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Biogeographic variability of coastal perennial grasslands at the European scale

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Abstract

Question: Coastal environments have often been described as azonal. While this characteristic is clear for the foredune system, it seems less evident for more inland fixed dunes, which host habitats of major conservation concern, whose features seem to be more related to local climatic conditions. We hypothesized that, unlike other coastal habitats, dune perennial grasslands differ floristically and structurally across their European range and that patterns of variation are linked to the corresponding climate.

Location: European coasts (Atlantic Ocean, Baltic, Mediterranean, Black Sea).

Methods: We used a large data set of phytosociological relevés, representative of coastal grasslands throughout their European range. The role of climatic variables (temperature, precipitation and continentality) in determining the variability in species composition and vegetation structure (by means of life forms) was investigated through CCA, DCA and GLM. The degree of concentration of species occurrences within groups was calculated through the Phi coefficient.

Results: Through multivariate analyses we identified seven major types of coastal grassland, corresponding to different geographic areas. The groups significantly differed in their climatic envelope, as well as in their species composition and community structure.

Conclusion: Our results confirm the hypothesis that coastal dune perennial grasslands are subjected to local climate, which exerts significant effects on both floristic composition and community structure. As a consequence, coastal grasslands are particularly prone to the effect of possible climate change, which may alter species composition and distribution, and lead to shifts in the distribution of native plant communities.

KEYWORDS
azonal habitats, climatic gradient, dune habitats, endemism, habitat classification, meta-analysis, phytosociological data, vegetation gradient, vegetation structure

1 | INTRODUCTION

Coastal dune systems are distributed in almost all latitudes, and are characterized by high ecological diversity in terms of geomorphological dimensions, environmental heterogeneity and compositional variation (van der Maarel, 2003; Martínez, Psuty, & Lubke, 2004). Coastal dune habitats have often been described as azonal (Acosta, Stanisci, Ercole, & Blasi, 2003; Noirfalise, 1987; Wiedemann & Pickart, 2004), i.e. as linked to non-climatic environmental stress factors or extreme soil conditions (Walter, 1985). Indeed, the vegetation of beaches and foredunes is usually characterized by habitat specialists (Maun, 1994) with a broad to global distribution (e.g. *Cakile maritima*, *Ammophila arenaria*, *Elytrigia juncea*; Wiedemann & Pickart, 2004; Davy, Scott, & Cordazzo, 2006; Carboni, Zelený, & Acosta, 2016), resulting in low compositional variation at a continental scale (Doing, 1985), although examples of biogeographic vicariance have been described (Géhu, 1986). In contrast, communities of fixed dune systems have been described as subject to local climate, geomorphology, lithology and site history (Houston, 2008; Provoost, Ampe, Bonte, Cosyns, & Hoffmann, 2004; Sburlino, Buffa, Filesi, & Gamper, 2008), suggesting a stronger influence of environmental factors and past climatic events that drove floristic migrations (Buffa, Filesi, Gamper, & Sburlino, 2007; Martínez et al., 2004).

Species-rich perennial dune grasslands, where a matrix of perennial species is colonized by ephemeral species in spring and early summer, represent one of the most valuable and diversified habitats of the semi-fixed or fixed dune sector (Doing,1985). They mainly occupy the transition zone along the sea–inland vegetation zonation, developing between the herbaceous vegetation of the foredune and the scrub of the fixed dune. Being less exposed to the severe coastal environmental conditions, they normally present a higher vegetation cover and higher species richness compared to other early successional dune habitats (Del Vecchio, Pizzo, & Buffa, 2015; Houston, 2008; Sburlino, Buffa, Filesi, Gamper, & Ghirelli, 2013). Moreover, they often grow in an undulating landscape with variable exposure and slope, resulting in a high variability of microclimates. Thanks to these features, they host a large variety of species, often rare, endemic or endangered, and a very high number of different plant communities (Bioret, Lazare, & Géhu, 2011; Del Vecchio, Giovi, Izzi, Abbate, & Acosta, 2012; Del Vecchio, Mattana, Acosta, & Bacchetta, 2012; Martínez et al., 2004), which, alongside serious anthropogenic threats, makes them habitats of major conservation concern (Bakker et al., 2016; Janssen et al., 2016).

Previous research on coastal fixed dune perennial grasslands mainly concentrated on the description of vegetation composition and on the syntaxonomic classification at local to national levels (e.g. Brullo, Giusso del Caldo, Siracusa, & Spampinato, 2001; Colasse & Delassus, 2014; Gamper, Filesi, Buffa, & Sburlino, 2008), using the Braun-Blanquet approach (Dengler, Chytrý, & Ewald, 2008; Westhoff & van der Maarel, 1973), or on ecology, management and conservation strategies (e.g. Del Vecchio, Slaviero, Fantinato, & Buffa, 2016; Isermann, Koehler, & Mühl, 2010; Provoost et al., 2004). However, despite their evident diversity, no comparative studies, analysing the variability of coastal perennial grasslands across their European range have been carried out yet.

Two comprehensive, pan-European hierarchical habitat classification schemes are widely used in Europe: the EUNIS habitat classification (Davies, Moss, & Hill, 2004) and the Annex I of the EU Habitats Directive (92/43/EEC) (European Commission 1992, 2013). EUNIS splits dune perennial grasslands into four geographic types: “Northern fixed grey dunes”, “Biscay fixed grey dunes”, “Mediterraneo-Atlantic fixed grey dunes” and “East Mediterranean fixed grey dunes”. Annex I of the Habitats Directive recognizes only two types of dune perennial grassland: the habitat “2130*–Fixed coastal dunes with herbaceous vegetation–grey dunes” along the coasts of the Baltic and North Sea, Atlantic Ocean and Black Sea, and “2210–*Crucianellion maritimae* fixed beach dunes” in the Mediterranean. The dune perennial grassland types of both classifications encompass a wide geographic distribution, from the Baltic to the Mediterranean Sea. Recently, Schaminée et al. (2016) reviewed the EUNIS grassland types based on vegetation plots and proposed to reorganize dune perennial grasslands into three types: “B1.4a–Atlantic and Baltic coastal stable dune grassland (grey dunes)”, “B1.4b–Mediterranean and Macaronesian coastal stable dune grassland (grey dunes)” and “B1.4c–Black Sea coastal dune grassland (grey dunes)”.

From this starting point, this study aimed to analyse the variability of dune perennial grasslands, relating it to climate gradients throughout their European distribution range. We hypothesized that, unlike other coastal habitats, perennial dune grasslands are subjected to the local climate, which exerts significant effects on both floristic composition and community structure.

2 | METHODS

2.1 | Data collection

We collected phytosociological relevés of dune perennial grasslands from the entire European distribution range from published literature and from unpublished data, available from the European Vegetation Archive database (EVA; Chytrý et al., 2016) and provided by some authors of this article. We considered as “dune perennial grasslands” the vegetation that grows between the foredune and the scrub of the fixed dune, with a cover of perennial species >25% of the total vascular species cover. The origin, number of relevés and syntaxa of each data source are provided in Appendix S1. For alliances delimitation and nomenclature we followed Mucina et al. (2016).

From an initial database of 4,500 relevés, we removed relevés with anomalous size (surface <1 or >25 m^2; e.g. Haveman & Janssen, 2008; Gigante, Attorre, et al., 2016) and uncertain information on geographic position or on the year in which they were performed. Furthermore, we removed all non-vascular species from relevés, because they had not been consistently sampled throughout the data set. We performed geographic resampling in order to avoid spatial autocorrelation by randomly selecting one relevé per cell from a 1 km × 1 km grid. After this procedure, we obtained a database of 605 relevés × 586 species (see Figure 1 for the geographic distribution of relevés). Preliminary analysis of the data set showed that neither remaining variation in plot size nor the year of surveying influenced the floristic composition (Pearson correlation; data not shown).

We associated with each relevé (1) latitude and longitude; (2) mean annual temperature and precipitation using Worldclim (Fick & Hijmans, 2017) at 1 km^2 resolution grid (ArcGis 9.2); (3) a continentality index, defined as the annual range of the extreme temperature values divided by the sine of the latitude (Kc index; Conrad, 1946); (4) the syntaxon at the alliance level as indicated by authors who made the relevé, conforming nomenclature to Mucina et al. (2016). We chose the alliance rank because it has been proved to be the most appropriate to

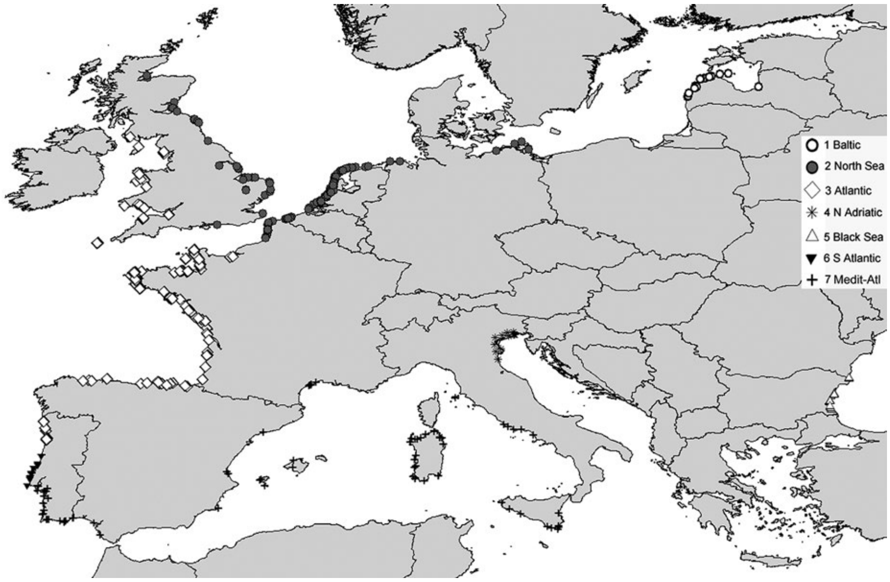

FIGURE 1 Geographic distribution of the relevés. Different symbols refer to the grouping that emerged after multivariate analyses. White dots = group 1, Baltic Sea; Grey dots = group 2, North Sea; Diamonds = group 3, Atlantic; Asterisks = group 4, N Adriatic; White triangles = group 5, Black Sea; Black triangles = group 6, S Atlantic; Crosses = group 7, Medit-Atl

describe the variability of vegetation across wide geographic ranges, such as the European scale of investigation (Faber-Langendoen, 2015; Jennings, Faber-Langendoen, Loucks, Peet, & Roberts, 2009). Finally, we associated to each species (1) the life form (Raunkiær, 1934), as a synthetic indication of adaptation to environmental conditions, especially climate (Kent & Coker, 1992); (2) the distribution type, according to Tutin et al. (2001) and Euro+Med.

2.2 | Data analysis

To test our hypothesis we performed a CCA (on presence–absence data; PC-ORD 5.1 software; MjM Software Design, Gleneden Beach, OR, US; 999 randomizations), using the mean annual temperature, mean annual precipitation and Kc index as climatic data. To define the groups in the CCA diagram we performed a cluster analysis on the relevés × climatic data matrix (using Ward's clustering method, Euclidean distance, on square root-transformed data; PC-ORD 5.1). Furthermore, we performed unconstrained ordination (DCA; on presence–absence data; PC-ORD 5.1) to compare constrained (CCA) with an unconstrained approach (DCA).

For each species in each group obtained by the CCA we calculated the Phi coefficient (JUICE 7.0 software; Tichý, 2002; Tichý & Chytrý, 2006). Being based on the degree of concentration of species occurrences, the Phi coefficient can be considered as a fidelity measure of a species in a given group of relevés (Tichý, 2002). The phi value of 40 was used as the lower threshold to identify the diagnostic species in each group. The value of the Fisher exact test was set at 0.001.

In order to detect differences in the structure of sand perennial grasslands, we performed a PERMANOVA (Past 3.0 software) among the groups, followed by post-hoc Tukey test, using the frequency of life forms (in particular chamaephytes, hemicryptophytes and therophytes) as dependent variables, and the groups identified by the CCA as grouping variable. To analyse the contribution of climate variables in determining the distribution of life forms, we performed GLM (on square root-transformed data; R package MASS; Venables & Ripley, 2002; R Foundation for Statistical Computing, Vienna, AT) using the frequency of life forms as dependent variables and the climatic variables (mean annual temperature and mean annual precipitation) as independent variables.

The species distribution area and the alliances were used as general descriptors of the variability within each group.

3 | RESULTS

3.1 | Variability of perennial grasslands across the European distribution range

According to the floristic and climatic variability, and to the groups evidenced by the cluster analysis (percentage chaining = 0.47; clustering level = 90%) we could identify seven major groups in the CCA ordination space (Figure 1, see Appendix S2 for the scatter plot of relevés and technical results). The first axis was predominantly determined by the mean annual temperature and the Kc index, while the second axis was determined by the mean annual precipitation (Appendix S2). The correlation of the climatic variables with the unconstrained ordination (DCA ordination axes; Appendix S2) confirmed the result obtained using the constrained method (CCA).

The groups corresponded to different geographic areas arranged along a latitudinal and longitudinal gradient (Figure 1): (1) the first (1 Baltic) corresponded to the relevés distributed along the coasts of the Baltic Sea; (2) the second (2 North Sea) included relevés from the North Sea and the east coast of Great Britain; (3) the third (3 Atlantic) included the West Atlantic coast, from the Channel and the west coast of Great Britain downward to the Bay of Biscay and on to approximately Porto district, Portugal; (4) the fourth group (4 N Adriatic) corresponded to the North Adriatic region (Italy), which represents the north-eastern part of the Mediterranean Basin; (5) the fifth group (5 Black Sea) corresponded to the Black Sea coast; (6) the sixth group (6

S Atlantic) included the relevés of the South Atlantic coast in Portugal; (7) the seventh group (7 Medit-Atl) mainly sorted the relevés from the Mediterranean coast, but it also included the southernmost part of the Atlantic coast of Spain and Portugal.

The groups showed differences in their climatic envelope, summarized in Table 1. The groups arranged from north to south along an increasing gradient of mean annual temperature and continentality, with group 1 showing the minimum and group 7 the maximum values. Mean precipitation values displayed a maximum at intermediate latitudes, and decreased eastwards, along the longitudinal gradient, with the western coasts of Europe, bordering the Atlantic Ocean, and the N Adriatic coastline showing the highest values of precipitation.

3.2 | Diagnostic species

The diagnostic species of each group, their Fidelity index values and their distribution area are summarized in Table 2. Each group was characterized by diagnostic species with a narrow distribution area, in some cases endemic. The values of the Fidelity index were high, especially for the groups 1 Baltic, 4 N Adriatic, 5 Black Sea and 6 S Atlantic, with the Black Sea group having the highest number of diagnostic species. A similar pattern was observed at the syntaxon level of alliance, since each group showed a dominance of one alliance. A synoptic table showing the frequency of species in each group is provided in Appendix S3.

3.3 | Climatic variables and vegetation structure

We found differences in the frequency of life forms among groups (PERMANOVA; $F = 53.32$, $p = .0001$). In particular, chamaephytes increased in frequency southwards, while hemicryptophytes and therophytes evidenced an opposite trend (Figure 2).

Linear models showed that temperature was the most important driver of life form frequency, with a significant influence on all of them (see Appendix S4 for technical results). Chamaephytes increased at higher temperatures, while hemicryptophytes and therophytes decreased. Precipitation mainly affected therophyte frequency, which increased with increasing precipitation. Hemicryptophytes showed the same trend, although the effect was less strong.

4 | DISCUSSION

Our results confirm the hypothesis that coastal dune perennial grasslands are subjected to the local climate, which exerts significant effects on both floristic composition and community structure. Although some species are widely distributed (e.g. *Artemisia campestris*, *Carex arenaria*, *Cerastium semidecandrum*), most of them show narrower geographic ranges and are related to specific climatic conditions or local biogeographic or geological histories (Piñeiro, Fuertes Aguilar, Draper, & Nieto Feliner, 2007). Our results are in line with those of Jiménez-Alfaro, Marcenò, Guarino, and Chytrý (2015) who found a greater effect of climatic variables on fixed dune communities with respect to shifting dunes.

The analysis of the relationships between vegetation and climatic variables allowed us to identify seven groups of perennial grasslands, which depict a clear geographic gradient, mainly determined by latitude and continental position, running from the coasts of the Baltic and North Seas, through those of the West Atlantic Ocean, North Adriatic and Black Sea, downward to the Mediterranean coast and the southern coast of the Atlantic Ocean.

Although detailed comparisons are difficult, as classifications may not use the same variables or the same spatial resolution, our results are consistent with the thermotypes of Europe proposed by Rivas-Martínez, Penas, and Díaz (2010), in particular as far as boundaries are concerned. Especially, our data support the existence of a large intermediate zone, extending from the English Channel down to approximately the Porto district, which corresponds to the "Thermotemperate" zone proposed by Rivas-Martínez et al. (2010). The transition zone extends eastward to the North Adriatic region and the Black Sea area.

Each climatic zone proved to be rather homogeneous when considering the floristic composition. Diagnostic species showed a geographically well-delimited distribution, for most part coincident with that of the group, with a remarkable richness in endemic species. The high values of the Fidelity index confirm that identified diagnostic

TABLE 1 Values of temperature, precipitation and continentality index for the seven groups of relevés evidenced by the multivariate analyses

	Annual temperature			Annual precipitation			Continentality index		
		Range			Range			Range	
Group	Mean ± *SD* (°C)	Min	Max	Mean ± *SD* (mm)	Min	Max	Mean ± *SD*	Min	Max
1 Baltic	6.4 ± 0.2	6.1	6.6	54.4 ± 1.6	51.6	57.0	14.1 ± 0.1	13.9	14.1
2 North Sea	9.5 ± 0.7	8.1	10.7	60.1 ± 6.5	45.3	70.8	17.0 ± 1.2	14.0	21.3
3 Atlantic	11.8 ± 1.5	7.4	14.8	80.8 ± 13.6	60.9	127.7	20.2 ± 4.2	13.6	30.4
4 N Adriatic	13.4 ± 0.1	13.2	13.5	80.4 ± 12.5	63.3	93.7	25.3 ± 1.1	23.9	26.7
5 Black Sea	12.8 ± 0.5	12.1	13.3	44.3 ± 3.3	39.3	47.7	26.5 ± 1.9	22.5	29.1
6 S Atlantic	15.3 ± 0.1	15.1	15.3	61.9 ± 5.0	54.3	69.7	25.2 ± 2.4	21.9	29.0
7 Medit-Atl	16.8 ± 0.9	14.5	18.5	46.9 ± 8.3	23.7	71.5	32.1 ± 5.0	20.3	43.0

species were present in almost all relevés of the group, and allowed us to characterize each geographic area from the floristic point of view. Moreover, the analysis of diagnostic species distribution area supported the distinctiveness of the Black Sea region, recognized by almost all climatic, environmental and biogeographic stratifications of Europe (EEA 2005; Metzger, Bunce, Jongman, Mücher, & Watkins, 2005; Rivas-Martínez et al., 2010) as well as the climatic and floristic peculiarities of the western coast of Europe, bordering the Atlantic

TABLE 2 Variability of the groups at species and syntaxonomical level. The table shows the diagnostic species, with the relative Phi value (threshold value = 40; Fisher exact test = 0.001), diagnostic species distribution area at European level (Euro+Med; Tutin et al., 2001), and the alliances described in each area, with their percentage of frequency. Nomenclature and syntaxa delimitation follow Mucina et al. (2016).

Group	Diagnostic species	Distribution area	PHI value	Alliances	Frequency (%)
1 Baltic	*Festuca polesica*	Eurosiberian	96.1	*Koelerion glaucae* Volk 1931	100.0
	Koeleria glauca	Eurasiatic	87.8		
	Hieracium umbellatum	Eurasiatic	62.4		
	Thymus serpyllum s.l.	Eurasiatic	60.3		
	Pulsatilla pratensis	Eurasiatic	54.8		
	Arabidopsis arenosa	Eurasiatic	48.7		
	Anthyllis vulneraria subsp. *maritima*	Eurosiberian	48.7		
	Dianthus arenarius	NE Europe	42.0		
	Tragopogon heterospermus	Baltic endemic	42.0		
2 North Sea	*Myosotis ramosissima*	Broad distribution	55.2	*Koelerion arenariae* Tx. 1937 corr. Gutermann et Mucina 1993	97.9
	Jacobaea vulgaris	Eurasiatic	53.1		
	Cerastium semidecandrum	Eurasiatic	49.6	*Corynephorion canescentis* Klika 1931	2.1
	Festuca rubra	Broad distribution	48.2		
	Erophila verna	Broad distribution	47.9		
	Carex arenaria	Subatlantic	47.6		
	Phleum arenarium	Subatlantic	46.0		
	Erodium cicutarium	Broad distribution	44.7		
	Sedum acre	Eurasiatic	42.3		
	Galium verum	Eurasiatic	42.0		
	Aira praecox	Subatlantic	41.5		
	Veronica arvensis	Broad distribution	41.1		
	Poa pratensis	Eurasiatic	40.3		
3 Atlantic	*Mibora minima*	W Europe	52.5	*Euphorbio portlandicae-Helichrysion stoechadis* Sissingh 1974	64.9
	Euphorbia portlandica	W Europe	51.0		
	Thymus praecox	Most of Europe	48.1	*Koelerion arenariae* Tx. 1937 corr. Gutermann et Mucina 1993	35.1
	Ononis spinosa	Mediterranean	45.5		
	Arenaria serpyllifolia	Broad distribution	42.1		
	Helichrysum stoechas	Mediterraneo-Atlantic	42.1		
4 N Adriatic	*Fumana procumbens*	SE Europe	81.2	*Syntrichio ruraliformis-Lomelosion argenteae* Biondi, Sburlino & Theurillat in Sburlino et al., 2013	100.0
	Carex liparocarpos	SE Europe	67.0		
	Silene vulgaris	Broad distribution	63.7		
	Sanguisorba minor	Broad distribution	61.6		
	Scabiosa triandra	S Europe	56.9		
	Vulpia fasciculata	Mediterraneo-Atlantic	56.4		
	Petrorhagia saxifraga	Mediterranean	50.2		
	Teucrium chamaedrys	Mediterranean	45.2		
	Helianthemum nummularium subsp. *obscurum*	SE Europe	42.6		
	Silene otites	Most of Europe	40.9		
	Medicago minima	Eurasiatic	40.9		

(Continues)

TABLE 2 (Continued)

Group	Diagnostic species	Distribution area	PHI value	Alliances	Frequency (%)
5 Black Sea	*Jurinea kilaea*	Endemic Black Sea	80.3	*Sileno thymifoliae-Jurineion kilaeae* Géhu et Uslu ex Mucina 2016	72.0
	Silene thymifolia	Endemic Black Sea	75.0		
	Lepidotrichum uechtritzianum	Endemic Black Sea	72.2	*Elymion gigantei* Morariu 1957	28.0
	Centaurea arenaria	South-Eastern Europe	66.5		
	Odontarrhena borzaeana	SE Europe	60.3		
	Peucedanum arenarium	SE Europe	60.3		
	Linaria genistifolia	SE Europe	57.0		
	Cionura erecta	SE Europe	57.0		
	Secale sylvestre	SE Europe	57.0		
	Silene euxina	Endemic Black Sea	53.6		
	Verbascum purpureum	Endemic Black Sea	50.0		
	Festuca vaginata	SE Europe	50.0		
	Cynanchum acutum	Broad distribution.	50.0		
	Artemisia campestris	Broad distribution	42.8		
	Erysimum diffusum	SE Europe	42.0		
	Medicago falcata	Eurasiatic	42.0		
6 S Atlantic	*Armeria welwitschii*	Endemic (PT)	88.0	*Corynephorion canescentis* Klika 1931	70.0
	Sedum sediforme	Mediterraneo-Atlantic	74.6		
	Herniaria ciliolata subsp. *robusta*	W Europe	66.1	*Helichrysion picardii* (Rivas-Mart., M. Costa et Izco in Rivas-Mart. et al. 1990) Rivas-Mart. et al. 1999	30.0
	Iberis procumbens	W Europe	60.3		
	Corynephorus canescens	W Europe	53.8		
	Helichrysum italicum	Mediterraneo-Atlantic	56.1		
	Malcolmia littorea	W Europe	32.3		
	Anagallis monelli	Mediterranean	50.4		
	Calendula suffruticosa	W Europe	48.7		
	Seseli tortuosum	Mediterranean	43.5		
	Halimium calycinum	Endemic (PT, ES)	42.8		
7 Medit-Atl	*Lotus cytisoides*	Mediterranean	46.1	*Crucianellion maritimae* Rivas Goday & Rivas-Martínez 1958	76.2
	Crucianella maritima	Mediterranean	46.7		
	Anthemis maritima	W Europe	43.9	*Corynephorion canescentis* Klika 1931	23.8
	Pancratium maritimum	Mediterranean	43.5		

Ocean (Beatty & Provan, 2013; Minckley, Haws, Benedetti, Brewer, & Forman, 2015). Either paleogeographic events (such as the Ice Age of the Quaternary period) and the current climatic conditions (in particular the North Atlantic Oscillation–NAO) associated with high precipitation rates (Batten, Zhou, & Li, 2014; Minckley et al., 2015; Webb & Bartlein, 1992) are probably related to the floristic identity of this area.

Furthermore, this study also provided new evidence of the biogeographic originality of the Italian sector of the Northern Adriatic Sea, already recognized for other northeastern Italian ecosystems (Buffa & Villani, 2012). These peculiarities, which contribute to define coastal ecosystems strongly atypical within the Mediterranean context (Buffa, Mion, Gamper, Ghirelli, & Sburlino, 2005; Buffa et al., 2007; Gamper et al., 2008; : Sburlino et al., 2008, 2013), were previously highlighted by Béguinot (1913, 1941), and later by Marcello (1960). Based on floristic studies, both authors described the 'Venetian biogeographic lacuna'. In fact, many typical Mediterranean plant species found on both sides of the Adriatic Sea (such as *Crucianella maritima*, *Helichrysum stoechas*, *Maresia nana*, *Matthiola tricuspidata*) were not present in the Venetian coasts, which are exposed to cold north-easterly winds, but sheltered from the influence of warm, south-westerly ones. These climatic features promote sub-Atlantic climatic conditions, rather than Mediterranean conditions. Paleogeographic events during the Tertiary period, such as opening and closure of marine corridors as well as the appearance and disappearance of water bodies between Europe and West Asia (up the Caspian Sea), may also have contributed to the floristic differences found along the longitudinal gradient considered in this study (Ivanov et al., 2011; Müller, Geary, & Magyar, 1999).

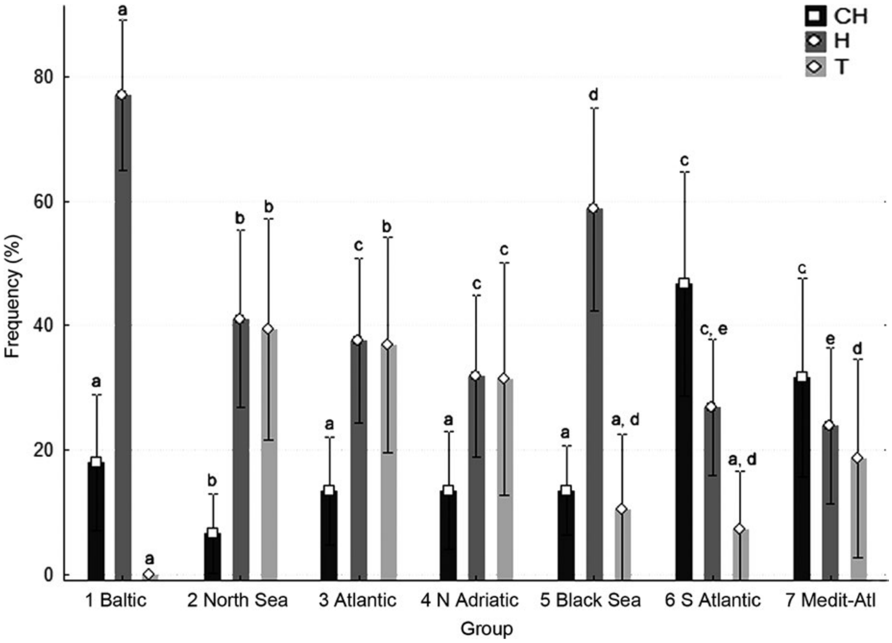

FIGURE 2 Mean ± *SD* of life forms frequency values within each group. Bars with different letters are significantly different according to post-hoc Tukey test

Although mosses and lichens were not included in this research, it is worth highlighting their potential role in a further differentiation of sand dune perennial grasslands within the European range. According to literature considered in this study, mosses and lichens are a typical component in sand dune perennial grasslands of North and West Europe. They were still present in the Northern Adriatic area, while they completely disappeared from the Mediterranean one.

Major features of each group were also confirmed by the relevant number of autonomous syntaxa at alliance level, often endemic or confined to geographic regions. It is the case e.g. of *Koelerion glaucae*, mainly distributed in Northeast Europe, *Euphorbio portlandicae-Helichrysion stoechadis*, endemic to the Atlantic coast (Géhu, 2000), or *Syntrichio-Lomelosion argenteae*, limited to the north Adriatic coast (Sburlino et al., 2013). Note also that the groups of relevés identified by the analysis of the relationships between vegetation and climatic variables in most cases correspond to specific alliances. This result confirms the usefulness of the alliance rank, which is usually floristically better separated compared with higher vegetation ranks (Gigante, Foggi, Venanzoni, Viciani, & Buffa, 2016; Jennings et al., 2009) and contributes to highlight environmental gradients and biogeographic regions (Willner et al., 2017).

Besides the taxonomic or syntaxonomic differentiation, the analysis of the vegetation structure revealed functional information through life forms (Del Vecchio, Prisco, Acosta, & Stanisci, 2015; Duckworth, Kent, & Ramsay, 2010; Fantinato et al., 2016; Pierce et al., 2017; Slaviero, Del Vecchio, Pierce, Fantinato, & Buffa, 2016). Although chamaephytes, hemicryptophytes and therophytes always represented the main life forms, they were differentially distributed among the groups, with chamaephytes prevailing in the southernmost zones (Mediterranean and S Atlantic), while hemicryptophytes and therophytes dominate in the northern, western and easternmost zones, and this pattern is strongly related to temperature values. In fact, these results are consistent with previous studies (Moles et al., 2014; van Ommen Kloeke, Douma, Ordoñez, Reich, & van Bodegom, 2012; Swenson & Enquist, 2007), demonstrating that temperature is more related to plant traits than precipitation.

Our study evidenced that the use of large phytosociological databases may represent a valuable tool to detect vegetation variation at continental scale and provide fine-scale information for exploring large-scale ecological patterns and processes and for increasing the accuracy of land categorization. Our results rather conform to the recent revision of the EUNIS grassland habitats classification provided by Schaminée et al. (2016). Conversely, the Annex I habitat types seem too broad to account for the variability we found. Considering that Annex I habitat types represent a selected list of habitats of conservation interest, a more detailed classification becomes crucial to provide an effective system for the description and monitoring of habitat types at European, national and regional context. Our study can thus contribute to improve the classification of perennial dune grasslands, providing information on indicator species, structural characteristics and their geographic range across Europe.

Overall, our study demonstrated that climate parameters such as temperature and precipitation have a significant effect on perennial dune grasslands, influencing the species pool, the presence of floristic and coenological peculiarities, and defining the vegetation structure. Although further research is needed to take into account other possible drivers of variation, our results might support the zonality of dune perennial grasslands envisaged by previous authors (Houston, 2008; Provoost et al., 2004; Sburlino et al., 2008). From a biodiversity conservation point of view, this would raise concerns with respect to global warming. Due to the important role of climatic parameters in determining the vegetation pattern, coastal grasslands may suffer the influence of climate change more than other coastal habitats (Bakker et al., 2016; Prisco, Carboni, Jucker, & Acosta, 2016). Rising temperatures and changes in precipitation can substantially alter the composition, distribution and abundance of species, which can eventually lead to shifts in the distribution of native plant communities (Nordstrom, 2014) and make dune perennial grasslands a key habitat for assessing the long-term impact of global warming on coastal biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1 Reference list of published literature used to build the database

APPENDIX S2 Scatter plots of relevés and technical results of multivariate analyses

APPENDIX S3 Synoptic table of species frequency in each group

APPENDIX S4 Model results

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