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Caspian remnant coastal dunes: how do natural and anthropogenic factors impact on plant diversity and vegetation?

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ABSTRACT

This vegetation–environmental relation study is the first large-scale survey along 34 cross-shore transects in 650 km-coastal dune remnants of the south Caspian Sea, Iran. The five vegetation zones dedicated here seem to be driven by both zonal (climate, distance to the sea and pH) and azonal (salinity) factors. To assess conservation status, different attributes of *H*dune diversity index, endemicity index (EI) and Naturalness (*N*) were estimated based on endemic, alien and total species contributions per plot. Contrary to *H*dune index, EI followed a decreasing pattern across the coast–inland gradient, whereas *N* shows a unimodal pattern of distribution with the highest value at the mobile dune zone. Two main gradients of salinity and alkalinity shaping floristic composition are more prominent than climate, distance to the sea and the anthropogenic factors particularly when a full range of coastal habitats are considered. Human-related factors only partially explain the variability of the vegetation data and negatively affect naturalness and endemicity indices, even though their impact on community composition is aggravated in the western parts of the Caspian coasts. Both *N* and EI indices can be suggested as bioindicators for proper conservation strategies to preserve the last fragments of sand dunes of the Caspian Sea.

KEYWORDS

Coastal dunes; littoral zonation; alien species; endemicity index; naturalness index; Southwest Asia.

INTRODUCTION

Coastal habitats are characterized by some important ecological and biodiversity values, particularly the occurrence of narrowly endemic species and considerable morpho-dynamic impacts and they also provide robust protection against extreme marine processes (e.g. sea level rise and storms) (van der Maarel and van der Maarel-Versluys 1996; Miller et al. 2010; Bertoni et al. 2014; Pinna et al. 2015; Chung et al. 2015; Bilkovic et al. 2016).

Plant communities are considered essential components of coastal habitats (Wolfe and Nickling 1993; Acosta et al. 2007, 2009), and their composition is influenced by the interactions of several factors, the most important of which are substrate incoherence, the effects of high wind speeds, salt spray and sand accumulation (Martinez and Psuty 2004; Attorre et al. 2013; Fenu et al. 2013a; Tordoni et al. 2021).

Continuous diverse habitats across the coastal dunes which are mainly controlled by a complex coastal environmentalgradient, have led to creating a precise sequence of ecologically distinct plant communities from the seashore to the inland, the so-called coastal zonation (e.g. Acosta et al. 2009; Kim and Yu 2009; Monserrat et al. 2012; Fenu et al. 2013a; Marceno et al. 2018; Malavasi

et al. 2018; Sperandii et al. 2018). This coastal zonation reflects the progressively more sheltered environments that are created with increasing distance from the coastline (e.g. Maun 2009; Fenu et al. 2013a; Fantinato et al. 2018; Calderisi et al. 2021). Usually the entire coastal vegetation zonation includes the following: (1) an upper beach or drift line (strand line) zone of the beach, where extreme environmental conditions exist; (2) the embryonic dune, where the first stage of dune development occurs; (3) the mobile dune, which is considered an important part of developed sand dunes, where sand deposition is heavy; (4) the transitional dune and backdune a mixed community of mobile and fixed dunes; (5) the fixed dunes, which is characterized by dune shrublands (Barbour 1992; Imeri et al. 2010; Ciccarelli 2014). In addition to the zonal vegetation (those influenced by local coastal systems on a normal sea–land gradient), there are also some fixed dune slacks occasionally occurring in the coast–inland gradient (Maun 2009; Sarmati et al. 2019; Bazzichetto et al. 2020).

Several studies found a strong correlation of edaphic factors with different vegetation zones characterized by specific plant communities (Fenu et al. 2012; Ruocco et al. 2014; Valles et al. 2015; Bazzichetto et al. 2020), whereas some other surveys presented other environmental drivers, such as distance to the sea, wind-related factors and dune geomorphology, as being important for influencing the composition of the vegetation zonation (e.g. Acosta et al. 2007; Silva et al. 2008; Kim and Yu 2009; Monserrat et al. 2012; Fenu et al. 2013a). It was also shown that the presence of invasive and native species that have quite different impacts on coastal vegetation zonation can be driven by various environmental factors (e.g. Tordoni et al. 2018). Moreover, human-related activities cause intensive environmental degradation in coastal ecosystems (Santoro et al. 2012; Malavasi et al. 2013; Doxa et al. 2017), where a higher rate of accessibility and exploitation is observed compared to other terrestrial ecosystems (e.g. Ciccarelli et al. 2017; Delgado-Fernandez et al. 2019). This has progressively led to increasing incidence of early successional species, reduced natural sand dynamics, the spread of alien and nutrient demanding species and the disappearance of coastal zonation (e.g. Roeland and Piet 1995; Cakan et al. 2011; Provoost et al. 2011; Marcantonio et al. 2014; Sciandrello et al. 2015; Del Vecchio et al. 2015; Parra-Tabla et al. 2018; Tordoni et al. 2018; Fantinato 2019; Delbosc et al. 2021).

Plant diversity assessment among different vegetation zones of the coastal sand dunes is the most important prerequisite to determine the dunes' vulnerability to natural dynamic processes and anthropogenic factors (Honrado et al. 2010; Ciccarelli and Bacaro 2016; Parra-Tabla et al. 2018). Since both plant species richness and species assemblages in sand dunes have been partially to significantly affected by human activities (Carboni et al. 2009; Attorre et al. 2013; Ciccarelli et al. 2017), detecting diversity characteristics of coastal vegetation zones is regarded as an undeniably key factor in assessing coastal dunes' integrity (Del Vecchio et al. 2015). Different attributes of plant diversity (*H*dune, naturalness and endemicity indices) have been used for evaluating the conservation status of coastal habitats, particularly in the Mediterranean coastal dune ecosystems where the value of each of these indices is considered an indicator of anthropic pressures (Grunewald and Schubert 2007; Ciccarelli 2014; Pinna et al. 2015, 2019; Calderisi et al. 2021). These modified plant diversity indices can also be used as easily accessible bioindicators for conservation status in other coastal regions where a variety of pressures and human activities might lead to a severe impact on the vegetation zonation. In harsh environmental conditions such as the coastal dunes (Attorre et al. 2013), the estimation of the *H*dune index is more appropriate than the Shannon diversity index (Shannon and Weaver 1949). The endemicity index (EI) and the naturalness index (*N*) represent the rate of endemic species and the percentage cover of non-native species in each plant community, respectively.

The Caspian Sea is the largest enclosed water body in the world, and its coasts never experience tides (Kaplin and Selivanov 1995; Froehlich et al. 1999; Peeters et al. 2000). Factors influencing the

Caspian Sea environment are quite different from those commonly occurring in oceanic areas (Khoshravan et al. 2019, 2020, 2021). The presence of the complex orography near the sea could strongly affect the local coastal climate and lead to a particular mesic climate in the area (Zohary 1973; Djamali et al. 2011; Akhani et al. 2010; Gholizadeh et al. 2020). In addition, low or lack of salinity of entering rivers as well as the high evaporation rate of this closed sea could differentiate this basin from other comparable areas like the Mediterranean basin and the Red Sea. Consequently, a different set of environmental and human-related factors could be expected to drive plant community zonation in the south Caspian coastal system. The south Caspian coastal systems (N Iran) encompass various types of ecosystems, including lagoons, spit–lagoon complexes, sand dunes, wetlands and sand spits (Leroy et al. 2011; Naderi Beni et al. 2013; Naqinezhad 2012b; Haghani et al. 2016; Rezaei et al. 2019). Sand dunes are one of the most sensitive ecosystems of the south Caspian coasts; once widely distributed, due to human-related activities, they are now restricted to fragmentary remnants in few coastline areas (e.g. Frey and Probst 1974; Naqinezhad et al. 2006; Tegetmeyer et al. 2007; Atamov 2007; Nouri et al. 2008; Naqinezhad 2012a; Ravanbakhsh et al. 2015, 2016). During the last several decades, dune degradation has been occurring at an accelerating rate along the south Caspian basin, and it is projected that the dunes could entirely disappear due to human activities within a short period if the coastal management is not properly carried out (Khoshravan and Farshchi 2015). Despite several sporadic local floristic-vegetation studies being conducted along the south Caspian coastline (Frey and Probst 1974; Shokri et al. 2004; Ejtehadi et al. 2005; Naqinezhad et al. 2006; Asri et al. 2007; Naqinezhad 2012a, 2012b; Ravanbakhsh et al. 2015, 2016; Saeidi Mehrvarz et al. 2016; Mahdavi and Bergmeier 2016; Mahdavi et al. 2017), there is still a lack of a multidisciplinary approach integrating the floristic composition of vegetation zonation, climate and soil parameters, diversity indices and different disturbance factors.

Given that the fragmented coastal dune systems of the south Caspian Sea host valuable biodiversity, intense anthropogenic pressures on the coastal dunes lead to prioritizing decisions on vulnerability assessments of these dune habitats, detecting their conservation status based on modified diversity indices (i.e. *H*dune diversity index, *H*dune-max diversity index, *E*dune diversity index, EI and *N*) in each plant community, and devising strategies in response to environmental changes. Here we have used surveys of 227 plots in 34 cross-shore transects from remnant sand dunes in northern Iran, aiming to (1) identify the vegetation zonation of South Caspian coastal dune systems along the coast–inland gradient using classical vegetation type classification and indicator species specification, (2) assess how different attributes of plant diversity (*H*dune, naturalness and endemicity indices) vary among different plant communities and consequently indicate the conservation status and (3) characterize the relationships of vegetation zones in terms of natural and anthropogenic factors.

Materials and methods

Study area

The study was carried out in the coastal dune systems of the south Caspian Sea (N Iran), stretching from Miankaleh Biosphere Reserve (36° 54′ N, 54° 00′ E) in the Mazandaran province to Astara (38° 23′ N, 48° 52′ E) in the Gilan province with an approximate length of 650 km (Figure 1). The eastern parts of the study area feature Mediterranean pluviseasonal-oceanic bioclimate (mean annual temperature = 17 °C) and precipitations (mean annual rainfall = 754 mm), whereas the western parts are mostly characterized by a temperate oceanic bioclimate (mean annual temperature = 15.8 °C) and precipitations (mean annual rainfall = 1423 mm) (Djamali et al. 2011). Moreover, the eastern parts are characterized by a steep coast–inland gradient with well-developed sand hills, whereas the sand dunes of the western parts formed on more or less flat

surfaces without any obvious developed hills and consequently encompasses vast area of embryo dunes (see Khoshravan and Farshchi 2015). Two protected areas, Miankaleh Biosphere Reserve and Boujagh National Park are included within the study area. Miankaleh Biosphere Reserve (also called as Miankaleh peninsula or Gorgan Bay) is one of the nine Biosphere Reserves in Iran and covers an area of approximately 688 km^2; it was designated as a protected area in 1970 and considered as a UNESCO biosphere reserve in 1976 (Ramsar convention Bureau 2002). Boujagh National Park has a total area of 32.8 km2; it is located in the middle of the western part, and is characterized by various habitat types of aquatic wetlands, wet sand dunes and flat sand dunes (Naqinezhad et al. 2006).

Data sampling

In order to identify the relevant plant communities and the vegetation zones in the coastal dune systems, we selected remnants and the most pristine sand dunes for data sampling. A total of 34 transects perpendicular to the coasts consisting of 277 plots (designed as "alternate-plot transects" *sensu* Del Vecchio et al. 2019) were placed under the stratified random sampling method. Each stratum corresponded to a specific habitat, and several plots were randomly sampled in each stratum based on the habitats width in the spring/summer spanning from 2010 to 2017. Spatial intervals between the studied plots located in the transects were not always the same, as the occurrence of some disturbances, such as fires in some transects and the presence of artificial forests of *Alnus subcordata* between two natural vegetation zones/habitats, could lead to a wider interval between some studied transects. Our sampling allowed us to assess the full spectrum of the coastal vegetation zonation from the seashore to the inland (Supplementary Table S1). Transects varied in length from 10 to 5562 m depending on differences in the coastal system morphology, vegetation cover and disturbance level. We allocated the transects through different habitats to ensure that our sampling contained different coastal habitats from the pioneer zone of the drift line to the backdune (Maun 2009; Miller et al. 2010). However, the backdune was mostly experiencing severe habitat degradations, meaning that only one or two plots could be allocated in these parts.

To ensure recording of the plant diversities across the sampled plots, we used 25 m^2 square-shape plot sizes for coastal grasslands (a total of 193 plots) and 100 m2 plots for remnant coastal shrubby vegetation (84 plots). Shrubby vegetation was only assessed in the Miankaleh Biosphere Reserve and Astara coastal regions. In each plot, the coverage of all vascular plant species was either estimated using direct cover percentage or visually recorded using the Braun-Blanquet scales (Braun-Blanquet 1964). The Braun-Blanquet values obtained were transformed into mean values of percentage cover categories (i.e. *r*: 0.1; +: 1; 1: 2.5; 2: 15; 3: 37.5; 4: 62.5; 5: 87.5). The plots' distances from the coastline and their coordinates were recorded using Garmin Geko 201 GPS. The whole procedure of data collection over different years was conducted and supervised by the second author in the framework of various small projects.

For each plant species recorded in the plots, it was indicated whether it is a species native or alien to coastal dune systems of the south Caspian Sea using available floras (Rechinger 1963–2015; Assadi et al. 1988–2014); endemic plants were further highlighted in the dataset. Species name were standardized using The Plant List (The Plant List 2013) and IPNI (IPNI 2020) databases. In each plot, three soil samples at a depth of 15 cm were taken and mixed before lab analyses. Soil samples were only available for 227 recently-collected plots. Soil pH was calculated in a suspension of 1:1 soil: water ratio at 25 °C by a pH meter glass electrode (Handbook of soil analysis 1980) and electrical conductivity (EC (ds/m)) with an EC meter in a saturation extract at 25 °C. Climate variables, including mean annual temperature (*T*) and annual precipitation, were obtained from the CHELSA database version 1.2. (http://chelsa-climate.org; Karger et al. 2017).

We established six main categories of different anthropogenic drivers based on personal knowledge of coastal habitats, including trampling, human settlements, grazing, sand exploitation, coastal erosion and paths/roads using different levels according to the following scale: absent (0), low (1), moderate (2) and high (3). To ensure replicability of this approach, we consulted all disturbance factors already applied in other coastal studies (e.g. Mediterranean area, Ciccarelli 2014). Moreover, species-related diversity indices including species richness, *H*dune, *H*dune-max, Edune, EI, *N* and total cover were calculated per plot. *H*dune, a modified version of the Shannon diversity index and *E*dune, a modified Evenness index, were described by the appropriate biodiversity indices with the advantage of focusing the natural fragmentation of coastal habitats and the changes to coastlines with different levels of disturbance (Grunewald and Schubert 2007; Ciccarelli 2014; Pinna et al. 2015, 2019). The *H*dune index was calculated following the formula: *H*dune = $-\Sigma\ Pi \times \ln Pi$, where *Pi* = % cover of the *i*th plant species. From *H*dune it is possible to obtain *H*dune-max, which is a combination of total cover and number of species. *H*dune-max was calculated following the formula: *H*dune-max = $-s \times [(\Sigma Pi)/s)] \times \ln[(\Sigma Pi)/s)]$, where *s* = number of plant species. It is indicated that *H*dune is more appropriate than the Shannon diversity index (Shannon and Weaver 1949) through harsh environmental conditions such as the coastal dunes (Attorre et al. 2013). Evenness (*E*) is an index often used as a parameter for community structure, being independent of species richness (Grunewald and Schubert 2007). Grunewald and Schubert (2007) modified *E* (*E*dune) and calculated it as a ratio between *H*dune and *H*dune-max.
In addition, to explore the endemic and natural plant coverages as indicators of a coastal dune system's conservation status, the endemicity and naturalness indexes (EI; Pinna et al. 2019) were calculated for each plot. Both indices were calculated based on the percentage cover of endemics or alien plants along each plot, according to the following formula (Grunewald and Schubert 2007; Pinna et al. 2019):
EI _ *H*dune (considering only the endemic plant species) / *H*dune
N = *H* dune (dune without alien plant species)/ *H*dune

Data analysis

To determine the main plant communities across the coast-inland gradient, a total of 277 collected plots and 368 plant species were subjected to a divisive type of classification (Modified TWINSPAN) embedded in the JUICE version 7.1 program (Tichy 2002; Roleček et al. 2009). The Advantage of TWINSPAN analysis for vegetation zonation is that it introduces groups of diagnostics, constant and dominant species (altogether forming the set of "indicator species") and the coincidence of produced plant communities within the available sea–inland zonal gradient (Zoladeski 1991; Chuman and Romportl 2010). Similar to the European and Mediterranean coastal dune vegetation, coarsely-classified plant communities by using the hierarchical divisive classification method of TWINSPAN (Hill 1979) in the current study largely correspond to the major vegetation zones occurring on a sea–inland gradient (Marceno et al. 2018). Three pseudospecies cut levels 0%, 5% and 25%, and *total inertia* were used in the TWINSPAN analysis. Diagnostic species were identified using the *phi*-coefficient as a fidelity measure based on log-transformed cover data (Chytry et al. 2002). The sizes of all groups were standardized to an equal size and the Fisher exact test ($p < .05$) was applied (Tichy and Chytry 2006). Species with a *phi*-coefficient higher than 0.15 were considered diagnostic for a particular group. For translation of the TWINSPAN results into vegetation units, we chose the highest division that still yielded floristically well-characterized terminal clusters with their own diagnostic species (Dengler et al. 2005). The habitat profile and the authors' field experience were used during the division to find comprehensive and ecologically interpretable results of classification. For all other analyses we used a subset of 227 plots for which soil data were also available.

To determine the most important variables affecting the plant communities in the south Caspian dune systems, canonical correspondence analysis (CCA; ter Braak 1986) was performed. Transformation of the plant community data was carried out using the Hellinger method (Legendre and Gallagher 2001). Pairwise correlations of all studied variables were checked and the variables with a high Pearson correlation (i.e. annual precipitation and mean annual temperature; $r = -0.98$) were removed from further analyses. Therefore, effects of the environmental variables (mean annual temperature, *T*, annual precipitation, distance to sea, pH and EC and six anthropogenic-related drivers) on species composition were tested with a permutation test under the reduced model with 999 permutations. The most parsimonious model was fitted using a stepwise algorithm, through forward and backward selection of explanatory variables, based on the lower value of the Akaike Information Criterion (AIC; Akaike 1974). CCA analyses were separately repeated for western and eastern coastal transects. Compositional beta-diversity was estimated by calculating the rate of compositional turnover using permutational multivariate analysis of variance (PERMANOVA) using the "*adonis*" function from the "*vegan*" package in R (Anderson 2001; Anderson et al. 2008; Oksanen et al. 2020). To test for differences in environmental and diversity-related variables among plant communities, we applied the Kruskal–Wallis test followed by Tukey *post hoc* test pairwise comparisons, adjusting the significance test with the Bonferroni correction.

Moreover, variance partitioning (Borcard et al. 1992) of the community matrix by two explanatory matrices, that is, the natural matrix (comprising mean annual temperature, pH, EC, distance to the sea) and the anthropogenic-related matrix (comprising the six categories described above) was done to compare the fractions of natural and anthropogenic factors and their combined effects (Peres-Neto et al. 2006). A Venn diagram (Okland 2003) was used to illustrate the fractions of the factors for all data as well as for western and eastern coastal data. CCA and variance partitioning analyses were calculated using the *vegan* package (Oksanen et al. 2020). As there is an increasing number of documents showing the influence of spatial autocorrelation in community ecology (e.g. Kuhn 2006; Peres-Neto and Legendre 2010; Bacaro et al. 2016), we examined it in the neighbouring transects following the methodology proposed by Ciccarelli (2014), using the "*adespatial*" package (Dray et al. 2021). For this, Moran's I statistic using 999 random permutations was applied on a matrix of geographic coordinates in the transects related to the percentages of community coverage found in each transect. All analyses were performed in the free statistical software environment R 4.1.1 (R Development Core Team 2021).

Results

The identified plant communities and the environmental relationships

A total of 368 plant species belonging to 62 families and 218 genera were identified in the south Caspian coastal sand dune systems (see Supplementary Table S2). Based on constancy and fidelity measures for the species, five main plant communities were identified using the modified TWINSPAN analysis (Figures 2 and 3, Table 1; Supplementary Table S3).

The plant communities included the following: (I) *Salicornia iranica* Akhani–*Juncus acutus* L. was found in salt marshes habitats covered mostly by halophytes; this plant community is between coastal shrublands and Gorgan Bay and is frequently occupied by *Salicornia iranica*, *Limonium meyeri* (Boiss.) Kuntze, *Juncus littolaris* C.A. Mey., *Juncus acutus* and *Bassia crassifolia* (Pall.) Soldano. (II) *Convolvulus persicus* L.–*Tournefortia sibirica* L. was found in the upper beach zone or the embryonic dune with major rhizomatous pioneer species in the strandline, next to sea water and affected by harsh environmental conditions (high wind velocity and sand movement). (III) *Artemisia campestris* subsp. *inodora* Nyman–*Daucus littoralis* Smith subsp. *hyrcanicus* Rech. F. was found on mobile dunes mostly dominated by dune builder plant species (e.g. *Artemisia campestris*

subsp. *inodora, Daucus littoralis* subsp. *hyrcanicus*, *Imperata cylindrica* (L.) Raeusch.); this community is the most important part of dunal development characterized by heavy sand accumulation. (IV) *Juncus acutus–Rubus sanctus* Schreb. was found in the transition dune and/or backdune where sandy soil and fixed soil meet each other with *Juncus acutus* and *Petrorhagia saxifraga* (L.) Link. Finally, (V) a *Punica granatum* L. community was found on fixed dunes prominently occupied by shrublands, in this plant community huge and dense populations of *Punica granatum* seemingly are dominant.

Diagnostic species of each plant community are reported in the synoptic table (Supplementary Table S3). Only two transects belonging to Miankaleh Biosphere Reserve (numbers 2 and 3) include all these plant communities (see Supplementary Table S4).

All of the Moran's *I* indices of spatial autocorrelation regarding the five different plant communities (vegetation zones) in the transects were not significant (*p* value >.05), which indicated that there were not any spatial autocorrelations among transects (Supplementary Table S5). Our comparative detrended correspondence analysis (DCA; Hill and Gauch 1980) of both vegetation datasets (277 plots without soil data and 227 plots with soil data) indicated that the distribution pattern of the studied plots was almost the same within these five communities. This analysis confirmed that the vegetation zonation dedicated to plots with complete environmental variables matched with the whole vegetation dataset (see Supplementary Figure S1). The five plant communities recognized in the TWINSPAN analysis were confirmed in a direct gradient analysis of the CCA analysis (Figure 4). Both the first and second axes of the CCA analyses almost equally contributed to the differentiation of the floristic composition of the studied plant communities. CCA analysis showed that EC and pH along with mean annual temperature and distance to the sea were the most important variables affecting the vegetation composition (see Table 2). The first axis showed a gradient of soil salinity clearly separating the plant community I (dune slacks or salt marshes community) from the other four plant communities (Figure 4). The second axis was dedicated to distance to the sea, and alkalinity separated the plant communities according to the sea-inland gradient. Grazing, paths/roads and trampling were the most important anthropogenic factors affecting dune communities (Table 2). Nevertheless, variance partitioning confirmed that the share of anthropogenic factors explaining the total variability (3%) was much less than environmental variables (soil, climate and distance to sea) (Figure 4). The share of different variables explaining the vegetation data differed in a separate CCA and variance partitioning analyses of the western and eastern parts of the Caspian coasts. The western coastal parts represented only two vegetation zones; they were mainly affected by their distance to the sea, the only significant environmental variable, as well as some anthropogenic factors (Figure 5). Moreover, the PERMANOVA revealed that the floristic composition (i.e. beta-diversity) differed significantly between the five plant communities according to the environmental characteristics (Table 3). Corresponding to the CCA and variance partitioning analyses, environmental features contribute more to beta-diversity than anthropogenic factors. Furthermore, the Kruskal–Wallis test showed that most of the environmental and species diversity data varied within paired communities (Supplementary Figure S2).

Pattern of diversity among the identified plant communities

Diversity indices among different transects highlighted those located in the eastern coastal areas; in particular, transects of Miankaleh Biosphere Reserve encompassed the highest values of diversity indices (Supplementary Table S6). The diversity indices for each plant community showed that *H*dune increased from plant community II to V, that is, from the upper beach to the inland areas (Table 4). The most homogeneous plots in terms of plant coverage (the highest *E*dune) were located in the most extreme environmental conditions of plant communities I (salt marshes

community) and II (upper beach community) (Table 4). *N* exhibited almost equally high values in all plant communities, with the highest records in plant communities I (salt marshes) and III (mobile sand dune), whereas the lowest values occurred in the shrublands (plant community V). Interestingly, endemicity was the highest in plant communities near the sea (i.e. plant community II) and drastically decreased in plant communities IV and V (i.e. transition dune and/or backdune and fixed dunes) (Table 4; Supplementary Figure S2). The Kruskal–Wallis test showed that all diversity indices were significantly different among the plant communities (Supplementary Figure S2).

Discussion

Plant community zonation and environmental interaction

On the south coast of the Caspian Sea, an increasing development of the prevailing wind regime controls hydrodynamic processes from the eastern to the western parts of the coastline (Khoshravan and Farshchi 2015). This subsequently created a correspondence in dissimilar hydrodynamic forces and resulted in different dune morphology and vegetation zonation (Abuodha et al. 2003). As a result, a full gradient of the plant community described in this paper is not evenly distributed throughout east-west coastal systems. The studied transects exhibit varying patterns of the typical sequence of coastal dune plant communities, ranging from the absence of the upper beach and mobile dune communities (plant communities II and III) to the presence of the complete sequence. For example, salt marshes (plant community I), large, undulating hills of mobile dunes (plant community III) and shrublands (plant community V), are hardly found in the western coastal area. Moreover, in some places, fixed dunes and back dunes could replace the upper beach and embryo dunes in the western parts of south Caspian coastal systems, where natural erosion was more consistent (Khoshravan and Farshchi 2015).

Generally, the first zone (corresponding to the plant community II) was mainly colonized by rhizomatous plant species such as *Tournefortia sibirica* and *Convolvulus persicus* that can be considered ecosystem engineers that are able to stabilize sands against strong winds. In fact, the presence of such rhizomatous plants, a common feature in dune systems worldwide (e.g. Fenu et al. 2012, 2013a), plays an important role in the further development of dune morphologies. This zone can be identified as a pioneer zone with primary stabilizing plants, and their survival depends on their ability to tolerate salt spray, strong winds, sandblast and occasional inundation by sea water (Maun 2009; Ravanbakhsh et al. 2015; Ciccarelli 2015). Consistent sand dunes, which only occurred along zone III (*Artemisia campestris* subsp. *inodora–Daucus littoralis* subsp. *hyrcanicus* community) in the eastern parts, represent shifting dunes where *Daucus littoralis* subsp. *hyrcanicus* and *Artemisia campestris* subsp. *inodora* were considered important elements affecting the formation and expansion of sand dunes. They contribute to further stabilized sands and improve dune morphology, and positive interaction among them results in significant dunes development (Martinez and Psuty 2004; Asri et al. 2007; Naqinezhad 2012b; Lithgow et al. 2013). *Artemisia campestris* subsp. *inodora* is a dominant psammophilous species exclusively occurring in the large sand dunes of eastern coastal parts, where dominant hydrodynamic forces created large mobile dunes (Naqinezhad et al. 2006; Naqinezhad 2012a; Ravanbakhsh et al. 2015; Saeidi Mehrvarz et al. 2015, 2016). The *Juncus acutus–Rubus sanctus* plant community (zone IV) is the largest plant community located in more stabilized soil/sands towards the inland. The floristic composition of this zone varies from the western to eastern parts of the south Caspian Sea. Whereas large tussocks of *Juncus acutus* and *Juncus maritimus* Lam. mostly dominate along the western parts on rather wet or brackish stabilized soils of the fixed dune or backdune, a higher cover of *Rubus sanctus* mostly dominates in the eastern coastal areas, where a transitional form of vegetation gradient from the mobile dune plant community to dune shrublands is observed.

Significant anthropogenic effects (paths/roads and trampling) are considered to be the reason for the high cover of *Rubus sanctus* in this community, as the latter species was frequently recorded as a ruderal species after disturbances in the ecosystems (e.g. Saeidi Mehrvarz et al. 2015, 2016). Moving further towards the backdune, soils became completely stabilized and had a lower salinity, which resulted in remarkable vegetation cover.

The floristic composition of this community is quite distinctive and the occurrence of large stands of shrubs particularly *Punica granatum* could provide microhabitats for uncommon sand dune plants (Ejtehadi et al. 2005; Asri et al. 2007; Saeidi Mehrvarz et al. 2015). Our study revealed that the vegetation zonation occurring in the Caspian coastal dune system seems to be driven by both zonal (e.g. climate, distance from the sea and pH) and azonal (salinity = EC) factors due to its geomorphological complexity (see Khoshravan et al. 2020, 2021). Salt marshes community (*Salicornia iranica–Juncus acutus*) was clearly distinctive in terms of floristic composition and mainly occurred at the endpoints of the transects located in the Miankaleh Biosphere Reserve where Gorgan Bay's indentation provides a vast salty habitat. However, this azonal community could also sporadically distribute to other coastal zones, depending on salt-water discharges in the inland areas. High rainfall, particularly in late winter, in this zone allowed the occurrence of some annual non halophytic species (Asri et al. 2007). Excluding the salt marshes zone in the Caspian dune systems, other vegetation zones are clearly located on a gradient from the upper beach (near the coastline) to the fixed dune and shrublands (see the second axis of CCA, Figure 4). The climatic variable, which was represented here as mean annual temperature (highly negatively correlated with annual precipitation) is considered as one of the most important environmental variables affecting floristic composition, particularly on the eastern coasts of south Caspian Sea (see Table 2). Both soil and climate factors were not significant in the western section of the Caspian Sea, partly due to higher habitat and vegetation homogeneity as well as the occurrence of only two out of the five major vegetation zones in these areas (see Figure 5). Consistent with other coastal regions (Ciccarelli 2014), a CCA analysis along with variance partitioning showed that natural variables (climate, soil and distance to sea) explained most of the species composition variation in the communities.

The natural variables shaping the natural heterogeneity over the coast–inland environmental gradient is generally considered the main driver of biodiversity patterns, and other landscape spatial patterns of dune communities, such as habitat loss and fragmentation, can be considered to have a weak effect on plant diversity (Malavasi et al. 2018; Calderisi et al. 2021). The CCA analysis also revealed that the most important anthropogenic variables in the studied habitat–environmental relationships were grazing, trampling and paths/roads, which was partly consistent with some Mediterranean coastal systems (De Luca et al. 2011; Attorre et al. 2013; Ciccarelli 2014; Pinna et al. 2019; Calderisi et al. 2021). The main adverse effect of trampling is the partial or total destruction of vegetation; another effect is soil compaction, which increases soil density but decreases porosity, an unfavorable condition, especially for plant communities of embryonic and mobile dunes that are adapted to substrate instability and sand burial (Maun 2009; Santoro et al. 2012; Fenu et al. 2013b). Livestock grazing along coastal habitats, particularly in the Miankaleh Biosphere Reserve, altered the dunal vegetation pattern, causing vast areas considerably covered by ruderal plants (Tamartash et al. 2009). Moreover, non-native species would be able to be established in grazed area because of contaminated stock fodder and their seed easily spread through coastal habitats by livestock movement (Will and Tackenberg 2008; Cossu et al. 2020). In addition, habitat functions can be severely damaged under pressure of paths/road as many roads accompanied by recreational activities, constructions and many other coastal resorts (Davenport and Davenport 2006; Delbosc et al. 2021).

Distance from the coastline significantly affects the plant community composition only in a magnitude after the effects of soil and climatic factors. This is consistent with the results of Fenu et al. (2013a) and Ciccarelli (2014), which revealed that plant community distribution along the coast–inland gradient cannot be sufficiently explained only by the distance from the shoreline at the local scale and that other environmental variables such as soil properties, could be considered the most determinant factors for community zonation (Ruocco et al. 2014). Nevertheless, the distance to the sea is the only significant natural variable affecting the sand dunes of the western coastal region; the impacts of anthropogenic disturbances are comparatively larger in these areas (see Figure 5), likely due to the higher habitat homogeneity and more exposed and accessible landscapes.

Plant diversity characteristics and conservation status

Our study showed that the plant diversity followed an increasing pattern from the coastline (plant communities II and III) to the inland (plant communities IV and V). This was predictable, as the inland areas are naturally less stressful environments (e.g. Attorre et al. 2013; Fenu et al. 2013a; Pinna et al. 2015, 2019; Yousefi Lalimi et al. 2017; Sperandii et al. 2018). However, other factors, particularly anthropic pressures, might also be reasons for this gradient. The high values of plant diversity indices in the inland plant communities (IV and V) coincide with the increasing intensity of some anthropogenic factors, such as grazing, paths/roads and trampling (see Figures 4 and 5; Supplementary Figure S2). The increase in species richness under moderate grazing is mostly related to an increase in annual ruderal plants by reducing the density of the dominant species in addition to increasing the soil disturbance, which provides suitable conditions for establishing this life form (Talebi et al. 2021). *H*dune diversity index contributes applicability to differentiate zones with different disturbance levels (Grunewald and Schubert 2007) and a medium degree of human disturbances in the Mediterranean sand dunes causes an increase in the coastal floristic richness and coverage (Ciccarelli 2014; Pinna et al. 2019).

The EI showed an opposite trend to the *H*dune diversity index along the coast-inland gradient. This index decreases when moving from plant community II (upper beach zone) to the inland zones. The high presence of endemic species in the upper beach areas has already been reported in other dune systems (Pinna et al. 2019; Calderisi et al. 2021), is a way to identify the areas that are more important for implementing an adequate management and conservation strategy (Pinna et al. 2019). Plant communities I and II suffer harsher environments due to salt spray, poor-nutrient soil in embryo dunes and high EC in salt marshes, which filter out species by providing less favourable conditions for plants and effectively reducing the species pool and hence taxonomic diversity (*H*dune). This finally resulted in a small number of adapted species with limited distribution; that is, the endemic species (Acosta et al. 2009; Fenu et al. 2013b; Ciccarelli 2014; Valles et al. 2015). The *N* index is generally high in the Caspian sand dune systems, and the small variability of *N* is likely due to the low incidence of alien taxa in different plant communities, which has already been pointed out in other coastal sand dunes (see Attorre et al. 2013; Ciccarelli 2014; Malavasi et al. 2018; Pinna et al. 2019; Calderisi et al. 2021). Quite different to the rather linearly decreasing pattern of the Endemicity index towards the inland areas, *N* shows a unimodal pattern of distribution, with the highest value at the middle, where the mobile dune zone (plant community III) occurs (Table 4; Supplementary Figure S2). This specific pattern indicates that the two extreme ends of the coast–inland gradient tend to be affected by more alien species, likely due to more anthropic pressures in these zones. This emphasizes the conservational importance of coastal edge zones, where a high number of visitors could expand alien species and subsequently reduce naturalness. However, as mentioned above, these habitats can also filter out many species in favour of a small number of adapted endemic species. Interestingly, salt marshes (plant

community I) as an azonal community showed the highest naturalness. This could be a consequence of the evenly distributed cover of halophytes in the community and salt avoidance by many alien species (Asri et al. 2007).

Conclusions

During recent decades, along the south Caspian basin, outbound tourism, the expansion of urban areas and the spread of agriculture and afforestation activities have strongly led to the disappearance of both inland and coastal vegetation zones. Still, some fragmented dune relicts with high conservational importance preserve invaluable coastal biodiversity. To determine dunes' vulnerability to natural dynamic processes and anthropogenic factors, five major plant communities corresponding to five coastal zones were identified across the sea–inland gradient. Different attributes of plant diversity (*H*dune, naturalness and endemicity indices) proved to be used as bioindicators for conservation planning in Caspian dune systems. The floristic composition of all these coastal communities has been driven by two gradients of salinity and alkalinity being more prominent than the distance to the sea and the anthropogenic factors. It was indicated that grazing, paths/roads, and trampling were the most important disturbance factors affecting dune systems, particularly in inland communities. Likewise, naturalness and endemicity could be also affected by these anthropogenic effects. While most of the anthropogenic factors have no effect or even positive effect on species richness and diversity indices, they negatively affect naturalness and endemicity in the coastal dune systems. However, the naturalness is generally high despite the high touristic significance of the Caspian coastal system and anthropogenic factors only partially explain the variability of the vegetation data. Both naturalness and endemicity indices can be used by managers as a biological proxy to identify more sensitive coastal dunes and to promote appropriate management strategies to preserve the last remnants of sand dunes.
Managers should protect the last remnants of pristine sand dune habitats in order to maintain higher naturalness and endemicity and to reduce further habitat fragmentations and loss. Although vegetation of the drift-line and embryonic dunes are poor of taxa with low coverage, they represent an important ecosystem that must be considered in conservation programs (Acosta et al. 2009; Ciccarelli 2014). Besides, a stricter conservation procedure is needed for shrublands and salt marshes habitats where higher species diversity is recorded.

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The authors declare no conflict of interest.

Authorship contributions

AN conceptualized, designed and coordinated the work. AN, ST, ZK and NV collected the field data. HM, AN, GF and ST performed statistical analyses. ST prepared the original draft with main contribution by AN (lead), GF and HM. All authors reviewed the manuscript and contributed.

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TABLES

Table 1. Southern Caspian Sea habitat types and plant communities found in the study areas along the sea-inland gradient.

	Salt marshes (I)	Upper beach (II)	Mobile dunes (III)	Transition dunes, and/or backdunes (IV)	Fixed dunes of shrublands (V)
Plant community description	Dune slack plant community mostly covered with halophytes next to Gorgan Bay	Vegetation of drift line majorly characterized by rhizomatous perennial species through alkaline soil	Most developed sand hills distinguished by dune builder species where heavy sand accumulation occurred	Perennial community of Transition dune where shifting and fixed sand meet each other	Formations of small trees or shrubs in dense populations is accompanied by herbaceous species through fixed sand
Main diagnostic species	*Salicornia iranica, Juncus acutus, J. littoralis, Limonium meyeri*	*Convolvulus persicus, Tournefortia sibirica*	*Artemisia campestris* subsp. *inodora, Daucus littoralis* subsp. *hyrcanicus*	*Juncus acutus, Rubus sanctus*	*Punica granatum*
Location	East	West and east	With a higher concentration in the Eastern transects	West and east	East (only in two transects of Miankaleh Biosphere Reserve)

I–V represents the number used for plant community.

Table 2. Results of the CCA analysis based on AIC value.

Environmental variables (AIC = 1903.75)	AIC	*F*	*p* Value	%-variance
EC (ds/m)	1897.9	7.8773	.005**	26.60
pH	1900.2	5.5832	.005**	18.41
Temperature (°C)	1900.6	5.1259	.005**	16.41
Distance to the sea (m)	1901	4.7555	.005**	8.08
Grazing	1901.5	4.2615	.005**	6.13
Path/road	1902	3.6935	.005**	5.35
Trampling	1902.3	3.4284	.005**	4.58
Close to human settlement	1903.6	2.1278	.005**	3.39
Sand exposure	1904.5	1.2615	.280	2.11

Total inertia is 19.37.
**$p \leq .01$

Table 3. Results of PERMANOVA comparing differences in the species composition between five major plant communities studied in south Caspian coastal region.

Environmental and anthropogenic variables	SumsOfSqs	MeanSqs	R^2	*F*
EC	5.92	5.92	0.06	17.64***
Distance to sea	4.06	4.06	0.04	12.09***
pH	4.04	4.04	0.04	12.05***
Grazing	2.13	2.13	0.02	6.35***
Path/road	1.97	1.97	0.02	5.87***
Close to human settlement	1.83	1.83	0.02	5.46***
Temperature (°C)	1.76	1.76	0.02	5.23***
Trampling	1.71	1.71	0.02	5.09***
Sand exposure	0.67	0.67	0.01	1.98**

**Significance levels: $p < .01$.
***Significance levels: $p < .001$.

Table 4. The mean values (±standard deviation) of the diversity indices for conservation status assessment of each plant community along south Caspian coast.

Plant community	H_{dune}	$H_{dune\text{-}max}$	E_{dune}	*N*	Endemicity index
I: *Salicornia iranica–Juncus acutus*	3.31 (0.93)	4.40 (1.20)	0.75 (0.07)	0.98 (0.03)	0.09 (0.04)
II: *Convolvulus persicus–Tournefortia sibirica*	0.78 (0.44)	1.10 (0.63)	0.75 (0.17)	0.85 (0.12)	0.22 (0.26)
III: *Artemisia campestris* subsp. *inodora–Daucus littoralis* subsp. *hyrcanicus*	1.66 (1.07)	2.84 (1.71)	0.60 (0.14)	0.91 (0.09)	0.07 (0.07)
IV: *Juncus acutus–Rubus sanctus*	3.45 (2.96)	5.42 (3.80)	0.60 (0.16)	0.86 (0.11)	0.02 (0.04)
V: *Punica granatum* community	8.12 (1.63)	11.22 (2.24)	0.72 (0.03)	0.84 (0.03)	0.02 (0.01)

N, naturalness.

FIGURES

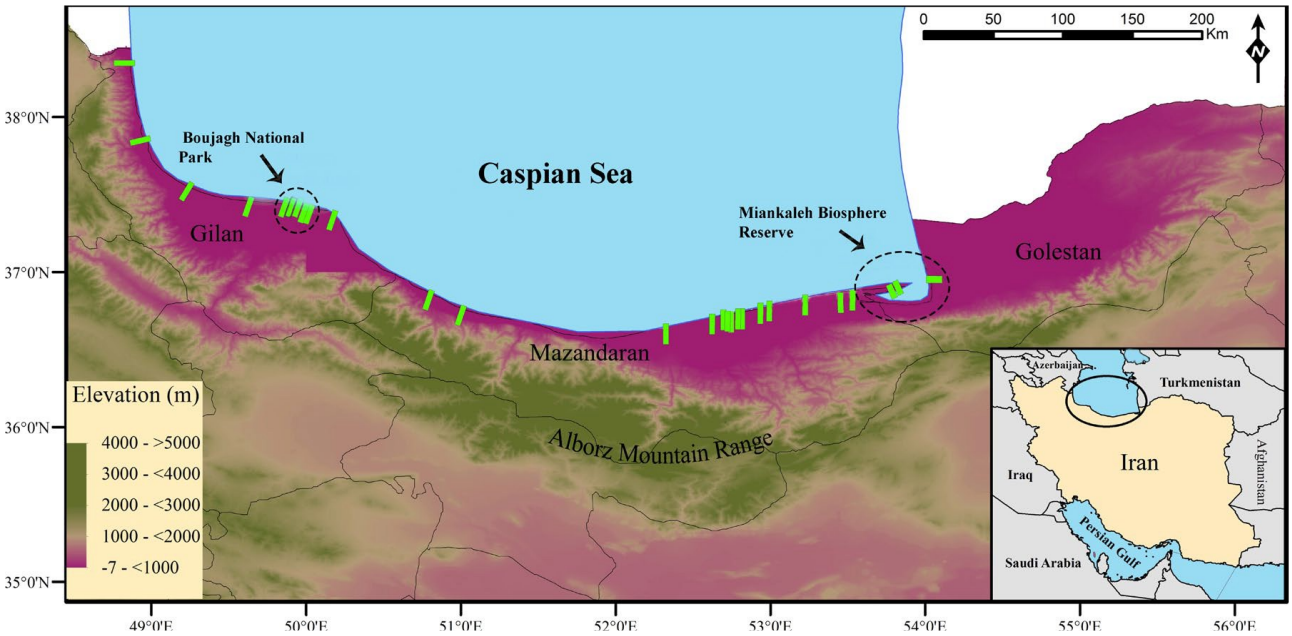

Figure 1. M ap of the study area. Vertical bars along the shore show the location of the studied transects along southern Caspian Sea coast in three provinces (Gilan, Mazandaran and Golestan) in north of Iran. The dashed areas are two main protected areas, Miankaleh Biosphere Reserve and Boujagh National Park.

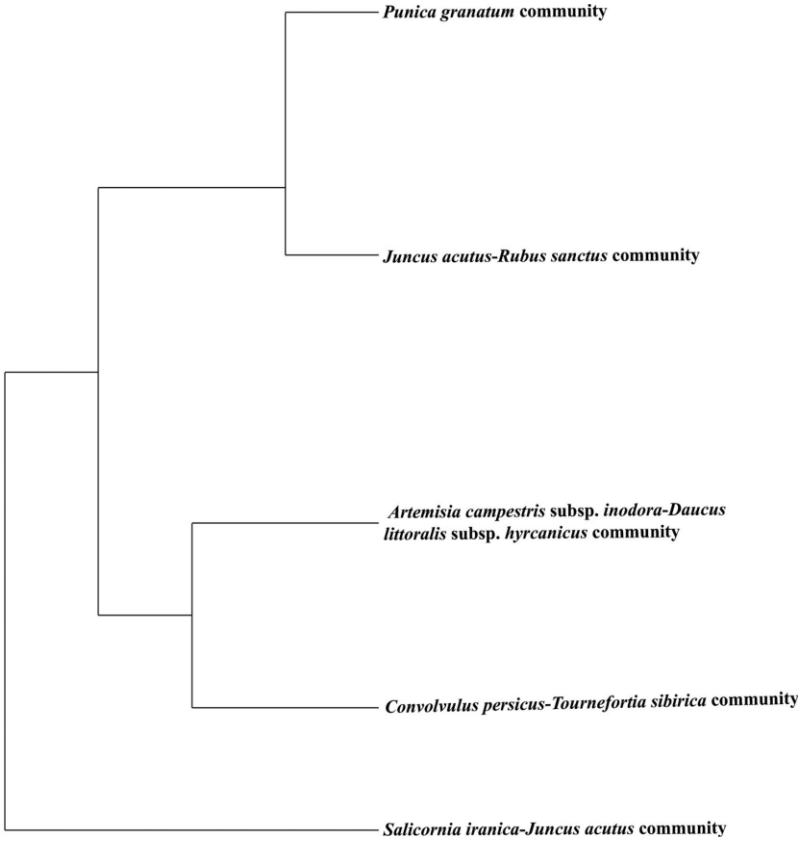

Figure 2. TWINSPAN dendrogram representing five plant communities of the coastal sand dune of south Caspian Sea.

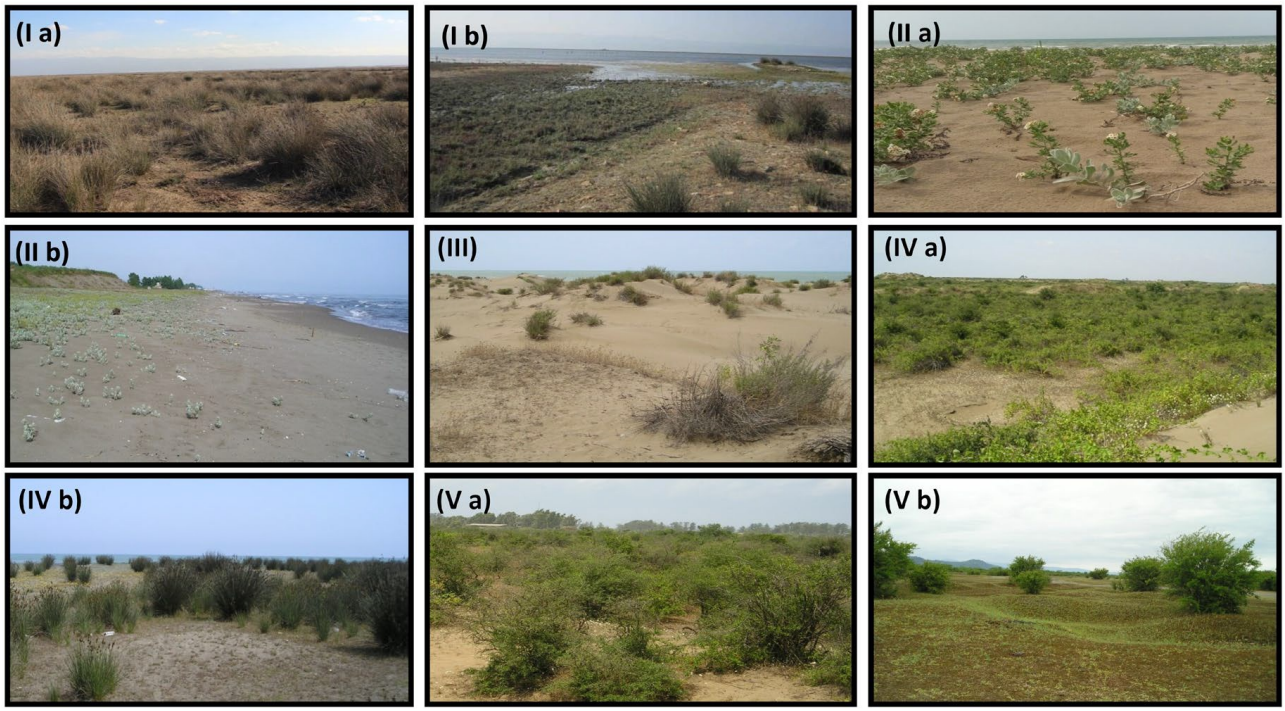

Figure 3. The plant community zones of the studied coastal areas. Ia, Ib: *Salicornia iranica–Juncus acutus* community in different parts of Miankaleh Biosphere Reserve. IIa, IIb: *Convolvulus persicus–Tournefortia sibirica* community and endemic *Convolvulus persicus*, III: *Artemisia campestris* subsp. *inodora–Daucus littoralis* subsp. *hyrcanicus* community, IVa: *Juncus acutus–Rubus sanctus* community in Miankaleh Biosphere Reserve, IVb: *Juncus acutus–Rubus sanctus* community with dominance of *Juncus acutus* in Boujagh National Park where mobile dune are entirely disappeared, Va: dense *Punica granatum* community in Miankaleh Biosphere Reserve and Vb: *Punica granatum* community in Astara.

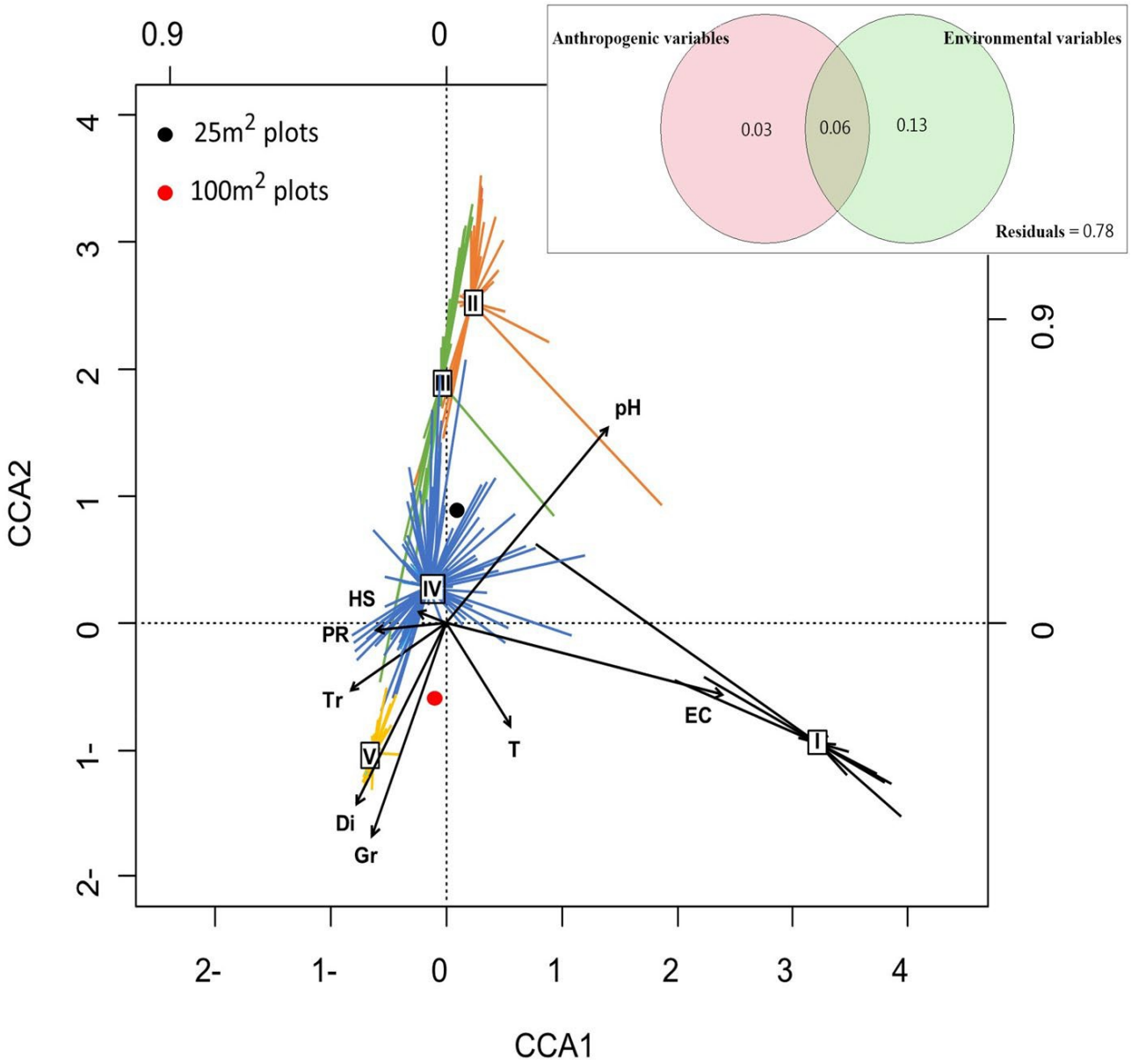

Figure 4. Canonical correspondence analysis (CCA) of the studied plots and variables. Numbers indicates vegetation plant communities according to Supplementary Table S3. Arrows represent the environmental variables. Eigenvalues of constrained and unconstrained axes were 0.68 and 0.66 for the first axis and 0.49 and 0.61 for the second axis. Plot size was used as a dummy variable. Venn diagram showing the variance partitioning of conditional and shared effects of the groups of environmental and anthropogenic variables as fractions of the total inertia was shown in the inset of figure. Tr (Trampling), HS (Close to Human settlement), Gr (Grazing), PR (Path/Road), Di (Distance from the sea), T (Temperature), Hd (Hdune). (I) *Salicornia iranica–Juncus acutus* community; (II) *Convolvulus persicus–Tournefortia sibirica* community; (III) *Artemisia campestris* subsp. *inodora–Daucus littoralis* subsp. *hyrcanicus* community; (IV) *Juncus acutus–Rubus sanctus* community along transition dune and/or backdune and (V) *Punica granatum* community.

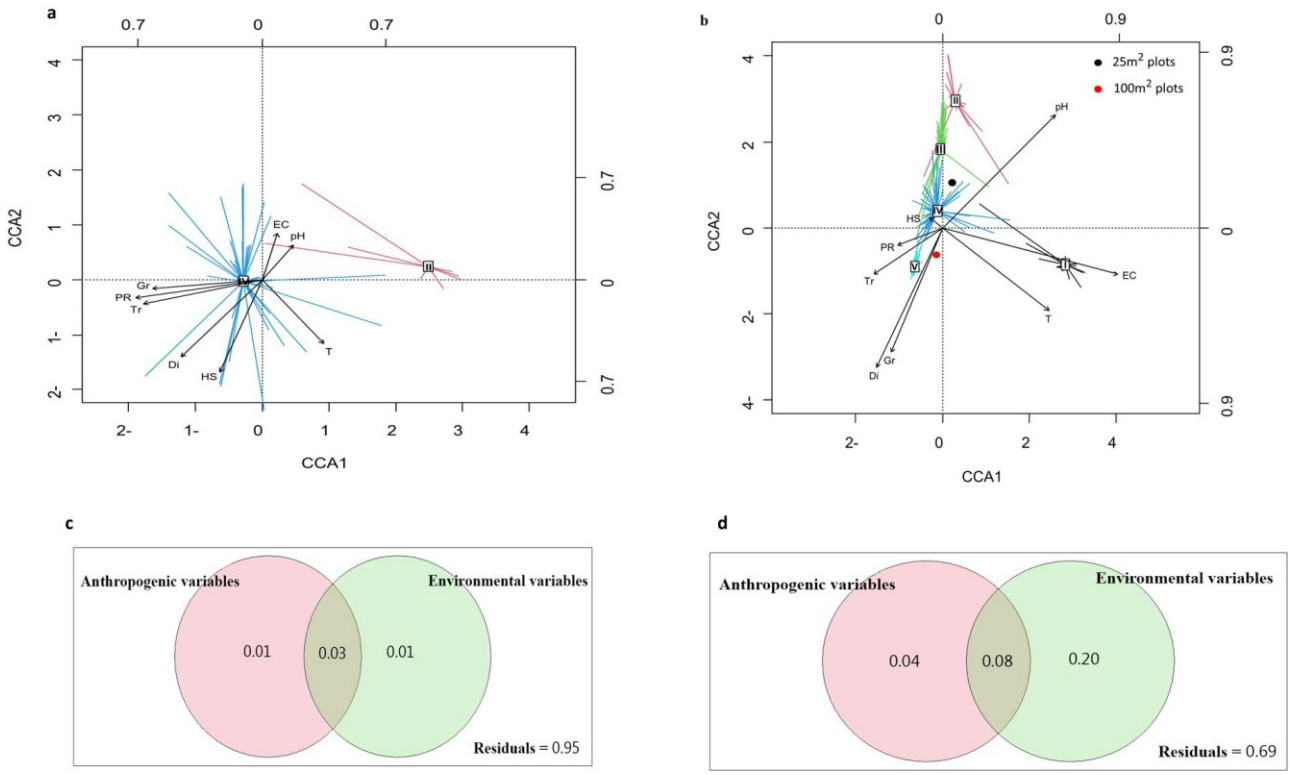

Figure 5. Canonical correspondence analysis (CCA) of the studied plots and variables in two western (a) and eastern (b) coastal parts. Numbers indicates vegetation plant communities according to Supplementary Table S3. Arrows represent the environmental variables. Eigenvalues of constrained and unconstrained axes were 0.68 and 0.72 for the first axis and 0.46 and 0.69 for the second axis in the western part and 0.75 and 0.65 for the first axis and 0.54 and 0.56 in the eastern part. Plot size was used as a dummy variable. Venn diagram showing the variance partitioning of conditional and shared effects of the groups of environmental and anthropogenic variables as fractions of the total inertia in the inset of figures ((c) for western and (d) for eastern coastal parts). Tr (Trampling), HS (Close to Human settlement), Gr (Grazing), PR (Path/Road), Di (Distance from the sea), T (Temperature), Hd (Hdune). (I) *Salicornia iranica–Juncus acutus* community; (II) *Convolvulus persicus–Tournefortia sibirica* community; (III) *Artemisia campestris* subsp. *inodora–Daucus littoralis* subsp. *hyrcanicus* community; (IV) *Juncus acutus–Rubus sanctus* community along transition dune and/or backdune and (V) *Punica granatum* community.