

Research Article

Evidence of short-term response of rocky cliffs vegetation after removal of invasive alien *Carpobrotus* spp.

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Abstract

Invasive alien plant species are among the major drivers of change in natural ecosystems; therefore, their eradication or control is a common and effective conservation tool to reverse biodiversity loss. The LIFE LETSGO GIGLIO project was implemented with the objective of controlling the invasion of *Carpobrotus* spp., among the most threatening invasive alien species in Mediterranean ecosystems, on the Island of Giglio (Tuscan Archipelago, Italy). The management of *Carpobrotus* spp. was conducted across an area of approximately 33,000 m² of coastal habitats. The main intervention was conducted during the winter of 2021–2022, primarily through manual removal, with a limited use of mulching sheets. Subsequent years saw the continued removal of seedlings.

We monitored the habitats of vegetated sea cliffs and coastal garrigues (both protected under Directive 92/43/EEC), as these were the two habitats most affected by the control actions. A total of 24 permanent plots were sampled annually from 2020 to 2023 in a Before-After-Control-Impact (BACI) design. We analysed the variation pre- and post-removal of *Carpobrotus* spp. cover and litter and of native plant cover and diversity, as well as the changes in the composition of native plant communities.

Our results show that already two years after the main intervention of removal, thus in the short term, the community's composition shifted considerably towards the pre-invasion set of species. This recovery was also evident in terms of diversity indices, although the impact of *Carpobrotus* spp. on ecological parameters (mainly soil) favoured nitrophilous species. Furthermore, we highlight the need for yearly removal of *Carpobrotus* spp. seedlings for the next 5–10 years, in order to continue promoting the recovery of native communities.

Key words: Ecological restoration, island ecosystem, Mediterranean, N2000 habitats, plant community, plant management

Introduction

Invasive alien plants (IAPs) are one of the major drivers of change in natural ecosystems (IPBES 2019) and represent one of the most severe threats to biodiversity (CBD 2018). There is strong evidence of the negative impacts of IAPs on islands, which are more vulnerable to biological invasions than the mainland (IPBES



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2023), but there is also increasing evidence for the effectiveness of eradication and maintenance management of invasive species on islands (Simberloff et al. 2018). Despite the persistence of certain challenges, such as the persistent seed bank (Munné-Bosch 2023) or the unaffordable costs of long-term management (Lorenzo and Morais 2023), islands represent the optimal context for successful control outcomes (Simberloff et al. 2018). For these reasons, eradicating or controlling introduced plants and animals from island contexts is a common and effective conservation tool to reverse biodiversity loss (Ruffino et al. 2015).

Carpobrotus acinaciformis (L.) L.Bolus, *C. edulis* (L.) N.E.Br., and their hybrids (hereafter collectively referred to as *Carpobrotus*) are among the most threatening invasive alien species in Mediterranean ecosystems (Acosta et al. 2006; Carranza et al. 2010; Santoro et al. 2011; Celesti-Grapow et al. 2016). These species are native to South Africa and were introduced to Europe for ornamental purposes at the end of the 17th century (Campoy et al. 2018). The invasion by *Carpobrotus* causes significant ecosystem changes at different scales, leading to a decrease in native plant richness and diversity (Santoro et al. 2011; Fried et al. 2014; Badalamenti et al. 2016; Mugnai et al. 2022; Lazzaro et al. 2023). The impacts include alterations in soil pH, salinity, moisture level, nutrient content, and microbial activity (Santoro et al. 2011; Novoa et al. 2013; Badalamenti et al. 2016; Vieites-Blanco and González-Prieto 2018). These may result in inhibiting native plants' germination, survival, growth, and reproduction (Vilà et al. 2006; Conser and Connor 2009; Affre et al. 2010; Novoa et al. 2013) and in the facilitation of nitrophilous species (Fried et al. 2014; Badalamenti et al. 2016; Lazzaro et al. 2023). Due to these peculiarities, the genus *Carpobrotus* has the highest number of records of control actions (Brunel et al. 2013). Eradication and control methods used on *Carpobrotus* range from chemical to mechanical methods, such as mulching and manual removal (Lazzaro et al. 2020a; Fos et al. 2021, 2022). Manual removal is considered an effective and cost-efficient method to control *Carpobrotus* invasion both in the short and long term (Munné-Bosch 2023). However, it also generates disadvantages, such as the formation of large quantities of waste material, resulting in additional management time and labour (Campoy et al. 2018; Chenot et al. 2018; Lazzaro et al. 2023). Integrating manual removal with mulching sheets can enhance effectiveness in suppressing *Carpobrotus* and facilitate the recovery of native vegetation (Lazzaro et al. 2023; Nascimento et al. 2023).

A focal point in the experiences of eradication or control of these IAPs is represented by the recovery or restoration of native communities. An increasing body of knowledge in *Carpobrotus* removal projects conducted on significant invaded surfaces shows that the recolonizing by native species occurs after the species removal, both on sand dunes (Andreu et al. 2010; Lazzaro et al. 2020), as well in low matorral (Buisson et al. 2021) or rocky cliffs vegetation (Lazzaro et al. 2023). These experiences seem to confirm that in the absence of other invasive species and with low post-removal disturbance, active revegetation through sowing or transplanting is not necessary to achieve diverse native plant communities, although the speed of development may vary. While there are some published experiences on these interventions, more are needed, and the availability of data in both the long and short term is essential to plan effective actions on these IAPs.

Within this work, we focus on the short-term effects of *Carpobrotus* control interventions conducted within the EU LIFE project LIFE18 NAT/IT/000828 “Less alien species in the Tuscan Archipelago: new actions to protect Giglio island habitats”,

on Giglio island (Tuscan Archipelago, Italy). In particular, our study builds upon the work of Mugnai et al. (2022), who highlighted the important impacts of these species on rocky cliff habitats, which caused a decrease in species richness, community diversity, and abundance, as well as a compositional shift in invaded communities.

In line with the above, the present study aimed to i) verify the short-term effectiveness of the intervention on *Carpobrotus*, evaluating the temporal changes in its cover and litter, as well as the recovery of native plant communities in terms of ii) plant abundance, species richness and diversity after the intervention, iii) species composition and iv) increase of nitrophilous species. Toward these aims, we monitored a series of vegetation plots within two coastal habitats invaded by *Carpobrotus* on Giglio Island.

Methods

Study area

Giglio Island (WGS84: 42.35527°N, 10.90134°E) is the second largest island of the Tuscan Archipelago (Italy) with a surface area of 21.2 km² and a perimeter of 28 km (Baldini 1998). Almost all Giglio Island's land surface, approximately 21 km², falls within the Natura 2000 Special Area of Conservation (SAC/SPA IT51A0023), with a portion of it, covering 8.9 km², being part of the Tuscan Archipelago National Park.

The island is mainly mountainous, with steep and rocky slopes up to the coastline. The climate of Giglio Island is Mediterranean, with mild, rainy winters and hot-arid summers, peaking in July and August (Baldini 1998; Foggi and Pancioli 2008). The vegetation is typically Mediterranean, with forests dominated by *Quercus ilex*, evolved scrubs of *Erica arborea* and *Arbutus unedo*, and other typical Mediterranean *Cistus* and *Helichrysum* garrigues (Foggi and Pancioli 2008). The coastal vegetation, of particular interest for this study, being the one invaded by *Carpobrotus* (see Fig. 1A, B), hosts a mosaic of habitats of conservation interest according to Directive 92/43/EEC "Habitat", including the habitat of Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp. (habitat code 1240 according to Dir. 92/43/EEC, hereafter referred to as Vegetated sea cliffs), and the habitat of Low formations of *Euphorbia* close to cliffs (hab. code 5320, hereafter referred to as Coastal garrigues). Vegetated sea cliffs are characterized by the presence of alophylous chasmophytes such as the endemic *Limonium sommierianum* Fiori and *Crithmum maritimum* L., with few other species very sporadic (f.e. *Lotus cytisoides* L., *Catapodium pauciflorum* (Merino) Brullo, Giusso, Miniss. & Spamp. or *Polygogon subspathaceus* Req.). This paucispecific habitat hosts species fully adapted to grow on rocky coasts and occupy the first colonizable zone in contact with the sea, forming a discontinuous belt along the entire perimeter of the island. Indeed, Vegetated sea cliffs are generally characterised by an almost total absence of soil and direct contact with seawater and marine aerosol, therefore requiring highly specialised species (Perrino et al. 2013). Coastal garrigues settle in the upper parts of rocky coasts, in a variable-width zone between the typical aeroalophilous vegetation of the Vegetated sea cliffs and the first elements of Mediterranean low and high maquis. These plant communities are characterized by a low, single-layer structure dominated by dwarf and small shrubs like *Helichrysum litoreum* Guss. and *Jacobaea maritima* (L.) Pelsér & Meijden., prostrate *Pistacia lentiscus* L., and host several other Mediterranean annual species.

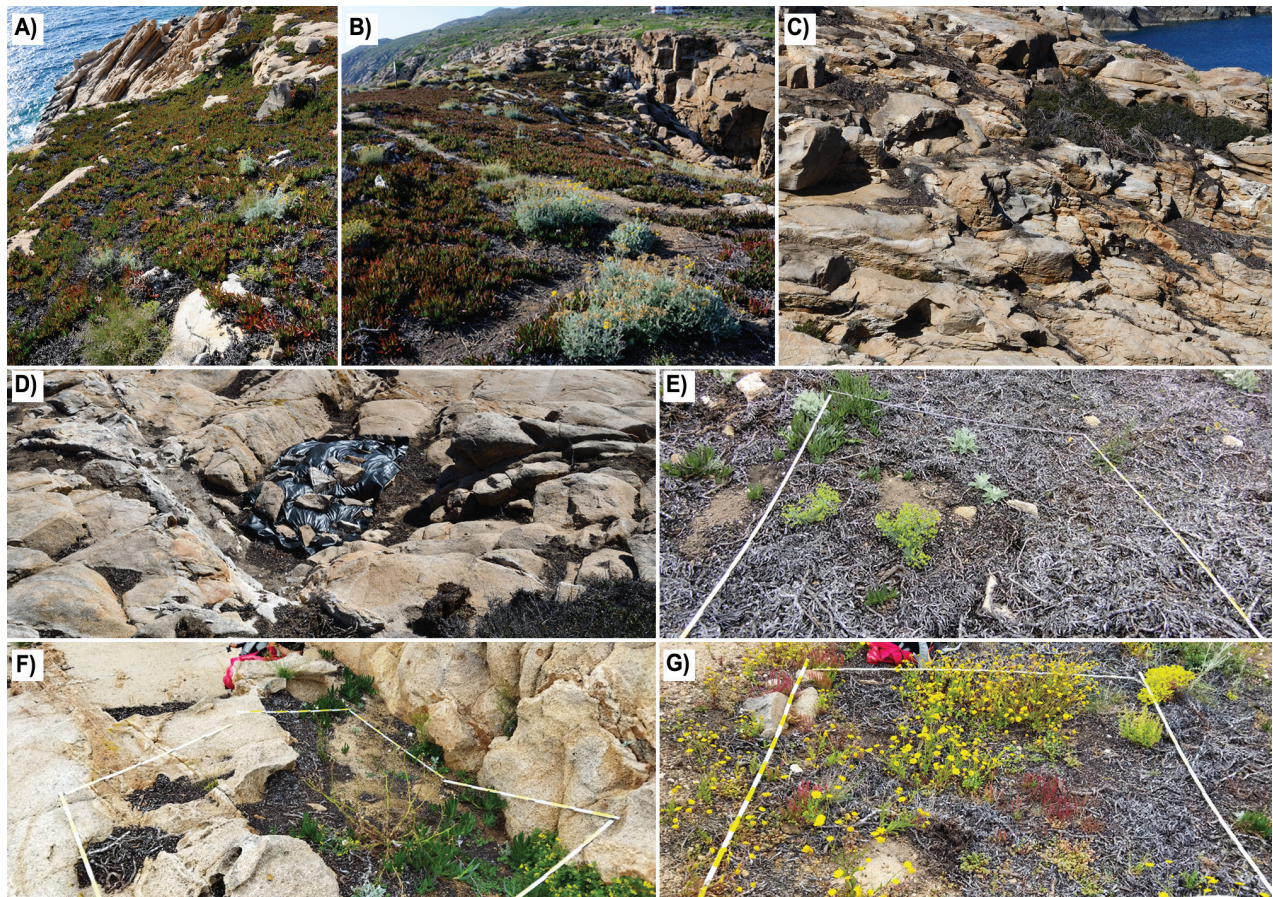


Figure 1. Some images of the interventions of *Carpobrotus* removal at Giglio Island **A, B** rocky cliffs invaded by *Carpobrotus*. In 2020 **C**, **D** images of the cliffs after the main intervention in early 2022 **E, F** monitoring plots after one year (2022) with the visible presence of *Carpobrotus* seedlings and **G** in 2023 with native vegetation.

The control of *Carpobrotus* at Giglio Island

The present study analysed the changes in *Carpobrotus* and native species presence and abundance during the actions of control of this invasive alien species, on the island of Giglio conducted within the EU LIFE project LIFE LETSGO GIGLIO “Less alien species in the Tuscan Archipelago: new actions to protect Giglio island habitats” (LIFE18 NAT/IT/000828). In the spring and summer of 2020, we conducted a preliminary phase of detailed mapping of the spread of *Carpobrotus* on the island. This involved the interpretation of aerial photos and surveys on the island. The initial distribution of this species on the island was recorded as approximately 61,000 m², with the majority occurring on cliffs or rocky areas. Approximately 50,000 m² of this area was found to be strictly invaded (Lazzaro et al. 2016; Mugnai et al. 2022). The intervention area extended over 33000 m² of coastal habitats, with an estimated net *Carpobrotus* surface of approximately 22000 m².

The main intervention for the removal began in the winter of 2021–2022 integrating two techniques: manual removal and covering with mulch sheets (landscape fabric, 105 g/m²). It should be noted that approximately 90% of the *Carpobrotus* on the island were removed manually, while mulching sheets were used only in a limited number of areas, mostly used to contain and isolate the waste material (Fig. 1C, D). The manual removal involved the entire plant, including roots, with the objective of eliminating all visible *Carpobrotus* live plants within

the intervention areas. As expected, regrowth of seedlings occurred in all the areas subjected to treatment, particularly in areas where the seed bank was present in the litter remaining on the ground (Fig. 1E, F). Hence, the project foresees continuous monitoring for three years following the main intervention and several rounds of follow-up interventions for the removal of new seedlings. Indeed, already in the first two years after the main intervention (from 2022 to 2023), any seedlings and resprouts were removed manually in April/May and, at the time of writing, continue to be removed annually (Fig. 1G). Furthermore, monitoring and the removal of seedlings will continue for at least five years after the main intervention.

Further technical details on the methods adopted are available in the executive project for the eradication (https://www.lifegogiglio.eu/wp-content/uploads/WEB_Relazione-illustrativa-generale_Carpobrotus-1.pdf).

Sampling design and data collection

The sampling was conducted at the promontory of “Punta Capel Rosso”, south of the island, largely invaded by *Carpobrotus*. In particular, the monitoring was carried out on both habitats, Vegetated sea cliffs and Coastal garrigues, as they were the two most invaded habitats of major conservation importance within the study area.

The monitoring began in 2020, and the impact assessment was carried out using the Before-After-Control-Impact (BACI), a suitable evaluation scheme consisting of pre- and post-intervention sampling of the restoration sites and control sites (Christie et al. 2019). The experimental sampling design has been implemented and maintained through a floristic survey of 2 × 2 m squared plots in two treatments: invaded (plots subjected to the removal) and control (plots in native vegetation). The sampling was stratified according to a random sampling design based on the surface of the habitats mapped concordant to the HaSCITu (Habitat in the Sites of Conservation Interest in Tuscany) program, and a detailed mapping of the distribution of *Carpobrotus* confirmed after several visits to the island before the commencement of the monitoring. Plots were paired, thus for each invaded plot a control plot was identified as close as possible. The sampling included a total of 24 permanent plots, 6 × 2 plots for Vegetated sea cliffs, and 6 × 2 plots for Coastal garrigues, evenly distributed between invaded and control.

Vegetation sampling was carried out during the vegetative season in May when most species were identifiable. Each plot was georeferenced and marked with a peg and a numbered nameplate. Data on native plant species occurrence and abundance was collected using a percentage scale, considering the overlapping of different species. Furthermore, the percentage of fresh *Carpobrotus* as well as its dead litter, was recorded. We present the data collected up to 2023, including thus 4 years of monitoring, resulting in the survey of 96 plots. A full list of species observed during the sampling within the two habitats between 2020 and 2023, is included in Suppl. material 1.

Statistical analysis

To verify the effect of *Carpobrotus* removal intervention on its cover and litter, and on the alpha diversity of native vegetation, we used a Repeated Measurement ANOVA-type modelling. We fitted a series of linear mixed models, with a random effect

factor on plot identity to account for the autocorrelation linked to the repetition of the samplings across the four years of surveying and including a covariance structure based on a Gaussian spatial autocorrelation of the observations accounting for the paired structure of the sampling design. For each of the two habitats separately, we assessed whether the cover and litter of *Carpobrotus* varied according to treatment and time. Similarly, we tested whether native species richness (SR), native diversity expressed as H' index, and native species abundance, expressed as the sum percentage cover of each species, changed before, during, and after the interventions using time and treatment (Invaded vs. Control) as fixed effect explanatory variables. When required, the variables were log or asin-transformed to achieve the normality of residuals.

We assessed the changes in the species composition of plots using multivariate analysis for the two habitat types. The analyses included only plots with at least one species (a total of 92 plots; 4 plots had no species in 2022, the year of main interventions). Plot species composition differences were analysed using a non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis dissimilarities calculated on abundance data (expressed as percentages). Nitrophilous species were defined as those with Ellemberg's ecological indicator value for eutrophication above 6 (Pignatti 2005; Ellemberg 2009), the relative abundance and frequency of nitrophilous species were calculated and, due to the differences in the two types of plant communities, we conducted all the analyses separately for the two habitats. Moreover, we evaluated the extent and the divergence of species composition variations according to time and treatment using a Principal Response Curve (PRC) analysis (ter Braak and Smilauer 2012). In this analysis, time was treated as a categorical variable and was used as a covariate. The significance of the effect of the treatment on the species composition was assessed with a permutation analysis using 9999 permutations due to the hierarchical structure of the data and allowing freely exchangeable permutation on the whole plot level, and no permutation at the split-plot level. Given the differences in the two types of plant communities within the two habitats, we conducted the PRC analysis separately for the two habitats.

All analyses were conducted in the R environment (R version 2023.06.2): the LME models were fitted using the 'nlme' package version 3.1-162 (Pinheiro and Bates 2006); the NMDS was produced using the 'vegan' package version 2.6-4 (Oksanen et al. 2020); PRC analysis was performed using 'prc' function in the 'vegan' package version 2.6-4, (Oksanen et al. 2020). All plots were drawn using 'ggplot2' package version 3.4.2. (Wickham 2016).

Results

The sampling resulted in the identification of 65 species in 96 plots. Within the invaded plots for both habitats, we observed a significant effect of time for both habitats (interaction terms Treatment: Year, see Table 1) with a decrease in *Carpobrotus* cover after the year of intervention, but a reappearance of *Carpobrotus* seedlings was recorded after two years (Fig. 2A). *Carpobrotus* litter increased in both Vegetated sea cliffs and Coastal garrigues treated plots after the intervention, and declined the following year. Within the Vegetated sea cliffs' control plots, some *Carpobrotus* litter was recorded after the intervention year (Fig. 2B). In the control plots of both habitats, no *Carpobrotus* cover was present in 2020, whereas *Carpobrotus* seedlings were found in the years after the intervention, with cover never exceeding 0.5%, except in one plot in Vegetated sea cliffs, which contained 6% *Carpobrotus* cover in 2023 (Fig. 2A, B).

Table 1. Repeated Measurement ANOVA table for the effect of Invasion Status (Control plots vs. Invaded plots) and Year (sampling year 2020, 2021, 2022, 2023) on *Carpobrotus* cover (%) and *Carpobrotus* litter cover (%), provided for Vegetated sea cliffs (Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp., habitat code 1240 according to Dir. 92/43/EEC) and Coastal garrigues (Low formations of *Euphorbia* close to cliffs, hab. code 5320). numDF: numerator degree of freedom; denDF: denominator degree of freedom. Significance codes: p -value <0.001 ‘***’; p -value>0.01 ‘**’; p -value <0.05 ‘*’.

Response	Habitat	Variable	numDF	denDF	F value	p value
<i>Carpobrotus</i> Cover (%)	Vegetated sea cliffs	Invasive Status	1	10	25.94	<0.001***
		Year	3	28	12.39	<0.001***
		Invasive Status: Year	3	28	18.35	<0.001***
	Coastal garrigues	Invasive Status	1	10	248.04	<0.001***
		Year	3	28	93.39	<0.001***
		Invasive Status: Year	3	28	107.17	<0.001***
<i>Carpobrotus</i> Litter Cover (%)	Vegetated sea cliffs	Invasive Status	1	10	16.12	0.002**
		Year	3	28	4.99	0.007**
		Invasive Status: Year	3	28	2.42	0.087*
	Coastal garrigues	Invasive Status	1	10	112.51	<0.001***
		Year	3	28	4.46	0.011**
		Invasive Status: Year	3	28	5.75	0.003**

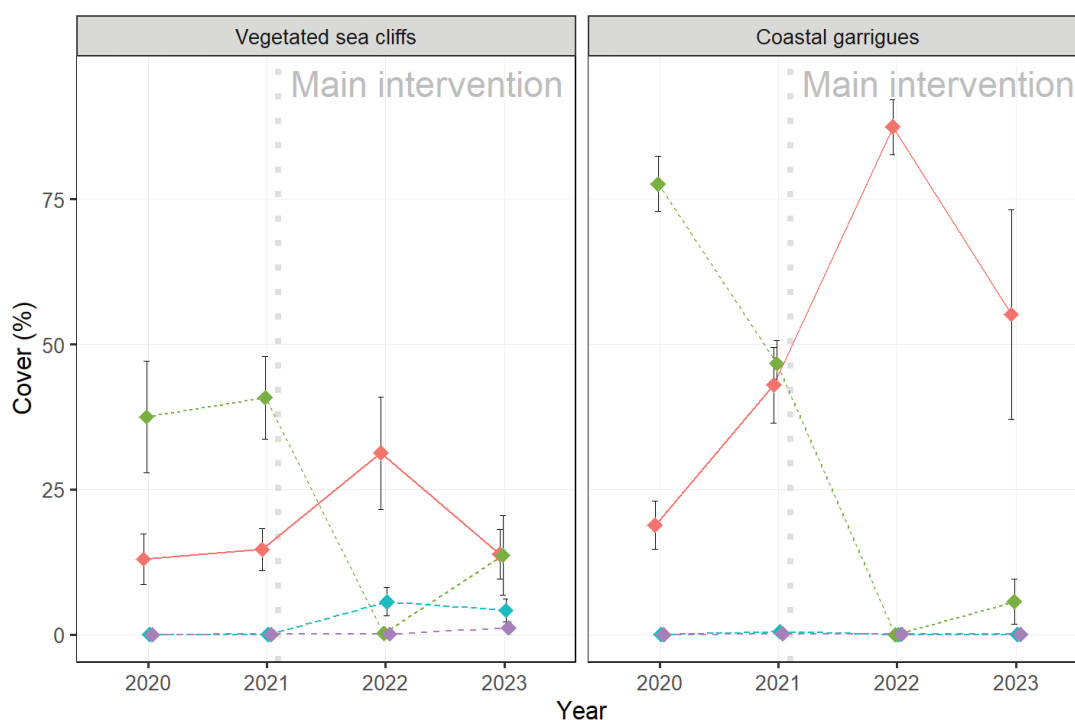


Figure 2. Litter cover of *Carpobrotus* and live *Carpobrotus* plants during 4 years of monitoring in the invaded and control plots of Vegetated sea cliffs (Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp., habitat code 1240 according to Dir. 92/43/EEC) and Coastal garrigues (Low formations of *Euphorbia* close to cliffs, hab. code 5320). The green dotted line represents live *Carpobrotus* plants in invaded plots, the red solid line represents the litter cover of *Carpobrotus* in invaded plots, the blue dashed line represents the litter cover of *Carpobrotus* in control plots and the violet long dashed line represents live *Carpobrotus* plants in control plots.

The native species cover was found to be significantly changed by time for Vegetated sea cliffs and by the interaction of time and invasive status for Coastal garrigues (respectively a p -value of <0.001 and 0.001, see Table 2). Moreover, the anal-

Table 2. Repeated Measurement ANOVA table for the effect of Invasion Status (Control plots vs. Invaded plots) and Year (sampling year 2020, 2021, 2022, 2023) on Native species cover (%), Species richness and Species diversity (Shannon Index), provided for Vegetated sea cliffs (Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp., habitat code 1240 according to Dir. 92/43/EEC) and Coastal garrigues (Low formations of *Euphorbia* close to cliffs, hab. code 5320). numDF: numerator degree of freedom; denDF: denominator degree of freedom. Significance codes: p -value <0.001 ‘***’; p -value>0.01 ‘**’; p -value <0.05 ‘*’.

Response	Habitat	Variable	numDF	denDF	F value	p value
Native Species Cover	Vegetated sea cliffs	Invasive Status	1	10	7.89	0.018**
		Year	3	28	8.21	<0.001***
		Invasive Status: Year	3	28	1.51	0.234
	Coastal garrigues	Invasive Status	1	10	22.46	0.001**
		Year	3	28	0.98	0.418
		Invasive Status: Year	3	28	7.68	0.001***
Species Richness	Vegetated sea cliffs	Invasive Status	1	10	0.01	0.921
		Year	3	28	22.71	<0.001***
		Invasive Status: Year	3	28	10.43	<0.001***
	Coastal garrigues	Invasive Status	1	10	48.92	<0.001***
		Year	3	28	10.76	<0.001***
		Invasive Status: Year	3	28	2.47	0.083*
Species Diversity (Shannon Index)	Vegetated sea cliffs	Invasive Status	1	10	0.15	0.709
		Year	3	28	25.66	<0.001***
		Invasive Status: Year	3	28	7.43	0.001**
	Coastal garrigues	Invasive Status	1	10	35.98	<0.001***
		Year	3	28	11.79	<0.001***
		Invasive Status: Year	3	28	8.43	<0.001***

ysis of species richness and diversity index showed significantly changes by time and by the interaction of time and invasive status for both Vegetated sea cliffs and Coastal garrigues (Table 2). The analysis of native species richness, diversity index, and native species abundance shows that the index values are higher in the Coastal garrigues control plots than in the invaded one (Fig. 3A–C). Still, after the year of intervention, the values in the invaded plots increased. Interestingly, after the year of intervention, the values of the Shannon index and native species richness values for Vegetated sea cliffs-invaded plots, exceed those of the controls.

The NMDS analysis (stress = 0.1441, non-metric fit $R^2 = 0.979$, linear fit $R^2 = 0.9$, see Fig. 4) showed a well-defined differentiation between the composition of the two habitats in control plots across the time, highlighting strong and short-term changes in the species composition after the removal of *Carpobrotus* within the invaded plot. It is interesting to note that in the top-left corner of Fig. 4, Vegetated sea cliffs and Coastal garrigues invaded plots appear in proximity and therefore like each other in composition, both are characterised by the abundant presence of *Carpobrotus*. However, after the *Carpobrotus* removal intervention, the differentiation between the invaded communities becomes more pronounced and the lines for invaded plots diverge (moving on both NMDS1 and NMDS2), getting closer in composition to their respective controls.

The PRC analysis of the composition of survey plots during the years is consistent with the mentioned trend of the fast-paced recovery of the invaded communities towards their habitat-related communities of the control plots. The analysis highlighted significant effects of treatment over time in both Vegetated sea cliffs (pseudo-F = 8.2, p value = 0.002) and Coastal garrigues (pseudo-F = 4.7, p value =

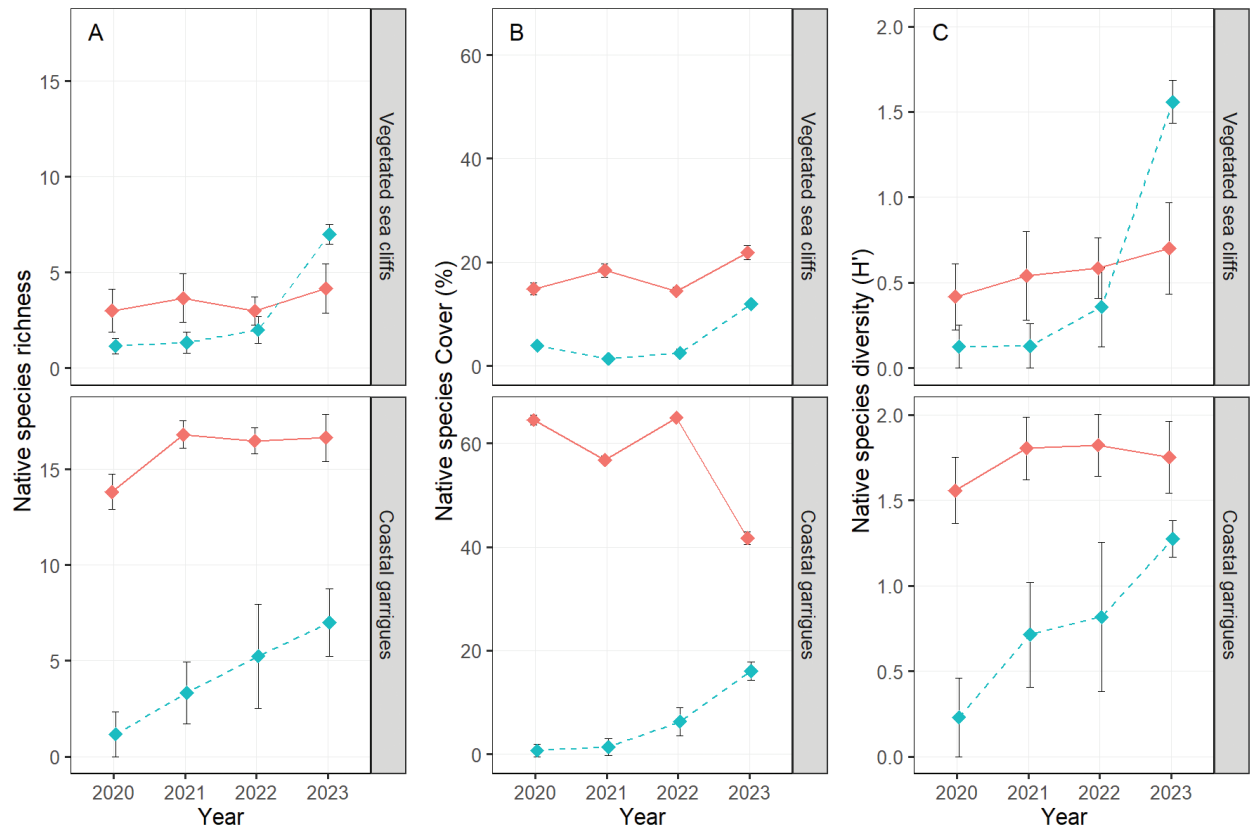


Figure 3. Native species richness, cover (%) and diversity (H') during 4 years of monitoring in the invaded and control plots of Vegetated sea cliffs (Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp., habitat code 1240 according to Dir. 92/43/EEC) and Coastal garrigues (Low formations of *Euphorbia* close to cliffs, hab. code 5320). **A** Native species richness **B** Native species cover (%) and **C** Native species diversity (H') in invaded (blue dashed line) and control plots (red solid line).

0.002). In both cases, a trend of convergence of the treated plots towards the control ones is visible (Suppl. material 2: fig. S1).

The cover of nitrophilous species was found to be significantly changed by time and by the interaction of time and treatment for Vegetated sea cliffs (respectively a p -value of 0.018 and 0.029, see Table 3), where the contribution of nitrophilous species in local communities increases drastically one year after *Carpobrotus* removal. Regarding Coastal garrigues, instead, we did not obtain significant values, even if there is a trend towards an increase that peaked in 2022, to then decline the following year, still maintaining values above that pre-intervention (see Fig. 5).

Discussion

Short-term effects after *Carpobrotus* control intervention

Our results build on the effects of *Carpobrotus* removal on coastal reef plant communities, based on a four-year survey period, focusing on describing and analysing the short-term response of native vegetation. Our results markedly indicated that the changes in community composition through the years correspond to a prompt recovery of the native plant communities following the removal of *Carpobrotus*. Prior to removal, both Vegetated sea cliffs and Coastal garrigues invaded communities were similar in composition, due to the very high impact of *Carpobrotus*

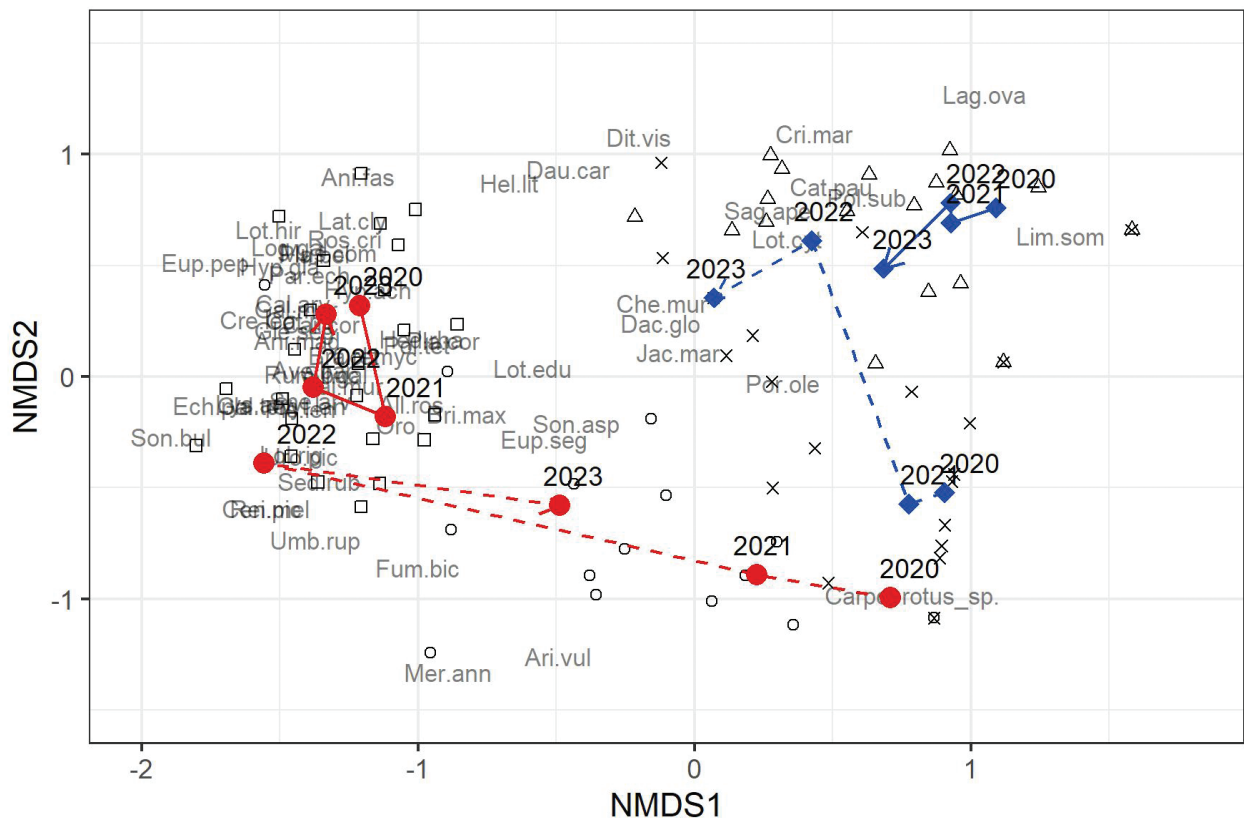


Figure 4. Non-metric multidimensional scaling (NMDS) ordination plot based on Bray–Curtis dissimilarities of the 96 sampled plots. Plots are grouped according to N2000 habitats and invasion status showing the years of monitoring. Solid lines represent control plots and dashed lines represent invaded plots. Blue lines and square symbols represent the Vegetated sea cliffs (Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp., habitat code 1240 according to Dir. 92/43/EEC) and red lines and round symbols represent the Coastal garrigues (Low formations of *Euphorbia* close to cliffs, hab. code 5320). Each symbol along lines indicates a year of monitoring. Codes of plant species are indicated in Suppl. material 1: table S3.

Table 3. Repeated Measurement ANOVA table for the effect of Invasion Status (Control plots vs. Invaded plots) and Year (sampling year 2020, 2021, 2022, 2023) on the relative abundance of nitrophilous species, provided for Vegetated sea cliffs (Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp., habitat code 1240 according to Dir. 92/43/EEC) and Coastal garrigues (Low formations of *Euphorbia* close to cliffs, hab. code 5320). numDF: numerator degree of freedom; denDF: denominator degree of freedom. Significance codes: *p*-value <0.001 ‘***’; *p*-value>0.01 ‘**’; *p*-value <0.05 ‘*’.

Response	Habitat	Variable	numDF	denDF	F value	<i>p</i> value
Relative abundance of nitrophilous species	Vegetated sea cliffs	Invasive Status	1	10	4.43	0.062
		Year	3	28	3.93	0.018*
		Invasive Status: Year	3	28	3.47	0.029*
	Coastal garrigues	Invasive Status	1	10	0.68	0.430
		Year	3	28	2.23	0.107
		Invasive Status: Year	3	28	0.64	0.594

at the alpha diversity level replacing and outcompeting characteristic native species as already shown in several similar contexts (Fried et al. 2014; Badalamenti et al. 2016; Mugnai et al. 2022). However, invaded plots of both types tended to converge towards their respective control plots during the following growing season after the removal of *Carpobrotus*. Following the removal, the Vegetated sea cliffs communities, were primarily colonised by *Jacobaea maritima* subsp. *maritima*, *Lotus cytisoides* and *Limonium sommierianum*, whereas those of Coastal garrigues

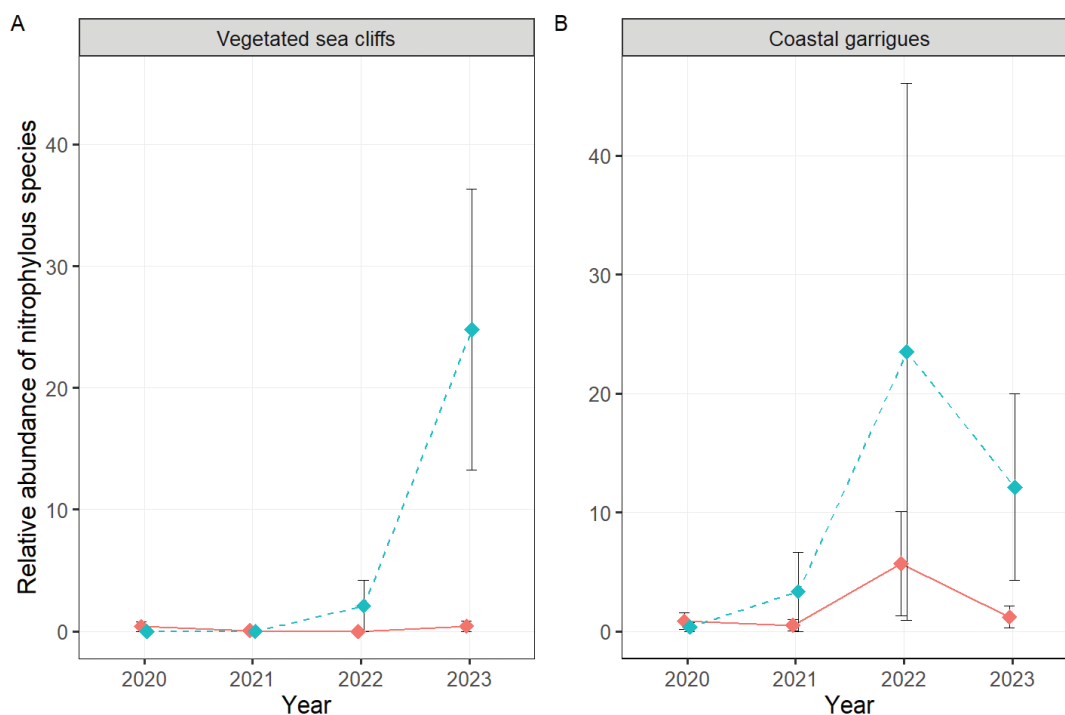


Figure 5. Relative abundance of nitrophilous species (%) for Vegetated sea cliffs (Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium* spp., habitat code 1240 according to Dir. 92/43/EEC) and Coastal garrigues (Low formations of *Euphorbia* close to cliffs, hab. code 5320) during 4 years of monitoring in the invaded (blue dashed line) and control plots (red solid line).

were characterised by *Helichrysum litoreum*, and *Pistacia lentiscus*, which are indicator species of the typical coastal vegetation (Foggi and Pancioli 2008). Moreover, some of these species have a high conservation and naturalistic value, such as *Limonium sommierianum*, as it is endemic to the Tuscan Archipelago (Baldini 1998). Similarly, on Bagaud Island (Var, France), following the removal of *Carpobrotus*, the post-eradication plant communities of rocky coastal cliffs exposed to sea spray tended to converge toward baseline communities characterised by species such as *Jacobaea maritima*, *Spergularia* spp. and *Polycarpon tetraphyllum* (Krebs et al. 2015). Hence, our data confirm once more the effectiveness of control actions in the case of *Carpobrotus* invasion. Indeed, the effectiveness of manual removal and mulching sheet on the removal of *Carpobrotus* has been already shown (see Lazzaro et al. 2023; Nascimento et al. 2023), but while other experiences have shown that the recovery of native communities can be achieved on a medium/long term (7 and 5 years after the interventions, respectively in Buisson et al. 2021 and Lazzaro et al. 2023), we show that already in two years native plants can colonize the areas where *Carpobrotus* had been manually removed.

Although the removal of *Carpobrotus* leads to an inevitable decrease in *Carpobrotus* coverage and a slow increase in the recolonization of native plants, the persistence of litter *in situ* can lead to a higher potential for reinvasion due to its large seed bank (Chenot et al. 2014). Indeed, as expected, in two growing seasons after removal, the emergence of seedlings of *Carpobrotus* has been observed within the survey plots and in all the study areas and appeared greater in the coastal garrigues and where litter was thicker and persistent after the interventions. Novoa et al. (2012, 2013) have shown that litter accumulation can repress the growth of native plants even after the removal of live plants, limiting the suitable area for the recolonisation of the natives.

However, removing the litter, other than adding a significant cost to the removal operation, may leave the soil subject to erosion (Chenot et al. 2018). On coastal reefs as per their exposure to atmospheric elements, the persistence of litter decreases quickly: we noted that litter cover diminished in 2023, probably due to soil runoff caused by wind and heavy autumn rains. Interestingly, with an opposite trend, litter was found in some control plots in Vegetated sea cliffs, with no live *Carpobrotus* present, probably transported from the invaded plots to the control plots during bad weather.

However, in one case, it has been shown that leaving the litter improves the germination of new *Carpobrotus* seedlings (Chenot et al. 2018) while, in another, the removal of both the living parts and the litter guarantees a more effective restoration of the native vegetation (Novoa et al. 2013), our results showed a good recovery of the native vegetation a few years after removal with a trend that increasingly approaches that of the control plots. In line with our results, Buisson et al. (2021) pointed out that coastal vegetation plant communities can recover and become relatively similar to the reference within a few years, while shrub communities may need more time to recover due to the competition from native herbaceous species. Buisson et al. (2021) and Campoy et al. (2018) suggested that *Carpobrotus* may have a persistent seed bank (> 5 years), but there are no exhaustive studies over a longer period. Gioria et al. (2012) placed *Carpobrotus edulis* in the category of short-term persistent seed banks, and Ruffino et al. (2015) reported that seeds of *Carpobrotus* can persist for 5 years after eradication. Numerous studies (Novoa et al. 2013; Ruffino et al. 2015; Buisson et al. 2021; Lazzaro et al. 2023) emphasised that it is, therefore, necessary to carry out regular monitoring of treated areas for 10 years before being able to assess the success of the eradication.

Effects on diversity indices and habitats composition

There are strong differences between Vegetated sea cliffs and Coastal garrigues habitats in terms of species richness and diversity (Foggi and Pancioli 2008; Mugnai et al. 2022), native species cover, and the response of their native communities to the removal of *Carpobrotus*. Moreover, the rapid response of the native vegetation follows the trend described by Buisson et al. (2021), Lazzaro et al. (2020a), and Andreu et al. (2010), confirming that, in the absence of post-removal disturbance, invaded and then treated areas can quickly and naturally revegetate, reaching levels of species richness and species diversity close to those of the corresponding control areas. Indeed, in the year following the removal of *Carpobrotus*, as shown in Fig. 2, species richness and diversity values in treated plots for Vegetated sea cliffs exceeded those of the control. This is likely due to the accumulation of *Carpobrotus* litter in areas that normally would not experience such soil buildup, which has allowed for the establishment of richer communities than those typically found in Vegetated sea cliffs. In 2023 there is also a slight divergence at the beta-diversity level, probably due to the entry of some ruderal and nitrophilous species, that are not typically found in either of these habitats, but which can be favoured by soil nutrient enrichment caused by *Carpobrotus* (Novoa et al. 2013; Fried et al. 2014; Malavasi et al. 2016; Lazzaro et al. 2023). The nitrophilous species with the highest cover values in both 2022 and 2023 are *Sonchus asper* (L.) Hill, *Polycarpon tetraphyllum* (L.) L., *Polypogon subspatheus*, *Mercurialis annua* L. and *Dactylis glomerata* L. all with Ellemberg's ecological indicator values fluctuating between 6 and 8. Similarly, also for Bagaud Island (Var, France), following the removal of *Carpobrotus*, there

was a shift of the post-eradication plant communities of the inner part of the island to the reference alonitrophilous ones. Although this inland area already had alonitrophilous herbaceous communities due to the presence of *Larus michahellis* (Naumann, 1840), there was no post-eradication community shift to low matorral communities, which are also present in this area (Krebs et al. 2015). Indeed, both *Carpobrotus* and *Larus michahellis* have been demonstrated to facilitate soil enrichment and entry of nitrophilous species (Novoa et al. 2013; Krebs et al. 2015).

Given the specialised flora that usually characterize the Vegetated sea cliffs, the occurrence of nitrophilous species in this habitat could probably be due to an unusual accumulation of *Carpobrotus* litter, which may have allowed the expansion of some non-characteristic species. In contrast, the relative abundance of nitrophilous species is reduced in habitat 5320 due to the greater complexity of this habitat, which develops on soils between the cliffs exposed to the action of the sea and the shrub communities of the more internal thermo-Mediterranean scrub (Perrino et al. 2013).

Conclusion

In conclusion, our results demonstrated that two years after the *Carpobrotus* removal, the habitat composition had shifted considerably towards a pre-invasion set of species. Furthermore, the recovery occurred also in terms of diversity indices, despite the initial impact of *Carpobrotus* on ecological parameters (mainly soil) favouring nitrophilous species in the early stages. We obtained significant and positive results in terms of native species re-establishment, in an optimistic short time, starting from the year following the removal. However, as the study focused on short-term patterns of regeneration following *Carpobrotus* management, the continuation of vegetation monitoring is pivotal to assess fully the recovery of native communities in the long term. Furthermore, the emergence of seedlings on the site due to the presence of litter and the persistence of the seed bank for many years, emphasises the importance of continued monitoring of the whole area for a long period (five to ten years from the main intervention), to ensure the seasonally repeated removal of new *Carpobrotus* spp. seedlings.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Alice Misuri: Methodology; Investigation; Visualization; Writing – Original Draft. Eugenia Siccardi: Methodology; Investigation; Visualization; Writing – Original Draft; Formal Analysis; Data curation. Michele Mugnai: Conceptualization; Methodology; Investigation; Visualization; Writing – review & editing. Renato Benesperi: Project administration; Validation; Writing – review & editing. Francesca Giannini: Project administration; Validation; Writing – review & editing. Michele Giunti: Project administration; Methodology; Validation; Writing – review & editing. Lorenzo Lazzaro: Project administration; Conceptualization; Methodology; Investigation; Writing – review & editing; Funding acquisition; Validation.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Data file used for analysis

Authors: Alice Misuri, Eugenia Siccardi, Michele Mugnai, Renato Benesperi, Francesca Giannini, Michele Giunti, Lorenzo Lazzaro

Data type: xlsx

Explanation note: **table S1**. Environmental variables for each plot; **table S2**. Species occurrences per plot; **table S3**. Species list and names abbreviation.

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Link: <https://doi.org/10.3897/neobiota.94.120644.suppl1>

Supplementary material 2

Principal response curves (PRC) showing the effect of the *Carpobrotus* removal on the plant species composition of the plots (only the 20 best fitting species are shown)

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Data type: pdf

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