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Article

Vegetation Characteristics and Recent Successional Trends of Sand Dune Habitats at the Bulgarian Black Sea Coast

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Abstract: Coastal dunes are valuable and vulnerable habitats that require scientific exploration and understanding of their natural processes; therefore, the aims of this study were to determine the current vegetation characteristics of dune habitats along the Bulgarian Coast in terms of species richness and cover of typical psammophytes and different non-psammophytic plant groups, and to analyze how they respond to certain environmental drivers. Data were collected from 12 dune systems. The research was focused on embryonic, white and grey dunes. The field work was conducted throughout July and August 2017. The vegetation was sampled at 154 phytosociological plots (5 m × 5 m). To understand how the vegetation responds to different drivers, we tested the correlation of defined species group richness and cover in relation to (1) the soil pH and EC values, (2) the distance from inland to the sea and (3) the range of different categories of land cover in the surrounding area. In order to track temporal vegetation changes, we compared the cover of defined species groups between 2003 and 2017. We registered a total number of 269 vascular plants, 12 bryophytes and 5 lichens. The strongest presence in all dune types, both in species richness and cover, was the group of grass- and shrubland plants. Weeds and ruderal plants had significant coverage in grey dunes, while the richness and cover of forest and alien plants were negligible among the studied dune habitats. The comparison of data between 2003 and 2017 revealed a substantial decline in the cover of psammophytes. We observed a clear pattern regarding the share of species richness of psammophytes and non-psammophytes among different locations. We detected that grey dunes were the most affected by the penetration of non-psammophytes.

Keywords: environmental gradients; land-use change; plant species groups; alien species; forest; grassland; shrubland; psammophytes; ruderal plants; weed plants; temporal vegetation dynamics; West Pontic coast

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1. Introduction

As transitional ecosystems between land and sea, coastal dunes are unique habitats that are distributed among almost all latitudes under a wide range of climatic and geologic conditions [1] and characterized by high ecological diversity in terms of environmental heterogeneity and variability of species [2,3]. The strong environmental gradients, which are a characteristic feature of coastal dunes, allow for the coexistence of different plant communities in a relatively small area [4,5].

Coastal dune systems provide important ecosystem services [6], such as groundwater storage [7], water purification and coastal defense [8,9] and opportunities for recreation and tourism [10–12]. At the same time, they appear among the most threatened ecosystems on earth [13,14]. As emphasized by Weinstein [15], there is an urgent need for real compromises and sacrifices that will be necessary to achieve a sustainable coastal ecosystem, one that is economically feasible, socially just and ecologically sound. All over Europe, a net loss of coastal dunes of 25% has been reported since 1900, and 55% of the remaining coastal dune area has lost its natural character [16]. The pursuit of economic development in coastal areas has resulted in extensive modifications of sand dune ecosystems [17]. The structure and functions of coastal landscapes have been severely modified by constantly growing tourism, the expansion of urban areas and the spread of agriculture and afforestation activities [18–21]. Human pressure, causing physical and chemical changes in coastal dune soils, has led to a decrease and even local extinction of some species [22], as well as fragmentation, modification, and in some cases, the destruction of typical dune plant communities [23,24]. Currently, it is known that habitat loss, land-use change, and invasive species are accelerating the global rate of species extinction [25], and there is growing concern about biodiversity loss affecting ecosystem services and generally threatening human well-being [26,27].

Threats affecting European dune systems, such as urbanization, the extraction of materials, recreational seashore activities (including mechanical impact caused by trampling, camping, etc.), pollution, invasive species and natural system modifications [17,28], have also been documented at the sand dunes on the Bulgarian Black Sea coast [29–36], especially during the last few decades. Changes in land use from natural and semi-natural areas to agricultural land and urbanized territories are responsible for permanent modifications in the geomorphology of coastal habitats, while other anthropogenic pressures, such as mechanical cleaning practices and off-road vehicle use, have an ecological and short-term impact on sand dunes and psammophytic communities [37].

In accordance with their conservation significance on a European level [14,38], coastal sand dune habitats are considered to be of conservation importance on a national level as well—they are listed in Annex 1 of the Biological Diversity Act [39] and are also included in the Bulgarian Red Data Book [30–36]. A substantial part of their area in Bulgaria is included in the Natura 2000 network—58% of embryonic dunes, 73% of white (shifting) dunes, 89% of grey (fixed) dunes, 100% of wooded dunes and 67% of humid dune slacks [40].

Psammophytes are the typical and characteristic plant species of the dunes that have evolved multiple adaptive strategies, showing a high degree of functional diversity and complexity [41]. They survive in a specific environment with harsh conditions, such as sand burial and substrate mobility, salt spray, a dry substrate with occasional high temperatures near the surface, soil salinity and nutrient deficiency, intense directed and reflected radiation and high winds [42]. Being confined to the heavily impacted coastal dune systems, nowadays, their populations suffer from direct destruction, habitat loss and pollution. They provide good opportunities to analyze plant succession and colonization, and because of this, coastal dune systems have been among the first studied in terms of these processes [43–46]. Sand dune habitats are a particularly suitable object for observation because vegetation and habitat changes on coasts are often drastic and fast [47]. Recently, studies on the presence and importance of alien species in coastal ecosystems have increased significantly [48–59], but, unfortunately, these are not the only risk factors for the fate of psammophytic vegetation. The natural and anthropogenic-induced processes of sand dune stabilization, accompanied by accumulation of organic matter [60], might create favorable conditions for the penetration of not only alien but also native plant species with different habitat type preferences. Limited numbers of studies deal with this problem [24,61–63], but we consider this issue important because the presence of non-psammophytes might cause changes in the structure and functions of coastal dune ecosystems.

Further protection of the valuable and vulnerable habitats that coastal dunes are requires scientific exploration and understanding of their natural processes in order to form the basis of appropriate conservation activities and management strategies. Therefore, the aims of this study were (1) to determine the current vegetation characteristics of sand dune habitats from the Bulgarian Black Sea Coast in terms of species richness and cover of typical psammophytes and different non-psammophytic plant groups, (2) to analyze how far the species richness and cover of the defined plant groups respond to certain environmental drivers, and (3) to establish temporal trends in the cover of different species groups by using our own samples and existing literature data from 2003, as criteria for their current status, future management and conservation measures.

2. Materials and Methods

2.1. Study Area

Out of the total coastal length of 4740 km of the Black Sea [64], the Bulgarian coastline consists of 412 km, located between Cape Sivriburun in the north to the Romanian border and Rezovska River mouth in the south to the Turkish border [65]. Cape Emine (the most eastern part of the Balkan Range) is a geographical barrier dividing it into southern and northern parts [66]. According to Popov and Mishev [67], sand dunes and beaches occupied 28% of the coastal strip with a total area of 16 km^2, but more recent studies show that, due to increased human activities, the total dune landscape is constantly diminishing, and dunes cover only 10% of the entire coastline; the total length of the sand dunes is 38.57 km and the total area is 8.78 km^2 [68]. Sand dunes at the northern part of the Bulgarian coast cover larger coastal areas compared to the numerous dune complexes from the southern part, which are formed in the inlets between small rocky capes and lagoons [68]. The longest beach strip is Kamchia Sands and Skorpilovtsi, with a length of 11.2 km [67]. Dune heights range from 2 to 44 m and the highest dune is at Arkutino [69].

Due to the importance of land–sea circulation systems, the Bulgarian Black Sea coastline is a separate climatic region within the Continental–Mediterranean climatic zone [70]. Warm summers and mild winters (with positive January temperatures) are typical, but the more northern areas are characterized by lower annual precipitation and lower average winter temperatures (480 mm, 0.6 °C, town of Balchik) compared to the southern ones (700 mm, 4 °C, town of Tsarevo) [70]. The coastal vegetation reflects these climatic differences, and commonly, the geographical border (Cape Emine) is also perceived as a phytogeographical border between the northern and southern parts of the coastline [71]. Currently, for dune vegetation, in particular, Tzonev et al. [72] assumed that the flora and vegetation of the large dune complex near the Kamchia River mouth, located north of Cape Emine, rather belong to the southern group of phytocoenoces.

According to the EUNIS habitat classification [73], Bulgarian sand dunes comprise the following habitats: N12 Mediterranean and Black Sea sand beach; N14 Mediterranean, Macaronesian and Black Sea shifting coastal dune; N17 Black Sea coastal dune grassland (grey dune); N1E Black Sea broad-leaved coastal dune forest; N1J Mediterranean and Black Sea moist and wet dune slack. These types respond to the following Natura 2000 habitats: Embryonic shifting dunes (habitat 2110); Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes) (habitat 2120); Fixed coastal dunes with herbaceous vegetation (grey dunes) (habitat 2130); Wooded dunes of the Atlantic, Continental and Boreal region (habitat 2180); Humid dune slacks (habitat 2190).

The Bulgarian Black Sea dune vegetation was last studied by Tzonev et al. [72] and classified into broadly accepted classes of European dune vegetation, including embryonic dunes of *Cakiletea maritimae*, represented by one alliance (*Euphorbion peplidis*) with one association (*Cakilo euxinae-Salsoletum ruthenicae*), and white and grey dunes of class *Ammophiletea*, with three alliances (*Elymion gigantei* with two associations, *Xanthio italici-Leymetum sabulosi* and *Medicago tenderiensis-Ammophiletum arundinaceae*; *Scabiosion ucrainicae* with three associations, *Alysso borzaeani-Ephedretum distachyae*, *Stachyo atherocalici-Caricetum ligericae* and *Festuca arenicola* community; *Sileno thymifolae-Jurinion kilaeae* with one association, *Aurinio uechtritziani-Artemisietum campestris*). A recent critical revision of the white and grey dune vegetation of Europe and extra-European parts of the Mediterranean Basin [74] confirmed the syntaxonomical scheme of Tzonev et al. [72].

2.2. Data Sampling and Processing

We selected 12 representative dune systems (Figure 1) to reveal the current vegetation characteristics of psammophytic communities of the Bulgarian Black Sea Coast. Our research was focused on Natura 2000 habitats 2110, 2120, and 2130 (referred to as embryonic, white and grey dunes, respectively, hereinafter), as they form the most substantial part of these large dune complexes (Figure 2).

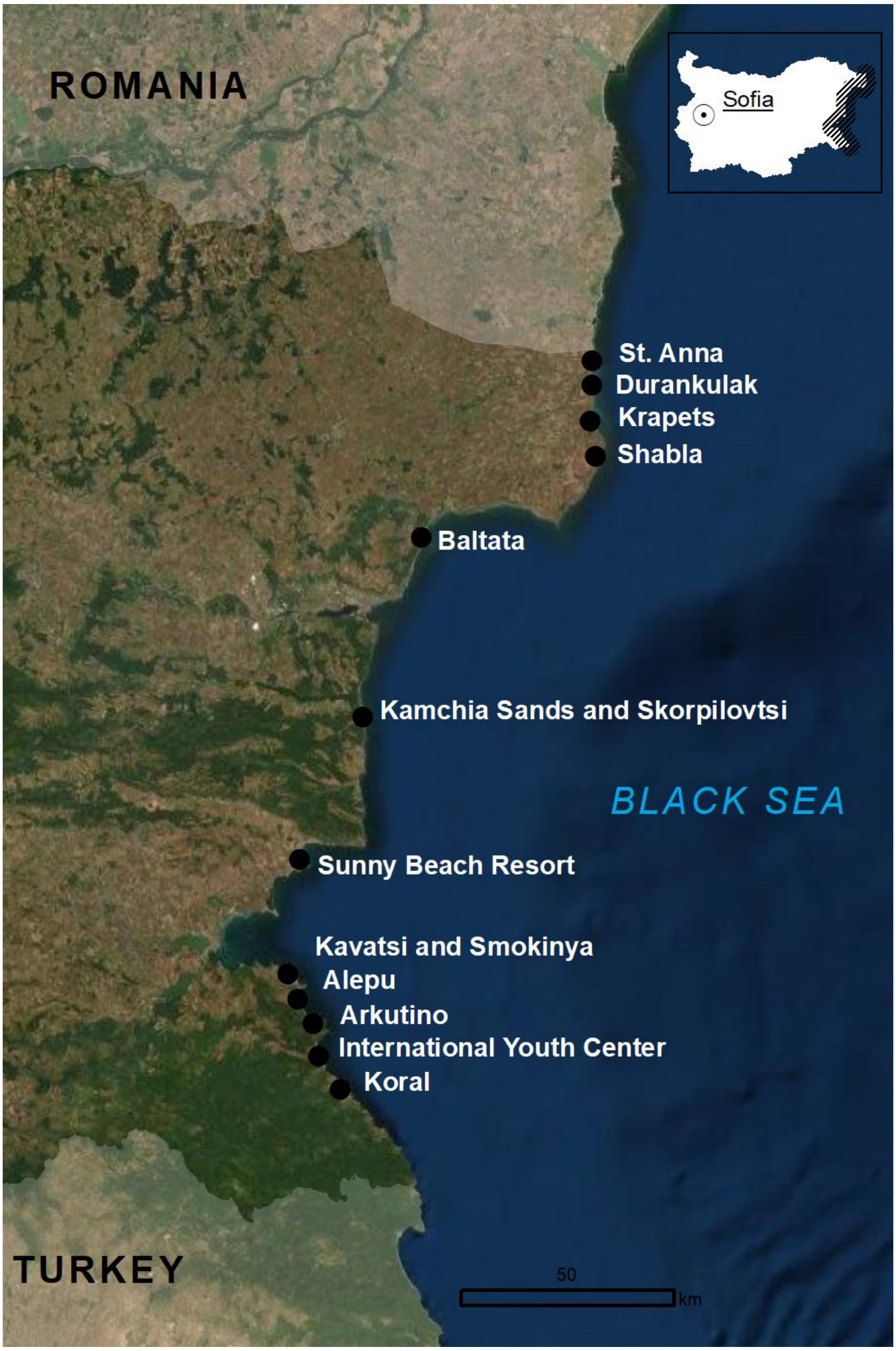

Figure 1. Map of the Bulgarian Black Sea Coast with the 12 studied locations marked. ArcGIS Desktop ver. 10, ESRI Basemap.

(**a**) (**b**) (**c**)

Figure 2. Typical profile of different dune habitats from the Bulgarian Black Sea Coast. (**a**) embryonic dunes; (**b**) white dunes; (**c**) grey dunes.

The field work was conducted throughout July and August 2017 because the majority of typical psammophytes develop and flower in this particular period. For the spring flowering plants, we conducted preliminary visits to the sites in April 2017 in order to properly identify their remnants registered in the plots. The vegetation was sampled at 154 phytosociological plots (5 m × 5 m). Of these, 102 were placed along 17 transects orthogonal to the seashore, with 20 m of distance between the plots, starting from inland to the sea, and ending at the upper active beach zone. The transects were located with consideration for the land cover categories in the dune system's adjacent territories; in most of the studied localities, we made one transect, but a few of the dune complexes bordered with a more heterogeneous territory, so we made more transects to cover those differences. The remaining 52 plots were visually determined as typical sections of the studied dune habitats that are present in the respective dune system. A complete list of vascular plants, bryophytes and lichens, the percentage cover of each vascular plant species, the total vegetation cover and separate cover of lichens and bryophytes and bare sand were recorded for each plot. Additionally, we recorded all vascular plants not registered in the plots in 5 m-wide transects parallel to the coastline in each habitat type. A mixed sand sample was collected from the upper horizon (up to 10 cm) from all four corners of each plot from the 17 orthogonal to the seashore transects. The 102 samples were subjected to analyses of the soil pH and electrical conductivity (EC) in the Research Geological Laboratory "GeoLab" of the Geological Institute at the Bulgarian Academy of Sciences, Sofia, following the requirements of the International Organization for Standardization (ISO) for "Determination of pH" (ISO 10390) and "Determination of the specific electrical conductivity" (ISO 11265).

For the purposes of the analyses, we classified all registered vascular plants either as typical coastal psammophytes (species occupying sandy substrates and playing an important role in dune formation), or as non-typical species, which we refer to as non-psammophytes. The latter were further assigned to one of the following groups according to their main habitat preference and using the approach of Valcheva et al. [63]: weeds and ruderals; grass- and shrubland plants; forest plants; alien (including invasive) species (see Supplementary ESM S1). Vascular plants nomenclature was applied according to Euro+Med PlantBase [75]. Bryophyte nomenclature was applied according to Hill et al. [76], while lichen nomenclature was applied according to Nimis and Martellos [77].

In order to analyze how sand dune vegetation responds to different landscape drivers, the range of land cover categories was calculated in a 1 km circular buffer around the starting point of every orthogonal transect for the years 2006, 2011 and 2017. Aerial photos from the period 2006–2017, as a part of the Integrated Administration and Control System (IACS) (data provided by the Ministry of Agriculture, Food and Forestry of the Republic of Bulgaria), were used to calculate the range of different land cover categories. The spatial resolution of the used photos was 0.4 m. The created layer had a minimum mappable unit of 1000 m^2. The following classification of land cover categories was used: (1) annual crops; (2) perennial crops and heterogeneous agricultural areas; (3) natural and semi-natural grass communities; (4) forest areas; (5) urbanized and anthropogenically disturbed territories; (6) roads and transport infrastructure; (7) water areas and wetlands. For a more precise border between the coastal dunes and inland areas, the Specialized Maps of the Dunes on the Black Sea Coast were used [78]. The areas covered by sand dunes and sea in the buffers were excluded for the purposes of the analysis. Data were generated using ArcGIS Desktop ver. 10.x [79] (see Supplementary ESM S2).

An analysis of similarities (ANOSIM) [80] was performed to prove the differences in species composition among the studied dune types. In addition, we used MDS (non-metric multidimensional scaling) to visualize the distances between the plots in different dune types based on the Bray–Curtis similarity index by species composition. We also used similarity percentage analysis (SIMPER) [80] to determine the non-psammophytes that contributed the most to the resemblances between plots from different dune types that were detected by the ANOSIM procedure. Both the ANOSIM and SIMPER analyses and the MDS visualization were carried out in PRIMER version 6.1.6 [81]. In STATISTICA [82], we carried out a test for normality (Kolmogorov–Smirnov) and after obtaining the results, we applied non-parametric Kruskal–Wallis ANOVA to test the significance of the differences in defined species group richness and cover among dune types. Additionally, differences between species richness and cover of psammophytes and non-psammophytes were graphically expressed by their mean values and standard deviations for every dune type from the 12 studied locations.

To understand how vegetation responds to different drivers, we tested the correlation of defined species group richness and cover (Spearman rank-order correlations) to (1) the pH and EC values, (2) the distance from inland to the sea and (3) the range of the different categories of land cover in the buffers of the transects for 2017. We then applied a regression, carried out in STATISTICA 13 [82]. In addition, the changes of different vegetation parameters against the distance from inland to the sea were graphically expressed by scatterplots for all the studied locations.

In order to track temporal vegetation changes, we compared the cover of defined species groups between 2003 and 2017 based on data from the sand dune vegetation study by Tzonev et al. [72], which included 86 phytosociological plots with the same size as ours (25 m^2) from 2017. The same number of plots (7 from embryonic, 19 from white and 60 from grey dunes) from the same or the closest possible locality were extracted randomly for the purpose of the analyses from the data we collected in 2017. Since Tzonev et al. [72] excluded bushes and forests in their research work, we also omitted all forest species registered in the plots from 2017. For further calculations, we transformed all cover values from both our original percentage data from 2017 and the Braun–Blanquet cover classes [83] data from 2003 [72] to median values (Table 1), following the approach of Vittoz and Guisan [84]. For a graphical representation of the changes in cover among defined species groups between 2003 and 2017 for each dune type (by their mean values and standard deviations), we used STATISTICA [82].

Table 1. Transformation from Braun–Blanquet cover classes [83], estimated in plots from 2003 [72], and percentage values in our plots from 2017 to median values used for analyses.

Braun–Blanquet Class	Cover (%)	Value Taken for Analyses (%)
r	<0.1	0.1
+	0.1–1	0.5
1	1–5	2.5
2	5–25	12.5
3	25–50	37.5
4	50–75	62.5
5	75–100	87.5

3. Results

3.1. Vegetation Characteristics

We registered a total number of 269 vascular plants in all 12 studied locations. Among them, 48 species were identified as typical psammophytes, 41 were weeds and ruderals, 142 were considered typical for grasslands and shrublands, 20 were characteristic for forests and 20 were alien (including invasive) plants (see Supplementary ESM S1). We also recorded 12 bryophytes and 5 lichens in the plots (Supplementary ESM S1).

The ANOSIM analysis and MDS-visualization revealed differences in species composition among the studied dune types (embryonic, white, grey) (R = 0.371; p = 0.01) as well as between grey and white dunes (R = 0.164; p = 0.01), grey and embryonic dunes (R = 0.713; p = 0.01) and embryonic and white dunes (R = 0.485, p = 0.01) (Figure 3).

We found that while the species richness of psammophytes did not differ much among different dune types, their cover varied significantly—the highest was registered in grey, and the lowest in embryonic dunes (Table 2). The species richness and cover of non-psammophytes were highest in grey dunes and lower throughout white and embryonic dunes (Table 2). The strongest presence in all dune types, both in species richness and in cover, was the group of grass- and shrubland plants. Weeds and ruderal plants had significant cover in grey dunes, while richness and cover of forest and alien plants were negligible among the studied dune habitats (Table 2). The richness and cover of lichens and bryophytes were concentrated in grey dunes (Table 2).

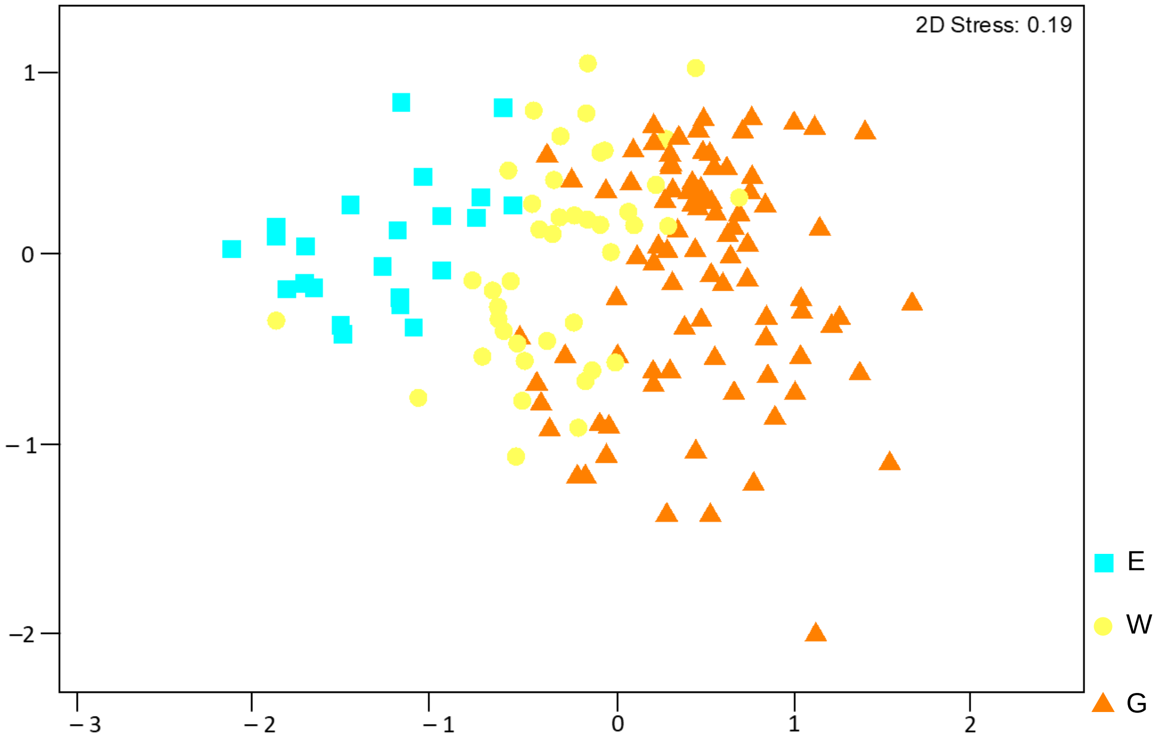

Figure 3. MDS—visualization of the distances between plots in different dune types (coded as follows: E—embryonic, W—white and G—grey dunes) based on the Bray–Curtis similarity index by species composition.

Table 2. Vegetation characteristics of studied dune habitats. Means and standard deviations are given; *p*-values derived from Kruskal–Wallis ANOVA (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$).

	Embryonic Dunes	**White Dunes**	**Grey Dunes**	***p***
Number of Cases (Plots)	**24**	**42**	**88**	
Parameters	**(Mean ± SD)**	**(Mean ± SD)**	**(Mean ± SD)**	
Species richness of vascular plants	7.5 ± 2.5	10.2 ± 3.2	13.0 ± 5.9	***
Species richness of psammophyte plants	6.5 ± 2.4	6.8 ± 2.3	5.3 ± 2.6	**
Species richness of non-psammophytes	1.0 ± 1.0	3.4 ± 2.5	7.6 ± 5.5	***
Species richness of weeds and ruderal plants	0.3 ± 0.6	0.3 ± 0.6	1.2 ± 1.7	**
Species richness of grass- and shrubland plants	0.2 ± 0.4	2.9 ± 2.2	6.1 ± 4.0	***
Species richness of alien plants	0.5 ± 0.5	0.1 ± 0.3	0.2 ± 0.5	***
Species richness of forest plants	0.0 ± 0.0	0.0 ± 0.2	0.2 ± 0.4	*
Species richness of lichens and bryophytes	0.0 ± 0.0	0.0 ± 0.2	1.4 ± 1.1	***
Total vegetation cover (%)	14.5 ± 8.2	36.4 ± 14.2	67.4 ± 24.2	***
Cover of psammophyte plants (%)	13.2 ± 7.4	29.9 ± 12.6	33.5 ± 18.9	***
Cover of non-psammophytes (%)	1.1 ± 2.2	6.8 ± 7.2	21.9 ± 26.1	***
Cover of weeds and ruderal plants (%)	0.1 ± 0.3	0.3 ± 1.0	5.2 ± 15.6	**
Cover of grass- and shrubland plants (%)	0.4 ± 1.6	6.1 ± 6.8	14.3 ± 18.5	***
Cover of alien plants (%)	0.6 ± 1.5	0.3 ± 1.4	1.2 ± 4.7	**
Cover of forest plants (%)	0.0 ± 0.0	0.0 ± 0.2	1.2 ± 5.2	*
Cover of lichens and bryophytes (%)	0.0 ± 0.0	0.0 ± 0.2	28.4 ± 28.8	***
Cover of open sand (%)	85.5 ± 8.2	63.6 ± 14.2	32.6 ± 24.2	***

The SIMPER analysis results demonstrate that the non-psammophytes that contributed the most to the species composition similarity between plots in grey dunes were *Alyssum hirsutum* (10.15%), *Anisantha tectorum* (7.28%), *Lomelosia argentea* (6.14%), *Teucrium polium* (3.34%), *Chondrilla juncea* (2.35%), *Anthemis arvensis* (1.53%), *Silene conica* ssp. *cono-*

maritima (1.29%), *Linaria genistifolia* (1.22%), *Erysimum diffusum* (1.21%) and *Medicago falcata* (1.14%). For plots in white dunes, they were *Alyssum hirsutum* (8.38%), *Euphorbia seguieriana* (4.11%), *Linaria genistifolia* (3.9%), *Medicago falcata* (3.5%) and *Astragalus onobrichys* (1.12%). For plots in embryonic dunes, *Xanthium orientale* ssp. *italicum* (6.5%) accounted the most for the species composition similarity.

In the 12 studied locations, the species richness of psammophytes and non-psammophyte species was more or less the same (Figure 4a), but the cover of typical psammophyte plants prevailed in all locations except in Krapets (Figure 5a). Both the richness and the cover of non-psammophytes were low in plots from embryonic dunes from all studied locations (Figures 4b and 5b), and in plots from white dunes, their richness and cover were considerable in some of the dune systems at the northern part of the coast, including Baltata, Durankulak, Shabla and St. Anna (Figures 4c and 5c). The species richness of non-psammophytes was higher than the richness of psammophyte species in plots from grey dunes from all dune systems except Arkutino (Figure 4d), while the cover of non-psammophytes prevailed only in plots from Krapets (Figure 5d).

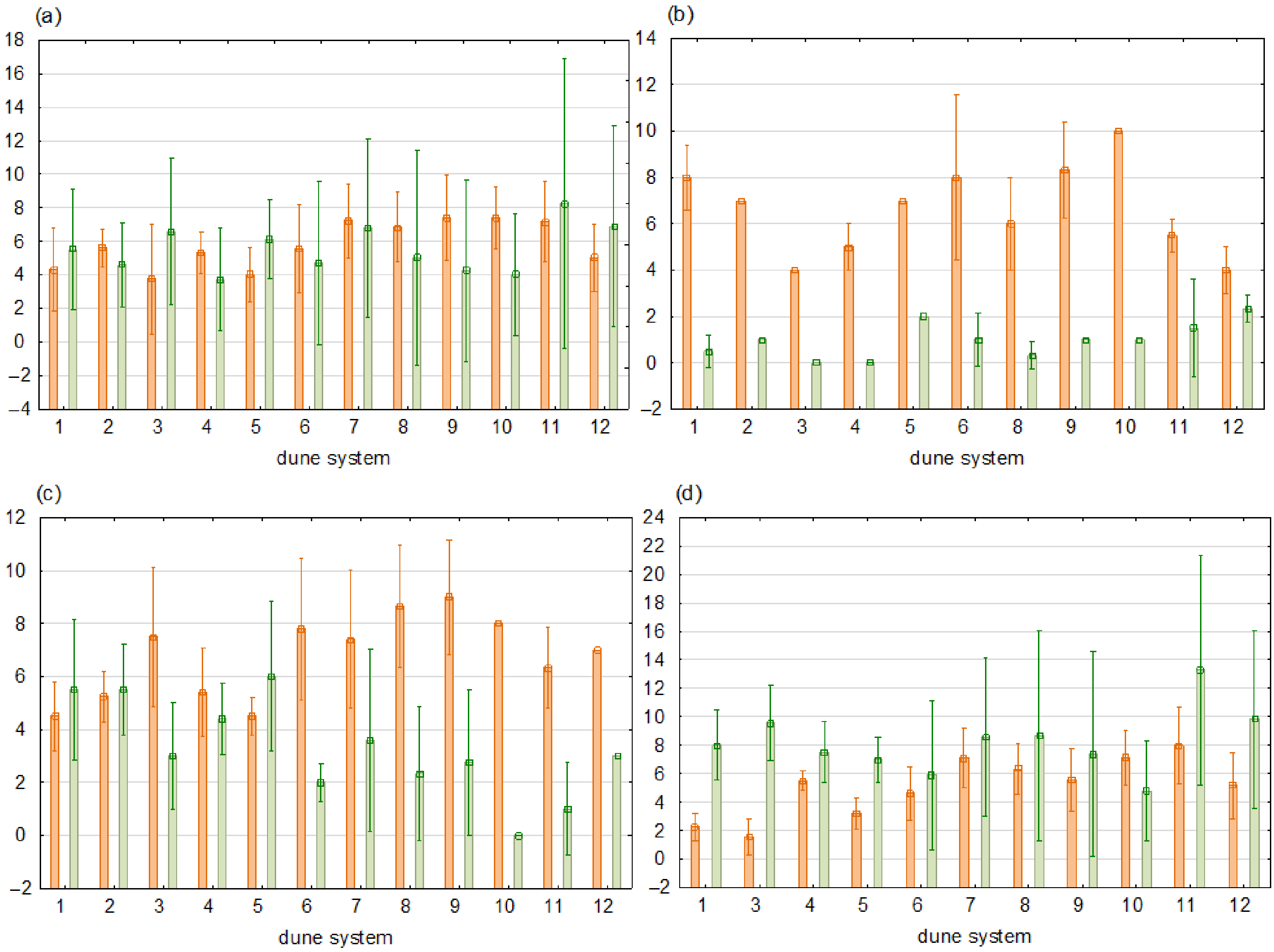

Figure 4. Mean species richness (columns) and standard deviations (whiskers) of psammophytes (orange) and non-psammophytes (green) grouped by the 12 studied locations (numbered as follows: 1—St. Anna; 2—Durankulak; 3—Krapets; 4—Shabla; 5—Baltata; 6—Kamchia Sands and Skorpilovtsi; 7—Sunny Beach Resort; 8—Kavatsi and Smokinya; 9—Alepu; 10—Arkutino; 11—International Youth Center; 12—Koral) for (**a**) all habitat types; (**b**) embryonic dunes; (**c**) white dunes; (**d**) grey dunes.

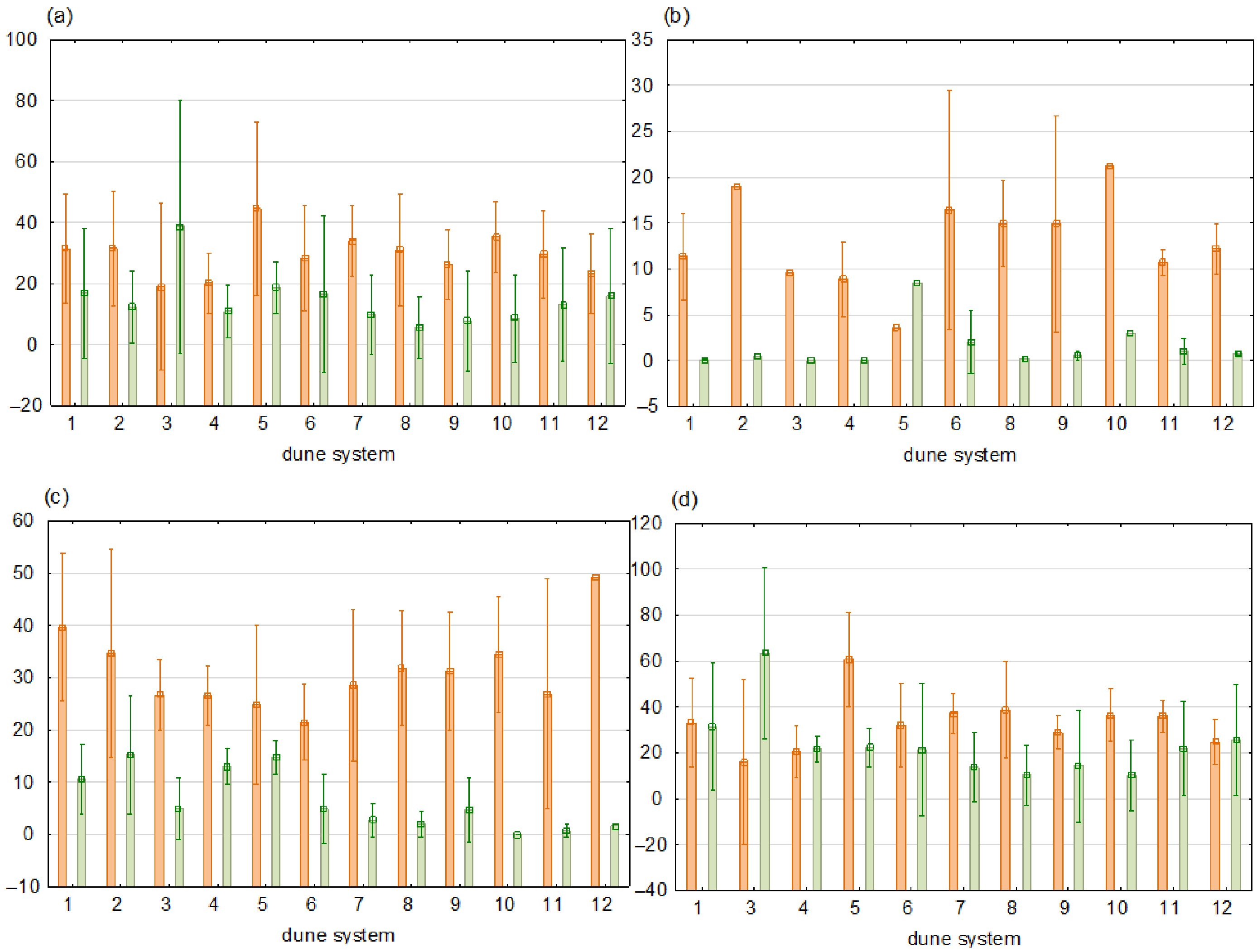

Figure 5. Mean cover (columns) and standard deviations (whiskers) of psammophytes (orange) and non-psammophytes (green) grouped by 12 studied locations (numbered as follows: 1—St. Anna; 2—Durankulak; 3—Krapets; 4—Shabla; 5—Baltata; 6—Kamchia Sands and Skorpilovtsi; 7—Sunny Beach Resort; 8—Kavatsi and Smokinya; 9—Alepu; 10—Arkutino; 11—International Youth Center; 12—Koral) for (**a**) all habitat types; (**b**) embryonic dunes; (**c**) white dunes; (**d**) grey dunes.

3.2. Environmental Drivers

The results from soil sample analyses show the prevailing alkaline character of the Bulgarian coastal dunes (the only exception was the dune system of Kamchia Sands and Skorpilovtsi, where the reaction varied from slightly acidic through neutral to alkaline) (Figure 6a), along with very low ECs among studied locations (the highest values were measured at Krapets and Durankulak) (Figure 6b). Soil reaction became more alkaline and EC values were lower closer to the sea. Statistically significant results from correlation and regression analyses of different vegetation parameters and soil pH and EC are shown in Table 3. Correlations for soil pH were weak, and for EC stronger correlations were registered for the species richness and cover of weeds and ruderal plants, the richness of grass- and shrubland plants and non-psammophytes in general, as well as for total vegetation cover (Table 3).

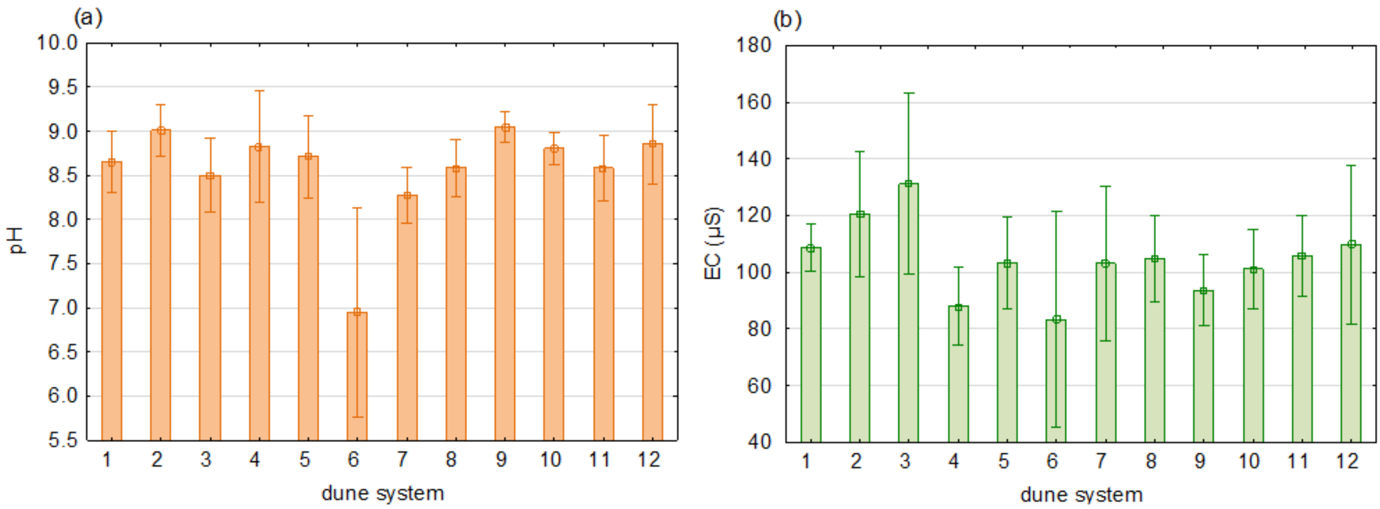

Figure 6. Mean values (columns) and standard deviations (whiskers) of (**a**) soil pH and (**b**) soil EC in the 12 studied locations, which are numbered as follows: 1—St. Anna; 2—Durankulak; 3—Krapets; 4—Shabla; 5—Baltata; 6—Kamchia Sands and Skorpilovtsi; 7—Sunny Beach Resort; 8—Kavatsi and Smokinya; 9—Alepu; 10—Arkutino; 11—International Youth Center; 12—Koral.

Table 3. Correlations and regressions of richness and cover of different species groups in relation to the soil pH and EC values. Only statistically significant results at $p < 0.05$ are shown.

Number of Cases (Plots): 102	**pH**				**EC (µS)**			
Parameter	**Spearman Rank Correlations**	**Multiple R**	**Multiple R^2**	**Adjusted R^2**	**Spearman Rank Correlations**	**Multiple R**	**Multiple R^2**	**Adjusted R^2**
Species richness of vascular plants	-	-	-	-	0.342	0.315	0.099	0.09
Species richness of psammophyte plants	-	0.269	0.072	0.063	-	0.241	0.058	0.049
Species richness of non-psammophytes	−0.253	-	-	-	0.498	0.46	0.212	0.204
Species richness of weeds and ruderal plants	-	-	-	-	0.41	0.566	0.321	0.314
Species richness of grass- and shrubland plants	−0.262	-	-	-	0.432	0.365	0.133	0.125
Species richness of forest plants	-	-	-	-	0.267	0.334	0.112	0.103
Total vegetation cover (%)	−0.281	0.202	0.041	0.031	0.499	0.471	0.222	0.214
Cover of non-psammophytes (%)	−0.293	-	-	-	0.331	0.587	0.345	0.338
Cover of weeds and ruderal plants (%)	-	-	-	-	0.45	0.391	0.153	0.145
Cover of grass and shrubland plants (%)	−0.273	0.209	0.044	0.034	0.232	0.455	0.207	0.199
Cover of alien plants (%)	-	0.235	0.055	0.046	-	-	-	-
Cover of forest plants (%)	-	-	-	-	0.27	0.21	0.044	0.034

The results for different vegetation characteristics in relation to the distance from inland to the sea show an increase in species richness of psammophytes, while the total vegetation cover and the cover of non-psammophytes, lichens and bryophytes decreased from inland to the sea. Changes in different plant group species richness in relation to the distance from inland to the sea differed among the studied locations (Figure 7). There was a more obvious pattern in changes of their cover along the vegetation zone gradient in the 12 dune systems, where total vegetation cover decreased and bare sand increased against the sea, but the cover of psammophytes displayed different rates of change in the studied localities (Figure 8).

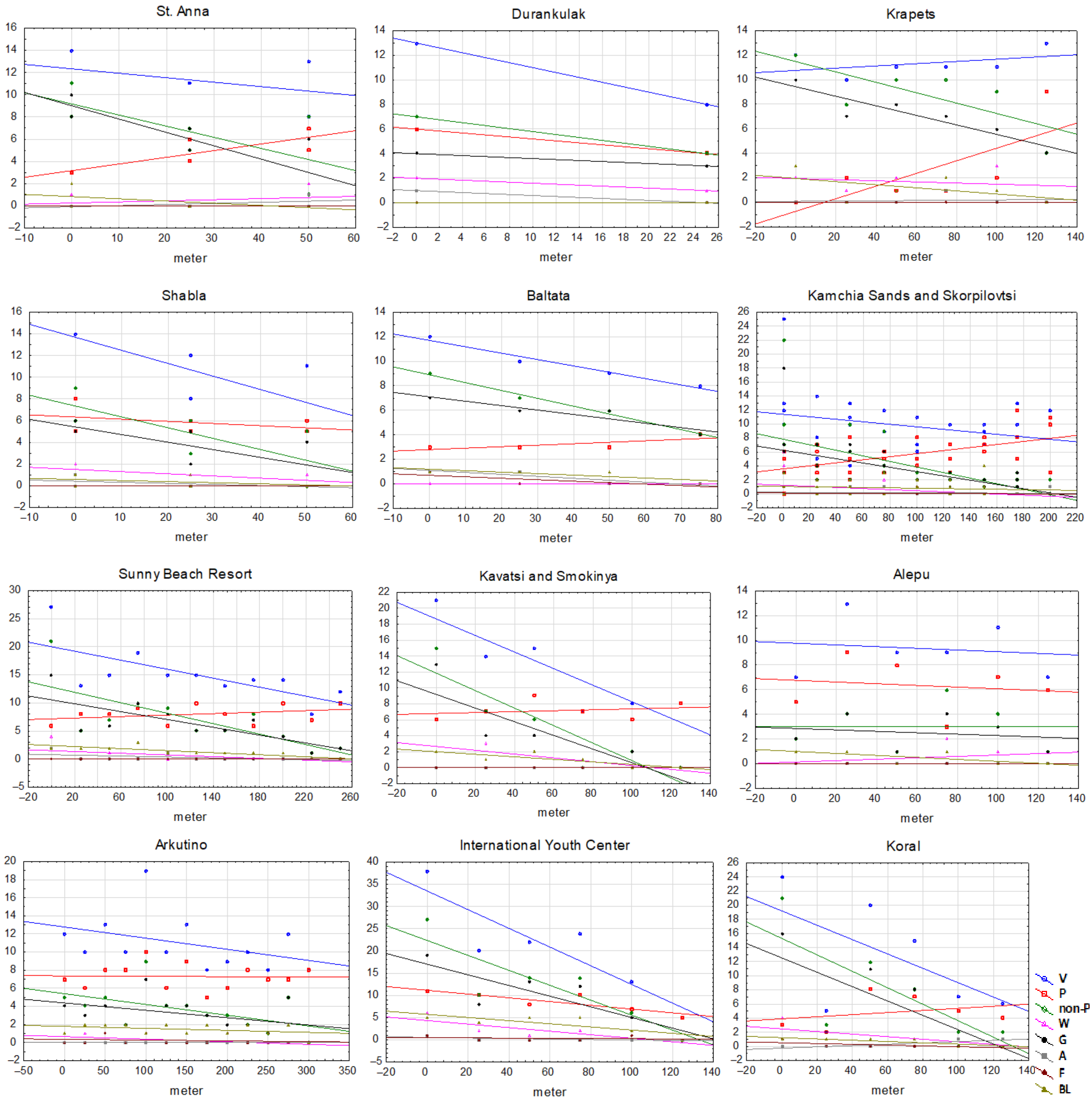

Figure 7. Species richness of different plant groups (coded as follows: V—all vascular plants: P—psammophytes, non-P—non-psammophytes; W—weeds and ruderals, G—plants typical of grasslands and shrublands, A—alien (including invasive) species; F—forest species; BL—bryophytes and lichens) in relation to the distance from inland to the sea (m), for all studied locations.

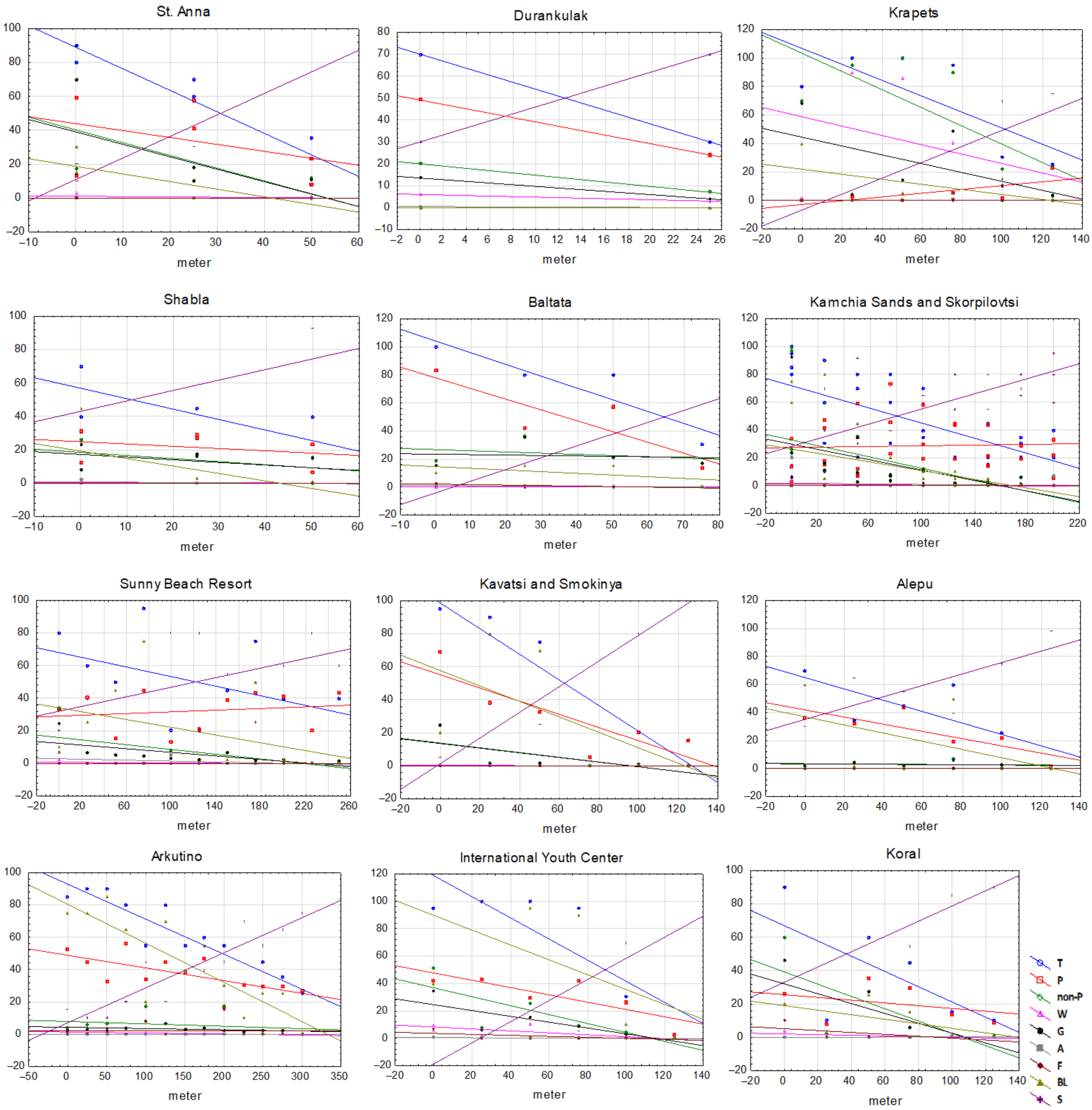

Figure 8. Cover of different species groups and bare sand (%) (coded as follows: T—total vegetation cover: P—psammophytes, non-P—non-psammophytes; W—weeds and ruderals, G—plants typical of grasslands and shrublands, A—alien (including invasive) species; F—forest species; BL—bryophytes and lichens; S—bare sand) in relation to the distance from inland to the sea (m), for all studied locations.

There were no remarkable changes in the land cover types in the buffers around the studied transects for the period of 2006–2017 (Figure 9a–g; Supplementary ESM S2). We detected a decrease in the area of natural and semi-natural grass communities (Figure 9c) and an increase in the area of urbanized and anthropogenically disturbed territories (Figure 9e,f). The results show a larger share of annual crops in the buffers from the northern dune systems (Figure 9a), while roads and transport infrastructure, as well as urbanized territories, covered larger areas in the buffers from the southern ones (Figure 9e,f).

The most significant decrease in natural and semi-natural grass communities (Figure 9c) was detected at Baltata, Kavatsi and Smokinya and Alepu. Some increase in the forest area was detected at Baltata (Figure 9b).

The results for the correlation of richness and cover of different species groups to the range of different categories of land cover in the buffers show that land cover types slightly affected dune vegetation. With the enlargement of the area covered by annual crops, the species richness of psammophytes and the richness and cover of lichens and bryophytes decreased, while the cover of non-psammophytes (mostly weeds and ruderals) increased. The enlargement of the area covered by roads and urbanized territories in the buffers supported an increase in the total number of vascular plants (Table 4).

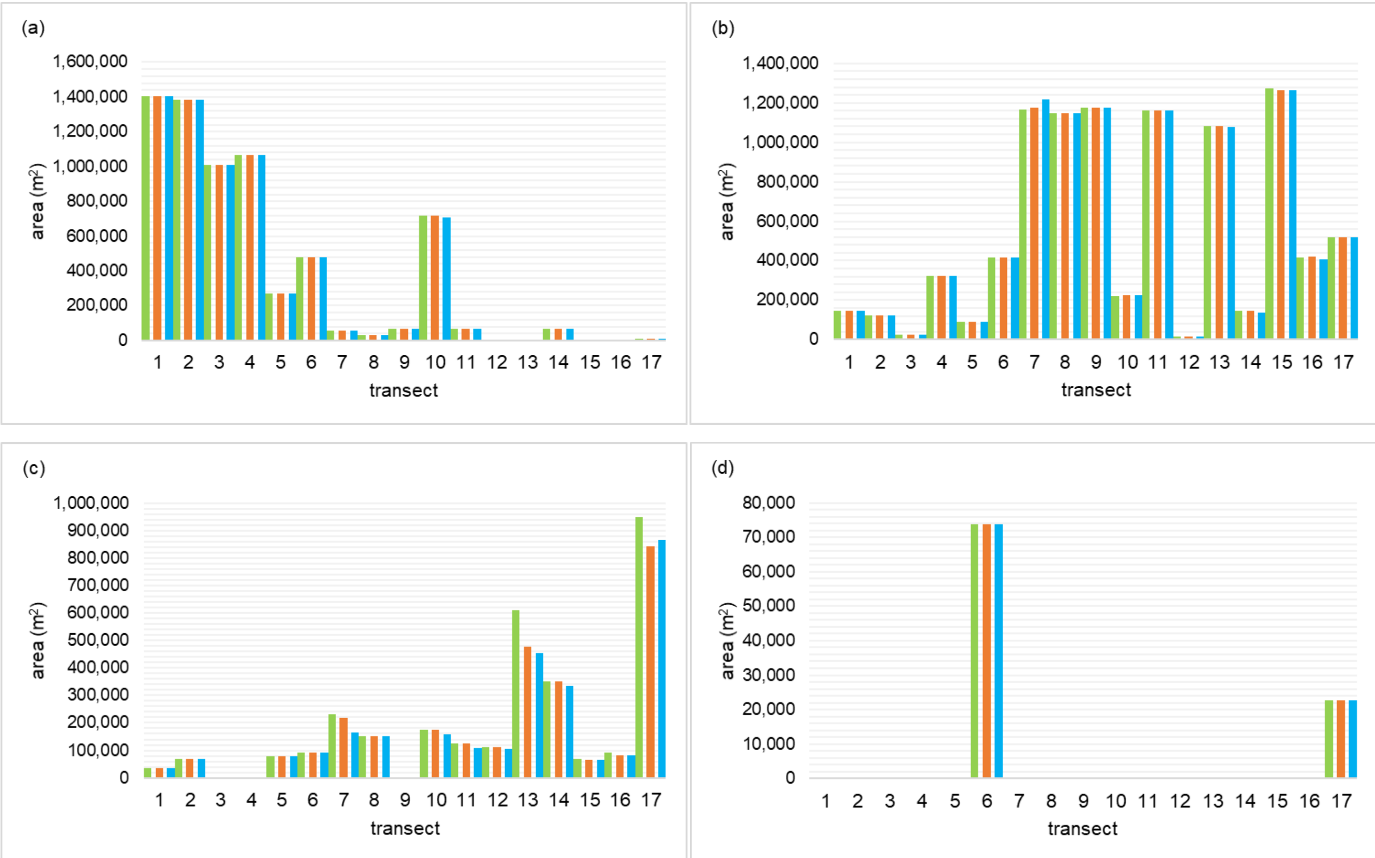

Figure 9. *Cont.*

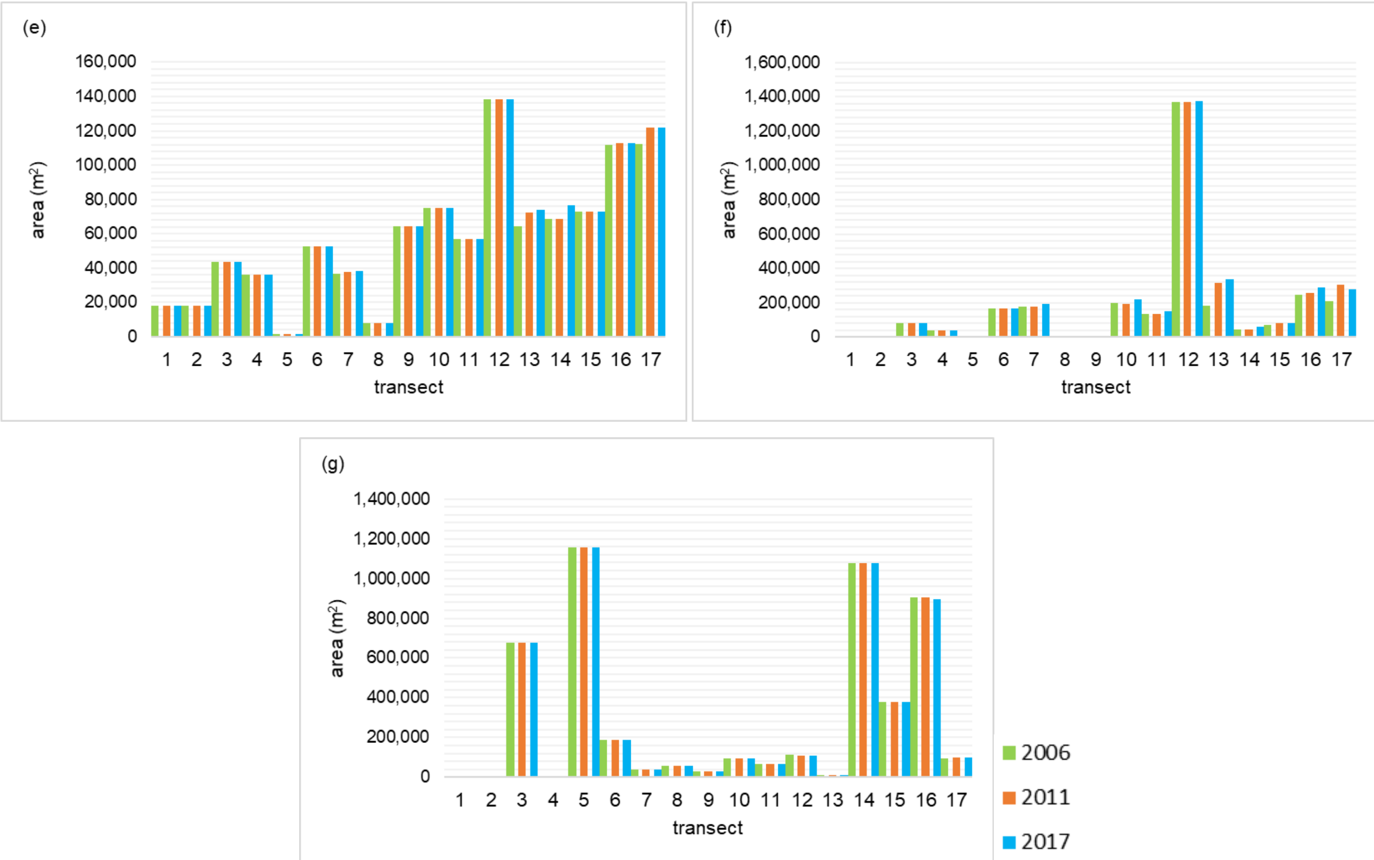

Figure 9. Changes in different categories of land cover between years 2006, 2011 and 2017—(**a**) annual crops, (**b**) forest areas, (**c**) natural and semi-natural grass communities, (**d**) perennial crops and heterogeneous agricultural areas, (**e**) roads and transport infrastructure, (**f**) urbanized and anthropogenically disturbed territories, (**g**) water areas and wetlands—in the buffers of 17 transects (1—St. Anna—north; 2—St. Anna—south; 3—Durankulak; 4—Krapets; 5—Shabla—north; 6—Shabla—south; 7—Baltata; 8—Kamchia Sands—north; 9—Kamchia Sands—south; 10—Skorpilovtsi—north; 11—Skorpilovtsi—south; 12—Sunny Beach Resort; 13—Kavatsi and Smokinya; 14—Alepu; 15—Arkutino; 16—International Youth Center; 17—Koral) (see Supplementary ESM S2).

Table 4. Correlation and regression of richness and cover of different species groups in relation to the range of different categories of land cover (in m^2) in the buffers of the transects in 2017. Only statistically significant results at $p < 0.05$ are shown. Result values are coded as follows: 1—Spearman rank correlations; 2—multiple R.

Number of Cases (Plots): 102	Annual Crops		Urbanized and Anthropogenically Disturbed Territories		Roads and Transport Infrastructure	
Parameter	**1**	**2**	**1**	**2**	**1**	**2**
Species richness of vascular plants	−0.206	-	0.289	0.284	0.342	0.332
Species richness of psammophyte plants	−0.486	0.357	-	-	-	-
Species richness of lichens and bryophytes	−0.449	0.252	-	-	-	-
Cover of non-psammophytes (%)	0.28	0.331	-	-	-	-
Cover of weeds and ruderal plants (%)	-	0.327	-	-	-	-
Cover of grass- and shrubland plants (%)	0.29	0.226	-	-	-	-
Cover of lichens and bryophytes (%)	−0.421	0.236	-	-	-	-

3.3. Recent Successional Trends

The comparison of the data between 2003 and 2017, in general, revealed a substantial change in the cover of psammophytes, which halved over time, unlike the cover of the other species groups, which remained relatively stable (Figure 10a). An even more drastic decrease in the cover of psammophytes was detected in embryonic and white dunes, in addition to a decrease in the total vegetation cover (Figure 10b,c). The total vegetation cover in grey dunes remained the same, but there was an increase in the cover of bryophytes (Figure 10d). The cover of weeds and ruderals, grass- and shrubland species and alien (including invasive) plants remained stable in the studied dune habitats over time (Figure 10b–d).

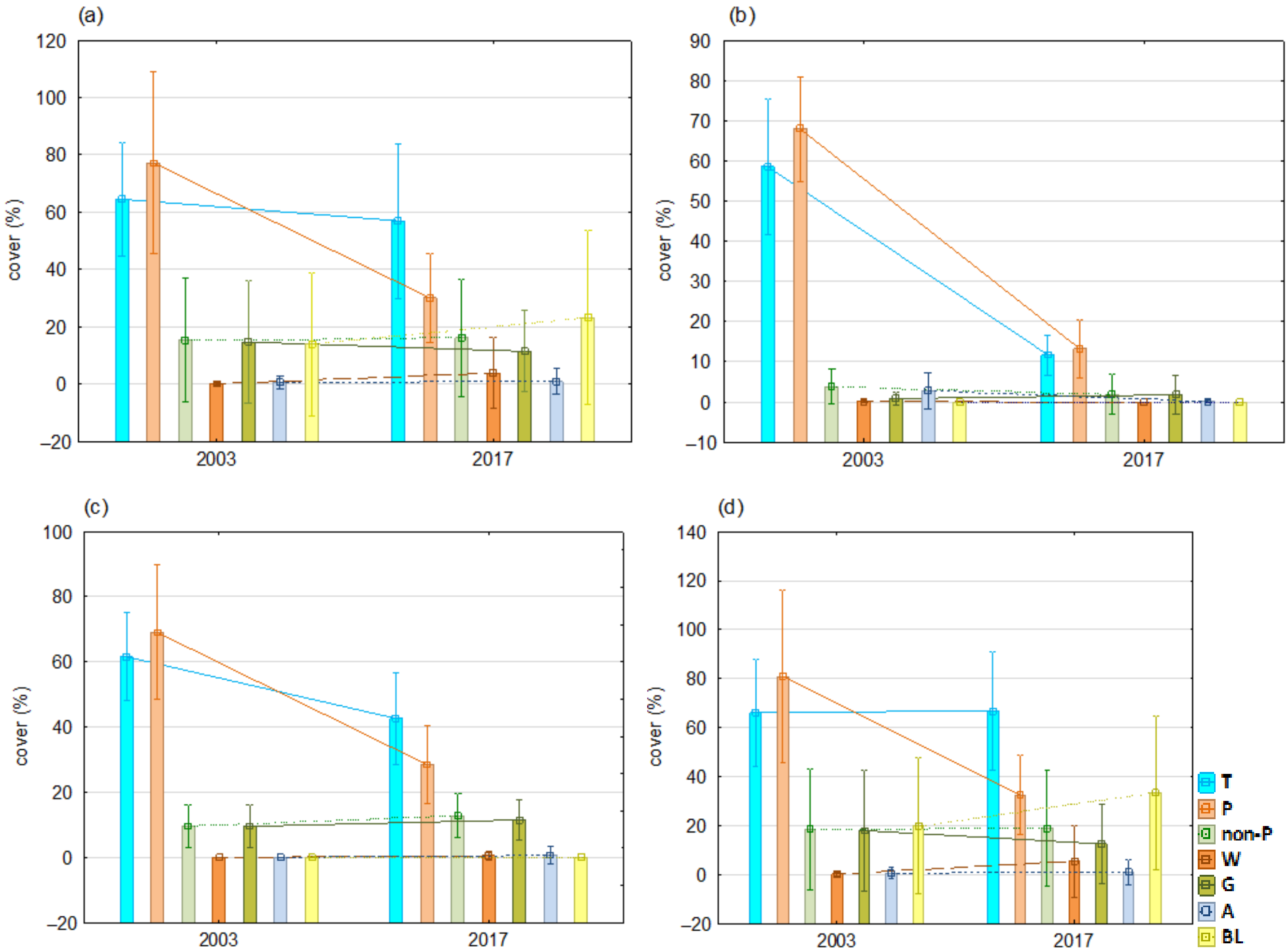

Figure 10. Dynamics of mean cover (columns) and standard deviations (whiskers) of different species groups (coded as follows: T—total vegetation cover: P—psammophytes, non-P—non-psammophytes; W—weeds and ruderals, G—plants typical of grasslands and shrublands, A—alien (including invasive) species; BL—bryophytes and lichens) between original plots from 2017 and plots from 2003 (Tzonev et al. 2005) for (**a**) all habitat types; (**b**) embryonic dunes; (**c**) white dunes; (**d**) grey dunes.

4. Discussion

4.1. Vegetation Characteristics

The results from our study provide evidence for relatively preserved coastal dune vegetation, so far, in Bulgaria. The presence of psammophytes is a useful biological indicator for the degree of disturbance within the dunes and a measure of their conservation value [84]. Although a relatively small number, the psammophytes we registered represent the core group of characteristic plant species for the Bulgarian coastal dunes. Our previous study on coastal flora showed that these species have remained consistent in sand dune vegetation over time [63]. The cover of psammophytes prevailed in the studied dune habitats and generally in all studied dune locations. Plant species richness and cover in the different dune habitats were not homogenous and increased in a gradient from the sea line towards the inland, which supports findings for other regions [21,85–87]. Our results complement previous findings, demonstrating that not only is the abundance of typical species important but so is their cover, as it is a crucial element in the evolution of dune landscapes [88]. The species richness and cover of non-psammophytes, which were registered in all dune types, could be used as an indicator of successional changes in the studied habitats. We detected that grey dunes were the most affected by the penetration of non-psammophyte species; their numbers prevailed in all studied locations, with only one exception. This supports the findings of Castillo and Moreno-Casasola [61] that ruderal/secondary species occupy more stabilized habitats. A significant presence of weeds and ruderal plants was registered only in grey dunes. During the last couple of decades, many sand dune areas (especially in the northern part of the Bulgarian Coast) have been bordered by agricultural land, and the increase in the cover of weeds and ruderal plants could be explained by the increasing range of annual crops in the buffers. This supports the suggestion of Castillo and Moreno-Casasola [61] that the increase in croplands, pastures and secondary vegetation will increase the ruderal/secondary species component and modify the composition of the vegetation cover in grey dunes. In addition, human activities, in general, favor the presence of weeds and ruderal species, many of which produce small, easily dispersed seeds [61]. Grass- and shrubland plants as a group had the strongest presence in all dune types, but again, grey dune vegetation was the most influenced. Grey dunes normally present a higher vegetation cover and higher species richness compared to other early successional dune habitats [62,85,86,89], as they often grow in an undulating landscape with variable exposure and slope, resulting in high variability of microhabitats [90]. The presence of grass- and shrubland species, common for the *Koelerio-Corynephoretea canescentis* and *Festuco-Brometea* vegetation classes, is typical for Black Sea coastal dune vegetation, especially for the dunes of northern alliances, such as *Cynodonto-Teucrion polii* and *Scabiosion ucranicae*, which have been linked with the lower sand salinity due to the general lower salinity of Black Sea water [74].

Despite the fact that, at a European level, alien plant invasions in coastal dune habitats are considered to be the focus of invasion management strategies [59], the presence of alien (including invasive) species registered in our study could be considered as low, both in species richness and in cover. Nevertheless, the possibility of invasive plant species, in particular, contributing to the development of negative successional trends against typical psammophytic vegetation in the future should not be underestimated given their potential to produce a decline of native taxa and to damage native communities [91,92]. For example, the only alien species involved in a negative successional trend in Bulgarian embryonic dunes, the North American *Xanthium orientale* subsp. *italicum*, was mentioned by Davidov [93] as one of the "occasional species" that are not adapted to the physical conditions of coastal sands and appear sporadically over the years. Eighty years later, doing [94] listed this species among the most typical neophytes for southern European coasts. Furthermore, half of the alien species we registered are considered among the 150 most widespread alien plants in Europe (*Ailanthus altissima*, *Amaranthus retroflexus*, *Cuscuta campestris*, *Erigeron canadensis*, *E. sumatrensis*, *Mahonia aquifolium*, *Oenothera biennis*, *Robinia pseudoacacia* and *Rosa rugosa*) [95]. Alien species are, in some cases, intentionally planted on dunes for ornamental purposes, but more commonly, they are unintentionally dispersed by human visitors [96]. We observed that such intentionally introduced ornamental species currently have self-established populations in some of the studied locations, including *Mahonia aquifolium* (at Sunny Beach Resort), *Sedum sediforme* (at International Youth Center) and *Yucca filamentosa* (at Sunny Beach Resort and Arkutino), all registered in grey dunes. Although in the currently known populations in Bulgaria, the ornamental *Rosa rugosa* does not show any invasive behavior [97], on the Atlantic and Baltic coastal dune grasslands, it forms dense stands with a high impact on the native vegetation [98,99] and it is considered a major threat to the biological diversity of the Dutch coastal dunes [100]. *Pinus pinaster*, a Mediterranean species, which was widely used for afforestation in South Bulgaria and the Black Sea Coast during the period of 1960–1985, is, nowadays, considered highly invasive in most of the areas outside of its native range [101,102]. Petrova et al. [103] reported its high invasion success and impact on the natural vegetation as problematic in two particular areas—the coastal dune habitats of Kamchia Sands and in an inland dune habitat near the town of Beloslav. We believe that a possible reason for the acidic reaction, measured only in some of the plots from Kamchia Sands, might be the plantation of *P. pinaster* in this location, which is its largest area of establishment observed so far in Bulgaria—almost 50 ha [104], with dense stands, predominantly 45–50 years old, planted on flat grey dunes [103].

4.2. Environmental Drivers

As pointed out by Carboni et al. [105], well-adapted native species, such as psammophytes, are in a fragile equilibrium with their natural environment and are extremely sensitive to human-driven modifications; therefore, the comprehension of all environmental drivers affecting their development is important. For the Bulgarian Black Sea Coast, we established that the substrate reaction and conductivity did not vary much among the different studied locations (Figure 6), and respectively, did not significantly affect the richness and cover of psammophytes, but we confirmed the alkaline character of the coastal sands in the Pontic basin [106]. However, we detected that substrate reactions and conductivity vary along the sea inland gradient, resulting in an increase of psammophytes richness from the grey towards the white and embryonic dunes. We observed that the richness and cover of grass- and shrubland plants were positively affected by the higher mineralization (higher EC values, Table 3) in grey dunes, and that their cover increased with the range of annual crops in the buffers (Table 4). The abundance and cover of native plants typical for grasslands and shrublands in grey dunes are facilitated by the adjacent surrounding species pool of grasslands and urban zones, and this particular group seems to be the most immediate threat to the psammophytic vegetation, especially in the event of further stabilization of the sand substrate [107]. In addition, both the richness and cover of weeds and ruderal species were positively affected by the higher mineral richness (expressed by EC values, Table 3) measured in grey dunes. As the most distanced from the sea line, respectively, from the large tourist flow, the grey dunes are less affected by a direct anthropogenic impact, but rather suffer indirectly from the diverse human activities in the surrounding areas. Sarmati et al. [108] reported that in coastal dune habitats, where the anthropogenic disturbance is high, an impoverished species pool is likely to occur, which is reflected in the increase of non-typical species, such as alien and ruderal plants. Furthermore, Panitsa et al. [109] registered a higher number of ruderals near urban, suburban, cultivated and coastal areas in Greece.

4.3. Recent Successional Trends

The comparison of the vegetation data between 2003 and 2017 showed that the total vegetation cover remained unchanged. However, a significant change occurred in the cover of typical psammophyte species, which has seriously declined in all dune types (Figure 10). The dune habitats at the front part (closer to the sea) are very important for the conservation of the characteristic psammophytic biodiversity. At the same time, embryonic and white dune communities are certainly the most exposed not only to natural but also to anthropogenic sources of disturbance, such as seaside mass tourism [52,110–112]. A likely reason for the severe decline in the cover of psammophytes registered in the embryonic and white dunes is anthropogenic pressure; in this regard, we did not even establish embryonic dunes at the end of the transect from the largest beach resort in Bulgaria—Sunny Beach. Several studies have already provided evidence of the negative impact of tourism-related activities, such as trampling on sand dune habitats [28,57,113,114], and some of them have shown a reduction in species cover [23,112,115]. A decrease in the abundance and cover of characteristic psammophytic species has also been reported for other regions. Sperandii et al. [116] observed a significant decrease in the species richness and cover of the dune grasslands habitat and revealed a negative trend for several species (e.g., *Ammophila arenaria*), which is diagnostic for mobile dunes. Sarmati et al. [108] reported a decrease in diagnostic species present in coastal dune habitats where the anthropogenic disturbance is high. Sperandii et al. [110] detected a significant decrease in the cover of some diagnostic species for upper beach and embryonic dune habitats, such as *Ammophila arenaria*, *Salsola kali* and *Euphorbia peplis*, and revealed that all diagnostic species experiencing a statistically significant change in time decreased in their occurrence and/or in their cover. The vegetation data comparison between 2003 and 2017 also showed that, aside from typical psammophyte plants, the cover of other plant groups has undergone negligible changes over time. We consider increases in the cover of bryophytes and lichens in grey dunes to be related to the natural successional processes of stabilization and nutrient enrichment. Although the presence of non-psammophytes enlarges all vegetation diversity, in the case of psammophytic vegetation, it rather poses interesting problems for coastal dune conservation [61]. The detected changes strengthen the conviction that resurveying historical vegetation data can provide unique insights into vegetation successional trends in relation to environmental changes over time [117], and studies focusing on the assessment of temporal vegetation changes should be conducted to develop a better understanding of coastal dune ecosystem dynamics [118].

Supplementary Materials: The following are available online at http://www.mdpi.com/xxx/s1. **ESM S1:** Original data from 2017 from 12 dune systems along the Bulgarian Black Sea Coast. The studied locations are numbered as follows: 1—St. Anna; 2—Durankulak; 3—Krapets; 4—Shabla; 5—Baltata; 6—Kamchia Sands and Skorpilovtsi; 7—Sunny Beach Resort; 8—Kavatsi and Smokinya; 9—Alepu; 10—Arkutino; 11—International Youth Center; 12—Koral. The 17 orthogonal transects correspond to the following numbers: 1—St. Anna—north; 2—St. Anna—south; 3—Durankulak; 4—Krapets; 5—Shabla—north; 6—Shabla—south; 7—Baltata; 8—Kamchia Sands—north; 9—Kamchia Sands—south; 10—Skorpilovtsi—north; 11—Skorpilovtsi—south; 12—Sunny Beach Resort; 13—Kavatsi and Smokinya; 14—Alepu; 15—Arkutino; 16—International Youth Center; 17—Koral. Sand dune habitat types are coded as follows: E—embryonic, W—white and G—grey dunes. Different species groups are coded as follows: P—psammophytes, W—weeds and ruderals, G—plants typical of grasslands and shrublands, F—plants typical of forests, A—alien (including invasive) species, B—bryophytes, L—lichens. **ESM S2:** Shapefiles showing the changes in different categories of land cover (annual crops, forest areas, natural and semi-natural grass communities, perennial crops and heterogeneous agricultural areas, roads and transport infrastructure, urbanized and anthropogenically disturbed territories, water areas and wetlands, other (including sand dunes), sea) between the years 2006, 2011 and 2017 in the buffers of 17 transects (1 km circular buffers around the starting point of every transect) in 12 dune systems from the Bulgarian Black Sea Coast.

Author Contributions: All authors contributed to the study's conception and design. Field data collection was done by M.V. and partly by D.S. and I.A. Data preparation and analyses were performed by M.V., except the data extraction and processing of land-use types, which were performed by N.T. The first draft of the manuscript was written by M.V. All authors have read and agreed to the published version of the manuscript.

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