Mixed responses of ant communities to the eradication of black rats and iceplants on a small Mediterranean island

Romane Blaya, Olivier Blight, Sébastien Aurelle, Julie Braschi, Laurence Berville, Philippe Ponel, Elise Buisson

Mixed responses of ant assemblages to Carpobrotus spp. and Rattus rattus eradications on a small Mediterranean island

Romane Blaya (romane.blaya@gmail.com)
Avignon Université, Aix Marseille Univ, CNRS, IRD, IMBE
Olivier Blight
Avignon Université, Aix Marseille Univ, CNRS, IRD, IMBE
Sébastien Aurelle **Julie Braschi**
Avignon Université, Aix Marseille Univ, CNRS, IRD, IMBE
Philippe Ponel **Laurence Berville**
Avignon Université, Aix Marseille Univ, CNRS, IRD, IMBE
Elise Buisson
Avignon Université, Aix Marseille Univ, CNRS, IRD, IMBE

Research Article

Keywords: Formicidae, Restoration, Exotic, Monitoring, Community Recovery

Posted Date: November 7th, 2023

DOI: https://doi.org/10.21203/rs.3.rs-3551654/v1

Additional Declarations: No competing interests reported.

Abstract

Eradication of invasive alien species (IAS) is often proposed to restore invaded ecosystems, with information on subsequent ecosystem recovery key to conservation policies. Although ants perform major ecological functions in the ecosystem, their response to IAS eradication has received relatively little monitoring. This study investigated ant response to *Carpobrotus* spp. (iceplant) and *R. rattus* (black rat) eradications on the small Mediterranean island of Bagaud (Var, France). Ant assemblages were monitored over a ten-year period, including two years before eradications, at six different sites, two invaded by *Carpobrotus* spp., two under high *R. rattus* pressure, and two control sites. We found inter-annual variations in ant assemblages but no before-after eradication trend at both control and rat eradication sites. However, there was a clear increase in ant species richness and abundance after the *Carpobrotus* eradication. A trend toward more homogeneous assemblages was observed, with an enhanced core of common Mediterranean ant species. Xerophilous and thermophilous species such as *Pheidole pallidula*, *Messor bouvieri*, and *Plagiolepis pygmaea* were more abundant, consistent with the return of native vegetation communities and possibly warmer and dryer microclimatic conditions. The trend was even stronger on the denser and thicker *Carpobrotus* eradication patch. Increased ant foraging activity is a good sign of restoration success, influencing different functions of the ecosystem, such as seed dispersal or nutrient cycling.

1. Introduction

Islands represent a major challenge for biodiversity conservation, hosting high levels of endemism that exceed those of mainland regions - for example, eight times higher for vertebrates (Kier et al. 2009). Yet much of this biodiversity is being lost, threatened by multiple factors including biological invasions (Fernández-Palacios et al. 2021). Compared to mainland regions, islands suffer higher invasion rates (Dawson et al. 2017), with invasive alien species (IAS) identified as one of the main causes of species extinctions (Pyšek et al. 2020). Invasions often cause changes in community structure and modify abiotic characteristics of ecosystems (Strayer et al. 2006; Pyšek et al. 2012). Insular ecosystems are remarkably vulnerable due to their small size, small populations and vacant niches without competitors or predators (Fernández-Palacios et al. 2021; Russell et al. 2017).

Considered as a hotspot of biodiversity, the Mediterranean basin and its numerous islands (>10,000) are highly threatened by invasions (Myers et al. 2000; Hulme et al. 2008) and could be the ecosystems most impacted by IAS by 2100 (Sala et al. 2000). Many islands are now faced with numerous interacting invasive species, such as plants and seed dispersers, which pose a severe threat to the native biodiversity (Courchamp et al. 2011; Russell and Kaiser-Bunbury 2019).

Such invasive meltdown was described for two invasive taxa, the black rat (*Rattus rattus*) and iceplants (*Carpobrotus* spp., Aizoceae), which promote each other (Bourgeois et al. 2005). The black rat (*Rattus rattus*) is considered as one of the 15 most prevalent IAS on islands (Russell et al. 2017). It has colonized most of the Mediterranean islands over the last 2,000 years (Ruffino et al. 2009), with direct effects on

biodiversity, through predation. The black rat is widely known to prey on seabird eggs and chicks, and on large-bodied invertebrates, such as beetles, spiders, gastropods (Caut et al. 2009; Nascimento et al. 2019). It also has indirect effects by dispersing invasive plant seeds, including *Carpobrotus* species (Bourgeois et al. 2005; Shiels 2011).

Also known as iceplants or hottentot figs, *Carpobrotus* species were introduced to Europe in the seventeenth century from South Africa, Australia or Chile for ornamental and soil stabilization purposes (Campoy et al. 2018). *Carpobrotus acinaciformis*, *Carpobrotus edulis* and their hybrids (*Carpobrotus* aff. *acinaciformis*) have now colonized a large portion of the western Mediterranean coast (Suehs et al. 2004; Campoy et al. 2018). They establish in various coastal environments, from sandy dunes to rocky cliffs, forming dense monospecific mats with an abundant litter (Campoy et al. 2018). The succulent species of *Carpobrotus* (Aizoceae) are a major threat to native biodiversity in Mediterranean coastal ecosystems (Hulme et al. 2008; Carboneras et al. 2018). They shift soil chemical parameters (Novoa et al. 2013a; Vieites-Blanco and González-Prieto 2018), decrease plant diversity (Badalamenti et al. 2016), and reduce invertebrate abundance and modify community composition (Rodríguez et al. 2020).

In order to mitigate the adverse impacts of IAS on biodiversity, control or eradication operations are carried out, prioritizing the most prevalent IAS, including the black rat and the iceplant (Carboneras et al. 2018). In the Mediterranean Basin, controls and eradications have generally led to a positive response in terms of biodiversity (Jones et al. 2016). *Carpobrotus* eradications have been shown to positively impact native plants (Lazzaro et al. 2020; Buisson et al. 2021). *Rattus rattus* eradications have benefited reptiles (Krebs et al. 2015) and breeding bird populations (Howald et al. 2010; Bourgeois et al. 2013). However, while several studies investigated invertebrate recovery after rat eradication (St Clair et al. 2011; Ruscoe et al. 2013) and *Carpobrotus* removal (St Clair et al. 2011; Braschi et al. 2021b, a), these did not include ants.

Ubiquitous and abundant, ants play a key role in ecosystem functioning, in soil structure, as predators, or as promoters of plant dispersion (Del Toro et al. 2012; De Almeida et al. 2020). They are sensitive and respond quickly to environmental change, which makes them good bioindicators (Majer 1983; Andersen et al. 2002). Habitat structure, microclimate, resource availability and competitive interactions are indirect factors responsible for ant community modifications (Andersen 2019). The decrease in ant diversity correlated with habitat simplification and loss of resources like seeds points to the need to monitor ant communities, a crucial component of the ecosystem, in restoration projects (Underwood and Fisher 2006). Very few studies focus on ant response to plant or mammal IAS eradication (Parr et al. 2010; Osunkoya et al. 2011; Lenda et al. 2013), although ant monitoring is a relevant way of assessing ecosystem change (Kaspari and Majer 2000).

The aim of this study was to explore ant responses to *Carpobrotus* spp. and *R. rattus* eradications on the small Mediterranean island of Bagaud (Var, France). Ant assemblages were compared over a ten-year monitoring period, including two years before eradications, at six different sites on the island: two sites

invaded by *Carpobrotus* spp., two sites under high *R. rattus* pressure, and the last two as controls. We hypothesized that : (i) Ant species richness would increase after the IAS eradication at the four invaded sites and remain stable at the control sites; (ii) Ant abundance would increase at the eradication sites and remain stable at the control sites; and (iii) The composition of ant assemblages would change after the IAS eradication at the four invaded sites and remain stable at the control sites; (iv) The magnitude of changes in ant assemblage structure and composition would be greater after the eradication of *Carpobrotus* spp. than of *R. rattus*, as *Carpobrotus* spp. would induce more habitat modifications.

1. Materials and methods

1.1 Study area

Bagaud island is a small uninhabited Mediterranean island of 58 ha located in the Hyères archipelago (Var, France), which is part of the Port-Cros National Park. It is a strict biological reserve with restricted access since 2007. The continent is 7.5km away and the main nearest island, Port-Cros, is 1 km away. The archipelago has a Mediterranean climate with annual mean temperatures ranging between 13.5 and 19.5°C and an average 621.5 mm of precipitations per year (1991-2020, Ile du Levant weather station, Infoclimat). Vegetation on Bagaud island is typical of Mediterranean regions, with dominant matorral and halophilous plants on the rocky shores. In addition to its rich native plant communities, the invasive plant species *Carpobrotus edulis* and *Carpobrotus* aff*. acinaciformis* were introduced in the nineteenth century by military engineers. Intended to stabilize the soil around the island's forts, these species covered 2-ha of the island at their worst. The only non-flying mammal of the island, the black rat (*R. rattus*), was also introduced, probably during the Roman period (Ruffino et al. 2015). It preys on *Carpobrotus* spp. fruits as well as potentially on various seeds, beetles, geckos, and seabird eggs and chicks (Ruffino et al. 2015). Eradications of *Carpobotus* spp. and *R. rattus* were carried out on the island in late 2011 and 2012.

1.2 Study sites

We monitored the temporal dynamics of ant communities via three treatments: (1) *Carpobrotus* spp. removal (hereafter CA), (2) *Rattus rattus* removal (hereafter RR) and (3) control sites with no eradication action (hereafter CO) (Fig.1). Limited availability of sites led us to select two sites per treatment only. The two *Carpobrotus* spp. removal sites were selected for size, large enough to set up transects of 10 pitfall traps (see section 1.3). The two *Rattus rattus* removal sites were selected as having the highest rate of *Rattus rattus* captures and being accessible for arthropod sampling.

Carpobrotus spp. was eradicated from study sites CA1 and CA2 between November 2011 and February 2012. Plants were uprooted and left to compost on the site to avoid further dissemination (Chenot et al. 2018). Control operations have been conducted every year since then to prevent the recolonization of the area from the seed bank (Ruffino et al. 2015; Buisson et al. 2021).

Rats were trapped from September 2011 to June 2012 at RR1 and RR2 sites. Rat eradication was carried out first via trapping sessions and later supplemented by rodenticide (Ruffino et al. 2015). Twenty permanent bait stations were set up along the coast under biosecurity measures (Ruffino et al. 2015). Traces on baits were spotted again in 2013, and while biosecurity increased, rat traces became significantly more numerous in 2017, fluctuating thereafter (Braschi 2021).

Our two control sites were selected as presenting the lowest rates of rat captures, i.e. below 37 individuals / hectare (Ruffino et al. 2015), and no *Carpobrotus* ever reported. CO1 and CO2 sites represent the island's two main vegetation types (low and high matorrals). A habitat description for each study site (CA1 and CA2, RR1 and RR2, CO1 and CO2) is available in Table 1.

1.3 Sampling design

Ants were collected using pitfall traps, a method commonly used to sample ground-dwelling arthropods and which has proved efficient in assessing ant species richness and spatial patterns (Steiner et al. 2005; Salata et al. 2020). The two first years of sampling, 2010 and 2011, were pre-eradication, while the following four surveys were carried out post-eradication, i.e. in 2013, 2015, 2017, and 2019. Each year, 10 pitfall traps (5 cm diameter and 10 cm depth), half-filled with ethylene-glycol, were installed 5 meters apart on a 45-meter transect on each site. They were collected every three weeks, four times from late April to late June / early July, and again collected between mid-September and mid-October, a total of four sampling periods. Ants were counted and identified to species level or to species-group level, following Lebas et al. (2016).

1.4 Data analysis

Statistical analyses were performed using R version 4.2.2 (2022-10-31). The temporal dynamics of ant communities was studied for each site independently. Sites were not statistically compared with each other due to the limited number of true site replicates (see section 1.2) (as in Braschi et al. 2021b, a). First, changes in species richness and total abundance of ants over time were assessed. Each trap's species richness was calculated. Raw ant counts were not used because these depend on species-specific social behavior (Steiner et al. 2005) and do not reflect the natural unit of ant diversity, the individual nest (Gotelli et al. 2011). Thus, the abundance of each species was transformed on a 7-score scale (Hoffmann et al. 2000): 1 = 1 ant; 2 = 2-5 ants; 3 = 6-10 ants; 4 = 11-20 ants; 5 = 21-50 ants; 6 = 51-100; and 7 > 100 ants. Total abundance was obtained by summing the species scores for each trap. Each site was studied independently, using a generalized linear mixed model from the glmmTMB R package (Brooks et al., 2017), with a negative binomial distribution (logit link) with either species richness or total abundance as response variables. The year was set as a fixed factor and the period of sampling and the trap number were set as random factors. Multiple comparisons between years were performed using the Sidak method.

The assemblage compositions of all sites were compared over the six years of survey using the non-metric multidimensional scaling (NMDS) approach with the vegan package (Oksanen et al. 2022). For this analysis, abundance classes were averaged over the four sampling periods of each year for each trap. Assemblages were represented using a Bray-Curtis dissimilarity matrix. Overall significant difference between assemblages was assessed using PERMANOVA, followed by pairwise adonis tests (Martinez Arbizu 2020). Further individual species abundance analyses were conducted for the sites showing significant dissimilarity. SIMPER analysis (Clarke 1993) was used to identify species contributing up to 75% of the assemblage dissimilarity between the pre-eradication grouped years and the post-eradication grouped years. Their individual abundance response to the year factor was assessed using glmmTMB with the same features as the total abundance models.

2. Results

A total of 35,414 specimens, 24 species, and 13 genera were identified during the study (Appendix A). The majority of the individuals belonged to the Myrmicinae family (25,944 individuals), followed by Formicinae (9,491 individuals), and a few Ponerinae were also counted (28 individuals). CO2 had the most species, 18, and CA2 had the least, 11 species. *Pheidole pallidula* was the most abundant and frequently found species. Statistical results of the fitted models are available in Appendix B.

2.1 Species richness and total abundance

RR2 had the overall highest mean species richness, with an average of 4.90 ± 1.98 species caught per trap, against 2.38 ± 1.25 for RR1, the overall lowest value. Species richness per trap remained unchanged during the pre-eradication surveys in 2010 and 2011 at all the studied sites. The two *Carpobrotus* removal sites showed a significant increase in species richness per trap after the eradication (Fig 1). In 2013, CA2 species richness was not significantly different from either the pre-eradication years or from all the post-eradication years. Only in years 2015 to 2019 was species richness significantly higher than in 2010. At CA1, the species richness of 2013 was significantly higher than that of 2010. Years 2015 and 2017 showed significantly higher values compared to the pre-eradication years, and values in 2019 were significantly higher than all the other years, reaching an average of 5.06 species per trap. RR2 mean species richness per trap changed slightly over time, with significantly higher values in 2019 than in 2013 and 2017 (Fig 2). The other sites did not show any significant differences between years.

RR2 also had the overall highest mean abundance, an average abundance of 10.55 ± 5.18, against the overall lowest average of 4.87 ± 2.91 per trap at CO2 (Fig 3). Total ant abundance per trap increased significantly after the eradication at CA1 (Fig 3). Abundance levels in 2010 and 2011 were significantly lower than in any other year of sampling. They were up to 5 times lower than in 2019, when total abundance reached 11.75 ± 4.13. The mean total abundance of 2019 traps was also significantly higher than in 2013 and 2015. CA2 also showed a slight increase in total ant abundance over the years, 2010 mean total abundance being significantly lower than in the other years. It then significantly increased in

2011 and 2013 and again in 2015 and 2019. At RR1, RR2 and CO1, abundances fluctuated, with no particular trend (Fig 3), although they were significantly higher in 2019 compared to 2010 at both RR1 and RR2. Ant abundances did not change over the years at CO2.

2.2 Assemblage composition

The assemblages of CA1, CA2, RR2 and CO2 showed a significant percentage of variance according to year grouping. With an R^2 of 32%, CA1 assemblages differed the most across years, followed by CA2 with 19% and RR2 and CO2 with respectively 14% and 15%. At the two *Carpobrotus* eradication sites, 2010 and 2011 assemblages were the most heterogeneous (Fig 4). The CA1 assemblages of 2010 and 2011 were similar to each other but both different from all the subsequent years (2013-2019). The assemblage composition of 2019, the most homogeneous, was significantly different from all the previous years. Assemblages shifted over the years, from heterogeneous pre-eradication assemblages driven by *Hypoponera eduardi* to more homogeneous ones with a strong species core composed of *Pheidole pallidula, Plagiolepis pygmaea, Crematogaster scutellaris,* and *Crematogaster sordidula.* This trend was weaker at CA2, where polygons overlapped much more. The 2010 assemblage composition differed from all the subsequent years and the 2011 composition was only significantly different from 2019. The pairwise analysis also showed significant differences between 2013, 2015, and 2019. Like CA1, the CA2 assemblages became more homogeneous over the years, except for 2017, where the polygon was larger than in 2015. At RR2, the assemblage composition of 2010 was significantly different from all the other years except 2011. The assemblage of 2013 only differed from 2010 and 2017. With the largest polygon, the 2015 assemblage composition was the most heterogeneous (Fig 4). At CO2, the assemblages of 2010 and 2011 were significantly different from 2017 and 2019. At RR2 and CO2, polygons overlapped much more than at the *Carpobrotus* eradication sites (Fig 4).

2.3 Individual species abundance

At the CA1 site, three species contributed to 75% of the pre-/post-eradication assemblage dissimilarity: *P. pallidula, Messor bouvieri,* and *P. pygmaea*. For these three species, individual mean abundance increased after the eradication (Fig 5). This trend was stronger for *P. pallidula* and *P. pygmaea,* both showing abundance levels close to zero before *Carpobrotus* eradication, significantly lower than in the subsequent years. Their abundance steadily increased, reaching 4.12 ± 1.18 and 2.22 ± 1.48, respectively, in 2019. At CA2, the same three species contributed to most of the dissimilarity between pre- and post-eradication years. While *P. pygmaea* abundance did not change over the years, *P. pallidula* began to be significantly more abundant from 2015 on and *M. bouvieri* from 2017 on (Fig 5). At RR2, 75% of the pre-/post-eradication dissimilarity was attributed to six species: *P. pallidula*, *Lasius* gr. *grandis*, *M. bouvieri*, *C. scutellaris*, *P. pygmaea,* and *Camponotus sylvaticus*. Unlike the *Carpobrotus* eradication sites, no before-after trend was observed (Fig 5). The abundance level of *P. pallidula* was significantly lower in 2013 compared to 2010 and 2011. *Lasius* gr. *grandis* was significantly more abundant in 2019 compared

to 2013 and 2017. *Messor bouvieri* abundance was significantly lower in 2015 and 2017 compared to 2010. In contrast, *P. pygmaea* was less abundant in 2010 compared to all subsequent years except 2013, while *C. sylvaticus* abundance was higher in 2013 than in 2010, 2011, and 2017. Concerning CO2, among the three main species contributing to pre-/post-eradication dissimilarity, only *C. sordidula* abundance was significantly influenced by year (Fig 6). It was significantly less abundant in 2010 and 2011 compared to the subsequent years.

3. Discussion

The objective of the study was to assess changes in ant assemblage structure and composition after simultaneous eradication of *Carpobrotus* and *R. rattus* on a small Mediterranean island. As we expected, the temporal dynamics of ant assemblages showed a stronger trend toward pre-/post-eradication dissimilarity at *Carpobrotus* eradication sites (CA1 and CA2) than at rat eradication sites (RR1 and RR2).

At the control sites (CO1 et CO2), assemblage structures and compositions either remained stable or changed slightly, usually without showing any particular trend. At both sites, species richness remained stable and assemblage composition showed a strong overlap over the years. *Crematogaster sordidula* abundance was an exception, increasing for unknown reasons after 2011 at CO2.

Buisson et al. (2021) showed that the plant communities of Bagaud island remained relatively stable outside the *Carpobrotus* removal sites. The absence of habitat modifications or perturbations is consistent with relative stability in control assemblages. However, the slight changes in assemblage structure and composition observed across the years reflect a change in ant foraging activity, affecting trapping success (Steiner et al. 2005). These changes could be explained by climate variations (Pelini et al. 2014; Resasco et al. 2014) and/or by demographically volatile species (Samways 1990). The Mediterranean climate is known for the strong inter-annual variability of temperatures and precipitations (Deitch et al. 2017), and these parameters can strongly influence ant foraging activity (Whitford and Ettershank 1975; Levings 1983; Lasmar et al. 2021). Increased temperature can positively influence foraging activity, increasing ant abundance and diversity, with responses varying according to the thermal tolerance of the species (Stuble et al. 2013). In Mediterranean open vegetation, temperature is the main driver of changes in ground ant communities (Retana and Cerdá 2000). Apart from climatic variability, resource availability can also be a strong driver of demographic changes and foraging behavior in ants (Bernstein 1979; Davidson et al. 1985; Traniello 1989). Moreover, some species show changes in their nest distributions from year to year and highly flexible behavior (Gordon 1991).

Our sampling is composed of common Mediterranean heat-tolerant species that could benefit from open and dry habitats to increase their activity (Cros et al. 2016). According to the Porquerolles weather station, 2011 was the wettest and one of the coldest years of our study (Table 2). Xerophilous and thermophilous species could have reduced their foraging activity because of non-favorable climatic conditions, reducing their probability of being trapped, and explaining the slightly lower overall ant abundance that year. Nevertheless, the low abundance of *Crematogaster sordidula* in both 2010 and 2011 compared to the rest

of the sampling is surprising, as the climate differed between these two years, 2011 being warmer and much dryer. Yet *Crematogaster sordidula* mean abundance did not exceed an average of one worker caught per trap. As its most common habitats are open and well exposed (Retana et al. 2015), workers could occasionally visit the high matorral site to forage from the nearby open areas which represent a favorable nesting habitat. A new nest closer to the sampling site could explain the higher worker abundance after 2011.

Similarly, no before-after pattern was observed at the rat eradication sites. Overall, 2019 had higher levels of abundance and species richness, and assemblages were more homogeneous. Individual responses were mixed, depending on species identity and sites. Although eradications initially decreased rat densities on Bagaud island, the population density rose again in 2015 and 2017. The lack of response from ants to rat eradication in the first years is consistent with previous findings that ants are not commonly a prey of *Rattus rattus* (Courchamp et al. 2011; Riofrío-Lazo and Páez-Rosas 2015). Moreover, ant abundance and species richness were already at similar or higher levels than those of the control sites. Other studies on rat eradication or exclusion failed to show any response in ant abundance (Sinclair et al. 2005; Vergara et al. 2021). One of them even showed a decrease in ant abundance, attributed to either the rodenticide or to ant behavioral change in response to higher resource availability (Rate 2009).

Variation in ant abundances and ant species richness at the rat eradication sites could, once again, be correlated with climatic variability. A warmer and dryer climate was recorded in 2019, especially compared to 2010 and 2013. Concerning individual species abundances, *Lasius* gr. *grandis* and *Plagiolepis pygmaea*, which are both thermophilous Mediterranean species, showed abundance variations consistent with higher activity under a warmer climate (Majeed et al. 2021; Santos et al. 2022). However, no particular trend was observed in *Pheidole pallidula* and *Camponotus sylvaticus* abundance variations. Abundance variability in such dominant and highly competitive species (Retana et al. 2015) has already been observed, with worker numbers multiplying as resource availability increases (Samways 1990). Similarly, the granivorous ant *Messor bouvieri* is highly dependent on seed availability (Willott et al. 2000), which can be influenced by vegetation dynamics and climate variation through complex interactions (Carmona et al. 2015).

The fact that inter-annual variations without a before-after trend were observed at the control and rat-invaded sites indicates that the changes observed in ant assemblages at *Carpobrotus* spp.-invaded sites can be attributed to the *Carpobrotus* eradication. Indeed, while the pool of species found at the CA sites did not change after eradication, we observed a shift toward more homogeneous assemblages. *Carpobrotus* eradication promoted an abundant species core composed of common xerophilous Mediterranean ant species. This trend was stronger at the *Carpobrotus* eradication site located on the cliff top and surrounded by low matorral (CA1), where we observed an overall steady increase in ant abundances.

These changes in the ant assemblages can be explained by modification of the ecosystem after eradication. As a succulent and with its ability to create dense litter and mats, *Carpobrotus* induces

changes at the soil surface: it reduces evapotranspiration, incident solar radiation, and thus temperature (Molinari et al., 2007; Novoa et al., 2013). Native vegetation quickly recovered after eradication, inducing changes in habitats, from poor and homogeneous dense mats of *Carpobrotus* to higher plant species richness, a decrease in litter cover, and fluctuation of bare ground cover with seasons and years (Buisson et al. 2021). At a small scale, the return of native vegetation added habitat structure and resource diversity, and allowed a return to the warmer and dryer microclimate that benefits most Mediterranean ants.

Ants are sensitive to habitat disturbance through the indirect effects of change in habitat structure, microclimate, resource availability, and competitive interactions (Andersen 2019). Ant species richness and abundance are closely correlated to vegetation variables, such as vegetation cover and strata (Retana and Cerdá 2000; Lassau and Hochuli 2004). Diversified plant communities promote more heterogeneity in the vegetation structure, with varying plant heights and microhabitats (Buisson et al. 2021), which has already been shown to promote ant species diversity in various ecosystems (Vasconcelos et al. 2008; Hill et al. 2008; Martello et al. 2018).

The dynamics of the resource use of many ant species is strongly influenced by microclimatic conditions (Cerdá et al. 1998), in particular by fine-scale temperature changes (Stuble et al. 2013) and by microhabitat formation (Luque and Reyes López 2007). The diversification of vegetation also influences nest site availability (Herbers 1989) and temporal spread of certain food resources, such as nectar or seeds, contrasting with the few weeks of *Carpobrotus* flowering during spring (Campoy et al. 2018). The increased post-eradication abundance of ant species with a specialized diet, such as *Plagiolepis pygmaea* that feed on liquid food and *Messor bouvieri* that feed on seeds (Arnan et al. 2014), confirm the benefits of habitat diversification. However, removing the abundant litter produced by *Carpobrotus* might be detrimental to other specialized species, such as the hypogaeic species *Hypoponera eduardi* characteristic of the pre-eradication assemblages of this site (CA1).

While our results clearly showed the benefits of *Carpobrotus* eradication on ant occupancy at CA1 located on the cliff top and surrounded by low matorral, there was less evidence of benefits at CA2. This coastal site had patchy vegetation with some native species before eradication and higher rock cover, which remained at the same level throughout the study (Buisson et al. 2021). The eradication of *Carpobrotus* spp. probably did not trigger enough changes to the ecosystem to induce modifications in ant assemblage composition and structure.

4. Conclusion

Carpobrotus spp. eradication, and thus habitat change, was a stronger driver of change in the ant assemblages than climate. Our results suggest that the restoration of diversified ant assemblages, with higher foraging activity, was more effective at CA1, where *Carpobrotus* was denser and thicker. Increased ant activity goes hand-in-hand with strong habitat transformation and the return of native and diversified plant communities. Higher levels of multifunctionality are reached in species-rich ecosystems (Lefcheck

et al. 2015) and many functions also depend on abundance (Soliveres et al. 2016). As ecosystem engineers, ants are known to participate in seed dispersal, and to improve soil structure and nutrient cycling (Folgarait 1998). Thus, increasing ant activity and richness at eradication sites may contribute to an increase in functions performed, including the enhancement of soil quality (Nkem et al. 2000) and seed-dropping frequency (Arnan et al. 2010). Ants play an active role in ecosystem recovery, and their quick response to the eradication here points to their efficacy as bioindicators when assessing restoration success.

Our data come from eradications carried out on a single small Mediterranean island, and this study should therefore be replicated on other islands to confirm our results. The harmful effects of *Carpobrotus* are leading to an increasing number of eradication campaigns, particularly in the Mediterranean. Ant monitoring would appear to be a relevant means of monitoring such restoration and conservation strategies.

Declarations

Acknowledgements

We thank Port-Cros National Park and Naturalia-Environment for providing financial support for the study. We are grateful to all those who helped with field work and sorting insects from traps, as well as to Marjorie Sweetko for English language revision.

References

1. Andersen AN (2019) Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group. Journal of Animal Ecology 88:350–362. https://doi.org/10.1111/1365-2656.12907
2. Andersen AN, Hoffmann BD, Müller WJ, Griffiths AD (2002) Using ants as bioindicators in land management: simplifying assessment of ant community responses. Journal of Applied Ecology 39:8–17. https://doi.org/10.1046/j.1365-2664.2002.00704.x
3. Arnan X, Cerdá X, Retana J (2014) Ant functional responses along environmental gradients. Journal of Animal Ecology 83:1398–1408
4. Arnan X, Retana J, Rodrigo A, Cerdá X (2010) Foraging behaviour of harvesting ants determines seed removal and dispersal. Insect Soc 57:421–430. https://doi.org/10.1007/s00040-010-0100-7
5. Badalamenti E, Gristina L, Laudicina VA, et al (2016) The impact of Carpobrotus cfr. acinaciformis (L.) L. Bolus on soil nutrients, microbial communities structure and native plant communities in Mediterranean ecosystems. Plant and Soil 409:19–34
6. Bernstein RA (1979) Schedules of Foraging Activity in Species of Ants. Journal of Animal Ecology 48:921–930. https://doi.org/10.2307/4204

7. Bourgeois K, Ouni R, Pascal M, et al (2013) Dramatic increase in the Zembretta Yelkouan shearwater breeding population following ship rat eradication spurs interest in managing a 1500-year old invasion. Biol Invasions 15:475–482. https://doi.org/10.1007/s10530-013-0419-x
8. Bourgeois K, Suehs CM, Vidal E, Médail F (2005) Invasional meltdown potential: Facilitation between introduced plants and mammals on French Mediterranean islands. Écoscience 12:248–256. https://doi.org/10.2980/i1195-6860-12-2-248.1
9. Braschi J, Hélard O, Mazzia C, et al (2021a) Impacts of the removal of invasive Carpobrotus on spider assemblage dynamics. Biodivers Conserv 30:497–518. https://doi.org/10.1007/s10531-020-02102-6
10. Braschi J, Torres A, Fadda S, et al (2021b) Beetle assemblage dynamics after invasive ice plant (Carpobrotus) removal on a small Mediterranean island. Restoration Ecology 29:e13387. https://doi.org/10.1111/rec.13387
11. Brooks ME, Kristensen K, Benthem KJ van, et al (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378–400
12. Buisson E, Braschi J, Chenot-Lescure J, et al (2021) Native plant community recovery after Carpobrotus (ice plant) removal on an island — results of a 10-year project. Applied Vegetation Science 24:e12524. https://doi.org/10.1111/avsc.12524
13. Campoy JG, Acosta ATR, Affre L, et al (2018) Monographs of invasive plants in Europe: Carpobrotus. Botany Letters 165:440–475
14. Carboneras C, Genovesi P, Vilà M, et al (2018) A prioritised list of invasive alien species to assist the effective implementation of EU legislation. Journal of Applied Ecology 55:539–547. https://doi.org/10.1111/1365-2664.12997
15. Carmona CP, Mason NWH, Azcárate FM, Peco B (2015) Inter-annual fluctuations in rainfall shift the functional structure of Mediterranean grasslands across gradients of productivity and disturbance. Journal of Vegetation Science 26:538–551. https://doi.org/10.1111/jvs.12260
16. Caut S, Angulo E, Courchamp F (2009) Avoiding surprise effects on Surprise Island: alien species control in a multitrophic level perspective. Biol Invasions 11:1689–1703. https://doi.org/10.1007/s10530-008-9397-9
17. Cerdá X, Retana J, Manzaneda A (1998) The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117:404–412. https://doi.org/10.1007/s004420050674
18. Chenot J, Affre L, Gros R, et al (2018) Eradication of invasive Carpobrotus sp.: effects on soil and vegetation. Restoration Ecology 26:106–113. https://doi.org/10.1111/rec.12538
19. Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x
20. Courchamp F, Caut S, Bonnaud E, et al (2011) Eradication of alien invasive species: surprise effects and conservation successes. In: Island Invasives: Eradication and Management. pp 285–289

21. Cros S, Cerdá X, Retana J (2016) Spatial and temporal variations in the activity patterns of Mediterranean ant communities. Écoscience
22. Davidson DW, Samson DA, Inouye RS (1985) Granivory in the Chihuahuan Desert: Interactions within and between Trophic Levels. Ecology 66:486–502. https://doi.org/10.2307/1940397
23. Dawson W, Moser D, van Kleunen M, et al (2017) Global hotspots and correlates of alien species richness across taxonomic groups. Nat Ecol Evol 1:1–7. https://doi.org/10.1038/s41559-017-0186
24. De Almeida T, Blight O, Mesléard F, et al (2020) Harvester ants as ecological engineers for Mediterranean grassland restoration: Impacts on soil and vegetation. Biological Conservation 245:108547. https://doi.org/10.1016/j.biocon.2020.108547
25. Deitch M, Sapundjieff M, Feirer S (2017) Characterizing Precipitation Variability and Trends in the World's Mediterranean-Climate Areas. Water 9:259. https://doi.org/10.3390/w9040259
26. Del Toro I, Ribbons RR, Pelini SL (2012) The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecol News 17:133–146
27. Fernández-Palacios JM, Kreft H, Irl SDH, et al (2021) Scientists' warning – The outstanding biodiversity of islands is in peril. Global Ecology and Conservation 31:e01847. https://doi.org/10.1016/j.gecco.2021.e01847
28. Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7:1221–1224
29. Gordon DM (1991) Behavioral Flexibility and the Foraging Ecology of Seed-Eating Ants. The American Naturalist 138:379–411. https://doi.org/10.1086/285223
30. Gotelli NJ, Ellison AM, Dunn RR, Sanders NJ (2011) Counting ants (Hymenoptera: Formicidae): Biodiversity sampling and statistical analysis for myrmecologists. College of Arts and Sciences Faculty Publications
31. Herbers JM (1989) Community structure in north temperate ants: temporal and spatial variation. Oecologia 81:201–211. https://doi.org/10.1007/BF00379807
32. Hill JG, Summerville KS, Brown RL (2008) Habitat Associations of Ant Species (Hymenoptera: Formicidae) in a Heterogeneous Mississippi Landscape. Environmental Entomology 37:453–463. https://doi.org/10.1093/ee/37.2.453
33. Hoffmann BD, Griffiths AD, Andersen AN (2000) Responses of ant communities to dry sulfur deposition from mining emissions in semi-arid tropical Australia, with implications for the use of functional groups. Austral Ecology 25:653–663. https://doi.org/10.1111/j.1442-9993.2000.tb00071.x
34. Howald G, Donlan CJ, Faulkner KR, et al (2010) Eradication of black rats Rattus rattus from Anacapa Island. Oryx 44:30–40. https://doi.org/10.1017/S003060530999024X
35. Hulme PE, Brundu G, Camarda I, et al (2008) Assessing the risks to Mediterranean islands ecosystems from alien plant introductions. 39–56

36. Jones HP, Holmes ND, Butchart SHM, et al (2016) Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113:4033–4038. https://doi.org/10.1073/pnas.1521179113
37. Kaspari M, Majer JD (2000) Chapter 7: Using Ants to Monitor Environmental Change. In: Ants - Standards Methods for Measuring and Monitoring Biodiversity, Smithsonian Institution Press. pp 89–98
38. Kier G, Kreft H, Lee TM, et al (2009) A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences 106:9322–9327. https://doi.org/10.1073/pnas.0810306106
39. Krebs E, Abba A, Gillet P, et al (2015) Responses of reptile populations to the eradication of the Roof Rat (Rattus rattus) on Bagaud Island (Port-Cros National Park, Var, France). Rev Ecol-Terre Vie 70:99–109
40. Lasmar CJ, Bishop TR, Parr CL, et al (2021) Geographical variation in ant foraging activity and resource use is driven by climate and net primary productivity. Journal of Biogeography 48:1448–1459. https://doi.org/10.1111/jbi.14089
41. Lassau SA, Hochuli DF (2004) Effects of habitat complexity on ant assemblages. Ecography 27:157–164. https://doi.org/10.1111/j.0906-7590.2004.03675.x
42. Lazzaro L, Tondini E, Lombardi L, Giunti M (2020) The eradication of Carpobrotus spp. in the sand-dune ecosystem at Sterpaia (Italy, Tuscany): indications from a successful experience. Biologia 75:199–208. https://doi.org/10.2478/s11756-019-00391-z
43. Lebas C, Galkowski C, Blatrix R, Wegnez P (2016) Fourmis d'Europe occidentale. Delachaux et Niestlé
44. Lefcheck JS, Byrnes JEK, Isbell F, et al (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat Commun 6:6936. https://doi.org/10.1038/ncomms7936
45. Lenda M, Witek M, Skórka P, et al (2013) Invasive alien plants affect grassland ant communities, colony size and foraging behaviour. Biol Invasions 15:2403–2414. https://doi.org/10.1007/s10530-013-0461-8
46. Levings SC (1983) Seasonal, Annual, and Among-site Variation in the Ground Ant Community of a Deciduous Tropical Forest: Some Causes of Patchy Species Distributions. Ecological Monographs 53:435–455. https://doi.org/10.2307/1942647
47. Luque GM, Reyes López J (2007) Effect of experimental small-scale spatial heterogeneity on resource use of a Mediterranean ground-ant community. Acta Oecologica 32:42–49. https://doi.org/10.1016/j.actao.2007.03.003
48. Majeed W, Khawaja M, Rana N (2021) Assessing fluctuation of ant populations in a distinct ecological habitat to track climate change effects. Biodiversitas Journal of Biological Diversity 22:. https://doi.org/10.13057/biodiv/d220533
49. Majer JD (1983) Ants: Bio-indicators of minesite rehabilitation, land-use, and land conservation. Environmental Management 7:375–383. https://doi.org/10.1007/BF01866920

50. Martello F, de Bello F, Morini MS de C, et al (2018) Homogenization and impoverishment of taxonomic and functional diversity of ants in Eucalyptus plantations. Sci Rep 8:3266. https://doi.org/10.1038/s41598-018-20823-1
51. Martinez Arbizu P (2020) pairwiseAdonis: Pairwise multilevel comparison using adonis
52. Molinari N, D'Antonio C, Thomson G (2007) Carpobrotus as a case study of the complexities of species impacts. In: Ecosystem Engineers: Plants to Protists. Academic Press
53. Myers N, Mittermeier RA, Mittermeier CG, et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501
54. Nascimento T, Oliveira N, Fagundes AI, et al (2019) Diet selection of introduced black ratsRattus rattus L. in relation to plant availability on Berlenga Island, Portugal / Préférence alimentaire des rats noirs introduits Rattus rattus L. en relation avec la disponibilité de la flore sur l'île de Berlenga, Portugal. Ecologia Mediterranea 45:15–29. https://doi.org/10.3406/ecmed.2019.2072
55. Nkem JN, Lobry de Bruyn LA, Grant CD, Hulugalle NR (2000) The impact of ant bioturbation and foraging activities on surrounding soil properties. Pedobiologia 44:609–621. https://doi.org/10.1078/S0031-4056(04)70075-X
56. Novoa A, González L, Moravcová L, Pyšek P (2013a) Constraints to native plant species establishment in coastal dune communities invaded by Carpobrotus edulis: Implications for restoration. Biological Conservation 164:1–9. https://doi.org/10.1016/j.biocon.2013.04.008
57. Novoa A, Rodríguez R, Richardson D, González L (2013b) Soil quality: a key factor in understanding plant invasion? The case of Carpobrotus edulis (L.). Biol Invasions 16:429–443. https://doi.org/10.1007/s10530-013-0531-y
58. Oksanen J, Simpson GL, Blanchet FG, et al (2022) vegan: Community Ecology Package
59. Osunkoya OO, Polo C, Andersen AN (2011) Invasion impacts on biodiversity: responses of ant communities to infestation by cat's claw creeper vine, Macfadyenaunguis-cati (Bignoniaceae) in subtropical Australia. Biol Invasions 13:2289–2302. https://doi.org/10.1007/s10530-011-0040-9
60. Parr CL, Ryan BJ, Setterfield SA (2010) Habitat Complexity and Invasive Species: The Impacts of Gamba Grass (Andropogon gayanus) on Invertebrates in an Australian Tropical Savanna. Biotropica 42:688–696. https://doi.org/10.1111/j.1744-7429.2010.00637.x
61. Pelini SL, Diamond SE, Nichols LM, et al (2014) Geographic differences in effects of experimental warming on ant species diversity and community composition. Ecosphere 5:art125. https://doi.org/10.1890/ES14-00143.1
62. Pyšek P, Hulme PE, Simberloff D, et al (2020) Scientists' warning on invasive alien species. Biological Reviews 95:1511–1534. https://doi.org/10.1111/brv.12627
63. Pyšek P, Jarošík V, Hulme PE, et al (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology 18:1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

64. Rate SR (2009) Does rat control benefit forest invertebrates at Moehau, Coromandel Peninsula? DOC Research & Development Series
65. Resasco J, Pelini SL, Stuble KL, et al (2014) Using Historical and Experimental Data to Reveal Warming Effects on Ant Assemblages. PLOS ONE 9:e88029. https://doi.org/10.1371/journal.pone.0088029
66. Retana J, Arnan X, Cerdá X (2015) A multidimensional functional trait analysis of resource exploitation in European ants. Ecology 96:2781–2793. https://doi.org/10.1890/14-2326.1
67. Retana J, Cerdá X (2000) Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123:436–444. https://doi.org/10.1007/s004420051031
68. Riofrío-Lazo M, Páez-Rosas D (2015) Feeding Habits of Introduced Black Rats, Rattus rattus, in Nesting Colonies of Galapagos Petrel on San Cristóbal Island, Galapagos. PLOS ONE 10:e0127901. https://doi.org/10.1371/journal.pone.0127901
69. Rodríguez J, Novoa A, Cordero-Rivera A, et al (2020) Biogeographical comparison of terrestrial invertebrates and trophic feeding guilds in the native and invasive ranges of Carpobrotus edulis
70. Ruffino L, Bourgeois K, Vidal E, et al (2009) Invasive rats and seabirds after 2,000 years of an unwanted coexistence on Mediterranean islands. Biol Invasions 11:1631–1651. https://doi.org/10.1007/s10530-008-9394-z
71. Ruffino L, Krebs E, Passetti A, et al (2015) Eradications as scientific experiments: progress in simultaneous eradications of two major invasive taxa from a Mediterranean island: Simultaneous pest eradications in the Mediterranean. Pest Management Science 71:189–198
72. Ruscoe WA, Sweetapple PJ, Perry M, Duncan RP (2013) Effects of Spatially Extensive Control of Invasive Rats on Abundance of Native Invertebrates in Mainland New Zealand Forests. Conservation Biology 27:74–82. https://doi.org/10.1111/j.1523-1739.2012.01932.x
73. Russell JC, Kaiser-Bunbury CN (2019) Consequences of Multispecies Introductions on Island Ecosystems. Annu Rev Ecol Evol Syst 50:169–190. https://doi.org/10.1146/annurev-ecolsys-110218-024942
74. Russell JC, Meyer J-Y, Holmes ND, Pagad S (2017) Invasive alien species on islands: impacts, distribution, interactions and management. Environmental Conservation 44:359–370
75. Sala OE, Chapin III FS, Armesto JJ, et al (2000) Global Biodiversity Scenarios for the Year 2100. Science 287:1770–1774
76. Salata S, Kalarus K, Borowiec L, et al (2020) How estimated ant diversity is biased by the sampling method? A case study of Crete: a Mediterranean biodiversity hotspot. Biodivers Conserv 29:3031–3050. https://doi.org/10.1007/s10531-020-02014-5
77. Samways MJ (1990) Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. Oecologia 84:482–490. https://doi.org/10.1007/BF00328164
78. Santos JT, Brito EL da S, Santos GMM (2022) The role of vegetation structure and abiotic factors affecting the temporal dynamics of ant foraging. Sociobiology 69:e7422–e7422.

https://doi.org/10.13102/sociobiology.v69i2.7422

79. Shiels AB (2011) Frugivory by introduced black rats (Rattus rattus) promotes dispersal of invasive plant seeds. Biol Invasions 13:781–792. https://doi.org/10.1007/s10530-010-9868-7
80. Sinclair L, McCartney J, Godfrey J, et al (2005) How did invertebrates respond to eradication of rats from Kapiti Island, New Zealand? New Zealand Journal of Zoology 32:293–315. https://doi.org/10.1080/03014223.2005.9518421
81. Soliveres S, van der Plas F, Manning P, et al (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459. https://doi.org/10.1038/nature19092
82. St Clair JJH, Poncet S, Sheehan DK, et al (2011) Responses of an island endemic invertebrate to rodent invasion and eradication. Animal Conservation 14:66–73. https://doi.org/10.1111/j.1469-1795.2010.00391.x
83. Steiner FM, Schlick-Steiner B, Moder K, et al (2005) Congruence of data from different trapping periods of ant pitfall catches (Hymenoptera: Formicidae). Sociobiology 46:105–116
84. Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends in Ecology & Evolution 21:645–651. https://doi.org/10.1016/j.tree.2006.07.007
85. Stuble K, Pelini S, Diamond S, et al (2013) Foraging by forest ants under experimental climatic warming: A test at two sites. Ecology and evolution 3:482–91. https://doi.org/10.1002/ece3.473
86. Suehs CM, Affre L, Médail F (2004) Invasion dynamics of two alien Carpobrotus (Aizoaceae) taxa on a Mediterranean island: I. Genetic diversity and introgression. Heredity 92:31–40. https://doi.org/10.1038/sj.hdy.6800374
87. Traniello JFA (1989) Foraging Strategies of Ants. Annu Rev Entomol 34:191–210. https://doi.org/10.1146/annurev.en.34.010189.001203
88. Underwood EC, Fisher BL (2006) The role of ants in conservation monitoring: If, when, and how. Biological Conservation 132:166–182. https://doi.org/10.1016/j.biocon.2006.03.022
89. Vasconcelos HL, Leite MF, Vilhena JMS, et al (2008) Ant diversity in an Amazonian savanna: Relationship with vegetation structure, disturbance by fire, and dominant ants. Austral Ecology 33:221–231. https://doi.org/10.1111/j.1442-9993.2007.01811.x
90. Vergara OE, Nelson N, Hartley S (2021) Effects of mammal exclusion on invertebrate communities in New Zealand. Austral Ecology 46:776–791. https://doi.org/10.1111/aec.13020
91. Vieites-Blanco C, González-Prieto SJ (2018) Effects of Carpobrotus edulis invasion on main litter and soil characteristics in backdune and rocky coastal habitats with oceanic climate. Plant Soil 425:363–374. https://doi.org/10.1007/s11104-018-3598-5
92. Whitford WG, Ettershank G (1975) Factors Affecting Foraging Activity in Chihuahuan Desert Harvester Ants. Environmental Entomology 4:689–696. https://doi.org/10.1093/ee/4.5.689
93. Willott SJ, Compton SG, Incoll LD (2000) Foraging, food selection and worker size in the seed harvesting ant Messor bouvieri. Oecologia 125:35–44. https://doi.org/10.1007/PL00008889

.2307/4204" targettype="DOI" class="RefTarget">

- Bourgeois K, Ouni R, Pascal M et al (2013) Dramatic increase in the Zembretta Yelkouan shearwater breeding population following ship rat eradication spurs interest in managing a 1500-year old invasion. Biol Invasions 15:475–482. https://doi.org/10.1007/s10530-013-0419-x
- Bourgeois K, Suehs CM, Vidal E, Médail F (2005) Invasional meltdown potential: Facilitation between introduced plants and mammals on French Mediterranean islands. Écoscience 12:248–256. https://doi.org/10.2980/i1195-6860-12-2-248.1
- Braschi J, Hélard O, Mazzia C et al (2021a) Impacts of the removal of invasive Carpobrotus on spider assemblage dynamics. Biodivers Conserv 30:497–518. https://doi.org/10.1007/s10531-020-02102-6
- Braschi J, Torres A, Fadda S et al (2021b) Beetle assemblage dynamics after invasive ice plant (Carpobrotus) removal on a small Mediterranean island. Restor Ecol 29:e13387. https://doi.org/10.1111/rec.13387
- Brooks ME, Kristensen K, van Benthem KJ et al (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J 9:378–400
- Buisson E, Braschi J, Chenot-Lescure J et al (2021) Native plant community recovery after Carpobrotus (ice plant) removal on an island — results of a 10-year project. Appl Veg Sci 24:e12524. https://doi.org/10.1111/avsc.12524
- Campoy JG, Acosta ATR, Affre L et al (2018) Monographs of invasive plants in Europe: Carpobrotus. Bot Lett 165:440–475
- Carboneras C, Genovesi P, Vilà M et al (2018) A prioritised list of invasive alien species to assist the effective implementation of EU legislation. J Appl Ecol 55:539–547. https://doi.org/10.1111/1365-2664.12997
- Carmona CP, Mason NWH, Azcárate FM, Peco B (2015) Inter-annual fluctuations in rainfall shift the functional structure of Mediterranean grasslands across gradients of productivity and disturbance. J Veg Sci 26:538–551. https://doi.org/10.1111/jvs.12260
- Caut S, Angulo E, Courchamp F (2009) Avoiding surprise effects on Surprise Island: alien species control in a multitrophic level perspective. Biol Invasions 11:1689–1703. https://doi.org/10.1007/s10530-008-9397-9
- Cerdá X, Retana J, Manzaneda A (1998) The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117:404–412. https://doi.org/10.1007/s004420050674
- Chenot J, Affre L, Gros R et al (2018) Eradication of invasive Carpobrotus sp.: effects on soil and vegetation. Restor Ecol 26:106–113. https://doi.org/10.1111/rec.12538
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x
- Courchamp F, Caut S, Bonnaud E et al (2011) Eradication of alien invasive species: surprise effects and conservation successes. In: Island Invasives: Eradication and Management. pp 285–289
- Cros S, Cerdá X, Retana J (2016) Spatial and temporal variations in the activity patterns of Mediterranean ant communities. Écoscience

- Davidson DW, Samson DA, Inouye RS (1985) Granivory in the Chihuahuan Desert: Interactions within and between Trophic Levels. Ecology 66:486–502. https://doi.org/10.2307/1940397
- Dawson W, Moser D, van Kleunen M et al (2017) Global hotspots and correlates of alien species richness across taxonomic groups. Nat Ecol Evol 1:1–7. https://doi.org/10.1038/s41559-017-0186
- De Almeida T, Blight O, Mesléard F et al (2020) Harvester ants as ecological engineers for Mediterranean grassland restoration: Impacts on soil and vegetation. Biol Conserv 245:108547. https://doi.org/10.1016/j.biocon.2020.108547
- Deitch M, Sapundjieff M, Feirer S (2017) Characterizing Precipitation Variability and Trends in the World's Mediterranean-Climate Areas. Water 9:259. https://doi.org/10.3390/w9040259
- Del Toro I, Ribbons RR, Pelini SL (2012) The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecol News 17:133–146
- Fernández-Palacios JM, Kreft H, Irl SDH et al (2021) Scientists' warning – The outstanding biodiversity of islands is in peril. Global Ecol Conserv 31:e01847. https://doi.org/10.1016/j.gecco.2021.e01847
- Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers Conserv 7:1221–1224
- Gordon DM (1991) Behavioral Flexibility and the Foraging Ecology of Seed-Eating Ants. Am Nat 138:379–411. https://doi.org/10.1086/285223
- Gotelli NJ, Ellison AM, Dunn RR, Sanders NJ (2011) Counting ants (Hymenoptera: Formicidae): Biodiversity sampling and statistical analysis for myrmecologists. College of Arts and Sciences Faculty Publications
- Herbers JM (1989) Community structure in north temperate ants: temporal and spatial variation. Oecologia 81:201–211. https://doi.org/10.1007/BF00379807
- Hill JG, Summerville KS, Brown RL (2008) Habitat Associations of Ant Species (Hymenoptera: Formicidae) in a Heterogeneous Mississippi Landscape. Environ Entomol 37:453–463. https://doi.org/10.1093/ee/37.2.453
- Hoffmann BD, Griffiths AD, Andersen AN (2000) Responses of ant communities to dry sulfur deposition from mining emissions in semi-arid tropical Australia, with implications for the use of functional groups. Austral Ecol 25:653–663. https://doi.org/10.1111/j.1442-9993.2000.tb00071.x
- Howald G, Donlan CJ, Faulkner KR et al (2010) Eradication of black rats Rattus rattus from Anacapa Island. Oryx 44:30–40. https://doi.org/10.1017/S003060530999024X
- Hulme PE, Brundu G, Camarda I et al (2008) Assessing the risks to Mediterranean islands ecosystems from alien plant introductions. 39–56
- Jones HP, Holmes ND, Butchart SHM et al (2016) Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113:4033–4038. https://doi.org/10.1073/pnas.1521179113
- Kaspari M, Majer JD (2000) Chap. 7: Using Ants to Monitor Environmental Change. Ants - Standards Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, pp 89–98

- Kier G, Kreft H, Lee TM et al (2009) A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences 106:9322–9327. https://doi.org/10.1073/pnas.0810306106
- Krebs E, Abba A, Gillet P et al (2015) Responses of reptile populations to the eradication of the Roof Rat (Rattus rattus) on Bagaud Island (Port-Cros National Park, Var, France). Rev Ecol-Terre Vie 70:99–109
- Lasmar CJ, Bishop TR, Parr CL et al (2021) Geographical variation in ant foraging activity and resource use is driven by climate and net primary productivity. J Biogeogr 48:1448–1459. https://doi.org/10.1111/jbi.14089
- Lassau SA, Hochuli DF (2004) Effects of habitat complexity on ant assemblages. Ecography 27:157–164. https://doi.org/10.1111/j.0906-7590.2004.03675.x
- Lazzaro L, Tondini E, Lombardi L, Giunti M (2020) The eradication of Carpobrotus spp. in the sand-dune ecosystem at Sterpaia (Italy, Tuscany): indications from a successful experience. Biologia 75:199–208. https://doi.org/10.2478/s11756-019-00391-z
- Lebas C, Galkowski C, Blatrix R, Wegnez P (2016) Fourmis d'Europe occidentale. Delachaux et Niestl&#233
- Lefcheck JS, Byrnes JEK, Isbell F et al (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat Commun 6:6936. https://doi.org/10.1038/ncomms7936
- Lenda M, Witek M, Skórka P et al (2013) Invasive alien plants affect grassland ant communities, colony size and foraging behaviour. Biol Invasions 15:2403–2414. https://doi.org/10.1007/s10530-013-0461-8
- Levings SC (1983) Seasonal, Annual, and Among-site Variation in the Ground Ant Community of a Deciduous Tropical Forest: Some Causes of Patchy Species Distributions. Ecol Monogr 53:435–455. https://doi.org/10.2307/1942647
- Luque GM, Reyes López J (2007) Effect of experimental small-scale spatial heterogeneity on resource use of a Mediterranean ground-ant community. Acta Oecol 32:42–49. https://doi.org/10.1016/j.actao.2007.03.003
- Majeed W, Khawaja M, Rana N (2021) Assessing fluctuation of ant populations in a distinct ecological habitat to track climate change effects. Biodiversitas J Biol Divers 22. https://doi.org/10.13057/biodiv/d220533
- Majer JD (1983) Ants: Bio-indicators of minesite rehabilitation, land-use, and land conservation. Environ Manage 7:375–383. https://doi.org/10.1007/BF01866920
- Martello F, de Bello F, de Morini MS C, et al (2018) Homogenization and impoverishment of taxonomic and functional diversity of ants in Eucalyptus plantations. Sci Rep 8:3266. https://doi.org/10.1038/s41598-018-20823-1
- Martinez Arbizu P (2020) pairwiseAdonis: Pairwise multilevel comparison using adonis
- Molinari N, D'Antonio C, Thomson G (2007) Carpobrotus as a case study of the complexities of species impacts. Ecosystem Engineers: Plants to Protists. Academic Press

- Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501
- Nascimento T, Oliveira N, Fagundes AI et al (2019) Diet selection of introduced black ratsRattus rattus L. in relation to plant availability on Berlenga Island, Portugal / Préférence alimentaire des rats noirs introduits Rattus rattus L. en relation avec la disponibilité de la flore sur l'île de Berlenga, Portugal. Ecologia Mediterranea 45:15–29. https://doi.org/10.3406/ecmed.2019.2072
- Nkem JN, Lobry de Bruyn LA, Grant CD, Hulugalle NR (2000) The impact of ant bioturbation and foraging activities on surrounding soil properties. Pedobiologia 44:609–621. https://doi.org/10.1078/S0031-4056(04)70075-X
- Novoa A, González L, Moravcová L, Pyšek P (2013a) Constraints to native plant species establishment in coastal dune communities invaded by Carpobrotus edulis: Implications for restoration. Biol Conserv 164:1–9. https://doi.org/10.1016/j.biocon.2013.04.008
- Novoa A, Rodríguez R, Richardson D, González L (2013b) Soil quality: a key factor in understanding plant invasion? The case of Carpobrotus edulis (L). Biol Invasions 16:429–443. https://doi.org/10.1007/s10530-013-0531-y
- Oksanen J, Simpson GL, Blanchet FG et al (2022) vegan: Community Ecology Package
- Osunkoya OO, Polo C, Andersen AN (2011) Invasion impacts on biodiversity: responses of ant communities to infestation by cat's claw creeper vine, Macfadyenaunguis-cati (Bignoniaceae) in subtropical Australia. Biol Invasions 13:2289–2302. https://doi.org/10.1007/s10530-011-0040-9
- Parr CL, Ryan BJ, Setterfield SA (2010) Habitat Complexity and Invasive Species: The Impacts of Gamba Grass (Andropogon gayanus) on Invertebrates in an Australian Tropical Savanna. Biotropica 42:688–696. https://doi.org/10.1111/j.1744-7429.2010.00637.x
- Pelini SL, Diamond SE, Nichols LM et al (2014) Geographic differences in effects of experimental warming on ant species diversity and community composition. Ecosphere 5:art125. https://doi.org/10.1890/ES14-00143.1
- Pyšek P, Hulme PE, Simberloff D et al (2020) Scientists' warning on invasive alien species. Biol Rev 95:1511–1534. https://doi.org/10.1111/brv.12627
- Pyšek P, Jarošík V, Hulme PE et al (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob Change Biol 18:1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x
- Rate SR (2009) Does rat control benefit forest invertebrates at Moehau. Coromandel Peninsula? DOC Research & Development Series
- Resasco J, Pelini SL, Stuble KL et al (2014) Using Historical and Experimental Data to Reveal Warming Effects on Ant Assemblages. PLoS ONE 9:e88029. https://doi.org/10.1371/journal.pone.0088029
- Retana J, Arnan X, Cerdá X (2015) A multidimensional functional trait analysis of resource exploitation in European ants. Ecology 96:2781–2793. https://doi.org/10.1890/14-2326.1
- Retana J, Cerdá X (2000) Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123:436–

444. https://doi.org/10.1007/s004420051031

- Riofrío-Lazo M, Páez-Rosas D (2015) Feeding Habits of Introduced Black Rats, Rattus rattus, in Nesting Colonies of Galapagos Petrel on San Cristóbal Island, Galapagos. PLoS ONE 10:e0127901. https://doi.org/10.1371/journal.pone.0127901
- Rodríguez J, Novoa A, Cordero-Rivera A et al (2020) Biogeographical comparison of terrestrial invertebrates and trophic feeding guilds in the native and invasive ranges of Carpobrotus edulis
- Ruffino L, Bourgeois K, Vidal E et al (2009) Invasive rats and seabirds after 2,000 years of an unwanted coexistence on Mediterranean islands. Biol Invasions 11:1631–1651. https://doi.org/10.1007/s10530-008-9394-z
- Ruffino L, Krebs E, Passetti A et al (2015) Eradications as scientific experiments: progress in simultaneous eradications of two major invasive taxa from a Mediterranean island: Simultaneous pest eradications in the Mediterranean. Pest Manag Sci 71:189–198
- Ruscoe WA, Sweetapple PJ, Perry M, Duncan RP (2013) Effects of Spatially Extensive Control of Invasive Rats on Abundance of Native Invertebrates in Mainland New Zealand Forests. Conserv Biol 27:74–82. https://doi.org/10.1111/j.1523-1739.2012.01932.x
- Russell JC, Kaiser-Bunbury CN (2019) Consequences of Multispecies Introductions on Island Ecosystems. Annu Rev Ecol Evol Syst 50:169–190. https://doi.org/10.1146/annurev-ecolsys-110218-024942
- Russell JC, Meyer J-Y, Holmes ND, Pagad S (2017) Invasive alien species on islands: impacts, distribution, interactions and management. Environ Conserv 44:359–370
- Sala OE, Chapin FS III, Armesto JJ et al (2000) Global Biodiversity Scenarios for the Year 2100. Science 287:1770–1774
- Salata S, Kalarus K, Borowiec L et al (2020) How estimated ant diversity is biased by the sampling method? A case study of Crete: a Mediterranean biodiversity hotspot. Biodivers Conserv 29:3031–3050. https://doi.org/10.1007/s10531-020-02014-5
- Samways MJ (1990) Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. Oecologia 84:482–490. https://doi.org/10.1007/BF00328164
- Santos JT, Brito EL, da Santos S GMM (2022) The role of vegetation structure and abiotic factors affecting the temporal dynamics of ant foraging. Sociobiology 69:e7422–e7422. https://doi.org/10.13102/sociobiology.v69i2.7422
- Shiels AB (2011) Frugivory by introduced black rats (Rattus rattus) promotes dispersal of invasive plant seeds. Biol Invasions 13:781–792. https://doi.org/10.1007/s10530-010-9868-7
- Sinclair L, McCartney J, Godfrey J et al (2005) How did invertebrates respond to eradication of rats from Kapiti Island, New Zealand? New Z J Zool 32:293–315. https://doi.org/10.1080/03014223.2005.9518421
- Soliveres S, van der Plas F, Manning P et al (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459. https://doi.org/10.1038/nature19092

- St Clair JJH, Poncet S, Sheehan DK et al (2011) Responses of an island endemic invertebrate to rodent invasion and eradication. Anim Conserv 14:66–73. https://doi.org/10.1111/j.1469-1795.2010.00391.x
- Steiner FM, Schlick-Steiner B, Moder K et al (2005) Congruence of data from different trapping periods of ant pitfall catches (Hymenoptera: Formicidae). Sociobiology 46:105–116
- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends Ecol Evol 21:645–651. https://doi.org/10.1016/j.tree.2006.07.007
- Stuble K, Pelini S, Diamond S et al (2013) Foraging by forest ants under experimental climatic warming: A test at two sites. Ecol Evol 3:482–491. https://doi.org/10.1002/ece3.473
- Suehs CM, Affre L, Médail F (2004) Invasion dynamics of two alien Carpobrotus (Aizoaceae) taxa on a Mediterranean island: I. Genetic diversity and introgression. Heredity 92:31–40. https://doi.org/10.1038/sj.hdy.6800374
- Traniello JFA (1989) Foraging Strategies of Ants. Annu Rev Entomol 34:191–210. https://doi.org/10.1146/annurev.en.34.010189.001203
- Underwood EC, Fisher BL (2006) The role of ants in conservation monitoring: If, when, and how. Biol Conserv 132:166–182. https://doi.org/10.1016/j.biocon.2006.03.022
- Vasconcelos HL, Leite MF, Vilhena JMS et al (2008) Ant diversity in an Amazonian savanna: Relationship with vegetation structure, disturbance by fire, and dominant ants. Austral Ecol 33:221–231. https://doi.org/10.1111/j.1442-9993.2007.01811.x
- Vergara OE, Nelson N, Hartley S (2021) Effects of mammal exclusion on invertebrate communities in New Zealand. Austral Ecol 46:776–791. https://doi.org/10.1111/aec.13020
- Vieites-Blanco C, González-Prieto SJ (2018) Effects of Carpobrotus edulis invasion on main litter and soil characteristics in backdune and rocky coastal habitats with oceanic climate. Plant Soil 425:363–374. https://doi.org/10.1007/s11104-018-3598-5
- Whitford WG, Ettershank G (1975) Factors Affecting Foraging Activity in Chihuahuan Desert Harvester Ants. Environ Entomol 4:689–696. https://doi.org/10.1093/ee/4.5.689
- Willott SJ, Compton SG, Incoll LD (2000) Foraging, food selection and worker size in the seed harvesting ant Messor bouvieri. Oecologia 125:35–44. https://doi.org/10.1007/PL00008889

Tables

Table 1 : Site acronym with type and detailed description, main plant species identified by Buisson et al. (2021), and density of black rats (*Rattus rattus*) recorded by Ruffino et al. (2015)

Site name	Type of site	site Details	Vegetation	Rat density (individuals/ha) (Ruffino et al., 2015)
CA1	Carpobrotus eradication	Inland 0.5 ha patch of *Carpobrotus* aff. *acinaciformis* located on top of a 40 m high cliff	Low matorral vegetation surrounding the *Carpobrotus* patch. Recolonizing vegetation dominated by *Lotus creticus* subsp. *cytisoides, Sonchus asper* subsp. *glaucescens, Bromus diandrus* subsp. *diandrus*	between 46 and 60
CA2	Carpobrotus eradication	Coastal area with *Carpobrotus edulis* intermingled with small halophilous vegetation and rock patches	Coastal halophilous vegetation and low matorral inland. Main species are *Lotus creticus* subsp. *cytisoides, Sonchus asper* subsp. *glaucescens, Frankenia* sp.	below 37
RR1	Rat eradication	Nitrophilous grassland highly frequented by seagulls	Common species are *Hordeum murinum* subsp. *leporinum, Sonchus asper* subsp. *glaucescens* and *Lotus creticus* subsp. *cytisoides*	between 60 and 75
RR2	Rat eradication	Open low matorral vegetation	Small patches of grassland intermingled with shrubs *Lotus creticus* subsp. *cytisoides, Pistacia lentiscus*, and *Frankenia* sp.	between 46 and 60
CO1	Control	Low matorral vegetation	Shrubby vegetation with *Pistacia lentiscus*, *Smilax aspera* and *Myrtus communis*	below 37
CO2	Control	High matorral vegetation	Matorral vegetation with trees such as *Phillyrea* sp., *Pistacia lentiscus* and *Erica arborea*.	below 37

Table 2 : Summary of the main weather data from the Porquerolles weather station (9 kilometers from Bagaud island) during the four sampling periods (April to July and September to October)

	2010	2011	2013	2015	2017	2019	Mean over the six years
Mean maximum temperature (°C)	22.65	25.52	22.60	24.70	23.70	25.22	24.07
Mean minimum temperature (°C)	13.64	14.31	13.94	14.61	14.16	14.7	14.23
Annual cumulated precipitation (mm)	298.4	34.5	165.2	180.7	65.7	104.3	141.5

Figures

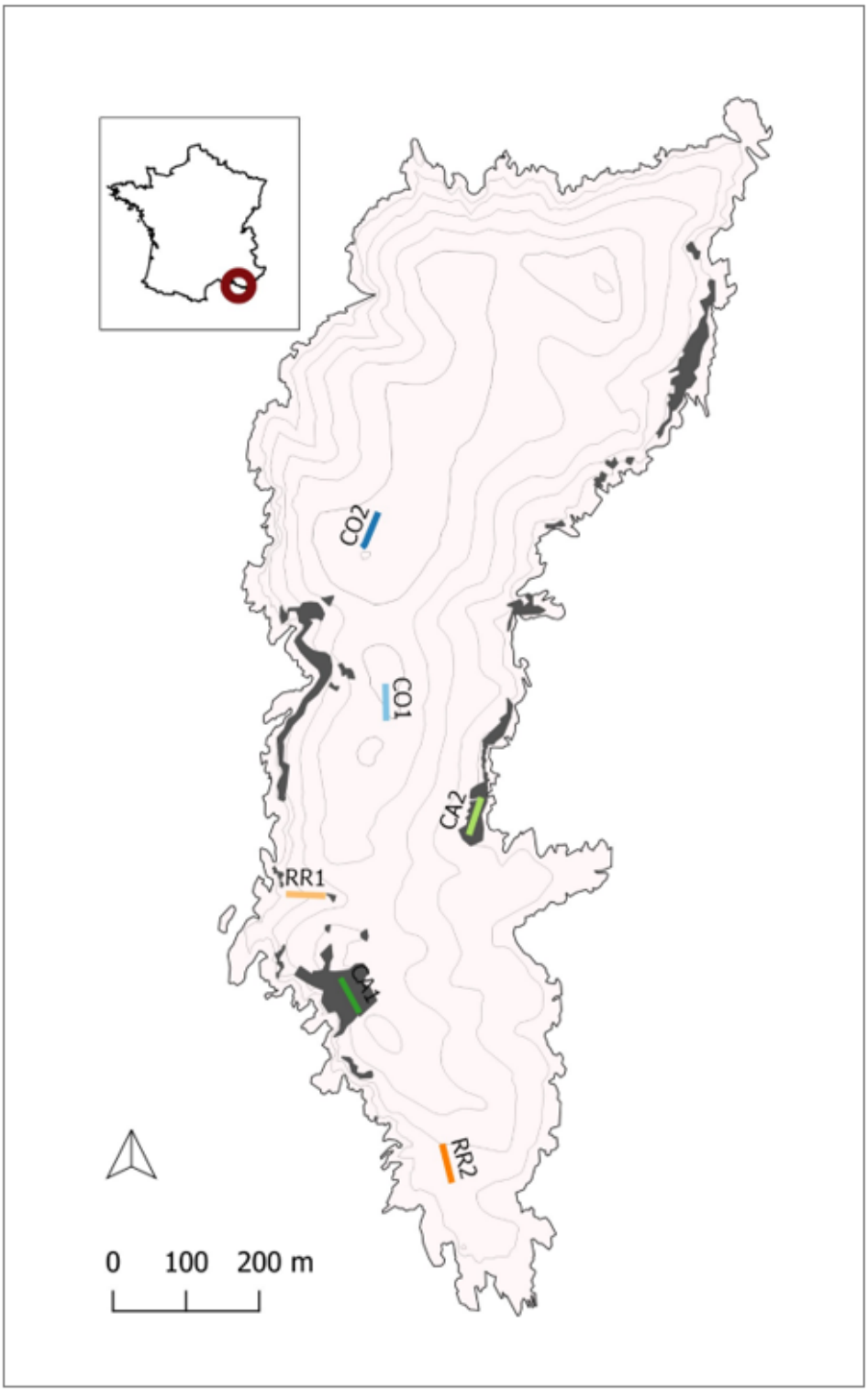

Figure 1

Map of Bagaud island, with area invaded by Carpobrotus spp. in dark grey and position of the six monitoring sites. Green lines indicate sites invaded by *Carpobrotus* spp. (CA1 and CA2), orange lines sites with high rat density *Rattus rattus* (RR1 and RR2), and blue lines controls (CO1 and CO2)

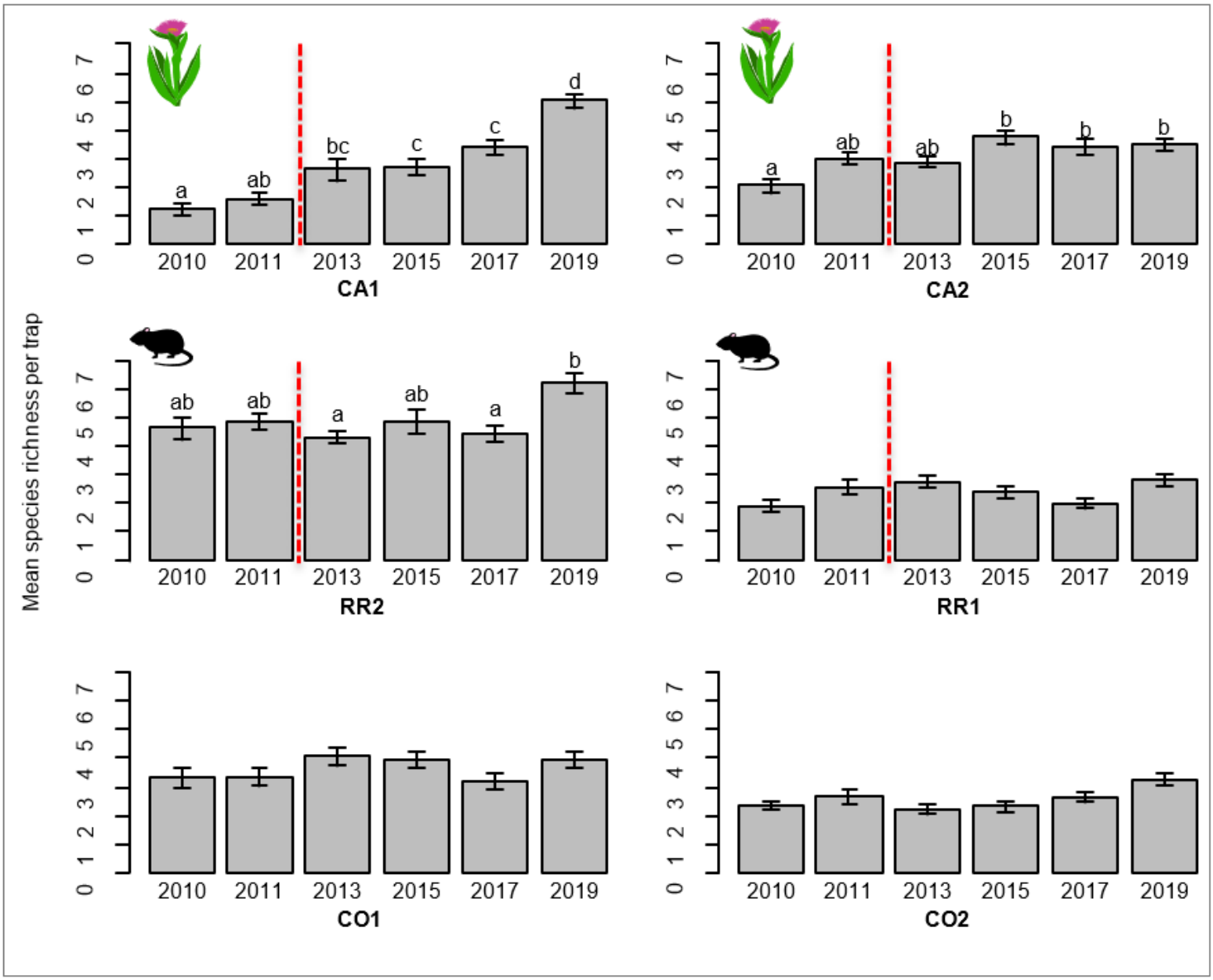

Figure 2

Mean ant species richness per trap over the six-year sampling at the six different sites (mean value ± se). The red dotted line indicates period of IAS eradication (between late 2011 and mid-2012). Black rat eradication took place at RR1 and RR2, *Carpobrotus* spp. eradication at CA1 and CA2. Letters above the bars indicate significant differences between years ($p<0.05$) assessed via a generalized linear mixed model and a negative binomial distribution

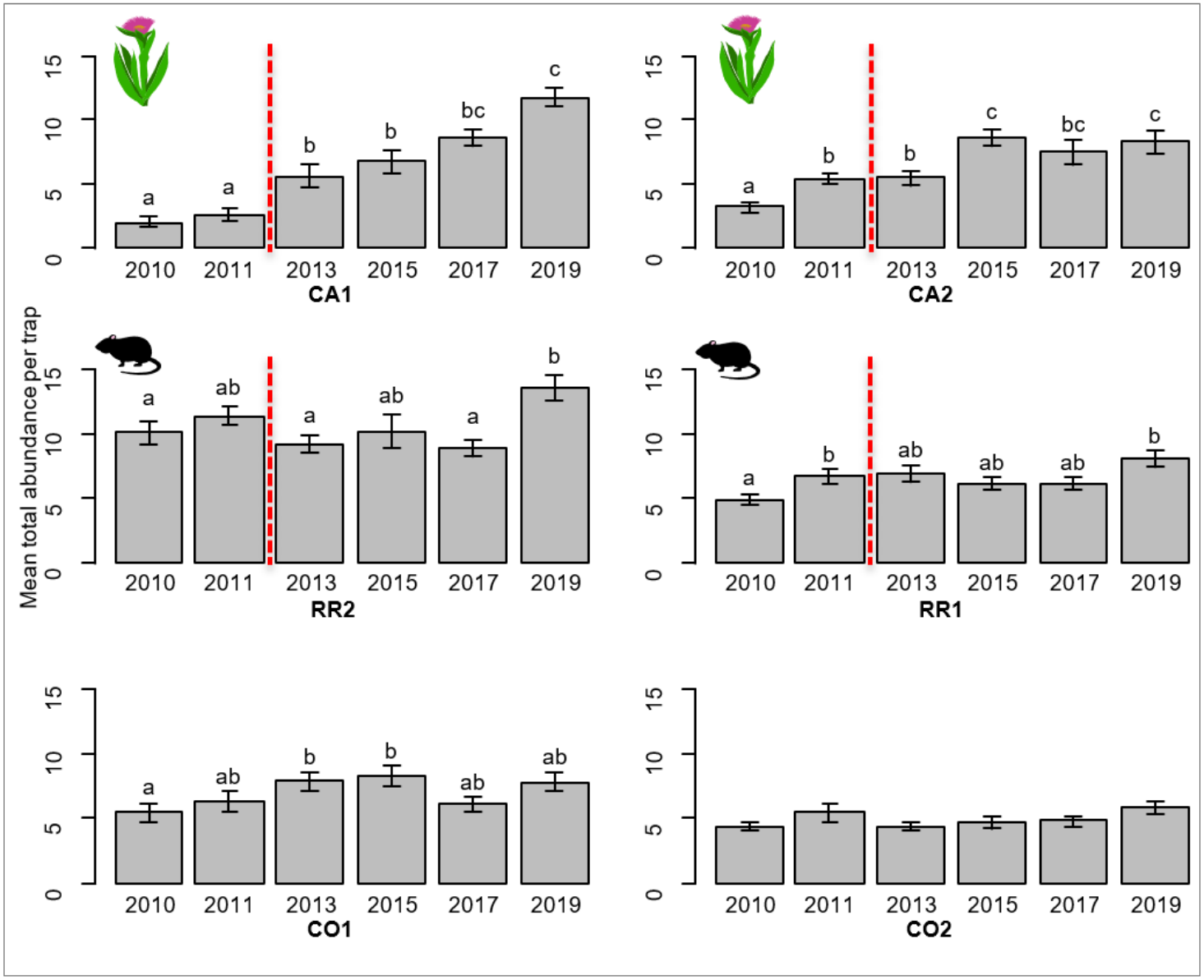

Figure 3

Mean ant total abundances per trap over the six-year sampling at the six different sites (mean value ± standard error). The red dotted line indicates period of eradication (between late 2011 and mid-2012), of black rats at RR1 and RR2 and of *Carpobrotus* spp. at CA1 and CA2. Tests were performed using GLMM. Letters above the bars indicate significant differences between years ($p<0.05$).

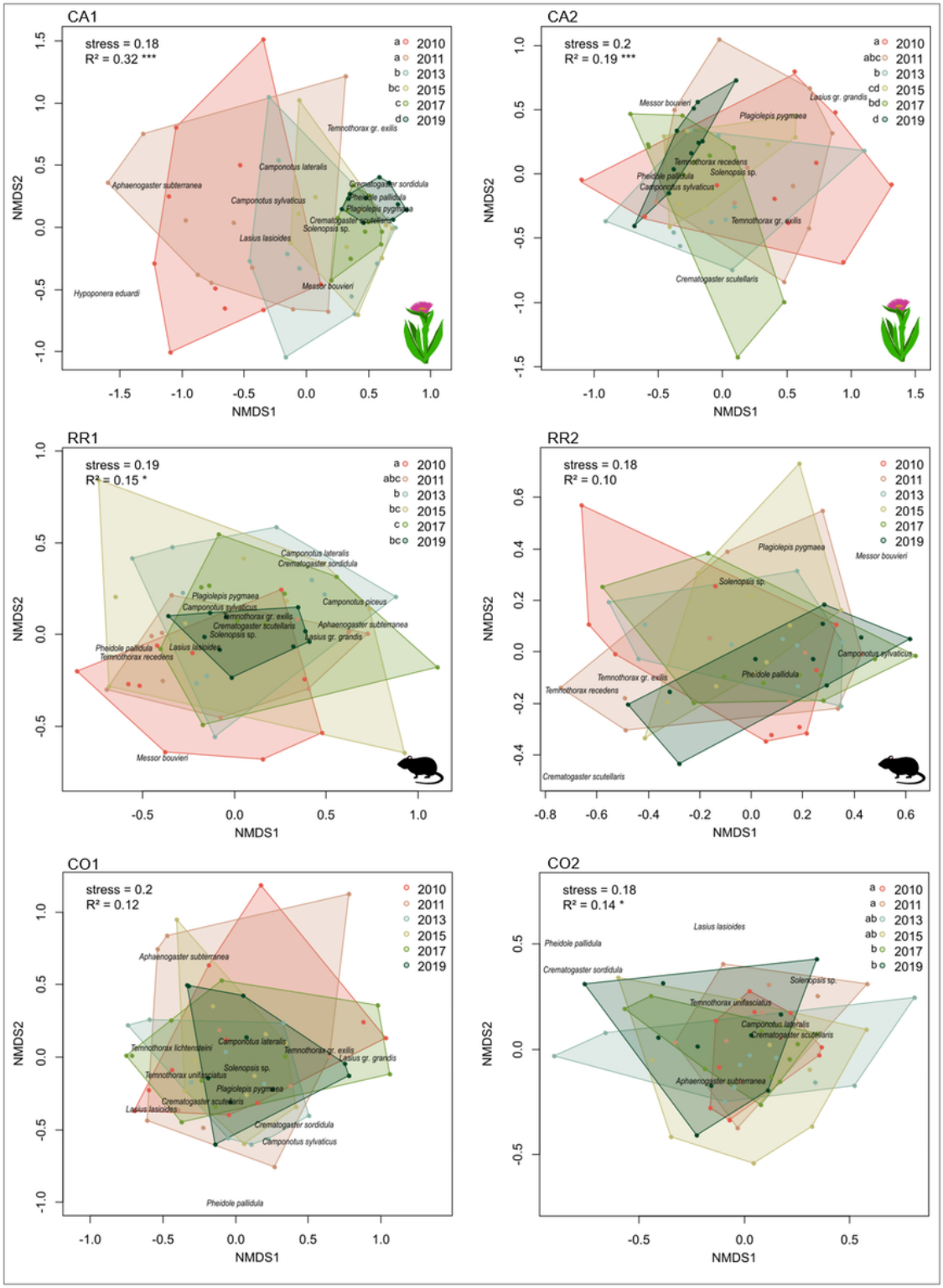

Figure 4

Non-metric multi-dimensional scaling (NMDS) ordination of ant assemblages based on Bray–Curtis dissimilarities with pitfall trap scaled abundances. Differences between the years' assemblages were assessed via the adonis2 (vegan) package, giving the R^2 and its significance (P<0.05*, P<0.01**, P<0.001***). Assemblages differed significantly according to year at the two *Carpobrotus* spp. eradication sites (CA1 and CA2), at one of the rat eradication sites (RR2 but not RR1), and at one of the control sites

(CO2 but not CO1). Letters next to the year entries indicate significant differences between years found with permanova.

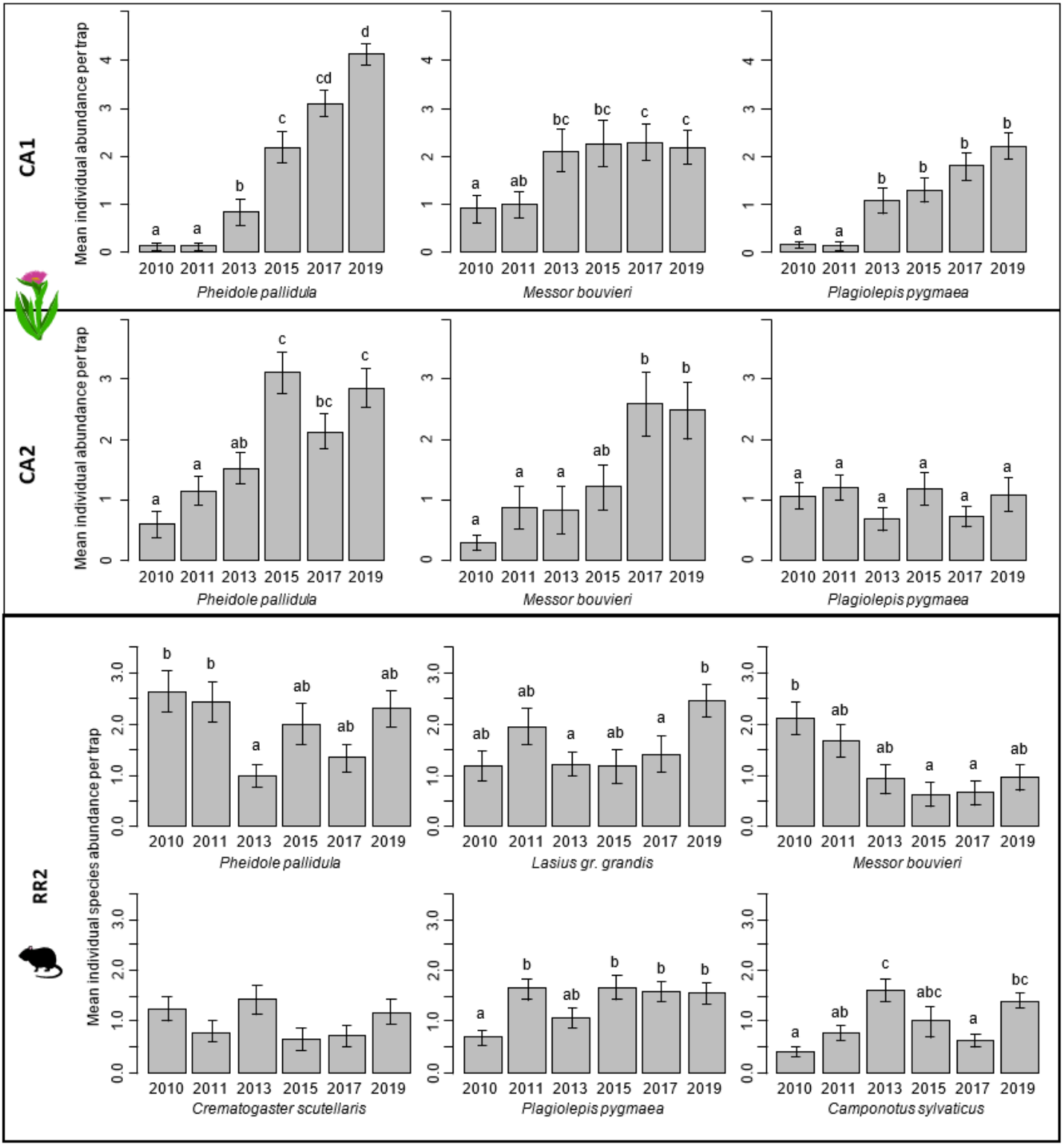

Figure 5

Mean level of abundance of individual species per trap over the six-year sampling (mean value ± standard error) at the two *Carpobrotus* eradication sites (CA1 and CA2) and at the second rat eradication

site (RR2). Only sites that presented significant assemblage dissimilarities were considered. Selected species were those contributing up to 75% to before-after eradication dissimilarity, according to SIMPER analysis. The red line indicates the eradication period (between late 2011 and mid-2012). Letters above the bars indicate significant differences between years ($p<0.05$) assessed with a generalized linear mixed model and a negative binomial distribution.

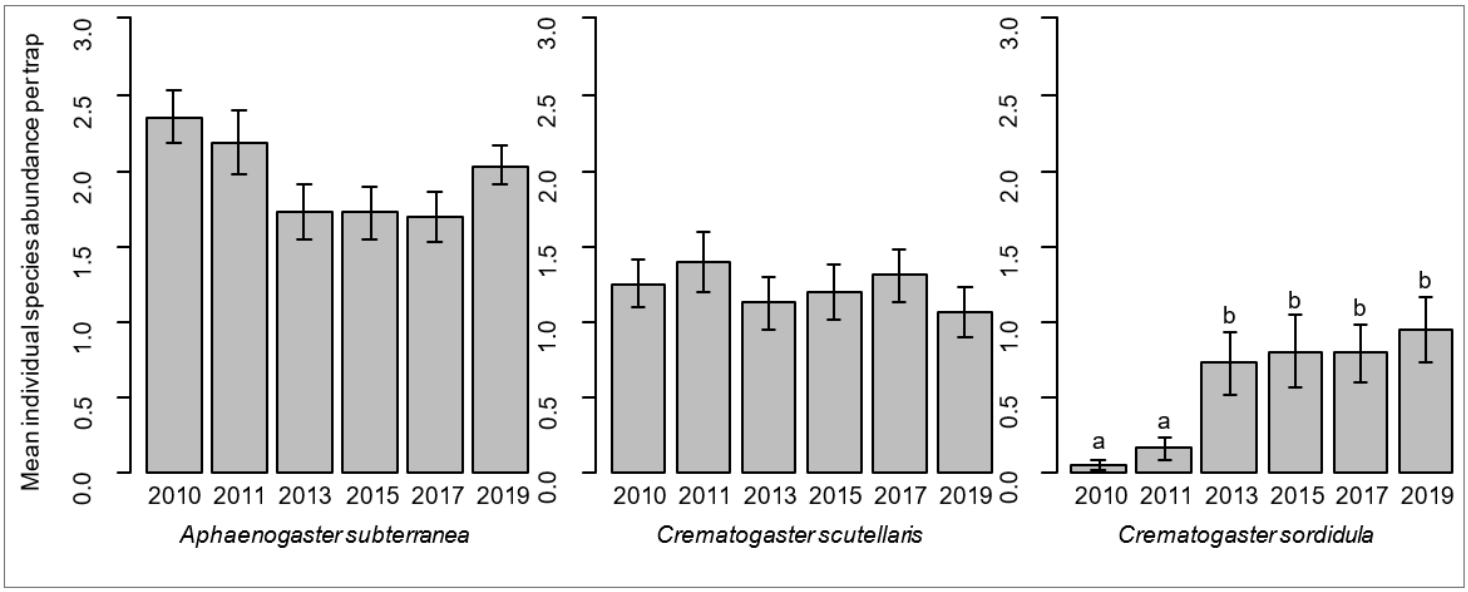

Figure 6

Mean level of abundance of individual species per trap over the six-year sampling (mean value ± standard error) at the high-matorral control site (CO2). Only sites that presented significant assemblage dissimilarities were considered. Selected species were those contributing up to 75% to the before-after eradication dissimilarity, according to SIMPER analysis. The red line indicates the eradication period (between late 2011 and mid-2012). Letters above the bars indicate significant differences between years ($p<0.05$) assessed with a generalized linear mixed model and a negative binomial distribution.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- AppendixA.docx