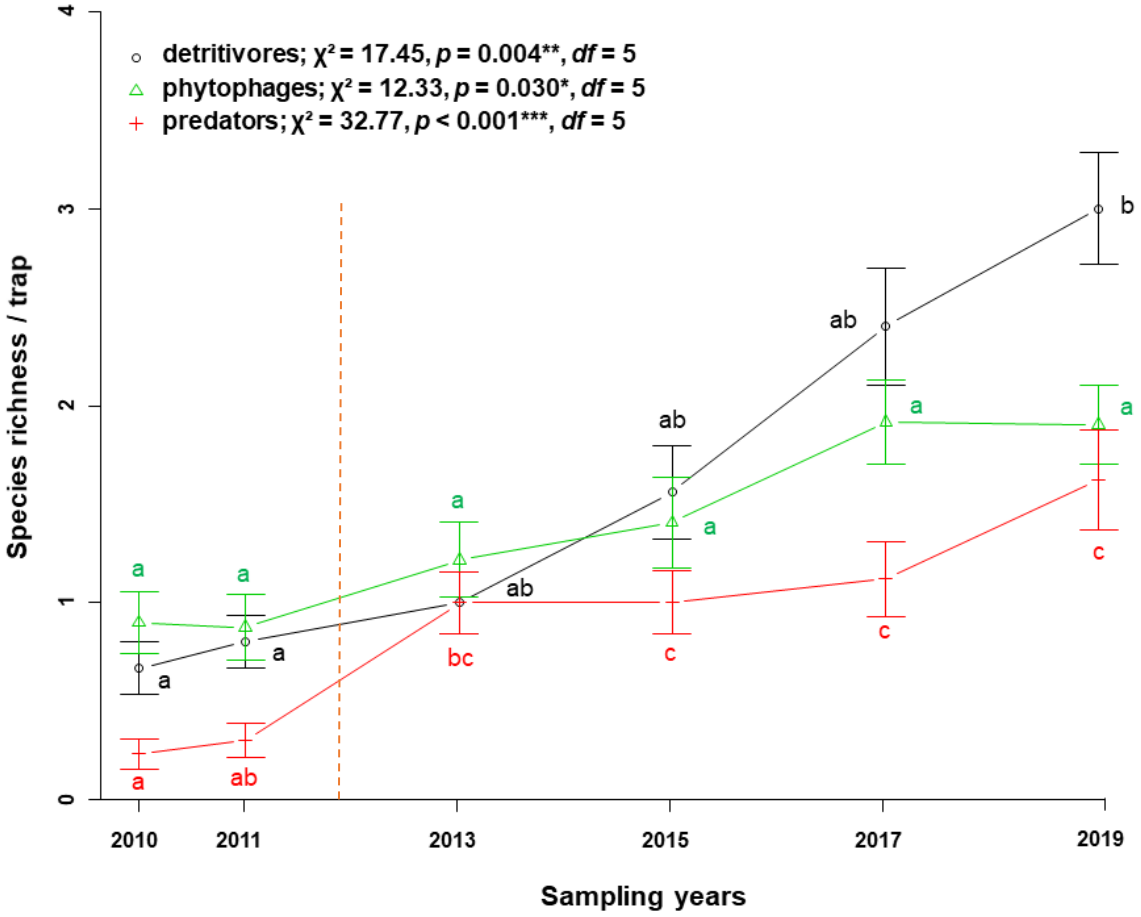


Figure 3. Annual beetle species richness (S) for the detritivores (black circles), herbivores (green triangles) and predators (red crosses) at the *Carpobrotus* removal site. The red dotted line represents the *Carpobrotus* removal period (winter 2011-12). Bars not sharing letters were significantly different between years ($p < 0.05$).

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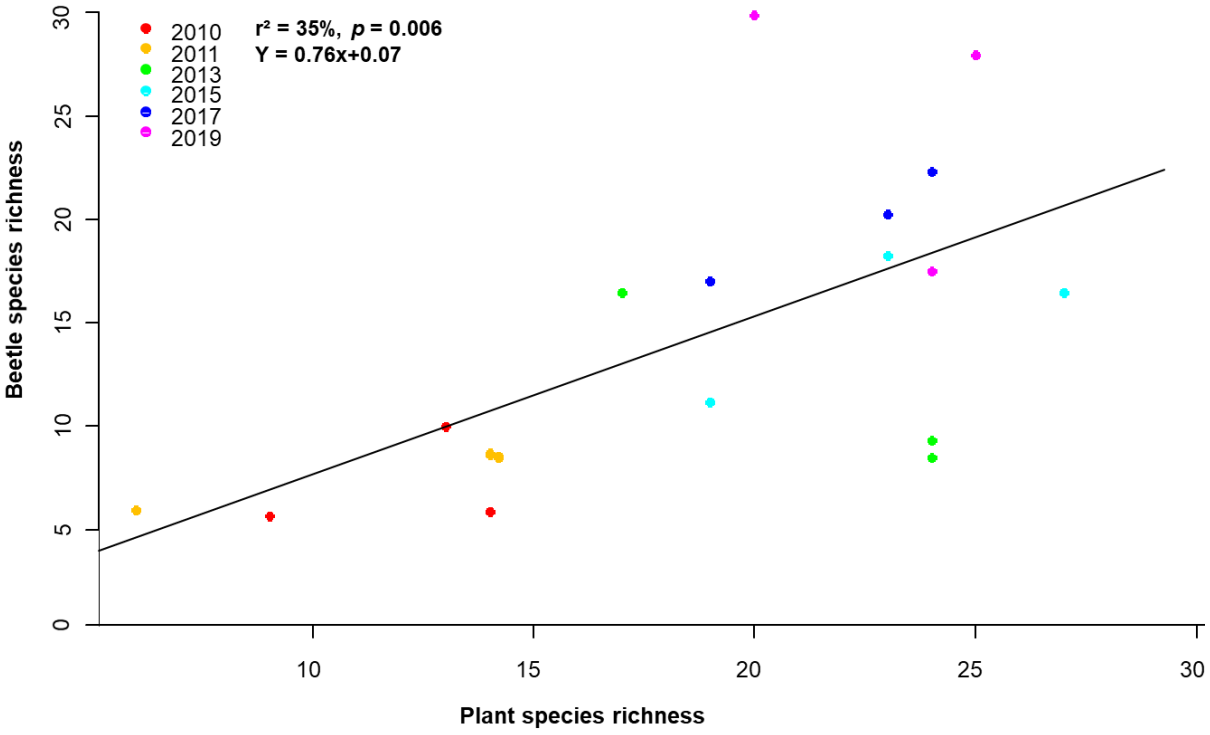


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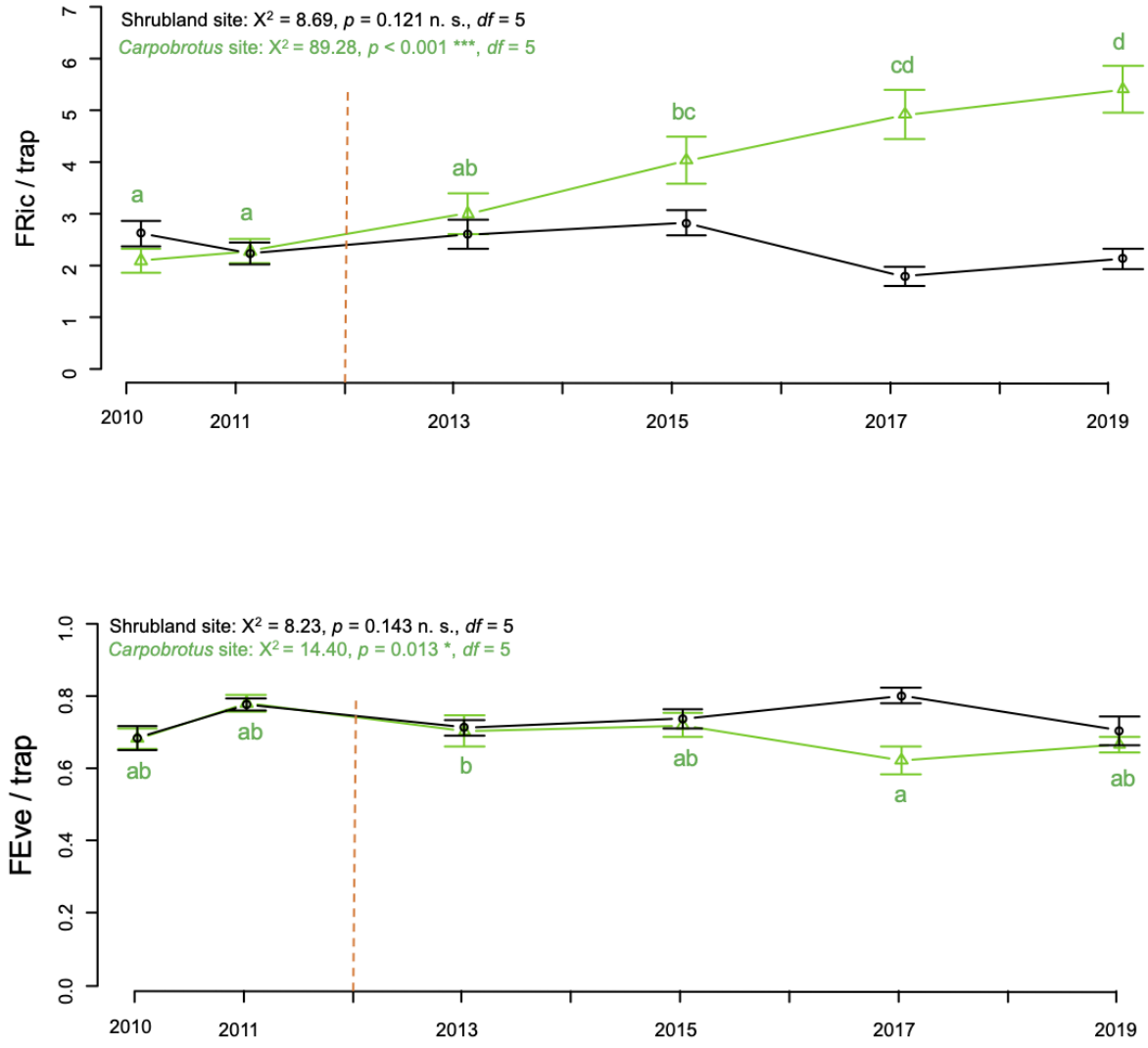
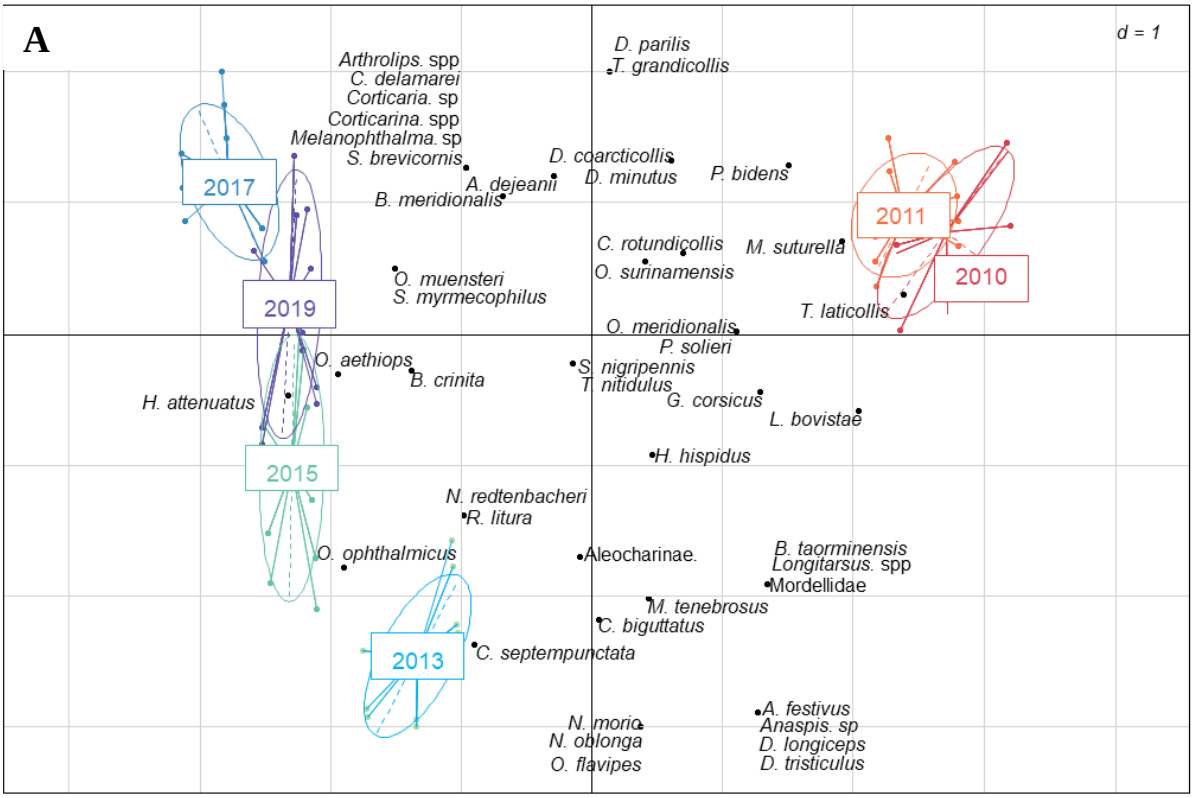


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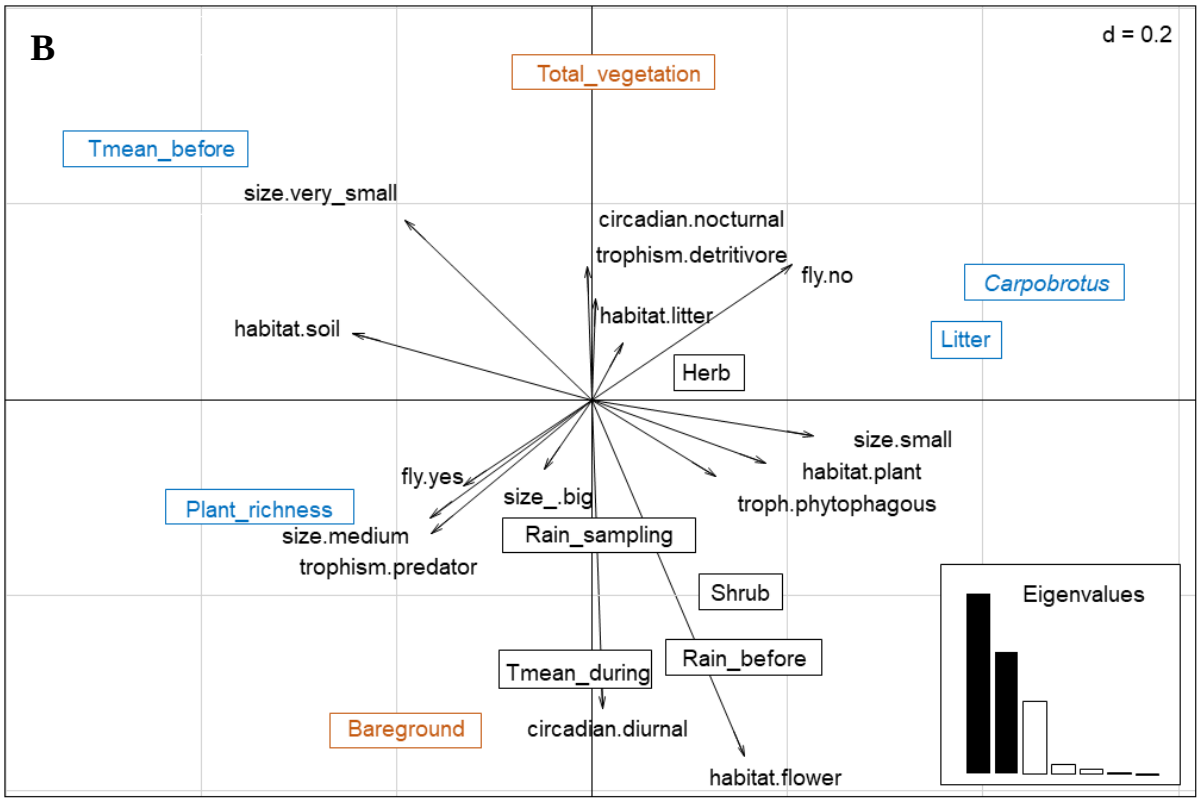


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