Native plant community recovery after *Carpobrotus* (iceplant) removal on an island – results of a 10-year project

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Abstract

Question

Species of the genus *Carpobrotus*, or iceplant, are succulent mat-forming perennial herbs often introduced for soil stabilization. They are common in coastal environments and may thus threaten island biodiversity. While their effects are well known on soils, plant communities and associated fauna, the effects of *Carpobrotus* control on vegetation recovery is poorly documented. The aim of the paper is to describe plant community trajectories after *Carpobrotus* removal.

Location

Bagaud: a 58-ha Mediterranean island, southern France.

Methods

Carpobrotus and its litter were removed in 2011-2012. Follow-up controls of germinations and resprouts were carried out from then on. Plant communities were surveyed every year two years before and seven years after *Carpobrotus* removal: on two ca. 0.5-ha sites (one coastal and one inland) and in three native plant communities used as potential references. Differences in resprouts, vegetation parameters, Bray–Curtis similarity indices between years were tested. Plant community dynamics was studied through a NMDS and two recovery indices.

Results

The removal of *Carpobrotus* and its litter led to the recovery of diverse native plant communities. To prevent *Carpobrotus* return and ensure success, follow-up controls were necessary for a period of at least seven years, but the amount of work decreased with time. The plant community recovering on the coastal site quickly reached a composition and structure similar to that of non-invaded coastal vegetation, although some slow-growing native species remain under-represented (e.g. *Crithmum maritimum* and *Limonium pseudominutum*). The plant community recovering on the inland site was still very different from the surrounding matorral vegetation because of its slow colonization dynamics, particularly in the presence of competitive herbaceous species.

Conclusion

Both sites now provide diverse native plant communities with a more diversified composition and structure (plant heights, litter, bare ground patches) than the plant communities which used to be associated with *Carpobrotus* mats.

Introduction

Invasive plant species constitute a major threat to biodiversity (Hejda *et al.,* 2009), particularly on islands which are i) characterized by a high proportion of endemic species, but a sometimes low species richness, ii) disharmonic systems (e.g. vacant niches) with poor competitors (Patiño *et al.,* 2017). The Mediterranean Basin covers 2% of the world land area and hosts 10% of the world plant species richness; islands in the Mediterranean Basin host many rare plants, with endemism often exceeding 10% (Médail and Quézel, 1997; Brundu, 2013). On the other hand, Mediterranean islands also have high percentages of exotic or invasive plant species. For example, i) Lloret *et al.* (2004) recorded over 400 exotic species on eight of the major islands of the Mediterranean Basin (Lesbos, Rhodes, Crete, Malta, Corsica, Sardinia, Majorca and Minorca), ii) Pretto *et al.* (2012) mentioned 154 exotic species on 37 small Mediterranean islands in Italy and iii) 109 exotic species were found on Porquerolles, an island part of the Hyères archipelago (France; Données Flore: CBNMed & CBNA (Admin.) 2020). Larger islands often support more exotic species because they have a greater habitat diversity, but small islands (< 1000 ha) are more vulnerable because of the disproportionate effects of invasive species on the local carrying capacity of the ecosystems (Médail, 2017).

Among the particularly noxious invasive plant species are species of the genus *Carpobrotus* (Aizoaceae), or iceplant (Giulio *et al.,* 2020). *Carpobrotus* species are succulent perennial herbs native to South Africa, Australia or Chile, introduced outside of their native range for ornamental or soil stabilization purposes (Campoy *et al.,* 2018). They form thick mats, grow in a wide variety of soils, habitats and climates. They are particularly successful in persisting and invading new areas because they combine a fast year-round clonal growth (up to 53 cm/yr) and an efficient sexual reproduction (up to 1800 seeds / fruits) (Campoy *et al.,* 2018). These two characteristics make *Carpobrotus* species hard to eradicate when they are well established because they can resprout from left-over fragments and they can germinate from their dense long-term seed bank. *Carpobrotus* species affect soil parameters: they increase litter, may change C and N fluxes as well as pH, Al, Fe, Ca, Na, Mg, Cu, Zn and P concentrations (Affre, 2011; Santoro *et al.,* 2011; Novoa *et al.,* 2013; Vieites-Blanco and González-Prieto, 2018a; Vieites-Blanco and González-Prieto, 2018b). They i) directly compete with native plants for space, water and light, reducing their establishment, growth and survival (Campoy *et al.,* 2018), ultimately decreasing native plant species richness and diversity up to the 'extirpation' of plant functional groups and life-forms (Vilà *et al.,* 2006; Affre, 2011; Fried *et al.,* 2014), ii) negatively impact arthropods and reptiles

(Orgeas *et al.,* 2007; Galán, 2008), and iii) change native pollinator networks (Moragues and Traveset, 2005; Affre, 2011).

Invasive species containment, control, removal or eradication are common management tools to restore island biodiversity (Genovesi, 2011; Simberloff *et al.,* 2013; Ruffino *et al.,* 2015). In a review on invasive plant control experiments, Kettenring and Adams (2011) found that most removal experiments were carried out in small plots, and that monitoring was carried out over brief periods (one growing season or less) and did not document native plant community recovery. Their review, based on 355 studies, did not mention *Carpobrotus* control. Many *Carpobrotus* removal projects have been implemented, and many of them by local stakeholders, but monitoring is either not carried out or not published (Campoy *et al.,* 2018). With the same search string as Kettenring and Adams (2011), we found three papers on *Carpobrotus* species removal published after 2009 (Andreu *et al.,* 2010; Magnoli *et al.,* 2013; Lazzaro *et al.,* 2020). These experiments removed respectively 300 ha, 380 m² maximum, and 8000 m² of *Carpobrotus*. The plant communities were monitored respectively for 1 year, 2 growing seasons and four years (one before and three after the removal). So these studies have larger removal areas and longer monitoring time scales than those recorded by Kettenring and Adams (2011).

The present study monitored plant communities within the framework of a *Carpobrotus* removal project which ran for nine years: two years before *Carpobrotus* removal and seven years after, on two ca. 0.5-ha (5000 m²) sites (Ruffino *et al.,* 2015). The removal project was conducted in a limited-access nature reserve located on Bagaud Island. The site location is therefore particularly advantageous for eradication success as recovery is more likely when anthropogenic disturbances are low (Prior *et al.,* 2018). The aim of the paper is to describe plant community trajectories after manual *Carpobrotus* uprooting. Here, we demonstrate slow but steady recovery of native vegetation up to seven years after *Carpobrotus* removal.

Material and methods

Study site

The island of Bagaud is a 58-ha limited-access nature reserve located in Port-Cros National Park, Hyères archipelago, in the Mediterranean, Southern France (43°00′42″N; 6°21′45″E). It is located 7.5 km from the mainland coast and has a maximum elevation of 57 m. The climate is Mediterranean, characterized by mild wet winters, and hot, dry summers, but being an island, with year-round high air humidity. The annual average temperature is ca. 15°C with daily maximum

summer temperature over 30°C. The average temperature of the coldest month is above 9°C (Krebs *et al.,* 2015). The Hyères archipelago is the home of several plant species which are narrow endemic species, endemic species from the Tyrrhenian area or from the west-Mediterranean area with highly fragmented distributions. These species are either i) found on peninsulas and islands (*Fumaria bicolor* Nicotra, *Crepis leontodontoides* All., *Romulea florentii* Moret) (Cruon (coord.) *et al.,* 2008) or ii) absent from the nearby mainland and only found on islands (*Teucrium marum* L., *Galium minutulum* Jord., *Delphinium requeni* DC.). Bagaud native vegetation is mainly composed of i) halo-resistant coastal plant communities hereafter named coastal vegetation (Crithmo-Lotetum cytosoidis Mol. Re. 1937), ii) low matorral vegetation with *Pistacia lentiscus, Myrtus communis, Phillyrea angustifolia* and *Olea europea*, and iii) high matorral vegetation with *Erica arborea, Arbutus unedo* and sometimes *Pinus halepensis* (Médail, 1998). The vegetation also includes halophilous to halo-nitrophilous grasslands, oak woodlands (Krebs *et al.,* 2014), and ca. 2-ha of *Carpobrotus edulis* and of the introgressed hybrid of *Carpobrotus edulis* × *Carpobrotus acinaciformis,* named *Carpobrotus affine acinaciformis.* The two species are called *Carpobrotus* hereafter (Suehs *et al.,* 2004a; Suehs *et al.,* 2004b; Chenot *et al.,* 2018).

Carpobrotus covered ca. 1-ha on cliffs (not included in this study) and ca. 1-ha that was easily accessible to monitor vegetation dynamics (Figure 1). All areas covered by *Carpobrotus* are intended to be treated by Port-Cros National Park to reach a *Carpobrotus*-free nature reserve in the long-term. Research was carried out in two accessible sites invaded by *Carpobrotus*, one coastal and one inland site, each composed of several patches (Figure 1). The coastal and inland *Carpobrotus* sites were studied separately because the environmental conditions and thus surrounding native plant communities were different for each site. On the coast, soils are thinner, the vegetation receives more sea spray and the surrounding native vegetation is coastal vegetation. Inland soils are deeper and the surrounding native vegetation is a low matorral with a few patches of halophilous grasslands with chamaephytes. In order to compare vegetation dynamics between the *Carpobrotus* removal sites and native vegetation, we also studied three uninvaded native plant communities: i) low matorral vegetation, thereafter named matorral vegetation, ii) coastal vegetation, and iii) halo-nitrophilous grassland vegetation.

***Carpobrotus* removal**
Carpobrotus was removed in 2011-2012, timed between October and February to minimize disturbance to the native flora (Ruffino *et al.,* 2015). Approximately one hectare of *Carpobrotus*

located in two accessible sites: one coastal site and one inland (Figure 1) was manually uprooted (*Carpobrotus* found on cliffs were removed later and are not part of this study). Because *Carpobrotus* litter contains a large amount of *Carpobrotus* seeds (Chenot *et al.,* 2014) and because it can hamper the recovery of native vegetation (Novoa *et al.,* 2012), removal of live shoots and rhizomes was followed by removal of dead shoots and litter. Removing litter can increase soil erosion (Chenot *et al.,* 2018), but this option was preferred for Bagaud island because accessible sites were not located on steep slopes. All plant material (estimated to 40 tons) was left to decompose in piles on Bagaud island to avoid the dispersal of fruits, seeds and fragments. Because *Carpobrotus* has a persistent seed bank and can resprout from forgotten fragments of rhizomes, follow-up controls were carried out every year, mainly in autumn, after 2012 (Ruffino *et al.,* 2015). Each time *Carpobrotus* plants were found on a site from which it had previously been removed, the number of germinations and the number of resprouts were removed and counted, and the area estimated. We then summed these counts in total number of individuals and total number of individuals / m².

Monitoring protocol

Plant communities were studied before (2010 and 2011) and after (2013 to 2019) *Carpobrotus* removal in spring (late April) each year. In order to compare recovering plant communities at the *Carpobrotus* removal sites with the native plant communities and to identify potential trajectories, we used a long-term protocol to study plant communities in the islands of the region (Baumberger *et al.,* 2012) using 100-m² circular permanent plots (Figure 1). Such plots were sampled in the *Carpobrotus* removal sites (six plots on the coast, four inland) as well as in the three native plant communities selected as references (four plots in each in coastal, halo-nitrophilous grassland and matorral vegetations) in 2010-2011 and then 2013-2019 (Krebs *et al.,* 2015).

To study plant community dynamics through time at the two *Carpobrotus* removal sites more precisely, we used a high number of smaller quadrats. Twenty-two (22) 4×4-m (16 m²) quadrats were sampled: 12 inland and 10 on the coast (Figure 1). In each quadrat or plot, the percent cover of each plant species was visually estimated. In each quadrat, percent cover of vegetation, *Carpobrotus* alone, bare ground and litter were also estimated. To do so, we used cover classes (i : < 1 % ; 1 : 1-10 % ; 2 : 11-25 % ; 3 : 26-50 % ; 4 : 51-75 %; 5 : 76-100 %) which allowed reducing the bias of having several observers estimating covers over nine years. For data analysis, i was replaced by 0.1. All species found during sampling are listed in Appendix S1 and

species nomenclature follows (Tison *et al.,* 2014). Species richness was calculated as the number of species in each 16 m² quadrat.

Data analysis

All analyses were run with R-3.6.2 (R Core Team, 2020). Differences in the number of *Carpobrotus* individuals removed / m² between years (2013 to 2019) were tested separately for the two *Carpobrotus* removal sites. We used Generalized Linear Models (GLM), one for each site, with years as a fixed factor (gamma error distribution). They were followed by pairwise contrast comparisons with a Tukey adjustment when significant (*emmeans*: Lenth *et al.,* 2020).

Differences in vegetation (species richness, percent cover class of vegetation, *Carpobrotus* alone, bare ground and litter) between years (2010 to 2019) were tested separately for the two *Carpobrotus* removal sites. We used Generalized Linear Mixed Models (GLMM), one for each variable and each site, with years as a fixed factor and quadrats as a random factor to take repeated measures into account (*glmmTMB:* Magnusson *et al.,* 2020; *car:* Fox *et al.,* 2020). They were followed by pairwise contrast comparisons with a Tukey adjustment when significant. The data used for these analyses were taken from the 16-m² quadrats and models were fitted with a Poisson error distribution.

Similarities between i) the coastal *Carpobrotus* removal site and coastal vegetation, ii) the inland *Carpobrotus* removal site and coastal vegetation, iii) the inland *Carpobrotus* removal site and halo-nitrophilous grassland vegetation, and iv) the inland *Carpobrotus* removal site and matorral vegetation were assessed using the Bray–Curtis similarity index calculated on cover classes (*vegan*: Oksanen *et al.,* 2019). The Bray–Curtis index is an appropriate index for beta diversity assessment (Legendre and Cáceres, 2013). We also calculated Bray–Curtis similarity indices within reference sites. This index ranges from 0 to 1, where 1 represents the greatest similarity between two vegetation types. We used two GLMM, one for each site, with either years or reference vegetation*years as a fixed factor(s) and quadrats as a random factor to take repeated measures into account. They were followed by pairwise contrast comparisons with a Tukey adjustment when significant. The data used for these analyses were taken from the 100-m² plots and models were fitted with a gamma or beta error distribution.

Plant community dynamics through time was analyzed using a non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis dissimilarities calculated on cover classes (*vegan*: Oksanen *et al.,* 2019). We used data taken in the 100-m² plots in all

vegetation types (the two *Carpobrotus* removal sites and the three native plant communities) between 2010 and 2019 after removing species found only once (118 species × 196 plots; 6 plots on the coastal *Carpobrotus* removal site, 4 inland *Carpobrotus* removal site, 4 in matorral, 4 in grassland, 4 in coastal vegetations = 22 × 9 years = 198 plots - 1 inland plot missing from the 2013 and 2014 survey). We tested for dissimilarity in community composition between vegetation types with a Permanova (pairwise distances calculated with pairwise adonis tests with Bray-Curtis distances and 999 permutations) (*pairwise adonis*: Martinez Arbizu, 2017).

To assess plant community recovery, we used two indices: $CSII_{norm}$ (normalized Community Structure Integrity Index) and HAI (Higher Abundance Index) (Jaunatre *et al.*, 2013) with the vegetation data (cover classes) taken in the 100-m² plots after *Carpobrotus* removal (2013 to 2019) (*Renaudpack2*: Jaunatre, 2020). To calculate these two indices, each community has to be characterized by a list of species each associated with a number (n) which reflects their abundance (e.g. biomass, abundance coefficient, percent cover). For a given species i, $\Delta i,j = |ni, AC - ni, j|$ the absolute difference between the abundance in the assessed community and the abundance in reference community j. A subscript indicates whether the abundance in the assessed community is lower (Δ^-i,j) or higher (Δ^+i,j) than in the reference community (see Jaunatre *et al.*, 2013 for details). The $CSII_{norm}$ measures the proportion of the species abundance of a native plant community present in the recovering community, where S the total number of species over all communities and K the total number of reference communities:

$$CSII = \overline{\left[\frac{\sum_{i=1...S}(n_i - \Delta_{i,j}^-)}{\sum_{i=1...S}n_{i,j}} \right]}^{j=1...K}$$

$CSII_{norm}$ theoretically ranges from 0 to 1, where 1 represents all species with the same abundance in both communities. HAI measures the proportion by which the species abundance in the recovering community exceeds that of the reference community:

$$HAI = \overline{\left[\frac{\sum_{i=1...S} \Delta_{i,j}^+}{\sum_{i=1...S} n_{i,AC}} \right]}^{j=1...K}$$

It also ranges from 0 to 1, where 1 corresponds to all species in the recovering community with

higher abundance than in the reference. Both indices (CSII$_{norm}$ and HAI) were calculated between samples (plots) of the two plant communities, but also within samples of each reference. We compared the values obtained for these indices between the native plant communities and the recovering community using GLMM, one for each index and each site comparison, with vegetation comparison (between or within)*years as fixed factors and plots as a random factor to take repeated measures into account. They were followed by pairwise contrast comparisons with a Tukey adjustment when significant and models were fitted with a gamma distribution. Comparisons included: the coastal *Carpobrotus* removal site with coastal vegetation and the inland *Carpobrotus* removal site with the three selected native plant communities.

Results

Carpobrotus *cost removal and follow-up controls*

The removal of *Carpobrotus* located in the accessible areas (11,000 m²) required 82 man.days and cost approximately 25,302€, 2.30€/m² or 74.5 man.days/ha (by comparison, removal of *Carpobrotus* on cliffs (8,000 m²), not included in the rest of the study, required 242 man.days as it required highly specialized rope-workers).

The follow-up control in the accessible areas required 131 man.days between 2013 and 2019, so approximately 65,500€, 5.95€/m², 119.1 man.days/ha over seven years, or 17.0 man.days/ha/yr. The mean number of individuals / m² (germinations and resprouts) removed during follow-up controls decreased between 2013 and 2014 (from 7.6±3.0 to 2.1±1.0 individuals / m² on average) and dropped after 2015 (to 0.47±0.2 individuals / m²) both on the coastal and inland *Carpobrotus* removal site (coast: χ^2=181.3, df=6, p<0.001; inland: χ^2=172.7, df=6, p<0.001; Figure 2; Appendix S2).

Dynamics of vegetation parameters

In the *Carpobrotus* removal sites, plant species richness was significantly lower before *Carpobrotus* removal (2010-2011) than in subsequent years (2013-2019) at both sites (coast: χ^2=53.56, df=8, p<0.001; inland: χ^2=155.68, df=8, p<0.001; Figure 3). Total vegetation cover and litter cover dropped in the year after *Carpobrotus* removal (2013) and slowly increased thereafter, but without reaching the highest percent covers from before removal. Overall, this difference across all years was not significant for total vegetation cover (Figure 4a). *Carpobrotus* cover decreased drastically after removal in 2011-2012 and remained low throughout the rest of the

study at both sites (coast: χ²=130.27, df=8, p<0.001; inland: χ²=179.70, df=8, p<0.001; Figure 4b). *Carpobrotus* litter removal greatly reduced litter cover, which kept decreasing until 2015-2016. Native plant litter then began to slowly build up from 2017 on (coast: χ²=35.27, df=8, p<0.001; inland: χ²=118.52, df=8, p<0.001; Figure 4c). Bare ground cover increased immediately after *Carpobrotus* removal in the inland *Carpobrotus* removal site; it declined in subsequent years with increasing native plant cover, but did not return to pre-removal levels (χ²=46.34, df=8, p<0.001; Figure 4d). Bare ground cover in the coastal *Carpobrotus* removal site remained low and constant (χ²=2.49, df=8, p=0.962; Figure 4d).

Plant community composition

Bray-Curtis similarity indices calculated between the coastal *Carpobrotus* removal site and the reference coastal vegetation increased with time and was significantly different between years before *Carpobrotus* removal and years from 2015 on (χ²=26.18, df=8, p<0.001; Figure 5a). By 2019, the similarity between these two sites reached 0.60. There was no significant differences in Bray-Curtis similarity indices within the reference coastal vegetation (χ²=11.57, df=8, p=0.172; Figure 5a). Bray-Curtis similarity indices calculated between the inland *Carpobrotus* removal site and the three potential references (coastal, halo-nitrophilous grassland and matorral vegetations) also increased with time (χ²=136.77, df=8, p<0.001; Figure 5b). Similarity of the inland *Carpobrotus* removal site to coastal vegetation was slightly, but not significantly higher (0.45 on average over all years) than with the halo-nitrophilous grassland (0.41 on average over all years). Similarity of the inland *Carpobrotus* removal site to matorral vegetation was significantly lower than to the two other native plant community types (0.30 on average over all years) (χ²=79.96, df=2, p<0.001; Figure 5b). There was no significant differences in Bray-Curtis similarity indices within each of two of the potential references (coastal and halo-nitrophilous grassland vegetations), but they increased slightly after 2015 in the matorral vegetation (χ²=40.98, df=8, p<0.001; Figure 5b).

The NMDS ordination separated all vegetation types (stress: 0.16; permanova$_{vegetation}$ p = 0.001; Figure 6). Axis 1 separates matorral vegetation from the rest of sites, where the vegetation is more open. It is characterized by perennial species such as *Brachypodium retusum, Cistus monspeliensis, Cistus salviifolius, Erica arborea, Euphorbia characias, Myrtus communis, Olea europaea, Rosmarinus officinalis, Teucrium marum, Phillyrea* sp.. Axis 2 separates i) both the coastal and the inland *Carpobrotus* removal sites in 2010 and 2011 characterized by *Carpobrotus*

dominance from ii) these same sites from 2013 to 2019, the coastal vegetation and the halo-nitrophilous grassland (Figure 6).

Plant community recovery

The highest value of post-removal $CSII_{norm}$ (the proportion of the species abundance of a native plant community present in the recovering community) was reached when comparing the coastal *Carpobrotus* removal site in 2019 and reference coastal vegetation (0.92) and this value was not significantly different from that of the reference coastal vegetation (Appendix S3). The $CSII_{norm}$ comparing the coastal *Carpobrotus* removal site and coastal vegetation increased slightly but steadily overtime and was significantly higher in 2019 than in 2013 ($\chi^2=28.42$, df=6, p<0.001; Appendix S3). The nine most dominant species of the reference coastal vegetation were well represented at the coastal *Carpobrotus* removal site: *Lotus creticus* ssp. *cytisoides, Sonchus asper* ssp. *glaucescens, Frankenia* spp., *Limonium pseudominutum, Senecio leucanthemifolius* ssp. *crassifolius, Crithmum maritimum, Catapodium marinum, Atriplex prostrata, Parapholis incurva*, although *Limonium pseudominutum* and *Crithmum maritimum* were under-represented (Figure 7a). The HAI (the proportion by which the species abundance in the recovering community exceeds that of the reference community) for these two vegetation types was relatively high (0.51) and significantly greater than that of the reference coastal vegetation ($\chi^2=68.73$, df=1, p<0.001; Appendix S3), because some species were over-represented, such as *Dactylis glomerata* ssp. *hispanica, Sonchus asper* ssp. *asper, Carpobrotus* germinations and resprouts, *Juncus acutus* (Figure 7a).

When comparing the inland *Carpobrotus* removal site with the three potential references, the value of post-removal $CSII_{norm}$ were 0.77 with coastal vegetation, 0.69 with halo-nitrophilous grassland vegetation and 0.33 with matorral vegetation. These values were significantly lower from that of the references (coastal vegetation: $\chi^2=64.50$, df=1, p<0.001; halo-nitrophilous grassland vegetation: $\chi^2=149.23$, df=1, p<0.001 and matorral vegetation: $\chi^2=109.90$, df=1, p<0.001, Appendix S3). The $CSII_{norm}$ comparing the inland *Carpobrotus* removal site and coastal vegetation increased slightly with time, 2013 being significantly lower from 2016 and 2017 ($\chi^2=15.70$, df=6, p=0.015; Appendix S3). The $CSII_{norm}$ comparing the inland *Carpobrotus* removal site and the halo-nitrophilous grassland also increased slightly with time, 2013 and 2014 being significantly lower from 2016 to 2019 ($\chi^2=13.14$, df=6, p=0.041; Appendix S3).

The two most dominant species of the coastal vegetation were well represented at the inland *Carpobrotus* removal site after removal: *Lotus creticus* ssp. *cytisoides*, and *Sonchus asper* ssp. *glaucescens. Senecio leucanthemifolius* ssp. *crassifolius, Catapodium marinum* and *Atriplex prostrata* were also well represented. *Frankenia* spp., *Limonium pseudominutum, Crithmum maritimum* and *Parapholis incurva* appeared under-represented. The HAI for these two vegetation types was high (0.54) and significantly greater than that of the reference coastal vegetation (χ^2=105.02, df=1, p<0.001, Appendix S3), thus showing that some species were over-represented: *Bromus diandrus* ssp. *diandrus*, *Smilax aspera* and *Carpobrotus* germinations and resprouts (Figure 7b).

The three most dominant species of the halo-nitrophilous grassland vegetation were well represented at the inland *Carpobrotus* removal site: *Sonchus asper* ssp. *glaucescens, Lotus creticus* ssp. *cytisoides* and *Senecio leucanthemifolius* ssp. *crassifolius. Sonchus bulbosus, Atriplex prostrata* and *Catapodium marinum* were also well represented. *Frankenia* spp., *Hordeum murinum* and *Malva arborea* appeared under-represented. The HAI for these two vegetation types was high (0.51) and significantly greater than that of the halo-nitrophilous grassland vegetation (χ^2=115.72, df=1, p<0.001, Appendix S3), thus showing that some species were over-represented: *Pistacia lentiscus, Smilax aspera, Jacobea maritima* ssp. *maritima, Euphorbia pithyusa* and *Carpobrotus* germinations and resprouts (Figure 7c).

Pistacia lentiscus, the most dominant species of the matorral vegetation, was well represented at the inland *Carpobrotus* removal site. *Smilax aspera, Sonchus bulbosus* and *Dactylis glomerata* ssp. *hispanica* were also well represented. Most other species found in matorral vegetation appeared under-represented (Figure 7D). The HAI for these two vegetation types was high (0.72) and significantly greater than that of the matorral vegetation (χ^2=475.35, df=1, p<0.001, Appendix S3), because many species were over-represented: *Bromus diandrus* ssp. *diandrus, Lotus creticus* ssp. *cytisoides, Jacobea maritima* ssp. *maritima* and *Carpobrotus* germinations and resprouts (Figure 7d).

Discussion

Native plant species colonization

Recovery of native vegetation after *Carpobrotus* removal was encouraging. All the plant species that colonized after *Carpobrotus* removal were native species, contrary to what Magnoli *et al.* (2013) found in northern California, on sites that had other invasive species before control (e.g.

Bromus diandrus). Species recolonized rapidly after removal; the number of species for 16 m²
reached 14.7 species on the coastal *Carpobrotus* removal site and 16.5 on the inland *Carpobrotus*
removal site as early as 2013. It reached 16.8 species on the coastal *Carpobrotus* removal site and
17.9 on the inland *Carpobrotus* removal site by 2019 (Figure 3). This rapid recovery of native
vegetation is similar to *Carpobrotus* removal projects implemented on sand dunes in Italy
(Lazzaro *et al.,* 2020) and in Spain (Andreu *et al.,* 2010). We thus confirm that in the absence of
other invasive species and where post-removal disturbance are low (Prior *et al.,* 2018), active
revegetation *via* sowing or transplanting is not necessary to reach diverse native plant
communities. Species commonly found recolonizing are known to be either in the seed bank, such
as *Atriplex prostrata*, *Frankenia* spp., *Lotus creticus* ssp. *cytisoides* (Chenot *et al.,* 2014), wind-
dispersed (*Senecio leucanthemifolius* ssp. *crassifolius*) or both (*Jacobaea maritima* ssp. *maritima,*
Sonchus asper ssp. *asper, Sonchus asper* ssp. *glaucescens*). Other species are tuberous species,
such as *Sonchus bulbosus*, and had probably been waiting to resprout from under the *Carpobrotus*
mats. Finally, some are perennial species which were present within the *Carpobrotus* patches and
survived its removal: *Dactylis glomera* ssp. *hispanica, Limonium pseudominutum, Pistacia
lentiscus*, or *Smilax aspera.*

Changes in litter and bare ground cover
Litter under *Carpobrotus* mats can cover up to 100% of the ground, as it was the case in the inland
Carpobrotus removal site. On the coastal *Carpobrotus* removal site, *Carpobrotus* mats were more
patchy because of high rock cover and low soil depth, and so was the litter (Figure 4). Litter
decreased in 2012 just after *Carpobrotus* removal as planned in the protocol (Ruffino *et al.,* 2015).
Although such data were not precisely recorded (we did not estimate *Carpobrotus* litter and native
plant litter separately), the progressive increase in litter after 2012 was from native plants as they
were colonizing and the leftover *Carpobrotus* litter kept decomposing as shown by Lazzaro *et al.,*
(2020). Concurrently, bare ground, which was lower at the inland *Carpobrotus* removal site due to
the higher cover of *Carpobrotus* mats, increased in 2013 just after removal and decreased again as
native species colonized. On the coastal *Carpobrotus* removal site, because of harsh conditions,
the plant community was more open and bare ground was higher than inland from the start. After
2012, bare ground on the coastal *Carpobrotus* removal site ended up stabilizing around what it
was before *Carpobrotus* removal. Inland however, bare ground remained higher than before 2012.
Altogether, removing the *Carpobrotus* mats and their litter induced the recolonization by native

species of various life-forms and sizes, producing litter with various decomposition rates (Fioretto *et al.,* 2005) that fluctuates with seasons, as some species are annuals and die during summer (e.g. *Atriplex prostrata, Senecio leucanthemifolius* ssp. *crassifolius*; Tela Botanica, 2020). This therefore allowed the recovery of plant communities that are more diverse and provide more microhabitats than the *Carpobrotus* mats.

Plant community recovery at the coastal site

It appears from the three calculated indices (Bray-Curtis similarity, CSII$_{norm}$ and HAI, Figures 5 and 7; Appendix S3) and from the multivariate analysis (Figure 6) that coastal vegetation is a good reference for the coastal *Carpobrotus* removal site. These two sites share a relatively similar environment, particularly the influence of sea spray. However, some species remained under-represented: *Crithmum maritimum, Hordeum murinum* ssp. *leporinum, Limonium pseudominutum*. *Hordeum murinum* ssp. *leporinum* has seeds with long barbed awns which makes them easily transported in animal fur, but not easily transported by insects (Iqbal *et al.,* 2019). On Bagaud island, there were no large mammals to disperse *Hordeum murinum* ssp. *leporinum* seeds until 2018 when wild boars (*Sus scrofa*) swam from the mainland to Port-Cros and Bagaud islands (Cottaz, 2018). This may explain the increase in this plant species cover in 2019 (Appendix S4). *Crithmum maritimum* and *Limonium pseudominutum* have low growth rates (Okusanya, 1979) which may explain why they are under-represented.

The Higher Abundance Index (HAI) was different between the coastal *Carpobrotus* removal site and coastal vegetation showing that some species were over-represented at the coastal *Carpobrotus* removal site compared to the reference. This may be partly due to the fact that these sites differ in topography: the coastal reference site is steeper and rockier and the coastal *Carpobrotus* removal site has more pockets of shallow soil, and with decomposing *Carpobrotus* litter. That may explain why perennial species (*Jacobaea maritima* ssp. *maritima, Pistacia lentiscus*) and ruderal species (*Bromus diandrus* ssp. *diandrus*) were more common at the coastal *Carpobrotus* removal site. *Bromus diandrus* ssp. *diandrus* increased progressively with a small peak in 2019 (Appendix S4) maybe due to the arrival of the wild boars and as it is easily dispersed in animal fur (Carlquist and Pauly, 1985).

Plant community recovery at the inland site

The inland *Carpobrotus* removal site did not converge towards the vegetation in its immediate surroundings, mainly composed of matorral vegetation. All analyses showed a great difference between the inland *Carpobrotus* removal site and matorral vegetation, which is certainly linked to the slow colonization dynamics of matorral species particularly in the presence of competitive herbaceous species (Holmgren *et al.,* 2000; Midoko-Iponga *et al.,* 2005). Indeed, *Bromus diandrus* ssp. *diandrus*, *Cynodon dactylon*, *Lotus creticus* ssp. *cytisoides* are well represented at the inland *Carpobrotus* removal site and may compete against the establishment of more typical matorral species, such as *Brachypodium retusum, Cistus monspeliensis, Myrtus communis, Pistacia lentiscus* and *Rosmarinus officinalis* which are under-represented. Some of these species also face additional challenges: i) *Pistacia lentiscus* has a short-term seed bank (García-Fayos and Verdú, 1998); ii) *Rosmarinus officinalis* has a short-term seed bank and a small proportion of viable seeds (Clemente *et al.,* 2007); iii) *Brachypodium retusum* has low seed production without fire (Vidaller *et al.,* 2019); and iv) although *Cistus* species have a long-term seed bank, they lack specialized structures for long-distance dispersal (Guzmán and Vargas, 2009).

The inland *Carpobrotus* removal site had a lower similarity with the coastal vegetation than the coastal *Carpobrotus* removal site (CSIInorm$_{2013-2019}$ 0.77 *vs.* 0.92). This was expected because the inland site lacks sea spray. It therefore logically lacked typical coastal species like *Crithmum maritimum*, *Frankenia* spp., *Limonium pseudominutum*, *Parapholis incurva* when compared with the coastal vegetation native plant community. Such species do poorly on the inland *Carpobrotus* removal site because i) they are not present in the surrounding vegetation, which is not directly under the influence of sea spray and ii) even if seeds could have reached the area, these coastal species are highly adapted to their environment and poor competitors elsewhere (Okusanya, 1979). Also, *Parapholis incurva* is a low-growing annual grass with little opportunity of wind dispersal and mainly has a short-term seed bank (Caballero *et al.,* 2005), which also contributes to explain why it does not colonize inland. There were more shrub species on the inland *Carpobrotus* removal site, which do not grow well on the very coast because they are not tolerant to salt (e.g. *Phillyrea angustifolia*; Tela Botanica, 2020). The inland *Carpobrotus* removal site also had some species in common with the halo-nitrophilous grassland (CSIInorm$_{2013-2019}$ 0.69), such as *Lotus creticus* ssp. *cytisoides* and *Sonchus asper* ssp. *glaucescens,* but did not have the most nitrophilous species, such as *Malva veneta* and *Beta vulgaris* ssp. *maritima* (Tela Botanica, 2020). However, *Bromus diandrus* ssp. *diandrus* and *Hordeum murinum* ssp. *leporinum* which are rather nitrophilous Poaceae (Tela Botanica, 2020) did substantially increase in 2019

(Appendix S4). This could be due to i) wild boar disturbances and seed dispersal in their fur, ii) the highly fluctuating cover of *Lotus creticus* ssp. *cytisoides* (Appendix S4) and particularly to its drastic decrease in 2018 and 2019, which may be linked with warmer winter temperature and thus reduced germination (Buisson *et al.,* 2018), or iii) both. Resampling in a few years will allow us to find out whether the plant communities of the inland *Carpobrotus* removal site will become closer to a halo-nitrophilous grassland.

Conclusion

The removal of *Carpobrotus* and its litter in areas with no other invasive species and where slopes are gentle can quickly lead to diverse native plant communities. Plant communities, such as coastal vegetation, composed of many pioneer species, may recover and be relatively similar to the reference in a few years. Plant communities with more shrubs may need more time to recover or may not recover if the succession is arrested by native competitive herbaceous species. To prevent *Carpobrotus* return, follow-up controls, i.e. removal of *Carpobrotus* germinations and resprout, were carried out along with monitoring. Studies on *Carpobrotus* seed bank longevity are scarce and the follow-up controls done in our study show that they are likely to have a persistent seed bank (> 5 years), as suggested by Campoy *et al.* (2018) and contrary to Gioria *et al.* (2012) study classifying *Carpobrotus edulis* in the category with short-term persistent seed bank. Follow-up controls will have to be continued until the exhaustion of the *Carpobrotus* seed bank but we showed that it becomes less work intensive three years after *Carpobrotus* removal. Still, based on 2019 figures concerning follow-up controls (Appendix S2) and dividing these by two to simulate the progressive exhaustion of the *Carpobrotus* seed bank, we speculate that an additional 50,000€ will be necessary to remove *Carpobrotus* germinations and resprouts in the next 10 years. This will be necessary to ensure eradication success.

Supporting information

Appendix S1. List of the sampled plant species

Appendix S2. Figures concerning follow-up controls

Appendix S3. Similarities between *Carpobrotus* removal sites and references

Appendix S4. Selected species cover variation with time

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Data statement

Data and codes are available upon request. Data also is made available *via* the online database of the French Botanical Conservatories, Silene-Flore (Données Flore: CBNMed & CBNA (Admin.), 2020).

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Figure 1. Map of Bagaud Island, with contour lines of elevation, areas invaded by *Carpobrotus* spp. (in black and white), and monitoring plots and quadrats. Research was thus carried out in two accessible sites: one coastal (c) and one inland (i), each composed of several patches.

Figure 2. Differences in the number of *Carpobrotus* individuals removed / m² (mean ± SE) during follow-up controls between years (2013 to 2019). Coast = at the coastal *Carpobrotus* removal site and Inland = at the inland *Carpobrotus* removal site. We used GLM (gamma error distribution), followed by pairwise contrast comparisons with a Tukey adjustment. Within each site, points sharing a letter were not significantly different from each other (p<0.05).

Figure 3. Differences in species richness between years (2010 to 2019) for the *Carpobrotus* removal sites. Mean of cover class ± SE. The red dotted lines represent *Carpobrotus* removal. Coast = at the coastal *Carpobrotus* removal site and Inland = at the inland *Carpobrotus* removal site. Species richness was calculated as the number of species in each 16 m² quadrat. We used GLMM (Poisson error distribution) followed by pairwise contrast comparisons with a Tukey adjustment when significant. Within each site, points sharing a letter were not significantly different from each other (p<0.05).

Figure 4. Differences in cover classes (a. vegetation and b. *Carpobrotus* alone, percent cover of c. litter and d. bare ground) between years (2010 to 2019) for the *Carpobrotus* removal sites (data taken from the 16-m² quadrats). Coast = at the coastal *Carpobrotus* removal site and Inland = at the inland *Carpobrotus* removal site. Mean of cover class ± SE. The red dotted lines represent *Carpobrotus* removal. We used GLMM (Poisson error distribution) followed by pairwise contrast comparisons with a Tukey adjustment when significant. Within each site, points sharing a letter were not significantly different from each other (p<0.05).

Figure 5. Differences in Bray-Curtis similarity indices between years (2010 to 2019), for *Carpobrotus* removal sites (a. coastal site, b. inland site) (data taken from the 100-m² plots). *C.* removal = *Carpobrotus* removal. Index means ± SE. The index ranges from 0 to 1, where 1 represents the greatest similarity between two vegetation types. The red dotted line represents *Carpobrotus* removal. We used GLMM (gamma error distribution) followed by pairwise contrast

comparisons with a Tukey adjustment. Points sharing a letter were not significantly different from each other (p<0.05). NS: not significant.

Figure 6. NMDS analysis based on Bray-Curtis dissimilarities and run on the data taken in the 100-m² plots in all vegetation types (the two *Carpobrotus* removal sites and the three native plant communities - 196 plots × 118 species) before 2010-2011 and after 2013- 2019 *Carpobrotus* removal. All vegetation types were significantly different (permanova$_{vegetation}$ p = 0.001). To make the figure clearer, plant species with subspecies names were shortened (e.g. *Hordeum murinum* ssp. *leporinum* written as *Hordeum leporinum*); please see Appendix S1 for plants full names.
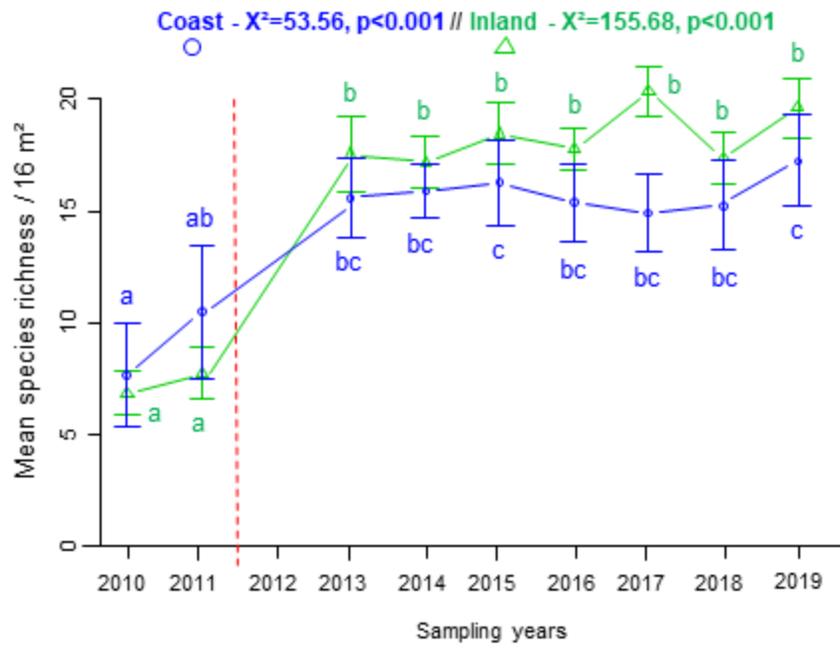
Figure 7. Mean abundances of reference communities and recovering communities between 2013 and 2019. On the left-hand side, grey areas represent mean abundances in the reference community. On the right-hand side, red areas represent mean abundances in the recovering community up to the mean abundances in the reference community; white areas represent mean missing abundances in the recovering community, and orange areas represent abundances which are higher than in the reference community. For clarity purposes, only species which occur in more than 3 plots are shown. a. Comparison between the coastal *Carpobrotus* removal site and coastal vegetation. b. Comparison between the inland *Carpobrotus* removal site and coastal vegetation. c. Comparison between the inland *Carpobrotus* removal site and halo-nitrophilous grassland vegetation. d. Comparison between the inland *Carpobrotus* removal site and matorral vegetation.

Iceplant removal
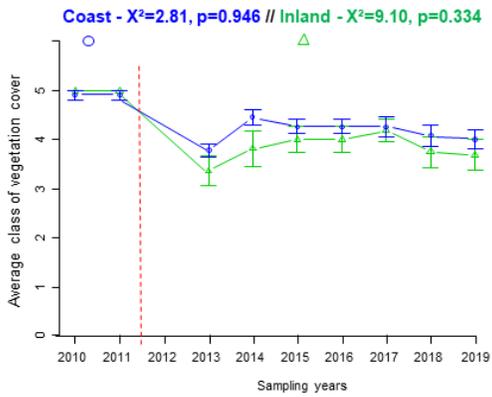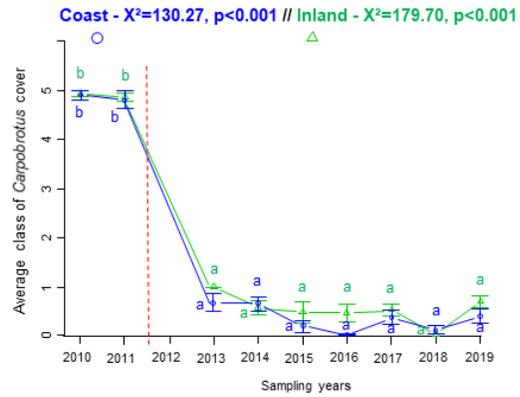
Carpobrotus-covered cliffs

Carpobrotus-covered accessible
 sites:
  c - coastal
  i - inland

100 m² circular permanent plots
  Inland Carpobrotus removal site
  Coastal Carpobrotus removal site
  Coastal vegetation
  Halo-nitrophilous grassland vegetation
  Matorral vegetation

16 m² permanent quadrats
  Inland Carpobrotus removal site
  Coastal Carpobrotus removal site
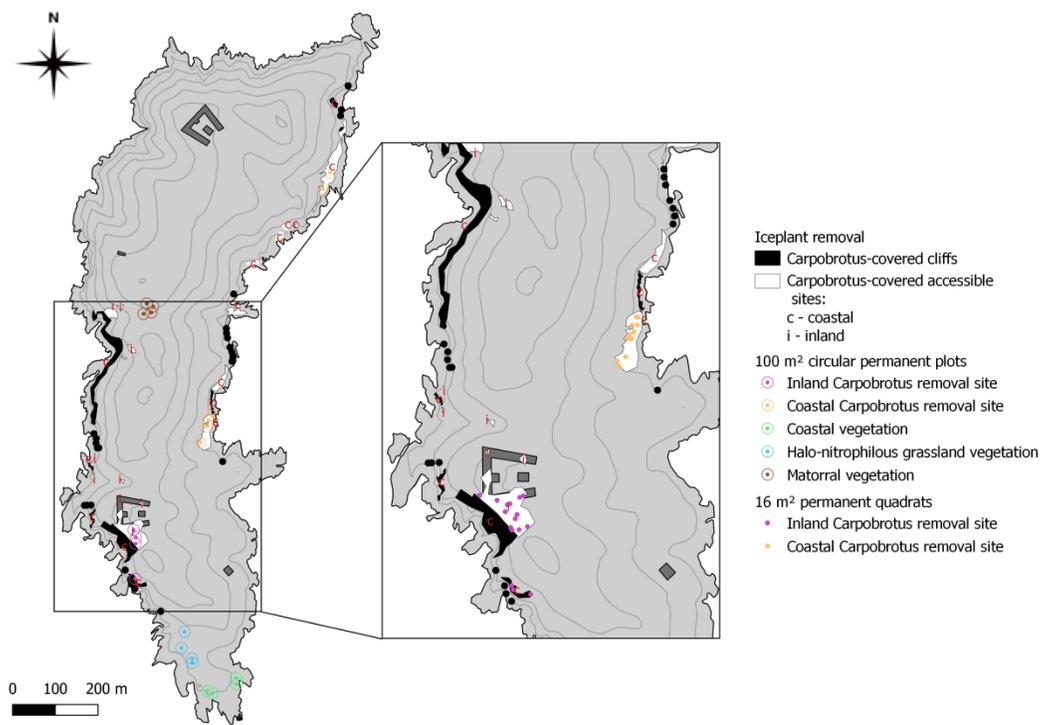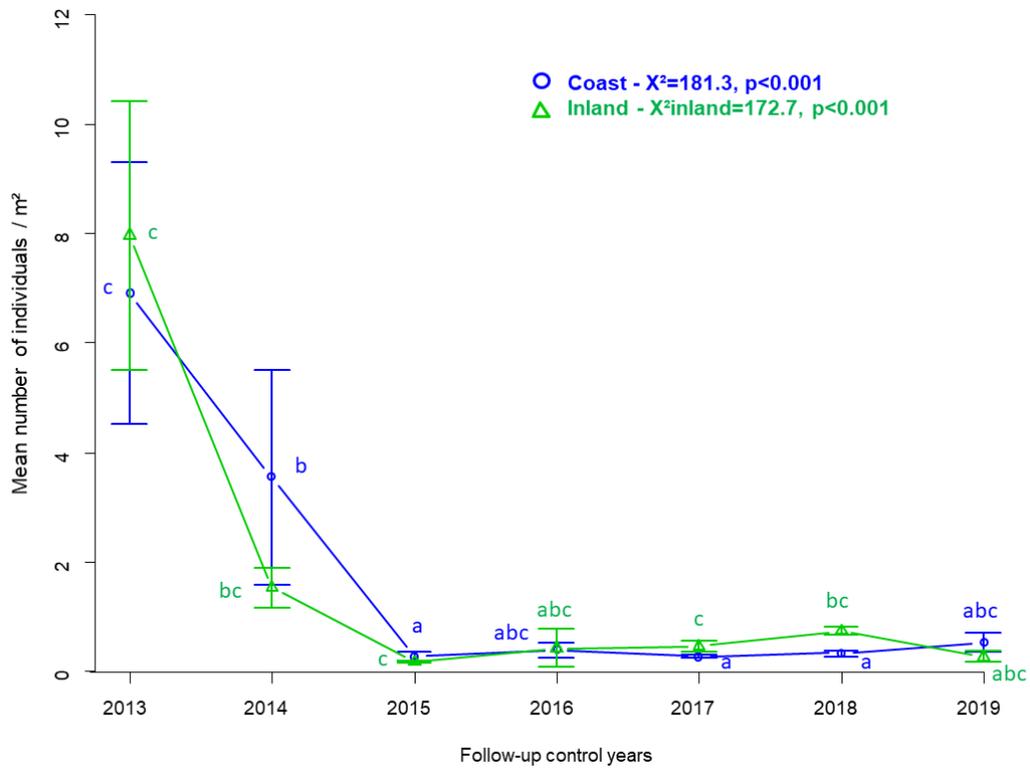
avsc_12524_f1.png
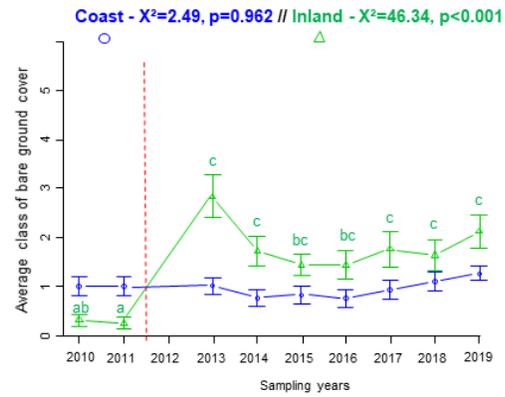
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avsc_12524_f3.tif

avsc_12524_f4.tif
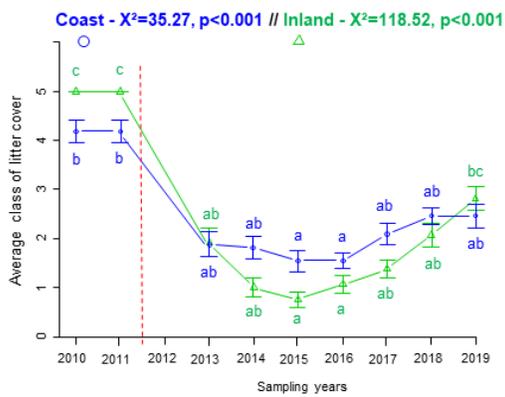
a. Similarity index of the coastal *Carpobrotus* removal site

▲ Coastal vegetation - χ^2_{year}= 11.57, p=0.172
○ Coastal *C.* removal site vs. coastal vegetation - χ^2_{year}=26.18, p<0.001
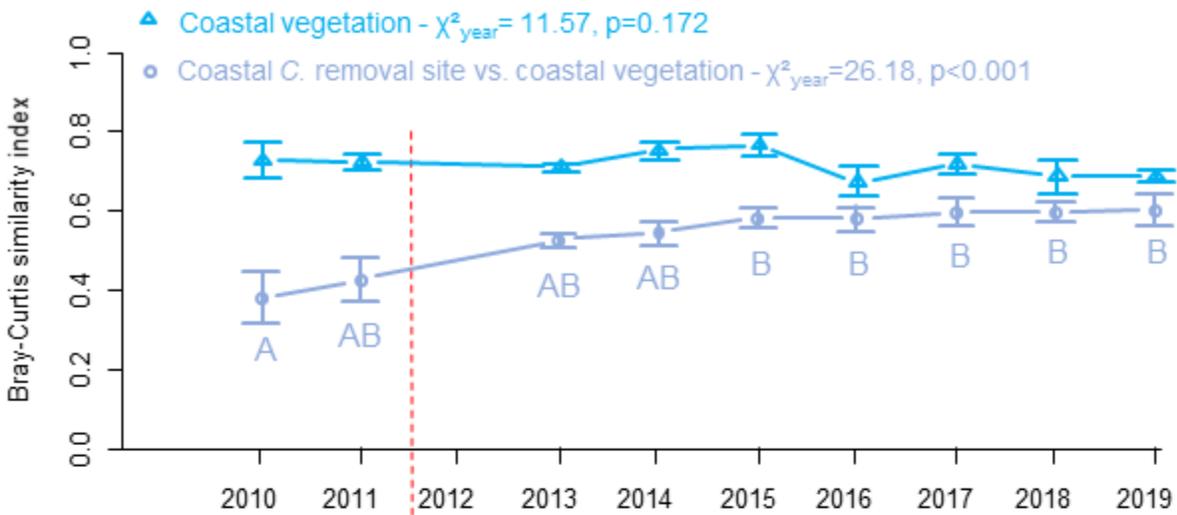
b. Similarity index of the inland *Carpobrotus* removal site

○ Coastal vegetation - χ^2_{year}= 11.57, p=0.172
△ Halo-nitrophilous grassland - χ^2_{year}= 16.11, p=0.041, post-hoc NS
+ Low matorral - χ^2_{year}= 40.98, p<0.001
✕ Inland *C.* removal site vs. coastal vegetation
◇ Inland *C.* removal site vs. halo-nitrophilous grassland
▽ Inland *C.* removal site vs. low matorral

χ^2_{year}=136.77, p<0.001
$\chi^2_{reference}$=79.96, p<0.001

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