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Impacts of the removal of invasive *Carpobrotus* on spider assemblage dynamics

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Abstract

Mediterranean island biodiversity is threatened by invasive plants, especially by *Carpobrotus* species. Invasive plant control is a major management tool for the restoration of invaded areas, but the effect of *Carpobrotus* removal on arthropods is poorly understood. In this study, we evaluate how spider assemblages are influenced by *Carpobrotus* removal on a Mediterranean island. A *Carpobrotus* patch was manually uprooted, followed by litter removal between November 2011 and February 2012. A nearby site with native matorral vegetation and no management was also studied. Spider communities were sampled using pitfall traps two years before removal (2010–2011), and then every two years after, between 2013 and 2019. Vegetation at the *Carpobrotus* site changed from a dense mat of *Carpobrotus* to a diverse halophilous grassland with some chamaephytes, while it remained stable in the matorral. Spider species richness increased significantly after removal and significant changes in assemblage composition were observed between pre- and post-removal years with a high turnover rate, while spider assemblages remained relatively stable in the matorral. Litter-dwelling spiders with trap strategies like *Oecobius navus* were the most reduced by *Carpobrotus* removal, while foliage-dwelling spiders which forage on plants like *Xysticus* benefited the most, likely due to vegetation opening and diversification of microhabitats. The increase in bare ground cover favoured *Aelurillus v-insignatus*, *Nomisia celerima* and *Zodarion elegans*, which are characterized by an affinity for dry sunny environments. Invasive *Carpobrotus* removal induced a rapid change (7 years) in spider assemblages as well as an enrichment in taxonomic and functional diversities.

Keywords Arachnids · Conservation management · Island · Invasive plant removal · Mediterranean type ecosystems · Restoration

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Introduction

Biological invasions by non-native plant species is a major direct driver of environmental change in ecosystems worldwide, causing declines in native species diversity, alterations in nutrient cycling and bottom-up impacts on higher trophic levels (Levine et al. 2003; Vilà et al. 2011; D'Antonio and Flory 2017). Island ecosystems in the Mediterranean Basin are particularly vulnerable to plant invasive species (Hulme et al. 2008). Indeed, Walsh et al. 2012 predict that islands with both a relatively high percentage of invasive species and many threatened or endemic species are more at risk. Island communities may also be more vulnerable to invasions due to vacant niches (Whittaker et al. 2017). Moreover, small islands (< 1000 ha) are more vulnerable than large ones because of the disproportionate effects of invasive species on the local carrying capacity of the ecosystems (Médail 2017).

Species of the genus *Carpobrotus* (ice plant) are among the most harmful invasive plants. They have strong negative impacts on biodiversity on both local and global scales (Vilà et al. 2006; Hulme et al. 2008; Celesti-Grapow et al. 2016). *Carpobrotus acinaciformis*, *Carpobrotus edulis* and their hybrids are mat-forming succulent plants (Aizoaceae) native to South Africa, introduced as ornamental plants and for soil stabilization purposes in many coastal regions of the world (Campoy et al. 2018). They form quasi-monospecific mats that exclude native species by competition, homogenize the landscape by eliminating micro-habitats, and modify soil properties (e.g. increasing soil salinity and producing allelopathic substances that inhibit the germination of native species seeds) (Conser and Connor 2009; Santoro et al. 2011; Novoa et al. 2012; Novoa and González 2014; Badalamenti et al. 2016; Vieites-Blanco and González-Prieto 2018; Campoy et al. 2018).

Invasive plant control is a major management tool for the restoration of invaded areas, but there has been limited experimental tests of the effects of invasive control (Kettenring and Adams 2011). Ideally, monitoring should be implemented before and after invasive plant control, not just on plant communities, but also on other taxa and different trophic levels to develop better guidelines for their management (Blossey 1999). Species of the genus *Carpobrotus* are being controlled or eradicated in many areas of the world using a wide variety of tools (e.g. uprooting, herbicide or biological control; Campoy et al. 2018). However, detailed monitoring is uncommon: Chenot et al. (2018) studied the effect of *Carpobrotus* removal on soil erosion and native vegetation by performing experiments in small plots over a short period; Krebs et al. (2015) and (Buisson et al. 2020) studied the effect of *Carpobrotus* removal on native plant recolonization on a 1-ha area, over several years.

While the effects of *Carpobrotus* on arthropod assemblages (Palmer et al. 2004; Orgeas et al. 2007; Rodríguez et al. 2019) and on the pollination of native species (Moragues and Traveset 2005; Bartomeus et al. 2008) have been studied by comparing areas with and without *Carpobrotus*, the effect of *Carpobrotus* control on arthropods is poorly known (Knapp 2014). However, despite the prominent role of spiders in most ecosystems, these invertebrates are still notably endangered as well as underrepresented in current conservation efforts (Branco and Cardoso 2020). The introduction of exotic species, including other spiders, animals, plants or fungi, may have direct or indirect impacts on native spiders, moreover for island populations (Borges et al. 2020).

Among arthropods, spiders are well studied in the context of habitat variations (Marc et al. 1999; Uetz et al. 1999; Pearce and Venier 2006; Buchholz 2010; Gerlach et al. 2013) notably because (i) they are taxonomically well known, abundant and inhabit a wide array of spatial and temporal niches (Kremen et al. 1993); (ii) their ecology is widely studied and they respond significantly to abiotic and biotic variations, disturbance and management,

even on small scales (Bell et al. 2001), and (iii) they can be easily collected using standardized sampling methods (Wise 1993). Consequently, spiders are valuable and useful to monitor habitat management and restoration practices (Pétillon et al. 2006; Cristofoli et al. 2010; Borchard et al. 2014; Hacala et al. 2019; Smith DiCarlo and DeBano 2019).

The aim of this study was to evaluate how spider assemblages were influenced by *Carpobrotus* removal on a small Mediterranean island. In particular, the objectives were to determine which spider species were the most impacted by the removal of this non-native plant. Sampling was performed 2 years before *Carpobrotus* removal and every 2 years after removal, over a 7 year period. We sampled (i) a site with a dense mat of *Carpobrotus* prior to removal and (ii) a site of native matorral vegetation (with no *Carpobrotus* removal). The latter site was not chosen as a restoration target, but rather as a local reference for normal variation in spider communities between years. We expected to find an enrichment in taxonomic and functional diversities of spider assemblages after *Carpobrotus* removal, depending on the relative success of vegetation recovery.

Methods

Study area

The study was conducted on Bagaud Island, a 59-hectare islet forming part of Hyères archipelago in the National Park of Port-Cros on the Mediterranean coast of France (43° 00′ N 6° 21′ E) (Ruffino et al. 2015). Bagaud Island is a strict biological reserve with prohibited access to the public. The island is 7.5 km from the coast and ca. 500 m from the main island of Port-Cros. The mean annual temperature is 16.6 °C with a mean annual precipitation of 724 mm (Porquerolles weather station, period from 2010 to 2019) and highly variable inter-annual rainfall, typical of the Mediterranean climate. The main habitat types are (i) high matorral (with trees, including *Pinus halepensis*, *Erica arborea*) (ii) low matorral (without trees, including *Cistus* spp., *Pistacia lentiscus*, etc.) and (iii) coastal vegetation characterized by halophilous species, each constituting rich native plant communities (Ruffino et al. 2015). A total of 2 ha of *Carpobrotus* was spread in various patches on the island as well as on the cliffs; the biggest patch, ca. 0.5 ha, was where this study was carried out.

Study sites

The two study sites had similar elevation, slope and soil type, approximately ca. 400 m apart:

(i) the *Carpobrotus* removal site is a ca. 0.5-ha patch of vegetation highly invaded by *Carpobrotus* spp., introduced on Bagaud Island in the mid-nineteenth century. *Carpobrotus* was manually uprooted between November 2011 and February 2012, producing 20 tons of *Carpobrotus* material, left in piles on Bagaud Island [the biomass was not exported to prevent the dissemination of fruits (Chenot et al. 2018)]. Regular control of the treated areas with systematic uprooting of new sprouts and shoots were implemented over the seven following years to ensure success (Ruffino et al. 2015).

(ii) the matorral site is a low matorral community without *Carpobrotus*, characterized by *Cistus monspeliensis*, *Cistus salviifolius*, *E. arborea*, *P. lentiscus*, *Phillyrea angus-*

tifolia, and *Smilax aspera*. Vegetation dynamics are slow at this site and this plant community was considered to be stable over the study period (Buisson et al. 2020). We suspect that vegetation of the *Carpobrotus* removal site will develop towards the community structure of this matorral site, but this was not expected to happen within 7 years. This site will be therefore used as a reference for the *Carpobrotus* removal site only in a much longer term than in this study period. For this study, it constituted a site where no management had occurred and where arthropod assemblages are only affected by natural variations.

Sampling design

Spiders were sampled using pitfall traps (10 cm deep and 5 cm diameter) filled with ethylene–glycol and a few drops of detergent. Pitfall traps were active continuously from mid-April to late-June, and were emptied every 3 weeks resulting in three sampling periods. For subsequent analyses, pitfall trap catches in each trap over the three sampling periods were pooled. On each site, ten traps spaced 5 m apart were placed on a transect geolocated with GPS and marked by stakes. Traps were sampled 2 years before *Carpobrotus* removal (2010, 2011), and then every 2 years thereafter (2013, 2015, 2017, 2019). Because we only sampled spiders with pitfall traps, we expected to catch more ground-dwelling spiders comparative to web-spinning species (sweep net sampling) or small litter spiders (Berlese sampling). We chose this sampling technique so that it would be the most consistent between years (i.e. litter being highly variable since *Carpobrotus* litter was removed with *Carpobrotus*). Spiders were first sorted by morphospecies (Oliver and Beattie 1996) then identified with the help of Roberts (2014), Nentwig et al. (2020), and Oger (2020). Only adult spiders were included in the analysis. Due to the difficulty of taxonomic identifications, some adults were pooled: by families (Dictynidae, Linyphiidae and Theridiidae) or genera (*Euophrys* and *Xysticus*) (see "Appendix 1").

Environmental variables

The total percent cover of the vegetation, the percent covers of each native shrub, all herbaceous species, *Carpobrotus* alone, bare ground and litter were visually estimated in three 100 m^2 plots (5.64 m circles). Plots were placed at each end of each transect as well as in the middle of the transects. We described each site using cover classes (i < 1%, 1: 1–10%, 2: 11–25%, 3: 26–50%, 4: 51–75%, 5: > 76%) before 2010–2011 and after (2013, 2015, 2017, 2019) removal. For the following statistical tests, the mean median value of each cover class was used (i = 0.5%, 1 = 5.5%, 2 = 17.5%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%). Plant species lists were generated in each plot to estimate plant species richness.

Minimum and maximum daily temperatures and daily rainfall data were obtained from the Porquerolles weather station and an average daily temperature was calculated.

Functional traits

Six functional traits of adult spiders were selected and assigned to species based on the literature. (i) Female body size was derived from Nentwig et al. (2020) and Le Péru (2007) in five classes (class 1: > 1 mm, class 2: 1–5 mm, class 3: 5–10 mm, class 4: 10–15 mm, class 5: > 15 mm). (ii) Four foraging strategies (hunting, run and kill, sit and wait, trap

strategy). (iii) Five habitat hygrometry affinities (dry, very dry, very wet, wet, no preference). (iv) Four circadian activity rhythms (diurnal, crepuscular, nocturnal, no preference) were derived from the ''Biological & Ecological functional Traits of Soil Invertebrates'' database (Hedde et al. 2012; BETSI 2020). (v) Ballooning or not (binary), which is the propensity to aerial dispersion of juveniles and adults, was taken from Bell et al. (2005). (vi) Kovoor and Muñoz-Cuevas (2000) detailed the vegetation strata affiliated to spider habitat preference: either on the vegetation or the ground ("Appendix 2").

Data analysis

Environmental variables

Differences in vegetation variables (vegetation percent cover and species richness) between years were tested separately for the two sites. We used Generalized Linear Mixed Models (GLMM), one for each variable and each site, with sampling year as a fixed effect and plots as a random effect, in order to take repeated measurements in the same plots over multiple years into account. These analyses were followed by pairwise comparisons with a Tukey adjustment. Models were fitted with a Poisson error distribution for species richness and a beta error distribution for the other variables. We used packages emmeans (Lenth et al. 2020), car (Fox and Weisberg 2020) and glmmTMB (Brooks et al. 2017).

To test the effects of environmental variables on spider abundances, we used the mvabund package (Wang et al. 2012) to create a Multivariate Abundance Data Object from the species abundance matrix. We fitted a multivariate linear model with environmental variable matrix as a fixed effect and a negative binomial distribution, followed by a test with the anova function, to make inferences about which environmental variables are associated with the multivariate abundances (Wang et al. 2012).

Taxonomic diversity and species abundances

Differences in spider taxonomic diversity [species richness, Simpson index 1/D, Shannon Evenness e^H between years were tested separately for the two sites. We used GLMMs as described above with traps as a random factor and a Poisson error distribution. To test variations in spider species abundance between years, we used a Generalized Linear Model (GLM) for Multivariate Abundance Data from the mvabund package (Wang et al. 2012) with sampling year as a fixed effect, followed by a test with the anova function. These GLMs were fitted with a negative binomial distribution.

Taxonomic composition and beta diversity

Spider assemblage composition was analyzed using one non-metric multidimensional scaling (NMDS) analysis at each site. NMDSs were run on presence-absence data and based on Jaccard dissimilarities (package vegan: Oksanen et al. 2019). To run these NMDSs, we removed all species with less than one individual in our data set. We tested for dissimilarity in community composition between years with a PERMANOVA (pairwise distances calculated with pairwise adonis tests with Jaccard distances and 999 permutations). We then partitioned beta diversity between years into its two components: the turnover (replacement of some species by others between sampling events) and nestedness (loss or gain of

species between sampling events) (package betapart: Baselga et al. 2018). We calculated these components using mean annual species abundances.

Functional diversity

Functional species richness (FRic) and functional evenness (FEve) were calculated using the function Distance-Based Functional Diversity Indices of FD package (Laliberté et al. 2014) and two matrices: a functional traits matrix and an abundance matrix of species with at least three individuals at each site. To find out if there were differences in FRic and FEve between years, we used a GLMM as described above with traps as a random effect with a Poisson error distribution for FRic and a beta error distribution for FEve.

Trait response to environmental gradient

In order to evaluate trait responses to environmental gradients, we analyzed simultaneously three matrices containing the following information: L (species abundance across samples), R (environmental characteristics of samples) and Q (species traits). We thus performed an RLQ analysis, which crosses traits and environmental variables weighted by species abundances, using the RLQ function of ade4 package (Dray et al. 2012).

All data analyses were conducted using the free software R-3.6.2 (R Development Core Team 2020).

Results

Changes in environmental variables and their effects on spider abundances

Most vegetation variables measured on the plant community at the matorral site did not differ significantly across years (e. g. total plant cover $\chi^2 = 0.001$, $p = 1.000$; shrub cover $\chi^2 = 8.53$, $p = 0.129$; plant species richness $\chi^2 = 7.54$, $p = 0.184$). Similarly, the percent cover of native shrubs and the total cover of herbaceous species in the *Carpobrotus* removal site did not vary significantly with time. However, total vegetation cover, *Carpobrotus* and litter cover were significantly higher before *Carpobrotus* control and dropped in 2013. Both total vegetation cover and litter cover had significantly increased by 2019 while *Carpobrotus* cover remained close to zero (Table 1). Bare ground cover first increased significantly in 2013 and then decreased (Table 1). Plant species richness significantly increased between before and after *Carpobrotus* removal from 10 to 23 species/100 m^2 plot (Table 1).

None of the vegetation variables had significant effects on spider mean abundances at the matorral site. The mean abundances of spiders at the *Carpobrotus* removal site increased significantly with increasing cover of herbaceous species ($F = 140.69$, $p = 0.002$), litter ($F = 68.03$, $p = 0.002$), shrubs ($F = 59.72$, $p = 0.016$), while they decreased with increasing *Carpobrotus* cover ($F = 58.08$, $p = 0.030$).

Autumn and spring rainfall averaged 725 mm over the 6 years of the study spread between 2010 and 2019. Rainfall in 2015 was 44% higher (1045 mm) than over the 6 years, and 45% lower in 2017 (390 mm) (Table 2). Rainfall during sampling (mid-April through to June) averaged 91 mm. It was high in 2010 (245 mm), nearly the average in 2013 and 2015, and very low in the 3 other years (Table 2).

Table 1 Environmental variables (mean values ± SE) of the plant community in the area invaded by *Carpobrotus* sp. before removal (2010, 2011) and after removal (2013 to 2019)

	2010	2011	2013	2015	2017	2019	χ^2	P
% cover vegetation	87.5 ± 0 [b]	87.5 ± 0 [b]	45.8 ± 14.4 [a]	70.8 ± 28.8 [ab]	87.5 ± 0 [b]	79.2 ± 14.4 [b]	39.8	***
% cover shrubs	13.6 ± 6.9	9.6 ± 6.9	7.8 ± 8.9	7.8 ± 8.9	7.8 ± 8.9	3.8 ± 3.2	10.08	n.s.
% cover herbs / grasses (including *Carpobrotus*)	87.5 ± 0 [a]	87.5 ± 0 [a]	45.8 ± 14.4 [a]	79.2 ± 14.4 [a]	60.2 ± 47.3 [a]	79.2 ± 14.4 [a]	14.63	* (post-hoc n.s.)
% cover *Carpobrotus*	79.3 ± 14.4 [b]	79.3 ± 14.4 [b]	5.6 ± 0.0 [a]	3.9 ± 2.9 [a]	2.1 ± 3.0 [a]	5.6 ± 0.0 [a]	450.21	***
% cover bare soil	0.1 ± 0 [a]	1.9 ± 3.2 [a]	39.3 ± 22.5 [c]	13.6 ± 6.9 [b]	5.6 ± 0.0 [ab]	13.6 ± 6.9 [b]	75.92	***
% cover litter	87.5 ± 0 [c]	87.5 ± 0 [c]	20.2 ± 16.2 [ab]	5.5 ± 0.0 [a]	9.5 ± 6.9 [a]	30.8 ± 11.5 [b]	188.86	***
# of plant species	12.0 ± 2.6 [a]	11.3 ± 4.6 [a]	21.7 ± 4.0 [b]	23.0 ± 4.0 [b]	22.0 ± 2.6 [b]	23.0 ± 2.6 [b]	23.93	***

Differences among years were tested with a GLMM with plots as a random factor to consider temporal correlation (% cover were analyzed with a beta distribution and species richness with a Poisson distribution). Between years effects were tested using a Tukey post-hoc test. Different letters indicate significant differences between treatments ($P < 0.05$). *n.s.* not significant. Environmental variables were stable for the plant community in the control area. Shading highlights greater values

Table 2 Summary of the main weather data (Porquerolles weather station)

	2010	2011	2013	2015	2017	2019	Mean over the 6 years
Autumn & winter rainfall (mm) from Sept to April	846.9	657	811.4	1044.7	390.4	598.6	724.8
Rainfall (mm) during sampling mid-April to end of June	244.9	26.2	107.7	149.8	13.1	3.3	90.8
Mean of average temperatures Sept to April (°C)	12.1	11.5	11.9	12.7	12.5	12.7	12.3
Mean of average temperatures during sampling mid-April to end of June (°C)	17.1	19.8	17.6	19.7	19	19.5	18.8

Rainfall and temperatures are given for (i) the autumn and winter preceding each sampling (September to April) and (ii) the sampling period (mid-April to end of June) precisely calculated for each year

Temperature before sampling (September to April) was lower the first 3 years (11.8 °C) then higher the last 3 years (12.6 °C) compared to the mean over the 6 years of the study (2010–2019: 12.3 °C) (Table 2), and it had significant positive effects on spider mean abundances at the restoration site ($F = 72.69$, $p = 0.003$). Temperature during sampling was lower than the long-term mean (18.8 °C) in 2010 (17.1 °C) and 2013 (17.6 °C) then above the other years (Table 2), and it had significant positive effects on spider mean abundances at the matorral site ($F = 69.96$, $p = 0.014$).

Spider diversity and variations in spider abundances

In total, we captured 1814 adult spider specimens in our plots, distributed in 51 taxa, none of which were exotic ("Appendix 1"). Higher abundance but lower richness was found at the *Carpobrotus* removal site (N = 1066, 34 taxa), than at the matorral site (N = 748, 41 taxa). At the *Carpobrotus* removal site, the most frequent species were *Oecobius navus* (53.9%) and *Dysdera erythrina* (15.3%) before restoration, and *Aelurillus v-insignitus* (24.0%) *Nomisia celerrima* (14.7%) and *Xysticus* spp. (10.4%) after restoration. At the

matorral site, the most frequent species were *O. navus* (29.4%), *A. v-insignitus* (12.3%), *Zodarion timidum* (12.3%) and *D. erythrina* (10.8%).

At the *Carpobrotus* removal site, species richness, Simpson diversity index (1/D) and Shannon Evenness (e^H) significantly increased after *Carpobrotus* removal, with the two first years (2010–2011) being different from the two last years (2017–2019) ($\chi^2 = 66.9$, $p < 0.001$, $\chi^2 = 23.7$, $p < 0.001$, $\chi^2 = 44.2$, $p < 0.001$ respectively; Fig. 1). At the matorral site, there were no significant differences between years in terms of species richness ($\chi^2 = 8.2$, $p = 0.14$), Simpson diversity index (1/D) ($\chi^2 = 0.4$, $p = 0.99$) or Shannon Evenness (e^H) ($\chi^2 = 2.9$, $p = 0.72$) (Fig. 1).

Abundances of spiders significantly differed between years at the *Carpobrotus* removal site (LRT = 436.2, p = 0.001): *O. navus* abundance decreased after restoration (LRT = 52.31, p = 0.001) and increased for *Cepheia longiseta* (LRT = 32.24, p = 0.001), *Nomisia celerrima* (LRT = 34.36, p = 0.003), *A. v-insignitus* (LRT = 29.38, p = 0.007), *Zodarion elegans* (LRT = 26.65, p = 0.018) and Linyphiidae spp. (LRT = 24.39, p = 0.027). *Xysticus* sp. were more abundant in 2015 and 2017 (LRT = 37.82, p = 0.002). Abundances of spiders differed significantly between years at the matorral site (LRT = 277.60, P = 0.001): Lyniphiidae spp. (LRT = 28.12, p = 0.002) were more abundant in 2013, 2017 and 2019, and *D. erythrina* (22.92, p = 0.005) in 2010 and 2015.

Assemblage composition

At the *Carpobrotus* removal site, the NMDS ordination clearly separated the years before (2010, 2011) and after restoration (2015, 2017, 2019), with the first post-removal year (2013) being intermediate (stress: 0.18; permanova p = 0.001; Fig. 2a). The last two years of sampling (2017 and 2019) also appear different from each other (Fig. 2a). The years before restoration are associated with species, such as *Atypus affinis, Hogna radiata, Heliophanus kochii, O. navus, Scytodes thoracica, Euophrys* spp. and Dictynidae. The years after restoration are associated with species, such as *A. v-insignitus*, *Arctosa villica, C. longiseta, Evarcha jucunda, Filistata insidiatrix, Nemesia congener, Nurscia albomaculata, Pulchellodromus pulchellus, Saitis barbipes*. Compositional variations in spider assemblages were better explained by species turnover between years (range 12.3 to 77.3%) than by the nestedness component of beta diversity (range 0.4 to 24.9%) (Table 3). Differences in turnover were greatest between pre- and post-*Carpobrotus* removal (range 45.2 to 77.3%) (Table 3).

NMDS ordination at the matorral site revealed the similarity of spider assemblages across years (stress: 0.16; permanova p = 0.009 but no significant differences between years; Fig. 2b). Compositional variations in spider assemblages were better explained by species turnover between years (range 19.7 to 41.7%) than by the nestedness component of beta diversity (range 0.8 to 21.6%) (Table 3).

Assemblage functional diversity

At the *Carpobrotus* removal site, functional richness (FRic) was significantly lower the 2 years before *Carpobrotus* removal and increased gradually over time ($\chi^2 = 29.57$, $p < 0.001$, Fig. 3), with functional evenness tending to be lower before *Carpobrotus* removal ($\chi^2 = 0.95$, $p = 0.052$). At the matorral site, there were no significant differences in functional richness nor evenness between years ($\chi^2 = 1.72$, $p = 0.880$ and $\chi^2 = 3.66$, $p = 0.590$, respectively).

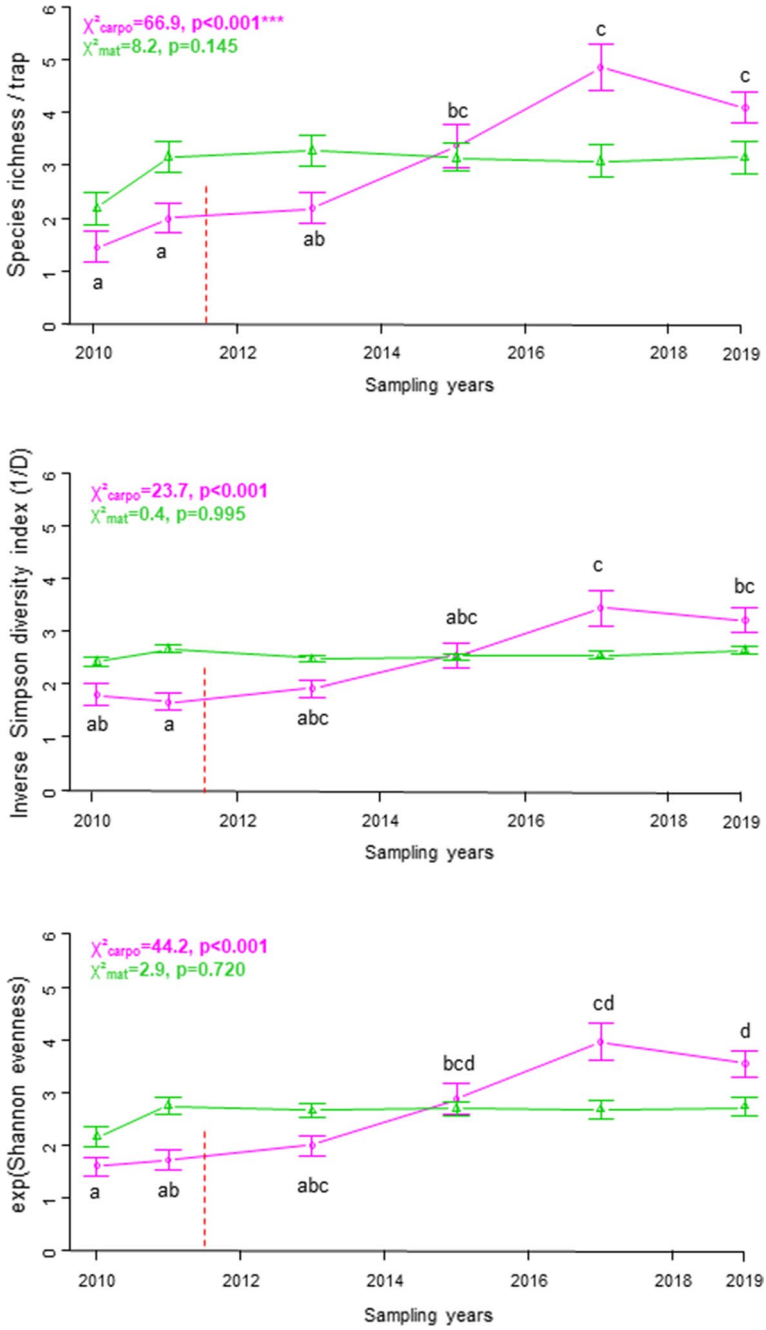


Fig. 1 Annual spider species richness (S) and species diversity (Simpson diversity index 1-D and Shannon evenness e^H (mean values + SE) for the *Carpobrotus* removal site (pink diamonds) and the matorral site (green triangles). The red dotted line represents the *Carpobrotus* removal period (winter 2011–2012). We used GLMM, one for each variable and each site, with years as a fixed factor and plots as a random factor, followed by Tukey test when significant. Models were fitted with a Poisson family. Bars not sharing letters were significantly different between years ($p < 0.05$)

Fig. 2 **a** NMDS ordination of spiders assemblage on presence/absence data at the *Carpobrotus* removal site (stress = 0.18, Permanova: p = 0.001***). 2010 and 2011 (pre-control years), colored in red, were significantly different from the post-control years (in green). Year entries represent the centroids for each sampling year, and the polygons surround the points corresponding to each sampling year. **b** NMDS ordination of spiders assemblage on presence/absence data at the control site (stress = 0.16, Permanova: p = 0.009; but no significant differences between years – see table above). Year entries represent the centroids for each sampling year, and the polygons surround the points corresponding to each sampling year

Trait response to environmental gradient

At the *Carpobrotus* removal site, the RLQ analysis (projected inertia (%): Axis 1 = 78.63, Axis 2 = 8.26, Fig. 4) separated the sites in two groups on the first axis: the pre-removal years 2010–2011, and the post-removal years 2013–2019. Pre-removal years were characterized by: high cover of litter and *Carpobrotus*, hygrophilous spiders such as *D. erythrina* and *Amaurobius erberi*, nocturnal and medium-size species with hunting or run and kill strategies. Year 2013 was characterized by a high cover of bare ground and a low plant species richness, with Linyphiidae species. Years 2015–2019 were characterized by: high plant richness and temperature before sampling, xerophilous spiders such as Z. *elegans*, *A. v-insignitus* and *Zelotes tenuis*, diurnal species with trap or sit and wait foraging strategies.

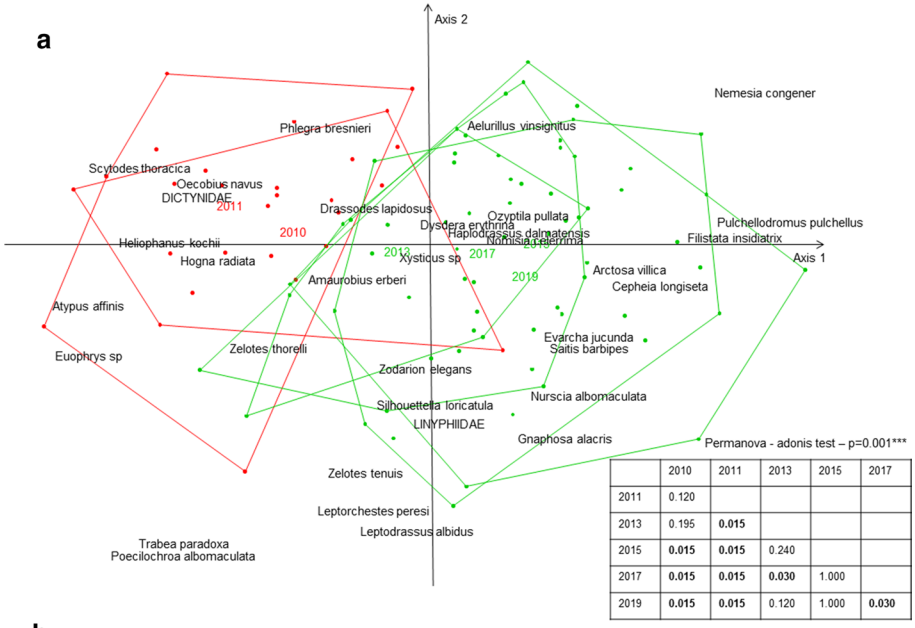
At the matorral site, the RLQ analysis (inertia: A × 1 = 63.2, A × 2 = 18.8) did not discriminate the years clearly.

Discussion

While rainfall was highly variable between years, which is typical of Mediterranean climates (Deitch et al. 2017), vegetation (species richness and percent cover of vegetation, native shrubs, native herbaceous species) and percent cover of litter and bare ground remained relatively stable at the matorral site. This is consistent with other shrublands under normal Mediterranean climatic variation (Rodriguez-Ramirez et al. 2017).

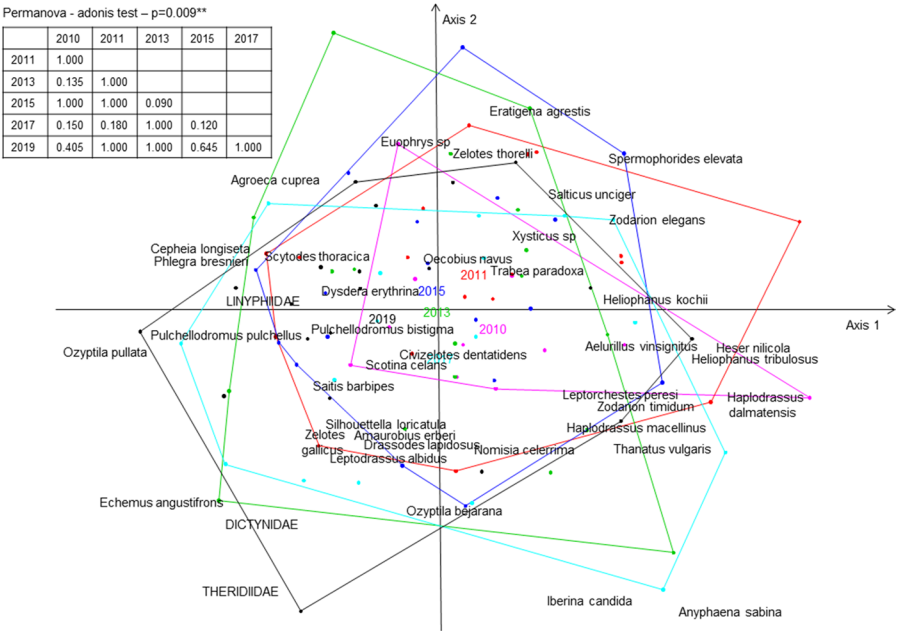
Spider alpha-diversity (spider richness, taxonomic and functional diversities) and assemblage composition also remained stable at the matorral site during the study. Spider assemblages can vary with habitat condition, vegetation structure and succession stages (Bonte et al. 2002): stable habitats without disturbance, such as shrublands, have more stable assemblages over time. As there was no *Carpobrotus* at this site and no disturbance or management, this relative stability in the face of climate variation was not surprising, given the stability of the vegetation. Woodlice variations are dependent on rainfall during sampling and could explain the variations in *D. erythrina* which feed mainly on these prey species (Cooke 1965). Considering the great taxonomic and ecological diversity within Linyphiidae (Draney 1997), the data analysis at the family level may hide possible interannual variations in the composition of Linyphiid assemblages that could be revealed by a lower taxonomic level study. Overall, this site did not undergo major changes in spider assemblages, and demonstrate their relative stability even with inter-annual climatic variations.

Vegetation and environmental parameters changed dramatically at the *Carpobrotus* removal site as a result of *Carpobrotus* removal. *Carpobrotus* cover was 75% lower in 2013 due to the removal of *Carpobrotus* in 2011–2012 and bare ground was nearly 40% higher. Open habitats containing a lot of bare ground are generally characterized by relatively species-poor spider communities where small r-selected Linyphiidae spp. and Synaphridae,



Permanova - adonis test – p=0.001***

	2010	2011	2013	2015	2017
2011	0.120				
2013	0.195	**0.015**			
2015	**0.015**	**0.015**	0.240		
2017	**0.015**	**0.015**	**0.030**	1.000	
2019	**0.015**	**0.015**	0.120	1.000	**0.030**



Permanova - adonis test – p=0.009**

	2010	2011	2013	2015	2017
2011	1.000				
2013	0.135	1.000			
2015	1.000	1.000	0.090		
2017	0.150	0.180	1.000	0.120	
2019	0.405	1.000	1.000	0.645	1.000

such as *C. longiseta,* can dominate (Bell et al. 2001; Buchholz 2010; Negro et al. 2013), as they build their webs over depressions in the soil and are known to be good aerial dispersers (Alderweireldt 1994). The opening up of the environment facilitates spider mobility

Table 3 Taxonomic turnover (replacement of some species by others between 2 years) and taxonomic nestedness (loss or gain of species between 2 years)—resultant components of taxonomic diversity on abundance data (a) at the *Carpobrotus* removal site (b) at the matorral site. Turnover is shown in dark grey and nestedness in light grey

(a)		Nestedness						(b)		Nestedness			
		2010	2011	2013	2015	2017	2019	2010	2011	2013	2015	2017	2019
	2010		11.2	5.8	12.7	24.9	8.9		8.5	21.6	12.6	12.7	9.9
Turnover	2011	48.2		4.4	0.4	6.3	0.5	36		13.5	3.8	3.6	3
	2013	51.1	56.3		7	20	4.6	26.3	25.5		8.6	8.5	9.8
	2015	45.2	73.9	39.4		22.1	2.1	29.3	19.7	36.4		0.8	0.3
	2017	45.7	76.6	44.4	12.3		21	33.5	41.7	29.9	42.8		1.2
	2019	54.7	77.3	43.4	40.1	26.8		43.1	29	29.8	34.4	34.2	

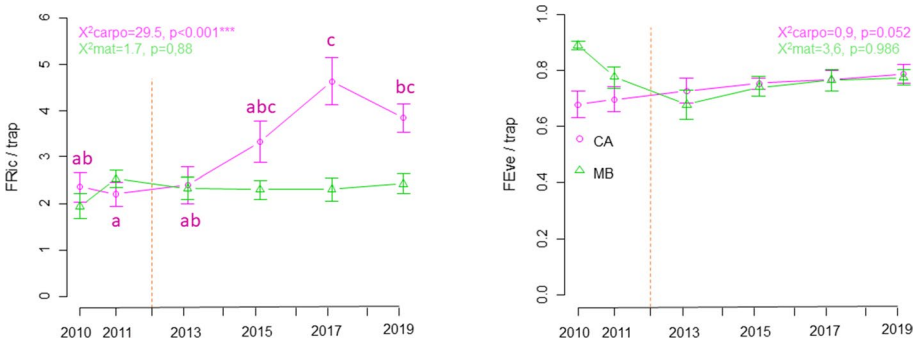


Fig. 3 Annual spider species functional richness (FRic ± SE) and evenness (FEve ± SE) for the *Carpobrotus* removal site (pink diamonds) and the matorral site (green triangles). The red dotted line represents the *Carpobrotus* removal period (winter 2011–2012). We used GLMM fitted with a Poisson family for FRic and fitted with a beta family for FEve, year as a fixed factor and plot as random factors, followed by pairwise contrast comparisons with a Tukey adjustment. Bars not sharing letters were significantly different between years ($p < 0.05$)

on the soil, as well as their catchability in pitfalls (Woodcock 2005; Brown and Matthews 2016). Temperature is also known to have potential effects on pitfall catches of epigeal arthropods (Saska et al. 2013).

Native vegetation, mainly herbaceous species, recolonized the site after *Carpobrotus* removal, doubling plant species richness (Buisson et al. 2020). The landscape therefore changed greatly from a dense mat of *Carpobrotus* to a diverse halophilous grassland with some chamaephytes, such as *Jacobaea maritima* ssp. *maritima, Lotus creticus* ssp. *cytisoides*, *Euphorbia pithyusa, Sonchus bulbosus* and *Bromus diandrus* ssp. *diandrus*. The vegetation was not only rich in species, but also in structure, providing various plant heights and microhabitats (less litter, but more diversified litter and more bare ground). Spider assemblages are known to vary with vegetation composition (Schaffers et al. 2008) and structure (Uetz 1991; Bell et al. 2001), that could explain the increase in spider species richness, the change in species composition and the high turnover of species between pre- and post-control years. With increasing vegetation cover, the habitat becomes more attractive for foliage-dwelling spiders and as a consequence, species richness increases

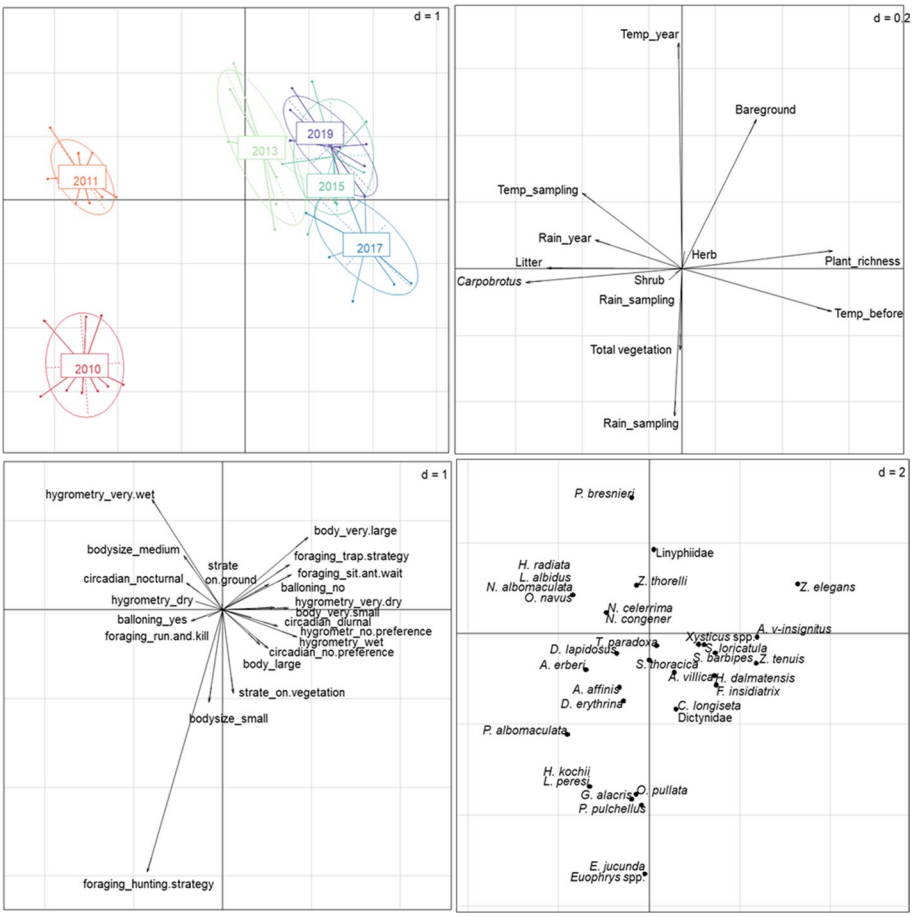


Fig. 4 RLQ analysis of spider species at the *Carpobrotus* removal site (projected inertia: Axis 1 = 78.63%, Axis 2 = 8.26%). The statistic measures the link between three tables: L (species abundance with more than three occurrences across samples, "Appendix 1"), R (environmental variables of samples, Tables 1 and 2) and Q (species traits on adult, "Appendix 2")

(Bell et al. 2001). Similar rapid changes in spider assemblages after invasive plant removal was also observed by Eckert et al. (2019) and Gratton and Denno (2005) only 6 years after the removal of invasive *Pinus* spp. and *Phragmites australis* respectively.

The species abundance most significantly affected by *Carpobrotus* removal was *O. navus*, a tiny cosmopolitan spider living in a tent-like web (Líznarová et al. 2013) that is frequently associated with litter (Nentwig et al. 2020). Its steady decline after *Carpobrotus* removal may have been caused by the marked decrease in *Carpobrotus* litter after 2013 that was slowly replaced by native herbaceous species' litter which is decomposable and less persistent than *Carpobrotus* litter. Variation in litter habitats have long been known to affect litter-dwelling spider species richness and composition, moreover, litter complexity appears to be the most influential variable in summer (Uetz 1979). Indeed, *Carpobrotus* forms litter that is present throughout the year while in the restored habitat, annual plants die and some perennial plants dry out in summer, making

the litter habitat more variable and perhaps less suitable for *O. navus*. *O. navus* may also have been partly replaced by a species with similar traits, *C. longiseta*. Other studies have reported negative indirect effects of invasive species eradication on native species (Zavaleta et al. 2001; Bergstrom et al. 2009; Skurski et al. 2014) and further investigation of species interactions, or more detailed species traits, might help understanding why one decreases while another increases.

On the other hand, *Carpobrotus* removal benefited spiders with ambush or trap strategies that forage primarily on vegetation, such as *Aelurillus v-insignatus* and *Xysticus* spp. (Jiménez-Valverde and Lobo 2007). Smith DiCarlo and DeBano 2019) have recently shown that *Xysticus* spp. are favored by increasing invasive plant litter cover, but the litter was produced by annual grass species such as *Bromus tectorum* in that study, very close to the native *B. diandrus* ssp. *diandrus* found on Bagaud Island after *Carpobrotus* removal. They may also take advantage of the richer vegetation structure, thus increasing the range of ambush possibilities on plants. As ground-dwelling hunters, *A. villica*, *N. celerrima* and *Z. elegans* depend on vegetation with patches of bare ground (Warui et al. 2005) that facilitate the running on the ground and the capture of prey. Ants, which exclusively constitute the diet of *Z. timidum* (Cushing 2012), increased significantly after restoration in our study (unpublished data). These three taxa, *A. v-insignitus*, *A. villica*, *N. celerrima* and *Z. elegans*, are also characterized by their affinity with dry and sunny environments (Roberts 2014).

This project followed the removal of a quasi-monodominant *Carpobrotus* mat that created a relatively moist environment with a thick very slowly decomposable litter. The environment was recolonized by grassland vegetation with a mix of annual and perennial herbaceous plants as well as small chamaephytes. This created a structurally diverse habitat in space and time, leading to an increase in the diversity of spider assemblages. Although the study site was located on an island, the size of the *Carpobrotus* patch was only 0.5 ha, compared to the size of the island (59 ha). The site was surrounded with native vegetation from where spiders could recolonize either on the ground or by ballooning. Future studies should be carried out in areas with larger *Carpobrotus* patches to determine whether recolonization can be as efficient as was observed in this study. These studies also need to be carried out on other islands and coastal areas of the Mediterranean to test the replicability of our results in other environments.

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Author contributions PP conceived and designed the research; JB, EB, OH performed sampling and sorted invertebrates; JB, OH, CM, PO identified spiders; JB, OH, EB analyzed the data; JB, EB wrote the paper; all authors edited the manuscript. All the authors read and approved the final version of the manuscript.

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Data availability Available upon request.

Ethical approval Invertebrates sampling was approved by the scientific board of the National Park of Port-Cros.

Appendices

Appendix 1

Species list and abundances by site. Both sites were sampled equally. Due to difficulties in taxonomic identification, the following species were pooled: *Altella lucida* and *Lathys stigmatisata* under the family Dictynidae; *Agyneta pseudorurestris*, *Agyneta rurestris*, *Cnephalocotes* sp., *Microctenonyx subitaneus*, *Tenuiphantes herbicola*, *Theonina cornix* and *Typhochrestus bogarti* under the family Linyphiidae; *Crustulina scabripes*, *Enoplognatha* mandibularis and *Lasaeola testaceomarginata* under the family Theridiidae; *Euophrys gambosa*, *Euophrys nigripalpis* and *Euophrys rufibarbipes* under the genus *Euophrys*; *Xysticus kochii* and *Bassaniodes bufo* (before *Xysticus bufo*) under the genus *Xysticus*.

	Carpobrotus removal	Matorral site	Sum	Relative abundance (%)
Oecobius navus	255	220	475	26.19
Aelurillus vinsignitus	190	92	282	15.55
Dysdera erythrina	95	81	176	9.70
Nomisia celerrima	113	8	121	6.67
Linyphiidae	51	51	102	5.62
Zodarion timidum	0	92	92	5.07
Drassodes lapidosus	77	14	91	5.02
Xysticus spp.	82	1	83	4.58
Euophrys spp.	16	30	46	2.54
Zelotes thorelli	15	27	42	2.32
Cepheia longiseta	39	1	40	2.21
Scytodes thoracica	17	21	38	2.09
Zodarion elegans	30	6	36	1.98
Saitis barbipes	1	24	25	1.38
Nurscia albomaculata	17	0	17	0.94
Arctosa villica	15	0	15	0.83
Silhouettella loricatula	11	2	13	0.72
Amaurobius erberi	2	7	9	0.50
Scotina celans	0	9	9	0.50
Haplodrassus dalmatensis	6	2	8	0.44
Pulchellodromus pulchellus	3	3	6	0.33
Zelotes gallicus	0	6	6	0.33
Agroeca cuprea	0	5	5	0.28

	Carpobrotus removal	Matorral site	Sum	Relative abundance (%)
Hahnia candida	0	5	5	0.28
Hogna radiata	5	0	5	0.28
Leptodrassus albidus	4	1	5	0.28
Phlegra bresnieri	4	1	5	0.28
Pulchellodromus bistigma	0	5	5	0.28
Spermophorides elevata	0	5	5	0.28
Dictynidae	3	1	4	0.22
Heliophanus kochii	2	2	4	0.22
Leptorchestes peresi	1	3	4	0.22
Eratigena agrestis	0	3	3	0.17
Haplodrassus macellinus	0	3	3	0.17
Ozyptila pullata	2	1	3	0.17
Thanatus vulgaris	0	3	3	0.17
Theridiidae	0	3	3	0.17
Atypus affinis	2	0	2	0.11
Civizelotes dentatidens	0	2	2	0.11
Gnaphosa alacris	2	0	2	0.11
Heliophanus tribulosus	0	2	2	0.11
Heser nilicola	0	2	2	0.11
Trabea paradoxa	1	1	2	0.11
Anyphaena sabina	0	1	1	0.06
Echemus angustifrons	0	1	1	0.06
Evarcha jucunda	1	0	1	0.06
Filistata insidiatrix	1	0	1	0.06
Nemesia congener	1	0	1	0.06
Ozyptila bejarana	0	1	1	0.06
Poecilochroa albomaculata	1	0	1	0.06
Zelotes tenuis	1	0	1	0.06
No. individuals	1066	748	1814	100.00
No. species	34	41	51	

Appendix 2: Functional traits matrix.

Taxa	Size class	Foraging	Strate	Hygrometry	Circadian activity	Ballooning
Aelurillus vinsignitus	Medium	Hunting strategy	On vegetation	Dry	Diurnal	Yes
Agroeca cuprea	Small	Run and kill	On ground	No preference	Nocturnal	Yes

Taxa	Size class	Foraging	Strate	Hygrometry	Circadian activity	Ballooning
Amaurobius erberi	Medium	Trap strategy	On ground	Very wet	Nocturnal	Yes
Anyphaena sabina	Medium	Run and kill	On vegetation	No preference	Crepuscular	Yes
Arctosa villica	Large	Run and kill	On ground	Dry	Diurnal	Yes
Atypus affinis	Large	Trap strategy	On ground	Dry	No preference	No
Cepheia longiseta	Very small	Trap strategy	On ground	No preference	No preference	Yes
Civizelotes dentatidens	Small	Run and kill	On ground	Dry	Nocturnal	No
Dictynidae	Small	Trap strategy	On ground	Very dry	No preference	No
Drassodes lapidosus	Large	Run and kill	On ground	Very dry	Nocturnal	Yes
Dysdera erythrina	Large	Run and kill	On ground	Wet	Nocturnal	Yes
Echemus angustifrons	Medium	Run and kill	On ground	Dry	Nocturnal	Yes
Eratigena agrestis	Large	Trap strategy	On ground	Dry	Nocturnal	Yes
Euophrys spp.	Small	Hunting strategy	On vegetation	No preference	Diurnal	Yes
Evarcha jucunda	Medium	Hunting strategy	On vegetation	Wet	Diurnal	Yes
Filistata insidiatrix	Large	Trap strategy	On ground	Wet	No preference	Yes
Gnaphosa alacris	Medium	Run and kill	On ground	Dry	Nocturnal	Yes
Haplodrassus dalmatensis	Medium	Run and kill	On ground	Dry	Nocturnal	Yes
Haplodrassus macellinus	Large	Run and kill	On ground	Dry	Nocturnal	Yes
Heliophanus kochii	Small	Hunting strategy	On vegetation	No preference	Diurnal	No
Heliophanus tribulosus	Medium	Hunting strategy	On vegetation	Very wet	Diurnal	Yes
Heser nilicola	Small	Run and kill	On ground	Dry	Nocturnal	Yes
Hogna radiata	Very large	Run and kill	On ground	Dry	Nocturnal	Yes
Iberina candida	Small	Trap strategy	On ground	Very dry	No preference	Yes
Leptodrassus albidus	Small	Run and kill	On ground	Dry	Nocturnal	No
Leptorchestes peresi	Medium	Hunting strategy	On vegetation	Dry	Diurnal	Yes
Linyphiidae	Small	Trap strategy	On ground	Dry	No preference	Yes
Nemesia congener	Very large	Trap strategy	On ground	No preference	No preference	Yes
Nomisia celerrima	Small	Run and kill	On ground	Dry	Diurnal	Yes

Taxa	Size class	Foraging	Strate	Hygrometry	Circadian activity	Ballooning
Nurscia albomaculata	Medium	Trap strategy	On ground	Dry	Nocturnal	Yes
Oecobius navus	Small	Trap strategy	On ground	No preference	No preference	Yes
Ozyptila bejarana	Small	Sit ant wait	On vegetation	Wet	Diurnal	Yes
Ozyptila pullata	Small	Sit ant wait	On vegetation	Dry	Diurnal	Yes
Phlegra bresnieri	Medium	Hunting strategy	On vegetation	Very wet	Diurnal	Yes
Poecilochroa albomaculata	Medium	Run and kill	On ground	Dry	Diurnal	Yes
Pulchellodromus bistigma	Small	Sit ant wait	On vegetation	Dry	Diurnal	No
Pulchellodromus pulchellus	Small	Sit ant wait	On vegetation	Dry	Diurnal	Yes
Saitis barbipes	Medium	Hunting strategy	On vegetation	No preference	Diurnal	No
Scotina celans	Small	Run and kill	On ground	Dry	Nocturnal	Yes
Scytodes thoracica	Small	Hunting strategy	On ground	No preference	Nocturnal	Yes
Silhouettella loricatula	Small	Run and kill	On ground	Dry	Nocturnal	Yes
Spermophorides elevata	Small	Trap strategy	On ground	Dry	No preference	Yes
Thanatus vulgaris	Medium	Sit ant wait	On vegetation	Dry	Diurnal	No
Theridiidae	Small	Trap strategy	On vegetation	Dry	No preference	Yes
Trabea paradoxa	Medium	Run and kill	On ground	Dry	Diurnal	Yes
Xysticus spp.	Medium	Sit ant wait	On vegetation	Wet	Diurnal	Yes
Zelotes gallicus	Medium	Run and kill	On ground	Dry	Nocturnal	Yes
Zelotes tenuis	Medium	Run and kill	On ground	Dry	Nocturnal	Yes
Zelotes thorelli	Medium	Run and kill	On ground	Dry	Nocturnal	Yes
Zodarion elegans	Small	Run and kill	On ground	Dry	No preference	Yes
Zodarion timidum	Small	Run and kill	On ground	Dry	No preference	Yes

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