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Impacts of the invasive alien prickly pear, *Opuntia stricta* (Haw.) Haw., on natural communities of Mediterranean insular habitats

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ABSTRACT

Opuntia spp. are important invasive alien plants threatening Mediterranean habitats, particularly in island ecosystems, but few studies have assessed their ecological impacts and relationships with invertebrate communities, focusing more on socio-economic impacts and loss of plant diversity. To fill this gap, we aimed to evaluate the impacts of *Opuntia stricta* (Haw.) Haw. on the native plant and invertebrate communities of Capraia, a small Mediterranean island of high naturalistic value in central Italy and particularly invaded by this species. We investigated the natural communities occurring in EU habitats of conservation interest, comparing the areas invaded by *O. stricta* with control one. To thoroughly evaluate the impacts of this species on biodiversity, we assessed multiple groups of organisms, specifically vascular plants, ants, and other soil microarthropods, by randomly sampling a total of 12 plots of 4 m^2 (6 invaded and 6 control plots). Samples were also collected to analyze soil physico-chemical properties. We estimated the abundance of all the groups and analyzed diversity indices and community composition. *O. stricta* seemed to significantly impact only plant communities (pseudo$F_{1,10} = 17.92$, $P = 0.01$), with a decrease in species richness in the invaded areas, but not on soil properties or invertebrate communities. However, the remarkable changes in the vegetation structure of the island's maquis could threaten natural habitats and consequently alter other parameters related to plants (e.g., shelters or resources for animals). Therefore, further studies could assess the indirect impacts of this alien species and verify the presence of complex processes resulting from its invasion.

1. Introduction

In recent centuries, the intentional and accidental introduction of plant species by humans has increased the risk of biological invasions worldwide, posing a substantial threat to biodiversity and native ecosystems (Pyšek et al., 2012, 2020; Vilà and Hulme, 2017; Rai and Singh, 2020). Understanding the impacts of these invasions on native communities, and the extent of those impacts, is particularly important in vulnerable and protected areas (Hulme et al., 2014; Foxcroft et al., 2017). Among such areas, islands are especially at risk. Due to their ecological isolation and high levels of endemism, islands are uniquely susceptible to biological invasions, which can disrupt native ecosystems and lead to disproportionate ecological consequences. Indeed, islands account for approximately 20 % of all reported impacts caused by

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invasive alien species (Celesti-Grapow et al., 2016; Russell et al., 2017; IPBES, 2023). In these insular systems, invasive species often exert particularly severe pressures on native biota, frequently contributing to local extinctions (Russell et al., 2017; Xu et al., 2022).

The Cactaceae family is among the most prominent in terms of invasive alien plants, given the growing interest in its species for ornamental purposes (Novoa et al., 2015). Notably, the genus *Opuntia* is one of the best-known plants for ornamental and economic-productive purposes, thanks also to their tolerance of high temperatures, aridity, and moderate salinity (Weber, 2017; Humphries et al., 2022). Specifically, the prickly pear *Opuntia stricta* (Haw.) Haw. is considered by the IUCN Invasive Species Specialist Group as one of the "100 of the World's Worst Invasive Alien Species" (Lowe et al., 2000). The ability of *O. stricta* to be competitive in harsher environments has favored its introduction in arid and semi-arid countries such as New South Wales in Australia, and South Africa and Kenya in Africa, and in Mediterranean and coastal climates, particularly in degraded and overgrown landscapes (Humphries et al., 2022; Vilà et al., 2003). The species' native distribution spans from south of Mexico to the southern United States, encompassing coastal regions along the Gulf of Mexico — including Texas, Louisiana, Alabama, and Florida — and extending along the Atlantic coast from Florida to South Carolina (Benson, 1982; Nobel, 2002). In Europe, several *Opuntia* species were introduced between the late 15th and early 16th centuries for various purposes, including fruit consumption, livestock forage, fencing, ornamental use, and the production of a red dye derived from the cochineal insect *Dactylopius coccus*. In the Mediterranean basin *O. stricta* is particularly widespread in Spain, Portugal, and Italy, mainly along the coasts and in island ecosystems (Lazzaro et al., 2014a; Novoa et al., 2015, Humphries et al., 2022) and is considered an invasive species in Italy (Galasso et al., 2018).

Despite being a widely common alien species with high reproductive and competitive abilities, most of the available studies focused on its distribution, dispersal patterns, and management techniques rather than on its ecological impacts (Foxcroft and Rejmánek, 2007; Foxcroft et al., 2017; Novoa et al., 2019; Pyšek et al., 2020; Venter et al., 2022). Indeed, few papers considered the impacts of *O. stricta* on vegetation: for example, Hunter et al. (2021) did not find a significant negative effect of *O. stricta* on species density on an Australian island, while Shackleton et al. (2017) provided evidence of negative socio-ecological impacts of *O. stricta* by showing a reduction in native plant populations, pasture conditions, human health, and humans and animals mobility in Kenya. The impacts on soil properties and fauna communities are even more understudied with some exceptions.

Novoa et al. (2021) demonstrated that the presence of *O. stricta* increases soil water content and nutrients, and alters bacterial communities in the African savannas. Such soil alteration could determine ecosystem changes in biogeochemical cycles and also affect soil microarthropods, which are strongly dependent on abiotic environmental conditions and are recognized as ideal biological indicators of many environmental and biotic stressors (e.g., Meyer et al., 2021; Junggebauer et al., 2024), including biological invasions (Lazzaro et al., 2018). Moreover, despite very few studies have been conducted in the areas invaded by *O. stricta*, its invasion might modify the local microenvironmental conditions and vegetation thus affecting the aboveground invertebrate fauna (e.g., Frenette-Dussault et al., 2013; Mugnai et al., 2021; Ozaki et al., 2022). For example, when considering the impacts of *O. stricta* on fauna communities, some differences were detected depending on the taxonomic group: Robertson et al. (2011) found that *O. stricta* density did not significantly affect spider species richness, density or assemblages, but that beetle assemblages were significantly affected. Surprisingly, no studies have investigated the effects of *O. stricta* on ant communities, despite ants being considered one of the best ecological indicators, due to their ubiquity, abundance, and sensitivity towards environmental changes (Masoni et al., 2017; Frasconi Wendt et al., 2021). In particular, they have proven to be very useful in assessing the impacts of invasive species on aboveground invertebrate communities (e.g., Lenda et al., 2013).

In light of this background and given the limited research conducted on *O. stricta,* it is therefore crucial to adopt a broad multi-taxa approach to adequately disentangle the impacts of this species on natural communities (Zamora-Marín et al., 2023). In particular, with this study we aimed to assess the impacts of *O. stricta* on Mediterranean insular ecosystem, evaluating whether its alteration of maquis vegetation leads to cascading effects on the invertebrate fauna, causing substantial ecological changes. To do so, we chose Capraia island, a small Mediterranean island in Tuscan Archipelago (Italy), which is highly threatened by *O. stricta*: the species has been present on the island since the 1980s (Viegi & Cela Renzoni, 1981; Guiggi, 2008) and has been widespread in recent decades, occupying 70 ha of the island's surface (3.6 %) and threatening almost half of the surface of natural habitats of conservation interest (sensu 92/43/EEC "Habitats" Directive) (Misuri et al., 2024). Hence, the island has been used as a model to evaluate i) the changes in soil properties due to *O. stricta* invasion and its impact on the diversity of ii) vascular plants and invertebrate communities such as iii) ants and iv) soil microarthropods.

2. Methods

2.1. Study area

Capraia is the third largest island in the Tuscan Archipelago (19,72 km2), the closest to the Corsican coast (more than 26 km) and the farthest from the Tyrrhenian coast (Fig. 1; Foggi & Grigioni, 1999).

It is a predominantly mountainous island reaching a maximum elevation of 445 m a.s.L. with Mt. Castello, characterized by a Mediterranean climate, with mild and rainy winters and hot and dry summers. Indeed, in Capraia Island the warm season typically extends from June to September, with August being the hottest month, when average daily maximum temperatures reach approximately 25 °C. Conversely, the cool season spans from November to April, with February representing the coldest month, characterized by average maximum temperatures of around 7 °C. Regarding precipitation, November is the wettest month, recording an average rainfall of approximately 90 mL, while July is the driest month, with an average precipitation of only 14 mL (Weatherspark, 2025).

The most representative vegetation consists of the evergreen shrubland of *Erica arborea* L. and *Arbutus unedo* L., which degrades into dynamically less evolved vegetation stages in rocky and steep areas (Foggi & Grigioni, 1999). It is an area of high naturalistic value with a significant number of local endemic flora also hosting terrestrial habitats of conservation interest, two of which (3170* and 6220*, see Sampling section) are priority habitats according to the European Habitat Directive 92/43/EEC. Moreover, Capraia Island is also included in the Italian National Park of the Tuscan Archipelago and in the European Natura 2000 network as Special Areas of Conservation (SAC)/Special Protection Areas (SPA) (IT5160006) (*sensu* 92/43/EEC "Habitats" Directive). There are currently no biocontrol agents acting on *Opuntia* on the island, so its spread in natural and semi-natural areas is not hindered, increasing the threat to habitats of conservation interest. For this reason, *Opuntia* removal action was included within the Life Tetide project "Turning Eradication Targets Into Durable Effects" (Project 101,113,950 — LIFE22-NAT-IT-LIFE TETIDE) launched in late 2023 and still ongoing.

2.2. Sampling

Sampling was conducted in May-July 2023 (9–13 May for plants, 16–20 May for soil fauna and 4–15 July for ants) in the northeastern part of the island in the flowering and later fruiting period (Fig. 1). The selection of this area was based on the following two criteria: i) the presence of the Mediterranean sclerophyllous vegetation, including habitat mosaics of 3120 ("Oligotrophic waters containing very few minerals generally on sandy soils of the West Mediterranean, with *Isoëtes*

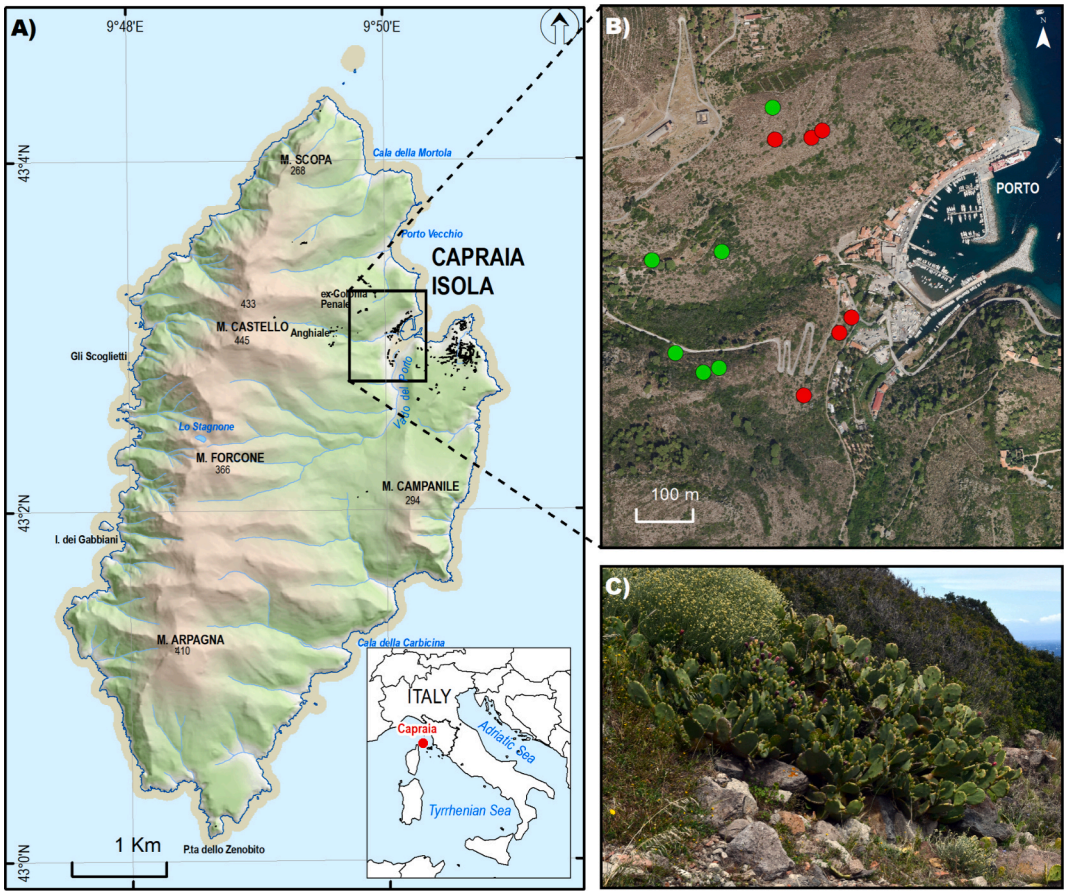

Fig. 1. Geographical setting of the study area. A Capraia Island and its location; B study area with green dots represent the control plots, and red ones represent the invaded plots; C example of Mediterranean shrubland invaded by *Opuntia stricta* (photo by Michele Mugnai). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

spp."), 3170* ("Mediterranean temporary ponds"), 6220* ("Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*"), and 8220 ("Siliceous rocky slopes with chasmophytic vegetation"); ii) a significant density of *O. stricta* (according to Misuri et al., 2024). As reported by Misuri et al. (2024), in fact, *O. stricta*, with over 70 ha, is the most widespread alien species that extends significantly outside the town in areas with natural vegetation, reaching the National Park territories in small and scattered patches. The estimated density of these patches is derived from an empirical estimate obtained from field observations by Misuri et al. (2024), based on the number and width of *Opuntia* clumps per area. See Fig. 1C for an example of habitats invaded by *O. stricta* (more pictures are available in Fig. S1).

Within the study area, we randomly placed a total of 12 square plots (2 m x 2 m), 6 in invaded areas and 6 in control (uninvaded) areas. Each plot was separated by at least 25 m, to ensure their independence in terms of sampling of the animal groups considered.

In each plot, 100 cm^3 of undisturbed soil cores were collected using Eijkelkamp cylinders: the metal cylinders were gently hammered vertically into the soil (taking care not to disturb the soil inside), then carefully removed, ensuring the soil inside remains intact and compact, and finally the soil cores were stored in sealed plastic bags and stored at room temperature. They were then dried at 105 °C until constant weight and the bulk density (BD) was calculated by the ratio between the dry weight and the soil core volume (Blake and Hartge, 1986). Soil texture was determined using the SediGraph method (Andreanelli et al., 2013) and the USDA classification (USDA, 2021). Particle size by sedimentation was also measured with the Sedigraph (Micromeritics Inc.) for automated analysis with X-ray diffraction. The Sedigraph uses a parallel X-ray beam to detect changes in suspended sediment concentration during settling. Samples of 5 g of bulk soil (< 2 mm) were used to obtain a soil suspension passed through a 250 µm wet sieve to detect medium, coarse and very coarse sands. Soil samples were homogenized at 500 µm and analyzed for carbon (C) and nitrogen (N) content by dry combustion with a Thermo Flash 2000 NC soil analyzer equipped with a thermal conductivity detector (Fisher Scientific, Waltham, MA, USA). A sub-sample of 20 to 40 mg was weighed into tin (Sn) capsules for total C and N determination and another sub-sample was pre-treated with 10 % HCl until complete removal of carbonates for total organic C (TOC) determination. The difference between total C and organic C represented the inorganic C concentration and was used to calculate the carbonate concentration. Soil moisture was measured in the field at 0–8 cm depth using a soil moisture meter (Delta T device). Soil pH was measured potentiometrically in a 1:2.5 soil–water suspension.

Undisturbed soil cores were incubated in the laboratory to measure the potential production of CO_2, N_2O, and CH_4, using a DX4040 FTIR Gas Analyzer (Gasmet Technologies Oy, Finland). Undisturbed soil samples were incubated in 1 L flasks and the instrument was connected to the lids with two Teflon tubes, creating a closed path between the instrument and the flasks. Prior to each use, the hardware status was checked, and zero calibration was performed with pure N (99.999 %). The instrument is equipped with Teflon tubes with quick-connect fittings and an on-board sample pump, which has a neoprene diaphragm membrane with a maximum pressure of 1.0 bar and a maximum flow of 2.0 L min^{-1}.

In each plot, we also recorded the occurrence and cover of plant species on a percentage basis. The identification of plant species was performed following Pignatti et al. (2017) and updated the nomenclature according to the Portal to the Flora of Italy (available at https

://dryades.units.it/floritaly, accessed on 01/06/2025). In addition, a 10 × 10 × 10 cm soil sample was dug with a spade from each plot, placed in a plastic bag and stored at room temperature. During the following days, we extracted microarthropods using a modified Berlese-Tullgren apparatus for seven days according to established procedures (Parisi et al., 2005, Menta et al., 2018), and then identified taxa under a microscope to order or class level following Angelini et al. (2002) and counted their abundance.

Ant communities were sampled placing four pitfall traps for each plot, one at each corner of the quadrat plot. Pitfall traps consisted of 50 ml tubes, with a diameter of 30 mm (size is sufficient for local myrmecofauna), filled with an 80 % diluted ethanol and 2 % glycerol solution and buried in the ground so that the rim of the trap was at the same level as the soil surface. The traps were collected after seven days, and the ants were determined at species level, (following the identification keys by Czechowski et al. (2012), Scupola (2018) and Lebas et al. (2019), which was then confirmed by a specialist. Since ants' abundance is highly affected by the closeness of pitfall traps to ant nests (Gotelli et al., 2011), we used incidence data, corresponding to the number of traps containing a species within each plot (from 0 to 4).

2.3. Statistical analysis

Soil variables were tested between the invaded and control sites using a set of analyses of variance (ANOVAs), after checking for assumptions (not significant outliers, normality and homogeneity of variance). To assess the impact on community diversity, we calculated numerical diversity indices at the plot level for each group considered (i.e., plants, soil microarthropods, and ants), including species richness, the Shannon-Wiener diversity index (H'), and Pielou's evenness index (J). For each index, differences between invaded and control sites were tested using ANOVA, after checking for assumptions. Since for the Pielou's evenness index of plants we found significant difference between variances across groups, we used the Welch ANOVA test.

To assess the impacts of *O. stricta* on the species composition of investigated communities, we used a non-metric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarity index (abundance data expressed as percentages for plants, raw abundances for soil microarthropods, and incidences for ants), selecting the function *metaMDS* of the R package vegan (Oksanen et al., 2024). To test these differences, for each group separately, we used a permutational multivariate analysis of variance (PERMANOVA) using 9999 permutations on the Bray–Curtis dissimilarity indices as response variables and the site as predictor for each group separately, using the function *adonis2* of the R package vegan (Oksanen et al., 2024).

All analyses were conducted using the R software (version 4.3.2; R Core Team, 2023) and all plots were produced using the *ggplot2 R* package (Wickham, 2016).

3. Results

In total we recorded 111 plant species (see Tab. S1 for the full list of species recorded in control and invaded sites), among which *O. stricta* was the only invasive alien species, along with 12 ant species and representatives of 26 different orders of soil microarthropods.

We found no differences in the measured soil variables, except for TOC (total organic C) ($F_{1,10} = 34.19$, $P < 0.001$) and C:N ($F_{1,10} = 14.69$, $P < 0.01$), both higher in control sites than in invaded ones (Fig. 2, Tab. S2, Figs. S2 and S3).

Diversity indices did not differ significantly between control and invaded areas, neither for plants, nor for ants, and soil microarthropod communities (Fig. 3, Tab. 1).

However, for plant communities, we found a trend towards higher values for the Pielou's uniformity index in the invaded areas (Fig. 3, Tab. 1).

The results of the multivariate analyses varied according to the taxonomic group (Fig. 4).

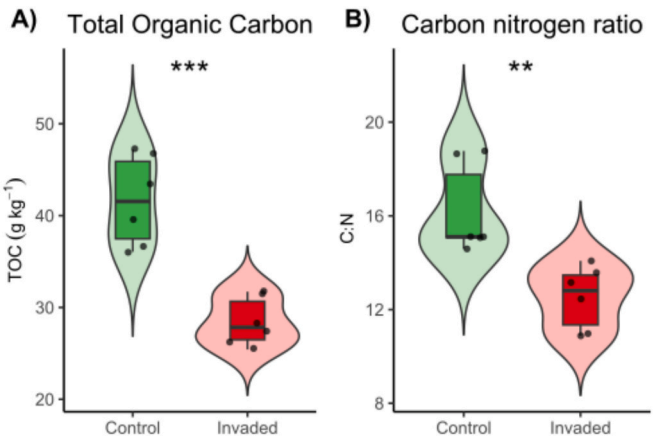

Fig. 2. Comparison between control (green boxplots; n = 6) and invaded (red boxplots; n = 6) plots in terms of A Total Organic Carbon (TOC) and B Carbon nitrogen ratio (C:N) using analyses of variance (ANOVAs). Asterisks denote statistically significant differences between the two communities (p value: * < 0.05; ** < 0.01; *** < 0.001). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

For plants, the community composition differed significantly between sites ($pseudoF_{1,10} = 17.92$, $P = 0.01$). Moreover, we can observe a higher overdispersion of control points compared to the invaded ones which results in more clustered in the compositional space (Fig. 4A). However, in contrast with plant communities, we found no significant differences between sites for both soil microarthropod ($pseudoF_{1,10} = 1.05$, $P = 0.40$) and ant communities ($pseudoF_{1,10} = 1.91$, $P = 0.15$), resulting in an overlap of invaded and control communities in compositional space (Fig. 4B and C).

4. Discussion

A growing number of studies have investigated the effects of invasive plants on multiple taxa (Schirmel et al., 2016), however, the impacts of *O. stricta* have been barely studied, despite its crucial role as an alien species worldwide. In this study, we assessed the impacts of *O. stricta* on soil parameters as well as on different components of the community (plants, ants, and soil microarthropods). Our results showed that *O. stricta* affected only a few soil parameters and plant community composition but not diversity indices or other groups' community composition.

Although a few studies showed soil chemical transformation by other invasive plants such as *Robinia pseudoacacia, Acacia dealbata*, and *Carpobrotus* spp. (e.g. Lazzaro et al., 2014b, 2018, Badalamenti et al., 2016), little information is available for *O. stricta*. Modifications of soil properties are strictly related to the chemical transformations and organic matter inputs from plant species, which trigger specific ecological mechanisms. For instance, *R. pseudoacacia,* as a nitrogen-fixing species, modifies several soil variables, resulting in acidification, increased nitrogen content, and high litter accumulations: this causes a negative impact on soil fauna, affecting not only microarthropods but also soil microbiota (Lazzaro et al., 2018). For *Carpobrotus* spp., the large increase in litter quantity actively changes the composition of the soil microbiota community, impacting the soil microclimate and leading to alterations in soil fungal and bacterial communities (Lazzaro et al., 2014b; Badalamenti et al., 2016). In our study, we found a significant difference only in TOC and C:N ratio between invaded and control areas, suggesting a lower amount of organic matter inputs in invaded areas compared to control ones. This aligns with previous studies carried out in arid ecosystems, which have shown that cacti typically provide minimal shade and produce limited aboveground litter, resulting in soils

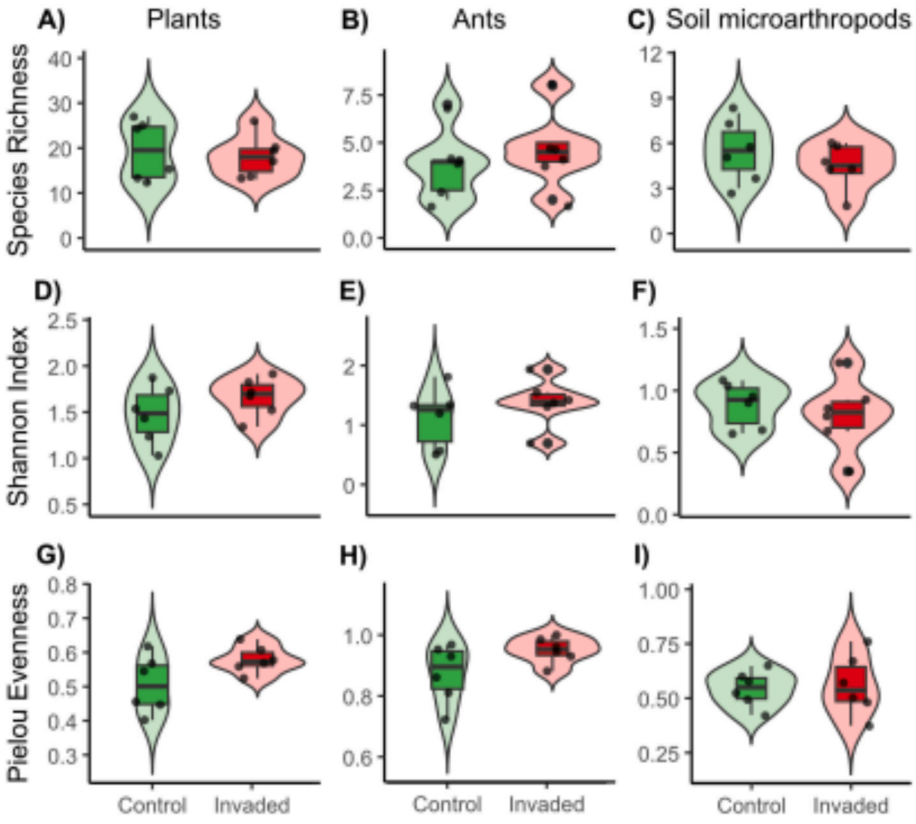

Fig. 3. Diversity indices (Species richness, Shannon-Wiener index and Pielou's evenness index) in the control (green boxplots; n = 6) and invaded (red boxplots; n = 6) communities for plants (A, D, G), ants (B, E, H) and soil microarthropods (C, F, I). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
The effect of invasion status (control plots vs. invaded plots) on Species richness, Shannon-Wiener index (H') and Pielou's evenness index (J) using Repeated Measurement ANOVA. df: degree of freedom; Sum Sq: sum of squares; Mean Sq: mean sum of squares; F value: the overall F-statistic of the ANOVA model. For Pielou's evenness index of plants the following statistics refers to the Welch One-Way ANOVA: statistic = 3.77; DFd = 7.16; p value = 0.092).

Group	Index		df	Sum Sq	Mean Sq	F value	*p* value
Plants	Species Richness	Type	1	4.080	4.083	0.122	0.735
		Residuals	10	336.170	33.617		
	Shannon Index	Type	1	0.111	0.111	1.595	0.235
		Residuals	10	0.700	0.070		
Ants	Species Richness	Type	1	2.083	2.083	0.576	0.465
		Residuals	10	36.167	3.617		
	Shannon Index	Type	1	0.198	0.198	0.952	0.352
		Residuals	10	2.079	0.208		
	Pielou Evenness	Type	1	0.018	0.018	3.220	0.103
		Residuals	10	0.054	0.005		
Soil Microarthropods	Species Richness	Type	1	4.080	4.083	0.122	0.734
		Residuals	10	336.170	33.617		
	Shannon Index	Type	1	0.020	0.020	0.344	0.570
		Residuals	10	0.580	0.0580		
	Pielou Evenness	Type	1	0.001	0.001	0.063	0.808
		Residuals	10	0.129	0.0129		

with moisture and nutrient levels similar to those in bare areas (Butterfield and Briggs, 2009; Neffar et al., 2013). However, Novoa et al. (2021) recorded higher soil moisture and nutrient levels (organic matter, nitrogen, phosphorus, phosphatase, β-glucosidase, and urease activities) in savanna areas of South Africa where *O. stricta* is invasive. This discrepancy is probably due to the different ecosystems invaded. In our case, in fact, *Opuntia* does not produce monospecific stands, but it creates scattered clumps of varying dimensions (Misuri et al., 2024) mixed with Mediterranean scrub dominated by shrubs and herbaceous species. The latter, in fact, can produce a layer of litter to replace the loss of organic substance. The study area of Novoa et al. (2021), on the other hand, consists of typical savanna vegetation with poor herbaceous cover and an uneven distribution of trees, where the influence of *O. stricta* may therefore be more relevant.

Regarding the impacts on plants, our results highlighted that invaded areas are characterized by a greater compositional evenness (i.e., more

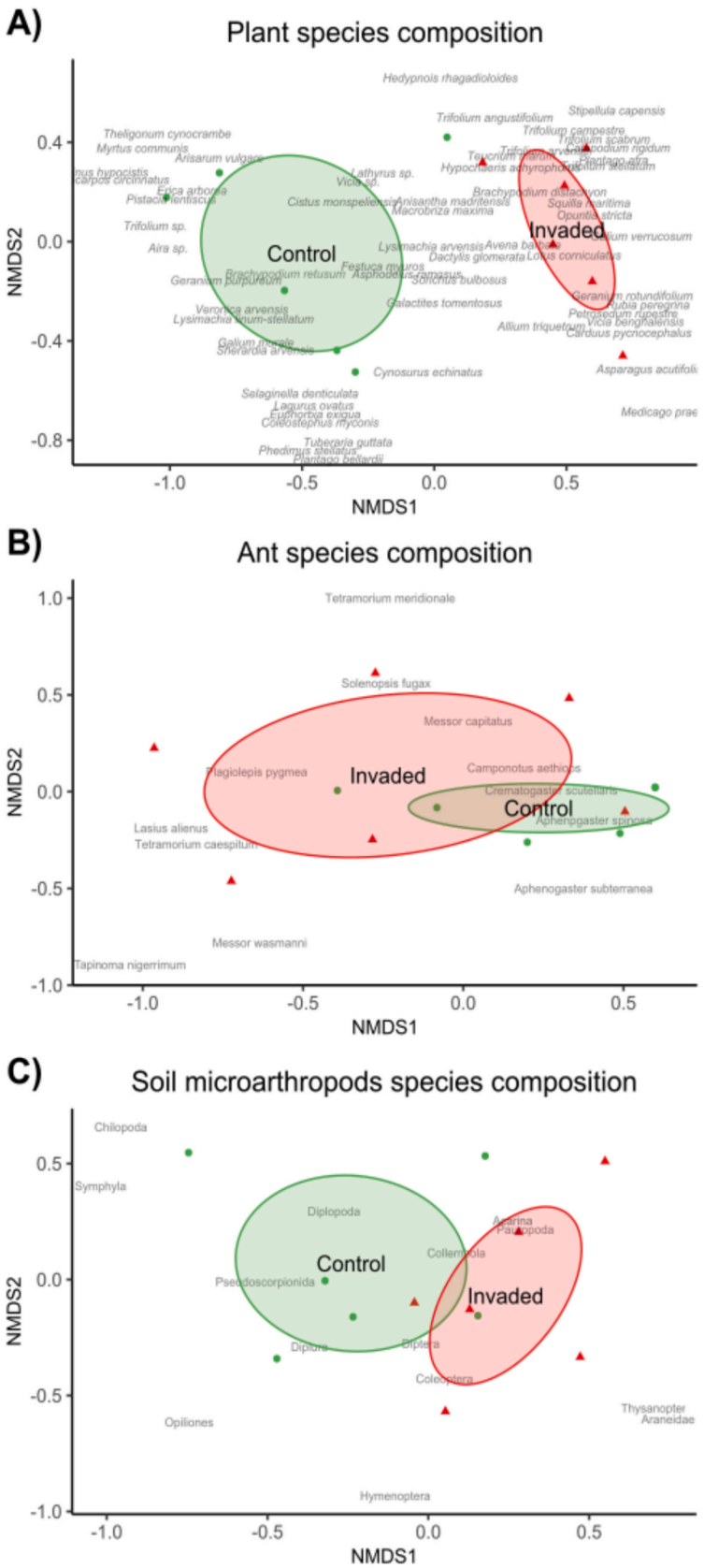

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination plot based on Bray–Curtis dissimilarities for A plant, B ant and C soil microarthropod communities. Ellipses represent standard deviation coded in green for control plots (n = 6) and in red for invaded plots (n = 6). Circles represent control plots while triangles represent invaded ones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

clustered plots in NMDS space, Fig. 4A) compared to control areas, thus highlighting a strong homogenization of the flora by *O. stricta*. Moreover, this species tends to occupy free patches with shallower soils, where Mediterranean shrub species such as *Erica arborea* L., *Myrtus communis* L., and *Pistacia lentiscus* L. are less abundant. Consequently, the invaded communities resulted in a changed species composition and a reduced number of plant species. Such an effect was also found also by Shackleton et al. (2017) who demonstrated how the villagers in the eastern part of Africa perceived a reduction of native plant occurrence due to the presence of *O. stricta*. At the same time and in contrast, for some pastoralists, *O. stricta* seemed to act as a nurse plant protecting native plant species, especially shrubs and trees, from livestock (Shackleton et al., 2017). This action seemed to be effective only for those native species that grow between or near individual plants and/or cactus stands and that already compete for space, light, and nutrients with invasive ones. Similarly, in Eritrea *Opuntia ficus-indica* (L.) Mill. likely provides shelter for species sensitive to herbivory while competing for space with browsing-tolerant species, this presumably explaining the absence of significant impact on native species diversity and richness (Tesfay and Kreyling, 2021). In Kenya, plant communities invaded by *O. ficus-indica* also had significantly higher native species richness and diversity because *O. ficus-indica* protected native species from grazing (Oduor et al., 2018). However, our study plots were located in semi-natural areas where livestock grazing is absent. We also observed in the field that *O. stricta* has an advantage in areas where there are more rock outcrops and less maquis cover, replacing the latter in the successional vegetation stages. Similarly, Erre et al. (2009) reported that *Opuntia* is commonly associated with evergreen sclerophyllous shrubs in degraded Mediterranean scrub, while it is rarely present in mature scrublands dominated by climax species such as holm oak and cork oak. Furthermore, they noted that although the genus *Opuntia* is highly adaptable to arid and semi-arid environments, including Mediterranean ecosystems, low winter temperatures represent the main limiting factor for its growth and distribution. The genus also shows a high tolerance to drought, with as little as 10 mm of monthly rainfall being sufficient for its survival. Considering that climate change is driving an increase in winter temperatures and more frequent drought events, the expansion of *Opuntia* in the Mediterranean Basin is likely to be increasingly favored.

Contrary to the homogenization caused by other invasive plant species (McKinney and La Sorte, 2007, Muthukrishnan and Larkin, 2020), for example, *Carpobrotus* spp. (Mugnai et al., 2022), which significantly alter soil chemistry and vegetation structure (Badalamenti et al., 2016, Vieites-Blanco and González-Prieto, 2018), our results indicated that *O. stricta* had moderate effects compared to other species. In fact, the plant community invaded by *O. stricta* is ecologically similar to the control in terms of edaphic parameters, but floristically different. Likewise, *O. ficus-indica* led to a significant homogenization of species composition in Eritrea, not affecting species richness and Shannon index (Tesfay and Kreyling, 2021). However, such relative change in plant communities might be highly detrimental in the context of a small Mediterranean island that is highly vulnerable to invasions (Celesti-Grapow et al., 2016). Indeed, although we did not detect significant differences in species richness and diversity index between the invaded and control areas, this shift in plant composition could highly threaten the quality of the habitats, not only for vascular plants but also for the associated fauna communities.

Structural and functional diversity of plant communities, as well as plant species richness, are considered drivers of herbivore, predator, and parasitoid diversity (Schuldt et al., 2019). The arrival of an invasive alien plant can change the well-established link between abiotic characteristics and soil invertebrates, inducing a cascading effect (Pyšek et al., 2012; Schirmel et al., 2016; Lazzaro et al., 2018), often significantly altering ecosystem dynamics both above and below ground (Schirmel et al., 2016). For example, the difference in organic matter content between invaded and control plots can affect microarthropod communities (e.g., Potapov et al., 2017). Indeed, soil fauna tends to aggregate in soils rich in organic matter, where both detritivores and predators also interact with the soil microbiome (Rusek, 1998). Nevertheless, we did not find a significant effect of the presence of *O. stricta* on either soil microarthropods or ants. This may be due to the overall similarity between invaded and control plots in terms of edaphic variables, as discussed above. A limited number of studies have shown similar results, with no effect of alien species on microarthropods. For example, Rusterholz et al. (2014) conducted a study focusing on mites and springtails in a deciduous forest and emphasized that the presence of the invasive alien *Impatiens glandulifera* Royle did not significantly alter the diversity of the considered taxa in the leaf litter and upper soil layer. This finding reinforced the idea that not all invasive alien plants have an evident and direct impact on soil fauna. However, the identification of taxa at high taxonomic levels (i.e., class, order) might mask effects on lower taxonomic levels (e.g., families, species). Further research is needed to evaluate this issue in depth in the future, as highlighted by Sciandra et al. (2024). Moreover, although no effects were found on soil fauna, other methods could help assess potential impacts on other soil organisms, like microbiota. Their composition and abundance, in fact, may vary with aridity gradients and the water and nutrient levels near *Opuntia* roots (Gargouri et al., 2021, Novoa et al., 2021).

Our study revealed no clear effect of *O. stricta* on ant community composition either. In the literature, contrasting results exist regarding the impact of invasive alien plants on ant communities. For instance, *Rosa rugosa* Thunb., an alien species along the Baltic coast, had no significant effect on ant communities (Grses et al., 2021), while *Elaeagnus umbellata* Thunb. and *Solidago* sp. negatively influenced both the number of species and community, as well as ant nest distribution and foraging distance (Lenda et al., 2013, Li et al., 2017). Moreover, Robbins and Miller (2009) observed several ant species collecting extrafloral nectar seasonally produced by *O. stricta*, demonstrating that this species can attract various arthropods through nectar production. However, we did not observe the same phenomenon in our study, probably due to the different timing of sampling compared to nectar production. Furthermore, by analyzing the diversity and the species composition solely, it might underestimate possible changes in trophic networks due to its invasion, justifying the need of specific studies. Moreover, ant diversity might be more influenced by other environmental parameters, instead of presence of plant alien species: for example, ant communities may be more closely related with micro-topography (Mugnai et al., 2021), explaining some outlier with high species richness (e.g. CONT_11 and INV_8) both present in invaded and not invaded patches.

Another interesting point worth considering is the effect of alien plants on plant-pollinator interactions. Indeed, other species of the genus *Opuntia* have been shown to be visited by many pollinator species, mostly generalist pollinators (Padrón et al., 2009, Lo Verde and La Mantia, 2011). This could have important implications for both native plants, which may be visited less when *Opuntia* is present, and for the pollinators themselves, potentially altering their interaction network (Padrón et al., 2009; Kovács-Hostyánszki et al., 2022). These aspects deserve *ad hoc* studies to comprehensively understand the potential impact of *O. stricta* on native plants' populations and pollinator communities (e.g. bees, butterflies).

5. Conclusion

Opuntia stricta significantly reduced the C input to soil and altered plant community composition, but not soil microarthropod and ant communities. Although in this context *O. stricta* seemed to have a lower impact on certain taxa compared to other invasive plants, we cannot exclude that additional taxonomic groups not considered in our study may be directly or indirectly affected by the presence of *O. stricta* (Litt et al., 2014, Schirmel et al., 2016). In conclusion, our study provides a first assessment of the relationships between *O. stricta* and some abiotic and biotic components in invaded ecosystems and indicates the further factors to investigate for a more complete and better understanding of its

invasion. Further study might detect the temporal changing of patches invaded by *O. stricta*, considering his fast growing and its role in seasonal variation of flora and fauna.

CRediT authorship contribution statement

Alice Misuri: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Elena Tricarico:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization. **Lorenzo Lazzaro:** Writing – review & editing, Validation, Conceptualization. **Sara Forni:** Writing – original draft, Visualization, Methodology, Investigation. **Eugenia Siccardi:** Writing – review & editing, Validation, Investigation. **Marco Morbidelli:** Validation, Methodology, Investigation. **Alberto Masoni:** Validation, Methodology, Investigation. **Giacomo Santini:** Writing – review & editing, Validation, Conceptualization. **Giuseppe Mazza:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization. **Alessandra Lagomarsino:** Writing – review & editing, Validation, Methodology, Investigation. **Silvia Landi:** Writing – review & editing, Validation, Methodology, Investigation. **Paride Balzani:** Writing – review & editing, Writing – original draft, Validation. **Renato Benesperi:** Validation, Project administration. **Daniele Viciani:** Validation, Project administration. **Claudia Becagli:** Validation, Methodology, Investigation. **Michele Mugnai:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2025.127110.

Data availability

Data will be made available on request.

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