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RESEARCH ARTICLE

Effects of simulated climate change on soil characteristics under *Carpobrotus edulis* invasion in a coastal backdune

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Abstract

Background and aims Along coastal habitats worldwide, *Carpobrotus edulis* is a highly invasive and detrimental species, that acts as an ecosystem engineer by modifying many soil properties for its own benefit. However, the combined effects of *C. edulis* and climate change on soil characteristics remain largely unknown.

Methods To address this knowledge gap, we set up a factorial field experiment with five treatments and eight replicates per treatment: natural vegetation as an uninvaded control under current climate conditions, *C. edulis* under current climate conditions, and *C. edulis* subjected to increased temperature (+ 2 ºC), decreased rainfall (- 33%), and both factors combined (+ 2 ºC and - 33% rainfall). The soil 0–5 and 5–10 cm layers were sampled after 14 months and analysed for 21 properties.

Results Although the effect of depth on soil characteristics was greater in most cases, the treatments significantly affected soil pH_{KCl}, electrical conductivity, organic $\delta^{13}C$, NH_4^+-N, NO_3^--N and available Al, Ca, Cu, Fe, Mg, Mn, P, and Zn. The discriminant analyses clearly differentiated the invaded from the uninvaded soils, reinforcing the view of *C. edulis* as an ecosystem engineer and highlighting the significant role of the species in shaping ecosystem dynamics. Besides, the analyses indicated that decreased precipitation had a greater impact on invaded soils than increased temperature, and suggested a synergistic effect of both climatic treatments.

Conclusion These findings underline the complex interactions between invasive species and climate change, highlighting the need for specific management strategies to mitigate *C. edulis* impacts on soil health and ecosystem integrity.

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Introduction

Soil properties are impacted by a number of global change factors induced by human activities, affecting the plant-soil interface (Bi et al. 2024; Fuchslueger et al. 2024). Climate change-induced environmental changes (for example, temperature increases and droughts) can influence nutrient cycling and availability (Chatterjee and Saha 2018). However, the nature of these alterations can vary depending on changes in climatic conditions, habitat, or plant cover (Matías et al. 2011). A drier climate can reduce microbial activity, causing an accumulation of nutrients in the soil, which will be more susceptible to leaching or erosion (Matías et al. 2011). Higher temperatures might result in a more rapid decomposition and mineralization, increasing nutrient availability and the rate of N mineralization and nitrification (Elbasiouny et al. 2022). However, a combination of higher temperature with lower soil moisture can reduce microbial activity and decomposition (Elbasiouny et al. 2022). In back dunes, changes in soil properties can affect the early stages of succession, influencing species composition and abundance and the entrance of alien species (Trotta et al. 2024).

Another major ecological stressor, biological invasions, can also impact soil chemical composition and nutrient availability (Ehrenfeld 2010). In fact, biological invasions frequently have stronger ecological effects than climate change (Lopez et al. 2022). Although climate change usually reduces the impact of invasions, in approximately 25% of cases there is a synergistic interaction (Lopez et al. 2022). Understanding how climate change will affect the impact of these invasions is necessary for guiding conservation and management policies (Côté et al. 2016).

One of the most invasive species worldwide is *Carpobrotus edulis* (L.) N.E. Br. (ice plant), a succulent plant from the Aizoaceae family, native to South Africa and introduced to temperate coastal regions of Eurasia, America, Africa, and Oceania (Campoy et al. 2018). Its success is attributed to its rapid growth, characterized by the formation of a dense mat, and the release of allelopathic compounds, which confers it a highly competitive ability (Maltez-Mouro et al. 2010; Novoa et al. 2012; Traveset et al. 2008). In addition, high rates of seed dispersal (Bourgeois et al. 2005), and significant ecophysiological plasticity (Fenollosa and Munné-Bosch 2019) give *C. edulis* a high capacity to invade habitats, functioning as an ecosystem engineer (Conser and Connor 2009). It modifies both plant (Santoro et al. 2012) and animal (Galán 2008) communities, affecting water and light availability (Molinari et al. 2007), and altering soil properties (Vieites-Blanco and González-Prieto 2018a) and microbiota (Badalamenti et al. 2016).

The effects of *C. edulis* invasion on soil depend on the substrate characteristics; its impacts are more pronounced at the surface and are mostly determined by the chemical properties of its necromass (Vieites-Blanco and González-Prieto 2018a). Soils with low organic matter and nutrient availability seem to be the most affected when comparing different dune soils (Novoa et al. 2014; Santoro et al. 2011), although comparisons between back dunes and rocky areas suggest otherwise (Vieites-Blanco and González-Prieto 2018a). *Carpobrotus edulis* effects include changes in soil pH, organic matter content, and macro- and micronutrient availability (Conser and Connor 2009; Novoa et al. 2014; Vieites-Blanco and González-Prieto 2018a). The impacts of the invasion have been observed in both the topsoil (0–5 cm) and subsoil (5–10 cm), although with a higher intensity in the topsoil (Vieites-Blanco and González-Prieto 2018a). Its invasion also alters soil microbiota composition and structure, as well as microbial activity related to nutrient cycling (Gómez-Rodríguez et al. 2024; Rodríguez-Caballero et al. 2020). Through its influence on the physicochemical and biological properties of soils, *C. edulis* affects both gross and net fluxes of the N cycle, limiting N availability (Vieites-Blanco and González-Prieto 2018b). The persistence of these effects after *C. edulis* removal, along with the fact that they facilitate its invasion, can sabotage restoration efforts and hinder natural vegetation recolonization (Conser and Connor 2009; de la Peña et al. 2010; Molinari et al. 2007).

Less is known about how climate change will affect *C. edulis* invasion. While the species benefits from increased temperatures, which enhance its photochemical efficiency and growth, it is less responsive to reductions in precipitation (Campoy et al. 2021). The influence of climate change on the invasion's impact on soil remains to be explored. As most alterations in soil appear to be necromass-mediated, an increase in *C. edulis* growth rate under warmer conditions could magnify its impacts on soil, leading to significant changes in nutrient dynamics and overall soil composition. By examining changes in soil chemical characteristics in the topsoil (0–5 cm) and subsoil (5–10 cm) (the most affected soil layers by necromass and plant roots, respectively) under predicted climate scenarios, this study aims to elucidate how expected climatic conditions (i.e., increased temperature, reduced precipitation, and their concurrence) will impact the effects of *C. edulis* invasion on soil properties and macro- and micronutrient availability. This knowledge is crucial for developing strategies to mitigate the ecological impacts of *C. edulis* under shifting climate conditions.

Material and methods

Study site

The experimental field plot was located over a coastal back dune on Sálvora island (42°28′44″N, 9°0′34″W, Galicia, NW Spain), a small uninhabited island which is part of the Galician Atlantic Islands National Park (Fig. 1). The island was invaded by *C. edulis* for about 80 years, covering an invaded area of around

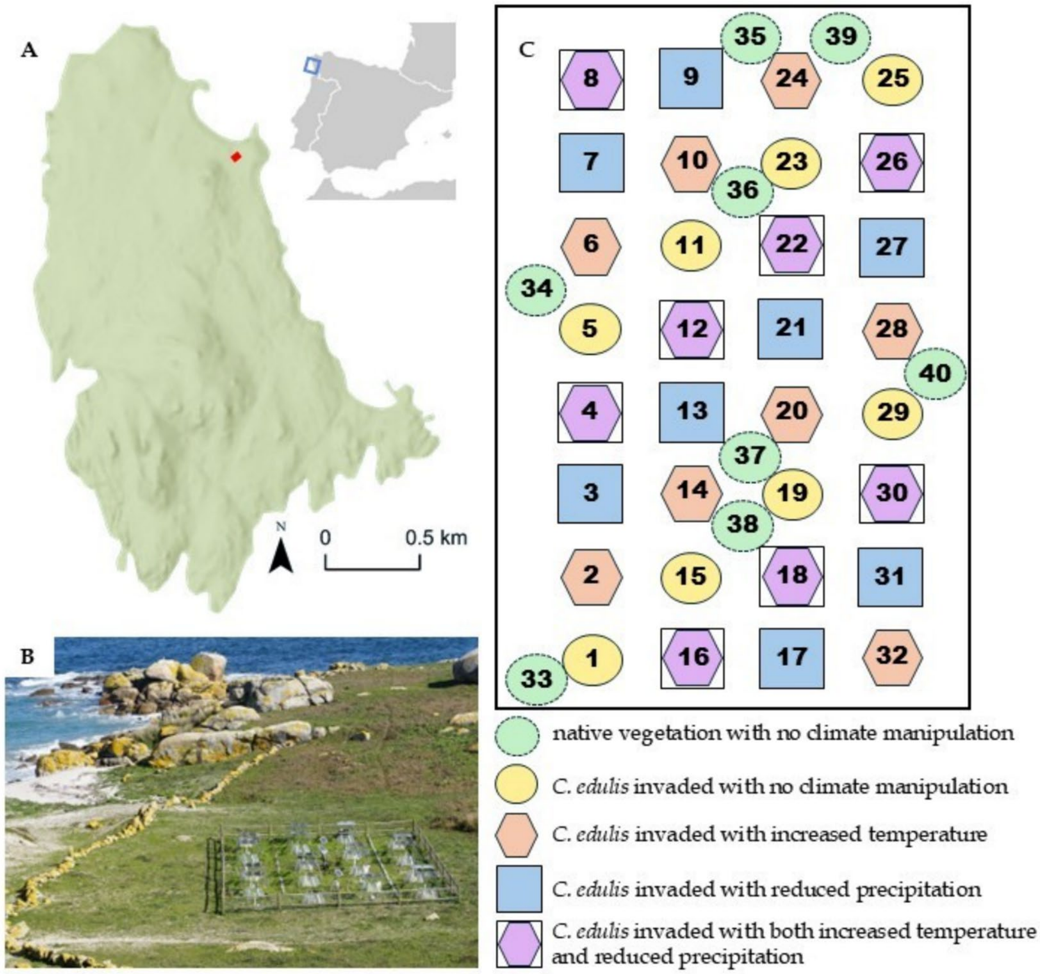

Fig. 1 Map of Sálvora island and its location in NW Spain (blue square), with the study site represented with a red rectangle (**A**), and close-up (**B**) and treatments (**C**) of the study site

30,000 m^2, before being mechanically removed in 2017. The field plot was established in an area with no signs of previous invasion (Ministerio para la Transición Ecológica y el Reto Demográfico 2025). The climate in the area is warm temperate with dry and warm summers or '*Csb*' type of Köppen-Geiger, with 1193 mm of mean annual rainfall and mean temperature ranging from 10 ºC in January to 20 ºC in August (AEMET-IMP 2011). The soil type is an Eutric Arenosol (IUSS Working Group 2014).

Forty subplots (1.55 m × 1.75 m) were established from September 2015 to November 2016 for a factorial experiment considering two depths (0–5 and 5–10 cm layers) with five treatments (Box 1) and eight replicates per treatment: natural vegetation under current climate conditions as uninvaded control (NV) (see Table S1 for vegetation characterization), *C. edulis* under current climate conditions (CC), and *C. edulis* under climate conditions modified according to the predictions for the study area (EEA 2017), i.e., 2 ºC increased temperature (CT), 33% decreased rainfall (CP) and 2 ºC increased temperature and 33% decreased rainfall (CTP); for more details see Campoy et al. (2021).

Box 1 Abbreviations of the treatments used in the manuscript

Abbreviation	Meaning
NV	natural vegetation under current climate conditions
CC	*C. edulis* under current climate conditions
CT	*C. edulis* under 2 ºC increased temperature
CP	*C. edulis* under 33% decreased rainfall
CTP	*C. edulis* under 2 ºC increased temperature and 33% decreased rainfall

Soil sampling and analyses

At the end of November 2016, just after the manual removal of both natural vegetation and the *C. edulis* plants that had grown in the plot for 14 months, soil samples were collected separately from the 0–5 cm (hereafter referred to as topsoil) and 5–10 cm (from now on referred to as subsoil) layers in each subplot (n =40). Four soil subsamples were taken with a stainless-steel probe (4 cm Ø) and mixed in the field into a composite sample per plot and depth. In the laboratory, the soils were sieved (< 2 mm), homogenized, and then divided into fresh subsamples (kept at 4 ºC) for inorganic N measurements and air-dried subsamples for the other analyses.

A pH-meter and a conductometer (both from Metröhm, Switzerland) were used for measuring soil pH in H_2O and 0.1 M KCl (1:2.5 soil:solution ratio), and soil electrical conductivity (1:5 soil:water ratio), respectively. Soil humidity was determined by drying soil samples at 105 ºC for 5 h.

Total C and total N of soils, as well as their ^{13}C and ^{15}N isotopic signatures, were measured in finely ground sub-samples (< 100 µm) with a CE 1108 elemental analyser (Carlo Erba, Italy) coupled on-line to a Delta C isotopic ratio mass spectrometer (Finnigan Mat, Germany). We also measured organic C and organic δ ^{13}C after $CaCO_3$ removal with 20% HCl, using the'capsule method'of Brodie et al. (2011). An elemental reference material (Soil 3 from Eurovector, Italy) and two isotopic standards [IAEA-CH- 6 and IAEA-CH- 7 (for δ ^{13}C) or IAEA-N1 and IAEA-N2 (for δ ^{15}N), alternately, from the International Atomic Energy Agency, Vienna, Austria] were included in each set of 10 samples to check the accuracy of the results; if necessary, drift correction was applied against internal standards during the run.

After extraction with 2 M KCl (1:5 soil:solution ratio) and filtration (glass microfiber filters Whatman GF/A, Ø 125 mm), the inorganic N species were sequentially liberated with two consecutive microdiffusions in hermetic glass jars by adding MgO (NH_4^+-N) and MgO +Devarda's alloy (NO_3^--N). Both N forms were trapped as NH_3 into 10 mL of 0.004 M H_2SO_4 in a Teflon bottle suspended in the glass jars and measured by back titration of the H_2SO_4 excess with 0.004 M NaOH. Three blanks and three NH_4NO_3 standards were included in each batch to subtract N from reagents and to check for N recovery.

The multi-elemental extraction method of García-Marco et al. (2020)-with a mixture of 1 M NH_4Ac and 0.005 M DTPA (soil:solution ratio of 1:5)- was employed to extract the soil available Al, Ca, Co, Cu, Fe, K, Mg, Mn, Na, Ni, P and Zn, which were measured with a simultaneous ICP-OES (Varian Vista Pro, Australia). A calibration curve prepared with certified standards of all elements was measured beforehand and one of the calibration solutions was routinely included in each set of 30 samples as a quality control and, when necessary, the calibration curve was measured again.

Samples were analysed in duplicate, and the mean was used for the statistical analysis.

Statistical analysis

An exploratory data analysis was carried out to detect outliers and anomalies that could affect the results, as well as to check the fulfillment of the assumptions of normality (Shapiro–Wilk's W test) and homogeneity of variances among groups (Levene's test); when these assumptions were not fulfilled (electrical conductivity, NH_4^+-N, total N, Na, K, P, Cu, Mg, Mn and Zn), the original data were transformed by Tukey's ladder of powers. Data were examined by two-way ANOVA with treatment (CC, CT, CP, and CTP) and depth (0–5 and 5–10 cm) as factors, and significant differences between the group means at $p < 0.05$ were stablished with the Bonferroni's test. A one-way ANOVA was used to check the effect of the invasion (NV vs CC) at each soil depth. The partial eta-squared (η^2) statistic was used to determine the proportion of the variation accounted for by each factor or interaction in both ANOVAs.

After checking the multivariate normal distribution with the Mardia's test and the equality of the group covariance matrices with the Box's *M* test, canonical discriminant analyses were done separately for each soil depth (0–5 and 5–10 cm) with the seven variables that showed the highest differences between treatments in the ANOVAs: Al, Mn,$\delta^{13}C$, NH_4^+-N, Zn, electrical conductivity and Mg, with Fe being used instead of Mg in the 5–10 cm layer.

The statistical analyses were performed with IBM SPSS 29.0 and the MVN package in the R environment (R Core Team 2022).

Results

The main characteristics of the studied soils are shown in Supplementary material, Table S2. Both treatment and soil depth and their interaction had a significant influence on soil pH_{KCl}, but the effect of soil depth ($p < 0.001$; 70.5% of the variance explained) was much stronger than that of treatment ($p < 0.01$; 19.2% of the variance explained) and the depth x treatment interaction ($p < 0.001$; 27.4% of the variance explained) (Supplementary material, Table S3). While no differences among treatments were found in the topsoil, a moderate (0.1–0.2 pH units) but significant acidification was observed in the subsoil for the CC treatment compared to CP and CTP, the CT treatment having intermediate pH values (Fig. 2). Analysing all treatment and depth categories together, the two-way ANOVA showed lower mean pH_{KCl} in CC than CTP, as well as in topsoil than subsoil. Similar trends were found for pH_{H2O}, though these differences were not statistically significant (Supplementary material, Table S3). Despite the significant effects of treatment ($p < 0.005$) and soil depth ($p < 0.05$) on electrical conductivity, these factors explained only a small proportion of its variance (21.4% and 7.4%, respectively). The lowest values were recorded in CC (0–5 cm), but the differences with the other treatments were scarcely significant (Fig. 2). The two-way ANOVA showed lower mean electrical conductivity in CC than in CTP, and in the subsoil than in the topsoil (Fig. 2, Table S3). No treatment or treatment x depth effects were found for the organic C. In contrast, soil depth had a significant effect ($p < 0.001$) explaining 48.4% of the variance, as organic C levels were higher in the topsoil than in the subsoil (Fig. 2; Table S3). Regarding the $\delta^{13}C$ isotopic signature, soil depth was a more important factor than treatment (60.3% vs. 14.9% of variance explained; $p < 0.001$ and $p < 0.05$, respectively). The subsoil was less ^{13}C depleted than the topsoil, and the CC was less depleted than CT (Fig. 2; Table S3).

The two-way ANOVA showed a similar trend for NH_4^+-N and NO_3^- -N in the topsoil, with the highest values found in CTP, the lowest in CC, and intermediate values in CT and CP (Fig. 2; Table S3). Conversely, no differences were observed in the subsoil for the NO_3^- -N (Fig. 2; Table S3). Jointly considering all cases, treatment explained 29.4% of the NH_4^+-N variance ($p < 0.001$), while depth explained 44.0% of the variance ($p < 0.001$), with lower mean levels in the subsoil than in the topsoil. Concerning the NO_3^- -N content, treatment explained 13.5% of the variance, soil depth explained 11.1% of the variance and their interaction explained 13.8% of the variance ($p < 0.05$ in all cases), with slightly lower mean NO_3^--N levels in the topsoil than in the subsoil (Table S3). Like for organic C, soil depth also

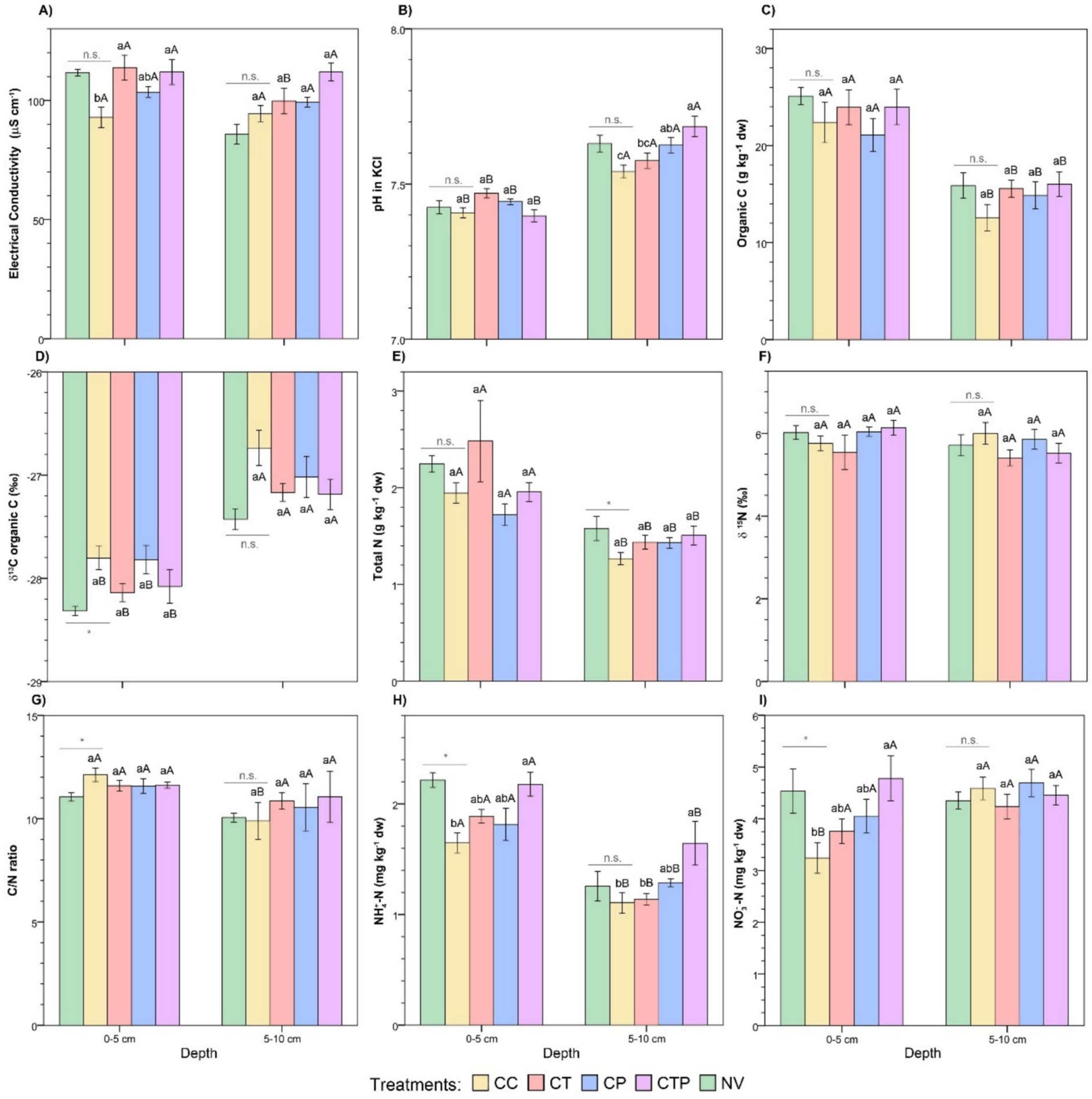

Fig. 2 Effect of treatments on the electrical conductivity, pH in KCl, organic C content, $\delta^{13}C$, organic N, ^{15}N, C/N ratio, NH_4^+-N and NO_3^- -N (corresponding to graphs **A** to **I**, in this order) in the 0–5 cm and 5–10 cm soil layers. Bars represent means ± SE. Different letters indicate significant post hoc differences at $p \leq 0.05$ among soil depths for a same treatment (capital letters) and among treatments for a given depth (lowercase letters). Asterisks indicate significant differences at $p \leq 0.05$ between native vegetation with no climate manipulation (NV) and *C. edulis* invaded with no climate manipulation (CC) plots for a given depth, while n.s. means no significant difference. Treatments: CC, *C. edulis* invaded with no climate manipulation; CT, *C. edulis* invaded with increased temperature; CP, *C. edulis* invaded with reduced precipitation; CTP, *C. edulis* invaded with both increased temperature and reduced precipitation

explained around half of the organic N variance (59.1%; $p < 0.001$), with higher contents in the topsoil than in the subsoil. None of the factors, nor their interaction (treatment x depth) had significant effect on the $\delta^{15}N$ isotopic signature (Fig. 2; Table S3). A small but significant effect of depth on C/N ratio was found (8.5% of the variance explained, $p < 0.05$), with higher values on the topsoil. Despite the significant effects of treatment ($p < 0.05$) and depth ($p < 0.001$) on the soil available P, these factors explained only a small fraction of the variance (15.3% and 24.9%, respectively). The mean P levels were significantly lower in CP than in CC treatment, as well as in the subsoil than in the topsoil (Fig. 3; Table S3).

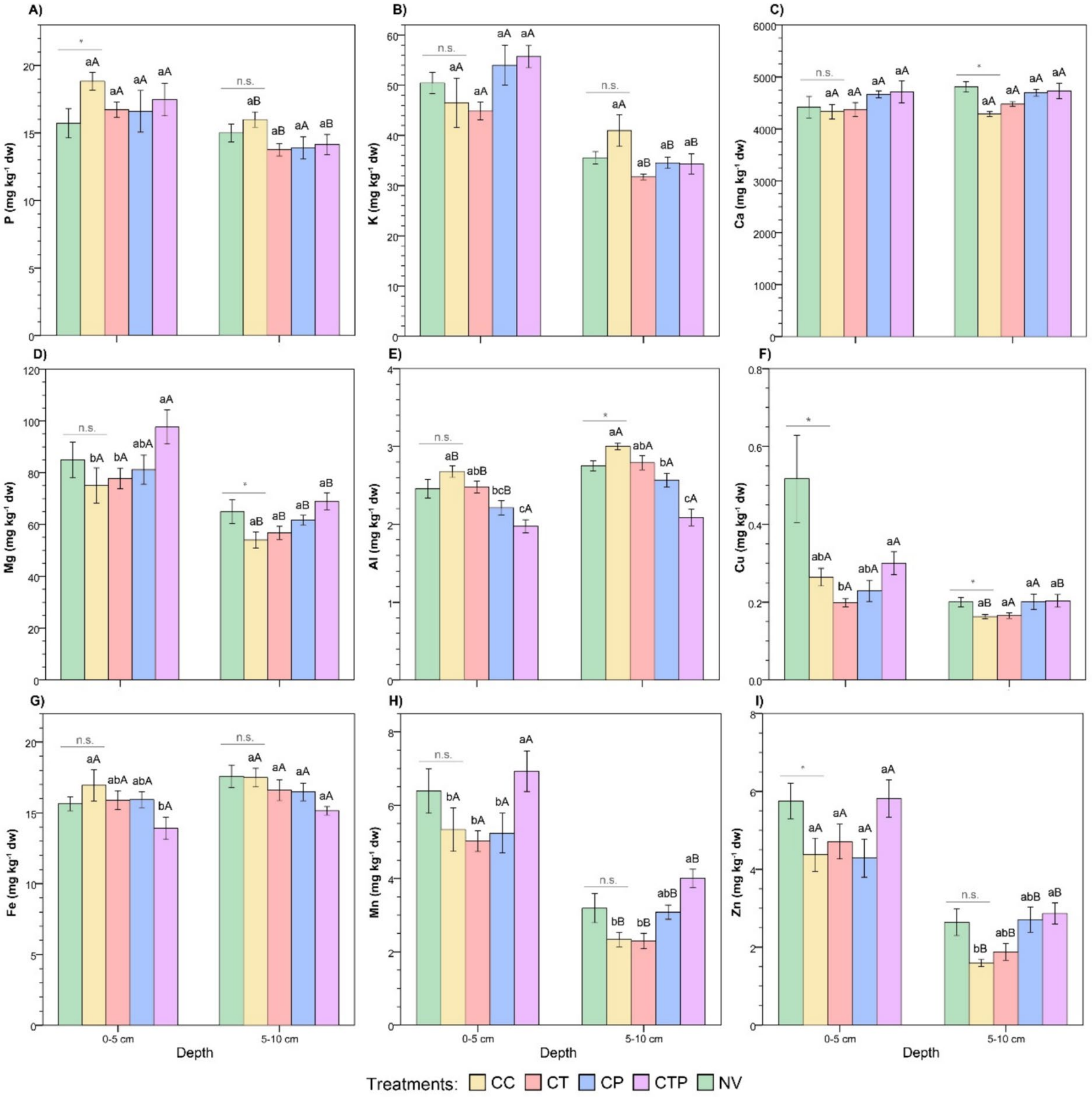

Fig. 3 Effect of treatments on the available contents of P, K, Ca, Mg, Al, Cu, Fe, Mn and Zn (corresponding to graphs **A** to **I**, in this order) in the 0–5 cm and 5–10 cm soil layers. Bars represent means ± SE. Different letters indicate significant post hoc differences at $p \leq 0.05$ among soil depths for a same treatment (capital letters) and among treatments for a given depth (lowercase letters). Asterisks indicate significant differences at $p \leq 0.05$ between native vegetation with no climate manipulation (NV) and *C. edulis* invaded with no climate manipulation (CC) plots for a given depth, while n.s. means no significant difference. Treatments: CC, *C. edulis* invaded with no climate manipulation; CT, *C. edulis* invaded with increased temperature; CP, *C. edulis* invaded with reduced precipitation; CTP, *C. edulis* invaded with both increased temperature and reduced precipitation

No effects of treatment on available K were found, while depth explained almost half of its variance (43.0%; $p < 0.001$), with lower values in the subsoil than in the topsoil (Fig. 3; Table S3). No significant effects of treatment, depth, or their interaction, were found for the available Na content (Table S3). The treatments had a small influence on available Ca, accounting for 21.8% of the variance explained ($p < 0.01$). However, mean values were significantly lower in the CC treatment than in CP and CTP treatments (Fig. 3), and no significant effects of soil depth or the treatment x depth interaction were observed (Table S3). Regarding available Mg, its concentrations were significantly affected by both factors, with the effect of soil depth (47.9% of variance explained; $p < 0.001$) being twice that of treatment (27.5% of variance explained; $p < 0.001$). The levels of available Mg were lower in CC and CT than in CTP, and in the subsoil than in the topsoil (Fig. 3; Table S3).

The available Al content was significantly affected by both treatment and depth factors ($p < 0.001$), with treatment explaining twice as much variance as depth (66.0% vs. 28.3%). Al levels were slightly lower in the topsoil than in the subsoil, with the lowest values recorded in the treatments with decreased precipitation (i.e., CP and CTP) (Fig. 3; Table S3). Both factors also significantly affected the available Cu content, though the effect of treatment (16.3% of variance explained; $p < 0.05$) was smaller than that of soil depth (29.9% of variance explained; $p < 0.001$). Overall, mean Cu levels in CT were lower than in CTP, and in the subsoil than in the topsoil. Soil available Fe levels were significantly affected by treatment (21.2% of variance explained; $p < 0.005$), with values in CTP being lower than those in CC (Fig. 3; Table S3). Like Cu, the available Mn levels were influenced by both treatment and soil depth ($p < 0.001$), but the effect of treatment was only half that of soil depth (36.5% vs. 67.4% of variance explained). Mn levels were also lower in CC, CP and CT than in CTP, and in the subsoil than in the topsoil (Fig. 3; Table S3). For the available Zn, the trends observed were similar to those of Cu and Mn, with 21.7% and 64.7% of variance explained by treatment and depth, respectively ($p < 0.001$ in both cases), lower in CT and CC than in CTP and in the subsoil than in the topsoil (Fig. 3; Table S3). The concentrations of Co and Ni were at or below the detection limits in all samples.

The *C. edulis* invaded plots (CC) did not show differences with native vegetation plots (NV) in pH, electrical conductivity, organic C, $\delta^{15}N$ or available Fe, K, Mn and Na (Table S4). In the topsoil, the invasive *C. edulis* increased the C/N ratio, the $\delta^{13}C$ and the available Al and P, while reducing inorganic N (both NH_4^+ and NO_3^-) and Zn availability (Fig. 2 and 3, Table S4). In the subsoil, the invasive *C. edulis* reduced the availability of Ca and Mg (Figs. 3, Table S4). *Carpobrotus edulis* reduced the availability of Cu in both the topsoil and subsoil (Fig. 3, Table S4).

Table 1 shows the structure matrix with the pooled within-groups correlations between discriminating variables and canonical discriminant functions for the topsoils and subsoils, obtained with the canonical discriminant analyses (CDA). Figures 4 and 5 illustrate the respective plots of the first two discriminant functions for each soil layer. In the topsoil, function 1 explained 63.9% of the variance, primarily distinguishing the soils based on the opposing levels of extractable Al ($r = -0.665$) and extractable NH_4^+-N and Mg ($r = 0.255$ to $r = 0.268$). Function 2, which

Table 1 Canonical discriminant analyses for the topsoil and subsoil with the seven variables that showed the highest differences between treatments in the ANOVAs. The structure matrix presents the pooled within-groups correlations between discriminating variables and canonical discriminant functions

	0–5 cm layer		5–10 cm layer	
	Function 1	Function 2	Function 1	Function 2
Electrical conductivity	0.175	– 0.207	0.392	0.494
$\delta^{13}C$ organic	0.054	0.401	– 0.049	0.587
NH_4^+-N	0.255	– 0.514	0.292	– 0.056
Extractable Al	– 0.665	0.297	– 0.724	0.365
Extractable Mg	0.268	– 0.202		
Extractable Mn	0.186	– 0.298	0.486	– 0.438
Extractable Zn	0.118	– 0.365	0.310	– 0.466
Extractable Fe			– 0.292	– 0.135

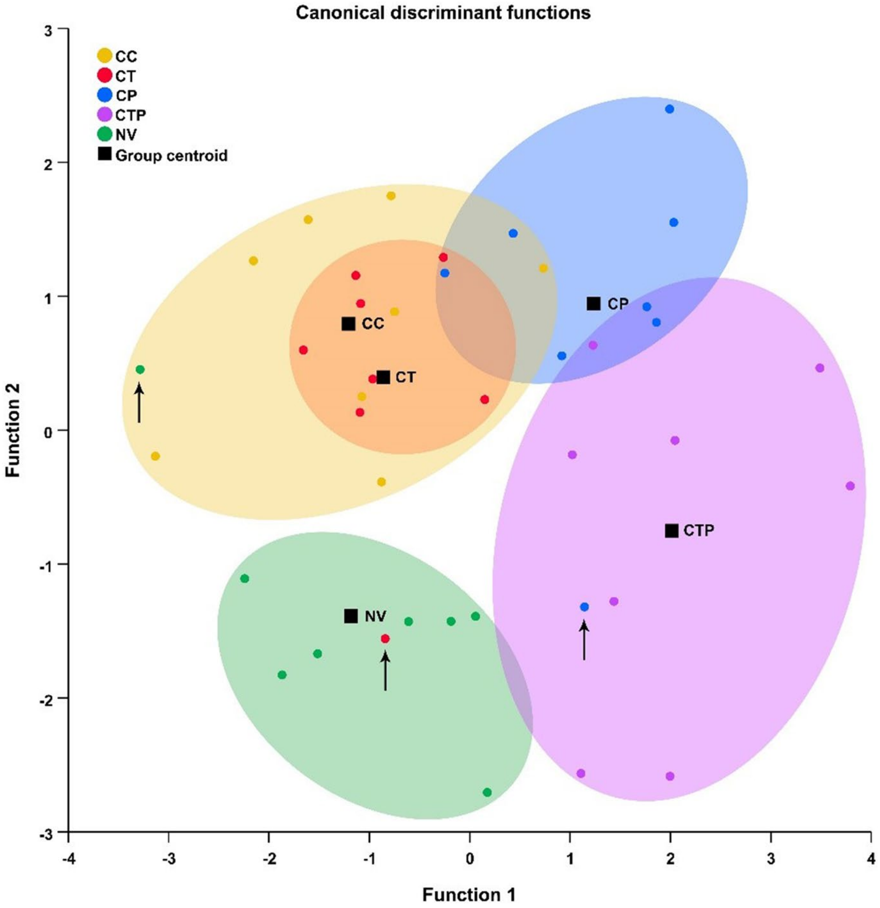

Fig. 4 Canonical discriminant analysis plot of the first two discriminant functions showing the differences between the studied treatments based on the physicochemical and chemical properties of the 0–5 cm soil layer. The arrows indicate the three samples wrongly grouped. Treatments: NV, native vegetation with no climate manipulation; CC, *C. edulis* invaded with no climate manipulation; CT, *C. edulis* invaded with increased temperature; CP, *C. edulis* invaded with reduced precipitation; CTP, *C. edulis* invaded with increased temperature and reduced precipitation

explained 29.0% of the variance, discriminated the soils primarily according to the levels of NH_4^+-N ($r = -0.514$), extractable Zn ($r = -0.365$) and organic $\delta^{13}C$ ($r = 0.401$) (Table 1). In Fig. 5, function 1 discriminated the subplots with *C. edulis* according to the climatic treatments, ranging from CC to CTP, with CT and CP treatments in intermediate positions. Function 2 clearly discriminated the topsoils under current climate conditions based on the type of vegetation, differentiating between native species and the invasive *C. edulis*, with only one case misclassified. Regarding the subsoils, the importance of extractable Al as a discriminating variable was comparable to that in the topsoils, whereas those of electrical conductivity, organic $\delta^{13}C$, extractable Zn and extractable Mn increased and that of NH_4^+-N decreased (Table 1). In the subsoils, functions 1 and 2 also explained high proportions of the variance (71.8% and 19.6%, respectively), but the discrimination of samples (Fig. 5) was less clear, though still comparable to that observed in the topsoils (Fig. 4).

Discussion

With scarce exceptions, the published studies have reported that *C. edulis* invasion usually promotes soil acidification (Badalamenti et al. 2016; Conser and Connor 2009; Gómez-Rodríguez et al. 2024; Molinari et al. 2007; Novoa et al. 2013, 2014; Rodríguez-Caballero et al. 2020; Santoro et al. 2011; Vieites-Blanco and González-Prieto 2018a; Vilà et al. 2006; Winsemius et al. 2015). One possible cause of this reduction in soil pH is the increased uptake of basic cations by the invader, as found by Vieites-Blanco

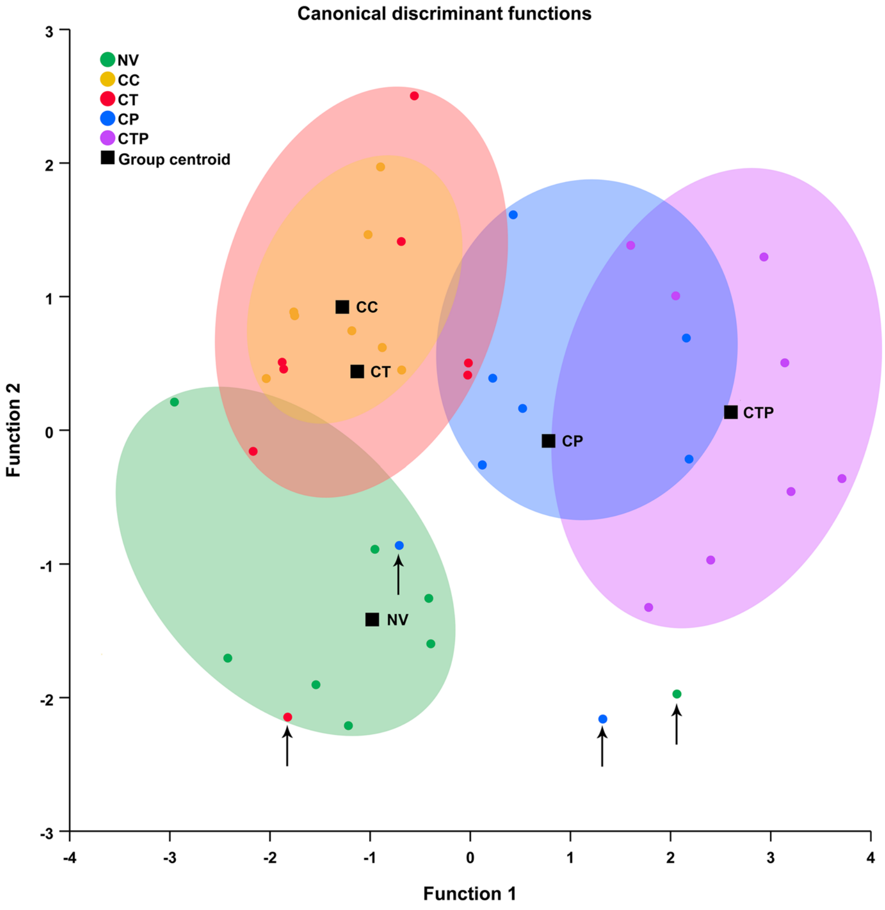

Fig. 5 Canonical discriminant analysis plot of the first two discriminant functions showing the differences between the studied treatments based on the physicochemical and chemical properties of the 5–10 cm soil layer. The arrows indicate the four samples wrongly grouped. Treatments: NV, native vegetation with no climate manipulation; CC, *C. edulis* invaded with no climate manipulation; CT, *C. edulis* invaded with increased temperature; CP, *C. edulis* invaded with reduced precipitation; CTP, *C. edulis* invaded with increased temperature and reduced precipitation

and González-Prieto (2018a). Another potential cause is the rhizodeposition of acidifying substances by *C. edulis* and/or the release of organic acids during the decomposition of its necromass, as several authors have reported a high production of organic acids by *C. edulis* (Novoa et al. 2014; Santoro et al. 2011). Considering the pH differences between the soil layers, and the limited accumulation of *C. edulis* necromass due to the short duration of the experiment (14 months), our results – although not significant at $p < 0.05$—suggest that soil acidification during the invasion began in the subsoil layer, likely due to the increased cation uptake and/or rhizodeposition of acidic substances by the invasive plant. Our results under different climate scenarios indicated a significant reduction of the acidifying effect of *C. edulis* in the CP (– 33% precipitation) and CTP (+ 2 ºC & – 33% precipitation) treatments. The lower precipitation in the CP and CTP subplots could have decreased leaching of basic cations (such as Ca and Mg) and mitigated the acidification produced by *C. edulis*.

Unlike previous studies with longer *C. edulis* invasion periods (Vieites-Blanco and González-Prieto 2018a), we found significant effects of treatment and soil depth on electrical conductivity; however, these effects explained a small proportion of the variance and did not exhibited a consistent relationship with either *C. edulis* or climatic conditions, at least within the range of predicted changes for the study area.

Both increases (Novoa et al. 2013, 2014; Santoro et al. 2011; Vilà et al. 2006) and decreases (Vieites-Blanco and González-Prieto 2018a) in soil organic matter have been reported in areas invaded by *C. edulis*. In our study, we did not observe a significant effect of the treatment on soil organic C, which may be attributed to the short duration of the experiment. Agreeing with the usual progressive increase of soil δ^{13}C with depth (Brunn et al. 2016; Philben et al.

2022), we found clearly less negative $\delta^{13}C$ values in the subsoil than in the topsoil. In a previous study on back dunes from the same region, Vieites-Blanco and González-Prieto (2018a) reported no differences in $\delta^{13}C$ between soils under native vegetation and *C. edulis* after 6–15 years of invasion. In contrast, despite the shorter invasion period in our study (14 months), we observed significant differences in $\delta^{13}C$ in the topsoil where lower $\delta^{13}C$ values were recorded in NV than in CC, both under current climatic conditions, with treatments involving modified climate (CT, CP, and CTP) showing intermediate values. These results are likely related to the facultative crassulacean acid metabolism (CAM) of *C. edulis*, which has a less negative ^{13}C isotopic signature (− 25 ‰, Herrera 2009) than most C3 plants (− 20 to − 35‰, Dawson and Siegwolf 2007). The decrease in ^{13}C produced by *C. edulis* is, nonetheless, of only around 0.5 units, as the contribution of CAM-fixed CO_2 to total C fixation in *C. edulis* is around 3% (Herrera 2009). However, the trend observed in CT, CP, and CTP is contrary to the expectations, as the discrimination against ^{13}C usually decreases in plants under water stress (Dawson and Siegwolf 2007). This unexpected trend of $\delta^{13}C$ under the modified climate conditions could be explained by a proportionally stronger reduction of CAM than C3 photosynthetic activity.

Along the coastal dunes of the Iberian Peninsula, the reported effects of *C. edulis* on soil NH_4^+-N and NO_3^- -N levels are largely variable (Novoa et al. 2014; Vieites-Blanco and González-Prieto 2018a). The tendencies we observed in the concentrations of both inorganic N forms (NV > CC; CC < CTP and intermediate values in CT and CP) suggest that the increase in gross NH_4^+-N immobilization and the decrease in gross autotrophic nitrification triggered by *C. edulis* invasion (Vieites-Blanco and González-Prieto 2018b) could be less important under the future climate conditions predicted for the study area, although Fernández-Alonso et al. (2021) reported a decline in potential nitrification along an aridity gradient. The effect of increased temperature coincides with the expected increase in NO_3^- resulting from enhanced nitrification, but does not correspond with the expected decrease in NH_4^+ due to a greater N uptake by plants (Chatterjee and Saha 2018).

The decrease of organic N concentration with depth, which is usually observed in dune soils (Brunn et al. 2016), could explain half of the organic N variance in our case. Regarding the treatment effect, it was too low to cause significant differences; however, NV had higher organic N values than CC in the subsoil, which is consistent with the findings of Vieites-Blanco and González-Prieto (2018a). Contrarily to these authors, we found a significant effect of *C. edulis* invasion on available P in the soil, which increased in the topsoil. However, this macronutrient did not vary under the studied scenarios of invasion and climate change, agreeing with García-Velázquez et al. (2020), who did not find significant changes in labile P across an aridity gradient in coastal dunes from the Iberian Peninsula.

The lack of invasion effects on soil available K and Na is consistent with the absence of significant changes reported for invaded dune areas of the same region (Vieites-Blanco and González-Prieto 2018a). Also like in the dune soils studied by these authors, we found a non-significant decrease in available Ca and Mg under *C. edulis* compared to native vegetation in the subsoil. The combined effect of increased temperature and reduced precipitation increased the Mg availability.

The non-significant increase we found in available Al in CC compared to NV in the topsoil agreed with the results of Vieites-Blanco and González-Prieto (2018a). However, in the subsoil the invasion slightly increased Al availability. Regarding the *C. edulis* invaded subplots and irrespectively of soil depth, it is remarkable the consistent effect of the tested climate change scenarios on the available Al, decreasing in the order CC > CT > CP > CTP, with significant differences between the first and the latter two treatments. Among soil cations, Al is the most strongly held and, thus, it must be the least affected by the changes in leaching intensity in treatments with reduced precipitation. Therefore, the reduction in available Al (an ‘acid’ cation) could be an indirect effect of reduced precipitation through a decrease in the leaching of ‘base’ cations (Ca, Mg, K, Na) and the subsequent rise of soil pH.

Due to the high and variable Cu levels in the topsoil of NV, the results on this micronutrient are difficult to interpret. However, the findings pointed to significant differences between NV and CC (contrarily to Vieites-Blanco and González-Prieto 2018a), with a decrease with invasion and little or no effect of the predicted climate change scenarios. Although Vieites-Blanco and González-Prieto (2018a) reported a significant decrease in available Fe in *C. edulis* invaded soils, we did not find significant differences, likely due to the short invasion time. In the *C. edulis* invaded subplots, the trend of available Fe resembles that of Al (CC > CT, CP > CTP), but the differences were significant only between CC and CTP in the topsoil. The levels of available Mn and Zn shared a common tendency of higher levels in NV than CC (only significant in the topsoil for Zn) and lower levels in CC and CT than CTP. However, there were few significant differences associated with either *C. edulis* invasion, as previously observed in dune soils by Vieites-Blanco and González-Prieto (2018a), or the studied climate scenarios.

The canonical discriminant analyses clearly differentiated the topsoil of subplots invaded by *C. edulis* from that under natural vegetation and, to a lesser extent, this differentiation also extended to the subsoil. These results supported the consideration of *C. edulis* as an ecosystem engineer capable of modifying key ecosystem properties for its own benefit (Conser and Connor 2009; Molinari et al. 2007), including the main soil characteristics (Vieites-Blanco and González-Prieto 2018a, 2018b) that in coastal dune ecosystems are considered the most determinant factors of plant community zonation (Ruocco et al. 2014). In the soils we studied, these soil properties encompassed the amounts of extractable Al, NH_4^+-N, Mg, Mn and Zn, as well as the $\delta^{13}C$ isotopic signature of the organic C and the electrical conductivity. Regarding the combined effects of the climatic treatments and *C. edulis* invasion on soil properties, the canonical discriminant analyses showed a significantly greater influence of decreased precipitation (CP) than of increased temperature (CT), with the joint influence of both treatments (CTP) seeming to be more synergistic than additive.

Conclusions

Soil acidification already started in the first year of *C. edulis* invasion and by the subsoil, pointing to enhanced cation uptake and/or acidic rhizodeposition by the invader as the (early) factors behind soil acidification, which was reduced under the most severe climatic conditions (i.e., increased temperature and decreased precipitation). In invaded soils, the combined effect of increased temperature and reduced precipitation led to a decrease in plant uptake and/or base cation leaching by rain, resulting in a reduction in the availability of Al and an increase in soil pH. The lowest and highest $\delta^{13}C$ values were observed in soils under natural vegetation and *C. edulis,* both under current climatic conditions, while invaded soils with modified climates exhibited intermediate values. Data on soil NH_4^+-N and NO_3^- -N suggest that the increased NH_4^+-N immobilization and the decreased autotrophic nitrification triggered by *C. edulis* invasion may be less significant under the future climate conditions predicted for the study area. The canonical discriminant analyses clearly differentiated the soils under *C. edulis* from those under natural vegetation, supporting the consideration of *C. edulis* as an ecosystem engineer capable of modifying key soil properties for its benefit. Additionally, the analyses demonstrated a more pronounced influence of decreased precipitation compared to increased temperature, along with a synergistic effect of both treatments. These findings underscore the complex interactions between invasive species and climate change, highlighting the need for additional field studies to enhance our understanding of these dynamics and their impacts on ecosystems. In addition, it is essential to develop targeted management strategies to mitigate the effects of *C. edulis* invasion on soil health and ecosystem integrity.

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Data availability The data obtained in this study are available at Figshare (https://doi.org/10.6084/m9.figshare.28458404).

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

References

AEMET-IMP (2011) Iberian climate atlas. Air temperature and precipitation (1971–2000). Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid. https://doi.org/10.31978/784-11-002-5

Badalamenti E, Gristina L, Laudicina VA, Novara A, Pasta S, La Mantia T (2016) The impact of *Carpobrotus* cfr. *acinaciformis* (L.) L. Bolus on soil nutrients, microbial communities structure and native plant communities in Mediterranean ecosystems. Plant Soil 409:19–34. https://doi.org/10.1007/s11104-016-2924-z

Bi M, Li H, Meidl P, Zhu Y, Ryo M, Rillig MC (2024) Number and dissimilarity of global change factors influences soil properties and functions. Nat Commun 15:8188. https://doi.org/10.1038/s41467-024-52511-2

Bourgeois K, Suehs CM, Vidal E, Médail F (2005) Invasional meltdown potential: facilitation between introduced plants and mammals on French Mediterranean islands. Ecoscience 12:248–256. https://doi.org/10.2980/i1195-6860-12-2-248.1

Brodie CR, Casford JSL, Lloyd JM, Leng MJ, Heaton THE, Kendrick CP, Zong YQ (2011) Evidence for bias in C/N, delta C-13 and delta N-15 values of bulk organic matter, and on environmental interpretation, from a lake sedimentary sequence by pre-analysis acid treatment methods. Quatern Sci Rev 30:3076–3087. https://doi.org/10.1016/j.quascirev.2011.07.003

Brunn M, Condron L, Wells A, Spielvogel S, Oelmann Y (2016) Vertical distribution of carbon and nitrogen stable isotope ratios in topsoils across a temperate rainforest dune chronosequence in New Zealand. Biogeochemistry 129:37–51. https://doi.org/10.1007/s10533-016-0218-4

Campoy JG, Acosta ATR, Affre L, Barreiro R, Brundu G, Buisson E, Gonzalez L, Lema M, Novoa A, Retuerto R, Roiloa SR, Fagundez J (2018) Monographs of invasive plants in Europe: *Carpobrotus*. Botany Letters 165:440–475. https://doi.org/10.1080/23818107.2018.1487884

Campoy JG, Lema M, Fenollosa E, Munné-Bosch S, Retuerto R (2021) Functional responses to climate change may increase invasive potential of *Carpobrotus edulis*. Am J Bot 108:1902–1916. https://doi.org/10.1002/ajb2.1745

Chatterjee D, Saha S (2018) Response of soil properties and soil microbial communities to the projected climate change. In: Bal SK, Mukherjee J, Choudhury BU, Dhawan AK (eds) Advances in crop environment interaction. Springer Singapore, Singapore

Conser C, Connor E (2009) Assessing the residual effects of *Carpobrotus edulis* invasion, implications for restoration. Biol Invasions 11:349–358. https://doi.org/10.1007/s10530-008-9252-z

Côté IM, Darling ES, Brown CJ (2016) Interactions among ecosystem stressors and their importance in conservation. Proc R Soc B Biol Sci 283:20152592. https://doi.org/10.1098/rspb.2015.2592

Dawson TE, Siegwolf RTW (2007) Using stable isotopes as indicators, tracers, and recorders of ecological change: some context and background. In: Todd ED, Rolf TWS (eds) Terrestrial ecology. Elsevier, pp 1–18. https://doi.org/10.1016/S1936-7961(07)01001-9

de la Peña E, de Clercq N, Bonte D, Roiloa S, Rodríguez-Echeverría S, Freitas H (2010) Plant-soil feedback as a mechanism of invasion by *Carpobrotus edulis*. Biol Invasions 12:3637–3648. https://doi.org/10.1007/s10530-010-9756-1

EEA (2017) Climate change, impacts and vulnerability in Europe 2016. An indicator-based report. European Environment Agency, Luxembourg. https://doi.org/10.2800/534806

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80

Elbasiouny H, El-Ramady H, Elbehiry F, Rajput VD, Minkina T, Mandzhieva S (2022) Plant nutrition under climate change and soil carbon sequestration. Sustainability 14:914

Fenollosa E, Munné-Bosch S (2019) Increased chilling tolerance of the invasive species *Carpobrotus edulis* may explain its expansion across new territories. Conserv Physiol 7. https://doi.org/10.1093/conphys/coz075

Fernández-Alonso MJ, Rodríguez A, García-Velázquez L, Dos Santos E, de Almeida L, Lafuente A, Wang JT, Singh B, Fangueiro D, Durán J (2021) Integrative effects of increasing aridity and biotic cover on soil attributes and functioning in coastal dune ecosystems. Geoderma 390. https://doi.org/10.1016/j.geoderma.2021.114952

Fuchslueger L, Solly EF, Canarini A, Brangarí AC (2024) Overview: global change effects on terrestrial biogeochemistry at the plant–soil interface. Biogeosciences 21:3959–3964. https://doi.org/10.5194/bg-21-3959-2024

Galán P (2008) Efecto de la planta invasora *Carpobrotus edulis* sobre la densidad del eslizón tridáctilo (*Chalcides striatus*) en una localidad costera de Galicia. Bol Asoc Herpetol Esp 19:117–121

García-Marco S, Abadín J, Couto-Vázquez A, Martín À, González-Prieto SJ (2020) Bioavailability of macro- and micro-nutrients chemically extracted in acidic soils for wheat. J Plant Nutr Soil Sci 183:705–717. https://doi.org/10.1002/jpln.201900590

García-Velázquez L, Rodríguez A, Gallardo A, Maestre FT, Dos Santos E, Lafuente A, Fernández-Alonso MJ, Singh BK, Wang JT, Durán J (2020) Climate and soil microorganisms drive soil phosphorus fractions in coastal dune systems. Funct Ecol 34:1690–1701. https://doi.org/10.1111/1365-2435.13606

Gómez-Rodríguez C, Retuerto R, Campoy JG, Rodríguez-Echeverría S (2024) Low impact of *Carpobrotus edulis* on soil microbiome after manual removal from a climate change field experiment. NeoBiota 95. https://doi.org/10.3897/neobiota.95.118238

Herrera A (2009) Crassulacean acid metabolism and fitness under water deficit stress: if not for carbon gain, what is facultative CAM good for? Ann Bot 103:645–653. https://doi.org/10.1093/aob/mcn145

IUSS Working Group WRB (2014) World Reference Base for Soil Resources 2014. International soil classification system for naming soils and creating legends for soil maps. FAO, Rome

Lopez BE, Allen JM, Dukes JS, Lenoir J, Vilà M, Blumenthal DM, Beaury EM, Fusco EJ, Laginhas BB, Morelli TL, O'Neill MW, Sorte CJB, Maceda-Veiga A, Whitlock R, Bradley BA (2022) Global environmental changes more frequently offset than intensify detrimental effects of biological invasions. Proc Natl Acad Sci 119:e2117389119. https://doi.org/10.1073/pnas.2117389119

Maltez-Mouro S, Maestre FT, Freitas H (2010) Weak effects of the exotic invasive *Carpobrotus edulis* on the structure and composition of Portuguese sand-dune communities. Biol Invasions 12:2117–2130

Matías L, Castro J, Zamora R (2011) Soil-nutrient availability under a global-change scenario in a Mediterranean mountain ecosystem. Glob Change Biol 17:1646–1657. https://doi.org/10.1111/j.1365-2486.2010.02338.x

Ministerio para la Transición Ecológica y el Reto Demográfico (2025) Actuaciones PIMA Adapta en el P.N. de las Islas Atlánticas de Galicia: Eliminación de exóticas invasoras. Available at: https://www.miteco.gob.es/es/parques-nacionales-oapn/red-parques-nacionales/seguimiento/seguimiento-ecologico/red-seguimiento/pima-adapta/pima-iatlanticas-exoticas.html. Accessed 25/02/2025

Molinari N, D'Antonio C, Thomson G (2007) 7 - *Carpobrotus* as a case study of the complexities of species impacts. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers: plants to protists. Theoretical ecology series. Academic Press, London, pp 139–162

Novoa A, Gonzalez L, Moravcova L, Pysek P (2012) Effects of soil characteristics, allelopathy and frugivory on establishment of the invasive plant *Carpobrotus edulis* and a co-occuring native *Malcolmia littorea*. Plos One 7:e53166

Novoa A, Gonzalez L, Moravcova L, Pysek P (2013) Constraints to native plant species establishment in coastal dune communities invaded by *Carpobrotus edulis*: Implications for restoration. Biol Conserv 164:1–9

Novoa A, Rodriguez R, Richardson D, Gonzalez L (2014) Soil quality: a key factor in understanding plant invasion? The case of *Carpobrotus edulis* (L.) N.E.Br. Biol Invasions 16:429–443

Philben M, Bowering K, Podrebarac FA, Laganière J, Edwards K, Ziegler SE (2022) Enrichment of ^{13}C with depth in soil organic horizons is not explained by CO_2 or DOC losses during decomposition. Geoderma 424:116004. https://doi.org/10.1016/j.geoderma.2022.116004

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rodríguez-Caballero G, Caravaca F, Díaz G, Torres P, Roldán A (2020) The invader *Carpobrotus edulis* promotes a specific rhizosphere microbiome across globally distributed coastal ecosystems. Sci Total Environ 719:137347. https://doi.org/10.1016/j.scitotenv.2020.137347

Ruocco M, Bertoni D, Sarti G, Ciccarelli D (2014) Mediterranean coastal dune systems: Which abiotic factors have the most influence on plant communities? Estuar Coast Shelf Sci 149:213–222. https://doi.org/10.1016/j.ecss.2014.08.019

Santoro R, Jucker T, Carranza ML, Acosta ATR (2011) Assessing the effects of *Carpobrotus* invasion on coastal dune soils. Does the nature of the invaded habitat matter? Community Ecol 12:234–240

Santoro R, Jucker T, Carboni M, Acosta ATR (2012) Patterns of plant community assembly in invaded and non-invaded communities along a natural environmental gradient. J Veg Sci 23:483–494

Traveset A, Brundu G, Carta L, Mprezetou I, Lambdon P, Manca M, Médail F, Moragues E, Rodríguez-Pérez J, Siamantziouras A-S, Suehs C, Troumbis A, Vilà M, Hulme P (2008) Consistent performance of invasive plant species within and among islands of the Mediterranean basin. Biol Invasions 10:847–858. https://doi.org/10.1007/s10530-008-9245-y

Trotta G, Vuerich M, Pellegrini E, Vilà M, Asquini E, Cingano P, Boscutti F (2024) Containing alien plants in coastal dunes: Evidence from a soil manipulation experiment. J Environ Manage 366:121780. https://doi.org/10.1016/j.jenvman.2024.121780

Vieites-Blanco C, González-Prieto SJ (2018a) 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

Vieites-Blanco C, González-Prieto SJ (2018b) Effects of *Carpobrotus edulis* invasion on soil gross N fluxes in rocky coastal habitats. Sci Total Environ 619–620:966–976. https://doi.org/10.1016/j.scitotenv.2017.11.154

Vilà M, Tessier M, Suehs CM, Brundu G, Carta L, Galanidis A, Lambdon P, Manca M, Medail F, Moragues E, Traveset A, Troumbis AY, Hulme PE (2006) Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. J Biogeogr 33:853–861

Winsemius S, Stein C, Parsons L, Minnick S, Ryan A, Suding K (2015) Plant-soil interactions and implications for restoration of coastal sand dunes in Point Reyes National Seashore. California Native Plant Society Conference, Los Angeles