Turkish Journal of Botany

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Research Article

Turk J Bot
(2022) 46: 346-360
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doi:10.55730/1300-008X.2714

Ellenberg ecological indicator values, tolerance values, species niche models for soil nutrient availability, salinity, and pH in coastal dune vegetation along a landward gradient (Euxine, Turkey)

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Received: 30.01.2022 • **Accepted/Published Online:** 04.07.2022 • **Final Version:** 29.07.2022

Abstract: Coastal dunes are characterised by plant species adapted to harsh conditions. Salinity and other factors (soil pH, nutrients, and climate events) vary along the landward gradient. The current study investigated the effects of environmental factors on the occurrence and composition of coastal dune plants. Ellenberg ecological indicator values (EIVs), species tolerance values (TVs), and species niche models for salinity, nutrient availability, and soil reaction were determined. EIVs were estimated using weighted averages based on the species cover-abundance for each plot. Species TVs were calculated considering the cover-abundance and EIVs (pH, nutrient, and salinity). Species niche models were determined with the general linear model (GLM). GLM was computed using mean community EIVs, canopy height, and climatic variables. We found that salinity (S) and pH (R) EIVs decreased along the seaside-inland gradient while nitrogen (N) EIVs increased. TVs for S increased landward while S and R TVs decreased. According to GLM, niche models of 28 species for salinity, 25 species for pH, and 21 species for nutrient were significant. In summary, salinity and pH are the main drivers shaping coastal dune zonation and plant community.

Key words: Dune plants, dune zones, habitat suitability, Mediterranean-type climate, oceanic climate

1. Introduction

Coastal dunes are unique ecosystems (Kennish, 2001; Spanou et al., 2006), and they have high plant biodiversity (Stancheva et al., 2011; Cakan et al., 2011). They are characterised by a specialized flora (Acosta et al., 2005, 2009; Carranza et al., 2008) and comprise different habitat types in relation to environmental heterogeneity (Everard et al., 2010; Tomaselli et al., 2011; Jimenez-Alfaro et al., 2015). Seventeen habitat types have been distinguished in European dune ecosystems (Carranza et al., 2008; Marcenò et al., 2018). In the current study, seven habitat types were determined (EU Habitat 1210, 2110, 2120, 2130, 2160, 2210, and 2230). Coastal dune ecosystems have large nature conservation value and include rare species (Jones et al., 2011; Malpas et al., 2013). These species offer important ecosystem services, such as stabilizing substrates (Beaumont et al., 2014). Additionally, coastal dunes are among the most important natural environments (Martìnez and Psuty, 2004), and they exhibit some of the most endangered and/or vulnerable taxa worldwide (Defeo et al., 2009; Van der Biest et al., 2020) due to natural and anthropogenic disturbance (Malavasi et al., 2014) as well as alien plant invasions (Giulio et al., 2020; Guarino et al., 2021). Therefore, these ecosystems are the most threatened ecosystems (EEA, 2008; Nordhaus et al., 2018).

Coastal dune ecosystems are stressful habitats due to the negative effects of abiotic and biotic factors (Ağır et al., 2019). Geology, climate, vegetation, and sea-level change make coastal dunes a dynamic ecosystem (Miller et al., 2010; Miller, 2015). Sand burial (Maun, 2009), nutrient limitations (Ruocco et al., 2014), substrate instability (Isermann, 2011), and salt spray (Lane et al., 2008) affect the coastal dune along the seashore-inland gradient. As a result, the typical dune zonation includes five vegetation types: drift line, embryonic and main (foredunes), and transitional and fixed (grassland dunes).

Climate (Ihm et al., 2001), hydrology (Bruelheide, 2003), and salinity (Kreyling et al., 2008) may also be important drivers of plant distribution and vegetation composition in coastal ecosystems (Wang et al., 2013). Previous studies show that annual precipitation and temperature regimes are important climatic variables (Brunetti et al., 2006) along with the rapid population growth (Diffenbaugh et al., 2008) and urbanization

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changes (Carrete et al., 2009). Also, the direct ecological effects (temperature and precipitation) of global change on coastal dunes can influence the seasonality of the vegetation (Sobrino Vesperinas et al., 2001; UNEP, 2010; Provoost et al., 2011).

Changes in salinity cause significant changes in the vegetation composition along the landward gradient (Del Vecchio et al., 2016). However, the distribution of dune plants may also be affected by nutrient availability and physicochemical parameters (Wagner et al., 2007). High water levels also control nutrient status, reduce organic matter mineralization and maintain low phosphorus and nitrogen concentrations (Lambers et al., 2008). In grassland dunes (transitional and fixed), the buffering effect of groundwater rich in carbonates ensures the survival of basophilic wetland plants (Sival et al., 1996).

Ellenberg ecological indicators values (EIVs) are the most frequently used bioindication tool in Europe. They are widely used to predict the responses of plants to environmental changes (Prach, 1993; Pignatti et al., 2001; McGovern et al., 2011; Newton et al., 2012; Wesche et al., 2012; Häring et al., 2014; Krause et al., 2015). EIVs characterise plant species on an ordinal scale, reflecting the realized suitable niche for nutrient (N), moisture (F), light (L), temperature (T), reaction/pH (R), salt (S), and continentality (K) (Ellenberg, 1988; Hill et al., 2004). Coastal ecosystems have a high plant biodiversity due to the heterogeneity of habitat niches; therefore, EIVs of the species are very different.

Ellenberg's indicator values (EIVs) have been used to estimate the value of a particular environmental factor at a particular site by averaging the indicator values for this factor across all species in the vegetation (ter Braak and Gremmen, 1987; Sürmen et al., 2014; Marcenò and Guarino 2015). The relative impacts of the different environmental factors affect the distribution of coastal dune plants, and the interaction between environmental factors is important to predict the responses of coastal dune plants to environmental changes (Pignatti, 2005; Jantsch et al., 2013). It may be a useful tool for assessing and evaluating land use and vegetation changes (Szymura et al., 2014; Breg Valjavec et al., 2017; Breg Valjavec et al., 2018).

Plant ecological niches provide the basis for the use of bioindication with EIVs. The species composition of a particular community enables the characterisation of various types of environmental factors: grasslands (Schaffers and Sýkora, 2000; Chytrý et al., 2009), forest (Szymura et al., 2014), mires (Navrátilová et al., 2017) or coastal dunes (Jones et al., 2004). Plants' niches in natural communities represent their physiological growth limits, and ecological indicators describe plant niches (Landolt et al., 2010). Smart et al. (2010) improved plant niche models using EIVs and climatic factors. In these models, EIVs corresponding to fertility, moisture, and pH were used as predictor variables in GLM in combination with climatic variables (annual precipitation, maximum and minimum temperatures) and canopy height.

The current study describes the ecological differentiation of plant species along the landward gradient by using EIVs, tolerance values (TVs), and GLM models for salinity, nutrient availability, and soil pH.

2. Materials and methods

2.1. The study area

Coastal dune vegetation was studied in the Central Black Sea Region (Euxine) of Turkey (Figure 1). The deltas of Yeşilırmak and Kızılırmak rivers enclose the eastern and the western part of the study area. The length of the studied coastal dunes is approximately 160 km from Yakakent (41°63′18.99″N, 35°55′40.72″E) to Terme (41°14′79.28″N, 37°15′75.39″E) districts. The coastal areas include five different dune zones [drift line (A), embryonic (B), main (C), transitional (D), and fixed (E)]. The width of the dune zones in the studied areas varies between 170 and 1.110 m along the seashore-inland gradient.

The study areas have different climatic features. Those in the western part experience a Mediterranean-type climate, with 672 mm annual rainfall and 15.1 °C mean annual temperature, and remarkable drought. The eastern part experience an oceanic climate, with 922 mm mean annual rainfall and 13.5 °C mean annual temperature, without a pronounced drought during the summer months.

2.2. Vegetation sampling and data analysis

The study was carried out in 7 different regions and aimed to obtain at least 10 square vegetation plots for each zone in each area (Figure 1). A total of 320 square vegetation plots were used in this study. Vegetation plots were taken along seashore-inland gradient, included all dune zones (drift line, embryonic, main, transitional, and fixed dunes) in the study area. Plot size (2 × 2 m) was determined by the minimal area method (Braun-Blanquet, 1964). The vegetation composition of each plot was sampled by using the Braun–Blanquet method from April to September 2014–2016 (Mueller Dombois and Ellenberg, 1974). EU Habitat types, plant associations, and characteristics of the studied area are listed in Table 1 based on previous studies (Ağır et al., 2014; Ağır et al., 2016).

Sand samples were collected from each plot at 0–20 cm depth. The sand samples were air-dried and sieved through a 2-mm screen. pH was measured in sand:water extracts at 1:2.5 (w:v) with a Beckman pH meter. Electrical conductivity (dSm^{-1}), an aqueous extract was obtained through an orbital shaker at 120–140 cycles/min and was determined using a Jenway analyzer. Sand nitrogen content (%) was determined by the micro Kjeldahl method (Kaçar, 2012).

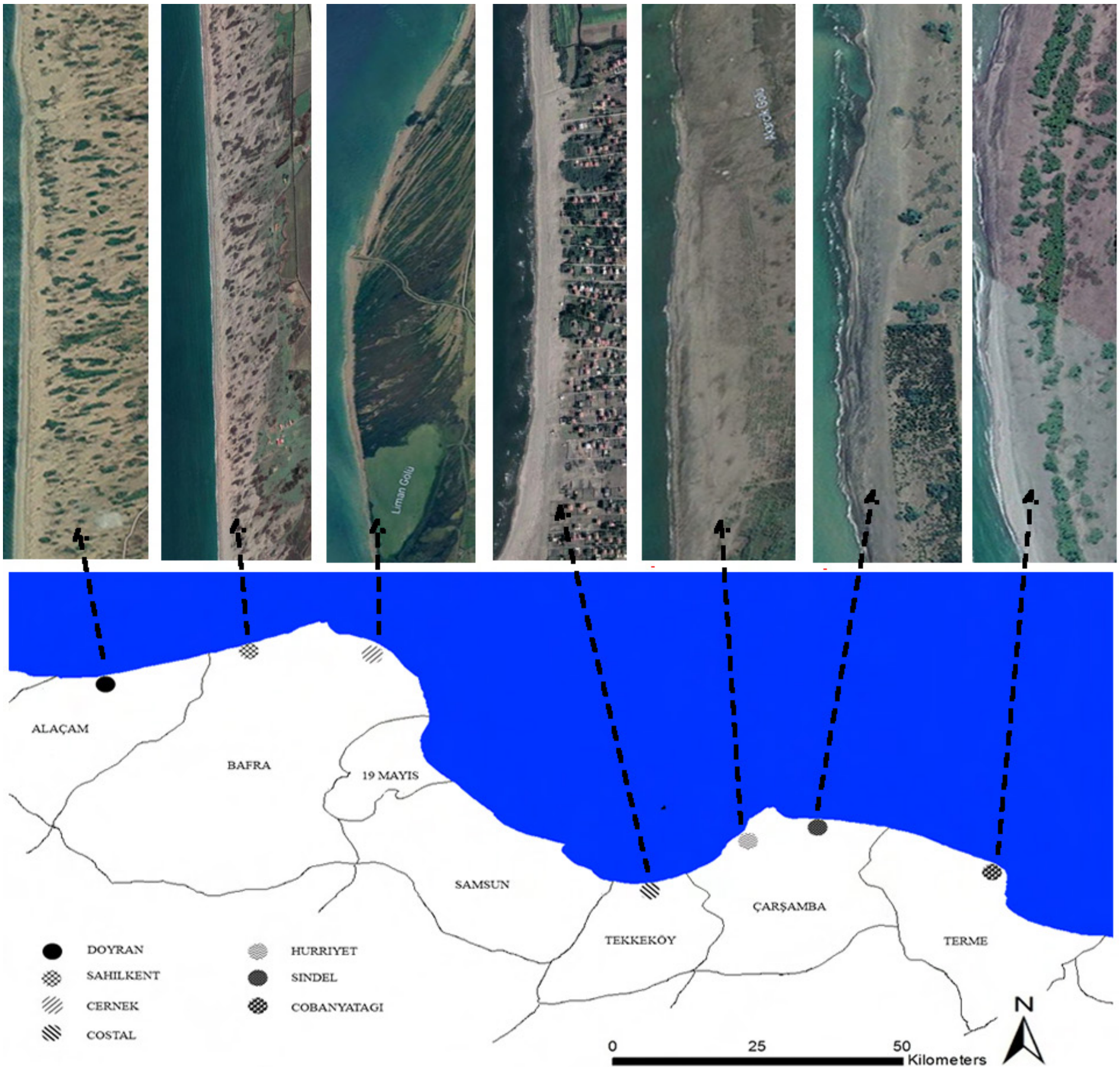

Figure 1. Coastal dune vegetation of Central Black Sea Region of Turkey was studied (Google Earth, 2021).

Ellenberg's indicator values of plant species are obtained from ecological observations in the field and measurable environmental factors of their habitats. The specific environmental factors of the areas where the species is distributed are measured, and the optimum environmental factor value preferred by the species is calculated. An indicator number is assigned according to the scale proposed by Ellenberg using the calculated value (Ellenberg, 1991; 1992). In this study, each species's optimum environmental factor value for ecological factors (soil pH, soil nitrogen, and soil salinity) was calculated by weighted averages of environmental factors measured and species cover-abundance value (Obidziński, 2004; Kasprowicz, 2010). Then, the EIV was assigned by considering the place of the calculated value in the scale suggested by Ellenberg.

$$\text{Weighted average} = \sum_{i=1}^{n} (\text{rij} \times \text{xi}) \Big/ \sum_{i=1}^{n} rij$$

"rij" is the response of the species i in sample plot j, "xi" is the indicator value of species i on the formula.

Sand pH, nitrogen content, and salinity tolerance (Tv) values of species were calculated using the following formula.

$$\text{Tv} = \left(\sum_{i=1}^{n} \text{Yik}(\text{pHi} - \text{Rk})^2 \Big/ \sum_{k=1}^{n} \text{Yik} \right)^{1/2}$$

Variable "Y" is the species abundance and "R" is the species indicator value. Parameter "i" stands for relevés (i = 1,. . ., n) and "k" for plant taxa (k = 1,. . ., p) (Balkovič et al., 2012).

Table 1. Main properties of studied coastal dune zones.

Association number	Plant associations	Dune zones	Habitat types	Characteristic species
As. 1	*Salsolo ruthenicae – Cakiletum maritimae*	Drift line (A)	EU Habitat 1210	*Salsola ruthenica, Cakile maritima, Tournefortia sibirica* var. *sibirica, Xanthium strumarium* subsp. *cavanillesii, Calystegia soldanella*
As. 2	*Euphorbio paralias – Eryngietum maritimi*			*Eryngium maritimum, Euphorbia paralias, Digitaria ischaemum, Parapholis incurva, Apocynum venetum*
As. 3	*Achilleo maritime – Elymetum farcti*	Embryonic (B)	EU Habitat 2110	*Agrostis stolonifera, Crepis foetida* subsp. *rhoeadifolia, Elymus farctus* subsp. *bessarabicus* var. *bessarabicus, Glaucium flavum, Juncus littoralis, Achillea maritima* subsp. *maritima Raphanus raphanistrum*
As. 4	*Medicagini marinae – Ammophiletum arundinace*		EU Habitat 2120	*Ammophila arenaria* subsp. *arundinacea, Cynanchum acutum* subsp. *acutum, Cynoglossum creticum, Gundelia tournefortii, Hypochoeris radicata, Medicago marina, Medicago polymorpha* var. *polymorpha, Pancratium maritimum, Schoenoplectus triqueter, Scolymus hispanicus, Stachys annua* subsp. *annua* var. *annua*
As. 5	*Sileno otitis – Vulpietum fasciculatae*	Main (C)	EU Habitat 2130	*Cenchrus incertus, Centaurea iberica, Cionura erecta, Cyperus capitatus, Echinops orientalis, Euphorbia peplis, Silene otites, Vulpia fasciculata, Xanthium spinosum*
As. 6	*Verbasco thapsus – Eleagnetum rhamnoidi*	Transitional (D)	EU Habitat 2160	*Crataegus monogyna* var. *azarella, Eleagnus rhamnoides, Imperata cylindrica, Medicago x varia, Petrorhagia saxifraga, Phleum exaratum* subsp. *exaratum, Teucrium chamaedrys* subsp. *chamaedrys, Trifolium stellatum, Verbascum sinuatum* var. *sinuatum*
As. 7	*Sophoro alopecurioides – Elymetum elongati*	Fixed (E)	EU Habitat 2210	*Anagallis arvensis* var. *arvensis, Daucus broteri, Elymus elongatus* subsp. *elongatus, Medicago littoralis* var. *littoralis, Plantago scabra, Polypogon monspeliensis, Silene dichotoma* var. *dichotoma, Sophora alopecuroides* var. *alopecuroides*
As. 8	*Euphorbio terracinae – Laguretum ovati*		EU Habitat 2230	*Anchusa hybrida, Cota tinctoria* var. *tinctoria, Bromus racemosus, Echium plantagineum, Euphorbia terracina, Jurinea kilaea, Kickxia commutata* subsp. *commutata, Lagurus ovatus, Prunella vulgaris, Satureja hortensis, Teucrium polium, Trifolium arvense* var. *arvense, Trifolium resupinatum* var. *resupinatum*

Niche models of each species were calculated using binary logistic generalized linear models (GLMs). GLMs were performed using seven explanatory variables (EIVs, climate variables, and cover-weighted canopy height). We estimated relationships between each species and seven explanatory variables using the GLM niche model proposed by Jarvis et al. (2016). GLM models were developed to show the relationships between environmental variables and species niches and if species niches change along the landward gradient.

Statistical analyses were done by SPSS v. 22 (SPSS Inc., 2012) and R v.3.0.2 statistical software (R Foundation for Statistical Computing, 2013). Firstly, distributions of EIVs were represented for each dune zones using the box-plot graphical method. One-way ANOVA investigated the differences in tolerance values among dune zones. Secondly, the GLM niche model was computed in R programme (v.3.0.2).

3. Results

Four main groups were determined statistically along the landward gradient according to N weighted average values (Figure 2). The first group is EU Habitat 2230 (As. 8 *Euphorbio terracinae – Laguretum ovati*). N weighted average values of EU Habitat 2230 varied from 0.091% to 0.100%. EU Habitat 2160 (As. 6 *Verbasco thapsus – Eleagnetum rhamnoidi*) in transitional dune zone and EU Habitat 2210 (As. 7 *Sophoro alopecurioides – Elymetum* *elongati*) in fixed dune zone are the second group. N weighted average values of the EU Habitat 2210 varied from 0.050% to 0.060%, and the EU Habitat 2160 varied from 0.044% to 0.057%. The third group consists of three EU habitats (2210, 2120, and 2130). N weighted average values of the EU Habitat 2130 (As. 5 *Sileno otitis – Vulpietum fasciculatae*) varied from 0.021% to 0.037%. The EU Habitat 2120 (As. 4 *Medicagini marinae – Ammophiletum arundinace*) varied from 0.016% to 0.030 %, and the EU Habitat 2110 (As. 3 *Achilleo maritimo – Elymetum farcti*) varied from 0.020% to 0.030%. The last group consists of two plant associations (As.1 *Salsolo ruthenicae – Cakiletum maritimae* and As. 2 *Euphorbio paralias – Eryngietum maritimi*) belonging to the EU Habitat 1210. N weighted average values of the last group varied from 0.007% to 0.016%.

Four main groups were determined statistically along the landward gradient according to pH weighted average values (Figure 3). The first group is the drift line zone. This zone hosts of two plant associations (As. 1 and As. 2) belonging to the EU Habitat 1210. The pH weighted average values varied from 9.43 to 9.80. The second group is EU Habitat 2110 (As. 3) in the embryonic dune zone. pH weighted average values of this group varied from 8.15 to 9.15. The EU Habitat 2120 (As. 4) in embryonic, the EU Habitat 2130 (As. 5) in the main dune, and the EU Habitat

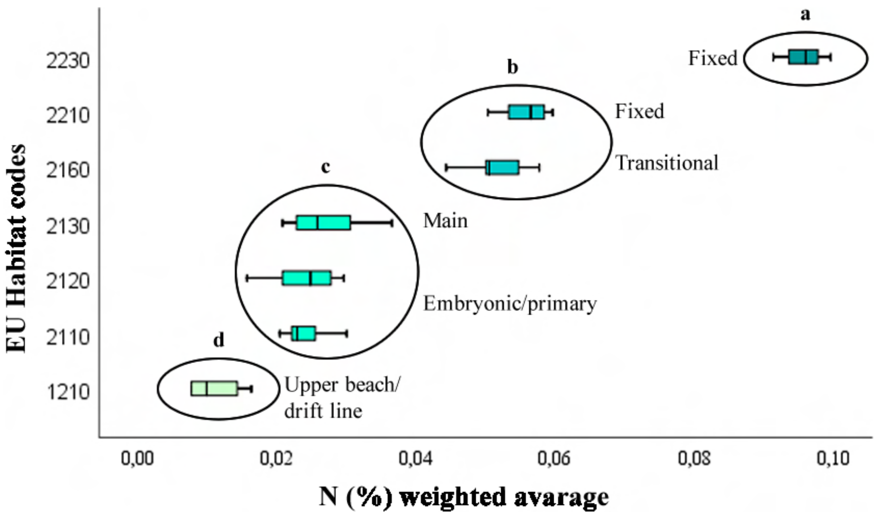

Figure 2. Distribution of N weighted average values along the sea-inland gradient according to coastal dune zones and EU Habitat code (Different lower cases show statistically significant differences, $p < 0.05$).

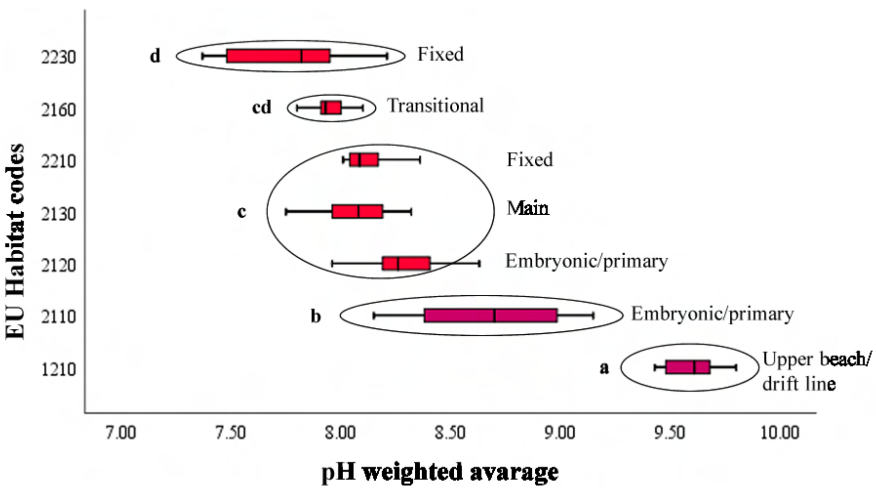

Figure 3. Distribution of R weighted average values along the sea-inland gradient according to coastal dune zones and EU Habitat code (Different lower cases show statistically significant differences, $p < 0.05$).

2210 (As. 7) in fixed dune zones form the third group. pH weighted average values of the third group ranged from 7.75 to 8.63. The last group is the EU Habitat 2230 (As. 8). pH weighted average values of the last group ranged from 7.37 to 8.21. The EU Habitat 2160 (As. 6) did not form a separate group in the transitional dune.

Four main groups were determined statistically along the landward gradient according to the EC (Electrical conductivity) weighted average values (Figure 4.). The first group consists of three plant associations (As. 1, As. 2 in EU Habitat 1210, and As. 3 in EU Habitat 2110). EC weighted average values of species drift line zone varied from 14.29 to 17.38 dSm^{-1}. EC weighted average values of EU Habitat 1210 in the first group varied 15.23–16.05 dSm^{-1}. EU Habitat 2120 (As. 4) in the embryonic dune zone is the second group, and EC weighted average values varied from 11.35 to 13.75. Main and transitional dune zones form the third group. EC weighted average values varied from 8.15 to 9.03 in the main dune and 7.29 to 8.19 in transitional dune zones. The last group consists of fixed dune zone. EC weighted average values of EU Habitat 2210 varied from 5.02 to 5.83. Values of EU Habitat 2210 varied from 4.30 to 5.95.

As far as EIVs are concerned, there are four different values (1, 2, 3, and 4) for N, three different values (7, 8, and 9) for R, and five different values (4, 5, 6, 7, and 8) for S were determined (Table 2). In the drift line dune zone, N was determined as 1 and R as 9. However, As. 1 had R = 8, and As. 2 had R = 7. Species of embryonic dune zone had N = 2. As for R, As. 3 had 8, and As. 4 had 9. As for S, As. 3 had 7, and As. 4 had 6. N, R, and S EIVs of species in the main dune zone were 2, 8, and 5, respectively. EIVs of species in the transitional dune zone were determined as 3 for N, as 8 for R, and 5 for S. In the fixed dune zone, S was determined as 4 for all habitat and plant association, whereas N and R were 3 and 8 for As. 7 and, 4 and 7 for As. 8, respectively (Table 3).

We found significant statistical differences among coastal dunes according to species tolerance values for nitrogen content (N) and salinity (S) between dune zones, While species tolerance values for sand pH (R) were not significant (Table 4). The highest sand salinity and pH tolerance values were found in the drift line dune. The lowest sand pH (R) and soil salinity (S) tolerance values were found in the main dune zone. Fixed dune species had the highest tolerance values for sand nitrogen concentration, while the lowest tolerance values were found in the drift line dune zone (Figure 5).

According to GLM, niche models of 28 species for sand salinity, 25 species for sand pH and 21 species for sand nutrient were found to be significant. *Parapholis incurva* and *Apocynum venetum* showed significant tolerance for all ecological indicators in the drift line dune zone. In the embryonic dune zone, only one species (*Cynoglossum creticum*) showed significant tolerance for all ecological indicators. There were significant niche models of six species for salinity, four species for pH, and five species for nutrients in the main dune zone, respectively. *Crataegus monogyna* var. *azarella*, *Eleagnus rhamnoides*, and *Trifolium stellatum* showed significant tolerance for all ecological indicators in the transitional dune zone. In the fixed dune zone, niche models of 8 species for salinity, ten species for pH, and seven species for nutrient were found to be significant (Table 5).

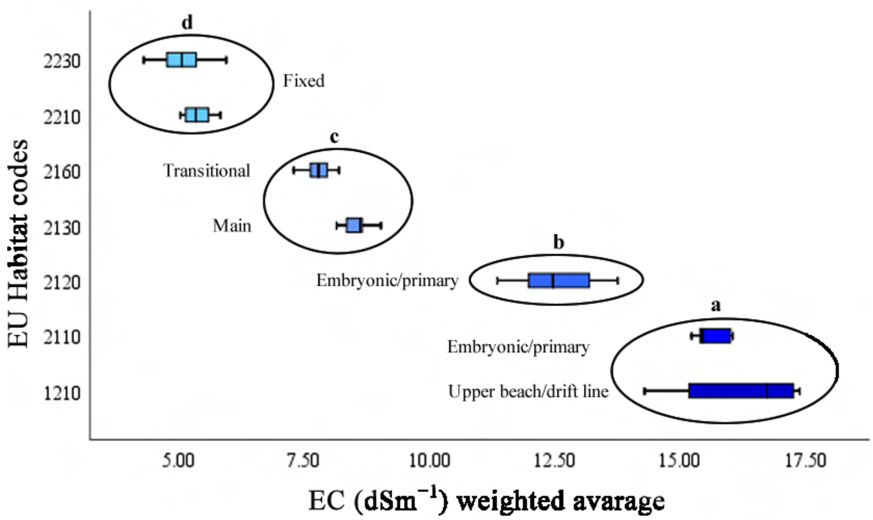

Figure 4. Distribution of S weighted average values along the sea-inland gradient according to coastal dune zones and EU Habitat codes (Different lower cases show statistically significant differences, $p < 0.05$).

Table 2. Calculated Ellenberg ecological indicator values in this study.

N EIVs		**R EIVs**		**S EIVs**	
1	Indicator of extremely infertile sites	**9**	Indicator of basic reaction, always found on calcareous or other high-pH soils	**8**	Species more or less permanently inundated in sea water
2	Between extremely infertile and more/less infertile sites	**8**	Between 7 and 9	**7**	Species of lower saltmarsh
3	Indicator of more or less infertile sites	**7**	Indicator of weakly acid to weakly basic conditions; never found on very acid soils	**6**	Species of midlevel saltmarsh
4	Between more/less infertile and intermediate fertility sites	-		**5**	Species of the upper edge of saltmarsh
-		-		**4**	Species of salt meadows and upper saltmarsh

Table 3. Ellenberg ecological indicator values of coastal dune vegetation.

Association number	**Plant associations**	**Dune zones**	**Habitat types**	**N EIVs**	**R EIVs**	**S EIVs**
As. 1	*Salsolo ruthenicae – Cakiletum maritimae*	Drift line (A)	EU Habitat 1210	1	9	8
As. 2	*Euphorbio paralias – Eryngietum maritimi*			1	9	7
As. 3	*Achilleo maritimo – Elymetum farcti*	Embryonic (B)	EU Habitat 2110	2	8	7
As. 4	*Medicagini marinae – Ammophiletum arundinace*		EU Habitat 2120	2	9	6
As. 5	*Sileno otitis – Vulpietum fasciculatae*	Main (C)	EU Habitat 2130	2	8	5
As. 6	*Verbasco thapsus – Eleagnetum rhamnoidi*	Transitional (D)	EU Habitat 2160	3	8	5
As. 7	*Sophoro alopecurioides – Elymetum elongati*	Fixed (E)	EU Habitat 2210	3	8	4
As. 8	*Euphorbio terracinae – Laguretum ovati*		EU Habitat 2230	4	7	4

Table 4. Statistically significant differences in tolerance values (Ntv, Rtv, Stv) among the dune zones using one-way ANOVA.

ANOVA						
		Sum of squares	df	Mean square	F	Sig.
Ntv	Between Groups	54.473	4	13.618	171.060	0.000*
	Within groups	4.856	61	0.080		
	Total	59.329	65			
Rtv	Between Groups	1.001	4	0.250	1.452	0.228ns
	Within groups	10.513	61	0.172		
	Total	11.514	65			
Stv	Between Groups	19.293	4	4.823	4.050	0.006*
	Within groups	72.651	61	1.191		
	Total	91.943	65			

* $p < 0.01$, ns: nonsignificant.

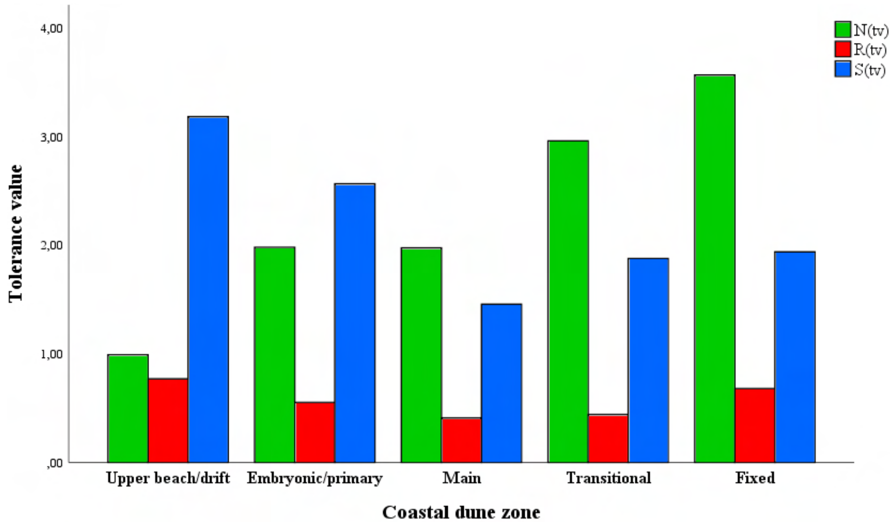

Figure 5. The changes in tolerance values for sand pH (R), nitrogen content (N), and salinity (S) in coastal dune zones of the study area.

4. Discussion

4.1. Ellenberg's ecological indicators

It has been found that EIVs (N, R, and S) differed along the landward gradient. In this study, we revealed ecological differentiation considering dune zones and EU habitat types because EIVs portrayed well the 'preferences' of a particular plant species for a specific soil pH, soil salinity, and soil nutrient concentrations (Del Vecchio et al., 2016).

EIVs for soil nutrients varied from 1 to 4 along the landward gradient. Especially, foredunes (drift line, embryonic and main dunes) and grassland had different ecological values. Soil fertility was intermediate in fixed and transitional dunes, while soil fertility in embryonic and main dunes was found to be low. These results are similar to the EIVs for Mediterranean fore and grassland dunes. Mediterranean dunes reported similar results (Feola et al., 2011). Previous studies (Schaffers and Sykora, 2000; Feola et al., 2011) showed that EIVs for soil nitrogen might be used properly as a suitable predictor of coastal dune zonation. Additionally, nutrient EIVs indicate that low availability of soil organic matter concentrations in earlier succession phases. The habitat EU 2160 (*Verbasco Thapsus – Eleagnetum rhamnoidi*) instead, represents the climax phase (Tzonev et al., 2005). Grassland dune habitats (EU 2160, EU 2210, EU 2230) are characterised by a more coherent and compacted substrate (Ağır et al., 2014). Foredune habitats (EU 1210, EU 2110, EU 2120, and EU 2130) are characterised by unstable substrate and wave effects. Harsh conditions, especially unstable substrate and wave effects, cause infertility. Organic matter decomposition is slower in foredunes (Ağır et al., 2019).

Soil reaction (R) decreased along the landward gradient (Ağır et al., 2019; Forey et al., 2008; Isermann, 2011), with an evident correlation to the calculated R value. On the contrary, according to previous studies, organic matter concentration gradually increased from the seaside to inland (Wilson and Sykes, 1999; Sykora et al., 2004; Emilio et al., 2006). Sand pH decrease from seaside to inland gradient due to the decline of the deposition of the marine aerosol (Maun, 2009) and the consequent release of organic acids by the vegetation (Ruocco et al., 2014). Black dunes are progressively less exposed to severe environmental constraints (Ciccarelli, 2015). Low pH in dune zones might be attributed to the deposited sediments and low organic matter content in the seaside (Pan et al., 2016), and soil pH plays the principal role in driving plant species composition on coastal dune vegetation (Angiolini et al., 2018).

The present study showed that habitat types and vegetation composition changed with the distance from the seashore and soil salinity (Ihm et al., 2001; Bruelheide, 2003; Kreyling et al., 2008; Wang et al., 2013; Jarvis et al., 2016). Salinity is affected by various factors, such as vegetation type, weather condition, soil features and anthropogenic factors, etc. (Silvestri et al., 2005; Tho et al., 2008; Chen et al., 2013). Considering the climatic and soil features, the effect of salinity is decreased during the rainy season and exposure to alluvial currents in the main dune and grassland dune zones. In coastal dune systems, tidal flooding or saline intrusion from seawater and salt spray can lead to increased salinity in coastal dunes (Dwyer et al. 2021). While species belonging to Euphorbio *Euphorbio paralias – Eryngietum maritimi* and *Salsolo ruthenicae – Cakiletum maritimae* (EU 2120) adapted to harsh conditions in drift line, regularly inundated by seawater and intense aerosol deposition. However, species

Table 5. Relationships between each species and seven explanatory variables using GLM niche model.

Habitat types	Species	Zone	S EIV	R EIV	N EIV
EU 1210	*Cakile maritima* Scop.	A	ns	ns	ns
EU 1210	*Calystegia soldanella* (L.) R.Br.	A	*	ns	ns
EU 1210	*Digitaria ischaemum* (Schreber ex Schweigger) Mühlenb.	A	***	ns	ns
EU 1210	*Eryngium maritimum* L.	A	***	ns	ns
EU 1210	*Euphorbia paralias* L.	A	ns	**	ns
EU 1210	*Parapholis incurva* (L.) C.E. Hubbard	A	**	*	*
EU 1210	*Polypogon monspeliensis* L. (Desf.)	A	ns	ns	ns
EU 1210	*Salsola ruthenica* L.	A	*	ns	ns
EU 1210	*Apocynum venetum* L.	A	***	***	***
EU 1210	*Xanthium strumarium* subsp. *cavanillesii* (Schouw) D.Löve & Dans.	A	ns	ns	***
EU 1210	*Tournefortia sibirica* L.var. *sibirica*	A	ns	ns	*
EU 2110	*Achillea maritima* (L.) Ehrend. & Y.P.Guo subsp. *maritima*	B	**	ns	ns
EU 2110	*Agrostis stolonifera* L.	B	ns	*	*
EU 2110	*Crepis foetida* L. subsp. *rhoeadifolia* (M.Bieb.) Čelak.	B	ns	*	ns
EU 2110	*Elymus farctus* (Viv.) Runemark ex Melderis subsp. *bessarabicus* (Savul. et Rayss) Melderis var. *bessarabicus*	B	ns	ns	ns
EU 2110	*Glaucium flavum* Crantz	B	ns	ns	ns
EU 2110	*Juncus littoralis* C. A. Meyer	B	ns	*	***
EU 2110	*Raphanus raphanistrum* L.	B	ns	ns	ns
EU 2120	*Ammophila arenaria* (L.) Link subsp. *arundinacea* H. Lindb. Fil.	B	ns	ns	ns
EU 2120	*Cynanchum acutum* L. subsp. *acutum* L.	B	***	**	ns
EU 2120	*Cynoglossum creticum* Mill.	B	***	***	***
EU 2120	*Gundelia tournefortii* L.	B	ns	ns	ns
EU 2120	*Hypochoeris radicata* L.	B	*	ns	ns
EU 2120	*Medicago marina* L.	B	ns	ns	ns
EU 2120	*Medicago polymorpha* L.var. *polymorpha*	B	ns	ns	ns
EU 2120	*Pancratium maritimum* L.	B	ns	ns	ns
EU 2120	*Schoenoplectus triqueter* L.	B	ns	ns	ns
EU 2120	*Scolymus hispanicus L.*	B	ns	ns	ns
EU 2120	*Stachys annua* L. (L.) subsp. *annua* var. *annua*	B	ns	ns	ns
EU 2130	*Centaurea iberica* Trev. ex Sprengel	C	***	***	***
EU 2130	*Cenchrus incertus* M. A. Curtis	C	***	***	***
EU 2130	*Cionura erecta* (L.) Griseb.	C	ns	ns	ns
EU 2130	*Cyperus capitatus* Vandelli	C	***	ns	*
EU 2130	*Echinops orientalis* Trautv.	C	***	***	***
EU 2130	*Euphorbia peplis* L.	C	***	***	***
EU 2130	*Silene otites* (L.) Wibel	C	*	ns	ns
EU 2130	*Vulpia fasciculata* (Forsskal) Fritsch	C	ns	ns	ns
EU 2130	*Xanthium spinosum* L.	C	ns	ns	ns
EU 2160	*Crataegus monogyna* Jacq. var. *azarella*	D	***	***	***
EU 2160	*Eleagnus rhamnoides* (L.) A.	D	***	***	***

Table 5. (Continued).

EU 2160	*Imperata cylindrica* (L.) Raeusch.	D	ns	ns	ns
EU 2160	*Medicago x varia* Martyn	D	ns	ns	ns
EU 2160	*Petrorhagia saxifraga* (L.) Link	D	*	ns	ns
EU 2160	*Phleum exaratum* Hochst. ex Griseb. subsp. *exaratum*	D	ns	ns	ns
EU 2160	*Teucrium chamaedrys* L. subsp. *chamaedrys*	D	ns	ns	ns
EU 2160	*Trifolium stellatum* L.	D	***	***	***
EU 2160	*Verbascum sinuatum* L.var. *sinuatum*	D	*	ns	ns
EU 2210	*Anagallis arvensis* L.var. *arvensis*	E	ns	*	ns
EU 2210	*Daucus broteri* Ten.	E	ns	ns	ns
EU 2210	*Elymus elongatus* (Host) Runemark subsp. *elongatus*	E	ns	ns	ns
EU 2210	*Medicago littoralis* Rohde ex Lois. var. *littoralis*	E	***	***	***
EU 2210	*Plantago scabra* Moench.	E	***	***	***
EU 2210	*Polypogon monspeliensis* L. (Desf.)	E	ns	ns	ns
EU 2210	*Silene dichotoma* Ehrh.var. *dichotoma*	E	ns	*	ns
EU 2210	*Sophora alopecuroides* L.var. *alopecuroides*	E	*	*	ns
EU 2230	*Anchusa hybrida* Ten.	E	ns	ns	ns
EU 2230	*Bromus racemosus* L.	E	ns	ns	ns
EU 2230	*Cota tinctoria* var. *tinctoria* L.	E	ns	ns	ns
EU 2230	*Echium plantagineum* L.	E	***	***	***
EU 2230	*Euphorbia terracina L.*	E	***	***	***
EU 2230	*Jurinea kilaea* Azn.	E	***	***	***
EU 2230	*Kickxia commutata* (Bernh. ex Reichb.) Fritsch subsp. *commutata*	E	***	***	***
EU 2230	*Lagurus ovatus* L.	E	***	***	***
EU 2230	*Prunella vulgaris* L.	E	ns	ns	ns
EU 2230	*Satureja hortensis* L.	E	ns	ns	ns
EU 2230	*Teucrium polium* L.	E	***	***	***
EU 2230	*Trifolium arvense* L.var. *arvense*	E	ns	ns	ns
EU 2230	*Trifolium resupinatum* L.var. *resupinatum*	E	ns	ns	ns

in fixed dune habitats *Sophoro alopecuroides – Elymetum elongati* (EU 2210) and *Euphorbio terracinae – Laguretum ovati* (EU 2230) are adapted to lower salinity (Prisco et al., 2012).

Species in the drift line zone have high EIVs for salinity. The soil is not stable in this zone because of active sand accumulation and reduction in vegetation cover (Gallego-Fernández and Martínez, 2011). Foredune habitats are highly related to variations in substrate coherence (Santoro et al., 2012), wind effects, and environmental stress from seashore to inland (Acosta et al., 2003; Frederiksen et al., 2006; Bazzichetto et al., 2016; Šilc et al., 2018). Especially grassland dune zone had the lowest salinity. Hence, soil salinity decreases along the seashore-inland gradient, and the weighted average S of species in the grassland dune zone is lower than the species of foredune zones.

4.2. Tolerance value

Tolerance values (TVs) for soil nitrogen increased, while TVs for soil salinity decreased along the seashore-inland gradient. However, tolerance values for soil reaction (pH) show a fluctuating distribution between coastal dune zones.

It has been found that salinity and nitrogen are the essential environmental factors determining plant distribution. Nitrogen availability is the dominant environmental factor restricting plant biomass production in saline vegetation (Ungar, 1991; Minden, 2010).

Salinity tolerance values were found to be highest in the drift line, but nitrogen tolerance values were found to be lowest in this zone. This can be explained by nitrogen uptake from the soil is inhibited by high salinity conditions (Howes et al., 1986; Minden, 2010). The availability of nitrogen plays a major role in the control mechanism of halophytes, which has already been pointed out in many other studies (Rozema et al., 1985; Bakker et al., 1993; van Wijnen and Bakker, 1997; Sperandii et al., 2019).

4.3. Niche model

In this study, 28 plants for salinity, 25 plants for pH, and 21 plants for nutrient values were significant according to the GLM niche model considering all dune zones. Previous studies showed that salinity is the most important factor in coastal plant niches (Batriu et al., 2011; Yuan et al., 2012, Jarvis et al., 2016). This finding supports that the Ellenberg salinity (S) score range is wider than the Ellenberg nitrogen (N) and soil pH (R) range.

In the drift line zone, species had specific adaptations to high salt concentrations, and they had the highest Ellenberg salinity scores. For example, *Calystegia soldanella*, *Digitaria ischaemum*, *Eryngium maritimum*, *Parapholis incurva, Salsola ruthenica*, *Apocynum venetum* subsp. *sarmatiense* had a high Ellenberg salinity score as compared to other zones. The main reason for this difference is that some species are distributed in other dune zones. Some studies showed that some species have lower salinity tolerance, although they have a high Ellenberg score. Jarvis et al. (2016) found that *Euphorbia paralias* exhibited more limited salt-tolerance, but it has a high S value. *Euphorbia paralias* L, *Parapholis incurva*, *Apocynum venetum* subsp. *sarmatiense* showed sensitive ecological requirements concerning soil pH, while *X. strumarium* subsp. *cavanillesii*, *Tournefortia sibirica* var. *sibirica*, *Parapholis incurva* and *Apocynum venetum* subsp. *sarmatiense* showed sensitive ecological requirements concerning soil nitrogen content. The number of species were increased due to the litter accumulation, which plays a major role on soil conditions in coastal dune habitats (Angiolini et al., 2018).

In embryonic dune zone, there are two different habitat types: EU 2110 (*Achilleo maritimo–Elymetum farcti*) and EU 2120 (*Medicagini marinae–Ammophiletum arundinace*). *Achillea maritima* subsp. *maritima* in EU 2110, *Cynanchum acutum* subsp. *acutum*, *Cynoglossum creticum* and *Hypochaeris radicata* in EU 2120 were found to be significant according to salinity. *Agrostis stolonifera*, *Crepis foetida* subsp. *rhoeadifolia*, *Juncus littoralis* in EU 2110 habitat and *C. acutum* subsp. *acutum*, *Cynoglossum creticum* in EU 2120 habitat were found to be significant considering pH. Finally, *Agrostis stolonifera*, *Juncus littoralis* in EU 2110 habitat, and *Cynoglossum creticum* in EU 2120 habitat were found to be significant considering N.

Angiolini et al. (2018) found that embryonic dune species need various ecological requirements (pH and organic matter). The fact that the niche models of other species in this zone are not significant may be due to the decrease or disappearance of the plant species here in some localities with beach arrangement studies. Peña-Alonso et al. (2018) showed that the frequency of mechanical beach cleaning reduces the presence of plants by 70%. In this study, we found that the frequency of mechanical beach cleaning reduces the presence of plants by 75% (Sürmen et al., 2019).

The main dune zone, especially *Centaurea iberica*, *Cenchrus incertus*, *Echinops orientalis*, *Euphorbia peplis* were significant, considering S, pH, and N. *Cyperus capitatus* was found to be significant for salinity and nitrogen. In this zone, soil characteristics constrain the survival and establishment of plant species due to soil pH and $CaCO_3$ content (Vallés et al., 2015). Vallés et al. (2015) found that some species (*Cyperus capitatus* and *Silene nicaeensis*) in the main dune zone are adapted to the harsh environmental factors. Angiolini et al. (2018) found that mobile dune species show the highest probability of occurrence at low EC values. Some species belonging to transitional and fixed dune zones (*Lagurus ovatus* and *Medicago littoralis* var. *littoralis,* respectively) were also found in the mobile dune zone. Ciccarelli (2015) showed that mobile dune species are affected by $CaCO_3$, highlighting species niche separation within the given macrohabitat, probably due to competition for physical space with the competitive, stress-tolerant species.

The transitional dune zone is where environmental constraints are generally reduced (Salinity, pH, and N), so plant species are gradually shaping the plant community (Vallés et al., 2015). In this zone, most pioneer communities are replaced by perennial plant communities that prefer relatively stable and fertile soils (Ercole et al., 2007; Angiolini et al., 2018). For example, *Crataegus monogyna* var. *azarella* and *Eleagnus rhamnoides* were found to be significant according to salinity, pH, and nitrogen. Fink and Scheidegger (2018) have revealed that there will be a wide variety of areas of suitable habitats predicted for species in this zone.

The moisture held in the soil in the fixed dune zone is high, and the soil is more developed; structurally becomes a suitable environment for many species (Carboni et al., 2016). Additionally, many species coexist, although ecological requirements overlap. The present study determined two habitat types (EU 2210 and 2230) and twenty species in the fixed dune zone. Especially pH and salinity are decisive for the existence of species. But it is not possible to say this for nitrogen. Because the litter of perennial plants in this zone plays an important role in edaphic features (Angiolini et al., 2018). *Medicago littoralis* var. *littoralis*, *Plantago scabra*, *Sophora alopecuroides* var. *alopecuroides* (EU 2210) and *Echium plantagineum*, *Jurinea kilaea*, *Kickxia commutata* subsp. *commutata*, *Lagurus ovatus*, *Teucrium polium* (EU 2230) were found to be significant considering pH and salinity. Preston et al. (2002) showed that salinity might limit species distribution in the fixed dune. Considering the dune species' different EC, pH, and N requirements, it can be said that the EC and pH factors are more determinant among these variables.

In summary, several environmental factors were revealed to be key factors in the formation of coastal dune habitats, while the ecological requirements of the species were used to explain this result. Ellenberg's ecological indicators, tolerance value, and niche model findings showed that coastal dune zones and plant communities changed along the sea-inland gradient. While the indicator values (R, S, and N) were clearly differentiated between the dune zones, it was observed that the pH fluctuated between the dune zones considering tolerance values. According to niche models, it was found that salinity and pH are more effective in the distribution of species.

The biodiversity values of natural dune zones should be done especially by protecting the interconnection of habitats in different dune zones. In particular, studies on the effects of the beach facilities arrangement (recreation and tourism, the value of the existence of biodiversity) should be carefully implemented and dune zones should be protected from further encroachment.

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