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Relationship Between Plant Strategy Types and Soil Characteristics in Backdunes and Foredunes

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Abstract

Dune ecosystems support limited plant diversity under harsh conditions. This study examines the distribution of competitor, stress tolerator, and ruderal (CSR) strategies in foredune and backdune areas and their relationships with soil variables. Seasonal variations in soil properties and plant strategy types were assessed using canonical correspondence analysis (CCA) and similarity percentage analysis (SIMPER). The Bray–Curtis similarity index showed a 67% dissimilarity between foredune and backdune plant strategies. Most soil variables exhibited significant seasonal changes ($p < 0.05$), except phosphorus (P) and calcium carbonate ($CaCO_3$). Competitive and stress-tolerant species were positively associated with pH, salinity, and $CaCO_3$ but negatively correlated with total nitrogen (TN), phosphorus (P), potassium (K), and moisture. In contrast, ruderal and mixed CSR species were linked to higher nutrient levels and moisture. Our findings highlight the adaptive resilience of dune species and the influence of soil conditions on plant community structure. Even without external disturbances, species well-adapted to harsh dune conditions can dominate, illustrating the dynamics of dune succession.

Keywords Dune · Plant functional types · CSR strategies · Soil · Succession

Introduction

Coastal dunes, dynamic ecotones between marine and terrestrial ecosystems, shift in response to environmental changes (Carboni et al., 2009; Schwarz et al., 2018). These ecosystems, shaped by salt spray, drought, nutrient deficiency, high temperature, intense light, wind, and substrate mobility, support only species with specialized survival strategies. Plants evolve physiological, morphological, and reproductive adaptations to persist in harsh conditions (Bermúdez & Retuerto, 2014; García-Mora et al., 1999; Hesp, 1991). Environmental pressures shape species composition, favoring those with shared traits (Cornwell et al., 2006; Keddy, 1992; Mayfield et al., 2005). Classifying plants into functional types (PFTs) based on shared traits provides valuable insight into community and ecosystem structure (Díaz & Cabido, 2001; Lavorel et al., 1997).

Grouping plants based on functional traits simplifies the interpretation of plant communities. This approach aids in assessing ecosystem functions, as different plant strategies contribute uniquely to nutrient cycling and energy flow through primary production and decomposition (Díaz & Cabido, 1997). The CSR model categorizes plant strategies as competitive, stress-tolerant, or ruderal, depending on stress and disturbance levels (Grime, 1974; Grime et al., 1997; Hodgson et al., 1999; Grime, 2001). By providing a flexible framework for species distribution in heterogeneous environments, the CSR classification illustrates how plants adapt through evolutionary processes (Bornhofen et al., 2011; Grime, 1977; Pierce et al., 2017).

Stress and disturbance drive dune plant succession, with stress factors such as high temperatures, high irradiance,

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nutrient limitation, and water scarcity, while disturbance factors include seawater inundation, grazing, strong winds, and human activity (Hesp, 1991; Maun, 2009). The CSR model is particularly relevant in such dynamic ecosystems, where species coexist despite environmental pressures (Acosta et al., 2005; Maun, 2009). Predicting these distribution patterns is crucial for conservation and management of fragile dune environments.

Climate is the primary abiotic factor influencing plant establishment and distribution, while soil—largely shaped by climate—regulates nutrient availability and water retention. In coastal dunes, nutrient input differs from that in terrestrial ecosystems, with meteorological inputs (e.g., aerosols in spray and fog) surpassing substrate weathering. Factors such as bulk precipitation, seawater inundation, detritus deposition, and sand movement contribute to nutrient availability, creating a mosaic soil condition. Certain nutrients (e.g., Na, K, Cl, Mg) reach high levels, while others (e.g., N, P, organic matter) remain limited (Barbour et al., 1985). The relationship between soil and plant species is reciprocal: dune soil conditions influence plant establishment, while plants contribute to sand accumulation and dune formation (Moreno-Casasola, 1986).

Studying functional characters is crucial to understanding the processes involved in the formation of plant communities under natural stress conditions (Feagin & Wu, 2007; Gallego-Fernández & Martinez, 2011; Chelli et al., 2019; Ciccarelli & Bona, 2022). While plant functional groups have been widely studied (Díaz Barradas et al., 1999; García-Mora et al., 1999; Acosta et al., 2006; Feagin & Wu, 2007; Novo et al., 2004; Gallego-Fernández & Martínez, 2011; Bermúdez & Retuerto, 2014), fewer studies have specifically examined the relationship between CSR strategies and soil factors (Brunbjerg et al., 2012; Ciccarelli, 2015; Lee et al., 2020; Macedo et al., 2010; Son et al., 2020). This study analyzes how soil characteristics, such as pH, organic matter, and moisture, influence the distribution of CSR strategies in foredune and backdune areas, contributing to a better understanding of plant adaptation under environmental stress (Brunbjerg et al., 2012; Grime et al., 1997; Lee et al., 2020). Given the ecological importance of coastal dunes in buffering inland areas from erosion and saltwater intrusion, as well as supporting biodiversity, understanding the link between CSR strategies and soil variables is critical for conservation planning (Hesp & Martinez, 2007; Defeo et al., 2009; Pugnaire & Luque, 2001; Macedo et al., 2010).

This study hypothesizes that variations in soil characteristics between foredune and backdune areas shape the distribution of CSR plant strategies (competitor, stress-tolerator, and ruderal). Specifically, key soil properties such as pH, moisture, organic matter, and nutrient content (e.g., total nitrogen, phosphorus) are expected to drive the prevalence of these strategies. Stress-tolerant species should dominate foredunes with higher salinity, whereas ruderal and competitive species will be more abundant in nutrient-rich backdunes. Additionally, seasonal fluctuations in soil properties may drive shifts in CSR strategy distributions, while plant-soil feedback in backdunes influences soil characteristics, shaping the composition of CSR strategies in these areas.

Materials and Methods

Study Area

The study area, located near the Aksaz Wetland (Sinop, Türkiye), is subject to significant human impact. It features two streams, Sırakaraağaçlar and Karasu, along with several drainage channels that open to the sea. These streams connect with the Black Sea during autumn, winter, and early spring and close in late spring and summer. The study area encompasses a foredune of 27 ha and a backdune of 13 ha (4 km long and of variable width, between 42°01′64.2″N–34°04′55.8″E and 44°02′33.3″N–35°02′39.9″E) (Fig. 1). The study area is characterized by a sub-Mediterranean climate. According to the data from the Sinop Meteorology Station, annual precipitation is 720.15 mm, with the highest monthly average of 103.91 mm in October and the lowest of 27.22 mm in May. The average annual temperature is 14.96 °C, with the highest recorded mean maximum of 28.1 °C in August and the lowest mean minimum of 5.05 °C in February. A brief dry period occurs between mid-May and mid-August. The region is influenced by dominant north and northwest winds, with an average wind speed of 3.0 m/s.

The coastal dunes in this area exhibit a typical zonation pattern, where foredunes are exposed to high levels of wind and salt stress, while backdunes provide more stable and nutrient-rich conditions. Soils in the foredune are primarily composed of well-drained, coarse sand with low organic matter content, whereas backdune soils contain higher levels of fine sediment and organic material, supporting increased plant diversity. The foredune area hosts a vegetation community composed of psammophyte and halophyte species adapted to sand movement, dominated by typical dune and salt-tolerant plants. In contrast, the backdune area hosts a plant community adapted to transitional and humid habitats, consisting of mesophytic species that contribute to a vegetation structure indicative of more stable dune conditions.

Evaluating the Distribution of CSR Strategies

For the foredune and backdune areas, a total of 20 permanent sample plots were established to assess plant diversity, with ten plots located in the foredune and ten in the backdune. The distance of the plots from the shoreline varies, with

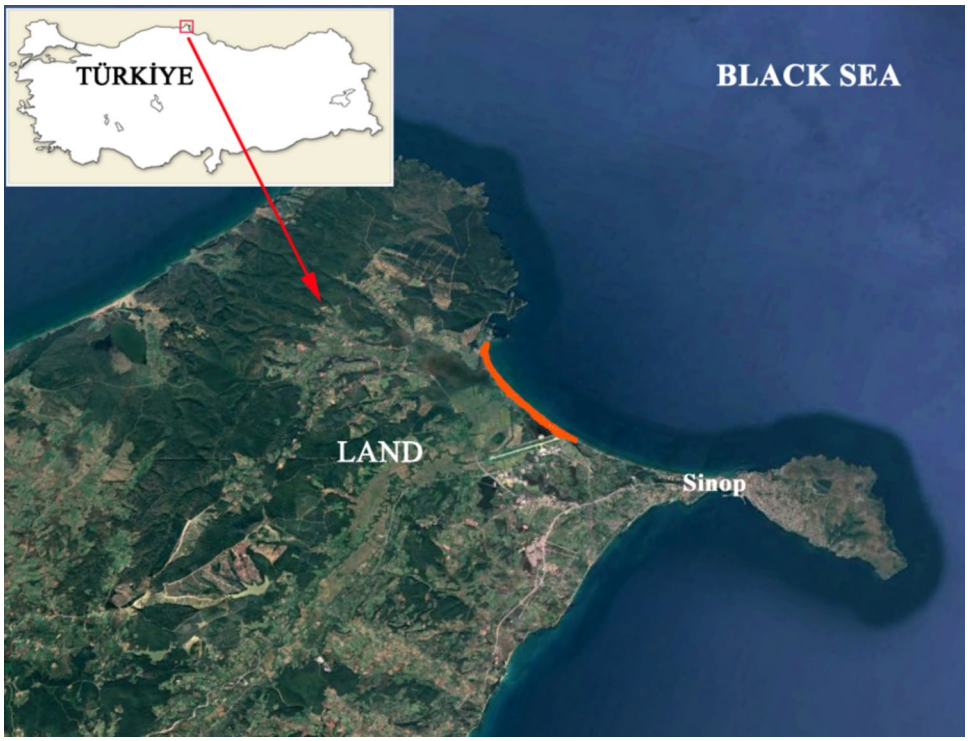

Fig. 1 Map of the study area in Sinop, Türkiye, with the sampling location marked in red. The inset shows the location of the study area within Türkiye

foredune plots positioned approximately 30–70 m from the sea and backdune plots located around 70–100 m inland. The plot size was determined using the minimal area method, resulting in 50-m^2 plots for both sites. The percentage cover of each plant species was recorded monthly over a 2-year period. Plant species were identified according to the "Flora of Turkey and the East Aegean Islands" (Davis, 1965–1985; Davis et al., 1988; Güner et al., 2000), and the taxonomic nomenclature adhered to that of Güner et al. (2012).

In this study, we used the Hodgson et al. (1999) approach for CSR classification, which incorporates seven functional traits (canopy height, leaf dry matter content (LDMC), flowering period, flowering initiation, leaf dry weight, lateral spread, and specific leaf area (SLA)). While Pierce et al. (2017) proposed a simplified approach using only three traits (leaf area (LA), SLA, and LDMC), we opted for the method of Hodgson et al. (1999) as it provides a more comprehensive evaluation of plant strategies in heterogeneous coastal dune environments. The additional traits considered in the Hodgson et al. (1999) approach offer valuable ecological insights, particularly in dynamic landscapes where plant responses to environmental gradients are complex. Given that our study aimed to analyze plant-soil interactions across different dune zones, we determined that a broader trait set would enhance the ecological interpretation of CSR strategies in this system.

For phenological observations, at least ten individuals of each species were marked, and observations were made at 15-day intervals. Canopy height was measured using a measuring tape, and the lateral spread of the plant was visually estimated by measuring the maximum horizontal distance covered by the plant, including stems and vegetative extensions, using a tape measure. To determine leaf traits, at least three mature leaves per plant were collected from three individuals of each species. The collected leaves were wrapped in damp paper and rehydrated overnight at 4 °C (Pérez-Harguindeguy et al., 2013). The fresh leaves were then weighed using a digital analytical balance (Shimadzu AW320) to the nearest 0.0001 g before being pressed. The leaf area was measured using a CI202 Leaf Area Meter (CID Inc., NW Camas, WA, USA). The leaves were dried at 60 °C until they reached a constant weight and then weighed again. The dry matter proportion (%) was calculated by dividing the leaf mean dry weight by the leaf mean fresh weight and multiplying by 100. The specific leaf area (SLA) was calculated by dividing the leaf mean area by the leaf mean dry weight. The CSR strategies of the studied species were determined according to Hodgson et al. (1999). Trait values were entered into a standardized Excel-based tool specifically designed for CSR classification, which calculates species' positions within the CSR triangle based on their functional traits. The tool applies the predefined equations from Hodgson et al. (1999) to assign competitive (*C*), stress-tolerant (*S*), and ruderal (*R*) scores for each species.

Evaluating the Soil Variables

Soil variables influence plant community and ecosystem dynamics by shaping the conditions under which different plant strategy types thrive or struggle. For example, pH affects the nutrient availability, and high or low pH can limit the uptake of essential nutrients, while cation exchange capacity reflects soil's ability to retain and supply positively charged ions. Likewise, organic matter serves as a reservoir of nutrients and supports beneficial microbial activity. To determine the soil properties of the study area, soil samples were collected from the permanent plot areas during November, May, August, and February. The roots of most of the plant species distributed in the dune area extend to a depth of 50–60 cm, while the roots of the species in the backdune are at a depth of 15–20 cm. Therefore, soil sampling was carried out at depths of 50–60 cm for the foredune and 15–20 cm for the backdune, where roots are dense. These samples were air-dried and sifted using a 2-mm sieve before being sent to the laboratory for analysis. The analysis determined soil moisture, organic matter, total nitrogen (N), ammonium (NH_4-N), nitrate (NO_3), phosphorus (P), pH, sodium (Na), potassium (K), calcium (Ca), calcium carbonate ($CaCO_3$), magnesium (Mg), salinity, saturation, and cation exchange capacity (CEC). The methods that were used in soil analysis are summarized in Table S1 (Supplementary materials).

Statistical Analysis

The cover data of the CSR types underwent a transformation into $\log_{10}(x+1)$, and the Bray–Curtis similarity matrix was utilized to determine similarity/dissimilarity. A nonparametric two-way similarity analysis (ANOSIM) was conducted to determine if the differences among the floristic composition of communities were significant using a similarity matrix. The similarity percentage analysis (SIMPER) was employed to demonstrate the contribution of strategy types to differences among communities. SIMPER analysis was used to identify the CSR types that most contribute to similarity/dissimilarity among different communities among sample plots within each dune sector as well as between the foredune and backdune communities. In this analysis, the mean abundance of each CSR type (MA), mean similarity of sampled sites (MS), contribution of each CSR type to community similarity (R), percentage contribution of each CSR type to community similarity (CoP), total contribution of CSR types to similarity (CP), mean differences in abundance between communities (MD), ratio of mean differences to standard deviation (D/SD), the contribution of CSR types to dissimilarity among communities (C), and sum of the contribution of CSR types to dissimilarity (CP) were computed. Thus, the average percentages of similarity/dissimilarity between communities were calculated, and it was revealed which species contributes the most to these differences.

Following the transformation of the data according to $\log(x+1)$, an independent-sample *t*-test was employed to identify differences in soil properties between the foredune and backdune areas across different seasons.

Canonical correspondence analysis (CCA) analysis was performed to analyze the relationship between the distribution of CSR strategy types and environmental data as the gradient length exceeded 3 standard deviations, indicating unimodal species-environment relationships. The analysis was conducted using the Canoco v4.5 package program, incorporating the percentage coverage of each CSR type.

Results

Distribution of CSR Strategies

In the foredune, 34 species were identified, while in the backdune, the count was significantly higher at 171 species. The backdune exhibited 17 distinct CSR strategy types, compared to 13 in the foredune. In the foredune, the most dominant species included *Pancratium maritimum* L., *Eryngium maritimum* L., and *Leymus racemosus* (Lam.) Tzvelev subsp. *sabulosus* (M. Bieb.) Tzvelev, and *Tribulus terrestris* L., which are primarily competitive and stress-tolerant species. These species are well adapted to the harsh foredune environment, where high salinity, wind exposure, and low nutrient availability create significant ecological challenges. Their dominance suggests that both competition and stress tolerance play key roles in species persistence and community structuring in this zone. In contrast, the backdune exhibited higher species diversity, with *Euphorbia helioscopia* L. subsp. *helioscopia*, *Erodium cicutarium* (L.) L'Hér. subsp. *cicutarium*, *Hordeum murinum* L. subsp. *glaucum* (Steud.) Tzvelev, *Trifolium resupinatum* L. var. *resupinatum*, and *Ornithogalum wiedemannii* Boiss. being the most common (Table 1). The backdune environment provides more stable and nutrient-rich conditions, allowing for the establishment of a greater number of ruderal and stress-tolerant species (Fig. 2).

The Bray–Curtis analysis revealed a similarity percentage of 65.38% among the sample plots in the foredune area and 75.93% in the backdune area (Fig. 3). The ANOSIM results indicated that the differences were statistically significant at $p < 0.1\%$ (global *R*, 0.989). The dissimilarity percentage between the foredune and backdune areas was found to be 67.04%. The Bray–Curtis dissimilarity of 67.04% between foredune and backdune areas highlights the high level of heterogeneity in species composition between these dune zones. This variation is likely driven by differences in soil

Table 1 Dominant plant species in the foredune and backdune areas, along with their common names and CSR strategy types

Scientific name	Common name	CSR strategy type
Foredune		
Eryngium maritimum	Sea holly	C/CR
Leymus racemosus subsp. *sabulosus*	Sand ryegrass	SC
Pancratium maritimum	Sea daffodil	C/CR
Salsola tragus subsp. *tragus*	Tumbleweed	R
Tribulus terrestris	Sea spurge	CR
Backdune		
Euphorbia helioscopia subsp. *helioscopia*	Sun spurge	R/CR
Erodium cicutarium subsp. *cicutarium*	Redstem filaree	R/CR
Hordeum murinum subsp. *glaucum*	Wall barley	R/CR
Ornithogalum wiedemtannii	-	R/CR
Trifolium resupinatum var. *resupinatum*	Persian clover	R/CR

Scientific names follow the standard botanical nomenclature, and CSR strategy types are classified according to Grime's framework

properties, disturbance regimes, and environmental stressors, which create distinct ecological conditions supporting different CSR strategy types.

In the foredune area, the C/CR, R, and R/CR strategy types contributed the most to similarity, with contributions of 54.94%, 15.20%, and 10.38%, respectively. In contrast, in the backdune area, the strategy types R/CR, R, and R/SR contributed 26.1%, 14.57%, and 12.29% to similarity, respectively (Table 2). The strategy types that contributed the most to the dissimilarity between the foredune and backdune areas were R/CR, S/SR, R, R/SR, CR/CSR, and C/CR, with contributions of 19.59%, 11.45%, 9.69%, 8.87%, 8.75%, and 7.43%, respectively (Table 3).

Results of Soil Analysis

The mean annual soil moisture were 7.24% in the foredune and 13.67% in the backdune area. The foredune soil was identified as strong alkaline and mild saline loamy, whereas mild alkaline and salt-free clay loamy in the backdune, according to the results (Table 4).

The differences in organic matter and pH between the two areas were statistically significant for all seasons ($p < 0.05$). Ca showed significant differences at $p < 0.05$ in winter, spring, and summer, while $CaCO_3$ differed in winter, summer, and autumn. CEC varied in winter, spring, and autumn; soil moisture in winter and spring; saturation in winter and summer; and salinity in summer; Mg in winter; and P in spring between the foredune and backdune areas. The results indicated that all soil variables, except for P for both areas and $CaCO_3$ for the backdune area, exhibited significant seasonal variations in each area ($p < 0.05$) (Fig. 4).

The Relationships Between CSR Strategy Types and Soil Variables

A CCA was performed to evaluate the relationship between the distribution of CSR strategy types and soil variables. The ordination plot separates the foredune and backdune areas along the environmental gradients, illustrating the distinct soil conditions that define these two areas. The first two axes of the CCA explained 66.6% of the relationships between strategy types and environmental factors (Table 5). The first canonical axis was statistically significant according to the Monte Carlo test ($p < 0.02$, $F = 0.764$). The ordination analysis differentiated the study areas based on TN, P, K, saturation, organic matter, moisture, Ca, $CaCO_3$, Mg, pH, salinity, and CEC (Fig. 5). Strong positive correlations were observed between the C/CR and SC strategy types and pH, salinity, and $CaCO_3$. This suggests that species employing

Fig. 2 Comparison of the foredune (left) and backdune (right) habitats in the study area. The foredune is dominated by *Pancratium maritimum* and other characteristic dune vegetation, while the backdune consists mainly of herbaceous vegetation. Scale bars represent 25 cm, adjusted to perspective

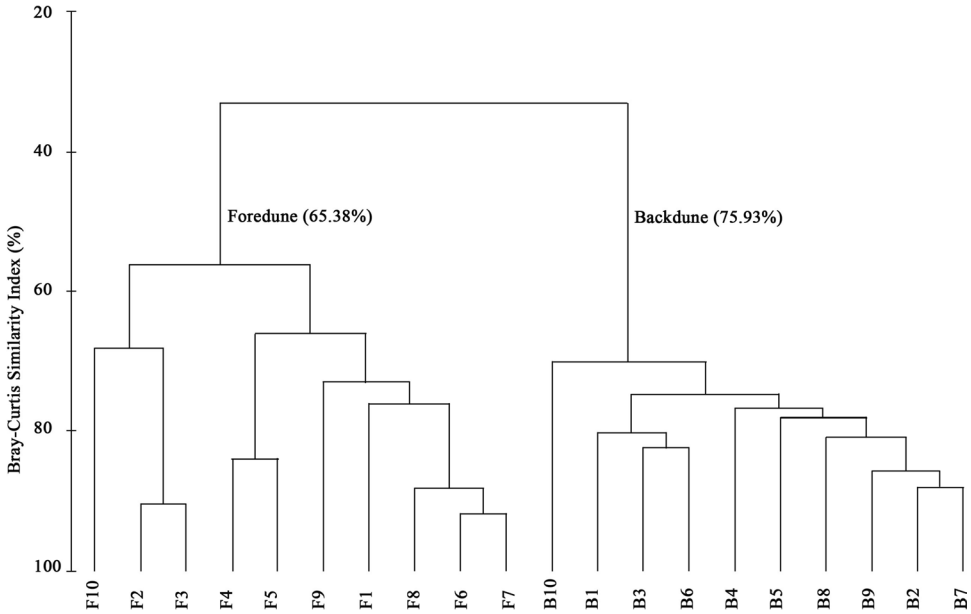

Fig. 3 Dendrogram based on the Bray–Curtis similarity index, illustrating the clustering of sample plots in the foredune and backdune areas according to the cover data of CSR strategy types (F, foredune; B, backdune)

Table 2 CSR strategy types contributing to similarity among sample plots within each study area

Species	*MA*	*MS*	*R*	*CoP*	*CP*
Foredune (average similarity, 65.38%)					
C/CR	25.02	35.92	2.89	54.94	54.94
R	1.21	9.93	3.94	15.20	70.13
R/CR	0.95	6.78	2.52	10.38	80.51
Backdune area (average similarity, 75.93%)					
R/CR	44.21	19.82	5.05	26.10	26.10
R	10.90	11.07	3.88	14.57	40.67
R/SR	5.88	9.33	5.59	12.29	52.96

MA mean abundance, *MS* mean similarity, *R* rate, *C* contribution, *CoP* contribution percentage, *CP* cumulative percentage

a competitor/stress-tolerator strategy thrive in the foredune areas, where these soil conditions are prominent. On the other hand, R/CR, R/CSR, SR/CSR, S/SR, SC/CSR, and CR/CSR strategy types showed strong correlations with TN, P, K, saturation, organic matter, moisture, and CEC. These variables are more abundant in the backdune areas, indicating that ruderal and stress-tolerant species dominate in environments with greater nutrient availability and moisture. Conversely, negative correlations were found between the C/CR strategy type and TN, P, K, saturation, organic matter, moisture, and CEC, as well as between the CR/CSR, R/CSR, SR/CSR, and S/SR strategy types and pH, salinity, and $CaCO_3$ (Fig. 5).

Discussion

The dominance of intermediate rather than primary CSR strategies in our study area likely results from allocation trade-offs throughout life cycle (Mustard et al., 2003), indicating no single evolutionary solution to various environmental conditions (Frenetto-Dussault et al., 2012; Ciccarelli, 2015). CSR strategies were more evenly distributed in the backdune (75.93%) than in the foredune (65.38%), possibly due

Table 3 CSR strategy types contributing to dissimilarity between foredune and backdune areas

Species	*MA*1	*MA*2	*MD*	*D*/*SD*	*C* (%)	*CP*
Group foredune-backdune (average dissimilarity, 67.04%)						
R/CR	0.95	44.21	13.13	3.56	19.59	19.59
S/SR	0.09	7.68	7.68	2.19	11.45	31.04
R	1.21	10.90	6.50	2.63	9.69	40.74
R/SR	0.58	5.88	5.95	3.44	8.87	49.61
CR/CSR	0.00	4.07	5.87	2.31	8.75	58.36
C/CR	25.02	5.78	4.98	1.29	7.43	65.79

MA1 mean abundance in foredune, *MA*2 mean abundance in backdune, *MD* mean differences, *D*/*SD* differences/standard deviation, *C* contribution, *CP* cumulative percentage

Table 4 Classification of soil types for the study areas

Parameter	Foredune		Backdune	
	Class	Value	Class	Value
pH	Strong alkaline	8.68 ± 0.25	Mild alkaline	8.00 ± 0.10
Salinity (%)	Mild saline	0.14 ± 0.09	Salt-free	0.01 ± 0.003
Saturation (%)	Loamy	39.89 ± 2.05	Clay-loamy	47.73 ± 4.47
CEC (meq/100 g)	Rich	7.47 ± 1.80	Rich	42.02 ± 8.20

Values represent means ± standard deviation, with soil classes provided for each parameter in both foredune and backdune areas

to anthropogenic influences or reduced dune mobility (Garcia-Mora et al., 2000). The most significant contributors to foredune-backdune dissimilarity were R/CR, S/SR, R, R/SR, CR/CSR, and C/CR strategies, reflecting differing stress and competition dynamics between these environments. In mobile dunes, plant distribution is often more heterogeneous and follows a random pattern (Conti et al., 2017). Similarly, the foredune in our study showed high spatial variability, likely influenced by the distribution of soil resources and ecological disturbances. However, the presence of competitive primary strategies in at least 25% of the foredune species suggests that disturbance levels, if present, are low. This heterogeneity may also be shaped by factors such as river inflows into the sea and spatial variation in wind and salt spray exposure (Zuo et al., 2009). Stressful environments can either reduce competition by promoting facilitation or intensifying competition (Bertness & Callaway, 1994; Berkowitz et al., 1995; Brunbjerg et al., 2012; Conti et al., 2017). While species in harsh environments generally exhibit lower competition tolerance, leading to competitive exclusion (Hart & Marshall, 2013), the greater abundance of competitive species in the foredune, despite its challenging conditions, aligns with this perspective.

Spatial heterogeneity of soil nutrient pools at different scales is a common characteristic of arid and semi-arid ecosystems (Hook et al., 1991; Schlesinger & Pilmanis, 1998). This heterogeneity plays a crucial role in vegetation dynamics, as variations in soil properties along successional gradients influence vegetation cover, which in turn alters soil characteristics (Olff et al., 1993; Zuo et al., 2009). In our study, OM, moisture, and Ca were higher in the backdune, whereas pH, salinity, CEC, and $CaCO_3$ were more pronounced in the foredune. Although nitrogen is widely recognized as a key limiting factor in plant growth (Willis et al., 1959; Willis, 1963; Kachi & Hirose, 1983; Dougherthy et al., 1990; Olff et al., 1993), no significant difference was found between the two regions. However, OM levels differed significantly, suggesting that the amount of OM alone does not equate to nutrient availability (Lane et al., 2008; Sýkora et al., 2004). This discrepancy may result from rapid nitrogen uptake by plants in the backdune or faster mineralization in the foredune. In their study, Zhu et al. (2021) found that in coarse-textured loamy soils, lower water availability reduces competition among decomposer microorganisms, increasing microbial diversity and accelerating nutrient cycling. Additionally, the presence of lime soil slows decomposition by providing larger surface areas for nutrient adsorption, potentially influencing mineralization rates. Considering that nitrogen-rich environments favor competitive species (Berendse, 1990; Vitousek & Walker, 1987), the higher representation of competitive strategies in the foredune suggests that mineralization in this area provides sufficient nitrogen to sustain competition-driven plant dynamics. However, further research is needed to confirm this process.

Soil pH, closely linked to texture, showed a decreasing trend toward the backdune, where species richness was higher. While some studies suggest a positive relationship between pH and species diversity (Isermann, 2005), others report the opposite trend (Lane et al., 2008). In the present study, the clay-loamy structure of the backdune likely contributed to lower pH due to carbonate and salt leaching, whereas $CaCO_3$ accumulation in the foredune maintained higher pH levels through buffering effect. Consistent with previous findings, OM and acidification emerged as significant drivers of succession (Angiolini et al., 2018; Berendse et al., 1998; Grime, 1973; Lane et al., 2008; Sýkora et al., 2004). Unlike $CaCO_3$, Ca is more abundant in the backdune, where it plays a key role in nutrient uptake and plant establishment. As one of the most important exchangeable cations in growth substrates, calcium directly influences nutrient availability by supporting plant colonization (Pausas & Austin, 2001).

The seasonal and spatial dynamics were observed by Feagin and Wu (2007) on the Gulf of Mexico's coastal dunes. They reported that temporal changes in soil moisture and salinity led to shifts in plant strategy dominance across the dune ecosystem. Similarly, in our study, seasonal fluctuations in soil variables such as moisture, salinity, and organic matter influenced the distribution of CSR strategies, with competitive species remaining dominant in foredunes during drier seasons, while ruderal species thrived in backdune during wetter periods. These findings demonstrate how temporal environmental changes drive plant community dynamics in coastal dune systems worldwide.

Fig. 4 Seasonal variations in variables within the study areas and differences observed within and between communities (A, autumn; W, winter; Sp, spring; S, summer; F, foredune; and B, backdune). Uppercase letters indicate significant differences between foredune and backdune, while lowercase letters represent significant differences between seasons within each community. Different letters denote statistically significant differences ($p < 0.05$)

Table 5 Results of canonical correspondence analysis (CCA) of community variables

Axes	1	2	3	4	Total inertia
Eigenvalues	0.289	0.143	0.061	0.050	0.667
Species-environment correlations	1.000	0.969	1.000	0.986	
Cumulative percentage variance					
Of species data	43.3	64.7	73.8	81.3	
Of species-environment relation	44.6	66.6	76.0	83.6	
Sum of all eigenvalues					0.667
Sum of all canonical eigenvalues					0.648

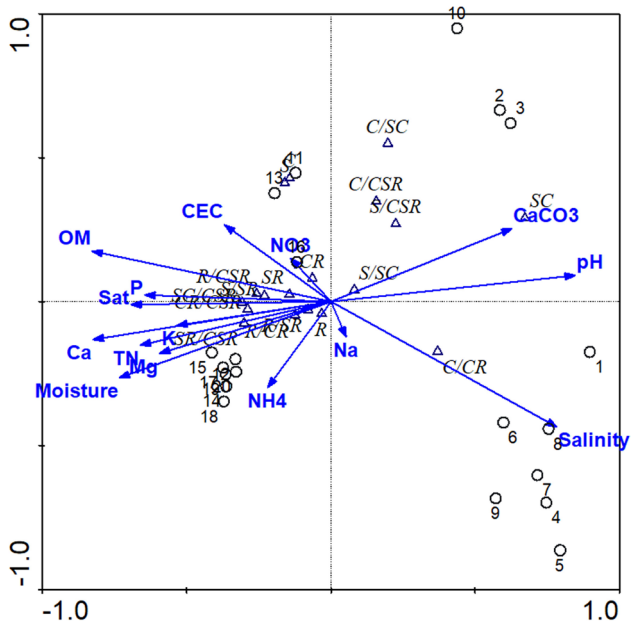

Fig. 5 Canonical correspondence analysis (CCA) ordination plot illustrating the relationships between CSR strategy types and soil variables. Numbered circles represent sample plots (foredune: 1–10; backdune: 11–18), while unnumbered triangles indicate CSR strategy types. The first canonical axis ($p < 0.02$, $F = 0.764$) significantly differentiates foredune and backdune areas along environmental gradients. This analysis highlights that competitor/stress-tolerator species are associated with high pH, salinity, and $CaCO_3$ in foredune areas, while ruderal and stress-tolerant species are linked to higher nutrient availability and moisture in backdune areas

This study provides novel insights into how environmental gradients shape CSR strategy distribution in foredune and backdune areas, emphasizing the role of salinity, moisture, and nutrient availability. Competitive and stress-tolerant species (C/CR and SC strategies) dominated the foredune, correlating with higher salinity, pH, and $CaCO_3$ levels, while ruderal, stress-tolerant, and competitive species (R/CR, R/CSR, SR/CSR, S/SR, SC/CSR, and CR/CSR strategies) were more prevalent in the backdune due to higher nutrient availability, moisture, and organic matter. CCA confirmed that pH, salinity, organic matter, and moisture drive CSR strategy distribution. Seasonal variations in soil properties further impacted species distribution, with ruderal species thriving in wetter backdune, while competitive and stress-tolerant species in foredune adapted to fluctuations in salinity and moisture. Additionally, plant-soil feedback in the backdune increased organic matter, reinforcing the establishment of ruderal and competitive species.

Salinity emerged as a key factor in structuring plant communities in dune ecosystems, acting as a crucial environmental filter in the foredune (Gallego-Fernández & Martinez, 2011). High salinity induces drought stress by increasing osmotic pressure (Maun, 2009), with peak salinity occurring in summer as soil moisture declines at the onset of the growing season. These variables were strongly correlated with the C/CR strategy, consistent with the findings of Son et al. (2020). Greater water loss through evaporation in the foredune, driven by higher temperature and sparse vegetation cover (Álvarez-Rogel et al., 2006; Ishikawa et al., 1995), exacerbates salinity levels. In contrast, salinity and moisture levels remain stable year-round in the backdune, where higher vegetation cover reduces evaporation (Liu et al., 2010; Zheng et al., 2015). This stability is consistent with patterns observed in other ecosystems where moisture gradients influence plant community composition and CSR strategy distributions (Zelnik & Čarni, 2008).

Previous studies in Mediterranean and Denmark dune ecosystems reported that stress-tolerant species dominate foredunes (Brunbjerg et al., 2012; Ciccarelli, 2015), whereas our study found that competitive species are more prevalent despite the high-stress conditions. This discrepancy may stem from regional differences in soil properties or species pools, particularly the relatively high pH and salinity levels in our study area, which may promote the establishment of competitive species (Lee et al., 2020; Son et al., 2020). Additionally, lower sea salt stress in the Black Sea Region may contribute to the prioritization of the C-strategy species. This finding highlights how the balance between stress and disturbance varies in environmental contexts (Petrů et al., 2006). Facilitative effects appear to increase in stressful environments, shifting species interaction from competition to facilitation (Montesinos, 2015). The greater species richness in the backdune supports this idea, suggesting that

facilitation plays a role in structuring plant communities under harsh conditions.

The C/CR strategy, which dominates the foredune, exhibited adaptations such as larger leaf area, high nitrogen uptake efficiency, and plasticity in aboveground-belowground allocation. These species endure harsh conditions like salt spray and repeated soil degradation, forming a distinct dominance hierarchy (Del Vecchio et al., 2021; Mustard et al., 2003). Dominant species not only contribute to dune stabilization but also mitigate the effects of marine stress making the backdune more suitable for plant colonization (Borsje et al., 2011; De Battisti & Griffin, 2020; Ellison et al., 2005; Fantinato et al., 2018). Burial-resistant species with deep root systems further enhance dune stability (Garcia-Mora et al., 1999, 2000). The strong presence of R/CR, R/CSR, SR/CSR, S/SR, SC/CSR, and CR/CSR strategies in the backdune underscores the role of disturbance in shaping plant communities. Ruderals and stress-tolerant species prioritize seed production and maintain high aboveground nitrogen levels by adjusting their subsoil belowground allocation, maximizing reproductive success in these dynamic environments (Mustard et al., 2003).

The findings of this study have important ecological and conservation implications for managing and preserving coastal dune ecosystems. Soil factors such as pH, CEC, organic matter, and salinity play a crucial role in determining the distribution of CSR strategy types, emphasizing the need for conservation strategies tailored to specific dune conditions. For example, the dominance of stress-tolerant species in high-salinity, low-nutrient foredunes suggests that these areas are more vulnerable to environmental disturbances such as climate change and human activities. In contrast, the presence of competitive species in backdunes with higher organic matter and moisture highlights the importance of soil fertility in promoting biodiversity and resilience. Regional differences, such as the role of pH role in limiting or supporting species diversity, further underscore the site-specific conservation strategies. To maintain stability and function, restoration efforts should focus on improving soil conditions that support diverse plant communities. Additionally, these findings contribute to predictive models of how dune ecosystems may respond to future environmental changes, helping to mitigate biodiversity loss and protect ecosystem services such as erosion control and habitat provision.

This study provides valuable insights for the conservation and management of coastal dune ecosystems by uncovering the relationships between plant strategy types and soil characteristics. Given the vulnerability of these ecosystems to climate change, urbanization, and tourism, sustainable management is crucial for maintaining ecological balance. The dominance of competitive and stress-tolerant species in the foredune underscores the need to minimize human disturbance in these fragile environments to support ecosystem stability. In contrast, the prevalence of ruderal and stress-tolerant species in the backdune suggests that maintaining nutrient-rich, moist soil conditions can enhance plant diversity through plant-soil feedback mechanisms. Therefore, protection strategies should focus on preserving natural plant cover in the foredune while supporting soil processes that sustain biodiversity in the backdune. The findings provide a scientific basis for conservation efforts aimed at ensuring the long-term resilience of coastal dune ecosystems and their critical services, including erosion control, habitat protection, and carbon storage.

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Data Availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of Interest The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Emire Elmas reports financial support was provided by the Scientific and Technological Research Council of Türkiye. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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