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The interplay of soil stress, growth and functional traits of the native *Cakile maritima* determines the alien plant invasion success in coastal dunes

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Abstract

Human activities are strongly affecting ecosystems worldwide, altering abiotic factors and often triggering massive habitat invasions, as in the case of coastal dunes. Moreover, biotic interactions with native dune species can either facilitate or hinder the invasion process. In order to curb the invasion of alien plants, it is therefore important to understand the interplay between biotic and abiotic factors during the colonization process. Our experiment investigated the cascading effects of soil stress, plant growth, and the functional traits of the key species *Cakile maritima*, on the alien and native plant community. In an island of the Marano's lagoon, Northern Adriatic Sea, we mechanically removed the vegetation in the back dune, triggering a new ecological succession. In the site we created a soil stress gradient by altering main soil properties (i.e. salt, nitrogen, and organic matter) with a randomized block design. Soil properties directly affected the plant functional traits of *C. maritima* and the diversity and composition of the whole community. Moreover, the cover, height, and functional traits of *C. maritima* showed a direct effect on native and alien species populations, likely competing with other native species, but only when soil conditions ameliorate, leaving free niches for the alien species colonization. These results showed a direct effect of soil on sand dune plant succession and diversity, but this was also indirectly mediated by the key species response. This study provided new information on the mechanisms of the coastal dune biological invasions, suggesting that induced soil stress can be effective to combat alien plant proliferation while maintaining native stress-tolerant species.

Keywords: biological invasion, *Cakile maritima*, coastal dunes, functional traits, plant-plant interactions, soil properties

沿海沙丘植物入侵受到土壤胁迫、本地海滨芥生长和功能性状相互作用的影响

摘要：人类活动对全球生态系统产生了深远影响，通常通过改变非生物因素引发大规模生物入侵，海岸沙丘生态系统便是典型案例。遏制外来植物入侵，关键在于明确物种定居过程中生物与非生物因素的交互作用机制。本研究探讨了土壤胁迫和关键物种—海滨芥(*Cakile maritima*)生长和功能性状对外来和本地植物群落级联效应。研究区域位于亚得里亚海北部马拉诺泻湖的一座岛屿，通过机械清除后沙丘区域的植被，开始新的生态演替过程。在该区域内，采用随机区组设计，通过改变土壤属性(即盐分、氮含量和有机质)，构建了土壤胁迫梯度。研究结果显示，土壤属性直接影响海滨芥功能性状，同时也直接影响整个植物群落多样性与组成。此外，海滨芥盖度、株高及功能性状对本地和外来物种种群产生直接影响，例如在土壤条件改善时与其他本地物种产生竞争，而土壤条件改善也会为外来物种定居提供空生态位。上述结果表明，土壤胁迫会直接影响沙丘植物演替和多样性，同时还会通过影响关键物种产生间接作用。本研究为理解海岸沙丘生物入侵机制提供了新认知，表明通过诱导土壤胁迫可在维持本地耐胁迫物种的同时，有效抑制外来植物的扩散。

关键词：生物入侵，海滨芥(*Cakile maritima*)，海岸沙丘，功能性状，植物间相互作用，土壤性质

INTRODUCTION

Dune systems sustain crucial functions in coastal areas, e.g. buffering against storm surge, waves, and erosion of the inland, while providing a unique habitat for flora and fauna (Sigren *et al.* 2014). They are characterized by strong environmental gradients, which determine the coexistence of various plant communities in a relatively small area (Acosta *et al.* 2009; Fenu *et al.* 2013b). Dune vegetation zonation is associated with tolerance to soil stress and disturbance produced by changes in soil salinity (also due to sea water spray), wind erosion, and wave flooding (Acosta *et al.* 2007; Barbour and DeJong 1977). Global changes are greatly impacting these gradients, due to the increase in frequency of extreme weather events (Vousdoukas *et al.* 2018). In addition, other anthropogenic drivers can affect the distribution of dune vegetation, such as the expansion of tourist facilities and urban settlements, which foster the spread of human-made habitats (De Luca *et al.* 2011). Also for these reasons, coastal dunes are among the most invaded habitats in Europe by alien plant species (Chytrý *et al.* 2008, 2009). Here, environmental stressors (e.g. nutrient availability, salt content, water availability) and biotic interactions (facilitation or competition) can co-occur and interplay at different ecological scales, driving the invasion processes and influencing the final invasion success (De Roy *et al.* 2013; Kotanen 1997; Trotta *et al.* 2024).

Soil properties represent the primary filter for the assembly of the dune plant community (Fenu *et al.* 2013a). They affect native species composition and diversity, while also exhibiting strong interactions with plant biological invasions. Here, soil salinity and nutrients are crucial for the invasion success (Vitti *et al.* 2020), especially at the early stage of the ecological succession (Lami *et al.* 2021; Trotta *et al.* 2024).

It is also true that the composition of a plant community can strongly depend on the plant-plant interactions, which can shape the final assembly of the community via competition/facilitation interactions. In particular, native species have been shown to help curb the alien plant invasion by reducing propagule pressure, especially when abiotic (e.g. climate) are close to the native species' ecological optimum (Trotta *et al.* 2023). Under these conditions, shifts in growth and functional traits of key native species may shape the outcome of the entire ecosystem, affecting the community diversity (Boscutti *et al.* 2018). These species to community feedbacks have been well observed in coastal ecosystems where the abiotic gradient can shift the role of dominant species from competitive to facilitative (Pellegrini *et al.* 2022), also in relation to the establishment of strong plant-soil feedbacks (Pellegrini *et al.* 2018). In this light, studying how the change in functional traits of native key/dominant species of the dune community can reveal some important ecological soil–plant relationships able to shape the properties of the entire plant community, with potential effects on alien plant invasion.

Dominant characteristic species of coastal dune habitats (sensu Habitat Directive) (Council Directive 92/43/EEC, 1992) play an important role in determining the structure and functioning of these systems as they, directly or indirectly, control the availability of resources for other species. These species are also called 'focal species' or 'keystone species' and are often used as biological indicators due to their strong sensitivity to any variation in ecological factors or habitats (Santoro *et al.* 2012). *Cakile maritima* Scop. is a common species found along maritime shorelines, associated with foredunes as one of the most important elements constituting the plant community (Doing 1985). Although the importance of the keystone species *C. maritima* has been studied (Trotta *et al.* 2025), little is known about how it can interplay with soil properties and how the abundance, growth and functional traits of this species can contribute to shaping the whole plant community via facilitative/competitive mechanisms. Recent studies have examined the role of dominant or keystone species in structuring coastal plant assemblages (e.g. Lami *et al.* 2021; Pellegrini *et al.* 2018); however, most have considered biotic interactions or abiotic filters in isolation or often neglecting the distinction between alien and native components. To our knowledge, no study has jointly evaluated how soil properties and key functional traits of *C. maritima* interact to shape both native and alien species richness and abundance at the community level. This gap is particularly relevant under current scenarios of accelerated biological invasions and climate-driven changes in coastal disturbance regimes, which can rapidly alter the balance between facilitation and competition in dune systems.

The present study aims at evaluating the relationships between soil conditions and stresses (represented by soil salinity, nitrogen and organic matter) and the growth, abundance, and functional traits of the key species *C. maritima*, investigating the cascading effects of these relationships at the community level. Within a causal network model, we hypothesized (i) that soil stress properties (salinity, nitrogen, organic matter) reduce the soil microbial activity (i.e. rate of decomposition). Moreover, (ii) we hypothesized that soil stress and changes in soil properties can directly reduce the growth (plant height), abundance, and functional traits of *C. maritima*, which, in turn, (iii) can decrease alien establishment, contributing to the final plant community composition. We tested our hypothesis with a Structural Equation Model (SEM), highlighting the weight and importance of each of the previously mentioned predictors on the growth of key species in dune systems, providing new insights into the abiotic and biotic processes driving biological invasion.

MATERIALS AND METHODS

Study area and species

The experiment was conducted in the back dune habitat of the barrier island of Sant'Andrea, in the Marano and Grado lagoon (Fig. 1a), for a total of 100 days. This particular ecosystem, recognized as a protected area by the Natura 2000 network, is located in Italy, in the region of Friuli Venezia Giulia (45°42′34.2″–45°43′15.0″ N, 13°10′53.0″–13°14′35.2″ E). It is located in the northern part of the Adriatic Sea, which exhibits a cyclonic circulation that determines a southward flow of nutrients along the western coast (Zavatarelli *et al.* 1998). Although the area is included in the Natura 2000 network and reachable only by boat, it is subject to anthropogenic pressures such as tourism during the growing season. Moreover, the island hosts a small wildlife-hunting estate, and it is relatively close to the nearby urban area of Lignano Sabbiadoro.

The lagoon experiences a humid sub-Mediterranean climate, with an annual mean temperature of 15.3 °C. Temperatures range from 3.1 °C in January to 29.0 °C in July. Most precipitation falls in autumn, with a secondary maximum in spring, giving an annual average of 974 mm. The seawater in front of the study site had an average salinity of 35 psu.

Winter and early-spring storms generated by the south-easterly wind Scirocco greatly contribute to shape the morphology of the islands and vegetation dynamics and zonation. By analyzing the distribution of vegetation, it is possible to identify three different areas on the barrier island: (i) the foredune, which includes the upper beach, the embryo and the mobile dunes; (ii) the back dune characterized by perennial communities; (iii) salt marshes, which are periodically submerged by the tides. The study was carried out in the second zone (i.e. the back dune), which is considered the most susceptible to biological invasions (Lami *et al.* 2021; Vitti *et al.* 2020). This

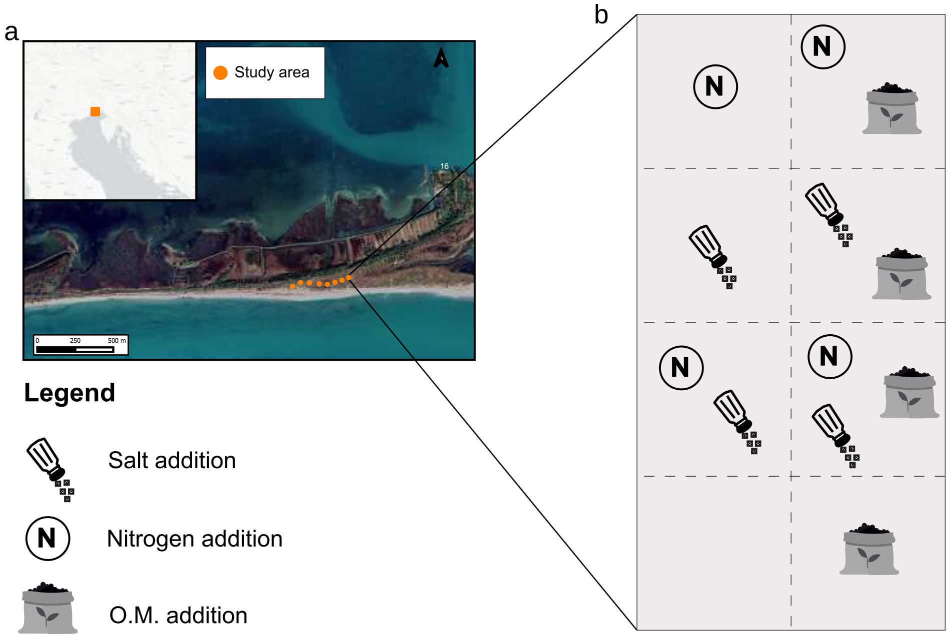

Figure 1: Experimental design: (a) study area located in the Marano and Grado lagoon, NE of Italy, at the Sant'Andrea barrier island, with the location of the 8 experimental blocks. In each block, the vegetation was removed, and (b) three soil treatments and their combinations were performed in plots of 1 m^2 (i.e. salt addition, nitrogen addition and organic matter addition).

area is classified as a Natura 2000 habitat (2120 shifting dunes along the coastline with *Ammophila arenaria*—white dunes) and belongs to the Ammophiletea Br.-Bl. et Tx. ex Westhoff class, following the classifications of Poldini *et al.* (1999) and Mucina *et al.* (2016).

Within the study area, soil from the back dune exhibited an average salinity of 43.6 μS cm^{-1}, along with mean concentrations of 0.56% organic carbon and 0.12% nitrogen. Conductivity was assessed using a CM35+ portable conductivity meter (Crison) on material collected from all external reference plots. For each sample, a 1:5 extract was prepared (10 g of dried soil combined with 50 mL of water), yielding a total of eight soil cores (see section 2.2 for experimental details).

The study key species was *C. maritima*, a succulent, annual plant found along the Atlantic and Mediterranean coasts of Europe, which shows wide intraspecific variability, reflected in its fruit and leaf traits (Davy *et al.* 2006). Colonization of *C. maritima* at the early stages of succession is favored by winds and tides, and its occurrence and abundance chiefly depend on the local soil conditions and dune stability. It thrives in ephemeral sandy habitats and in foredunes. Along the dune ecological succession, *C. maritima* poorly competes with perennial dune grasses (such as *Ammophila arenaria*), taking advantage of the consequences of soil disturbance, when existing vegetation cover is partially or completely removed, providing opportunities for its colonization (Davy *et al.* 2006).

Experimental set-up

In April 2022, an extreme disturbance event (i.e. a strong early-spring storm) was simulated on eight rectangular plots measuring 8 × 6 m (48 m^2) by removing the existing vegetation with a rototiller (see Supplementary Video SV1). The plots were manually cleared to remove any remaining clonal plant propagules and were fenced off.

The original soil properties were modified by adding: (i) organic matter (15 L m^{-2} of sphagnum peat, roughly +20% v/v in the top 7.5 cm of soil), (ii) salinity (260 g m^{-2} of NaCl), and (iii) nitrogen (50 g m^{-2} of $Ca(NO_3)_2$), to create different soil conditions (Fig. 1c). The organic matter was applied only at the start of the experiment, whereas salinity and nitrogen were additionally added as crystals after a cumulative rainfall of 8 mm. Pilot trials on dune soil to estimate the retention capacity of the addition of salt and nitrogen after an average rainfall event (between 8 and 10 mm) were preliminary conducted in a laboratory. Results suggested that the salt and nitrogen treatments should be repeated after rainfall events. Throughout the experiment, soil cores (12 cm deep, 5 cm in diameter) were collected and processed to track the effects of the treatments and assess soil parameters. For more details on the experimental design and sample collection and analyses, see Trotta *et al.* (2024).

Soil properties and microbial activity

In each of the 64 plots, a soil core was collected at the end of the soil manipulation (June 2022). In addition, 32 random cores were collected every 30 days during the experiment with the aim to continuously monitor the effects of the treatment. The soil organic carbon content (SOC) (%) was calculated as follows: sub samples of the homogenized cores, weighing between 5 and 10 mg, were ground with a ball mill and acidified with HCl to remove the inorganic Carbon fraction. Organic C was then measured with a CHNS elemental analyzer. The Cation Exchange Capacity (CEC) was determined according to standard protocol with $BaCl_2$ and triethanolamine (Gillman and Sumpter 1986). Briefly, about 2 g of dry soil were treated with 10% $BaCl_2$ and triethanolamine buffered at pH 8.1. Samples were then washed and treated with 25 mL of 0.05 mol L^{-1} $MgSO_4$. The CEC was then determined by titration. Soil Electrical Conductivity (hereafter EC, mS cm^{-1}) was used as a proxy of salinity, and it was measured in aqueous extract at a ratio of 1 to 5 (1 g soil to 5 mL water) using a conductivity meter (Crison). Soil pH was measured in an aqueous extract at a ratio of 1 to 2.5 with a pH meter (Crison). For both soil pH and EC, the suspension was mechanically stirred for about 2 h and allowed to settle for approx. 30 min before the measurement. In the case of EC, the suspension was also filtered. The content of N in the forms of nitrate (NO_3^--N) and ammonium (NH_4^+-N) was analyzed as a proxy of plant mineral N availability. The various forms of mineral nitrogen in the soil were extracted using a 0.5 mol L^{-1} KCl solution at 20 °C, with a 1:10 soil-to-solution ratio. The mixture was stirred for approximately 1 h at 20 °C, filtered through Whatman 32 paper, and the ammonium and nitrate concentrations were determined using a SKALAR San++ analyzer.

Soil microbial activity is an important soil parameter mainly affected by soil microbiota diversity and growth. It regulates soil nutrient cycles, the degradation of the organic matter and many plant-soil interaction processes. Soil microbial activity was measured in the experiment using the Tea Bag Index (TBI), which provides a measure of the rate of decomposition based on the weight loss of tea bags after a given period of incubation in the soil (100 days in the experiment; Keuskamp *et al.* 2013). In particular, the TBI allows for calculating the constant of decomposition (k rate) using two different types of tea with different decomposition rates according to the protocol guidelines.

Plant community

At the end of the experiment (i.e. 100 days), orthogonal photographs were taken of all the plots in order to survey plant community growth and composition, recording the occurrence and measuring the cover of vascular plant individuals present in each plot.

Images of each plot were collected using an RGB camera (Panasonic, model Lumix GH5) and processed to measure the species plant cover and number of individuals using the software ImageJ (Schneider *et al.* 2012), using a color filter followed by visual plant species identification. The mean plant height was measured in the field for each species, as the average of the occurring individuals (max. 5 random individuals were considered). At this stage, all the species were further divided into two groups according to their alien status following the Italian checklist of native (Bartolucci *et al.* 2018) and the regional checklist of alien species (Buccheri *et al.* 2018). The same references were used to standardize plant nomenclature. A complete list of occurrences is reported in the Supplementary Table S3. We would like to clarify that, in the study area, all alien plant species were considered invasive for the dune system, including some species classified as naturalized at the regional level. This is because the three species classified as naturalized are of particular concern owing to their strong invasive potential at our study site (Lázaro-Lobo *et al.* 2024; Zhang *et al.* 2024). This is particularly true given the proximity to human-disturbed systems (Lázaro-Lobo *et al.* 2020), which will perpetuate propagule pressure.

Cakile maritima growth, abundance and functional traits variation

At the end of the experiment, at least 3 fully developed leaves (up to 5 leaves) of *C. maritima* were collected for each plot. The collected leaves were analyzed to determine the following functional traits: (i) specific leaf area (SLA); (ii) pigment content; and (iii) leaf dry matter content (LDMC), which are commonly used to evaluate variability in plant functional traits in response to soil stress (Petrussa *et al.* 2013; Wilson *et al.* 1999).

The SLA (ratio of one-sided leaf area to its oven-dry mass cm^2 g^{-1}) (Pérez-Harguindeguy *et al.* 2013) is an important trait distinguishing fast-growing plants, characterized by high SLA values, from slow-growing plants with low values (Martin and Hine 2008). Within-species variability in SLA reflects its sensitivity to environmental stress (Debez *et al.* 2004). The LDMC (mg g^{-1}) was calculated as the oven-dry weight of the leaf (oven at 70 °C for 72 h; in mg), divided by its water-saturated fresh weight (g) (Pérez-Harguindeguy *et al.* 2013).

Three further leaves were sampled in each plot to quantify the pigment contents (i.e. chlorophylls, carotenoids, and flavonoids). Flavonoids are a large group of low molecular weight polyphenolic secondary metabolites, playing a significant role in various stages of plant growth and in response to environmental stresses (Filippi *et al.* 2021; Vuerich *et al.* 2024). Flavonoid content was measured according to the method proposed by Filippi *et al.* (2021). The plant material was ground in liquid nitrogen. Fifty milligrams of leaf powder were weighed, and 300 μL of methanol was added. The sample was centrifuged at 16 000 g for 5 min. Then, 50 μL of 1% diphenylboric acid 2-aminoethyl ester in ethanol was mixed with 100 μL of the supernatant. The mixture was placed in the wells of a plate and analyzed using a fluorescence spectrophotometer (VICTOR3 Multilabel Plate Reader 1420-011, Perkin Elmer). Results were expressed as microgram quercetin equivalents (QC-eq) per gram of fresh weight, using a quercetin (QC) calibration curve prepared from a 200 mmol L^{-1} QC stock solution in DMSO (dimethyl sulfoxide), diluted with methanol to generate the calibration points.

The levels of photosynthetic pigments (chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids) were determined through absorbance analysis (Marchiol *et al.* 2019). Samples were powdered in a mortar under liquid nitrogen. Twenty-milligram portions of the powder were mixed with 0.5 mL of 90% acetone containing 0.01 N ammonium hydroxide (NH_4OH), followed by 0.5 mL of 80% acetone after thorough homogenization. The mixtures were centrifuged at 14 000 g for 12 min, and about 500 μL of the supernatant (from 2 mL of 80% acetone) was collected for absorbance determination using an 8453 UV–visible spectrophotometer (Agilent Technologies). Supplementary Table S2 provides an overview of all measured variables and their units.

Statistical analyses

Statistical analyses were performed using R software (R Core Team 2024).

Plant community richness (i.e. number of species) was assessed using the '*vegan*' package and calculated for each plot (Oksanen *et al.* 2022). The collinearity of the independent variables was tested by the Pearson correlation test. Given that the total chlorophyll of *C. maritima* exhibits a higher correlation with chlorophyll a, chlorophyll b and carotenoids (respectively $r = 0.99$ ***; 0.88 ***; 0.81 ***) we decided to test only for total chlorophyll effects.

Causal relationships among the selected variables were analyzed using SEM (Grace 2006; Lamb *et al.* 2011), which combines multiple predictors and response variables into a single causal network (Grace *et al.* 2007; Lefcheck 2016). Specifically, Piecewise Structural Equation Models (hereafter PSEMs) were applied to examine possible causal relationships among the studied variables. PSEMs represent an extension of traditional SEMs that can account for data with nested structures (Lefcheck 2016).

After building a comprehensive model grounded in prior knowledge of potential interactions and including all hypothesized effects (Fig. 2), we applied a backward stepwise elimination procedure. This process, based on Fisher's C statistic ($P > 0.05$) and Shipley's test, was used to identify plausible models and evaluate potential missing paths (Shipley 2009). With this model we tested: (i) the effects of soil properties on all other variables considered, (ii) the effects of soil nutrients on all other variables considered, (iii) the effects of soil microbial activity on all other variables considered, (iv) the effects of the key species (i.e. *C. maritima*) on the plant community response.

In the SEM model, the soil properties were chosen as the driving independent factor able to influence both nutrients, soil microbial activity, plant traits and community. *C. maritima* development (i.e. cover and height) and stress traits were considered proxies of individual plant size (Lundholm *et al.* 2014; Navarro *et al.* 2010).

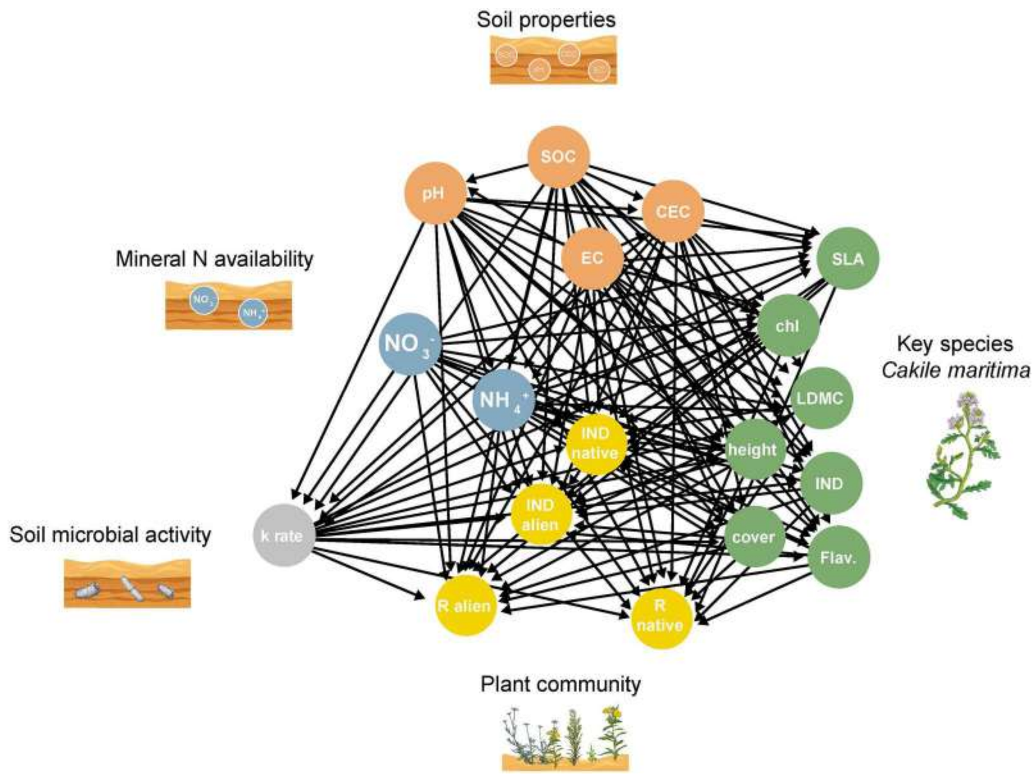

Figure 2: Overall model based on prior knowledge of interactions before testing. SOC = soil organic carbon; EC = soil electrical conductivity; CEC = cation exchange capacity; SLA = specific leaf area; Chl = chlorophyll content; LDMC = leaf dry matter content; Flav = flavonoid content; IND = number of individuals of *C. maritima*; R native = number of native species; R alien = number of alien species; IND alien = number of alien individuals per species; IND native = number of native individuals per species; k rate = measure of soil microbial activity; NO_3^--N = nitrate content; NH_4^+-N = ammonium content.

We hypothesized that soil properties, nutrients and activity could significantly influence the response of the key species, and thus project this influence on the response of the entire plant community.

The models in the PSEM were Linear Mixed Models (LMMs), accounting for the presence of plausible spatial autocorrelation due to the experimental design. LMMs were applied using the '*nlme*' package (Pinheiro *et al.* 2012). Blocks were included as random effects in the LMMs. Both linear and non-linear trends (i.e. log-transformed variables) were tested. Data normality was tested with the Shapiro–Wilk's test, and homoscedasticity was visually assessed using model residuals.

The PSEMs analysis was performed using the '*piecewiseSEM*' package for statistical analysis (Lefcheck 2016). The goodness of fit of the PSEMs was assessed using the χ^2 test ($P > 0.05$) in the 'lavaan' package (Rosseel 2012). The report of all interactions was created using the summary function on the PSEMs model.

RESULTS

The overall summary of the SEM is reported in Supplementary Table S1, while the significant effects of predictors on the response variables are shown in Fig. 3 (i.e. only when statistically significant).

Drivers of soil mineral nitrogen and soil microbial activity

Soil properties (i.e. SOC, pH and EC) significantly affected soil ammonium, CEC and soil microbial activity (i.e. k rate). Soil pH had a negative effect on the NH_4^+-N content (Std.estimate = −0.658, Fig. 3; Supplementary Table S1; Supplementary Fig. S1i). Moreover, SOC had a positive effect on the CEC (Std. estimate = + 0.24, Fig. 3; Supplementary Table S1; Supplementary Fig. S1c).

Soil microbial activity was negatively influenced by salinity (i.e. soil electrical conductivity) (Std.

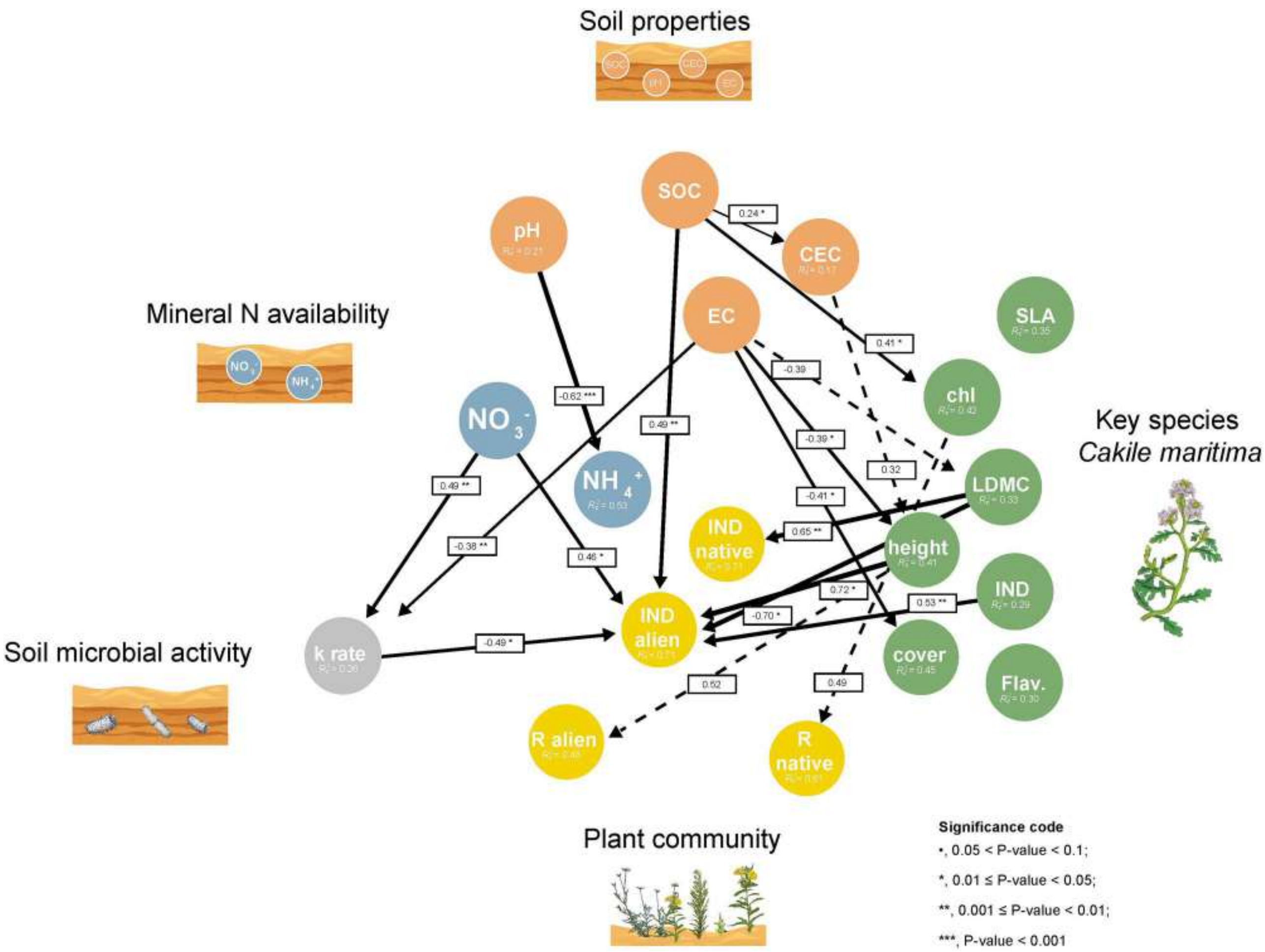

Figure 3: The structural equation model. Solid black arrows refer to statistically significant relationships ($P < 0.05$). Arrow thickness is proportional to the standardized effect size in the text box, along with its significance (•$0.05 < P < 0.1$; *$0.01 \leq P < 0.05$; **$0.001 \leq P < 0.01$; ***$P < 0.001$). Dashed arrows represent non-significant paths ($0.05 < P < 0.06$). Conditional R^2 (R^2_c) are also shown in the boxes. SOC = soil organic carbon; EC = soil electrical conductivity; CEC = cation exchange capacity; SLA = specific leaf area; Chl = chlorophyll content; LDMC = leaf dry matter content; Flav = flavonoid content; IND = number of individuals of *Cakile maritima*; R native = number of native species; R alien = number of alien species; IND alien = number of alien individuals per species; IND native = number of native individuals per species; k rate = measure of soil microbial activity; NO_3^- = nitrate content; NH_4^+ = ammonium content.

estimate = −0.38, Fig. 3; Supplementary Table S1; Supplementary Fig. S1b) but positively influenced by NO_3^--N content (Std.estimate = + 0.49, Fig. 3; Supplementary Table S1; Supplementary Fig. S1a), while pH, SOC and CEC did not show any direct effect on soil microbial activity.

Growth, abundance and functional traits variability of *C. maritima*

The growth (i.e. plant height) and abundance (i.e. plant cover, number of individuals) and functional traits variability (i.e. leaf traits) of the key species *C. maritima* were affected by soil features but not by mineral N content nor by soil microbial activity.

LDMC was negatively influenced by EC (Std.estimate = −0.399, Fig. 3; Supplementary Table S1, Supplementary Fig. S1d) while the total leaf chlorophyll content of *C. maritima* was positively influenced by SOC content (Std.estimate = + 0.41 Fig. 3; Supplementary Table S1; Supplementary Fig. S1g). SLA and flavonoid content were not significantly influenced by any tested soil factor, mineral N, or activity.

The *C. maritima* development (proxied by its final height and cover) was chiefly affected by soil salinity, while no significant relationship with soil mineral N and microbial activity was found.

The plant height of *C. maritima* was low at high levels of soil salinity (i.e. EC) (Std.estimate = −0.39,

Fig. 3; Supplementary Table S1; Supplementary Fig. S1e) but it was promoted by a high level of CEC (Std.estimate = + 0.32, Fig. 3; Supplementary Table S1; Supplementary Fig. S1h). The cover of *C. maritima* showed a negative relationship with soil salinity (Std.estimate = −0.41, Fig. 3; Supplementary Table S1; Supplementary Fig. S1f).

Finally, the germination of *C. maritima*, expressed as the number of individuals occurring in the plot, was not dependent on any of the tested soil variables.

The soil-to-plant interactions mediate the colonization of the plant community

The alien and native species pools of the newly established plant community were contrastingly affected by soil both directly and indirectly, by soil nutrient activity and the development and functional traits variation of the key species *C. maritima*.

The alien species richness was positively influenced by the height of the key species (Std.estimate = + 0.52, Fig. 3; Supplementary Table S1; Supplementary Fig. S2r). The number of alien individuals was positively influenced by SOC (Std.estimate = + 0.49, Fig. 3; Supplementary Table S1; Supplementary Fig. S2m), nitrate content (Std.estimate = + 0.46, Fig. 3; Supplementary Table S1; Supplementary Fig. S2L), the height (Std.estimate = + 0.72, Fig. 3; Supplementary Table S1; Supplementary Fig. S2n) and the number of individuals of *C. maritima* (Std.estimate = + 0.53, Fig. 3; Supplementary Table S1; Supplementary Fig. S2o), while it was negatively influenced by soil microbial activity (Std.estimate = −0.49, Fig. 3; Supplementary Table S1k) and *C. maritima* LDMC (Std.estimate = −0.70, Fig. 3; Supplementary Table S1; Supplementary Fig. S2q). Finally, the number of native individuals per species was positively influenced by *C. maritima* LDMC (Std.estimate = + 0.65, Fig. 3; Supplementary Table S1; Supplementary Fig. S2j), whereas no other tested soil or plant parameter was related to it.

DISCUSSION

The experiment provided new insights into the causal relationships between soil properties, shifts in plant functional traits, alien plant invasion, and the initial establishment of ecological succession. In particular, salinity directly affected the key species *C. maritima* in terms of growth, abundance, and functional traits. In turn, these effects contributed to shaping the plant community diversity and assembly. Specifically, *C. maritima* traits differentially promoted or inhibited the colonization of native and alien plant species. This was in line with our hypotheses and demonstrated that soil exerts a direct effect on plant succession and diversity of sand dunes but also an indirect effect mediated by the key species response.

Drivers of soil mineral nitrogen and soil microbial activity

In soils, nitrogen undergoes several transformations depending mainly on soil aeration and pH. Briefly, ammonium can be nitrified NO_3^- under aerobic conditions and partially via volatilization as NH_3 at increasing pH (Brady *et al.* 2008). Denitrification is also possible in dune systems, but only when anoxic conditions are established (Davidsson and Ståhl 2000). Here, nitrate is used as a terminal electron acceptor by denitrifying bacteria and is reduced to nitrite (NO_2^-), and then to nitrous oxide (N_2O) and elemental nitrogen (N_2).

In our experiment, the nitrate content was kept stable in Nitrogen-treated plots over time. Therefore, the possible effects of SOC or pH on soil nitrate were not tested in the statistical analysis.

Results showed, as hypothesized, that ammonium was negatively influenced by soil pH (Supplementary Table S1). It is well known that the NH_4^+ form is stable at acid and sub-neutral pH conditions but can be partially lost at pH larger than 7 (Avnimelech and Laher 1977; Radulov *et al.* 2011). In particular, at pH 9.25, about 50% of ammonium is transformed to NH_3 that can be lost by volatilization. Possible N losses can also be attributed to nitrification followed by denitrification or nitrate leaching from surficial soil. However, oxic conditions were ensured by the coarse, sandy soil and the limited amount of organic matter added to the treated plots. Thus, denitrification was unlikely to occur or to significantly affect our results.

Soil microbial activity, as expected, was negatively influenced by salinity (Supplementary Table S1). High sodium levels in the soil solution led to osmotic stress not only for plants but also for microorganisms (Mazhar *et al.* 2022; Paul and Frey 2023). Salinization can also affect the metabolism of the microorganisms due to specific ion toxicity and, hence, reduces soil microbial activity (Mazhar *et al.* 2022; Soriano 2012). The soil microbial activity (i.e. k rate) was instead boosted by an increase in nitrate content. This expected result is due to the relatively larger mineral nitrogen availability for the microbial community, also considering that nitrogen is a limiting nutrient in coastal sand dunes (Kachi and Hirose 1983). Microorganisms are efficient in the uptake of N even at low concentrations and are still more competitive than plants at high N levels (Kuzyakov and Xu 2013). This fact supports our results, i.e. the significant and positive effect of nitrate on soil microbial activity but not on plant growth. In general terms, it also explains the existence of mutualistic relationships (i.e. N_2 fixing bacteria) in the most varied environments.

Finally, as expected, we observed that SOC had a positive influence on CEC (Supplementary Table S1). This result is probably related to the fact that SOC contains a large amount of acidic functional groups (e.g. carboxylic and phenolic) that represent the largest part of CEC, especially in sandy soils that lack clay particles (Guan *et al.* 2006; Parfitt *et al.* 1995). Thus, an increase in organic matter will result in an increase in CEC with a positive influence on retention of many cationic nutrients.

Growth, abundance and functional traits variability of *C. maritima*

The growth (i.e. plant height), abundance (i.e. plant cover, number of individuals), and the functional traits of *C. maritima* (except for flavonoid content and SLA), as hypothesized, were negatively influenced by the EC. The negative response of *C. maritima* growth and abundance, measured as a reduction in plant height and cover, is consistent with previous studies showing a strong relationship between the biomass production and soil salinity, where biomass was high at moderate salinity (50 to 100 mmol L^{-1} NaCl), while decreasing at high salt content (Debez *et al.* 2004). In particular, it was demonstrated that the whole plant biomass and the leaf number were consistently affected, suggesting that salinity modified development through its effects on the initiation of new leaves. This is likely because leaf architecture does not depend on the salt concentration (Debez *et al.* 2004), as also confirmed by the lack of significant relationships between soil features and SLA found in our study. Instead, the LDMC of *C. maritima* decreased in soils with high EC, confirming the acclimation capacity of this halophyte species in adjusting the water content of the leaves. In detail, the decrease of LDMC might be related to the physiological adaptation of *C. maritima* leaves to salt, where most of the Na^+ ions transported in the leaves are removed from the leaf apoplast and efficiently internalized by the cells for water retention (Flowers *et al.* 1991; Munns and Passioura 1984). The total chlorophyll decreased with increasing salinity, consistently with other literature findings (Taïbi *et al.* 2016). Salinity exposure increases the generation of reactive oxygen species as byproducts that damage cellular components (Van Breusegem and Dat 2006). Reactive oxygen species cause chlorophyll degradation and membrane lipid peroxidation, reducing membrane fluidity and selectivity (Verma and Mishra 2005). In our case, the halophyte character of *C. maritima* resulted in a reduced effect of salts on its structure; the Std. estimate was indeed equal to 0.3312 (Supplementary Table S1). The amount of chlorophyll in leaf tissue is also influenced by nutrient availability and environmental stresses such as drought, salinity, cold and heat (Palta 1990). Our study showed a positive relationship between SOC and leaf chlorophyll content but not with other soil stressors (e.g. EC) (Supplementary Table S1). The addition of SOC to soils stimulates soil microbial activity, which, through soil mineralization, releases various nutrients that become available for plant development and photosynthesis, even though we did not find any direct relationship between soil nutrients, activity and leaf chlorophyll content. In addition, SOC and organic matter in general, improve the soil structure, favoring the soil efficiency in water and nutrient retention, boosting photosynthesis (thus chlorophyll production) and, ultimately, the overall plant growth.

Finally, CEC was also found to positively influence the height of *C. maritima* (Supplementary Table S1). The higher the CEC, the greater the number of nutrient cations that the soil is able to retain and thus make available to plants for their growth (Raman and Sathiyanarayanan 2009).

The soil-to-plant interactions mediate the colonization of the plant community

This study demonstrated that soil exerts a direct effect on sand dune plant succession and diversity, as hypothesized. This was particularly true for the alien species pool, whereas native species richness and density were less dependent on soil stress.

The number of alien individuals was negatively affected by soil microbial activity. Several studies have confirmed that soil communities can have profound effects on the invasions of ecosystems by alien species through a variety of pathways. For example, they can increase pathogen levels or disrupt root symbiont communities, thereby reducing nutrient uptake capacity, plant growth and hence community richness (Inderjit and van der Putten 2010). The results also highlighted that an increase in carbon and nitrogen content determines an increase in the number of alien individuals. As previously reported, the addition of organic carbon and nitrogen is determinant for the success of alien species in several ecosystems by ameliorating soil conditions, especially in stressed environments (Boscutti *et al.* 2020; Vitti *et al.* 2020). Finally, the number of native individuals per species was found to be positively affected by *C. maritima* LDMC, while alien individuals were negatively affected. This can be explained by the investment in conservative strategies by the key species (i.e. higher LDMC values) under strong environmental gradients (De Battisti 2021; De La Cruz *et al.* 2023; Flowers and Colmer 2008). While *C. maritima* height and cover were positively associated with alien species abundance, LDMC was negatively associated. These contrasting relationships likely reflect different underlying mechanisms: plant height and cover capture structural and demographic influences (e.g. canopy shelter, seed trapping) that can facilitate alien establishment (Johnston 2019; Rapson *et al.* 2023), whereas LDMC reflects a conservative resource-use strategy linked to environmental stress, which may favor stress-tolerant natives and exclude less-adapted aliens (Lami *et al.* 2021). Such conditions limit the growth of *C. maritima* while allowing space for natives and limiting the emergence of exotic seedlings, which often struggle under harsh environments (Trotta *et al.* 2024).

These findings suggest that, under favorable soil conditions, *C. maritima* does not interfere with (or even facilitate) alien species while containing the number of native species. Moreover, our results also showed that an increase in the number of individuals of *C. maritima* positively influenced the number of individuals of alien species. The behavior of *C. maritima* in relation to the native and alien pools might be explained by the stress-gradient hypothesis. This hypothesis is a general conceptual model that predicts how competitive and facilitative interactions among plant species change along gradients of biotic and/or abiotic stress (Armas *et al.* 2004; Bertness and Callaway 1994; Brooker *et al.* 2005; Forey *et al.* 2023). In this light, our findings showed that when environmental conditions are optimal for the *C. maritima* growth, this species contains other native species, probably as a result of efficient competition for the available resources. By contrast, this is not the case for alien species, probably more able to compete with *C. maritima* and other native species where the soil conditions are favorable (see also Trotta *et al.* 2024). On the other hand, when *C. maritima* declines, other native species take advantage of its presence, probably due to the occurrence of positive plant-plant interactions. Soil can exert important abiotic stress that triggers competitive and facilitation mechanisms, especially where strong local edaphic gradients are present (Zeil-Rolfe *et al.* 2024), such as in coastal systems (Pellegrini *et al.* 2022). Taken together, these results suggest that *C. maritima* plays a significant role in shaping community assembly in coastal ecosystems.

CONCLUSIONS

These results enhanced our understanding of the ecological processes involved in biological invasion at the early stages of succession, highlighting the crucial role of plant-soil interactions in the success of native and alien plants. Our results confirmed the strong influence of soil and its gradients on the initial establishment of plants during the ecological succession in dune ecosystems following soil disturbance. As a novelty, we were able to demonstrate that the responses of the key species *C. maritima* to soil stress, in terms of functional traits, growth and abundance, might reverberate through the entire plant community, giving new information on the processes acting during the dune alien biological invasions. Soil salinity was found to be an influential factor for the growth of native (including the key species) and alien species, suggesting that it may be manipulated to contrast alien or less salt-tolerant species. In contrast, the key species *C. maritima* seemed to compete mainly with other native species when soil condition ameliorates, leaving free niches for the alien species colonization. The understanding of the emerging interactions between biotic and abiotic processes might be promising for future applications, serving as an effective tool in the fight against biological invasions; however, its long-term efficiency still needs to be tested.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Video SV1: Video of the habitat and treatment used in the experiment.

Table S1: List of the summary of the PSEM tested.

Table S2: Description of the variables used.

Table S3: Complete list of the species found.

Figure S1: Plot of the Linear Mixed Models performed during the PSEM.

Figure S2: Plot of the Linear Mixed Models performed during the PSEM.

Authors' Contributions

Giacomo Trotta (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft), Paola Fabris (Writing—original draft), Marco Vuerich (Conceptualization, Data curation, Investigation, Methodology, Writing—review & editing), Elisa Pellegrini (Data curation, Investigation, Writing—review & editing), Elisa Petrussa (Investigation, Writing—review & editing), Edoardo Asquini (Writing—review & editing), Paolo Cingano (Data curation, Writing—review & editing), Marco Contin (Resources, Writing—review & editing), and Francesco Boscutti (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing—review & editing).

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Conflict of interest statement. The authors declare that they have no conflict of interest.

Data Availability

All the data are available at the public repository Mendeley Data, doi: 10.17632/spdtzdk9jr.2.

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