Research article

Containing alien plants in coastal dunes: Evidence from a soil manipulation experiment

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ABSTRACT

Biological invasion is recognised as one of the major threats to biodiversity, particularly in disturbance-prone ecosystems such as costal dunes. Many studies have associated alien plant invasion of dune ecosystem to human disturbances, but less is known about the role of soil properties in invasion after disturbance. Soil properties are crucial filters during plant succession and soil-related changes in the initial stage of species colonization might shape the final success of the invaders.

We performed a manipulative experiment aimed at elucidating the effects of soil properties on plant colonization processes in highly invaded dune systems, as a proxy for plausible management actions to curb the success of exotic plant species over native ones, which was measured through species richness and abundance.

In a barrier island of the Marano and Grado lagoon, Northern Adriatic Sea, we mechanically removed all the native and alien vegetation present in the back dune (also known as secondary dune), triggering a new ecological succession and further altered, for the following three months, soil properties by adding salt, nitrogen, and organic matter in a full factorial design with randomized blocks.

The soil treatments reduced the overall species richness and abundance of alien plants. Further, soil treatment interactions strongly shaped community evenness and species richness. Soil salinity had a positive effect on native cover while decreasing the overall number of alien species, especially in soil with added organic matter.

Our findings suggest that soil salinity, and its interplay with organic matter, might significantly reduce the initial success of alien species propagule pressure (i.e. alien plant germination), with likely implications for the trajectories of future plant communities. This study highlights that alien plant containment should be focused on early stages of succession, giving new perspective on future environmental management actions for dune restoration and conservation.

1. Introduction

Biological invasion is recognised as one of the major environmental issues of present days (Davis, 2003; Polce et al., 2023; Vilà et al., 2010; Xin et al., 2024), drastically reducing native biodiversity (Hughes et al., 2020; Hulme, 2009) and causing a global homogenization of biological systems (McKinney and Lockwood, 1999). The change in the vegetation composition after invasion can lead to major shifts in ecosystem integrity, functions and services, gradually decreasing the chance of reversing their impacts (Simberloff et al., 2013). It is well known that some habitats are highly prone to biological invasions, especially where natural or anthropic disturbances periodically trigger succession processes (e.g. rivers, coasts). Here, local factors, such as habitat type and soil disturbance, represent the most effective ecological filters that determine the success of alien species. Indeed, disturbance can create new availability of niches, enhancing the opportunity for new propagules to establish (Chytrý et al., 2009; Pyšek et al., 2010). This is especially true in the highly dynamic environments such as coastal dune ecosystems (Campos

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et al., 2004; Giulio et al., 2020), where the rapid intensification in human settlements and activities has caused the arrival and the spread of many alien plants (Carboni et al., 2010; Marcantonio et al., 2014; Pellegrini et al., 2021). In many invaded environments the alien species richness is higher at early stages of succession, but often subjected to strong ecological filters able to shape the vegetation trajectories over time (Mosanghini et al., 2023). Such empirical observations are not adequately supported by experimental evidence. For this reason, investigating the initial stages of plant succession might provide crucial insights into the processes of plant colonization by both native and alien species (Lami et al., 2021).

In the dune ecosystems, the interplay of strong abiotic factors creates steep sea-inland ecological gradients determining a complex landscape mosaic (Acosta et al., 2009). The main edaphic factors acting in dune systems are salinity, nutrients and organic matter (Fenu et al., 2013; Martínez and García-Franco, 2004). Generally nutrients and organic matter tend to increase with distance from the sea, while salinity decreases (Maun, 2009), but ecological succession can interfere with these ecological patterns. For instance, at intermediate and mature stages of many terrestrial ecosystems, high levels of soil nitrogen normally increase. This can enhance the invasion by nitrophilous alien species while decreasing overall plant diversity (Boscutti et al., 2020; Vitousek et al., 1997). This was partially contrasted by observed trends in some dune systems, where soil nutrient content favored native plants rather than alien (Vitti et al., 2020). In the same study, it has already been observed that soil salinity influences negatively the occurrence and abundance of salt-sensitive alien plants in coastal habitats. Soil organic matter seems also to be a driver of plant invasion in dunes, as it has been found in old successional stages, with more mature and organic matter rich soils, less invaded by alien plants (Lami et al., 2021).

The back dune ecosystems are highly susceptible to alien plant invasion (Tordoni et al., 2018). This can be explained by the back dunes being more stable and less subjected to extreme disturbance events (i.e. wash over events, salty winds, flooding stress), with moderate soil salinity and nutrient accumulation compared to foredune or saltmarshes environment (Vuerich et al., 2024), resulting in soils suitable for generalist species (Vitti et al., 2020). However, it is not yet known how these soil characteristics influence seedling emergence, and whether there are significant differences between alien and native species responses. Few studies have focused their attention on how the manipulation of soil properties can guide the plant community assemble and plant invasion in dune ecosystems (Cole et al., 2021).

The complex interplay between soil properties and plant community development has gained attention in research, yet gaps in knowledge persist regarding the effect at the early stage of colonization of dune ecosystem. For this purpose, we conducted a field experiment to test if changes in the main soil properties (i.e. soil salinity, nutrients, and organic matter) can modify the invasion of alien species in dune systems (i.e. restarting the invasion processes) and the possible contrasting responses of the native species community. To our knowledge, this study represents the first experimental approach to face dune invasion by soil manipulation, in future perspective of environmental management.

In dunes, the variation of soil properties after the succession restart can greatly shape the initial stages of plant communities, altering the success of germination and growth of alien and native pools. Our hypothesis is that the added nutrients, salt and organic matter have the potential to change the plant community, possibly promoting the richness and cover of native plants in contrast to alien species. In particular, we expect: i) soil salinity to decrease the richness and abundance of alien species; ii) nutrients to change the plant community favoring native plants (i.e. increasing plant abundance) and iii) organic matter, as a proxy for soil maturity, to reduce the occurrence of alien species. Additionally, we expect an interplay between those three soil properties, with possible additive effects between the treatments. Our hypothesis relies on the consequences of the sudden increase in niche availability due to disturbance, favoring the rapid colonization of generalist species,

such as annual plants (i.e. both native or alien) (Della Longa et al., 2020; Geppert et al., 2021; Lososová et al., 2004). We believe that our results will give new and important insight in the understanding of ecological invasion processes, with far reaching implications for mitigation and restoration programs in highly invaded dune ecosystems.

2. Material and methods

2.1. Study area

The experiment took place on the main barrier island (i.e. Sant'Andrea island) of the Marano and Grado lagoon (from 45° 43′ 15.0″N 13° 14′ 35.2″E to 45° 42′ 34.2″ N 13° 10′ 53.0″ E) in the Northern Adriatic Sea (Friuli Venezia Giulia, Italy) (Fig. 1). The site is recognised as a protected area in the Natura 2000 network (code IT3320037). The vegetation of the back dune in the island belong to the *Ammophiletea* Br.-Bl. et Tx. ex Westhoff et al., 1946 class according with Poldini et al. (1999) and Mucina et al. (2016), invaded by alien species such as *Amaranthus retroflexus, Ambrosia psilostachya, Amorpha fruticosa, Erigeron canadensis* and *Oenothera biennis*. The mean annual rainfall is 974 mm, with an average temperature of 15.3 °C, ranging from 3.1 °C in January to 29.0 °C in July. The average water salinity found in the Adriatic Sea near the study area is 35 psµ.

In this lagoon, tidal movements and alongshore sediment transport interact to make these islands a highly dynamic natural systems where both dune and halophilous species coexist. The zonation of the vegetation along the environmental sea–inland gradient can be divided into three main habitats: (i) foredune, including upper-beach, embryo-dunes and mobile dunes, frequently reached by seagrasses litter, (ii) back dune, defined as fixed dune encompassing those environments dominated by perennial communities of the inland, and (iii) salt marsh. These three main habitat types greatly differ in abiotic conditions, mainly due to disturbance regime and soil properties, such as nutrients, salinity, and organic substances. Our focus was on the back dune habitat (hereafter reference vegetation), the most susceptible to biological invasions and a possible crossway for the invasion of the other habitats (Lami et al., 2021). In the study area, the average soil salinity for the back dune was 43.6 µS cm^{-1}, the mean % of organic carbon is 0.56 and the mean % of nitrogen is 0.12. Conductivity was measured by a CM35 + portable conductivity meter (Crison) in soil samples taken from each external reference (5:1 extract using 10 g of dry soil and 50 mL of water per sample, a total of 8 soil cores). A description of how the external reference plot were chosen is reported in the following section.

2.2. Experimental design and setup

Before starting the experiment, some pilot trials were conducted in laboratory conditions to estimate the ability of the local sandy soil to retain experimentally added compounds. We added salt, nitrogen, and organic matter in pots with sandy soil collected from the experimental site simulating all the planned treatment combinations. We watered the pots simulating a rainfall event between 8 and 10 mm (i.e. the average amount of water falling during each spring rain event) and measured the salinity of the terrain assuming that the movement and percolation of salt and nutrients were similar to the field conditions. Pilot results showed soil to retain in the substrate the targeted compounds, confirming the effectiveness of treatments in altering soil properties.

The field experiment in the back dune vegetation started in the middle of April 2022, with the aim of simulate an extreme disturbance event caused by a strong spring sea storm able to trigger a new plant succession, events commonly occurring during autumn and early spring in the region (Sioni et al., 2023).

We selected 8 rectangular areas of 8 m by 6 m (48 m^2, i.e. experimental block). With a rototiller mounted on a tractor, all vegetation in the 8 blocks was removed and the bare soil was manually cleaned with rakes to take off remaining vegetal part of plants to avoid resprouting.
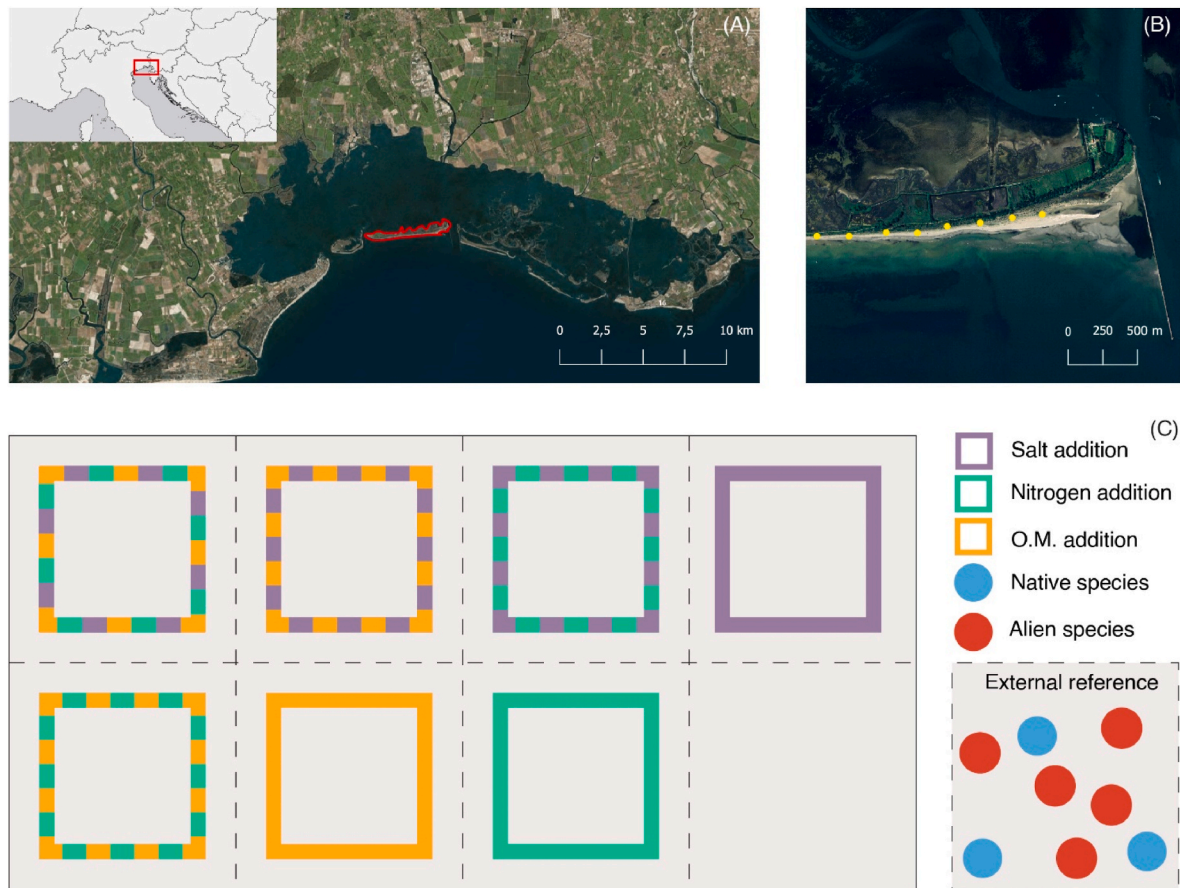
Fig. 1. Experimental design. (A) Study area located in the Marano and Grado's lagoon, NE of Italy at the Sant'Andrea barrier island, (B) location of the 8 experimental blocks (yellow dots), and (C) experimental design randomly applied to each experimental block. In each block the vegetation was removed, and three soil treatments and their combinations were performed in plots of 1 m^2 (i.e. salt addition, nitrogen addition and organic matter addition). An external reference plot was selected next to each block in the undisturbed reference vegetation.

Each block was divided in 8 plots of 1 m^2 (1 × 1 m) with at least 50 cm of distance between each. The bare soil was manipulated by altering (i) organic matter content, (ii) salinity, and (iii) nutrients (i.e. nitrogen fertilisation) with a full factorial design (Fig. 1). The treatments were randomly arranged in each block to avoid any response mediated by local factors. The soil treatments were the following. To increase the organic matter up to 20% in the first 7.5 cm of soil depth, a total of 15 l × m^{-2} of sphagnum peat (hereafter referred as organic matter) was added to each plot. This sphagnum peat has a composition of organic carbon on dry weight = 40 %; organic nitrogen = 4 %; pH = 4.5 and salinity = 0.3 µS cm^{-1}. Peat was used as source of organic matter similar to the content of the leaf litter (=seagrass wrack) of the locally most common seagrass species (Boscutti et al., 2015; Cingano et al., 2024), i. e., *Cymodocea nodosa* (leaf litter: organic carbon in dry weight = 51.0%, organic nitrogen = 4.7%, Peduzzi and Herndl, 1991). Seagrass litter was not used in our experiment to test separately the effects of salt and organic matter. The organic matter treatment was performed only at the beginning of the experiment. Soil salinity was increased with the aim of simulating the addition of sea water to the soil, by adding sea water at the start of the experiment containing crystal salt (NaCl) after a rainfall precipitation of 8 mm. In particular, given a mean rainfall event of about 8 mm and a salt concentration in the water around 35 g × l^{-1}, the total amount of salt was 260 g × m^{-2}. Finally, nutrient soil content was altered by adding commercial calcium nitrate (Ca(NO$_3$)$_2$) with a quantity of 50 g × m^{-2}; the crystals were solubilized with water during the experimental setup and then added in crystals after a rainfall cumulated of 8 mm. Throughout the entire experiment, soil cores were collected (i. e. 12 cm depth, 5 cm diameter), and processed to monitor the effects of

the treatments, confirming the consistent effect of each treatment over time (Figs. S1 and S2). In particular we tested the soil at the beginning of the experiment, after 45 days and at the end of the experiment (i.e. after 100 days). The first two core sampling events covered half of the treated plots (i.e. 32 soil cores each time) while at the end of the experiment all the 64 treated plot were tested by collecting a soil core. In the surroundings of each experimental block, we selected an undisturbed plot of 1 m^2 (hereafter referred as external reference).

2.3. Plant community data

During the experiment (i.e. from middle of April to middle of July 2022; 100 days of experiment), orthogonal pictures of each plot were taken with a RGB camera (Panasonic, model Lumix GH5) mounted on a tripod 2 m above the ground. Soil pictures and surveys were conducted in all the experimental and the reference plots. Only the photographs taken at the end of the experiment, after 100 days, were used to analyse the plant community.

Field surveys and picture analysis were used to record all the vascular plants occurring in the plot, to count the number of individuals and to measure the species cover (%), through the software ImageJ (Schneider et al., 2012). In particular, each photo was cut with a reference of 1 m^2, adjusted with the scale and filtered by colour threshold to select only plant parts. Once obtained the Region of Interest (ROI) of the vegetated areas in the images, a new manually selection, based on the species visual recognition was carried out, obtaining the value of cover for each species at the centimetre accuracy.

Species nomenclature was assigned according to the Italian native

checklist (Bartolucci et al., 2018), while the alien status was assigned according to the most recent regional alien species checklist (Buccheri et al., 2019). The abundance of each species was calculated as the number of individuals and the sum of the cover of individuals. Species richness (number of species), diversity (Shannon's index, calculated on species' cover) and evenness (Pielou's index, calculated on species cover) were considered as alpha-diversity indices, calculated separately for native and alien species. The beta-diversity (used as an index of species composition shifts) was analysed by comparing species dissimilarity between the treated plots and the external reference plot with the Jaccard index. The beta-diversity was calculated using the 'beta.pair' function of the 'betapart' package (Baselga et al., 2018). Due to the small number of species, the entire plant community was used to calculate the beta diversity index and further models, regardless of plant status (both alien and native).

Furthermore, to get more information on the effect of soil on plant invasion, we also considered the pooled beta-diversity for each status (i. e. native and alien), pooling all the 8 replicates. It is important to note that by pooling replicates, we were unable to test for changes in beta-diversity by status, obtaining a single value of distance from the external reference plots and treatment considered.

2.4. Statistical analysis

Abundance and diversity indices (i.e. Shannon's diversity index, species richness, Pielou's index) of the vegetation were calculated for each plot and separately for each plant status (i.e. native or alien). Because the Shannon's diversity index was highly correlated with species evenness ($r = 0.83$, $p < 0.01$) and richness ($r = 0.88$, $p < 0.01$), it was not considered any further for analysis.

Mean value of plant cover and number of individuals was provided as data to compare the situation outside the experimental block. We also reported the range of variation of the data considered, showing the minimum and maximum value. To test the effects of the soil disturbance treatment (i.e. restart of succession), the differences in plant community mean cover and number of individuals between paired treated and external reference plots were analysed with Wilcoxon signed-rank tests. The response of the vegetation indices (i.e. plant cover, number of individuals, species richness, evenness) to soil treatments (i.e., salt, nitrogen and organic matter), species status (i.e., alien or native), and their interactions were tested using linear mixed-effects models (LMM; $p \leq 0.05$). Beta-diversity LMM did not include species status. All LMMs were applied including the block id and plot id as nested random factors. LMMs were applied using the 'nlme' package (Pinheiro et al., 2022). We manually removed interaction terms from the final models when p-values were higher than 0.05, simplifying the model with a backward deletion procedure. All the full model are reported in the supplementary materials (Table S1). Statistical significance was assumed when the p-value was equal or lower than 0.05. The models' assumptions were verified using the diagnostic plots of the model residuals. Where model residuals violated any linear model assumption, variables were transformed using logarithmic, square root or exponential transformation. An outlier test was conducted when the points on the diagnostic plots were visually far from most of the residuals and the significant outliers were discarded.

The summary table of each model was reported with the function 'tab_model' of the 'sjPlot' package (Lüdecke, 2018). Graphic results were represented with the R package 'effects' (Fox and Weisberg, 2018). We calculated the mean value of the external reference plot for each variable considered and we displayed it in the graphs. All analyses were performed in R 4.2.2 (R Core Team, 2022).

3. Results

3.1. Effects of soil properties manipulation on plant abundance

In the external reference plots the overall mean number of individuals per plot was 26.4 (Min. = 5, Max = 63, std.Error = 6.25) and 9.9 (Min. = 0, Max = 22, std.Error = 3.34) for native species and 16.5 (Min. = 1, Max = 60, std.Error = 7.66) for alien species. The mean number of individuals in the soil disturbed plots (i.e. mean of all the treated plots), was significantly lower than the reference for the overall (Mean = 4.36, Min. = 0, Max = 59, p-value <0.001, std.Error = 0.75) and alien species (Mean = 5.13, Min. = 0, Max = 59, p-value <0.001, std.Error = 1.24), while it was similar for native species (Mean = 6.53, Min. = 0, Max = 43, p-value = 0.39, std.Error = 0.82). The overall cover values were consistent in both disturbed and reference vegetation plots (p-value >0.05). Cover of the reference plot was 7.17 % (Min. = 0%, Max = 14.5%, std.Error = 2.08%), 5.34 % (Min. = 0%, Max = 14.5%, std.Error = 2.31%) for native species and 1.82 % (Min. = 0%, Max = 10.1%) for alien species. Plant cover of the treated plots was without statistical difference compare with the external plots, with 6.70% (Min. = 0%, Max = 43.6%, std.Error = 0.59%), 5.05 % (Min. = 0%, Max = 43.6%, std.Error = 1.11%) and 1.86 % (Min. = 0%, Max = 12.9%, std. Error = 0.34) for native and alien species, respectively.

Soil treatments had a significant effect on plant abundance (i.e. number of individuals and plant cover) of both native and alien plant species. In particular, the number of individuals responded significantly to the interaction between salt addition and plant status (i.e. alien and native) (Table 1). The number of individuals of alien species showed a significant decrease when salt was added in the soil compared with the reference vegetation (Fig. 2a). The number of native individuals slightly decreased with salt addition reaching an overall value similar to the external reference plot.

Moreover, we found a significant interaction between plant status, salt and organic matter treatment on species cover (Table 1). Alien species exhibited a lower cover compared to native cover (Fig. 2b), and increased soil salinity reduced cover of alien plants. Natives reported an overall cover similar to or higher than the reference plot, while alien cover was lower. Furthermore, treatments with no organic matter and

Table 1
Summary of the best LMMs selected (i.e. simplified models when not significant) testing the effect of soil treatments (i.e. Salt [y] = salt addition, Nitrogen [y] = nitrogen addition, Organic matter [y] = organic matter addition, and Status [N] = native species) on log of number of individuals and log of area covered. Coefficients are estimated from the best linear mixed-effects models. Interactions of the full model were removed when p > 0.05.

| Dependent variable	Treatment	Estimates	CI	p
Log (n° of individuals)	(Intercept)	−1.05	−2.32–0.23	0.11
	Salt [y]	−2.27	−3.26–−1.27	**<0.001**
	Status [N]	2.48	1.48–3.48	**<0.001**
	Nitrogen [y]	−0.37	−1.08–0.33	0.30
	Organic matter [y]	−0.15	−0.85–0.56	0.68
	Salt [y] × Status [N]	1.48	0.07–2.89	**0.04**
Log (Area covered)	(Intercept)	−0.94	−3.20–1.32	0.41
	Salt [y]	−1.08	−3.98–1.82	0.46
	Status [N]	6.8	3.90–9.70	**<0.001**
	Organic matter [y]	0.04	−2.86–2.94	0.99
	Nitrogen [y]	−0.07	−1.53–1.39	0.93
	Salt [y] × Status [N]	−1.99	−6.09–2.11	0.34
	Salt [y] × Organic matter [y]	−0.32	−4.42–3.78	0.88
	Status [N] × Organic matter [y]	−3.35	−7.49–0.79	0.11
	Salt [y] × Status [N] × Organic matter [y]	6.03	0.20–11.85	**0.043**
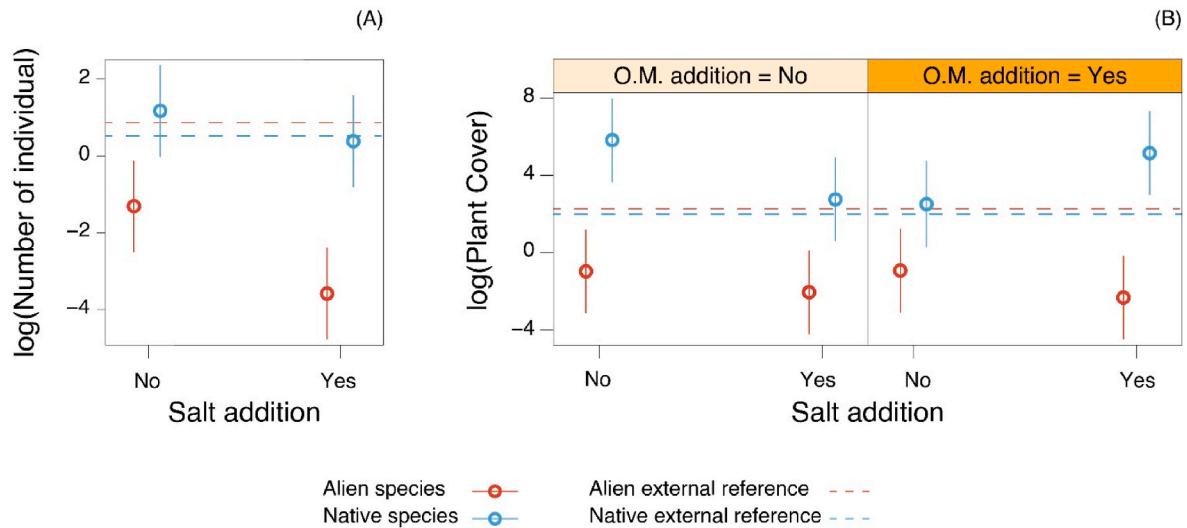
Fig. 2. (A) Effect of salt addition on the number of individuals (log-transformed) of alien and native species. (B) Effect of salt and organic matter addition interaction on the plant cover (log-transformed) of alien and native species. The dashed lines show the values from the undisturbed external reference plots. Confidence intervals (95%) are also shown. All the model presented were statistically significant.

no salt, on one hand, and treatments with organic matter and salt, on the other, enhanced native plant cover.

3.2. Effects of soil manipulation on alpha-diversity

In total, during the surveys we found 21 plant species (10 alien species of which 7 are considered invasive in the region and 11 native; see Table 2 for invasion status information). In particular, a total of 13 species were found in the external reference (i.e. 8 native and 5 alien), while 18 species were found in the treated plot (i.e. 9 native and 9 alien).

Native richness was higher than alien richness both in the external reference plots and treated plots (Fig. 3a). In the experimental plots, the most common species found was the native *Cakile maritima* (54.7% of the plots; Table 2), while in the reference plots the most frequent species was the alien *Oenothera biennis*, occurring in 87.5% of the plots. The proportion of annual and perennial species was similar both in the experimental (50 % of annuals and 50 % of perennials) and reference plots (46% annuals and 54% perennials).

We found a significant effect of salt, nitrogen and their interactions on species richness(Table 3). Salt decreased the species richness, especially when combined with nitrogen, independently of the species status (Fig. 3b). In contrast, the addition of soil organic matter had a non-significant effect on species richness.

The community evenness (Pielou's index) of alien and native species was affected by the interaction of all the soil treatments (Table 3). Alien species showed a lower value of evenness compared to native species in all experimental conditions, being similar when only organic matter was added in the soil (Fig. 3c). In particular, a concurrent addition of nitrogen and salt increased the native evenness, with a value above the reference vegetation. When organic matter was added, the effect of salt × nitrogen interaction was opposite, with a native evenness higher than alien where salt was not added to the soil. The alien evenness remained constant when nitrogen was added in both salt addition and organic matter treatments, considerably lower than the alien evenness in the reference vegetation. Instead, where no nitrogen and no organic matter was added, salt decreased the evenness both of native and alien species, but with the highest reduction for aliens. Both alien and native evenness were far lower compared to the reference plot. No difference in evenness between alien and native species was found when only organic matter was added, but when salt was added an opposite trend was found: the evenness of alien species decreased significantly, while that of native species increased.

3.3. Effects of soil manipulation on beta-diversity

Due to the low number of alien species occurring in some plots, the beta-diversity LMM was conducted without separating the alien and native pools. We found beta-diversity to be affected by the interaction between soil salinity, organic matter and nitrogen (Table 4). Plots with only vegetation removal (no addition of salt, nutrients or organic matter) were the most similar to the vegetation found in the external reference plots, showing the lowest beta-diversity (Fig. 4). Soil with the salt addition showed the highest beta-diversity in relation to external reference plot. All soils with added organic matter showed a consistent beta-diversity similarity, even when salt and nitrogen were added. Soil with no organic matter but nitrogen or salt treatment showed higher values of beta-diversity than soil added with organic matter.

To get more information on the effects of soil on plant invasion we further considered the pooled beta-diversity of each status (i.e. native and alien) (Fig. S3). We want to underline that by pooling the replicates we were unable to make statistics on the beta-diversity divided for status. The highest floristic distance of alien species (overall pooled beta-diversity) was found for treatments with salt and salt plus nitrogen (overall = 1), where none alien species of the treated plot was also occurring in the external reference plot. For native species the most distant community to the reference plot was obtained when nitrogen was added to the soil (overall pooled beta-diversity = 0.968).

4. Discussion

The findings of this experiment contribute to the mechanistic understanding of the influence of soil properties on plant invasions in coastal dune ecosystems. In particular, our experiment confirmed that the back dune salt and organic matter can constrain the alien cover, favoring native plants. Soil salinity seemed to act on limiting seedlings emergence, estimated as the number of individuals and reducing their growth (quantified as plant cover).

The plant abundance at early successional stages is an important feature for understanding the future trajectories of the succession (Estrada-Villegas et al., 2020). If the colonizer is an alien plant, its initial abundance can greatly affect their spread potential and, hence, the final success of biological invasion in the habitat (Lami et al., 2021). We found soil to significantly affect the plant abundance of native and alien plant communities, with salt addition able to curb both the number of individuals and cover of alien plants. This result is consistent to what

Table 2

List and percentage frequency of the species found during the experiment. The frequency are reported for the experimental block and for the external reference plots. We reported the status of each species and in case of alien we add the information for invasive species in the region.

Species	Family	Status	Species frequency (experimental block)	Species frequency (external reference)
Amaranthus retroflexus L.	Amaranthaceae	Alien	3.13	0
Ambrosia psilostachya DC.	Asteraceae	Alien (invasive)	15.63	37.5
Atriplex rosea L.	Amaranthaceae	Native	17.19	0
Cakile maritima Scop. subsp. *maritima*	Brassicaceae	Native	54.69	0
Cenchrus longispinus (Hack.) Fernald	Poaceae	Alien (invasive)	4.69	12.5
Cuscuta scandens Brot. Subsp. *cesattiana* (Bertol.) Greuter & Burdet	Convolvulaceae	Alien	9.38	0
Cynodon dactylon (L.) Pers.	Poaceae	Native	20.31	12.5
Cyperus capitatus Vand.	Cyperaceae	Native	31.25	25
Cyperus esculentus L.	Cyperaceae	Alien (invasive)	1.56	0
Erigeron canadensis L.	Asteraceae	Alien (invasive)	0	37.5
Lepidium virginicum L. subsp. *virginicum*	Brassicaceae	Alien	1.56	12.5
Lomelosia argentea (L.) Greuter & Burdet	Dipsacaceae	Native	0	37.5
Oenothera biennis L.	Onagraceae	Alien (invasive)	9.38	87.5
Plantago arenaria Waldst. & Kit.	Plantaginaceae	Native	0	12.5
Poterium sanguisorba L. subsp. *sanguisorba*	Rosaceae	Native	6.25	75
Robinia pseudoacacia L.	Fabaceae	Alien (invasive)	4.69	0
Salsola kali L.	Amaranthaceae	Native	4.69	0
Silene vulgaris (Moench) Garcke subsp. *tenoreana* (Colla) Soldano & F. Conti	Caryophyllaceae	Native	6.25	12.5
Soda inermis Fourr.	Amaranthaceae	Native	4.69	12.5
Poacynum venetum (L.) Mavrodiev, Laktionov &	Apocynaceae	Native	9.38	25

Table 2 (*continued*)

Species	Family	Status	Species frequency (experimental block)	Species frequency (external reference)
Yu.E. Alexeev *Xanthium orientale* L.	Asteraceae	Alien (invasive)	1.56	0

evidenced in other studies (Mayoral et al., 2021; Morais et al., 2012; Sykes and Wilson, 1989), actively acting to the potential propagule pressure of the alien species pool.

The number of individuals of native species in the disturbed plots was comparable to the target reference undisturbed plot, even when salt was added to the soil. Native species also reported an overall cover value higher or at least equal to the external reference plot. Furthermore, treatments with no organic matter and no salt, on one hand, and treatments with organic matter and salt, on the other, appear to be able to enhance native plant cover. Native species, hence, did not suffer a reduction in plant growth, as was evidenced for alien plants (Sykes and Wilson, 1989). Instead, it is plausible that the few species colonizing the plots under the salt treatment, e.g. *Cakile maritima*, can even enhance their growth rate, due to lower competition with fewer alien species (Borgnis and Boyer, 2016; Del Vecchio et al., 2018, 2021).

As hypothesized, the soil salinity strongly affected both alpha- and beta-diversity, the role of salinity was also enhanced or weakened by its interaction with the other soil properties modified in the experiment (i. e. organic matter and nitrogen availability).

Alien species represented the 48% of the total species richness in the studied dune system, much higher than the frequency of alien taxa at the regional (16%) and the national (12%) scale (Galasso et al., 2018), confirming these habitats to be among the most invaded habitats by aliens in Europe (Chytrý et al., 2008). The potential invasiveness of the habitat was confirmed by recent synthesis at continental level (Giulio et al., 2020). In the experimental disturbed plots native and alien species richness was lower than in the reference undisturbed plots, independently of the applied treatment. This showed that the soil disturbance, used to start the new ecological succession, originated a low biodiversity community, as already proved in other grass-dominated habitats (Geppert et al., 2021; Mosanghini et al., 2023). However, differently to other habitats, the number of alien species was significantly reduced in comparison to native ones, consistently with the result of field observation in similar ecosystems (Lami et al., 2021). Our results suggest that, during the early stages of succession, the success of exotic species is related to the local properties of the soil and may be also related to the availability of propagules in the seed bank. As hypothesized, soil salinity reduced the overall plant species richness, independently to the species status (i.e. native vs alien), especially when addition of nitrogen was also applied.

Soil salt content has been demonstrated to play a significant role in shaping plant zonation in coastal dunes (Ishikawa et al. 1995), where it creates challenging conditions primarily by increasing osmotic stress and hence reducing soil water availability. This is particularly pronounced in sandy soils, where the high porosity exacerbates the soil drought effects. Here only well adapted plants can colonize the bare soil, leading to a highly specialized habitat, as occurs in the foredune system (Ciccarelli, 2014). The addition of calcium nitrate to the soil decreased the overall number of species, and this was even more pronounced when salt was also added. Nitrogen is an essential nutrient for plant growth, but excess nitrogen can also have negative effects on plant diversity (Stevens et al., 2004). In our case, nitrogen addition seems to magnify the salt effect on plant diversity.

The evenness of the community (i.e. Pielou's index) was significantly affected by the interaction of the three soil factors and the species status. Nitrogen generally favored a more even native community while its effect on alien community was the opposite, especially when combined
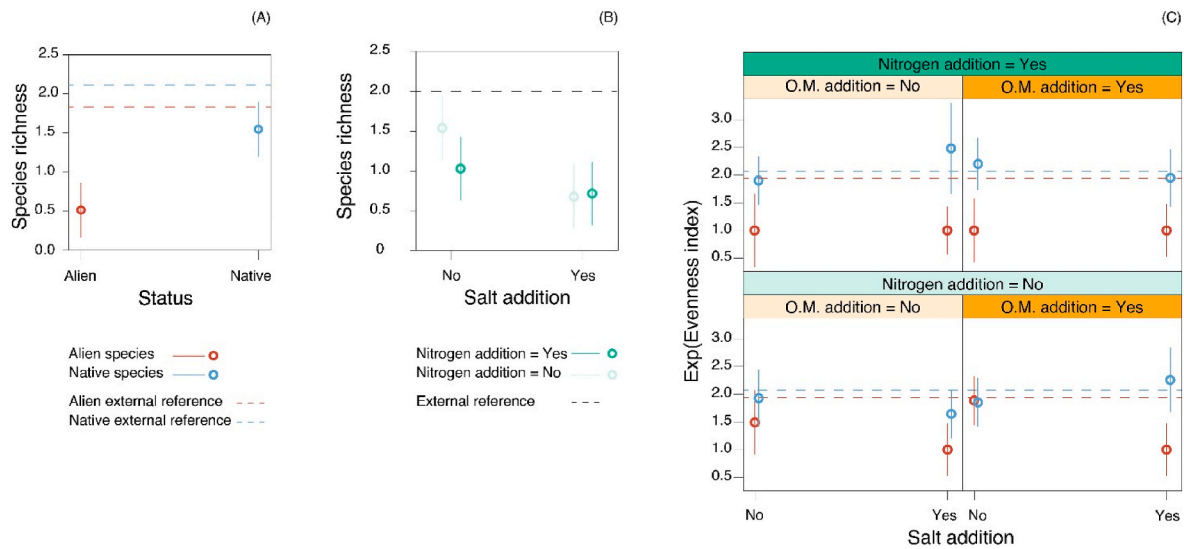
Fig. 3. soil and plant diversity. (A) Differences in species richness between the alien and native species. (B) Effects of the interaction between salt and nitrogen (i.e. calcium nitrate) on species richness. (C) Effects of the interaction between status, salt, nitrogen, and organic matter (i.e. added peat) on the evenness (Pielou's index, exponential transformation) of native and alien species. The dashed lines show the reference values obtained from the external plots. Confidence intervals (95%) are also shown. All the model presented were statistically significant.

Table 3
Summary of the best LMMs (i.e. simplified models when not significant) testing the effect of soil treatments (i.e. Salt [y] = salt addition, Nitrogen [y] = nitrogen addition, Organic matter [y] = organic matter addition, and Status [N] = native species) on species richness and Pielou index (exponential transformation). Coefficients are estimated from the best linear mixed-effects models. Interactions of the full model were removed when $p > 0.05$.

Dependent variable	Treatments	Estimates	CI	p
Species richness	(Intercept)	1	0.58–1.43	**<0.001**
	Salt [y]	−0.76	−1.08–−0.44	**<0.001**
	Nitrogen [y]	−0.48	−0.80–−0.16	**0.004**
	Organic matter [y]	0	−0.22–0.23	0.97
	Status [N]	1.07	0.84–1.29	**<0.001**
	Salt [y] × Nitrogen [y]	0.51	0.06–0.96	**0.028**
Exp (Pielou index)	(Intercept)	1.51	0.94–2.07	**<0.001**
	Salt [y]	−0.49	−1.18–0.21	0.17
	Status [N]	0.31	−0.42–1.04	0.40
	Organic matter [y]	0.36	−0.32–1.04	0.29
	Nitrogen [y]	−0.4	−1.23–0.43	0.34
	Salt [y] × Status [N]	0.34	−0.61–1.28	0.48
	Salt [y] × Organic matter [y]	−0.34	−1.26–0.58	0.46
	Status [N] × Organic matter [y]	−0.34	−1.26–0.59	0.47
	Salt [y] × Nitrogen [y]	0.41	−0.61–1.43	0.43
	Status [N] × Nitrogen [y]	0.47	−0.56–1.51	0.37
	Organic matter [y] × Nitrogen [y]	−0.5	−1.57–0.57	0.35
	Salt [y] × Status [N] × Organic matter [y]	0.85	−0.45–2.15	0.20
	Salt [y] × Status [N] × Nitrogen [y]	0.32	−1.09–1.73	0.65
	Salt [y] × Organic matter [y] × Nitrogen [y]	0.49	−0.89–1.87	0.48
	Status [N] × Organic matter [y] × Nitrogen [y]	0.82	−0.54–2.19	0.23
	Salt [y] × Status [N] × Organic matter [y]) × Nitrogen [y]	−1.88	−3.79–0.03	**0.05**

Table 4
Summary of the best LMMs (i.e. simplified models when not significant) testing the effect of soil treatments (i.e. Salt [y] = salt addition, Nitrogen [y] = nitrogen addition, Organic matter [y] = organic matter addition) on the beta-diversity (i. e. Jaccard index, square root-transformed). Coefficients are estimated from the best linear mixed-effects model. Interactions of the full model were removed when $p > 0.05$.

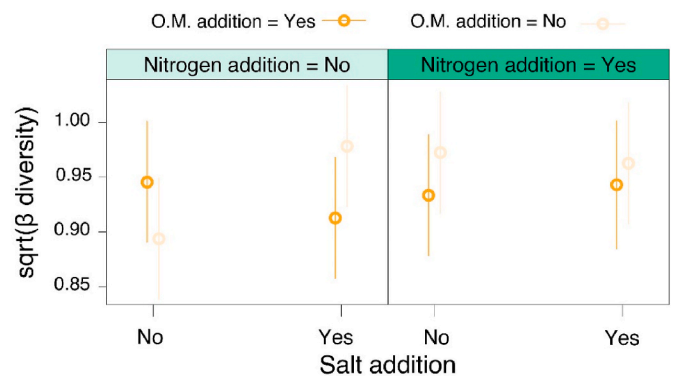| Dependent variable	Predictors	Estimates	CI	p
Sqrt (Jaccard)	(Intercept)	0.89	0.84–0.95	**<0.001**
	Salt [y]	0.09	0.02–0.15	**0.012**
	Organic matter [y]	0.05	−0.01–0.11	0.120
	Nitrogen [y]	0.08	0.02–0.14	**0.019**
	Salt [y] × Organic matter [y]	−0.1	−0.18–−0.01	**0.014**
	Salt [y] × Nitrogen [y]	−0.09	−0.18–−0.01	**0.046**
	Organic matter [y] × Nitrogen [y]	−0.09	−0.18–−0.00	0.054
	Salt [y] × Organic matter [y] × Nitrogen [y]	0.12	−0.01–0.24	**0.043**

Fig. 4. Soil and beta-diversity. Effects of the interaction between salt, organic matter and nitrogen (i.e. calcium nitrate) addition on beta-diversity index (sqrt transformed). Confidence intervals (95%) are also shown. All the model presented were statistically significant.

with salt addition, probably due to the occurrence and dominance of few alien species more tolerant to salt (Hesp, 1991). Considering both richness and evenness, salt seems to filter a community with low diversity that can either dominate the community, in the case of alien species, or share the ecological space, in the case of natives (i.e. higher evenness of native plants). In fact, in the disturbed plots, the alien community showed a lower evenness compared to the reference undisturbed plot, especially with salt addition. On the contrary, the natives had a similar evenness compared to the reference plot, especially when nitrogen was added to the soil. This also suggests that nitrogen may contribute to a more even sharing of ecological space for native species. The newly establishing succession thus appears to favor native alpha-diversity. On the contrary, salinity select some aliens to dominate over others, consistently to what observed in other ecosystems (Ehrenfeld, 2003).

Soil organic matter showed to affect species evenness, but no effect was observed on species richness. In particular, alien species had consistently lower evenness than native species under all experimental conditions, except when only organic matter was added to the soil. Here the higher organic matter content in the soil might ameliorate the soil conditions (e.g. water soil capacity, soil structure) (Hoffland et al., 2020) and, hence, enhancing the germination and growth conditions for more generalist alien species.

Soil disturbance significantly increased species composition distance (i.e. beta-diversity) with the reference undisturbed vegetation. The beta-diversity analysis confirmed that soil properties acted as a strong abiotic filter able to determine the community species assembly especially during the first stages of plant succession (Lami et al., 2021; Réjou-Méchain et al., 2014). Our findings suggest that salt is the most selective factor that greatly increased the differences in terms of species composition, while soils added with organic matter showed a more constant beta-diversity, even when salt and nitrogen were added. Species composition at the early stage of succession greatly depends on the success of seed bank germination (Jiménez and Armesto, 1992), crucial also in shaping the invasion success (Trotta et al., 2023). It seems that salt might filter the seed bank species germination selecting those species occurring in the reference vegetation more able to germinate in salty soils (Mariko et al., 1992). It is thus plausible that the soil seed bank of the back dune evenly exposed by the soil disturbance underwent the soil ecological filtering, able to affect the seed germination and, eventually, the final assembly of the new plant community (Bakker et al., 1996; Marteinsdóttir, 2014).

Soil organic matter has a great impact on soil functions acting as a buffer of the effect of many other soil properties (Hoffland et al., 2020). In our experiment, the addition of soil organic matter (i.e. peat) mitigated or amplified the effect of the other soil factors, probably by favouring the colonization of species of the mature reference vegetation, more sensitive to the soil alterations induced by the experiment. In fact, plots with no organic matter added but under nitrogen or salt treatment showed high values of overall beta-diversity.

Focusing on the response of native and alien species pools, we found alien species composition (i.e. beta-diversity) to be more strongly associated with salt and nitrogen than the native composition. In salty soils, the alien species composition was totally different to the reference plot, confirming this filter to select only for new entering well adapted alien species. Instead, nitrogen seems to exert a similar effect on native pools. As mentioned, nitrogen is a strong factor in determining plant diversity. The beta-diversity analysis stressed that nitrogen is also affects species composition, probably favouring the germination of particular pool of species particularly able to draw on this resource (Bird and Choi, 2017).

5. Conclusion

The differential responses of native and alien species to soil manipulations underscore the importance of considering the effects of soil

properties on species composition and abundance during the early stages of succession, with far reaching consequences for the ecological restoration and conservation of coastal dune ecosystems. Our findings suggest that in the back dune, where the soil conditions are not highly selective for opportunistic alien plants, we should focus our major efforts to deter alien plant invasion in coastal dunes. Here, disturbance might be used to constrain the abundance and diversity of alien species. Moreover, our results also suggest that the use of some local soil improvers (containing salt and nutrients, e.g. seagrass wrack) might be also added to soils to drive the first stages of succession after disturbance. These actions can be particularly suitable in the case of dune restoration actions of small-to medium-size sites, to influence the future trajectories of the succession. However, further research is needed to explore the long-term implications of soil manipulation on plant community resilience and ecosystem stability.

CRediT authorship contribution statement

Giacomo Trotta: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marco Vuerich:** Writing – review & editing, Visualization, Methodology, Conceptualization. **Elisa Pellegrini:** Writing – review & editing, Formal analysis, Data curation. **Montserrat Vilà:** Writing – review & editing, Validation. **Edoardo Asquini:** Writing – review & editing. **Paolo Cingano:** Writing – review & editing. **Francesco Boscutti:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

All the data are available at the public repository Mendeley Data, doi: https://doi.org/10.17632/ysv6f9srp5.1

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.121780.

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