Vegetation and functional diversity of sand dune habitats between and within different bioclimatic regions

Dissertation
for the award of the degree
"Doctor of Philosophy" Ph.D.
Division of Mathematics and Natural Sciences
of the Georg-August-Universität Göttingen

within the doctoral program Biology
of the Georg-August University School of Science (GAUSS)

submitted by
Parastoo Mahdavi

from Esfahan, Iran

Göttingen, 2017

Thesis Committee

Prof. Dr. E. Bergmeier, Abt. Vegetationsanalyse & Phytodiversität, Georg-August-Universität Göttingen

Prof. Dr. C. Leuschner, Abt. Ökologie & Ökosystemforschung, Georg-August-Universität Göttingen

Members of the Examination Board

Reviewer: Prof. Dr. E. Bergmeier, Abt. Vegetationsanalyse & Phytodiversität, Georg-August-Universität Göttingen

Second reviewer: Prof. Dr. C. Leuschner, Abt. Ökologie & Ökosystemforschung, Georg-August-Universität Göttingen

Further members of the Examination Board:

Prof. Dr. H. Behling, Abt. Palynologie und Klimadynamik, Georg-August-Universität Göttingen

Prof. Dr. T. Friedl, Abt. Experimentelle Phykologie und Sammlung von Algenkulturen der Universität Göttingen (EPSAG), Georg-August-Universität Göttingen

PD. Dr. M. Waltert, Blumenbach Institute for Zoology and Anthropology, Conservation Biology/Workgroup on Endangered Species, Georg-August-Universität Göttingen

Prof. Dr. H. Kreft, Abt. Biodiversität, Makroökologie und Biogeographie, Georg-August-Universität Göttingen

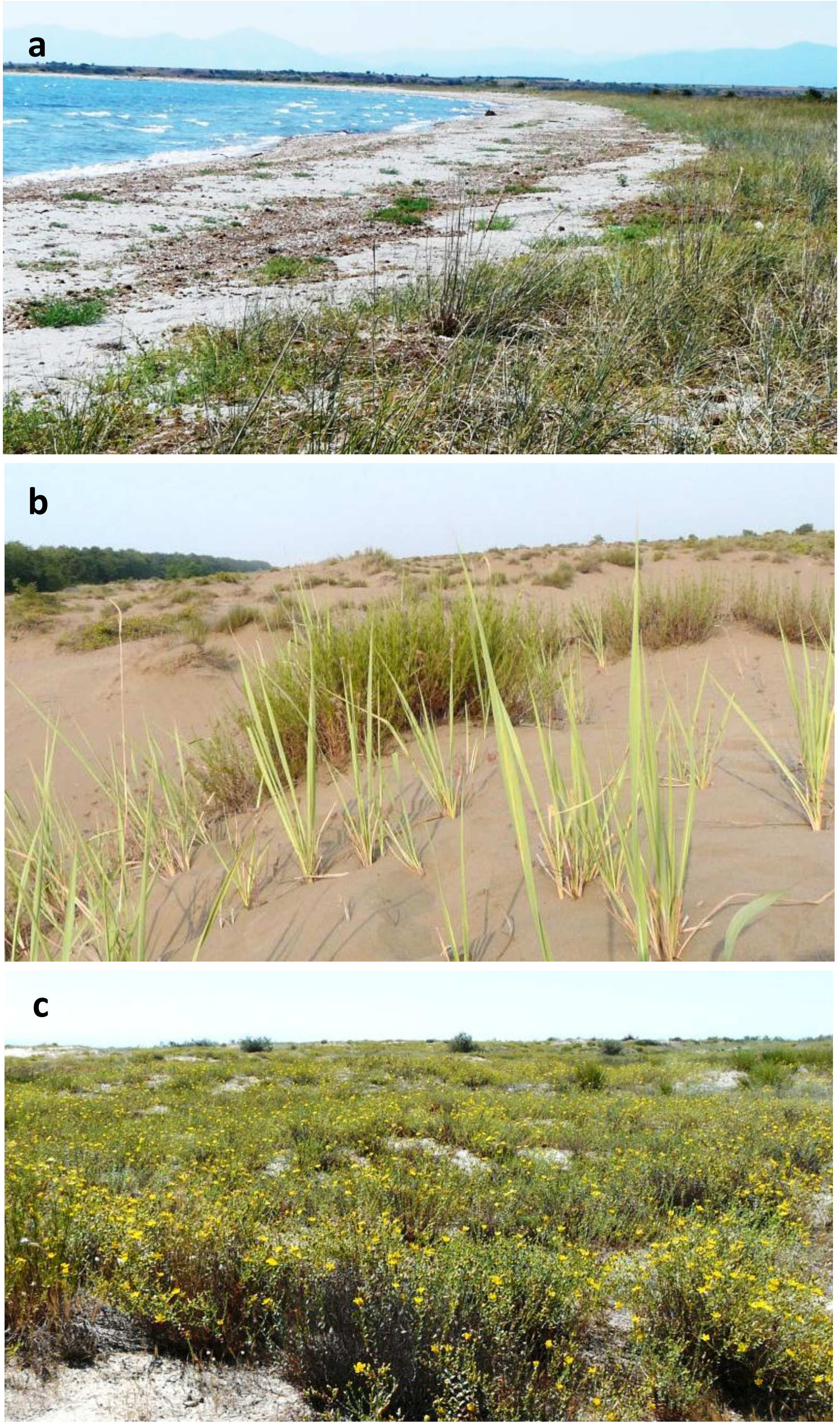
Date of the oral examiniation: 26.4.2017

"It is not the strongest of the species that survive,

nor the most intelligent,

but the one most responsive to change."

Charles Darwin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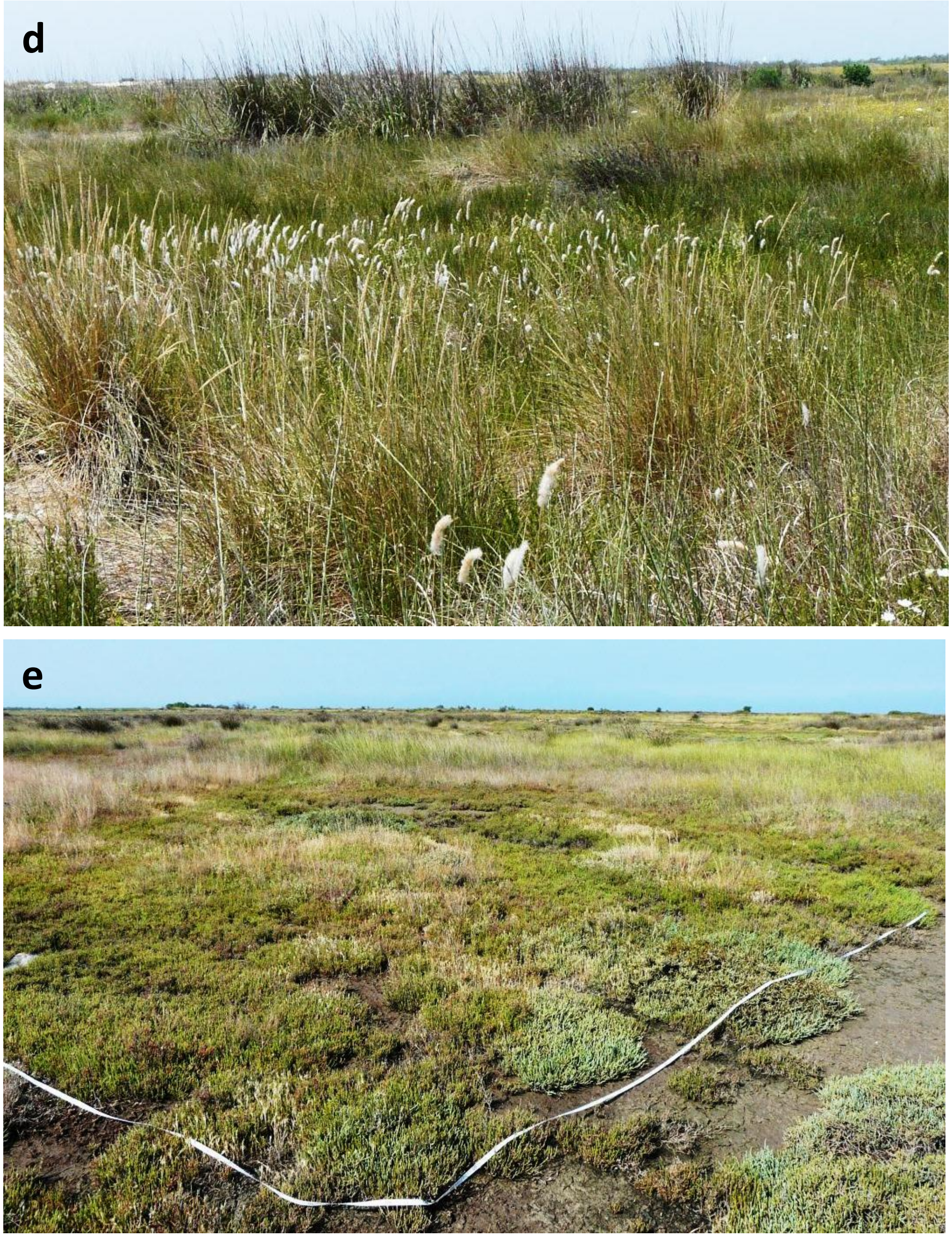

View of the main habitats occurring in sand ecosystems: a. driftline; b. mobile dune; c. stabilized dune; d. dune slack; e. salt marsh.

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Summary

Use of plant functional types has a long tradition in ecology from the time that von Humboldt offered the first physiognomic classification of plants based on growth form. In recent years, the application of functional traits in ecological studies increased and a variety of new measuring and statistical methods were developed. Functional groups comprise species with similar traits and thus similar response to environmental pressures and similar effects on ecosystem processes. Therefore, it is expected that they are affected rather by niche similarities than by biogeographic regions. However, the feasibility and applicability of functional groups at global scale and across different regions is still an open question.

Sand ecosystems are stress-prone habitats with quite low number of species, characterized by long environmental gradients on relatively small area and high ecological and habitat diversity. Considering these facts, sand ecosystems are a suitable model for ecological research. Furthermore, despite increasing attention to functional traits, the knowledge on functional ecology of sand ecosystems is limited. This thesis contributes to fill the gap on functional ecology of sand dunes by defining cluster-based functional groups of species and functional composition of plant communities across different biogeographic regions. Further, the effect of habitat and climatic region on functional groups and the similarity of sand habitats at species, community and functional level were investigated. Finally, the distribution of photosynthesis types across different sand habitats was examined. To achieve the targets, various sand habitat types (drift lines, mobile dunes, stabilized dunes, salt marshes, semi-wet sand and sandy disturbed habitats) across different climatic regions (Atlantic, Mediterranean, Hyrcanian and Irano-Turanian) were studied.

We found that sand ecosystems can be defined by sets of functional groups despite their regional climatic and species pool differences. It provides further support to the idea that classification of functional traits should be applicable to other regions. Based on our trait classification, sand dune ecosystems can be described with three main adaptive strategies among perennials and four strategy types in annuals. Ordination analysis of traits also shows that functional traits of the same habitat assembled together irrespective of their regions. This indicates that plant traits in sand ecosystems are grouped reflecting habitat affiliation rather than regional belonging.

Furthermore, we investigate the similarity of sand habitats at species, community and functional level. We found by changing the focus from species to community and to functional level, sand habitats of the same kind represent more similarity across regions. The highest habitat similarity was observed at functional level and the lowest at taxonomic level. The vegetation of all habitats at functional level is considered as azonal vegetation and independent from the climatic region. We found out that the more stress-prone a habitat, the more is its vegetation habitat-related and independent from the region. We

also tested the functional composition of the vegetation to compare plant communities across different regions. This is useful to understand and describe plant communities as trait groups reflect habitat and ecosystem conditions. However, species composition of habitats shows more region-related patterns. In this case, biogeographical distance prevails over environmental similarity.

We found C4 plants to have notable contribution to the vegetation cover in salt marshes, mobile dunes and disturbed sandy grounds despite their low number of species. Our results reveal that C4 species contribute most notably to the vegetation cover and less to the richness in comparison to C3 species. It indicates that environmental conditions (at least in some sand habitats) favor C4 plants to form dominant vegetation. Intensive light, high summer temperature and dryness are features of sand ecosystems which make C4 photosynthesis more efficient than the C3 pathway. We observed a general increasing trend in richness and cover of C4 species with increase of aridity. The highest proportion of C4 species occurred in C Iran, the driest and warmest study region.

Zusammenfassung

Die Verwendung von funktionellen Gruppen bei Pflanzen hat eine lange Tradition in der Ökologie, spätestens seit von Humboldt die erste physiognomische Klassifikation auf der Grundlage von Wuchsformen zusammenstellte. In den letzten Jahren wurden sie zunehmend benutzt, wobei eine Vielzahl neuer Meßverfahren und statistischer Methoden entwickelt wurde. Funktionelle Gruppen setzen sich aus Arten mit ähnlichen Eigenschaften zusammen und weisen demnach ähnliche ökologische Anpassungen auf und haben gemeinsame Auswirkungen auf Ökosystemprozesse. Deshalb kann man erwarten, daß ihre Zusammensetzung eher durch eine Ähnlichkeit des Standorts, als durch biogeographische Regionen geprägt wird. Vergleichbarkeit und Anwendbarkeit funktioneller Gruppen auf überregionaler oder gar globaler Ebene wurden aber bisher kaum untersucht.

Sandökosysteme sind von Streß geprägt und enthalten oft nur wenige daran angepaßte Arten. Dennoch treten lange ökologische Gradienten auf kleiner Fläche auf, die zu relativ hoher ökologischer und standörtlicher Vielfalt führen. Dies macht Sandökosysteme zu geeigneten Modellen für ökologische Forschungen. Des weiteren ist, trotz steigendem Interesse an funktionellen Gruppen, das Wissen um die funktionelle Ökologie von Sandökosystemen noch beschränkt. Die vorliegende Arbeit füllt zahlreiche Wissenslücken zur funktionellen Ökologie von Sandökosystemen. So werden funktionelle Artengruppen über Cluster-Analysen definiert und die funktionelle Zusammensetzung für Pflanzengesellschaften über mehrere biogeographische Regionen hinweg beschrieben. Weiterhin wird der Einfluß von Lebensraum und Klimaregion auf funktionelle Gruppen untersucht sowie die Ähnlichkeit von Sandlebensräumen jeweils für die Ebene der Pflanzenarten, der Pflanzengesellschaften und der funktionellen Gruppen untersucht. Schlußendlich wird auch die Verteilung von Photosynthesetypen in unterschiedlichen Sandlebensräumen dargestellt und diskutiert. Um die genannten Zielstellungen zu bearbeiten wurden verschiedene Lebensräume (Spülsäume, Wanderdünen, stabilisierte Dünenbereiche, Salzmarschen, (teil)feuchte Sandbereiche und gestörte Sandhabitate) in unterschiedlichen Klimaregionen studiert (Atlantische, Mediterrane, Hyrkanische und Irano-Turanische Region).

Wir zeigen, daß Sandökosysteme trotz großer Unterschiede bei regionalem Klima und Artenzusammensetzung durch Zusammenstellungen von funktionellen Gruppen definiert werden können. Dies untermauert, daß sich die Klassifikationen funktioneller Merkmale auf andere Regionen übertragen lassen. Durch Klassifikation funktioneller Merkmale können Sandökosysteme auf Grundlage von drei Anpassungsstrategien ausdauernder Arten und vier Strategietypen der Annuellen beschrieben werden. Ordinationsanalysen zeigen, daß sich funktionelle Merkmale unabhängig von der

Region gemeinsam anordnen. Das macht deutlich, daß Pflanzenmerkmale in Sandökosystemen eher eine Bindung an den Lebensraum als einen regionalen Bezug aufweisen.

Weiterhin verglichen wir Sandhabitate auf den Ebenen von Pflanzenarten, Pflanzengesellschaften und funktionellen Gruppen. Es ist erkennbar, daß bei einer Fokussierung auf Arten, Gesellschaften und zuletzt funktionelle Gruppen, die Ähnlichkeit zwischen gleichartigen Habitaten zunimmt. Die höchste Ähnlichkeit wurde auf funktioneller Ebene ermittelt, die niedrigste auf taxonomischer Ebene. Die Vegetation aller untersuchten Habitate auf der funktionellen Ebene, kann als azonal und damit unabhängig von der Klimaregion angesehen werden. Wir fanden zudem heraus, daß stärkere Stress-abhängigkeit der Vegetation, eine stärkere Bindung an den Lebensraum als an die Klimaregion bedingt. Wir testeten auch die funktionelle Zusammensetzung der Vegetation um unterschiedliche Regionen zu vergleichen. Dies ist nützlich um Pflanzengesellschaften ökologisch zu verstehen und zu beschreiben, da Merkmalsgruppen Habitat- und Ökosystembedingungen widerspiegeln. Allerdings weist die Artenzusammensetzung der Lebensräume in diesem Teil regionale Muster auf und es überwiegt die biogeographische Distanz im Gegensatz zu ökologischer Ähnlichkeit.

Wir fanden zudem heraus, daß C4 Pflanzen einen nennenswerten Beitrag auf die Vegetationsbedeckung von Salzmarschen, Wanderdünen und gestörten Sandbereichen haben, obwohl nur wenige solcher Arten auftreten. Unsere Ergebnisse zeigen, daß C4 Arten am stärksten die Bedeckung und beeinflussen und weniger die Artenvielfalt im Vergleich zu C3 Pflanzen. Dies zeigt, daß zumindest in einigen Sandlebensräumen C4-Pflanzen gefördert werden und dominieren können. Hohe Lichtintensität, hohe Sommertemperaturen und ausgeprägte Trockenheit sind typische Eigenschaften von Sandökosystemen, die C4-Photosynthese gegenüber dem C3-Weg effizienter machen. Wir konnten eine generelle Zunahme von Artenreichtum und Bedeckung von C4 Pflanzen mit zunehmender Trockenheit feststellen. Der höchste Anteil von C4 Arten trat im Inland von Iran auf, der trockendsten und heißesten Region.

Chapter 1

Introduction

Sand dune ecosystem

Ecosystem features

Sand dunes are sedimentary deposits occurring in different shapes and size. They are formed by interactions of wind and water erosion. Common in many parts of the world, they are found in coastal areas, inlands and along sandy river beds and valleys. Sediments in coastal dunes originate from glacial ice shelves and at present from cliff erosion, river discharges and input from tides and storm. In dry regions, the weathering of sand stones and rocks is the main source of sand. In rivers, water carries sands and deposits them on banks through overflow events (Maun 2009). In all cases, wind plays an important role in moving sands and shaping them to dunes. Vegetation also influences dune morphology through local changes in wind velocity and direction. It plays an important role in fixing the windblown deposit of sand (Danin 1996). Presence of particular plant communities in different zones are crucial for preserving the natural dune morphology (Acosta et al. 2007).

Another feature of sand dunes is symbiotic association of mycorrhizal fungi with the roots of higher plants. Mycorrhizal fungi have a vital role in establishment, survival and growth of plants. They increase the water and nutrient supply for the plants and in return they take organic compounds from the plants. The most common and widespread types of mycorrhizal fungi are arbuscular mycorrhizas. Mycorrhizal fungi strongly enhance the aggregation of sand particles. Similarly, microbiotic crust on the sand surface plays an important role in sand fixation. Disturbances can destroy the hyphal networks and thus the fungal communities (Danin 1996, Maun 2009).

Inland and coastal dunes are similar in main environmental pressures, physical structure, physiognomy, and plant strategies. In addition to different species composition, there are three main differences between these two types (Danin 1996): species of coastal sand dunes have to withstand salt spray and inundation by sea water in addition to sand burial. Climax vegetation in many coastal dune systems consists of phanerophytes whereas in inland dunes is mainly of chamaephytes. There is a persistent supply of organic matters from the sea in coastal dunes but such resources do not exist in desert dunes. Despite their variety in shape and form, all sand ecosystems are exposed to sand burial, salinity, aridity, lack of soil and nutrients and high wind velocity.

Although, the number of species in sand habitats is quite low due to harsh environmental conditions, sand ecosystems represent high ecological and biological diversity to both flora and fauna. Following the EU Habitats Directive (European Commission 2003) and EUNIS habitats (Schaminée et al. 2001) more than 10 habitat types are listed under coastal sand dunes and more than 5 habitat types for salt marshes and salt meadows of Europe. Sand dune ecosystems are a suitable model for ecological research because of their long environmental gradient, habitat diversity in relatively small areas and their low number of species in comparison to other ecosystems.

They provide important services such as sediment storage and transport, protection against wind erosion, waves and sea-level rise, water filtration and storage, carbon sequestration, provision of food, cultural services and they are essential breeding and nesting areas for wildlife (Defeo et al. 2009; Everard et al. 2010; Barbier et al. 2011). Many of these services are also applicable for inland dunes.

Sand dunes are one of the most endangered ecosystems worldwide which are in threat of habitat loss, fragmentation and biodiversity loss (flora and fauna) under high pressure of human activities (EEA 2008). Urbanization, agriculture, trampling and touristic development are the most important threats (Buffa et al. 2012; Pintó et al. 2014). Off-road vehicles which are commonly used in sandy area cause high ecological impact on the ecosystem. They disturb not only the physical features of the sand surface and stability of sand dunes but also destroy the vegetation and kill animals inhabiting such habitats (Defeo et al. 2009). Beach cleaning heavily affects the vegetation as it removes seedlings and young plants and increases sand erosion. Alteration of dune morphology through disturbances and human activities is highly correlated to changes in coastal vegetation zonation and loss of habitats (Acosta et al. 2007). Comparison of real vegetation with potential natural vegetation in Central Italy shows that only in few sites vegetation zones are relatively well-preserved (Acosta et al. 2004). Vegetation models predict that mobile and fixed dunes of Italy are under high pressure and will disappear without proper conservation plans only due to climate changes (Prisco et al. 2013). However, in many national Red Lists these habitats and their plant species are not well represented. Precise assessment of the dune systems is suggested by some researchers for conservation purposes (e.g. Pintó et al. 2014). Restoration of these vulnerable habitats and preservation of the remaining sites are important issues in order to sustain the sand ecosystem (Martinez et al. 2013).

Habitat diversity and survival strategies

Sand dunes are characterized by strong environmental gradients in a relatively small area. This creates a zonation and a wide range of habitats from dry shifting dunes to semi-wet dune slacks and saltmarshes (Doing 1985), mainly differentiated by salinity and drought gradient. Habitat heterogeneity results in vegetation diversity (Redžić 2007). Each zone provides specific environmental conditions, inhabited and shaped by particular plant communities.

Plant communities in sand dunes and saltmarshes have been documented for many regions especially in Europe (Mucina et al. 2016). However, further research is required in countries like Iran and Greece. In the following sections the ecological conditions determining plant species composition in each habitat zone and adaptive mechanisms of plants are described. Syntaxonomic details are provided in Chapter 3.

Drift lines

This habitat is characterized by narrow linear zone which occurs just above the normal upper tidal limits along the sea shores. They may be rich in pebbles and shingle and have always high amounts of organic matter (Sykora et al. 2003, European Commission 2013). Inundations and frequent disturbances through high tides and storms are common features of this zone which is not suitable for survival of most perennial plants (Grime 2006). Drift lines are sparsely inhabited by annual nitrophilous plants resistant to high salt concentration and frequent disturbances. Few species can complete their life cycle under such unfavorable conditions e.g. *Cakile maritima, Atriplex laciniata, Xanthium strumarium* and *Salsola kali*. However, the habitat shows the highest proportion of endangered species (Acosta et al. 2009) and properly listed as endangered habitat for Germany (Rennwald 2000) which is also the case for many regions.

Plants of drift line share common traits as adaptations to harsh conditions including short life cycle, good dispersal ability, seed dormancy and large seed size. Although, rate of mortality is usually high and plants' population vary year to year, but still some plants could complete their life cycle in short period within disturbances (Maun 2009). Species of *Cakile* have dimorphic two-segmented silique with an abscission layer between upper and lower part at maturity. They can float in water because of hard, corky and indehiscent pericarp. The upper part breaks off but the lower part remains on the parent plant. The upper fruit segment with thicker shell is well adapted to water dispersal (Barbour 1972). The larger seed size enable the upper fruit to grow under sand burial (Maun 2009).

Mobile dunes

Shifting dunes occur above the tidal limits and are characterized by sand accumulation and deflation. Sand burial and strong winds plays an important role in shaping the vegetation. In this zone disturbance is lower but wind velocity is higher. Sand accretion (to a certain extent) stimulates the growth of specific plants of mobile dunes, such as *Ammophila arenaria*, but also affects the composition and density of vegetation by reducing and eliminating species intolerant to sand burial (Maun 1998). Some species of this habitat are able to withstand sand burial as they can grow upwards rapidly and produce adventitious roots from the nodes of shoots (Fahn 1992). Another group can tolerate removal of sand from around the root by developing deep roots. Both horizontal and vertical root systems are common among plants on shifting dunes. Buds of these species are protected in the ground during the cold winter. Fragmentation of rhizomes and stolons facilitates dispersal and thus helps to establish new populations and colonies on bare sands (Maun 2009).

Dune slacks

They are depressions between dune hills where the water table is at or just below the sand surface. They are maintained by precipitation and ground water. Seasonal fluctuation of the water table is a feature of dune slacks. They are less exposed to erosion because of reduced wind velocity and soil moisture. There are different types of slack (from dry to flooded ones) depending on hydrological conditions. Water abstraction and drainage are threats to this habitat (Houston 2008). Compared to surrounding shifting dunes, they usually have higher species richness and/or biomass (Littmann & Veste 2005).

Stabilized dunes

Grey dunes or stabilized dunes are further developed dunes occupying the landward zone behind the mobile dunes. They are more stable and sand movement is not a limiting factor. Drought stress is the main environmental factor affecting the vegetation. Provoost et al. 2004 found that the surface temperature of stabilized dunes in Belgium reaches above 50°C. However, temperature declines rapidly below the sand surface. In depth of 5 cm from sand surface, temperature can drop about 10° (Maun 2009). Due to the more stable soil conditions, vegetation is denser compared to seaward zones.

Salt marshes

Salt marshes are permanently or temporarily wet habitats that may be associated with tidal flats, salt pans or salt lakes. They are common on both coastal and desert sand systems. Salt marshes accumulate organic matter and are temporarily inundated by salty or brackish water. High evaporation causes salt enrichment in both inland and coastal salt marshes (European Commission 2013). This highly stressful environment is generally species poor and its vegetation is sparse to rather close. Salinity gradients, flooding frequency and duration, soil texture and amounts of organic matter determine vegetation structure and productivity of the habitat (Pennings & Callaway 1992; Pennings & Bertness 2001; Mucina & O’Callaghan 2003). The vegetation is characterized mainly by succulent Chenopodiaceae such as *Sarcocornia fruticosa, Arthrocnemum macrostachyum, Halocnemum strobilaceum* and *Salicornia* spp.

Halophytes are differing in their tolerance to the concentration of salt. Salt tolerance often depends on various physiological and anatomical adaptations. Species show various degrees of succulency and usually possess a well-developed water storage tissue. Some are aphyllous or have small scale-like leaves while others have small thick leaves. Many coastal halophytes are densely covered by hairs, whereas inland halophytes are mainly glabrous and covered by a wax layer (Fahn 1992). Halophytes have different mechanism to achieve osmotic adjustment, including ion accumulation, synthesis or accumulation of organic compounds and water loss (Shannon 1997; Khan & Gul 2002). Salt exclusion by roots is the most common way for avoiding salt. Some halophytes are able to excrete salt to leaf surface through their salt glands (e.g. *Tamarix* and *Aeluropus*) or accumulate it in salt bladders (e.g. *Atriplex*). Salt bladders are modified epidermal hairs that usually consist of two cells, stalk cell and bladder cell, that accumulate salt to prevent high salinity in mesophyll cells. Some plants shed leaves with high salt concentrations. Seeds of some species like *Arthrocnemum macrostachyum*, *Cressa cretica*, *Suaeda fruticosa* and *Aeluropus lagopoides* remain dormant at high salinity but germinate when return to distilled water (Khan & Gul 2002).

Adaptive traits of plants as a key to understanding ecosystem function

As obtained from the last section, Environmental conditions and habitat characteristics act as a filter for species establishment and hence are important in shaping the vegetation. Adaptive strategies of plants have evolved under extreme conditions and are reflected in traits of plants. Therefore, plant traits can be used to find out about the vegetation dynamic and function of an ecosystem. The following sections describe functional traits and their importance in ecological studies.

Concept and definition of functional traits

Functional traits are characteristics of an organism which reveal function of that organism (Violle et al. 2007; de Bello et al. 2010). In plants, they consist of vegetative (whole-plant, leaf, stem and root traits), regenerative and ecophysiological traits which reflect adaptations to the environment (Cornelissen et al. 2003). Traits which can be measured relatively easily and quickly are so called ‘soft traits’ in contrast to ‘hard traits’ which may be more accurate indicators but are difficult or expensive to measure (Hodgson et al. 1999).

Plant functional traits such as life forms (Raunkiaer 1934) have been frequently used in ecological studies for a long time. However, in recent years, there is an increasing interest in using functional approaches to deal with different aspects of ecosystems and a variety of new methods have been developed and applied. Functional traits specifically allow simplifying and generalizing the ecosystem to a limited number of functional groups instead of dealing with large numbers of species (Gitay and Noble 1997).

Functional groups are species which respond similarly to environmental pressures or have similar effects on ecosystem processes and thus they can be divided to effect and response groups (Gitay and Noble 1997, Harrington et al. 2010). They can be identified as clusters through multivariate analysis of traits, without *a priori* classification (Hooper et al. 2002). However, this method is used in few studies. It was argued by some researchers that functional classification is context-dependent and thus useful functional groups at global scale may not be expected (Bugmann 1996; Noble & Gitay 1996). On the other hand, repeatable patterns of functional traits suggest that functional groups may be applicable across regions (Wright et al. 2004; Sasaki et al. 2011). Considering the definition of functional groups, it is expected that they are formed rather by habitat filters and niche similarities than by biogeographic regions (Cornwell et al. 2006; Lebrija-Trejos et al. 2010; Maire et al. 2012). For instance, in floristically different regions, similar trait combinations are associated with grazing (Díaz et al. 2001). However, global application of plant traits needs methodological standardization in definition of traits and their attributes, as well as rules for collecting and measuring (handbook of standardized traits by (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Unification of trait-related terminology should avoid misunderstanding and misinterpretation of functional studies. In this context, several concepts and glossary papers are published (Violle et al. 2007; Harrington et al. 2010). Global trait databases are the next step in functional studies on various scales (e.g. TRY, Kattge et al. 2011).

Ecological values of the functional approach

Functional approaches offers advantages in ecological studies. They are mainly used for dealing with community and ecosystem processes or for predicting ecological changes (reviewed in (Duckworth et al. 2000). In the following sections the importance of functional traits in ecological studies are summarized.

Functional groups respond well to the need of **generalization and globalization** in biogeography and ecology. In contrast to species-based approach, classified functional traits should be potentially applicable to other regions. Therefore, they are suitable for studies between regions which share no or only few species (chapter 2, Mahdavi & Bergmeier 2016). Functional traits are reflecting the environmental filters. Thus, using morphological and physiological traits to study communities can help in identification of general patterns in ecology and even may extend the ecological aspect into phylogenetic structures and trait evolution (McGill et al. 2006; Shipley et al. 2006). Another advantage of using functional groups based on cluster analysis is that new species can be added to the existing functional groups which is very useful in ecological studies (Fry et al. 2014).

Functional traits provide **new perspectives** in ecological studies. For example, functional approaches allow quantifying species niches in units of traits instead of environmental parameters. It was shown that mean trait values of a species determine its niche position along gradients and intraspecific trait variability determines its niche breadth (Violle & Jiang 2009). Trait syndromes are useful for defining the characters of a habitat. They refer to groups of co-occurring traits that express adaptation to particular environmental condition (Harrington et al. 2010). Furthermore, functional approaches are an effective complementary tool to traditional phytosociology for describing diagnostic species and vicariant plant communities especially when comparing different biogeographical regions (chapter 3, Mahdavi et al. 2017).

Functional diversity adds a new aspect to ecological diversity. It is a quite new concept dealing with niche partitioning and different species assemblage (Petchey 2004). The more species-rich a functional group, the more stable the ecosystem as species of the same function can replace each other and thus consequences of extinction are less serious (Duckworth et al. 2000). Community weighted trait mean which is a measure of functional diversity can be applied for assessing ecosystem properties and services (Díaz et al. 2007; de Bello et al. 2010). Diversity of functional traits of species in a community should be incorporated into conservation and restoration activities (reviewed in Cadotte et al. 2011). However, measuring functional diversity is a challenging task as many indices have been proposed using different methods for estimating the functional dissimilarity which can affect the results (Petchey et al. 2004; Ricotta 2005; Schleuter et al. 2010; Mason et al. 2013; de Bello et al. 2013). For choosing the proper diversity index these questions need to be considered: how many and which traits to use, how to combine traits which measured in different scale, and how to weight the traits by abundance of species (Lepš et al. 2006; Petchey & Gaston 2006; Mason & de Bello 2013).

Functional groups are especially useful for **modeling** biodiversity and **predicting** ecological changes (Lavorel & Garnier 2002; Boulangeat et al. 2012) as they reduce the number of variables to consider in the analysis. (Bonan et al. 2002 examined to consider landscape as patches of plant functional types for modeling climate and ecosystem. Plant traits are considered as a powerful tool for predicting species assemblages across different habitats and environmental gradients (Douma et al. 2012).

Beside species- and habitat-based approaches, functional traits can be considered as another component for the application in **nature conservation**. Functional groups are helpful when information about some species of the habitat are lacking. Species of the same functional group will receive the same management which facilitate delivery of preliminary recovery actions (Kooyman & Rossetto 2008). In this context, BIOPOP is a plant trait database made for species of Germany providing information for conservation purposes (Poschlod et al. 2003). Diverse researches suggest that functional groups can be used for identifying conservation priorities and suitable management policy and to evaluate the effect of environmental stress on target functional groups of habitat (e.g. García-Mora et al. 1999; Quétier et al. 2007).

C4 photosynthesis, a complex trait

Diversity of photosynthetic types

The oldest and most common photosynthesis type among plants is the C_3 pathway (Sage 2005). Carbon fixation in C3 pathway is started by Rubisco (ribulose 1,5-bisphosphate carboxylase/oxygenase) which is both, a carboxylase and oxygenase enzyme. Product of carbon fixation runs the Calvin cycle for producing sugar. Both carbon fixation and Calvin cycle occur in mesophyll cells. The oxygenate activity of Rubisco results in photorespiration and reduces the overall efficiency of photosynthesis.

C4 syndrome is a combination of anatomical, physiological and biochemical modifications in the photosynthetic pathway which increases the concentration of CO_2 around Rubisco and reduces photorespiration (Sage 2004). In contrast to C3 ones, the carbon fixation is performed by PEPC (phosphoenolpyruvate carboxylase) in mesophyll cells and results in a four-carbon organic acid (Oxaloacetate, OAA) which then is transformed and transfered to the bundle sheath cells (Covshoff et al. 2014). There, the four-carbon acid is decarboxylated to release CO_2 that is taken by Rubisco to start the Calvin cycle and produce sugar. Spatial separation of CO_2 uptake (mesophyll) and Calvin cycle (bundle sheath) provides high concentration of CO_2 for Rubisco and prevents its contact to O_2. Therefore, oxygenate activity of the enzyme is blocked leading to high photosynthesis efficiency.

Based on the type of the decarboxylation enzyme, three biochemical subtypes among C4 plants are identified: NADP-malic enzyme where OAA is converted to malate which is then transferred to interior compartment, NAD-malic enzyme where OAA is transformed to aspartate and the third one is phosphoenolpyruvate carboxykinase (PCK) which produces PEP during the carboxylation (Sage 2004; Christin & Osborne 2014). All three subtypes occur in grasses while eudicots have only NADP-ME and NAD-ME (Sage 2004). The most common subtype is NADP-ME which can be found in both monocots and dicots (Christin et al. 2009).

In most C4 plants, two distinct cell types are required for the function of C4 pathway. An inner layer (bundle sheath) consisting of enlarged, compact, thick-walled cells with high chloroplast content which is surrounded by an outer layer (mesophyll) with radiate, thin-walled cells (Muhaidat et al. 2007; Lundgren et al. 2014). This structure is known as Kranz anatomy with eight major types among different C4 lineage (Dengler & Nelson 1999). Five of these types occur in Chenopodiaceae (Atriplicoid, Kochioid, Salsoloid, Suaedoid, and Conospermoid) (Edwards et al. 2004).

In addition, a small group of plants with C4 pathway does not feature Kranz anatomy. In this group all C4 reaction occurs in a single cell. This group includes *Suaeda aralocaspica* (=*Borszczowia*) and three species of *Bienertia* (*B. sinuspersici, B. cycloptera, B. kavirense*) (Voznesenskaya et al. 2001; Sage 2016).

The third common type of photosynthesis is crassulacean acid metabolism (CAM). It is similar to C4 pathway in concentrating CO_2 and producing a four-carbon acid. However instead of a spatial separation as in C4 plants, CAM species exhibit a temporal separation of carbon fixation (during night) and Calvin cycle (during day) (Ehleringer & Monson 1993). Therefore, the stomata can stay close during the day while decarboxylation of four-carbon acid releases CO_2 and Rubisco operates under high concentration of CO_2. CAM is a highly efficient pathway in dry and hot regions and is frequently found in succulent plants such as Cactaceae, Bromeliaceae, Crassulaceae and Polypodiaceae (Ehleringer & Monson 1993).

Evolutionary pressure

Phylogenetic studies indicate that all C4 lineages evolved under low atmospheric CO_2 condition of the post-Oligocene (reviewed in (Sage & Stata 2015). The first origins of C4 grasses arose in the late Oligocene (ca. 30 million years ago) where the most severe drop in atmospheric CO_2 occurred; however C4 grasslands expanded in the late Miocene (5-8 million years ago) (Bouchenak-Khelladi et al. 2009). Low atmospheric CO_2 partial pressure (pCO_2) and high temperature are considered as a main selective force for driving evolution of C4 photosynthetic pathway (Ehleringer et al. 1997). C4 and C3 plants respond differently to variation in temperature and pCO_2. This concept is well explained in crossover temperature hypothesis (Ehleringer 1978). Crossover temperature is defined as a temperature at which the quantum yield of photosynthetic CO_2 fixation is equal for both C3 and C4 species at a certain pCO_2, which is at about 22°C (Collatz et al. 1998). Following this hypothesis, C3 plants have a higher efficiency below 22° C whereas above 30° C is in favor of C4 plants. Collatz et al. (1998) modeled the current distribution of C4 plants based on pCO_2 and crossover temperature in the past and provide a good base for predicting the changes in C3-C4 vegetation in the future. However, there are also other factors influencing the distribution of C4 plants as e.g. changing climate as well as fire and herbivory. The latter factors might be involved in the creation of open habitats which was required for C4 expansion at the Miocene as most C4 species cannot tolerate shade (Osborne & Beerling 2006). CO_2 enrichment, global climate warming, terrestrial eutrophication, bioinvasions and human altering of landscapes are significant modifiers of C3/C4 dynamics.

Origin and diversity of C4 plants

C4 photosynthesis has evolved independently more than 60 times in flowering plants and 22-24 times in grasses (Christin et al. 2013). All origins of C4 grasses occurred in PACMAD clade (Grass

Phylogeny Working Group II 2012), consisting of six subfamilies (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae and Danthonioideae; including both C3 and C4 species). Their sister clade BEP (Bambusoideae, Ehrhartoideae and Pooideae) diverged from PACMAD ca. 50 million years ago (Taylor et al. 2011). Phylogenetical evidences suggest that PACMAD lineages (whether they are C4 or not) are adapted to warmer regions while BEP lineages occurred in colder regions (Edwards et al. 2010). It is assumed that habitat preferences of C4 species is not only influenced by their photosynthetic trait but also is correlated with their phylogeny and other traits which they inherited from their C3 ancestors (Taub 2000). Phylogenetic analyses within lineages of PACMAD reveals that C4 lineages occur in drier habitats than their C3 relatives (Pau & Still 2014; Taylor et al. 2014). Therefore, distribution patterns of C3 and C4 grasses reflect the distribution patterns of Pooideae/PACMAD and it is not clear to what extent C4 syndrome is contributing to this trend (Edwards & Still 2008). Ecophysiological differences between subfamilies of PACMAD confirm that phylogeny is associated with habitat preferences of C4 lineages (Taylor et al. 2010). On the other hand, (Osborne & Freckleton 2009) showed that C4 photosynthesis is a pre-adaptation to arid condition explaining the high occurrence of C4 lineages in arid region. Their analysis on the phylogeny of grasses confirms that open habitats are necessary for selection of C4 pathway but the evolution may take place in arid, saline or mesic conditions of open habitats. However, when the pathway has evolved, C4 lineages have adapted more rapidly to arid and saline habitats than C3 lineages (Osborne & Freckleton 2009).

First origin of C4 plants date back to ca. 30 million years ago (Sage & Stata 2015). Although, first origins of monocots and dicots arose almost in the same time but some C4 lineages of dicots evolved more recently. The youngest being *Flaveria* that evolved 2 million years ago (Christin et al. 2011). The majority of C3 ancestors of C4 plants and C3-C4 intermediate forms have been identified among the eudicots such as the genera *Salsola, Heliotropium, Alternanthera, Moricandia, Mollugo* and *Flaveria* (Sage et al. 2011). In grasses however, there are only two C3-C4 intermediate genera: *Steinchisma* and *Neurachne* (Sage et al. 2011) and one species (*Alloteropsis semialata*) with C3, C4 and C3-C4 populations (Lundgren et al. 2016). Intermediate species are important for studying the evolutionary transition from C3 to C4.

C4 species occur in 16 families of dicots in which Chenopodiaceae and Amaranthaceae have the highest number of C4 species followed by Euphorbiaceae and Asteraceae. Other dicot families with recorded C4 species are: Zygophyllaceae, Brassicaceae, Scrophulariaceae, Acanthaceae, Boraginaceae, Polygonaceae, Caryophyllaceae, Aizoaceae, Gisekiaceae, Nyctaginaceae, Molluginaceae and Portulacaceae (Sage 2005).

Pre-adaptation of C4 photosynthesis to arid condition was shown also for dicots. Phylogenetic studies confirm that C4 lineages evolved from the C3 ancestors which already adapted to arid conditions (Christin & Osborne 2014). Similar results were gained for Chenopodiaceae, C3 chenopods that were more tolerant to salinity evolved as C4 halophytes (Kadereit et al. 2012). One should also consider that salinity is associated with aridity as it decreases water availability and causes physiological drought. Adaptation to arid condition is important for species to inhabit the arid interiors of continents where most C4 dicot lineages occur (Sage 2005). An evolutionary hypothesis for C4 halophytes is explained by the occurrence of *Bienertia* spp. and *Suaeda aralocaspica* (single-celled C4 species) in extreme saline soils beyond tolerance of C3 halophytes. Sage (2005) suggests some evolutionary stages of C3-C4 intermediates along salinity gradient which at each stage intermediate species colonized areas with greater salinity where their C3 relatives were unable to survive. This process is continued until full evolution of C4 pathway. Therefore, salinity should have worked as a selection pressure for the evolution of C4 pathway in C4 halophytes.

Considering diversity of C4 groups including biochemical and anatomical subtypes and different C4 lineages, it is suggested to integrate physiological and anatomical studies in a phylogenetic context to better understand the evolution of C4 plants (Christin, Salamin, et al. 2009; Christin et al. 2013).

Study area

Irano-Turanian region

The Alborz mountain range in N Iran, with the height of 5671 m at the peak of Demavand, works as a barrier and separates the humid part in south of the Caspian Sea from the interior part of the Iranian plateau. The northern part belongs to Euro-Siberian phytogeograophic region (Hyrcanian province) and the southern part belongs to the Irano-Turanian region.

The Irano-Turanian region is one of the hotspots of biodiversity and serves as a source of xerophytic taxa for neighboring regions (Manafzadeh et al. 2014; Manafzadeh et al. 2016). It is characterized by continental climate, low precipitation, hot and dry summer and cold winter, cushion form vegetation and dwarf shrubs with high number of endemic species (Zohary 1973). The Irano-Turanuan region forms a distinct bioclimatic area in SW and Central Asia which is more continental than Mediterranean climate and has different seasonality patterns of precipitation (Djamali et al. 2012).

Central Iran: southern shore of the Namak Lake (Daryacheh-ye Namak) in the Maranjab Desert (34° 9-19’N, 51° 30-56’E) was studies. It is a large saline playa surrounded by halo- phytic communities and sand dunes. Mean monthly temperatures vary between 5° C (January) and 33° C (July). The annual precipitation is 136 mm (http://www.chbmet.ir/iranarchive.asp).

Hyrcanian region

This region in Iran is extended along the southern shore of the Caspian Sea. The Western part of the Hyrcanian region has higher precipitation than the eastern part. The region is characterized by a warm humid climate with rainy summers and mild winters. The Hyrcanian forests are significant in the region and known as refugia for many relict elements. The large parts of the sand habitat along the coast are degraded and fragmented due to intensive human activities (Akhani et al. 2010).

N Iran: the SE Caspian Sea shore was investigated, including the Miankaleh Biosphere Reserve (36° 48-55'N, 53° 25'-54° 02'E) with 50 km of (semi-)natural coastline, and two other sites westward (36° 49'N, 53° 8'E, 36° 39'N, 52° 22'E). Miankaleh wildlife refuge is located in south-east of the Caspian Sea, with the total area of 68800 ha and consisted of two terrestrial and aquatic ecosystems. It is characterized by diverse habitats, supporting variety of wildlife, migratory birds and different vegetation and plant species. The mean temperature of the coldest month (January) is 8.7 °C and the warmest month is August with mean temperatures of ca. 28 °C. The mean annual precipitation is 789 mm (http://www.chbmet.ir/iranarchive.asp).

Mediterranean region

This region is known for high biodiversity and high rate of endemism (Médail & Quézel 1999). Disturbances such as fire and grazing play an important role in dynamic and structure of the vegetation (Cowling et al. 1996; Pausas et al. 2008). The climate is characterized by hot, dry summers and humid, cool winters.

NE Greece: The study area along the North Aegean coast runs approximately 300 km from south of Katerini (40° 09'N, 22° 33'E) eastward to Porto Lagos (40° 54'N, 25° 23'E). Mean monthly temperatures vary between 5-7 °C (January) and 25-27 °C (July). Mean annual rainfall is 400-600 mm (Lienau 1989).

Atlantic region

The region stretches along the North Sea and North-east Atlantic Ocean. It is characterized by oceanic climate, mile winters, cool summers, moderate rainfall throughout the year and westerly winds. The natural and semi-natural habitats are heavily fragmented through urbanization and agriculture and only isolated patches are existed (Sundseth 2009).

N Germany: The data from the coastal area along the North Sea from the island of Borkum (53° 36'N, 6° 43'E) eastward to the island of Fehmarn (54° 28'N, 11° 08'E) at the Baltic Sea coast was analyzed.

Mean monthly temperatures for the North Sea (Island of Norderney) vary between 3 °C (January) and 18 °C (July). Mean annual rainfall is about 801 mm, with higher amounts from July to December.

General description of methods

Data collection

Vegetation sampling

The field data were collected during the summer 2011 and 2012 in sand ecosystems of the Mediterranean, Hyrcanian and Irano-Turanian. In the Atlantic region, the data base of Coastal Vegetation Germany (GIVD code: EU-DE-035) was included in the analysis of the second study (chapter 3). In each region the following habitats were surveyed: drift lines, mobile dunes, semi-wet habitats (dune slacks), stabilized dunes, salt marshes and disturbed sandy grounds. The plots were made randomly in the homogenous vegetation types with distance of at least 50-100 m to avoid the spatial autocorrelation. The vascular plant composition was recorded in plots of 25 m^2 using Braun-Blanquet cover-abundance scale (Dierschke 1994). In addition, the total plant cover, the shrub and herb cover, the max. herb and shrub height and the environmental variables (geographic coordinates, slope, aspect, elevation a.s.l. and the soil texture) were recorded. The vegetation survey data sheet and the Braun-Blanquet cover-abundance scales are provided in the appendix A.

Plant nomenclature follows Flora Iranica (Rechinger 1963-2012), Dimopoulos et al. (2013) and Florenliste von Deutschland (Buttler et al. 2015) for Iran, Greece and Germany respectively; syntaxonomic nomenclature follows mainly Mucina et al. (2016) for Greece and Germany, and Asri (2003) for Iran.

Trait sampling

We used fourteen categorical traits for the functional trait analysis. Categorical traits can be measured or obtained from the literature and are especially useful for areas without established trait databases. They also facilitate repeating and comparing the approach in other areas. The traits were selected from different parts of plants to better reflect the adaptive response patterns of species to the environment (Cornelissen et al. 2003). For standardization, the protocol for functional traits (Pérez-Harguindeguy et al. 2013) was followed. The recorded species were assigned to the traits based on the given attributes in Table 1 (chapter 2). Original trait information was obtained mainly from the collected specimens and field observation, but also from floras (Rechinger 1963-2012) and other resources (especially for plant strategies and regenerative traits Grime et al. 2007; Klotz et al. 2002).

In case of the life form, we merged geophytes with hemicryptophytes as there are very few species of geophytes among the sampled species which we have preferred to merge them rather than omitting them from the study. The Plant height was mostly measured and partly taken from floras. They were divided then into four height classes as for our purposes it was sufficient to know whether plants in different habitats have small, medium or large size. To deal with such quantitative traits in analyses, they should be scaled from 0 (minimum value) to 1 (maximum value) and then the other heights could be scaled within this range (more information in (Lepš & de Bello 2008). For example, in our case class one is 0.25, class two is 0.5, class three is 0.75, and class four is 1. The data on the photosynthetic pathway of species were obtained from the literatures (more details in chapter 4, Table 2).

Data analysis

In this thesis, the collected data were examined mainly by means of multivariate analysis in forms of classification and ordination to find out the main gradients and/or groups. The general overview of the applied methods is provided in this section and the detailed information on the 'methods' section of each chapter.

The trait data built of all species and trait variables were classified by using cluster analysis (Ward's method with relative Euclidean distance) in order to define the functional groups of plants. The cluster cut level was determined manually so that the resulting groups were interpretable. Vegetation classification was performed separately for each region using TWINSPAN with three pseudospecies cut levels (0, 2, 5). After manual editing of generated groups, synoptic tables were created, and diagnostic species were determined using percentage frequency (constancy) values. The plant communities were assigned to the high-rank syntaxa and when possible to the association using the available literature.

We used Detrended Correspondence Analysis (DCA) to understand the distribution of functional traits and groups in sand habitats and to estimate the vegetation dissimilarities over regions and habitats. The DCA analysis was run on the matrix of specie-plot, trait-plot and FG-plot. The trait-plot matrix was built by multiplying the trait-species matrix by the matrix of species-plot. To make a FG-plot matrix for a given region, the composition of functional groups for each plot was calculated.

Objectives and thesis outline

The main aim of this thesis was to explore sand ecosystems beyond the regional borders by defining the main functional groups in the ecosystem using plant traits, to analyze the effect of habitat and region on adaptive characters of species, to discover the similarity of sand habitats at species, community and functional level, and to investigate the distribution of photosynthesis types across different sand habitats.

In **chapter 2**, the functional traits of plant species in sand ecosystems across different climatic regions are investigated. The main functional groups (group of species with similar functional traits) are defined by cluster analysis. It is hypothesized that functional groups and the functional affiliation of sand dune species are mainly determined by habitat characteristics and niches, independent of the climatic region in which they occur. To test this hypothesis, functional groups are examined in context of the habitat types (mobile dunes, stabilized dunes, salt marshes, semi-wet sand and sandy disturbed habitat) and climatic regions in which they occur (Mediterranean, Hyrcanian and Irano-Turanian) and results between inland and coastal sand systems are compared. Furthermore, the trait syndromes (groups of co-occurring traits that express adaptation to environmental condition) which are associated with particular habitats in sand dune systems are determined.

In **chapter 3**, the effect of habitat and region on sand dune vegetation is investigated by comparing its similarities at species, community and functional level. At each level similarity in habitats of the same kind across regions as well as in a given region across different sand habitats is considered. Four saline habitat types (drift lines, mobile dunes, stabilized dunes, and salt marshes) in four phytogeographic regions ranging from the Atlantic coasts to Irano-Turanian salt lake shores are examined. The plant communities for each habitat type are defined and the importance of using a functional approach in classical phytosociology is discussed. Specifically the chapter addresses the question whether vegetation of the same habitat type is similar across different phytogeographical regions and which kinds of similarity are more pronounced. It is analyzed to what extent sand habitats represent an azonal vegetation with respect to taxonomic (species and genera), syntaxonomic and functional similarity. Furthermore the syntaxonomical and functional analogues across regions are determined.

Focus of the study in **chapter 4** is on photosynthetic pathway trait and the distribution of C4 plants in habitats of sand dune ecosystems. Proportion of C4 plants and their contribution to total vegetation cover are analyzed. The habitat preferences of C4 plants, the potential drivers of C4 plants (such as aridity, salinity, temperature, and precipitation) are discussed. It is hypothesized that the hot and dry conditions of sand habitats favor plants with C4 photosynthetic pathway. C4 species cover, richness and C3/C4 ratio in five sand habitats is analyzed to answer the following research questions: How are C4 plants distributed in different habitats of sand ecosystems and what are their habitat preferences? Do C4 plants have larger biomass than ecologically similar C3 plants? Do regional climatic differences affect the occurrence and proportion of C4 plants?

In **chapter 5**, the main findings of the research are summarized and discussed in a wider ecological context. Open questions and future research perspectives are declared.

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Chapter 2

Plant functional traits and diversity in sand dune ecosystems across different biogeographic regions

P. Mahdavi, E. Bergmeier

Acta Oecologica 2016, 74: 37-45

http://dx.doi.org/10.1016/j.actao.2016.06.003

Abstract

Plant species of a functional group respond similarly to environmental pressures and may be expected to act similarly on ecosystem processes and habitat properties. However, feasibility and applicability of functional groups in ecosystems across very different climatic regions have not yet been studied. In our approach we specified the functional groups in sand dune ecosystems of the Mediterranean, Hyrcanian and Irano-Turanian phytogeographic regions. We examined whether functional groups are more influenced by region or rather by habitat characteristics, and identified trait syndromes associated with common habitat types in sand dunes (mobile dunes, stabilized dunes, salt marshes, semi-wet sands, disturbed habitats). A database of 14 traits, 309 species and 314 relevés was examined and trait-species, trait-plot and species-plot matrices were built. Cluster analysis revealed similar plant functional groups in sand dune ecosystems across regions of very different species composition and climate. Specifically, our study showed that plant traits in sand dune ecosystems are grouped reflecting habitat affiliation rather than region and species pool. Environmental factors and constraints such as sand mobility, soil salinity, water availability, nutrient status and disturbance are more important for the occurrence and distribution of plant functional groups than regional belonging. Each habitat is shown to be equipped with specific functional groups and can be described by specific sets of traits. In restoration ecology the completeness of functional groups and traits in a site may serve as a guideline for maintaining or restoring the habitat.

Key words Climatic region; Cluster analysis; Coastal vegetation; Functional group; Habitat filter; Sand dunes

Introduction

Plant functional traits efficiently support the study of ecological systems as they allow to explain and generalize the ecosystem by making use of a limited number of functional groups rather than dealing with a large number of species (Díaz Barradas et al. 1999; Petchey 2004; Grime et al. 1997). Plant traits are useful to better understand plant and ecosystem function (Díaz and Cabido 2001; Helsen et al. 2012), for predicting vegetation changes (Lavorel and Garnier 2002) and for nature conservation (Poschlod et al. 2003; Kooyman and Rossetto 2008). They are particularly suitable for large-scale studies with different environmental conditions and for comparing regions with no or few species in common (Dupré and Ehrlén 2002; Díaz et al. 2007a; Tecco et al. 2010).

There is a wide range of studies using plant traits, dealing with different scales and numerous though non-exhaustive aspects of ecosystems, including land use (Díaz et al. 1999; Verheyen et al. 2003; Quétier et al. 2007), grazing (Klimešova et al. 2008; Díaz et al. 2007), fire (Lloret and Vilà 2003; Keeley et al. 2011), community dynamics (Pillar et al. 2013), climate change (Box 1996; Díaz and Cabido 1997), ecosystem services (de Bello et al. 2010) and phylogenetic structure and evolution (Kraft and Ackerly 2010; Pillar and Duarte 2010). Surprisingly few studies deal with functional groups without *a priori* classification. García-Mora et al. (1999) and Gallego-Fernández and Martínez (2011), for instance, defined functional groups in the coastal vegetation of SW Spain and Mexico, respectively, by using functional trait classification. Some researchers classified functional traits to study responses to disturbance (Lavorel et al. 1999) or for predicting the landscape dynamics (Noble and Gitay 1996) but functional classification did not become a common method in ecological studies. It has been argued that regionally defined functional groups might not function at global scale (Bugmann 1996). Noble and Gitay (1996) emphasized that functional classification is context-dependent and that universal functional groups may thus not be expected to occur. However, repeatable patterns of functional traits have been observed by some researchers (Wright et al. 2004; Sasaki et al. 2011) suggesting that functional groups may be applicable across regions. As functional groups comprise species with similar response to environmental pressures and similar effects on ecosystem processes (Díaz et al. 2001; Harrington et al. 2010), it may be expected that they are formed rather by habitat filters and niche similarities (Cornwell et al. 2006; Lebrija-Trejos et al. 2010; Maire et al. 2012) than by the biogeographic region. For instance, Díaz et al. (2001) showed that in two regions with different floras similar combinations of traits were associated with grazing. Such studies across different regions are needed to assess the feasibility and repeatability of functional groups.

Despite increasing attention to functional traits the knowledge of functional groups in specific ecosystems such as sand dunes is limited (García-Mora et al. 1999; Gallego-Fernández and Martínez 2011). Sand dunes, whether coastal or inland, are known as stress-prone habitats distributed worldwide in different climatic and biogeographic regions. Regardless of their differences in species composition, sand dune ecosystems are well adapted to cope with extreme stress such as of water deficiency, salinity and lack of soil and nutrients, and with disturbances through wind erosion and sand burial. The special adaptations of psammophytes to sand ecosystems are well reflected in their traits (Danin 1996; Maun 2009) and can be applied for studying dune vegetation at larger scale by defining groups of species with similar functionality for the ecosystem. Similar habitats and vegetation zonation in sand dunes all over the world (Doing 1985; Acosta 2009) suggest their azonal character. We chose sand dune ecosystems reflecting extreme environmental conditions to explore the adaptation strategies of plants in three regions very different in climate and phytogeography. We aim to identify functional groups of plants in various common habitats of sand dune ecosystems (both inland and coastal) via classification. Easily measurable traits have been selected to study the ecological response of plants to the environmental pressures in the habitats of the three regions. We specifically ask the following questions: Are there specific groups of species with similar traits in sand dune ecosystems across different biogeographical regions? Are plant functional groups more influenced by the habitat types and their local properties than by the climatic region in which the plants occur? If yes, which functional groups and trait syndromes (groups of consistently co-occurring traits that express adaptation to environmental characteristics) are associated with particular habitats in sand dune systems?

We hypothesized that there are widely applicable plant species traits determined by habitat characteristics and niches in sand dune ecosystems, and that the adaptive response of plants to the environment in a certain habitat is similar across biogeographical regions.

Study area

Sand dune ecosystems in three regions have been studied: Mediterranean, Hyrcanian, and Irano-Turanian (Fig. 1). The regions are very different in climate, phytogeography and species composition but are all furnished with a similar set of psammophytic habitat types.

Mediterranean region: NE Greece, ca. 300 km along the North Aegean coast from south of Katerini (40º 09'N, 22º 33'E) via Thessaloniki eastward to Porto Lagos (40º 54'N, 25º 23'E); The area is characterized by Mediterranean climate with hot, dry summers and wet and cool, but almost frost-free winters; mean monthly temperatures vary between 6 °C (January) and 25-27 ºC (July); mean annual rainfall is 400-600 mm (Hellenic National Meteorological Service). The soil consists of fine quartz sands in dunes mixed with coarse sands and gravels in the stabilized dunes. Although not represented throughout, the vegetation zonation of sandy coasts includes drift lines (Euphorbion peplidis), mobile dunes (Ammophilion), stabilized hind dunes (Crucianellion maritimae) (Sýkora et al. 2003) and associated salt marshes (Salicornietalia fruticosae).

Hyrcanian region: NE Iran, SE Caspian Sea shore, Miankaleh Biosphere Reserve (36º 48-55'N, 53º 25'-54º 02'E), with 50 km of semi-natural coastline, and two other sites westward along the Caspian Sea (36º 49'N, 53º 8'E & 36º 39'N, 52º 22'E). The area has a warm humid climate with rainy summers and mild winters; mean annual temperature and rainfall are 17.9 ºC and 789 mm, respectively (based on the nearest meteorological station in Sari). The coldest month is January with a mean temperature of 8.7 °C and the warmest is August with 28 °C. The soils and vegetation zonation resemble that of the Mediterranean coasts but the plant community composition differs.

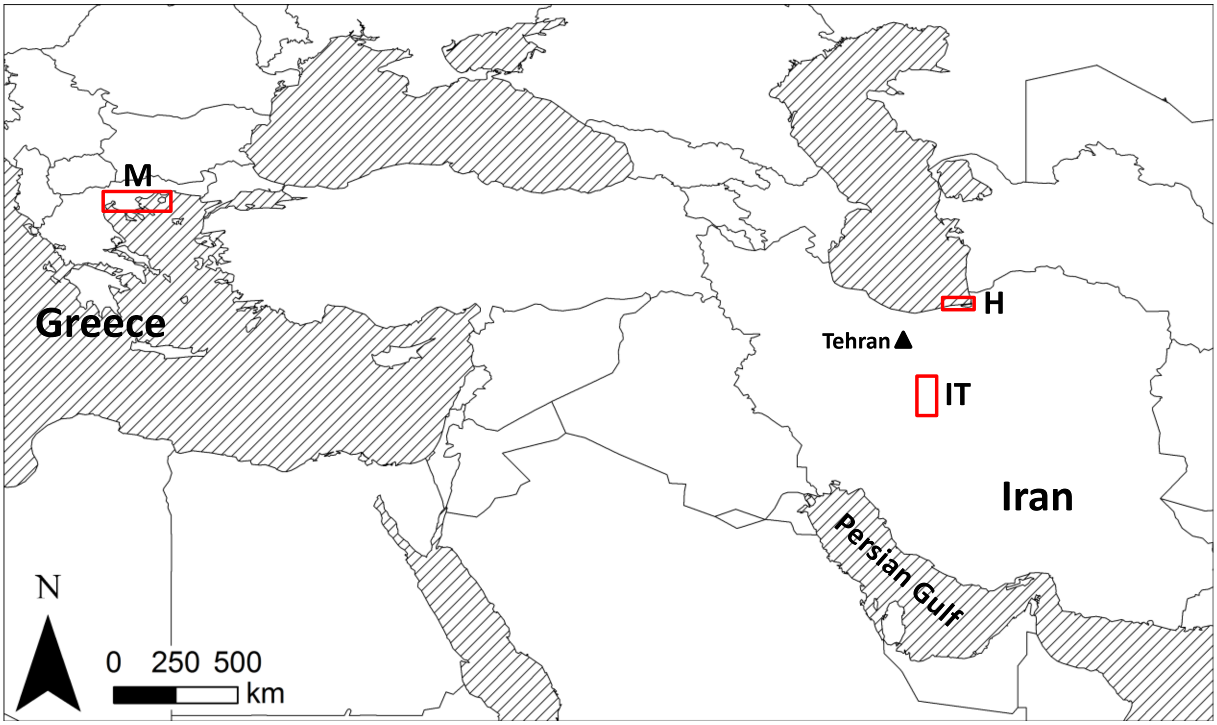

Fig. 1 Location of the study areas in the three climatic regions; M: Mediterranean (NE Greece); H: Hyrcanian (NE Iran); IT: Irano-Turanian (Central Iran)

Irano-Turanian region: Central Iran, southern shore of the Namak Lake (Daryacheh-ye Namak) in the Maranjab Desert (34° 9-19'N, 51° 30-56'E); large saline playa surrounded by halophytic communities and sand dunes. The area is characterized by continental climate with low precipitation, hot and dry summer and cold winter; annual temperature is 19 ºC and the annual precipitation is 136 mm. Mean monthly temperatures vary between 5 °C (January) and 33 °C (July). The vegetation zonation differs from the coastal dunes in species composition and by the absence of drift lines.

Methods

Data collection

The field data were collected during the summers 2011 and 2012 in sand ecosystems of the Mediterranean, Hyrcanian and Irano-Turanian region. The vascular plant composition and cover-abundance were sampled in plots of 25 m^2. Five common and widespread habitat types in sand dunes were defined based on Devillers & Devillers-Terschuren (1996; see also e.g. Doing 1985; Danin 1996; Maun 2009), comprising herbaceous and subshrub vegetation. We distinguished in each region (in brackets the corresponding EUNIS habitat type codes as in http://eunis.eea.europa.eu/habitats.jsp and plot numbers): 1. mobile dunes (B1.3, X35; 114 relevés); 2. stabilized dunes (B1.4; 46); 3. salt marshes (A2.5, D6.1; 95); 4. semi-wet sands (B1.8; 38) and 5. disturbed habitats (B1.1, H5.6; 21). In total, 314 relevés were collected: 161 relevés in the Mediterranean, 62 in the Hyrcanian and 91 in the Irano-Turanian region. Plant nomenclature follows Flora Iranica (Rechinger 1963-2012) for Iran, and Dimopoulos et al. (2013) for Greece.

Fourteen easily measurable categorical traits applicable for sand dune environments were chosen (Table 1). Categorical traits can be measured or obtained from the literature especially for areas without established trait databases. They also facilitate repeating and comparing the approach in other areas. The traits were selected from different parts of plants to better reflect the adaptive response patterns of species to the environment (Cornelissen et al. 2003). For standardization, the protocol for functional traits (Pérez-Harguindeguy et al. 2013) was followed. The observed species were assigned to the traits based on the given attributes in Table 1. Original trait information was obtained mainly from specimens collected and field observation, but also from floras (Rechinger 1963-2012) and other resources (especially for plant strategies and regenerative traits Grime 2001; Grime et al. 2007; Klotz et al. 2002).

Data analysis

In order to find the main functional groups (FG) of plant species, a trait database built of all species and trait variables was examined using cluster analysis (Ward's method with relative Euclidean distance; PC-ORD, McCune & Mefford 1999). The cluster analysis was also run for each region separately to compare the resultant groups with those of the whole dataset (graphs not shown). The cluster cut level was determined manually so that each group was represented in each region, and that the resulting groups were interpretable and in line with the field observations.

As the three regions had only few species in common, a species-plot database would not be informative for comparison. Therefore, the trait-plot matrix was built by multiplying the trait-species matrix by the matrix of species-plot. The matrix calculation was done using R, package SYNCSA (Debastiani and Pillar 2012). The trait-plot matrix was then analyzed by means of Detrended Correspondence Analysis (DCA) using CANOCO 4.5 (ter Braak & Šmilauer 2002) to understand the distribution of functional traits in sandy ecosystems.

Table 1 List of plant functional traits and their attributes used in this study. Original trait data were obtained from specimens and field observation, complemented by data from floras and other literature resources.

Functional traits	Attributes
Vegetative traits	
Life form	annual; chamaephyte; hemicryptophyte (incl. geophyte); phanerophyte
Plant height	1 = 1-30 cm; 2 = 31-60 cm; 3 = 61-100 cm; 4 = > 1m
Clonality	0 = no clonality; 1 = clonal plant
Plant strategy type	competitor (C); stress tolerant (S); ruderal (R); intermediate strategies CS; CR; SR; CSR
Regenerative traits	
Dispersal mode	anemochory; zoochory; no obvious dispersal agent (probably autochory)
Pollination mode	anemophilous; entomophilous, zoophilous, self-pollinated
Leaf traits	
Photosynthetic pathway	0 = C_3; 1 = C_4
Leaf and/or stem succulence	0 = not succulent; 1 = succulent
Reduced leaves	0 = no evidence of leaf reduction; 1 = reduced or no leaves
Hairiness	0 = glabrous; 1 = hairy
Thorniness	0 = no thorns; 1 = thorny
Wax-coating	0 = no wax; 1 = waxy
Stem and root traits	
Carbohydrate storage in thickened root and stem or long tap root	0 = no specialized storage organs; 1 = specialized organs
Rhizomatous plant	0 = non-rhizomatous; 1 = rhizomatous

The main functional groups were correlated to the habitats by means of multivariate analysis. The species-plot matrix was analyzed separately for each region using DCA. Rare species were downweighted. The functional groups (FG 1-7) obtained from the cluster analysis were used as external variable and plotted in the DCA scatter plot to illustrate which plant strategies were most successful in a given habitat type. To make a FG-plot matrix for a given region, the species list related to each FG and then to each plot was prepared. Further, the sum of the percentage cover values of species for a given FG was calculated and standardized to the relative values. The final matrix indicates the composition of FG for each plot in percentage values.

We used community-weighted trait mean values (Mason index), compatible with our categorical traits, to find out the trait syndromes in a given habitat. The trait value was weighted by the relative cover-abundance of the species (in percentage) and the related index was calculated using FunctDiv (Lepš et al. 2006).

Results

Floristic diversity

From a total of 309 species, 211 species were recorded in coastal sands of NE Greece, 66 species in NE Iran and 72 species in Central Iran. The species richness related to the same number of plots per region (62 randomly selected plots each) was more than two times higher in the Mediterranean area (173 species) than in the other two regions. The three areas had only few species in common, most of them distributed in the Mediterranean and the Hyrcanian areas (25 species), while only 9 species jointly occurred in the Mediterranean (M) and the Irano-Turanian (IT) and 6 species in the Hyrcanian and the Irano-Turanian areas. A high proportion of species in NE Greece belongs to the Mediterranean phytogeographical element (34%), followed mainly by M-IT (~16%) and ES (Euro-Siberian)-M-IT (~14 %). Species in N Iran comprise of different phytogeographical elements mainly recognized as IT (~18%), M-IT (13%), ES-M-IT (~14%), ES-IT (9%) and M (~6%) elements. Proportion of the Mediterranean element in N Iran is notable. Species of the IT element are dominant in C Iran (41%), followed with some distance by IT-SS (Saharo-Sindian) (17%) and ES-M-IT (~9%). Cosmopolitan species contribute 13% of the species recorded in sand dunes of N Iran, 9% in NE Greece and only 5% in C Iran. Other elements have low percentages in each region. The species belong to 46 plant families and 201 genera. Approximately 52 % of the species were annuals, 29 % perennial graminoids, 11.6 % woody plants, mostly low shrubs, and the rest were forbs.

Cluster analysis of functional traits

The psammophytes of the studied area were classified as seven main functional groups (FG; Table 2, Fig. 2), each consisting of plants with similar traits and thus similar functional potential for the ecosystem. At the first step of the cluster analysis, species were classed as two general plant groups of chiefly annuals and perennials, respectively. Perennials were then classified mainly based on stem and root traits into three FG: non-graminoid perennials, shrubs, and graminoids. The complete list of species per functional group is provided as supplementary material (Appendix B).

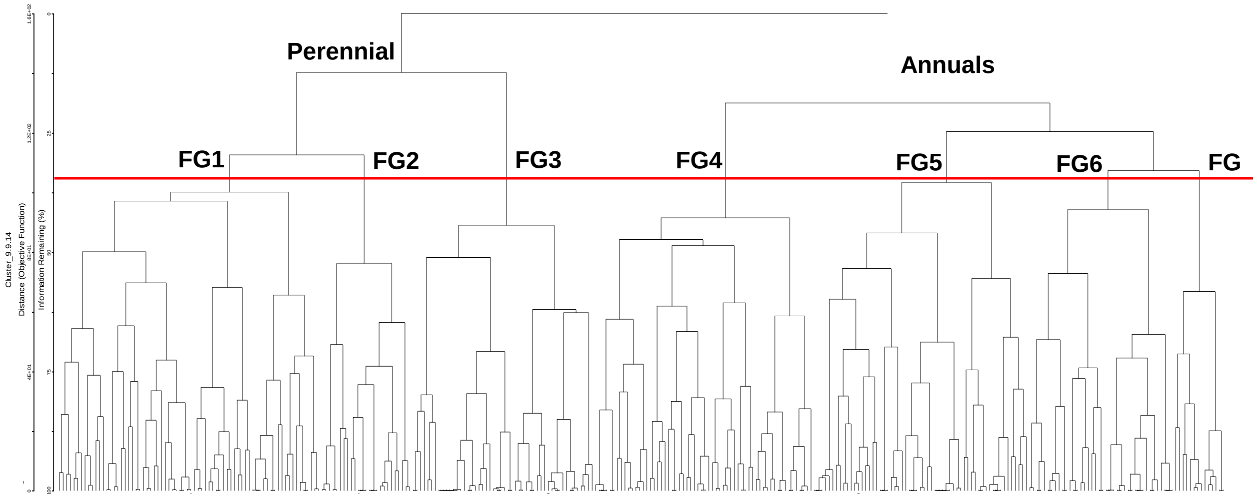

Fig. 2 Functional groups of species in sand dune habitats based on their trait similarities, using hierarchical cluster analysis (relative Euclidian distance, Ward's linkage method): FG1. Non-graminoid perennials; FG2. Shrubs; FG3. Perennial graminoids; FG4. Ruderals; FG5. Entomophilous therophytes; FG6. Short-lived grasses; FG7. Annual succulents. For the list of species in each group see Table S1.

FG1 comprises non-graminoid woody-based hemicryptophytes, geophytes, and dwarf shrubs, some of which cushion-shaped, generally with storage organs such as taproots, rhizomes, tubers or bulbs, or thickened stem bases. They are mainly stress-tolerant competitive species, many being more or less halo-tolerant, but only few are obligatory halophytes. A few sub-ruderal, disturbance-tolerant competitive grasses (Stipa capensis, Chrysopogon gryllus) and other competitors such as Cynanchum acutum, Alhagi maurorum and Eryngium campestre are also included (Table 2).

FG2 includes low to tall woody plants (15 cm to > 2 m) (Table 2). They tolerate dry conditions by reduced or succulent leaves, or stems covered by wax. Many are thorny. Succulents prevail in the salt marshes. They are adapted to the high salinity of the habitats by salt avoidance or salt tolerance.

FG3 comprises graminoids of mostly tall rhizomatous or more or less densely caespitose Poaceae, Cyperaceae and Juncaceae (Table 2). It includes two subgroups. While sedges and rushes occur chiefly in semi-wet or wet habitats, grasses prevail on dunes with mobile sands and other dry ground. They are clonal plants with carbohydrate stored in rhizomes or at the base of the tussocks. This strategy enables them to cope with perturbation and stress and to establish and persist in suitable patches. Wind dispersal facilitates the establishment of new colonies.

Annuals are classified into four FG (4-7, table 2), chiefly separated by habitat type and growth form.

FG4 includes almost exclusively annual or biennial herbs and grasses adapted to frequent disturbance. They are wind- or self-pollinated, and dispersed by wind.

Table 2 Plant functional groups obtained from cluster analysis with their description and some dominant species occurring in each group. C: competitor; S: stress-tolerant; R: ruderal; hem.: hemicriptophyte; cham.: chamaephyte; M: Mediterranean; H: Hyrcanian; IT: Irano-Turanian.

Functional group	**Description**	**Characteristic species**
Perennials		
1) Non-graminoid perennials	Sand dune/disturbed habitat, CS/CR cushions with long tap root and/or woody stem, non-graminoid hemicryptophytes or chamaephytes, entomophilous pollination, mostly dispersed by wind but partly without obvious dispersal agent, frequently covered by hair, C_3 photosynthesis	M: *Thymbra capitata, Artemisia campestris, Silene otites, Hypericum olympicum, Fumana procumbens, Scabiosa argentea, Centaurea diffusa, Cynanchum acutum, Eryngium campestre* H: *Argusia sibirica, Convolvulus cantabrica* IT: *Smirnovia turkestana, Heliotropium arguzioides, Alhagi maurorum*
2) Shrubs	Sand dune/salt marsh, CS Small to 3 m tall shrubs, with salt and drought adaptation, reduced leaves, succulent stem or leaves, covered with wax, mostly with anemophilous pollination and anemochorous dispersal, including C_4 shrubs	M*: Atriplex portulacoides, Ephedra distachya, Sarcocornia fruticosa, S. perennis, Halocnemum strobilaceum* H: *Ephedra procera, Lycium shawii* IT: *Haloxylon ammodendron, Calligonum crinitum, Ephedra strobilacea, Nitraria schoberi, Salsola rosmarinus*
3) Graminoids (grasses, sedges and rushes)	Sand dune/mesic habitat, CS/CR species with rhizome, clonal growth, anemophilous pollination, anemochorous dispersal, mostly glabrous, including C_4 grasses	M*: Ammophila arenaria, Cyperus capitatus, Elytrigia juncea* H & M: *Saccharum ravennae, Juncus* spp., *Scirpoides holoschoenus* IT: *Stipagrostis* spp., *Centropodia forsskalii* , *Cyperus eremicus*
Annuals		
4) Ruderals	Disturbed habitats, R Group of annuals with ruderal strategy, pollinated by wind or insects, both anemochory and zoochory is occurred, C_3 plants	M*: Bituminaria bituminosa, Eleusine indica, , Amaranthus albus, Echinochloa crus-galli, Sonchus asper* H: *Anagallis arvensis, Tragus racemosus, Xanthium strumarium* IT: *Chrozophora tinctoria, Centaurea bruguierana*
5) Entomophilous therophytes	Mostly on fixed dunes, S/SR Consist of small therophytes with entomophilous pollination and anemochorous dispersal, all with C_3 photosynthesis	M*: Jasione heldreichii, Malcolmia nana, Matthiola tricuspidata, Nigella arvensis, Medicago marina, Sideritis montana, Pseudorlaya pumila, Medicago littoralis* H : *Brassica tournefortii, Cakile maritime, Daucus guttatus, Spergularia bocconei* IT: *Acantolepis orientalis, Camelina rumelica, Isatis minima, Malcolmia africana*
6) Short-lived grasses	Mostly on mobile dunes, S Small psammophyte mostly of grasses, with anemophilous pollination and anemochorous dispersal, usually covered by hair, C_3 photosynthesis Short life span	M*: Briza maxima, Bromus diandrus, Dasypyrum villosum, Vulpia ciliata, Lagurus ovatus,* H : *Bromus racemosus, Cutandia memphitica, Parapholis incurva, Trisetaria linearis,* IT: *Bromus scoparius, Cutandia dichotoma, Schismus barbatus,* Non-grass spp.: *Mollugo cerviana* (M), *Plantago arenaria* (M, H), *Kochia stellaris* (IT)
7) Annual succulents	Salt marshes, S/SR Salt tolerant anuuals, with succulent leaves and/or stems, anemophilous pollination, anemochory or hydrochory dispersal but usually without obvious dispersal agent, divided to C_3 and C_4 subgroups	M*: Salicornia procumbens, Salsola soda, S. tragus, Suaeda maritima, S. splendens* H : *Salicornia iranica, Suaeda crassifolia* IT: *Suaeda arcuata, Salsola kali*

FG5 consists of non-ruderal therophytes and a few perennial herbs. They are commonly insect- or self-pollinated, and the dispersal strategy is mostly anemochorous or autochorous.

FG6 includes short-lived grasses, together with some dicots with inconspicuous flowers, with passive stress tolerance strategy, pollinated and dispersed by wind.

FG7 comprises annual succulents and sub-succulent plants inhabiting more or less disturbed sites in salt marshes or sometimes drift lines. They are tolerant to salt stress and frequently self- or wind-pollinated.

All seven functional groups are represented in all three studied biogeographic regions. Even after running the analysis separately for each region, the same functional groups were obtained (data not shown).

Trait distribution across habitats

The DCA of the species-plot matrix, run separately for each region, showed that the habitat types are well separated by species composition (Fig. 3a-c). The first axis in Fig. 3a (NE Greece) is interpreted as reflecting a gradient of water availability which is increasing towards salt marshes on the right side of the graph. Plants in coastal and inland dunes depend mostly on seasonal precipitation and salty or brackish temporarily available ground water resources while salt marshes are wet or semi-wet through surface waters over longer periods. The described pattern of trait distribution from NE Greece (Fig. 3a) was observed in the two other regions as well.

The DCA graphs also indicated the correlation of habitats with the functional groups. As shown in Fig. 3a, annual succulents (FG7) and shrubs (FG2) were more correlated with salt marshes while the FG3 subgroup of perennial grasses and the entomophilous therophytes (FG5) were chiefly associated with mobile dunes. Short-lived grasses (FG6) were found in stabilized dunes, non-graminoid perennials (FG1) in semi-wet habitats and annual ruderals (FG4) in disturbed habitats. The above mentioned correlation for NE Greece could be seen as well in the mobile dune, stabilized dune and salt marsh habitats of N and Central Iran (Fig. 3b & c). However, the low number of plots and therefore lower representativeness of species for semi-wet and disturbed habitats of those two regions resulted in a weak correlation of functional groups with these two habitats.

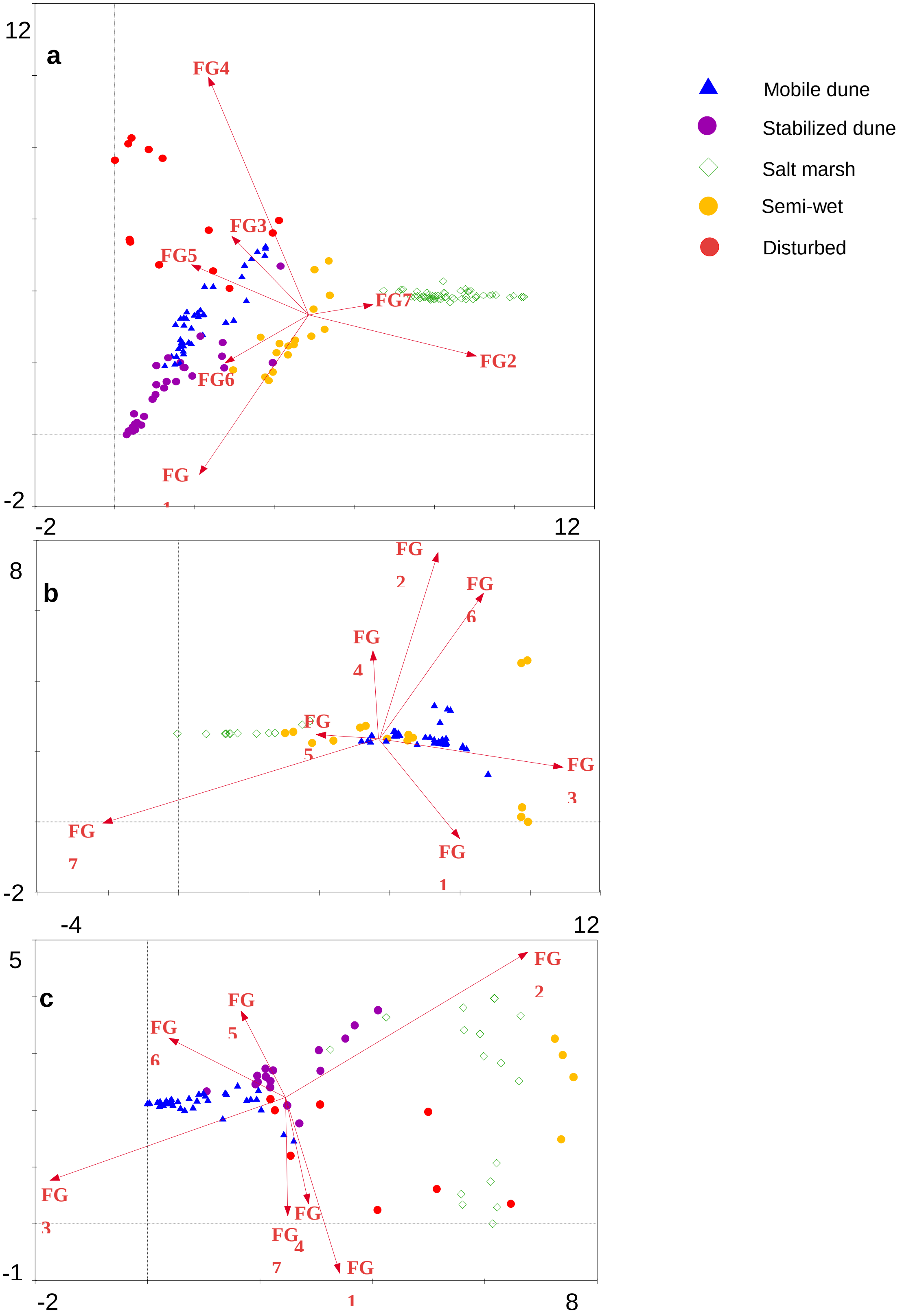

Fig. 3 Relation of habitats with functional groups (FG1-7) shown by DCA ordination of a species-plot matrix for each region: a. NE Greece; b. NE Iran; c. Central Iran. The eigenvalues for the first axes in a, b and c are 0.96 and the length of gradient for the first axis is 10.23 (a); 9.97 (b); 7.58 (c). Plots from disturbed habitats were excluded from analysis in NE Iran (b), as there were not enough representative plots for this type of habitat.

Trait distribution across regions

In order to compare the three regions in terms of their functional traits and to see how the traits were distributed across the three regions, we analysed the trait-plot matrix for the whole data set. The DCA ordination diagram (Fig. 4) showed that the traits were grouped reflecting patterns of habitat affiliation rather than regional belonging.

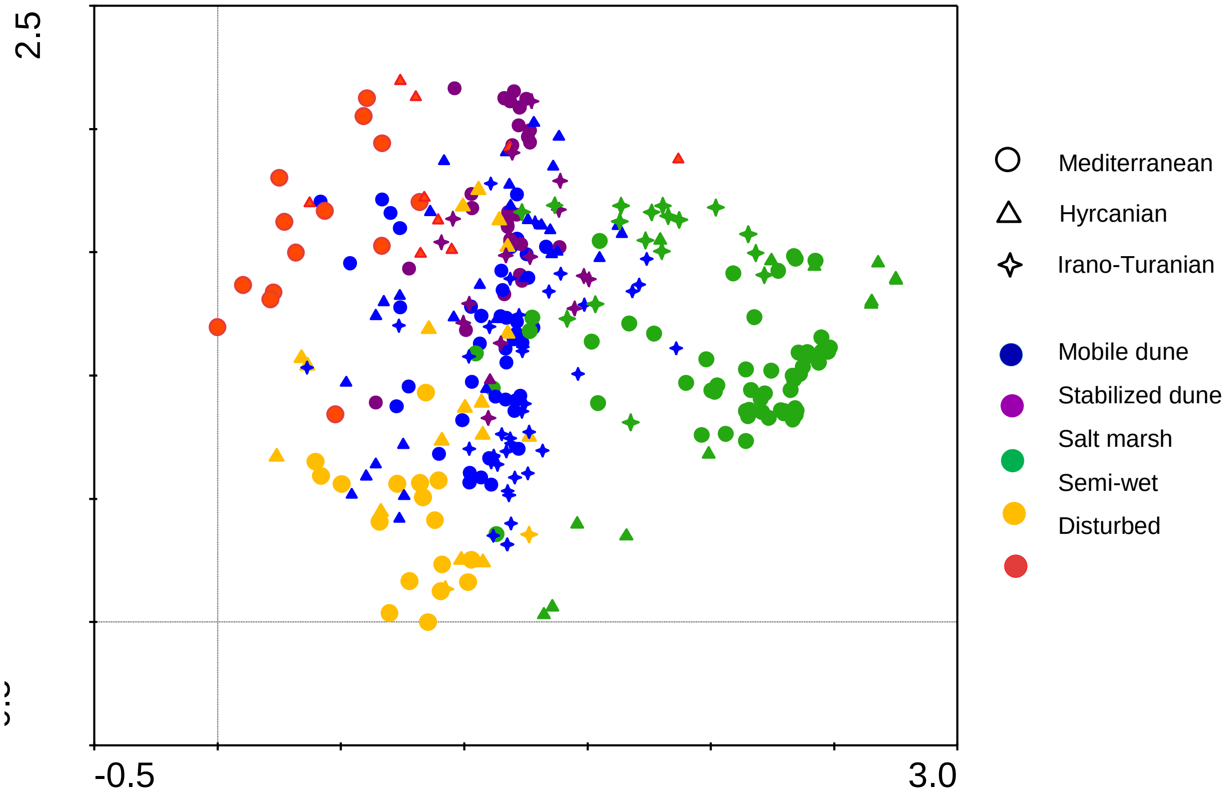

Fig. 4 DCA ordination of the trait-plot matrix for the combined data of three regions showing the distribution of traits among the sand dune habitats. Gradient length and eigenvalue for the first axis are 2.75 and 0.28, respectively.

The Irano-Turanian region of Central Iran, for instance, is much dryer than N Iran and NE Greece (136 mm vs. 780 and 500 mm, respectively) but the functional traits of the same habitats grouped together irrespective of their regions. Temperature differences among regions, both annual mean and mean minimum and maximum temperatures, were not reflected by functional trait distribution either. Species from a specific habitat have similar traits and function although they belong to different climatic regions with different species pools. For example, saltmarshes of the three regions grouped on the right side of the diagram as they share similar traits. The first axis can be interpreted as salinity gradient with a decreasing trend from right (salt marshes) to left. A gradient of dryness seems to rule the second axis with dryer habitats in the upper part and semi-wet to wet conditions in the lower part of the graph. Salt marshes have the highest salinity but moderate dryness. Wet sands and disturbed habitats which appear on opposite ends of the dryness gradient both display low salinity. The vegetation of stabilized dunes and mobile dunes show moderate salinity but the former which almost exclusively depends on precipitation water tends to be dryer than that of mobile dunes which is much more variable in terms of dryness.

Community weighted trait means

Community weighted trait mean values for the five studied habitats (table 3) indicated that dominant species in the mobile dunes tend to be taller than species in other habitat types and dispersed mostly by wind. Entomophilous species with dense indumentum and with thick storage stems or roots were found chiefly in stabilized dunes. Salt marshes were characterized by stress tolerant competitive species pollinated by wind. Succulent or reduced leaves covered by wax were common features among the species of this habitat. Semi-wet habitats were dominated by rhizomatous clonal plants pollinated mostly by wind. In disturbed habitats, ruderal competitors (CR strategy) were most prominent.

Table 3 Community weighted trait mean calculated for the five habitat types. For each trait, the highest value among the habitats is marked in bold. Abbreviation: Wind dis.: wind dispersal, Anem.: anemophilous, Ent.: entomophilous, CS: competitor-stress tolerant, CR: competitor-ruderal, Rhiz.: rhizomatous, TR/S: thick root/stem, RL: reduced leaves, SL: succulent leaves, Clon.: clonality, Cham.: chamaephyte, Hem.: hemicryptophyte

	Wind dis.	**Anem.**	**Ent.**	**CS**	**CR**	**Height**	**Rhiz.**	**TR/S**	**RL**	**SL**	**Hair**	**Wax**	**Clon.**	**Cham.**	**Hem.**
Mobile dune	**0.69**	0.72	0.29	0.59	0.01	**1.28**	0.56	0.23	0.11	0.07	0.42	0.29	0.53	0.13	0.58
Stabilized dune	0.54	0.48	**0.52**	0.36	0.03	0.89	0.26	**0.50**	0.18	0.05	**0.62**	0.29	0.28	0.33	0.30
Salt marsh	0.63	**0.88**	0.23	**0.69**	0.00	0.96	0.37	0.45	**0.51**	**0.75**	0.11	**0.83**	0.58	**0.56**	0.18
Semi-wet	0.59	**0.85**	0.22	0.44	0.04	1.05	**0.73**	0.19	0.16	0.01	0.38	0.37	**0.77**	0.02	**0.75**
Disturbed	0.55	0.60	0.39	0.11	**0.27**	0.90	0.34	0.33	0.06	0.21	0.40	0.24	0.16	0.20	0.45

Discussion

Functional groups across different regions

The results of our cluster analysis showed that similar plant functional groups of sand dune ecosystems occur across regions very different in species composition and climate. The plant functional groups obtained from cluster analysis (Fig. 2) are applicable for the three studied regions although the species numbers, floristic and plant community composition of the regions differ considerably. The functional groups represent various adaptive response types to stress-prone sand dune environments which are similarly realized in all study regions. For a given azonal ecosystem such as sand dunes it is shown that functional groups may be of universal relevance. Repeatability of the functional groups is an important issue if they are to be used in a global scale (Gitay & Noble 1997).

The groupings appear to be robust as we observed the same functional groups by running the analysis separately for each climatic region. By establishing functional groups with distinct combinations of traits for a given ecosystem complex or formation a comparison of ecological studies on a global scale is facilitated although they have few or no species in common. Duckworth et al. (2000) even argued for using plant functional groups as an alternative to species-based approaches in plant community research and biogeography. In our opinion, both approaches are supplementary.

In this study we showed that plant functional groups defined by using cluster analysis across different biogeographic regions are independent from the region. There are few studies using cluster analysis on functional traits in ecological studies (e.g. García-Mora et al. 1999). Alternatively, *a priori* groups, e.g. grasses, legumes and non-legume forbs, have been used (Lavorel et al. 1999; Lloret and Vilà 2003; McLaren 2006). Fry et al. (2014) discussed in detail the advantages of divisive hierarchical cluster analysis for creating functional groups in contrast to *a priori* grouping. They found strong similarity within groups generated from cluster analysis, indicating that each species was placed in the most appropriate group (Fry et al. 2014). It is also possible to assign new species to the existing functional groups by calculating the dissimilarity index and placing them alongside the group with the closest dissimilarity value (Fry et al. 2014). Functional groups derived from cluster analysis are more robust than *a priori* defined groups and therefore applicable to wider regions. In this study we used an agglomerative method for hierarchical clustering as a pre-defined number of groups was not desirable. We preferred to decide on the number of groups after the classification based on the interpretability of the clusters.

Danin (1996) classified psammophytes of inland desert dunes of Sinai and Negev using non-numerical methods. He described eight ecomorphological types of plants based on their root morphology and response to sand accumulation and deflation: A. perennial grasses requiring sand accumulation, B. species resistant to deep sand cover or removal (mostly shrubs), C. species of areas with moderate sand cover or removal, D. species actively resistant to sand deflation, E. passively resistant species to sand deflation, F. herbaceous perennials of stable sand sheets, G. shrubs of stable sand sheets, H. annuals. Our functional groups resulting from cluster analysis largely confirm but partly lump, partly split those plant types. Our FG3 (graminoids) is equivalent to group A; FG2 (shrubs) corresponds to groups B and G; and FG1 (non-graminoid perennials) includes groups C-F. Among the annuals we specified four different functional strategy groups (Table 2) rather than treating them as a single group. Our results, while found in wider regions and revealing more detailed groupings, are also generally congruent with three functional groups (winter annuals, perennials with spreading roots and plants capable of withstanding sand burial) derived from functional classification of coastal sand dunes of SW Spain (García-Mora et al. 1999).

Functional traits and habitat types

We observed that the functional affiliation of sand dune species is shaped by the habitat rather than by the climatic region. In contrast, the regional species composition is more influenced by climate and phytogeographical conditions as each region has its own species pool with very few species shared among regions. The highest number of common species among regions (25) was observed between subhumid NE Greece (M) and humid N Iran (H) while arid C Iran has very few species in common with the other regions. Climate-related effects on the species composition and on plant meta-communities have been shown for coastal habitats of the Iberian peninsula (Jiménez-Alfaro et al. 2015). Our multivariate analysis of the trait-plot and species-plot matrices for all studied regions (Figs. 3 and 4) revealed that functional traits as well as species were grouped irrespective of the region but subject to the habitat type in which they occur. Pervasive environmental factors across the habitats appear to be salinity and (seasonal) dryness. Gallego-Fernández and Martínez (2011) showed that the functional groups of Mexican coastal dunes were independent from taxonomic and phylogenetic affiliations but related with environmental filters. The effect of habitat filtering implies similar ecological needs of co-occurring species (Cornwell et al. 2006). Habitat filters shape the distribution of functional traits (Cornwell and Ackerly 2009; Bermúdez and Retuerto 2013) as well as of species (e.g. Grubb 1985). Confirming those studies, our comparative analysis (both cluster analysis and ordination, Figs. 2 and 4) demonstrates that regional differences did not influence the functional groups and trait assemblages, suggesting independency from climatic conditions. The results did not reveal trait-based differences between inland dunes (Irano-Turanian) and coastal dunes (Mediterranean and Hyrcanian) either.

Furthermore, habitats are distinct in the combination and proportion of plant traits. We defined the trait syndromes for each habitat type indicating which combination of traits is most successful and dominant in a given habitat (Table 3). For instance, rhizomatous chamaephytes with CS strategy, pollinated and dispersed by wind, with reduced or succulent leaves, are prominent under salt and drought stress. Describing the functional dimension of a habitat may provide a better perspective for maintaining or restoring the habitat or ecosystem (Garnier and Navas 2011).

Even though our results highlight the applicability of functional groups across regions and its correlation with habitat characteristics, further studies are needed to better understand the triangle spanned by species, traits, and habitats. The challenge will be to define more refined functional groups representative of ecosystem function, vegetation structure and plant biodiversity, and to develop new tools for modeling. Reliable attribute data of many species as yet insufficiently known will have to be collected (Rusch et al. 2003; Boulangeat et al. 2012). The functional approach may also be used to evaluate the degree of anthropogenic impact and the effects of environmental stress on target functional groups of potentially endangered habitats, thereby identifying conservation priorities and suitable management.

Conclusions

Our results provide further support to the idea that it is feasible to define and describe functional groups applicable at a large scale. Hierarchical cluster analysis is a simple but effective method for defining functional groups. Specifically, our study revealed that in sand dune ecosystems the plant traits are grouped reflecting habitat affiliation. Environmental factors and constraints such as sand mobility, soil salinity, water availability, nutrient status and disturbance are more important for the occurrence and distribution of plant functional groups than regional belonging, irrespective of the species pools. Even inland and littoral dunes do not seem to differ much regarding the observed patterns of traits and functional groups.

Furthermore, we defined trait syndromes in sand dune habitats by using community-weighted trait mean to perceive the effects of environmental stress on ecosystems caused by different disturbance regimes and land use (Hooper et al. 2002). Understanding the effect of environmental drivers on ecosystems is an important issue, both for preserving the present vegetation or for predictive purposes (e.g. consequences of global change). We consider functional traits as an effective tool for comparing ecosystem functions and processes, especially in regions with no or few species in common.

Acknowledgment

We would like to thank the Reinhold-und-Johanna-Tüxen-Stiftung for funding the field work in Iran for P.M. “Management Body of Delta Nestos, Lakes Vistonida-Ismarida” in Greece and departments of “Natural Resources of Esfahan” and “Nature Conservation of Mazandaran” in Iran are gratefully acknowledged for their help for visiting the areas. We would also like to thank Prof. Hossein Akhani for his support during the field work in Iran. We thank particularly Dr. Ioannis Tsiripidis and Dr. Georgios Fotiadis for their logistic support, discussions and their company at part of the field work in Greece. Advice by anonymous reviewers helped to improve an earlier version of the paper.

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Chapter 3

Sand habitats across biogeographical regions at species, community and functional level

Parastoo Mahdavi, Maike Isermann & Erwin Bergmeier

Phytocoenologia 2017, 47: 139-165

DOI: 10.1127/phyto/2017/0127

Abstract

Questions: To what extent does habitat similarity across different climatic regions support vegetation similarity at taxonomic, syntaxonomic and functional levels? Do different sand habitats share similarity patterns across regions? To what extent are sand habitats azonal with respect to taxonomic, syntaxonomic and functional similarity? What are the syntaxonomic and functional analogues? **Study area:** Coastal areas of N Germany, NE Greece, N Iran, and the Namak Lake shore in Central Iran. **Methods:** In four biogeographic regions (Atlantic, Mediterranean, Hyrcanian, Irano-Turanian) we collected 450 relevés representing four habitat types: drift lines, mobile dunes, stabilized dunes, and salt marshes. Plant communities were classified using TWINSPAN and assigned to syntaxa. High-rank syntaxa of each habitat were compared across four regions. Beta diversity was used to compare the species similarity between regions and habitats. We further compared trait-based functional groups across regions and habitats at the syntaxonomic level of class. **Results:** The floristic composition of sand habitats depended highly on the biogeographic region. At plant species and genus level, very low similarity was found between sand habitats of the same kind across regions as well as across habitats within a region. However, sand habitats of the same kind in different regions showed considerable functional similarity. Vegetation under particularly high stress, such as of salt marshes and drift lines, showed more syntaxonomic and functional similarities between regions than that of mobile and stabilized dunes, which was more determined by the regional species pool. **Conclusions:** The more stress-prone a habitat, the more is its vegetation habitat-related and the less dependent on the biogeographic region. All studied habitats are azonal but nuances are recognizable, and the concept of azonality is more generally applicable using functional traits as parameter. We further suggest using functional group proportions as a complementary tool to diagnostic species when comparing biogeographically distant, vicariant plant communities.

Keywords: Atlantic region; azonality; beta diversity; coastal vegetation; Irano-Turanian region; functional trait; Mediterranean region; saline habitat; salt marsh; sand dune; syntaxa

Nomenclature: *Flora Iranica* (Rechinger 1963−2012), Dimopoulos et al. (2013) and *Florenliste von Deutschland* (Buttler et al. 2015) for Iran, Greece and Germany, respectively; syntaxonomic nomenclature follows mainly Mucina et al. (2016) for Greece and Germany, and Asri (2003) for Iran.

Abbreviation: FG = Functional group

Introduction

Sand ecosystems, whether coastal or inland, comprise various habitat and vegetation types, showing a characteristic zonation, mainly differentiated by salt and drought gradients (Doing 1985; Carranza et al.

2008). Globally, they are frequently under pressure of urbanization, tourism and other human activities (Acosta et al. 2004; Pintó et al. 2014). This is a bothersome observation, not only for the sake of biodiversity but also as these ecosystems provide important services such as protection against wind erosion, waves and sea-level rise, water filtration and carbon sequestration, and they are indispensable breeding and nesting areas for wildlife (Defeo et al. 2009).

Sand ecosystems are specifically exposed to sand burial, salinity, dryness, lack of soil and nutrients, deflation, high wind speed, salt spray and inundation (Maun 2009). These factors shape a highly stressful environment for plants and greatly influence the vegetation composition and structure (Mucina et al. 2006). Specific plant communities are adapted to different habitats on sand, ranging from drift lines on the sea shores, mobile and stabilized dunes to salt marshes (Doing 1985; Acosta et al. 2007). Each zone provides specific environmental conditions inhabited and shaped by particular plant communities.

Drift lines are usually narrow linear habitats which occur just above the normal upper tidal limits along the sea shores. They may be rich in pebbles and shingle and have always high amounts of organic matter (Sýkora 2003, European Commission 2013). Inundation and frequent disturbances through high tides and storms are common features (Grime 2006). Drift lines are sparsely inhabited by annual nitrophilous plants resistant to high salt concentration and frequent disturbances.

Mobile dunes occur above the tidal limits and are characterized by sand accumulation and deflation. Sand burial and strong winds play an important role in shaping the vegetation. Sand accretion (to a certain extent) stimulates the growth of specific plants of mobile dunes, such as *Ammophila arenaria*, but also affects the composition and density of the vegetation by reducing and eliminating species intolerant to sand burial (Maun 1998).

Stabilized dunes are further developed dunes occupying the landward zone just behind the mobile dunes. Drought stress is the main environmental factor. Provoost et al. (2004) found that the surface temperature of stabilized dunes in Belgium could reach above 50 ºC. Due to the more stable soil conditions, the vegetation is denser if compared to seaward zones. The influence of salt is mainly by salt spray.

Salt marshes are permanently or temporarily wet littoral habitats. Coastal and desert salt marshes may be associated with tidal flats, salt pans or salt lakes. They accumulate organic matter and are temporarily inundated by salt or brackish water. High evaporation causes salt enrichment in both inland and coastal salt marshes (European Commission 2013). This highly stressful environment is generally species poor and the vegetation is sparse to rather close. Salinity gradients, flooding frequency and duration, soil texture and amounts of organic matter determine the vegetation structure and the productivity of the habitat (Pennings & Callaway 1992; Mucina & O’Callaghan 2003).

Azonality refers to vegetation of similar appearance and composition regardless of the climatic region, and littoral sand ecosystems are generally considered azonal (Ellenberg & Leuschner 2010). However, it has rarely been questioned whether there are nuances in the concept of azonality and on which vegetation parameters it may be based. We examined the effect of habitat and regionality on halophytic vegetation by comparing its similarities at the taxonomic, syntaxonomic and functional level. At each level we considered similarity in habitats of the same kind across regions as well as in a given region across different sand habitats. We specifically asked whether vegetation of the same habitat type is similar across different phytogeographical regions and which kinds of similarity are more pronounced. To what extent are sand habitats azonal regarding taxonomic (species and genera), syntaxonomic, and/or functional similarity? What are the taxonomic and functional analogues across climatic regions? Due to the omnipresent and prevalent salt effect on coastal and inland desert sand ecosystems, we hypothesized more syntaxonomic and functional similarity within a given habitat type across regions than among different habitat types within a given region. We tested four more or less saline habitat types (drift line, mobile dune, stabilized dune, and salt marsh) in four climatic and phytogeographic regions, ranging from the Atlantic coasts to Irano-Turanian salt lake shores.

Study areas

We studied coastal and halophytic inland sand ecosystems in four areas belonging to different climatic regions: Atlantic, Mediterranean, Hyrcanian and Irano-Turanian (Fig. 1).

In the Atlantic region, we analyzed data from coastal N Germany along the North Sea from the island of Borkum (53° 36' N, 6° 43' E) eastward to the island of Fehmarn (54° 28' N, 11° 08' E) at the Baltic Sea coast. Mean monthly temperatures for the North Sea (Island of Norderney) vary between 3 °C (January) and 18 °C (July). Mean annual rainfall is about 801 mm, with higher amounts from July to December.

The study area in the Mediterranean region is located in NE Greece, ca. 300 km along the North Aegean coast from south of Katerini (40° 09' N, 22° 33' E) eastward to Porto Lagos (40° 54' N, 25° 23' E). The area has hot and dry summers with wet, cool winters almost without frost. Mean monthly temperatures vary between 5−7 °C (January) and 25−27 °C (July). Mean annual rainfall is 400−600 mm (Lienau 1989).

In the Hyrcanian region, the SE Caspian Sea shore in N Iran was investigated, including the Miankaleh Biosphere Reserve (36° 48−55' N, 53° 25'−54° 02' E) and two other sites (36° 49' N, 53° 8' E, 36° 39' N, 52° 22' E). The area is characterized by a warm humid climate with rainy summers and mild winters. The mean temperature of the coldest month (January) is 8.7 °C and the warmest month is August with mean temperatures of ca. 28 °C. The mean annual precipitation is 789 mm (based on the nearest meteorological station in Sari).

In the Irano-Turanian region, the southern shore of the Namak Lake (Daryacheh-ye Namak) in the Maranjab Desert (34° 9−19' N, 51° 30−56 'E) in Central Iran was studied. The climate of the area is continental, characterized by low precipitation, hot and dry summers and cold winters. The mean temperature of the coldest month is ca. 5 °C (January) and that of the hottest month is 33 °C (July). The annual precipitation is 136 mm.

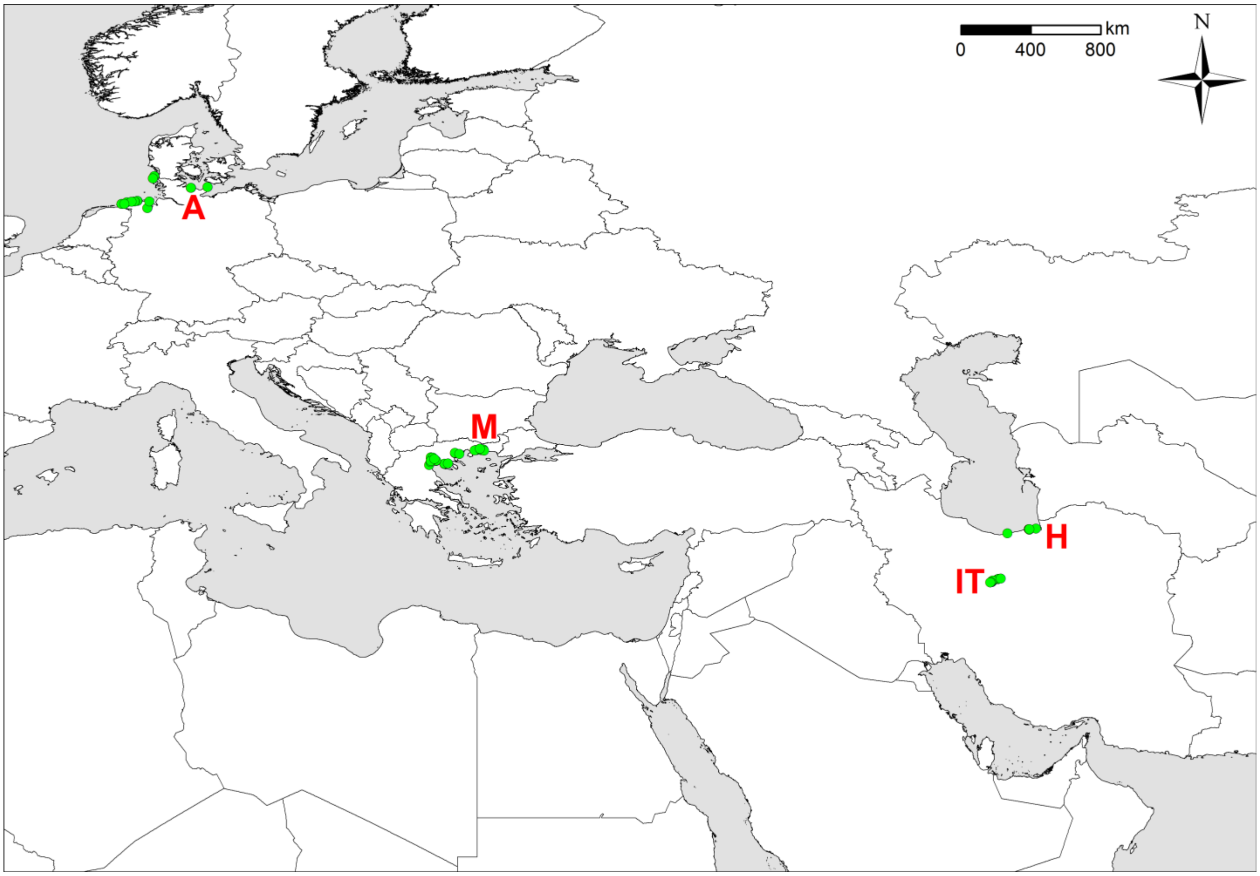

Fig.1 Location of the study areas in the four biogeographic regions: A: Atlantic (N Germany); M: Mediterranean (NE Greece); H: Hyrcanian (N Iran); IT: Irano-Turanian (Central Iran).

Methods

Data collection

The 319 vegetation plots in Iran and Greece were sampled in summer 2012 and 2013 using the Braun-Blanquet cover/abundance scale (Dierschke 1994). The 131 plots from Germany were compiled randomly from the database of Coastal Vegetation Germany (GIVD code: EU-DE-035). A surface area of 25 m^2 was applied for all plots. In each area, vascular plant cover-abundance data of four habitat types were collected: drift line, mobile dune, stabilized dune and salt marsh.

Data analysis

We classified the vegetation separately for each region in JUICE (Tichý 2002) using TWINSPAN (Hill 1979) with three pseudospecies cut levels (0, 2, 5). Subsequent manual editing of the generated groups included the merging of small group of one to three relevés with the larger sister group, and the division of a large group into two TWINSPAN-generated subgroups. Synoptic tables were created, and diagnostic species determined, using percentage frequency (constancy) values. The plant communities of each habitat type were compared between regions by using higher-ranking syntaxa. When possible, vegetation groupings were assigned at the association level using the available literature.

In order to compare the taxonomic similarity (species and genera) between different regions and habitats, beta diversity was calculated using the Bray-Curtis index (R software, package *vegan*; Oksanen et al. 2008). The gradient length in the first axis of a DCA (Detrended Correspondence Analysis) was used for estimating the vegetation dissimilarities over regions and habitats (CANOCO 4.5; ter Braak & Šmilauer 2002). All species were included in both analyses. The average species richness per plot was calculated for each vegetation class.

Furthermore, the habitat-region effect on vegetation was compared at the functional level. We defined the dominant plant functional group (FG) in a given community by calculating the proportion of seven functional groups derived from a hierarchical cluster analysis of a species-traits matrix (for details see Mahdavi & Bergmeier 2016): FG1, Non-graminoid perennials; FG2, Shrubs; FG3, Graminoid perennials; FG4, Annual ruderals; FG5, Entomophilous (insect-pollinated) annuals; FG6, Annual (non-ruderal) grasses; FG7, Annual succulents. The FG descriptors express the prevailing plant category (life form, growth form, strategy type) involved in the group (see Mahdavi & Bergmeier 2016). The complete list of species for each functional group is provided in Appendix B.

The percentage cover of the above functional groups was calculated for each relevé, and the average value was reported for a given community. For this purpose, the Braun-Blanquet scale was transformed to median percentage values (Dierschke 1994: 158). In order to test that differences between proportions of functional groups of each community were significant and did not occur by chance, the non-parametric Kruskal-Wallis test was used (R package *stats*, Hollander and Wolfe 1973).

The assignment of vegetation groupings from Iran and Greece to plant associations proved to be difficult and is to some extent tentative, as the phytosociological knowledge for these countries is as yet far from sufficient. We referred to the informal ‘community’ to distinguish undescribed vegetation units from valid associations. In addition to the main cited syntaxonomic nomenclature, other publications were also considered (e.g. Pott 1992; Rennwald 2000; Rivas-Martinez 2001; Alaie 2001; Sciandrello & Tomaselli

2013; Sýkora et al. 2013; Biondi et al. 2014). The authorities and the years of publication are provided in the syntaxonomic overview (Appendix C).

Results

Taxonomic diversity and similarity

Our beta diversity analysis confirmed that there is very low floristic similarity among regions and habitat types. Dissimilarity percentage values between habitats of the same kind in different regions (Table 1) varied from 85-100%. Similar results were found between different habitat types of a given region (data not shown).

Habitats of the same kind in different regions share only four genera (Table 2). *Cakile maritima* (with various subspecies) and the species group of *Salsola kali* are common to drift lines in all regions while different species of *Suaeda* and *Salicornia* occur in salt marshes. The highest number of common genera (12) occurs on salt marshes of the Mediterranean (NE Greece) and Hyrcanian region (N Iran), including *Aeluropus, Centaurium, Halocnemum, Hordeum, Juncus, Plantago, Polypogon, Puccinellia, Salicornia, Spergularia*, *Suaeda* and *Tripolium.* Mobile dunes have the lowest number of common genera (0-2). Stabilized dunes of the Mediterranean and Hyrcanian region have 7 genera in common: *Allium, Bromus, Corynephorus, Daucus, Ephedra, Plantago* and *Silene.* Table 2 also shows that the Mediterranean region has a high number of taxa in common with the Hyrcanian and Atlantic regions. As revealed in the synoptic tables (Tables 3-6), there are almost no common species between different habitats of a given region.

Table 1. Bray-Curtis index of beta diversity for each habitat type over the four regions: C-Ir: Central Iran; Ge: N Germany; Gr: NE Greece; N-Ir: N Iran. Encountered species richness for each habitat is given in parentheses.

Mobile dune (81)					Stabilized dune (164)				
	C-Ir	Ge	Gr	N-Ir		C-Ir	Ge	Gr	N-Ir
C-Ir	0.00				C-Ir	0.00			
Ge	1.00	0.00			Ge	1.00	0.00		
Gr	1.00	0.90	0.00		Gr	0.98	0.95	0.00	
N-Ir	0.99	1.00	0.96	0.00	N-Ir	0.99	1.00	0.88	0.00
Salt marsh (106)					Drift line (23)				
	C-Ir	Ge	Gr	N-Ir		Ge	Gr	N-Ir	
C-Ir	0.00								
Ge	1.00	0.00			Ge	0.00			
Gr	0.98	0.98	0.00		Gr	0.95	0.00		
N-Ir	0.91	0.95	0.88	0.00	N-Ir	0.85	0.92	0.00	

Table 2. Lists of genera (in bold) shared between regions followed by one or more species epithets separated by slash (/) for different regions. M: Mediterranean (NE Greece); H: Hyrcanian (N Iran); IT: Irano-Turanian (C Iran); A: Atlantic (N Germany).

	M/H	**M/IT**	**M/A**	**H/IT**	**H/A**	**IT/A**
Drift line	***Cakile*** *maritima,* ***Salsola*** *(tragus/kali),* ***Xanthium*** *strumarium*		***Cakile*** *maritima,* ***Salsola*** *(tragus/kali)*		***Cakile*** *maritima,* ***Salsola*** *kali*	
Mobile dune	***Bromus*** *diandrus*	***Bromus*** *(diandrus/chrysopogon),* ***Cyperus*** *(capitatus/ eremicus)*	***Ammophila*** *arenaria,* ***Elymus (Elytrigia)*** *(bessarabica, juncea/junceiformis),* ***Leymus*** *(racemosus/arenarius)*	***Bromus*** *(diandrus/chrysopogon)* ***Cutandia*** *(memphitica/dichotoma)*		
Stabilized dune	***Allium*** *(guttatum, sphaerocephalon/subnotabile),* ***Bromus*** *tectorum,* ***Corynephorus*** *divaricatus,* ***Daucus*** *guttatus,* ***Ephedra*** *(distachya/procera),* ***Plantago*** *arenaria,* ***Silene*** *conica*	***Ephedra*** *(distachya/ strobilacea),* ***Lomelosia*** *(argentea/olivieri)*	***Agrostis*** *(stolonifera, capillaris),* ***Corynephorus*** *(divaricatus/canescens),* ***Hypericum*** *(olympicum/perforatum),* ***Jasione*** *(heldreichii, montana),* ***Plantago*** *(arenaria, lanceolata),* ***Trifolium*** *(arvense, echinatum/dubium)*	***Ephedra*** *(procera/strobilacea)*		
Salt marsh	***Aeluropus*** *littoralis,* ***Tripolium*** *pannonicum,* ***Centaurium*** *(spicatum/erythraea),* ***Halocnemum*** *strobilaceum,* ***Hordeum*** *marinum,* ***Juncus*** *maritimus,* ***Plantago*** *coronopus,* ***Polypogon*** *maritimus,* ***Puccinellia*** *(festuciformis, distans),* ***Salicornia*** *(procumbens/iranica),* ***Spergularia*** *(media/ marina),* ***Suaeda*** *(maritima/crassifolia)*	***Aeluropus*** *littoralis,* ***Polypogon*** *(maritimus, monspeliensis),* ***Salicornia*** *(procumbens/persica),* ***Salsola*** *(soda/rosmarinus)* ***Suaeda*** *(maritima/spp.)*	***Tripolium*** *pannonicum,* ***Atriplex*** *(portulacoides/prostrata),* ***Elytrigia*** *(elongata/pycnantha, repens),* ***Limonium*** *(bellidifolium/vulgare),* ***Plantago*** *(coronopus, maritima),* ***Puccinellia*** *(festuciformis/distans, maritima),* ***Salicornia*** *(procumbens/stricta, europaea),* ***Spergularia*** *(marina, media),* ***Suaeda*** *maritima*	***Aeluropus*** *(lagopoides, littoralis),* ***Frankenia*** *hirsuta,* ***Phragmites*** *australis,* ***Polypogon*** *(maritimus, monspeliensis),* ***Salicornia*** *(iranica/persica),* ***Suaeda*** *(crassifolia/spp.)*	***Tripolium*** *pannonicum,* ***Phragmites*** *australis,* ***Plantago*** *(coronopus/maritima)* ***Puccinellia*** *(distans/distans, maritima),* ***Salicornia*** *(iranica/stricta, europaea),* ***Spergularia*** *(marina/marina, media),* ***Suaeda*** *(crassifolia/maritima)*	***Artemisia*** *(sieberi/maritima)* ***Phragmites*** *australis,* ***Salicornia*** *(persica/stricta, europaea,),* ***Suaeda*** *(spp./maritima)*

Syntaxonomic diversity and similarity

A long gradient (17.9) at the first DCA axis, considered as estimate of beta diversity, reveals the high compositional diversity in the vegetation between and within regions. While mobile dunes and stabilized dunes of different regions are separated, vegetation plots of salt marshes and drift lines from different regions are grouped together (Fig. 2). It may be assumed that the vegetation of drift lines and salt marshes is more associated with habitat features than with the other habitats studied in the same region. Mobile dunes and stabilized dunes, on the other hand, are more related to the regional species pool than to the same kind of habitats in other regions.

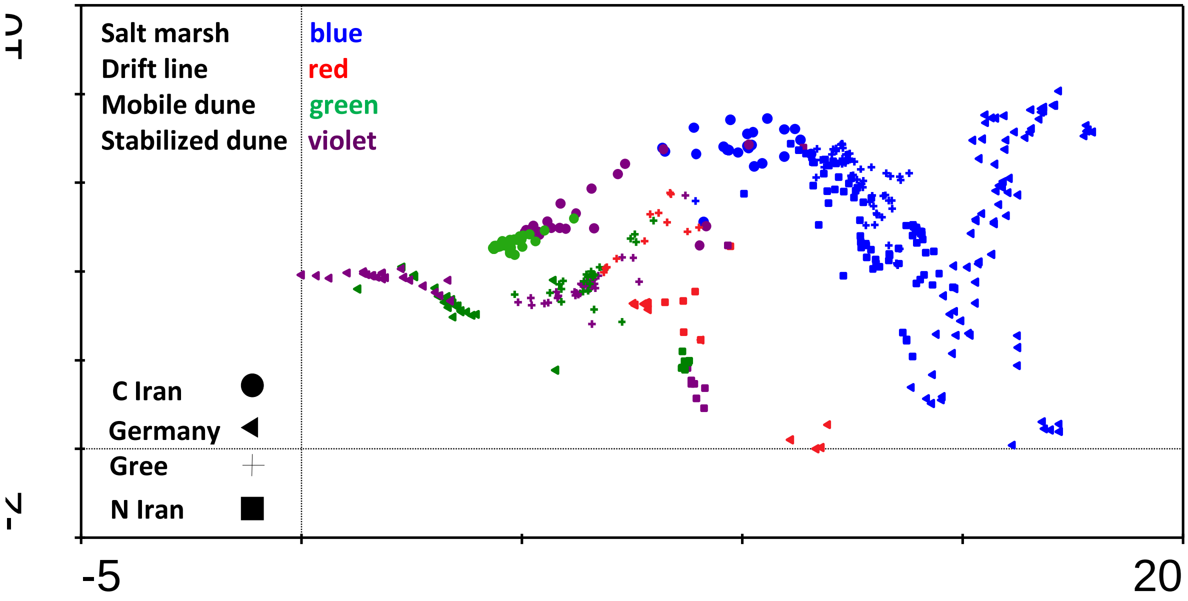

Fig. 2 DCA ordination of vegetation plots from four regions. Length of gradient in the first axis (17.9) is used as estimate of beta diversity to show the similarities between habitats of each region. Axis 2 gradient length is 8.1. The eigenvalue for the 1st and 2nd axes are 0.98 and 0.89 respectively.

In N Germany we classified 12 associations from 7 classes and 11 alliances (Table 3), in NE Greece 12 associations of 6 classes and 8 alliances (Table 4), in N Iran 13 communities of 7 classes and 10 alliances (Table 5), and in central Iran 12 communities in 5 classes and 7 alliances (Table 6). A syntaxonomic comparison of the investigated areas regarding a given habitat type showed that salt marshes and drift lines have more syntaxa in common than mobile and stabilized dunes. In the following sections, we describe the syntaxonomic spectrum of each habitat across the regions. A detailed syntaxonomic overview is provided in Table 7.

Table 3 Synoptic table of coastal vegetation in N Germany. Related habitats, classes and dominant functional group in each class are provided. High species constancy values in one column (or two) relative to the other columns are framed. In contrast, relatively high but unframed constancy values indicate much lower cover-abundance of the species concerned. ‘Other species’ with constancy of ≤20 % are listed at the bottom of the table. Detailed information on functional groups is given in Fig. 3. Habitat: d: drift line; f: stabilized (fixed) dune; m: mobile dune; s: salt marsh. Vegetation class: A: Cakiletea maritimae; B: Ammophiletea; C: Koelerio-Corynephoretea; D: Thero-Salicornietea; E: Juncetea maritimi; F: Salicornietea fruticosae; G: Phragmito-Magnocaricetea.

Community No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Number of relevés	8	24	18	5	8	9	7	20	13	8	6	5
Habitat	d	m	f	f	s	s	s	s	s	s	s	d
Functional group (FG)	4/5	3	3	3	7	3	7	2	3	7	3	4
Vegetation class	A	B	C	C	D	E	D	F	E	D	G	A
Cakiletum maritimae												
Cakile maritima	100	.	.	.	.	.	.	.	.	.	.	20
Elymus junceiformis	75	17	6	.	.	.	.	.	.	.	.	.
Salsola kali	25	.	.	.	.	.	.	.	.	.	.	20
Elymo arenarii-Ammophiletum arenariae												
Ammophila arenaria	13	100	67	20	.	.	.	.	.	.	.	.
Festuca rubra	.	54	39	20	.	.	.	.	23	.	.	.
Sonchus arvensis	.	29	.	.	.	.	.	.	.	.	.	.
Leymus arenarius	13	25	11	.	.	.	.	.	.	.	.	20
Calammophila baltica	.	33	34	.	.	.	.	.	.	.	.	.
Caricetum arenariae												
Carex arenaria	.	42	89	40	.	.	.	.	.	.	.	.
Corynephorus canescens	.	21	78	.	.	.	.	.	.	.	.	.
Cerastium semidecandrum	.	13	78	40	.	.	.	.	.	.	.	.
Viola canina	.	4	28	.	.	.	.	.	.	.	.	.
Myosotis ramosissima	.	8	22	.	.	.	.	.	.	.	.	.
Aira praecox	.	8	83	100	.	.	.	.	.	.	.	.
Airo-Festucetum												
Agrostis capillaris	.	.	28	100	.	.	.	.	.	.	.	.
Rumex acetosella	.	.	28	100	.	.	.	.	.	.	.	.
Festuca filiformis	.	.	.	60	.	.	.	.	.	.	.	.
Hypochaeris radicata	.	8	6	60	.	.	.	.	.	.	.	.
Achillea millefolium	.	.	.	60	.	.	.	.	.	.	.	.
Aira caryophyllea	.	.	.	60	.	.	.	.	.	.	.	.
Jasione montana s.l.	.	4	.	60	.	.	.	.	.	.	.	.
Plantago lanceolata	.	.	.	60	.	.	.	.	.	.	.	.
Trifolium dubium	.	.	.	60	.	.	.	.	.	.	.	.
Sagina procumbens	.	.	6	60	.	.	.	.	.	.	.	.
Holcus lanatus	.	4	6	60	.	.	.	.	.	.	.	.

Anthoxanthum odoratum	.	.	.	60	.	.	.	.	.	.	.	.
Trifolium pratense	.	.	.	40	.	.	.	.	.	.	.	.
Calluna vulgaris	.	8	.	40	.	.	.	.	.	.	.	.
Hypericum perforatum	.	.	.	40	.	.	.	.	.	.	.	.
Prunella vulgaris	.	.	.	40	.	.	.	.	.	.	.	.
Hieracium pilosella	.	.	.	40	.	.	.	.	.	.	.	.
Salicornietum strictae												
Salicornia stricta	.	.	.	.	100	22	43	5	.	13	.	.
Limonietum vulgaris												
Limonium vulgare	.	.	.	.	.	100	.	30	38	.	.	.
Puccinellia maritima	.	.	.	.	13	100	43	80	23	38	.	20
Spergularia media	.	.	.	.	.	56	.	20	.	.	.	.
Suaedetum maritimae												
Suaeda maritima	.	.	.	.	63	89	100	75	8	25	17	.
Spartina anglica	.	.	.	.	13	11	43	25	.	13	.	.
Halimionetum portulacoidis												
Atriplex portulacoides	.	.	.	.	.	56	14	90	8	.	17	.
Tripolium pannonicum	.	.	.	.	13	22	43	85	46	25	.	20
Juncetum gerardii												
Juncus gerardii	.	.	.	.	.	22	.	.	100	13	.	.
Glaux maritima	.	.	.	.	.	33	.	10	85	38	17	.
Plantago maritima	.	.	.	.	.	67	.	10	85	25	.	.
Agrostis stolonifera s.l.	.	.	.	.	.	.	.	5	54	38	17	.
Festuca rubra s.l.	.	8	6	.	.	22	.	20	38	.	.	.
Carex extensa	.	.	.	.	.	.	.	.	23	.	.	.
Carex distans	.	.	.	.	.	.	.	.	23	.	.	.
Armeria maritima	.	.	.	.	.	.	.	.	38	.	.	.
Salicornietum ramosissimae												
Salicornia europaea s.l.	.	.	.	.	13	78	71	30	31	100	.	78
Spergularia marina	.	.	.	.	.	33	14	.	.	63	.	.
Puccinellia distans	.	.	.	.	.	.	.	.	.	63	.	.
Bassia hirsuta	.	.	.	.	.	.	.	.	.	38	.	.
Scirpetum maritimi												
Bolboschoenus maritimus	.	.	.	.	.	.	.	.	23	50	100	.
Phragmites australis	.	.	.	.	.	.	.	.	8	.	33	.
Atriplicetum littoralis												
Atriplex prostrata s.l.	.	.	.	.	.	.	.	10	16	38	17	100
Atriplex littoralis	.	.	.	.	.	.	.	5	8	25	.	60
Other species												
Artemisia maritima	.	.	.	.	.	44	14	40	8	.	.	40
Triglochin maritimum	.	.	.	.	.	44	14	40	46	.	.	.

Species with low constancy:
Arabidopsis thaliana 2: 4, 3: 6; *Arenaria serpyllifolia* 2: 17, 3: 17; *Artemisia vulgaris 4*: 40; *Atrichum undulatum* 4: 20; *Atriplex glabriuscula* 10: 13; *Avenella flexuosa* 2: 8; *Bromus hordeaceus* 3:17; *Centaurium pulchellum* 9: 8; *Cerastium holosteoides 2*: 4, 3: 6; *Cirsium arvense 2*: 8; *Cirsium vulgare 2*: 4, 3: 6; *Cochlearia anglica 8: 5*; *Dactylis glomerata* 4: 20; *Draba verna* 3: 17; *Elymus athericus* 2: 4, 8: 5, 12: 20; *Elymus repens 3*: 6, 4: 20; *Epilobium angustifolium* 2: 13, 3: 6; *Erigeron canadensis* 2: 4, 3: 6; *Eryngium maritimum 2*: 4; *Festuca ovina* s.l. 3: 17; *Filago minima* 2: 4; *Galium aparine 2*: 4; *Galium mollugo* agg. 2: 8; *Galium verum* 2: 4, 3: 22; *Hieracium lachenalii* 4: 20; *Hieracium umbellatum* 2: 13; *Honckenya peploides* 3: 17; *Hypogymnia physodes 2*: 4; *Chenopodium glaucum 10*: 13; *Iris pseudacorus 3*: 6; *Juncus tenuis* 4: 20; *Koeleria arenaria* 3: 6, 4: 20; *Leontodon saxatilis* 2: 4; *Linaria vulgaris* 2: 13; *Lolium perenne 3*: 11; *Lophocolea bidentata* 2: 4; *Luzula campestris* 3: 17; *Odontites litoralis* 9: 8; *Oenothera ammophila* 2: 17; *Peltigera canina* 3: 6; *Plantago coronopus* 3: 6; *Plantago major s. intermedia 3*: 6; *Poa annua* 3: 17; *Poa humilis* 2: 4, 3: 11, 4: 20.; *Poa pratensis 2*: 4; *Pohlia nutans* 2: 4; *Polypodium vulgare* 2: 8; *Potentilla anserina* 9: 15, 11: 17, 12: 20; *Radiola linoides* 9: 8; *Rhytidiadelphus squarrosus* 2: 4, 3: 6; *Rubus caesius* 2: 8, 3: 11; *Rumex acetosella s. acetosella* 2: 4; *Rumex crispus* 2: 13; *Sagina maritima 1*0: 13; *Scleranthus perennis 4*: 20; *Scleropodium purum 3*: 6; *Sedum acre* 2: 17, 3: 11; *Senecio inaequidens 2: 4*; *Senecio jacobaea* 2: 13; *Senecio vernalis* 3: 6; *Senecio viscosus* 2: 4; *Senecio vulgaris* 2: 17; *Sonchus asper* 2: 4; *Spergularia media* 9: 15; *Stellaria graminea* 2: 4, 4: 20; *Taraxacum* spp. 2: 4, 3: 23, 4: 20; *Teesdalia nudicaulis* 2: 4; *Trifolium repens* 3: 17, 9: 15; *Tripleurospermum maritimum* 5: 20; *Tripleurospermum perforatum* 10: 13; *Urtica dioica* 3: 6; *Veronica arvensis 3*: 6; *Veronica officinalis* 3: 6; *Viola tricolor s. Curtisii* 2: 13, 3: 17.

Drift lines

The habitat is characterized by plant communities of the *Cakiletea maritimae* (Table 3, comm. 1; Table 4, comm. 8; Table 5, comm. 11), assemblages of annual plants dependent on nutrient input chiefly from seaweed and other organic material washed ashore. It is a naturally disturbed habitat in narrow bands near the sea, often heavily impacted by garbage. This habitat is fragmented and widely destroyed through tourist activities and beach cleaning at the coasts of Iran, Greece and Germany. The communities of *Cakile maritima* in the Mediterranean, Atlantic and Hyrcanian coasts are given in Table 7.

Mobile dunes

Ammophila arenaria, eponymous species of the class *Ammophiletea*, is a common and dominant species with two vicariant subspecies on mobile dunes of the Mediterranean (Table 4, comm. 10) and Atlantic coasts (Table 3, comm. 2). The *Ammophiletea* appear to be absent from the Hyrcanian region, where the class is replaced by the *Artemisietea lerchianae*. The latter is dominated by *Artemisia tschernieviana* (Table 5, comm. 13). The *Artemisietea lerchianae* form an Aralo-Caspian group of sub-halophilous plant communities on sandy soils (Rodwell et al. 2002). Mobile inland dunes of the Irano-Turanian region are characterized by the *Stipagrostietea pennatae*, with plant communities and species composition very different from those of the other regions. This class comprises communities mostly dominated by grasses such as *Stipagrostis pennata, S. karelinii, S. barbata and Centropodia forsskalii*, and by *Cyperus eremicus*. The latter may be seen as a geographical analogue of *Cyperus capitatus*, which is common in the Mediterranean *Ammophiletea* vegetation. There are no considerable syntaxonomic similarities between regions in this habitat type (Table 7). Photos of the mobile dune habitats and the prevailing vegetation are shown in Fig. 3a-d.

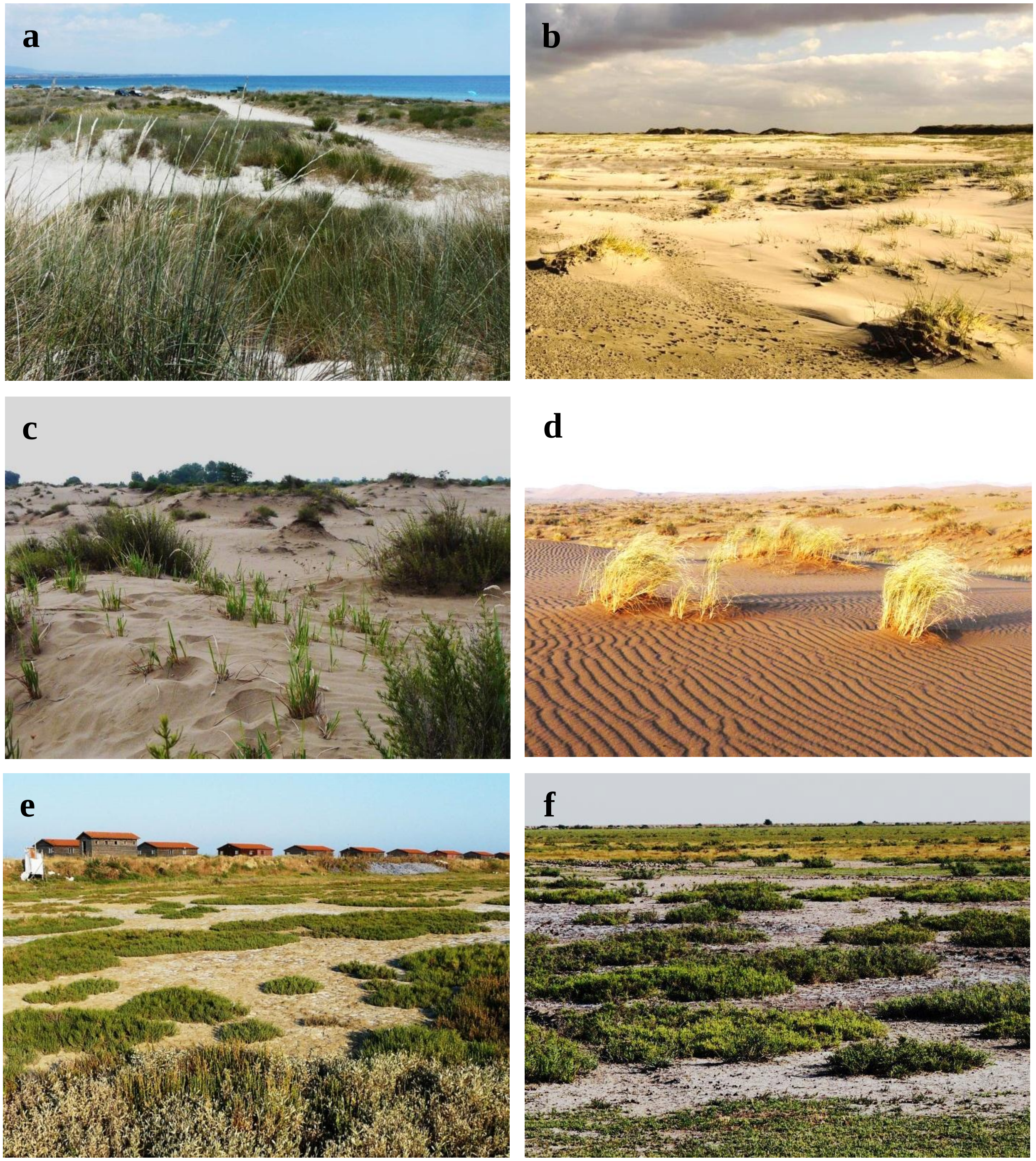

Fig. 3. Plant communities of mobile dunes (a-d) and salt marshes (e-f) of four biogeographic regions: a. Ammophiletea (NE Greece, Mediterranean region); b. Ammophiletea (N Germany, Atlantic); c. Artemisietea lerchianae (N Iran, Hyrcanian region); d. Stipagrostietea pennatae (C Iran, Irano-Turanian region); e. Salicornietea fruticosae (NE Greece); f. Kalidietea foliati (NE Iran). Photo 3b is created by C. Battmer.

Table 4. Synoptic table of coastal vegetation in NE Greece. Related habitats, classes and dominant functional group in each class are provided. High species constancy values in one column (or two) relative to the other columns are framed. In contrast, relatively high but unframed constancy values indicate much lower cover-abundance of the species concerned. 'Other species' with constancy of ≤20 % are listed at the bottom of the table. Detailed information on functional groups is given in Fig. 3. Habitat: d: drift line; f: stabilized (fixed) dune; m: mobile dune; s: salt marsh; Vegetation class: A: Salicornietea fruticosae; B: Thero-Salicornietea; C: Festuco-Puccinellietea; D: Cakiletea maritimae; E: Ammophiletea; F: Helichryso-Crucianelletea maritimae.

Community No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Number of relevés	10	4	8	4	14	11	10	13	5	27	9	18
Habitat	s	s	s	s	s	s	s	d	m	m	f	f
Functional group (FG)	2	2	7	3	2	2	2	3	3	3	1	1
Vegetation class	A	A	B	C	A	A	A	D	E	E	F	F
Arthrocnemo glauci-Halocnemetum strobilacei												
Halocnemum strobilaceum	100	75	.	.	21	.	.	.	.	.	.	.
***Arthrocnemum macrostachyum* comm.**												
Arthrocnemum macrostachyum	.	100	.	25	14	.	10	.	.	.	.	.
Suaeda splendens	.	25	25	.	.	.	10	.	.	.	.	.
***Salicornia procumbens* comm.**												
Salicornia procumbens	10	25	100	75	43	.	20	.	.	.	.	.
Suaeda maritima	20	.	88	75	50	.	20	.	40	.	.	.
Salsola soda	.	.	63	.	.	27	.	.	20	.	.	.
Petrosimonia brachiata	10	.	25	.	.	.	10	.	.	.	.	.
***Aeluropus littoralis* comm.**												
Aeluropus littoralis	.	.	63	100	29	55	40	.	.	.	.	.
Bupleurum tenuissimum	.	.	.	50	14	.	.	.	.	.	.	.
Polypogon maritimus	.	.	.	50	14	9	40	.	.	.	.	.
Juncus maritimus	.	.	.	25	14	.	10	.	20	.	.	.
Statico bellidifoliae-Salicornietum fruticosae												
Sarcocornia fruticosa	20	.	.	.	100	9	20	.	.	.	.	.
Limonium bellidifolium	.	.	.	50	29	.	.	.	.	.	.	.
Sarcocornio perennis-Puccinellietum convolutae												
Sarcocornia perennis	10	50	38	50	36	100	70	.	.	.	.	.
Tripolium pannonicum	.	.	13	.	.	27	10	.	.	.	.	.
Puccinellia sp.	.	25	25	25	29	45	20	.	.	.	.	.
Halimionetum portulacoidis												
Atriplex portulacoides	50	50	13	75	86	91	90	.	.	.	.	.
Limonium narbonense	.	.	13	25	29	55	70	.	.	.	.	.

Puccinellia festuciformis	.	.	.	50	21	27	60	.	.	.	.	.
Plantago coronopus	.	.	.	25	.	18	30	8	.	.	.	.
Spergularia media	.	.	.	25	.	9	40	.	.	.	.	.
Juncus acutus	.	.	.	25	.	18	30	.	.	.	.	.
Elymus elongatus	.	.	.	25	7	.	30	8	.	.	.	.
Salsolo-Cakiletum maritimae												
Cakile maritima	.	.	.	.	.	.	.	62	60	33	.	.
Matthiola tricuspidata	.	.	.	.	.	.	.	38	.	.	.	.
Glaucium flavum	.	.	.	.	.	.	.	23	.	4	.	.
Euphorbia peplis	.	.	.	.	.	.	.	23	.	.	11	.
Salsola tragus	.	.	.	.	.	9	.	77	100	52	.	6
Xanthium strumarium	.	.	.	.	.	.	.	38	40	15	.	.
Elymetum sabulosi												
Leymus racemosus subsp. *sabulosus*	.	.	.	.	.	.	.	.	100	7	.	.
Chenopodium album	.	.	.	.	.	.	.	31	100	4	.	.
Sporobolus pungens	.	.	.	.	.	.	10	62	80	19	.	.
Cynodon dactylon	.	.	.	.	.	.	10	23	40	.	11	17
Medicagini maritimae-Ammophiletum australis												
Ammophila arenaria subsp. *arundinacea*	.	.	.	.	.	.	.	.	20	85	.	.
Elytrigia juncea	.	.	.	.	.	.	.	54	40	59	11	11
Vulpia fasciculata	.	.	.	.	.	.	.	8	.	59	33	17
Eryngium maritimum	.	.	.	.	.	.	.	54	.	56	.	11
Achillea maritima	.	.	.	.	.	.	.	23	20	41	.	6
Verbascum pinnatifidum	.	.	.	.	.	.	.	23	.	56	11	11
Cyperus capitatus	.	.	.	.	.	.	.	31	.	78	33	22
Medicago marina	.	.	.	.	.	.	.	46	.	33	.	17
Cynanchum acutum	.	.	.	.	.	.	10	.	20	22	.	.
Malcolmia nana	.	.	.	.	.	.	.	.	.	26	.	6
Artemisietum campestris												
Artemisia campestris	.	.	.	.	.	.	.	.	.	26	67	28
Lomelosia argentea	.	.	.	.	.	.	.	.	.	26	67	17
Fumana procumbens	.	.	.	.	.	.	.	.	.	4	33	22
Daucus guttatus	.	.	.	.	.	.	.	.	.	4	22	6
Centaurea diffusa	.	.	.	.	.	.	.	.	.	4	33	28
Seseli tortuosum	.	.	.	.	.	.	.	8	20	26	44	39
Centaurea grisebachii	.	.	.	.	.	.	.	15	.	30	44	28
Plantago lagopus	.	.	.	.	.	.	.	8	.	4	22	.

Helianthemum salicifolium	.	.	.	.	.	.	.	.	.	.	44	.
Haplophyllum suaveolens	.	.	.	.	.	.	.	.	.	.	44	.
Silene otites	.	.	.	.	.	.	.	.	.	4	22	6
Trifolium arvense	.	.	.	.	.	.	.	.	.	15	22	6
Bromus tectorum	.	.	.	.	.	.	.	.	20	33	56	50
Ephedro distachyae-Silenetum subconicae												
Ephedra distachya	.	.	.	.	.	.	.	15	20	15	.	83
Thymbra capitata	.	.	.	.	.	.	.	.	.	.	11	56
Anthemis tomentosa	.	.	.	.	.	.	.	46	.	22	22	78
Corynephorus divaricatus	.	.	.	.	.	.	.	.	.	30	22	78
Hypericum olympicum	.	.	.	.	.	.	.	.	.	26	.	56
Sideritis montana	.	.	.	.	.	.	.	.	.	4	56	72
Erysimum calycinum	.	.	.	.	.	.	.	.	.	11	33	67
Jasione heldreichii	.	.	.	.	.	.	.	.	.	26	11	56
Silene dichotoma	.	.	.	.	.	.	.	8	.	37	22	61
Lagurus ovatus	.	.	.	.	.	.	.	8	.	22	22	61
Dasypyrum villosum	.	.	.	.	.	.	.	.	.	22	11	28
Eryngium campestre	.	.	.	.	.	.	.	.	.	.	11	22
Allium sphaerocephalon	.	.	.	.	.	.	.	.	.	.	.	22
Trifolium echinatum	.	.	.	.	.	.	.	.	.	.	22	39
Silene grisebachii	.	.	.	.	.	.	.	8	.	22	.	39
Silene conica	.	.	.	.	.	.	.	15	.	19	.	39
Phleum exaratum	.	.	.	.	.	.	.	.	.	4	11	33
Alkanna tinctoria	.	.	.	.	.	.	.	.	.	15	11	33
Astragalus sp.	.	.	.	.	.	.	.	.	.	4	11	22
Other species												
Hordeum marinum	.	25	13	.	7	27	30	8	.	.	.	.
Allium guttatum	.	.	.	.	.	27	.	.	.	4	.	17
Artemisia maritima agg.	.	.	.	.	.	.	30	8	.	.	.	.
Asperula tenella	.	.	.	.	.	.	.	.	.	.	.	28
Avena sterilis	.	.	13	.	.	.	10	.	.	.	22	11
Bothriochloa ischaemum	.	.	.	.	.	.	.	.	.	.	33	.
Chondrilla juncea	.	.	.	.	.	.	.	.	.	7	22	17
Elytrigia bessarabica	.	.	.	.	.	.	.	62	20	48	.	39
Orobanche sp.	.	.	.	.	.	.	10	.	.	.	.	33
Papaver dubium	.	.	.	.	.	.	.	.	.	.	11	28
Trifolium tomentosum	.	.	.	.	.	.	.	.	.	.	33	.

Species with low constancy:

Aegilops geniculata 11: 11; *Agrostis stolonifera 11*: 11; *Allium* sp. 6: 9, 7: 10, 8: 8, 12: 6; *Alyssum strigosum* 12: 6; *Alyssum umbellatum* 12: 6; *Anchusa* sp. 11: 11; *Anchusa undulata* 11: 11, 12: 11; *Apera intermedia* 5: 7, 7: 10; *Atriplex* sp. 4: 50; *Bassia hirsuta* 10: 4; *Bituminaria bituminosa* 11: 11; *Bromus diandrus* 10: 7, 11: 11, 12: 6; *Bromus intermedius* 7: 20, 8: 8; *Bromus japonicus* 11: 22; *Cachrys cristata* 12: 6; *Calystegia soldanella 8*: 8, 10: 4; *Carex divisa* 7: 10; *Cenchrus incertus* 10: 4; *Centaurea* sp. 12: 11; *Centaurium pulchellum* 10: 4; *Centaurium spicatum* 4: 25, 6: 9; *Chenopodium* sp. *7*: 10; *Cichorium intybus* 9: 20, 10: 4; *Cirsium* sp. 11: 11, 12: 6; *Cistus creticus* 11: 11; *Corispermum nitidum* 10: 7; *Coronopus didymus* 12: 6; *Crithmum maritimum* 8: 15; *Cuscuta* sp. 12: 6; *Cyperus* sp. *9*: 20; *Dianthus gracilis* 11: 11; *Dianthus monadelphus* 11: 11, 12: 11; *Dittrichia graveolens* 10: 7, 11: 11; *Dittrichia viscosa* 10:15, 12: 6; *Echinops* sp. 11: 11; Erigeron *canadensis 10*: 4; *Erodium cicutarium* 10: 15, 11: 11, 12: 11; *Euphorbia myrsinites* 12: 6; *Euphorbia paralias* 10: 15; *Filago gallica* 11: 11, 12: 11; *Filago vulgaris* 10: 4; *Fumana scoparia* 11: 11; *Geranium* sp. 10: 4; *Goniolimon incanum* 11: 11, 12: 6; *Goniolimon tataricum* 11: 11, 12: 11; *Hedypnois rhagadioloides* 8: 8; *Heliotropium europaeum* 8: 8; *Herniaria hirsuta 12*: 6; *Hypecoum procumbens 8*: 8, 10: 4; *Hypericum perforatum* 11: 11; *Juncus bufonius 7*: 10; *Juncus gerardii* 6: 9, 7: 10; *Juncus heldreichianus* 2: 25; *Juncus* sp. *7*: 10; *Jurinea mollis* 11: 11; *Kochia laniflora 4*: 25, 8: 8; *Limonium* sp. 7: 10; *Linaria* sp. 12: 6; *Lolium rigidum* 6: 9, 8: 8, 12: 6; *Lotus halophilus* 10: 4; *Medicago disciformis* 11: 11, 12: 17; *Medicago littoralis* 8: 8; *Medicago minima* 10: 4, 11: 11, 12: 6; *Medicago monspeliaca* 11: 11; *Melica ciliata 12*: 11; *Melilotus indicus 1*1: 11; *Milium vernale* 12: 6; *Mollugo cerviana* 10: 4, 12: 6; *Nigella arvensis* 10: 15, 12: 11; *Oenothera* sp. 11: 11; *Onobrychis caput-galli* 11: 22; *Osyris alba* 11: 11, 12: 6; *Pancratium maritimum* 8: 8, 10: 7, 12: 11; *Parapholis filiformis* 3: 13, 6: 9, 7: 20; *Petrorhagia illyrica* 12: 6; *Phragmites australis* 5: 7, 7: 10, 9: 20, 11: 11; *Plantago arenaria* 9: 20, 10: 11, 12: 17; *Plantago lanceolata 1*1: 22; *Polycarpon tetraphyllum* 10: 7; *Polygonum maritimum* 8: 8, 10: 7; *Portulaca oleracea 11*: 11; *Pseudorlaya pumila* 8: 8, 10: 7; *Scabiosa atropurpurea 1*1: 11; *Scabiosa webbiana* 11: 11; *Scirpoides holoschoenus* 7: 10, 10: 4, 11: 11; *Secale sylvestre* 10: 4; *Silene frivaldszkyana* 11: 11, 12: 6; *Silene gallica* 8: 8, 12: 6; *Silene supina 11*: 22; *Sonchus asper* 9: 20; *Sonchus oleraceus 12*: 6; *Sorghum halepense* 11: 11; *Spergularia bocconei* 3: 13, 4: 25; *Stipa capensis* 11: 11, 12: 11; *Teucrium capitatum 1*2: 6; *Thymus sibthorpii* 11: 11, 12: 17; *Trifolium angustifolium* 11: 11; *Trifolium physodes* 6: 9; *Typha* sp. *6*: 9; *Verbascum blattaria* 12: 6; *Vicia lutea 10*: 4; *Vulpia ciliata* 10: 4, 11: 11, 12: 6; *Xeranthemum inapertum* 12: 6.

Stabilized dunes

Among the study regions, stabilized dunes have almost no syntaxon in common. Dry perennial (and annual) grasslands prevail on so-called grey dunes of the North Sea (*Koelerio-Corynephoretea canescentis*, Table 3, comm. 3-4), dominated by *Aira praecox*, *Carex arenaria* and *Corynephorus canescens*, among others. In contrast, stabilized dunes of the Mediterranean are characterized mainly by dwarf shrub vegetation of the *Helichryso-Crucianelletea maritimae* (Table 4, comm. 11-12). Irano-Turanian vegetation of stabilized dunes is represented mainly by plant communities of two classes: the *Artemisietea sieberi* (Table 6, comm. 2,5,7,8), a widespread class of low-shrub vegetation covering most semi-desert areas in Iran (Zohary 1979), and the *Haloxyletea ammodendri* (Table 6, comm. 6,12), characterized by tall shrubs of *Haloxylon ammodendron* and *Calligonum crinitum*.

Although the regions do not share syntaxa (Table 7), vicariant communities (co-)dominated by *Ephedra* species are noteworthy, which form plant communities of different classes but similar in habit: *Ephedro distachyae-Silenetum subconicae* in NE Greece, *Ephedra procera* community in N Iran, and *Ephedretum strobilaceae* in central Iran.

Table 5 Synoptic table of coastal vegetation in N Iran. Related habitats, classes and dominant functional group in each class are provided. High species constancy values in one column (or two) relative to the other columns are framed. In contrast, relatively high but unframed constancy values indicate much lower cover-abundance of the species concerned. ‘Other species’ with constancy of ≤20 % are listed at the bottom of the table. Detailed information on functional groups is given in Fig. 3. Habitat: d: drift line; f: stabilized (fixed) dune; m: mobile dune; s: salt marsh; Vegetation class: A: *Juncetea maritimi*; B: *Thero-Salicornietea*; C: *Kalidietea foliati*; D: *Aeluropodetea littoralis*; E: *Saginetea maritimae*; F: *Cakiletea maritimae*; G: *Artemisietea lerchianae*.

Community No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Number of relevés	10	18	5	12	6	3	7	5	5	2	6	3	8
Habitat	s	s	s	s	s	s	s	s	s	s	d	f	f
Functional group (FG)	3	7	3	7/2	7/2	3	-	5	-	-	1/5	-	1
Vegetation class	A	B	A	C	C	D	C	E	E	E	F	?	G
***Juncus maritimus* comm.**													
Juncus maritimus	100	.	.	.	.	.	.	.	.	.	.	.	.
Polypogon monspeliensis	40	6	.	8	17	.	.	.	20	.	17	.	.
***Salicornia iranica* comm.**													
Salicornia iranica	90	100	100	67	33	33	86	40	60	100	.	.	.
Suaeda crassifolia	60	33	40	33	.	.	29	.	.	.	.	.	.
***Tripolium pannonicum-Salicornia iranica* comm.**													
Tripolium pannonicum	.	11	100	.	17	.	14	.	.	.	.	.	.
Puccinellia distans	.	44	80	17	17	.	43	.	20	.	.	.	.
Phragmites australis	10	6	80	.	17	.	14	20	.	.	17	.	.
***Halocnemum strobilaceum* comm.**													
Halocnemum strobilaceum	.	.	.	100	33	.	.	.	.	.	.	.	.
Koeleria nitidula	.	.	.	50	50	33	14	.	.	.	.	.	.
Frankenia pulverulenta	.	.	.	33	17	.	14	.	20	.	.	.	.
Centaurium erythraea	.	.	.	33	33	33	.	.	.	.	.	.	.
***Halostachys belangeriana* comm.**													
Halostachys belangeriana	.	.	.	67	100	67	.	20	.	.	.	.	.
Plantago coronopus	.	.	.	50	67	.	.	.	20	.	.	.	.
Aeluropodetum littoralis													
Aeluropus littoralis	.	.	.	17	.	100	.	.	.	.	.	.	.
Aeluropus lagopoides	.	.	.	58	50	67	14	.	.	.	.	.	.
***Petrosimonia brachiata* comm.**													
Petrosimonia brachiata	.	17	.	83	83	33	100	80	40	50	.	.	.
***Hordeum marinum* comm.**													
Hordeum marinum	.	.	.	67	50	100	57	100	40	.	.	.	.
Lolium rigidum	.	6	.	8	.	.	.	80	.	.	.	.	.
***Psylliostachys spicata* comm.**													
Psylliostachys spicata	.	6	.	17	17	.	14	.	100	50	.	.	.
***Frankenia hirsuta* comm.**													

Frankenia hirsuta	.	17	.	67	83	67	43	60	60	100	.	.	.
Sphenopus divaricatus	.	.	.	50	67	33	.	.	60	100	.	.	.
Spergularia marina	.	22	.	42	67	.	29	40	20	100	.	.	.
Henrardia persica	.	.	.	33	50	.	14	40	20	100	.	33	38
***Cakile maritima-Arguzia sibirica* comm.**													
Cakile maritima	.	.	.	.	.	.	.	.	.	.	83	.	.
Arguzia sibirica	.	.	.	.	.	.	.	.	.	.	83	.	13
Salsola kali agg.	.	.	.	.	.	.	.	.	.	.	83	.	.
Xanthium strumarium	.	.	.	.	.	.	.	.	.	.	33	.	.
***Ephedra procera* comm.**													
Ephedra procera	.	.	.	.	.	.	.	.	.	.	.	100	.
Catapodium rigidum	.	.	.	.	.	.	.	.	.	.	.	100	.
Corynephorus articulatus	.	.	.	.	.	.	.	.	.	.	.	100	.
Crepis foetida	.	.	.	.	.	.	.	.	.	.	17	100	25
Petrorhagia saxifraga	.	.	.	.	.	.	.	.	.	.	.	67	.
Allium subnotabile	.	.	.	.	.	.	.	.	.	.	.	67	.
Rostraria sp.	.	.	.	.	.	.	.	.	.	.	.	67	13
Plantago arenaria	.	.	.	.	.	.	.	.	.	.	17	100	88
Bromus tectorum	.	.	.	.	.	.	.	.	.	.	.	100	50
***Artemisia tschernieviana* comm.**													
Artemisia tscherviniana	.	.	.	.	.	.	.	.	.	.	50	.	100
Cutandia memphitica	.	.	.	.	.	.	.	.	.	.	17	33	100
Imperata cylindrica	.	.	.	.	.	.	.	.	.	.	.	.	88
Daucus guttatus	.	.	.	.	.	.	.	.	.	.	.	67	88
Bromus diandrus	.	.	.	.	.	.	.	.	.	.	.	.	63

Species with low constancy:
Alhagi maurorum 6: 33; *Alhagi pseudoalhagi 8*: 20; *Anagallis arvensis* 12: 33; *Atriplex* sp. 5: 17; *Atriplex tatarica* 5: 17; *Avena barbata* subsp. *wiestii* 5: 17; *Bassia hyssopifolia 3*: 20, 5: 17; *Brassica tournefortii* 13: 25; *Briza minor* 1: 10; *Bromus commutatus* 1: 20, 9: 20; *Bupleurum* sp. 4: 8, 5: 17; *Carex distans* 1: 10; *Centaurium pulchellum* 9: 20; *Climacoptera crassa 5*: 17, 7: 14; *Corispermum* sp. 11: 33; *Cynanchum acutum* 1: 20, 8: 20; *Cynodon dactylon* 5: 17, 12: 33; *Daucus* sp. *8*: 20; *Elymus* sp. 4: 8, 13: 13; *Filago arvensis 5*: 17; *Chondrilla juncea* 11: 17; *Juncus acutus* 1: 20, 11: 17; *Juncus heldreichianus* 1: 20; *Juncus hybridus 9*: 20; *Juncus littoralis* 1: 10; *Limonium gmelinii* 1: 10, 3: 33; *Medicago minima* 5: 17; *Melilotus officinalis* 5: 17, 8: 20; *Mulgedium tataricum 13*: 13; *Parapholis incurva* 9: 20; *Phalaris minor* 2: 11, 4: 8, 5: 17, 8: 20; *Plantago ovata* 4: 17; *Plantago* sp. 4: 8; *Polygonum patulum* 8: 20; *Polygonum* sp. 1: 10; *Polypogon maritimus* 4: 8; *Rhamnus pallasii 12*: 33; *Rumex crispus 7*: 14, 8: 20; *Rumex dentatus* 5: 17; *Silene conica* 12: 33; *Silybum marianum* 5: 17; *Sonchus* sp. *5*: 17, 12: 33; *Spergularia bocconii* 2: 11, 9: 29; *Spergularia diandra* 2: 6; *Tamarix meyeri* 1: 10; *Tamarix* sp. 7: 14; *Tetradiclis tenella* 9: 40; *Tragus racemosus* 11: 17; *Trisetaria linearis* 13: 25.

Salt marshes

This habitat shows the highest syntaxonomic similarity between regions. Pioneer annual vegetation on sea or lake shores with high salinity was identified as *Thero-Salicornietea* in all four regions (Table 7). Different species of *Salicornia* form vicarious plant communities in different phytogeographical regions. The class occurs in both coastal and inland salt marshes.

We assigned plant communities of woody halophytes in salt marshes of N Germany and NE Greece to the class *Salicornietea fruticosae* (Table 3, comm. 8; Table 4, comm. 1,2, 5-7), and such communities in N and central Iran to the *Kalidietea foliati* (Table 5, comm. 4-5; Table 6, comm. 3-4). These two classes are geographically separated. The former has been recorded in coastal areas, the latter in inland salt marshes. Although the two classes have almost no plant species in common (except *Halocnemum strobilaceum*), they share species with similar morphology and ecological needs (Fig. 3e, f).

The *Aeluropodetea littoralis* occur in alluvial temporarily flooded salt marshes in the Hyrcanian and Irano-Turanian regions. Saline habitats with fresh water influence are covered by *Juncetea maritimi* and *Phragmito-Magnocaricetea* reedbeds (Table 7). According to the European Vegetation Checklist (Mucina et al. 2016), *Juncetea maritimi, Phragmito-Magnocaricetea* and *Saginetea maritimae* are further classes common to all four or at least three regions (for the former two classes see also Akhani 2004), however without representative communities in our synoptic tables.

Table 6. Synoptic table of sand dune vegetation in Central Iran. Related habitats, classes and dominant functional group in each class are provided. High species constancy values in one column (or two) relative to the other columns are framed. In contrast, relatively high but unframed constancy values indicate much lower cover-abundance of the species concerned. 'Other species' with constancy of ≤20 % are listed at the bottom of the table. Detailed information on functional groups is given in Fig. 3. Habitat: d: drift line; f: fixed dune; m: mobile dune; s: salt marsh; Vegetation class: A: aff. *Tamaricetea salinae*; B: *Artemisietea sieberi*; C: *Kalidietea foliati*; D: *Haloxyletea ammodendri*; E: *Stipagrostietea pennatae*.

Community No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Number of relevés	5	6	8	13	3	5	2	12	15	13	8	3
Habitat	s	f	s	s	f	f	f	f	m	m	m	f
Functional group (FG)	3	2	2	2	2	2	2	2	3	-	3	2
Vegetation class	A	B	C	C	B	D	B	B	E	E	E	D
***Tamarix hispida* comm.**												
Tamarix hispida	100	17	13	8	.	.	.	.	.	.	.	.
Phragmites australis	80	.	.	.	.	.	.	.	.	.	.	.
Artemisietum sieberi												
Artemisia sieberi	.	100	.	8	33	.	.	8	.	.	.	.
Seidlitzietum rosmarini												
Seidlitzia rosmarinus	.	83	100	31	.	.	.	8	.	.	.	.
Alhagietum pseudalhagi												
Alhagi maurorum	.	33	25	92	.	.	.	.	.	.	.	33
Nitraria schoberi	.	.	.	46	.	.	.	.	.	.	.	.
Aeluropus lagopoides	20	17	.	46	.	.	.	.	.	.	.	.
Aeluropus littoralis	.	.	.	38	.	.	.	.	.	.	.	.
Cressa cretica	.	.	.	23	.	.	.	.	.	.	.	.
Ephedretum strobilaceae												
Ephedra strobilacea	.	33	.	.	100	.	.	.	.	.	.	.
Haloxyletum ammodendri												
Haloxylon ammodendron	.	17	.	.	67	100	.	.	.	8	.	.
Lomelosia olivieri	.	.	.	.	67	100	.	33	13	.	.	.
Kochia stellaris	.	.	.	.	.	40	.	33	.	8	.	.
Prosopidetum farctae												
Prosopis farcta	.	.	.	8	.	.	100	.	.	.	.	.
***Stipagrostis plumosa* comm.**												
Stipagrostis plumosa	.	.	.	.	.	80	50	100	93	23	13	.
Acantholepis orientalis	.	.	.	.	33	40	.	50	.	8	.	.
Gymnarrhea micrantha	.	.	.	.	.	.	.	25	.	.	.	.
Launaea acanthodes	.	.	.	.	33	.	.	25	13	.	.	.
***Centropodia forsskalii* comm.**												
Centropodia forsskalii	.	.	.	.	.	.	.	.	73	8	50	33
Schismus barbatus	.	.	.	.	33	80	100	58	73	31	.	.

Cutandia dichotoma	.	.	.	.	33	40	50	33	93	15	50	33
Cyperus eremicus **comm.**												
Cyperus eremicus	.	.	.	.	.	.	.	17	93	100	88	100
Stipagrostis karelinii **comm.**												
Stipagrostis karelinii	.	.	.	.	.	.	.	8	7	.	63	33
Stipagrostis barbata	.	.	.	.	.	.	.	8	13	.	50	67
Smirnovia turkestana	.	.	.	.	.	20	.	.	13	15	75	.
Heliotropium dasycarpum	.	.	.	.	.	.	.	.	7	15	25	.
Calligonum crinitum **comm.**												
Calligonum crinitum	.	.	.	.	.	.	.	17	20	8	13	100
Other species												
Aphanopleura breviseta	.	.	.	.	67	40	.	17	.	.	.	.
Astragalus squarrosus	.	.	.	.	.	40	.	33	27	15	.	.
Bromus chrysopogon	.	.	.	.	67	20	.	42	60	8	13	.
Bromus tectorum	.	.	.	.	.	.	.	.	27	15	.	.
Calligonum polygonoides	.	.	.	.	.	20	.	.	27	15	.	.
Chrozophora tinctoria	.	.	.	.	.	20	50	8	.	.	.	.
Cornulaca aucheri	.	.	.	.	.	40	.	8	.	.	.	.
Eremopyrum bonaepartis	.	.	.	8	33	40	50	42	.	.	.	.
Heliotropium arguzioides	.	.	.	.	.	20	50	8	13	8	25	33
Lappula sp.	.	.	.	.	.	.	.	8	27	15	25	67
Malcolmia africana	.	.	.	.	.	20	.	25	.	.	.	.
Peganum harmala	.	.	.	23	.	.	50	.	.	.	.	.
Salsola kali agg.	.	.	.	.	.	40	50	33	.	8	13	.
Senecio sp.	.	.	.	.	67	20	.	8	40	.	.	.
Stipagrostis pennata	.	.	.	.	.	20	.	8	20	31	25	.
Tribulus longipetalus	.	.	.	.	.	.	.	25	.	.	.	.
Tribulus terrestris	.	.	.	.	.	20	.	17	.	.	.	.

Species with low constancy:
Allium kotschyi 7: 50; *Allium* sp. 2: 17, 5: 33; *Arabidopsis pumila* 12: 33; *Arnebia* sp. 6: 20; *Beta vulgaris s. maritima* 4: 8; *Camelina* sp. 8: 17; *Centaurea bruguierana 8*: 8; *Climacoptera* sp. *4*: 8, 9: 7; *Convolvulus dorycnium* 8: 8; *Convolvulus chondrilloides 7*: 50, 9: 7; *Cynodon dactylon* 4: 23, 8: 8; *Echinops* sp. 9: 7, 10: 8; *Erodium cicutarium 6*: 20, 9: 7; *Fortuynia bungei* 2: 17, 8: 8; *Frankenia hirsuta* 4: 8; *Glycyrrhiza glabra* 4: 8; *Halimocnemis rarifolia* 4: 8; *Halothamnus subaphyllum 5*: 33; *Haplophyllum* sp. 7: 50, 8: 8; *Hyoscyamus species 6*: 20; *Isatis minima* 9: 7; *Juncus maritimus* 1: 20, 4: 8; *Koelpinia linearis* 5: 33; *Koelpinia* sp. *9*: 7; *Lactuca* sp. *10*: 8; *Launaea* sp. 8: 8; *Matthiola chenopodiifolia 7*: 50, 10: 8; *Panicum* sp. 4: 8; *Polygonum luzuloides 4*: 15; *Polypogon* sp. *4*: 8; *Populus euphratica1*4: 20; *Salsola praecox* 12: 33; *Schumannia karelinii* 6: 20, 10: 8; *Sonchus* sp. *4*: 8; *Suaeda arcuata* 4: 8; *Suaeda fruticosa* 4: 8; *Typha domingensis* 1: 20; *Xanthium strumarium* 4: 8; *Zygophyllum eichwaldii* 4: 8.

Table 7 Syntaxonomic comparison of vegetation in the four regions (A: Atlantic; M: Mediterranean; H: Hyrcanian; IT: Irano-Turanian). Mean species richness (SR) and dominant functional group (FG) for each class as well as endangered (**R**ed list) plant communities (only for N Germany) are provided in the table. NA: syntaxonomically not yet assigned.

SR	FG	Class	Order	Alliance	Association	A	M	H	IT	R
Drift line										
8.5	**4/5/3**	***Cakiletea maritimae***	*Atriplicetalia littoralis*	*Salsolo-Minuartion peploidis*	***Cakiletum maritimae***	*				
				Atriplicion littoralis	***Atriplicetum littoralis***	*				
			Thero-Atriplicetalia	*Euphorbion peplidis*	***Salsolo kali-Cakiletum* maritimae**		*			+
			NA	NA	***Cakile maritima-Arguzia sibirica* comm.**			*		
Mobile dune										
10.1	**3**	***Ammophiletea***	*Ammophiletalia*	*Elymion arenarii*	***Elymo-Ammophiletum***	*				
				Ammophilion	***Medicagini marinae-Ammophiletum australis***		*			
				Elymion gigantei	***Elymetum sabulosi***		*			
7.0	**1/6/3**	***Artemisietea lerchianae***	*Artemisietalia tschernievianae*	*Euphorbion seguierianae*	***Artemisia tschernieviana* comm.**			*		
5.7	**3**	***Stipagrostietea pennatae***	*Stipagrostietalia pennatae*	*Stipagrostion pennatae*	***Stipagrostis karelinii* comm.**				*	
					***Centropodia forsskalii* comm.**				*	
				NA	***Cyperus eremicus* comm.**				*	
Stabilized dune										
8.7	**3**	***Koelerio-Corynephoretea***	*Corynephoretalia canescentis*	*Corynephorion canescentis*	***Caricetum arenariae***	*				+
			Thero-Airetalia	*Thero-Airion*	***Airo-Festucetum***	*				
16.8	**1**	***Helichryso-Crucianelletea maritimae***	*Crucianelletalia maritimae*	*Crucianellion maritimae*	***Ephedro distachyae-Silenetum subconicae***		*			
					Artemisietum campestris		*			
9.0	**2**	**NA**	NA	NA	***Ephedra procera* comm.**			*		
6.4	**2**	***Artemisietea sieberi***	*Artemisietalia sieberi*	*Artemision sieberi*	***Artemisietum sieberi***				*	
				NA	***Stipagrostis plumosa* comm.**				*	
				Prosopidion farctae	***Prosopidetum farctae***				*	

SR	FG	Class	Order	Alliance	Association	A	M	H	IT	R
				Ephedrion strobilaceae	***Ephedretum strobilaceae***				*	
3.9	**2**	***Haloxyletea ammodendri***	*Haloxyletalia ammodendri*	*Haloxylion ammodendri*	***Haloxyletum ammodendri***				*	
					***Calligonum crinitum* comm.**				*	
Salt marsh										
4.0	**7**	***Thero-Salicornietea***	*Thero-Salicornietalia*	*Salicornion dolichostachyo-fragilis*	***Salicornietum strictae***	*				
				Salicornion ramosissimae	***Salicornietum ramosissimae***	*				+
					Suaedetum maritimae	*				+
				Thero-Salicornion	***Salicornia procumbens* comm.**		*			
				NA	***Salicornia iranica* comm.**			*		
				NA	***Salicornia persica* comm.**[1]					
6.2	**5**	***Saginetea maritimae***	*Frankenietalia pulverulentae*	*Frankenion pulverulentae*	***Hordeum marinum* comm.**[2]			*		
			NA	NA	***Psylliostachys spicata* comm.**			*		
			NA	NA	***Frankenia hirsuta* comm.**			*		
5.8	**2**	***Salicornietea fruticosae***	*Salicornietalia fruticosae*	*Salicornion fruticosae*	***Halimionetum portulacoidis***	*	*			+
					Statico bellidifoliae-Salicornietum fruticosae		*			
					Sarcocornio perennis-Puccinellietum convolutae		*			
				Arthrocnemion glauci	***Arthrocnemum macrost.* comm.**		*			
					Arthrocnemo glauci-Halocnemetum strobilacei		*			
5.9	**2/7**	***Kalidietea foliati***	*Kalidietalia foliati*	*Kalidion caspici*	***Halocnemum strobilaceum* comm.**[3]			*		
					***Halostachys belangeriana* comm.**			*		
					Alhagietum pseudalhagi				*	
				Seidlitzion rosmarini	***Seidlitzietum rosmarini***				*	
			NA	NA	***Petrosimonia brachiata* comm.**			*		
2.3	**3**	***Phragmito-Magnocaricetea***	*Scirpetalia maritimi*	*Scirpion maritimi*	***Scirpetum maritimi***	*				

SR	FG	Class	Order	Alliance	Association	A	M	H	IT	R
Salt marsh										
5.6	**3**	***Juncetea maritimi***	*Puccinellio maritimae-Salicornietalia*	*Armerion maritimae*	***Juncetum gerardii***	*				
				Festucion maritimae	***Limonietum vulgaris***	*				
			Juncetalia maritimae	*Juncion maritimae*	***Juncus maritimus* comm.**			*		
				NA	***Tripolium pannonicum-Salicornia iranica* comm.**			*		
10.2	**3**	***Festuco-Puccinellietea***	*Puccinellietalia*	*Puccinellion convolutae*	***Aeluropus littoralis* comm.**		*			
6.3	**3**	***Aeluropodetea littoralis***	*Aeluropodetalia littoralis*	*Aeluropodion littoralis*	***Aeluropodetum littoralis*** [4]			*		

Communities with superscript 1-4 did not occur in the synoptic table 6 (C Iran) but in literature for central Iran: 1 Akhani (2003); 2 Alaie (2001); 3 Akhani (2004); 4 Asri & Ghorbanli (1997).

Functional diversity and similarity

Although the four regions turned out to be quite different in terms of plant species pools and vegetation types (especially of mobile and stabilized dunes), the species of similar habitats may be functionally analogous. Common habitat features indeed resulted in similar functional groups of species. The proportion of different functional groups in classes and per region is shown in Fig. 4 and the prevailing functional group per class is given in Table 7. The significance of the differences between functional groups of each community was approved by the results of the Kruskal-Wallis test ($P < 0.01$).

Ammophiletea, *Artemisietea lerchianae* and *Stipagrostietea pennatae* are geographically distinct but very similar in having the highest proportion of graminoid perennials (FG3) (Fig. 3a-d, Fig. 4, Table 7), chiefly rhizomatous clonal grasses, wind pollinated and dispersed, and CS/CSR strategy. Such plants can cope with the extreme habitat conditions of mobile dunes, such as wind erosion, sand burial and water deficiency. Plant communities of the *Artemisietea lerchianae* include non-graminoid perennials (FG1) and shrubs (FG2) in addition to the graminoid perennials (FG3) with more or less the same proportion.

Plant communities on stabilized dunes are adapted to dry conditions with chiefly three groups of species: non-graminoid perennials (FG1), shrubs (FG2), and graminoid perennials (FG3), such as of the *Stipagrostis plumosa* community. Stabilized dunes of central Iran are dominated by shrubs (FG2) with reduced leaves, long roots and thickened stems/roots, mostly pollinated and dispersed by wind. The plant communities belong either to the class *Artemisietea sieberi*, characterized by small shrubs of up to 1 m, or to the *Haloxyletea ammodendri*, with shrubs up to 3 m tall. In Hyrcanian N Iran shrubs and graminoid perennials form communities on stabilized dunes, while in NE Greece graminoid (FG3) and non-graminoid perennials (FG1) prevail in this habitat type. *Helichryso-Crucianelletea maritimae* are dominated by cushions or prostrate plants with frequently dense indumentum, with long tap root and/or woody stem, mostly dispersed by wind but pollinated by insects. Graminoid perennials are dominant in stabilized dunes of N Germany. In the *Cakiletea maritimae*, the ruderal strategists (FG4) and insect-pollinated annuals are prominent functional groups (Fig. 2).

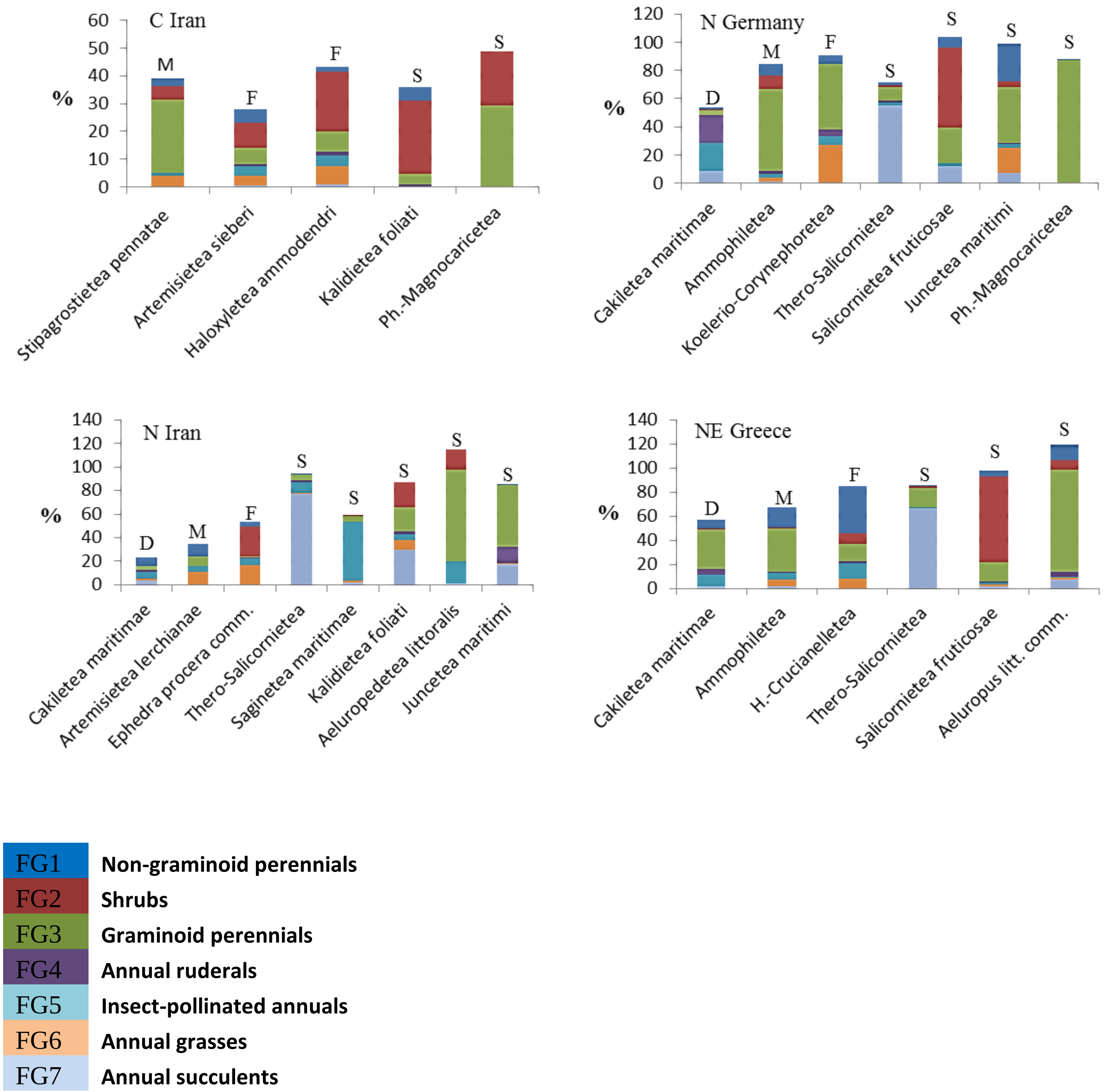

Fig. 4 Cumulative cover proportions (in %) of functional groups in the vegetation classes of each region. Habitat types above the columns: D: drift line; M: mobile dune; F: stabilized (fixed) dune; S: salt marshes. Total cover exeeds 100 % in some cases because of vegetation layer overlap. The differences between functional groups of each community were significant (Kruskal-Wallis test, P<0.01).

Plant communities on the salt marshes consist mostly of three functional groups. Annual succulents (FG7) occur in four regions and refer to the *Thero-Salicornietea*. Woody halophytes (FG2) with reduced leaves and/or succulent stems, adapted to high salinity, are most prominent in both coastal (*Salicornietea fruticosae*) and inland (*Kalidietea foliati*) salt marshes. Graminoid perennials (FG3) include rhizomatous or tussock-forming sedges and rushes of the *Juncetea maritimi* and *Phragmito-Magnocaricetea* (Table 7).

Discussion

Taxonomic and syntaxonomic similarities

Our findings show that the plant species composition of coastal and inland sand ecosystems is more related to the biogeographic (climatic) region than to habitat features. At both species and genus level, there is very low similarity in habitats of the same kind across regions as well as across such habitats within a region (Fig. 2, Table 1-2). As far as species and community composition are concerned, biogeographical distance, whether through climate or chorological and evolutionary history, prevails over environmental similarity. However, this effect varied among the four halophytic habitats. Mobile and stabilized dunes showed more region-related patterns at both taxonomic and syntaxonomic levels and their species composition thus reflected to some extent the biogeographic position of the area. Our results are in accordance with findings in the coastal vegetation of the Iberian Peninsula (Jiménez-Alfaro et al. 2015), where dune habitats were found to be controlled by climatic (temperature and precipitation) patterns, an effect that was more significant in stable dunes. In conclusion, the level of azonality of the vegetation of mobile and stabilized dunes, as appears from the amount of supraregional taxonomic and syntaxonomic dissimilarities and individuality, is lower than in the other sand ecosystems under study.

At syntaxonomic level, salt marshes and drift lines show considerable similarities between regions, whereas mobile and stabilized dunes have very little in common. Sand ecosystems in general are known as stress-prone habitats but among the four studied habitat types, salt marshes and drift lines are exposed to at least temporarily particularly high salinity (Pennings & Bertness 2001) and, as far as strandline vegetation is concerned, disturbance (Grime 2006). Extreme habitat conditions play an important role in forming plant associations (Mucina et al. 2006). The narrow ecological niche available in highly stressful habitats acts as an environmental filter, which selects the few tolerant species with morphological and physiological character traits that suit such habitats (Gallego-Fernández & Martínez 2011; Bermúdez & Retuerto 2013). Therefore, the more stress-prone a habitat, the more is its vegetation habitat-related and independent from the biogeographic region, virtually locked against the regional species pool. This explains why the highest numbers of species, genera and syntaxa in common at different biogeographical regions were recorded in salt marshes and drift lines, and it explains the low species richness of these habitats in comparison to others, e.g. 4-6 species per plot in salt marshes (similarly low numbers reported by, e.g., Isermann 2005 and Acosta et al. 2009). Therefore, from a taxonomic and syntaxonomic point of view, salt marsh and drift line vegetation show a particularly high degree of 'azonality'.

Functional similarity

Extreme environmental conditions have considerable effects on the morphology of plants and the functional composition of plant communities (de Bello et al. 2013), i.e. the proportion of functional groups. We observed that the prevailing vegetation of each habitat type has similar functional composition across different regions, while different sand habitats of one region have fewer functional groups in common. At the level of functional traits, the vegetation is more independent of the regional climate and biogeography, and highest trait similarities occurred among habitats of the same kind but of different regions. The filtering effect of habitat on plant functional composition was shown by Tecco et al. (2010), where no significant differences between functional attributes of herbaceous alien and native species of the same habitat under different climatic conditions were found. Regarding the functional aspect of vegetation and in contrast to the taxonomic and syntaxonomic perspective (see above), all studied ecosystems, including mobile and stabilized dunes, form azonal vegetation. They share functional groups of species independent from the climatic region.

In some cases, we noticed that a certain functional group (co-)dominated in vegetation types of different habitats. Graminoid perennials (FG3) for instance predominate in various habitats. Sedge and rush communities of wet salt marshes (*Juncetea maritimi*) as well as grass communities on mobile dunes (*Ammophiletea*), both FG3, are using similar strategies to overcome environmental stress. Equipped with storage organs (carbohydrate stored in rhizomes or at the base of the tussocks), plants can establish in stress-prone habitats and withstand periodical drought, while clonality enables them to occupy suitable places, withstand disturbance and to compete with other plants (CS or CSR strategy) in using the limited habitat resources (Maun 2009). Wind dispersal facilitates the establishment of new colonies. With help of these strategies, plants can overcome the harsh conditions of various habitat types, whether it is sand burial and erosion in mobile dunes or inundation and desiccation in salt marshes.

Similarly, in stabilized dunes as well as in salt marshes, FG2 plants (includes tall or low shrubs) figure prominently. By reduced leaves, photosynthetically active stems and/or succulent leaves, FG2 shrubs are well adapted to dry or saline habitat conditions. The high salinity of salt marshes as well as the dry conditions of stabilized dunes affects the availability of water, to which plants respond to by similar drought adaptation traits. Additional functional traits (and hence more sophisticated functional groups) may result in finer differentiation of functional vegetation characteristics in different habitats.

We believe that functional groups are useful to understand and describe plant communities as reflecting habitat and ecosystem conditions. Functional aspects of the vegetation can be applied in addition to species composition (and presence of diagnostic species) for defining high-rank syntaxa and also for comparing plant communities across different regions ('coeno-syntaxa', e.g. Deil 1989). While phytosociologists have used multiple morphological characters of vegetation to describe the 'texture' of plant communities since long ('synmorphology', e.g. Barkman 1979; Dierschke 1994), applying functional groups provides a wider range of character traits and a more consistent approach. For example, the woody salt marsh communities of the *Kalidietea foliati* and *Salicornietea fruticosae* are dominated by species of similar function (FG2). Plant communities of both classes have very similar ecological needs, plant morphology and trait characteristics as a response to similar environmental stress. The two classes represent the same kind of habitat and are to be considered as ecological counterparts and geographically vicariant syntaxa, which might even be combined into a single class, quite like some researchers include inland salt marsh shrub communities of the Iberian peninsula in the *Salicornietea fruticosae* (Fuente et al. 2013, Rufo et al. 2016).

A note on Halocnemum dominated vegetation

Plant assemblages dominated by *Halocnemum strobilaceum* (*Halocnemetum strobilacei*) are occurring in both inland and coastal areas of Iran as well as in European coastal salt marshes. The syntaxonomic position of the *Halocnemetum strobilacei* remains unclear, as it is grouped under different high-rank syntaxa in different regions. According to European authors (e.g., Rivas-Martínez et al. 2001), the *Halocnemetum strobilacei* belongs to the alliance *Arthrocnemion glauci* of the class *Salicornietea fruticosae*. In inland salt marshes of central Iran, the association of *Halocnemum strobilaceum* was first reported by Zohary (1973) under its own class '*Halocnemetea irano-anatolicae'*. This illegitimate name was changed into *Halocnemetea strobilacei* (yet without sufficient diagnosis) by Asri & Ghorbanli (1997) and then reduced to synonymy under *Salicornietea fruticosae* by Akhani (2004). Some authors (e.g. Schaminée et al. 2012; Mucina et al. 2016), assigned salt marsh communities dominated by *Halocnemum strobilaceum* with similar, if not identical, species composition into two alliances, the Caspian *Kalidion caspici* and the Mediterranean *Arthrocnemion glauci*, respectively. One solution is to consider all *Halocnemum*-dominated salt marsh communities with similar ecology as one association *Halocnemetum strobilacei* in the class *Salicornietea fruticosae* irrespective of its region or its location (Biondi et al. 2014). However, if *Halocnemum strobilaceum* turns out to be an aggregate of as yet undetected vicarious species (or subspecies) in different regions (see Biondi et al. 2013), similar to the *Salicornia europaea* aggregate (Kadereit et al. 2006), the syntaxonomic similarity of the respective communities would decrease as well. Pending molecular and in-depth morphological studies, the taxonomy of *Halocnemum* and the syntaxonomy of the '*Halocnemetum strobilacei'* remain open questions.

Conservation value

Coastal sand habitats rank among the most endangered and threatened ecosystems worldwide (EEA 2008). Urbanization, agriculture and touristic development are the most important factors leading to habitat degradation, fragmentation, and species and habitat loss (Buffa et al. 2012; Pintó et al. 2014). From the 11 associations of coastal sand habitats recorded by us in N Germany, five communities are listed as 'Endangered' (Rennwald 2000): three of salt marshes, one of drift lines and one of stabilized dunes. Yet in many national Red Lists these habitats and their plant species are not well represented (van der Maarel & van der Maarel-Versluys 1996). Based on our field observations, habitat loss and fragmentation is a serious problem particularly in coastal areas of N Iran and NE Greece, but also in Germany. The coastal vegetation in N Iran is already destroyed in many parts and in NE Greece under high pressure. Also the *Cakiletum maritimae* as well as several plant communities of stabilized dunes are highly vulnerable or threatened almost everywhere. Therefore, we emphasize the necessity of effective protection strategies for preserving the remaining sand dunes and salt marshes and restoring damaged habitats within and beyond our study areas.

Author contribution

P.M. conducted the research, performed analyses and wrote the manuscript, E.B. contributed in planning the research, revised and improved the manuscript, M.I. critically revised the manuscript and provided a regional dataset.

Acknowledgements

We would like to thank the Reinhold-und-Johanna-Tüxen-Stiftung for funding the field work in Iran for P.M. ‘Management Body of Delta Nestos, Lakes Vistonida-Ismarida’ in Greece and departments of ‘Natural Resources of Esfahan’ and ‘Nature Conservation of Mazandaran’ in Iran are gratefully acknowledged for their help for visiting the areas. The Editor’s and reviewer’s comments and corrections helped to improve the manuscript and are gratefully acknowledged.

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Chapter 4

Distribution of C4 plants in sand habitats of different regions

Parastoo Mahdavi & Erwin Bergmeier

Folia Geobotanica, 2017: accepted

Abstract

Sand dunes of warm regions provide suitable habitats for C4 plants because of improved water and nitrogen use efficiency of C4 plants under high temperature and high tolerance to ecological stress such as salinity, aridity and disturbance. In this study, we compared the distribution pattern of C4 plant species in sand dune ecosystems of three climatic regions (Mediterranean, Irano-Turanian and Hyrcanian) to find out the proportion and identify habitat preference of C4 plants in sand habitats. We analyzed the vegetation cover and richness of C4 and C3 species in five sand habitats. Our results revealed that C4 species have notable contribution to the vegetation cover despite of rather low contribution to the richness in comparison with C3 species. C4 plants were more prominent in mobile dunes, salt marshes and disturbed sandy ground; however, the habitat preference was different in each region. The abundance of C4 plants appears to be influenced by climatic conditions. We observed a general increasing trend in richness and cover of C4 plants with increase of aridity. Central Iran is the driest and warmest among our study regions and has the highest proportion of C4 species in terms of number and cover.

Keywords: C4 pathway, grass, chenopod, biomass, climate, habitat, sand dune, trait, Iran, Greece

Introduction

C4 photosynthesis is a complex trait, consisting of a combination set of anatomical and biochemical adaptations. It leads to concentration of CO_2 around the carbon-fixing enzyme Rubisco and reduction of photorespiration (Sage 2004; Christin & Osborne 2014). It has evolved independently more than 60 times in 19 families of flowering plants (Sage 2016) and 22-24 times in the Poaceae, the family with the most C4 species (GPWG II 2012). Although C4 species constitute only 3% of vascular plants, they account for about 25% of terrestrial primary production (Ehleringer & Monson 1993; Still et al. 2003). They also include economically important highly productive crops such as maize, sugarcane, sorghum, etc. (Osborne & Freckleton 2009).

Low partial pressure of atmospheric CO_2 (pCO_2) and high temperature are the main drivers of C4 evolution and expansion (Ehleringer et al. 1997; Sage 2005; Urban et al. 2015). First lineages of C4 grasses evolved about 30 million years ago, most likely in open habitats of warm regions (Osborne & Freckleton 2009; Sage 2016). The evolution of the C4 pathway in Chenopodiaceae originated probably from lineages inhabiting saline costal habitats (Kadereit et al. 2012). It has been shown that C4 photosynthesis can extend the ecological niche of plants (Lundgren et al. 2015). This hypothesis contributes to explaining the expansion of C4 species into a wide range of habitats and biomes (Sage et al. 1999; Christin & Osborne 2014). Moreover, the present distribution of C4 plants reflects present conditions regardless of changes in CO_2 concentration and temperature in the past (Auerswald et al. 2009).

The evolutionary, ecological and economical relevance of the C4 photosynthetic pathway attracted the attention of researchers from different points of view: effects of C4 plants in the evolution of mammals and humans (van der Merwe & Tschauner 1999); physiological advantages (Gowik & Westhoff 2011; Taylor et al. 2014); transgenic C4 crops and biofuels for higher production (Somerville et al. 2010; Lopes et al. 2011; van der Weijde et al. 2013), C4 rice engineering (Kajala et al. 2011; Peterhansel 2011); phylogeny of C4 plants (Edwards et al. 2010; Sage et al. 2011; Christin et al. 2013), and the effect of climate on the distribution of C4 plants (Collatz et al. 1998; Bremond et al. 2012). More than 50 years after the discovery of C4 photosynthesis (Hatch & Slack 1966), and after intensive researches (reviewed in Sage 2016 and Furbank 2016), the picture is comprehensive but not completed yet. Due to the taxonomical, anatomical and physiological diversity of C4 groups that evolved along different evolutionary pathways, a variety of ecological, geographical and habitat preferences are concerned. The current distribution of C4 plants, their ecology in different habitats and regions (especially outside the tropics) as well as C3/C4 dynamics are not well studied.

Sand dunes are known as stress-prone habitats associated with salinity and drought. Species inhabiting such habitats developed specific traits and adaptations, which enable them to use limited resources. Sand dunes of warm regions are suitable habitats for C4 plants because of their improved water and nitrogen use efficiency under high temperature (Ehleringer 1978; Long 1999) and high tolerance to ecological stress such as salinity, aridity and disturbance (Sage et al. 1999). The role, abundance and distribution of C4 plants in sand dunes are not well studied. The distribution of C4 grasses was modeled for West African coasts (Schmidt et al. 2011), and their ecological aspects were investigated in selected habitats of Costa Rica (Chazdon 1978). Outside tropics, floristic surveys showed a high presence of C4 plants in sandy and saline habitats of China and Mongolia (e.g. Pyankov et al. 2000; Wang 2007; Auerswald et al. 2009) . Most ecological studies referred to species richness and neglected abundance (e.g. Pyankov et al. 2010) although the latter is an important issue for ecosystem properties and services.

In this study we compared the distribution pattern of C4 plant species in three sand dune ecosystems across different climatic regions (Mediterranean, Irano-Turanian and Hyrcanian). In each region we analyzed the C4 species cover, richness and C3/C4 ratio in five sand habitats to answer the following: How are C4 plants distributed in different habitats of sand ecosystems and what are their habitat preferences? Do C4 plants have higher biomass than ecologically similar C3 plants? Do regional climate differences affect the occurrence and proportion of C4 plants?

Study area

We studied sand dune ecosystems in three regions (Fig. 1) very different in climate, phytogeography and species composition but similar in their set of psammophytic habitat types.

NE Greece: the study area along the North Aegean coast runs approximately 300 km from south of Katerini (40° 09'N, 22° 33'E) eastward to Porto Lagos (40° 54'N, 25° 23'E). The area is characterized by Mediterranean climate with hot, dry summers and wet and cool winter, almost without frost. Mean monthly temperatures vary between 5-7 °C (January) and 25-27 °C (July). Mean annual rainfall is 400-600 mm (Lienau 1989).

N Iran: the SE Caspian Sea shore was investigated, including the Miankaleh Biosphere Reserve (36° 48-55'N, 53° 25'-54° 02'E) with 50 km of (semi-)natural coastline, and two other sites westward (36° 49'N, 53° 8'E, 36° 39'N, 52° 22'E). The area belongs to the Hyrcanian phytogeographic region and is characterized by a warm humid climate with rainy summers and mild winters. The mean temperature of the coldest month (January) is 8.7 °C and the warmest month is August with mean temperatures of ca. 28 °C. The mean annual precipitation is 789 mm (http://www.chbmet.ir/iranarchive.asp).

Central Iran: the southern shore of the Namak Lake (Daryacheh-ye Namak) in the Maranjab Desert (34° 9-19'N, 51° 30-56'E) is a large saline playa surrounded by sand dunes and saltmarshes. The study sites belong to the Irano-Turanian region, characterized by continental climate, low precipitation, hot and dry summers and cold winters. The mean temperature of the coldest month is ca. 5 °C (January), while it reaches 33 °C (July) in the hottest month. The annual precipitation is 136 mm (http://www.chbmet.ir/iranarchive.asp).

Central Iran has significantly lower precipitation and higher temperature than N Iran (Table 1) as well as NE Greece. This is also reflected by the lower aridity index values of C Iran (Fig. 1).

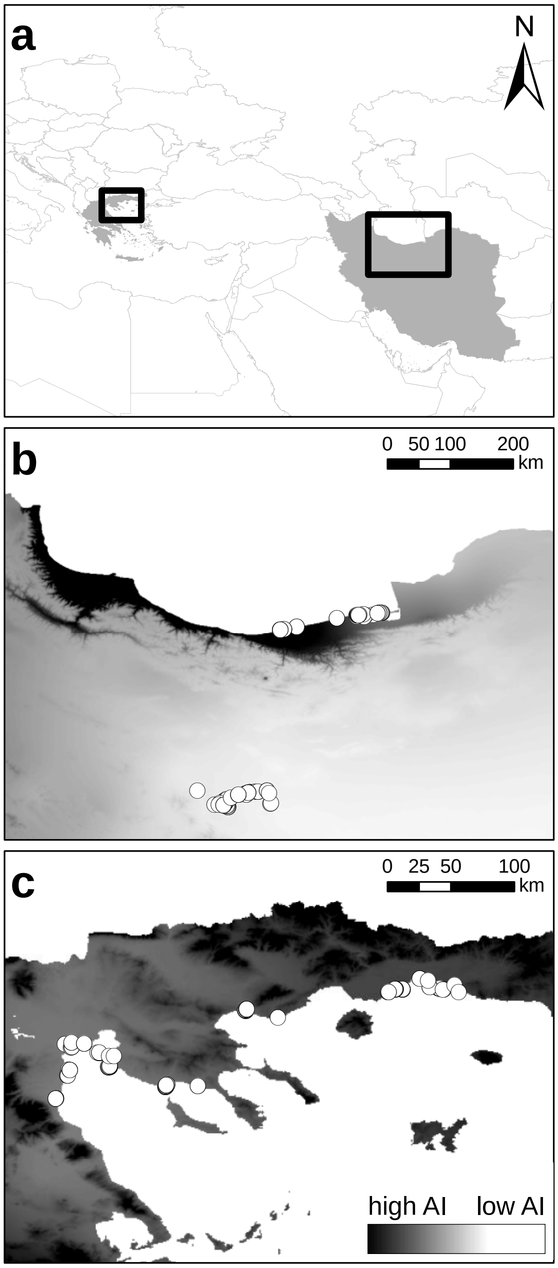

Fig. 1 Overview of the investigated area in Iran and Greece (a) with distribution of sampled plots (open circles) and aridity index (AI) differences between sites: North and Central Iran (b) and NE Greece (c). Low AI and lighter colors represent higher aridity; darker colors and high AI indicate more humid conditions.

Methods

Data collection

In total, 317 plots from N Iran (65), C Iran (91) and NE Greece (161) were analyzed. The plots (25 m^2) were sampled in summer 2011 and 2012 using the Braun-Blanquet cover/abundance scale for each species in plots of five habitat types where present: mobile dune, stabilized dune, semi-wet habitat (dune slack), salt marsh and disturbed ground. We assigned the regional species pools to the main C3 and C4 photosynthetic types chiefly based on the available literature. A list of the recorded C4 species, the biochemical subtype, and C4 identification references is provided in Table 1.

Table 1 List of recorded C4 species in the three investigated areas, their subtype and references: 1. (Akhani, Trimborn, & Ziegler, 1997); 2. (Akhani, Edwards, & Roalson, 2007); 3. Pyankov et al. 2000; 4. Pyankov et al. 2010; 5. Watson et al. 1992. Subtypes in subfamily Suaedoideae are based on (Muhaidat, Sage, & Dengler, 2007).

Species	**Subtype**	**Region**
Chenopodiacea		
Bassia laniflora (S.G. Gmel.) A.J. Scott [2]	NADP-ME	NE Greece
Bassia stellaris (Moq.) Bornm. [4]	NADP-ME	C Iran
Cornulaca aucheri Moq. [1]	NADP-ME	C Iran
Halimocnemis rarifolia (K. Koch) Akhani[2]	NADP-ME	C Iran
Halothamnus subaphyllus (C.A.Mey) Botsch.[1]	NADP-ME	C Iran
Haloxylon ammodendron (C. A. Mey.) Bunge ex Fenzl[3]	NADP-ME	C Iran
Petrosimonia brachiata (Pall.) Bunge[4]	NAD-ME	N Iran, NE Greece
Salsola kali L.[4]	NADP-ME	C Iran, N Iran
Salsola praecox Litv.[2]	NADP-ME	C Iran
Salsola soda L.[4]	NADP-ME	NE Greece
Salsola tragus L.[3]	NADP-ME	NE Greece
Seidlitzia rosmarinus Ehrenb. ex Boiss.[2]	NADP-ME	C Iran
Sorghum halepense (L.) Pers.[4]	NADP-ME	NE Greece
Suaeda arcuata Bunge[1]	NAD-ME	C Iran
Suaeda fruticosa Forssk. ex J.F. Gmel.[1]	NAD-ME	C Iran
Suaeda splendens (Pourr.) Gren. & Godr.[4]	NAD-ME	NE Greece
Poaceae		
Aeluropus lagopoides (L.) Trn. ex Thwaites[4]	NAD-ME	C Iran
Aeluropus littoralis (Gouan) Parl.[4]	NAD-ME	C Iran, NE Greece
Bothriochloa pertusa (L.) A. Camus[5]		NE Greece
Cenchrus incertus M.A. Curtis[4]	NADP-ME	NE Greece
Centropodia forsskalii (Vahl) Cope[5]		C Iran
Chrysopogon gryllus (L.) Trin.[5]		NE Greece
Cynodon dactylon (L.) Pers.[4]	NAD-ME	C Iran, N Iran, NE Greece
Digitaria sanguinalis (L.) Scop.[4]	NADP-ME	NE Greece
Echinochloa crus-galli (L.) P. Beauv.[3]	NADP-ME	NE Greece
Eragrostis minor Host[3]	NAD-ME	NE Greece

Species	**Subtype**	**Region**
Imperata cylindrica (L.) Raeusch.[4]	NADP-ME	N Iran, NE Greece
Paspalum distichum L.[4]	NADP-ME	N Iran, NE Greece
Saccharum griffithii Munro ex Aitch.[5]	NADP-ME	N Iran
Saccharum ravennae (L.) L.[4]	NADP-ME	N Iran, NE Greece
Saccharum spontaneum L.[4]	NADP-ME	N Iran
Setaria verticillata (L.) P.Beauv.[4]	NADP-ME	NE Greece
Sporobolus pungens (Schreb.) Kunth[4]		NE Greece
Stipagrostis barbata H. Scholz[5]	NADP-ME	C Iran
Stipagrostis karelinii (Trin. & Rupr.) H. Scholz[4]	NADP-ME	C Iran
Stipagrostis pennata (Trin.) De Winter[4]	NADP-ME	C Iran
Stipagrostis plumosa (L.) Munro ex T. Anderson[5]	NADP-ME	C Iran
Tragus racemosus (L.) All.[4]	NAD-ME	N Iran
Other families		
Cyperus capitatus Vand.[4]	NADP-ME	NE Greece
Cyperus eremicus Kukkonen		C Iran
Cyperus rotundus L.[4]	NADP-ME	NE Greece
Euphorbia peplis L.[4]	NADP-ME	NE Greece
Mollugo cerviana (L.) Ser.[3]	NAD-ME	NE Greece
Calligonum crinitum Boiss.[3]	NAD-ME	C Iran
Calligonum polygonoides L.[3]	NAD-ME	C Iran
Portulaca oleracea L.[3]	NAD-ME	NE Greece
Tribulus terrestris L.[3]	NADP-ME	C Iran, N Iran, NE Greece

Data analysis

In order to assess the proportion of C4 plants in different sand habitats, the C4 cover proportion was calculated by summing up the percentage cover (transformed cover/abundance scale values) of C4 plants in each plot. We used the percentage cover of species by proxy for aboveground biomass. Standardized percentage values of species per habitat and region were displayed using boxplots (Tableau, https://www.tableau.com). The significance of observed differences between habitats was tested using non-parametric Kruskal-Wallis test (R, stats package, Hollander & Wolfe 1973).

Further, we calculated the C4/C3 ratio for both species richness and percentage cover across habitats and regions, to assess the dominance and biomass of C4 plants compared to C3 species.

Climate data including mean annual temperature and precipitation sums were taken from CHELSA (Karger et al. 2016 a & b, www.chelsa-climate.org) and aridity index from CGIAR-CSI (Zomer et al. 2007 & 2008, www.cgiar-csi.org). The according values for each plot were extracted in ArcGIS 10.4 (ESRI 2011) and mean values calculated per region.

Results

Distribution of C4 plants in different habitats

The total number of C4 plants in C Iran (32%, 23 C4 species/72 species in total, based on the whole sample of 91 plots) was higher than in N Iran (14%, 10/72 species, 65 plots) and NE Greece (12%, 25/211 species, 161 plots). Based on species rank abundance curve (not shown), the first region was dominated by C4 species such as *Cyperus eremicus, Seidlitzia rosmarinus, Stipagrostis plumosa* and tall shrubs of *Haloxylon ammodendron* and *Calligonum* spp. In N Iran, C4 species of semi-wet habitats were frequent: *Saccharum ravennae* and *Imperata cylindrica. Aeluropus littoralis* and *Imperata cylindrica* were common in NE Greece. The highest C4 record was among monocots with 22 species of Poaceae and 3 species of Cyperaceae. Among dicots, Chenopodiaceae had most C4 records (16 species) and 7 species were found from other dicot families.

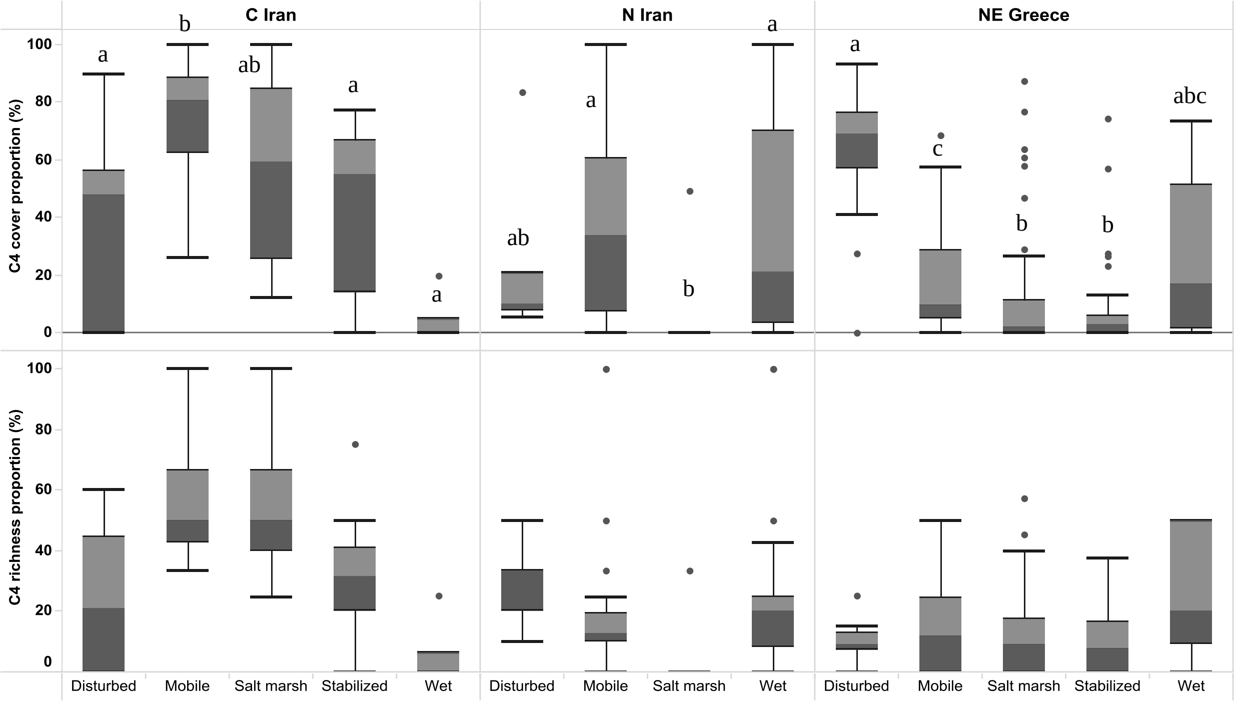

Fig 2. Boxplots of richness and cover proportion of C4 species in sand dune habitats of three regions. Boxes show the upper (light grey) and lower Quartile (dark grey), border of grey blocks represent the median, whiskers represent the maximum and minimum values and individual points are outliers. Letters indicate significant differences between habitats according to Kruskal-Wallis test (P<0.001).

The highest C4 richness (species number per plot) was recorded in disturbed sandy sites of N Iran and semi-wet habitats of NE Greece while in C Iran the highest numbers of C4 species occurred in mobile dunes and salt marshes (Fig. 2). Fixed dunes and saltmarshes in NE Greece, saltmarshes in N Iran and semi-wet habitats in C Iran showed the least C4 species records.

In terms of cover, the habitat preferences of C4 plants were different. In N and C Iran, C4 plants had the highest cover proportion in mobile dunes, followed by semi-wet habitats and salt marshes respectively (Fig. 2). In NE Greece, C4 plants were most abundant in disturbed habitats (Fig. 2).

Although richness of C4 species in sand habitats was in general lower than (or equal to) that of C3 plants, C4 plants have quite high cover. The mean C4 plant cover per plot in C Iran is about 61% corresponding to 50% of C4 species richness per plot. High cover of C4 plants is even more prominent in NE Greece, where 18% C4 plant cover is generated from only 0.1% of C4 plant richness per plot. In N Iran, C4 plants cover 30% per plot while their richness is 19% (Table 2).

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Table 2 Differences in climatic parameters between regions and average values of richness and cover proportion for C4 plants in each region (plot-based calculation).

Region		**C Iran**	**N Iran**	**Greece**
Number of plots per region (n)		89	65	161
Richness proportion C4 species	**Mean**	49.7	18.8	0.1
	Min	0.0	0.0	0.0
	Max	100.0	100.0	0.6
Cover proportion C4 species	**Mean**	60.8	30.0	18.2
	Min	0.0	0.0	0.0
	Max	100.0	100.0	93.1
Aridity index	**Mean**	712.1	5151.3	4303.4
	Min	585.0	3754.0	3668.0
	Max	802.0	8089.0	5223.0
Mean annual temperature [°C]	**Mean**	20.6	17.9	16.2
	Min	18.3	16.9	15.3
	Max	21.1	18.7	16.7
Mean annual precipitation [mm]	**Mean**	139.7	494.9	490.6
	Min	114.3	384.7	378.5
	Max	179.5	729.2	657.1

C4/C3 richness and cover ratio in comparison

The richness and cover ratio of C4 and C3 species provides further insight to dominance and distribution of C4 plants in different sand habitats. In saltmarshes of C Iran, richness and cover ratios had a similar value (ratio of 1) which means an equal proportion of C3 and C4 species in terms of number and cover. In mobile dunes, cover proportion of C4 plants was more than three times as that of C3 plants although they had the same number of species. Richness of C4 species was 40% of that of C3 species in both disturbed sites and stabilized dunes although the cover proportion of C4 plants was 90% of that of C3 plants in stabilized dunes and 75% in disturbed habitats. The lowest proportion of C4 plants occurred in semi-wet habitats, where richness and cover was 10% of that of C3 species (Table 3).

In N Iran, although the number of C4 species in mobile dunes was only 15% of C3 species numbers, C4 plants produced the same cover as C3 plants. C4 plants had also quite high cover in semi-wet habitats (70% of C3 species), while their richness was 20% of that of C3 species. In disturbed habitats, richness and cover proportion of C4 species were 30% of that of C3 species. The lowest richness and cover ratio was recorded in saltmarshes where C4 species occurred to less than 10% of C3 species (Table 3).

In NE Greece, richness ratios were generally low but C4 species had significant cover in disturbed habitats. While the richness of C4 species was about one third of that of C3 species, the cover was nearly two times of that of C3 species (1.85). In semi-wet habitats there were much fewer C4 species (richness ratio of 0.13) but their cover was 36% of that of C3 species (Table 3). Richness and cover ratios were almost equal in the other coastal sand habitats of NE Greece.

Table 3 Richness and cover ratio in sandy habitats of three study regions.

	Habitat	**Dist**	**Mob.**	**Salt.**	**Satb.**	**Wet**	**Total**
C Iran	**C4/C3 richness**	0.37	0.98	0.97	0.42	0.13	0.75
	C4/C3 cover	0.75	3.34	1.04	0.92	0.11	0.88
N Iran	**C4/C3 richness**	0.30	0.15	0.03	-	0.21	0.18
	C4/C3 cover	0.26	1.01	0.08	-	0.68	0.43
NE Greece	**C4/C3 richness**	0.30	0.20	0.15	0.05	0.13	0.14
	C4/C3 cover	1.85	0.21	0.14	0.11	0.36	0.37

Discussion

Distribution in sand habitats

We found notable presence of C4 plants in terms of vegetation cover in mobile dunes, saltmarshes and disturbed sandy ground, despite of their low number of species. At least in some habitats, the conditions for C4 plant dominance are favorable. This result is in consistence with a general trend for C4 plants to occur in hot, arid, saline and disturbed habitats (Ehleringer & Monson 1993). Relative high abundance of C4 species in sandy and saline habitats was observed as well in deserts of China (Wang 2007; Su et al. 2011).

Mobile dunes are more than other sand habitats subjected to water and nutrient shortage (Maun 2009). Nutrient and water use efficiency of C4 plants are well reflected in mobile sands in deserts of C Iran dominated by tall C4 shrubs of *Calligonum crinitum* and *Haloxylon ammodendron* forming communities on shifting dunes, and C4 graminoid communities such as of *Stipagrostis plumosa, S. karelinii, S. pennata* and *Cyperus eremicus* (Mahdavi et al. in press). In low-nutrient habitats C4 plants may use the nitrogen sources for developing the root system while the leaf area equals that of the C3 species (Christin & Osborne 2014). Biomass allocation in roots can be well observed in *Calligonum* and *Haloxylon* with thick, long and well developed root system but with reduced or no leaf system, adapted to the dry and nutrient-poor conditions of sandy soils.

Salinity stress is associated with limited water availability and drought adaptation and may have promoted the evolution of C4 halophytes (Sage 2005; Kadereit et al. 2012). Some C4 halophytes occur on extremely saline soils where no C3 halophytes can survive. (Kadereit et al. 2012) suggested that C4 lineages in Chenopodiaceae derived from C3 ancestors already adapted to saline/dry habitats. Given the current distribution and dominance of chenopods in diverse arid deserts, steppes and saline habitats, such pre-adaptation for shifting from coastal sites into dryer steppes and deserts is considered essential (Kadereit et al. 2012). In our study, the high presence of C4 species in saltmarshes of C Iran in terms of number and cover is evident (Fig. 2). Communities of *Seidlitzia rosmarinus* in C Iran and of *Aeluropus littoralis* in all three regions are examples of C4 vegetation in salt marshes (Mahdavi et al. in press).

Disturbed habitats are known for being inhabited by many C4 species (Collins & Jones 1985; Čarni & Mucina 1998). Disturbance influences the dynamics and expansion of C4 plants. It creates open habitats favorable to shade-intolerant C4 plants (Sage et al. 1999). C4 species in fertile and/or disturbed habitats may use the same amount of nitrogen to produce a larger leaf area than their C3 relatives (Christin & Osborne 2014). Plants in disturbed habitats grow rapidly and have short life histories to withstand unfavorable conditions. Therefore, the nitrogen use efficiency of C4 plants and the potential of high biomass production is an advantage in disturbed habitats. It explains the high C4 cover proportion of disturbed sandy grounds observed in our study. C4 plants have significant presence in disturbed habitats of NE Greece in terms of cover and of N Iran in terms of richness.

In both coastal regions of N Iran and NE Greece, there are patches of semi-wet habitats between mobile dunes inhabited by tall and dense clonal colonies of *Saccharum* spp. and *Imperata* cylindrica, which unlike other C4 species do not occur in dry habitats.

In general, we found that C4 abundance differed in the same habitat in different regions. However, the pattern in NE Greece and N Iran was more similar, probably due to higher climatic similarity of the two regions. Different habitat preference of C4 plants across regions may be partly due to climatic differences between regions and partly due to variation in C4 groups including different biochemical and anatomical subtypes, different lineages of C4 plants and taxonomic differences (monocots vs. dicots) which is resulted in different ecophysiological response to regional environmental conditions. Previously, we defined seven main functional groups in sand dunes by analyzing the functional traits of plants (Mahdavi & Bergmeier 2016). Three of them include C4 species: Shrubs, perennial graminoids and annual succulents. Each group, characterized by a set of traits common to both C3 and C4 species, indicates similar adaptations and niche preferences. It confirms that habitat preferences of C4 species are not only due to their photosynthetic pathway, but also connected to other traits inherited from their C3 ancestors (Christin & Osborne 2014).

C4 abundance and biomass

Our results revealed that C4 species contribute most notably to the vegetation cover and less to the richness in comparison to C3 species (Table 3). This pattern was more pronounced in the drier region (C Iran), where higher C4 cover and species numbers were observed. In some habitats, C4 plants even stand out in cover percentage against more species-rich C3 plants. High C4 cover proportion may be related to high individual biomass and/or because of the large population of some species. Similar results were obtained in the USA Central Plains Experimental Range, where 59% of the species were C3 but account for only 10% of the biomass (Paruelo & Lauenroth 1996).

It was shown that improved water and nitrogen use efficiency in C4 plants may enhance biomass allocation in C4 species, but productivity varies depending on environments (Ehleringer & Monson 1993; Long 1999; Christin & Osborne 2014). According to the crossover temperature hypothesis (Ehleringer 1978; Ehleringer et al. 1997), C3 grasses are competitive and dominant when daytime growing season temperatures are below 22°C. C4 grasses are dominant at temperatures above 30°C. (Winslow et al. 2003) argued that seasonal access to available water controls the relative C3 and C4 grass biomass. In this case, temperature causes temporal separation of the growing peaks of grasses where at high temperature (late summer) almost only C4 grasses have access to water and at lower temperature (early summer) C3 grasses. Water use efficiency of C4 plants is an advantage when water availability is limited. Most C4 species in our regions are late flowering plants and complete their life cycle in late summer when it is too dry for most C3 plants and their growing period is already over. The average summer temperature in our study regions is above the crossover temperature.

Furthermore, biomass allocation varies in different C4 groups. Taylor et al. (2010) showed that biomass allocation is greater in the NADP-ME C4 grass subtype than in other subtypes and C3 species. They discovered a distinct shift in biomass allocation and physiology associated with phylogenetic divergence between the grass tribe Paniceae and other PACMAD lineages (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae and Danthonioideae), suggesting the phylogenetic influence of different C4 lineages and their C3 ancestors on the ecological behavior of C4 plants (Christin & Osborne 2014). While our study cannot determine the share of each C4 group or lineage in the obtained results or specify the biomass strategy of C4 pants (shoot/root ratio), it confirmed the previous hypothesis that C4 plants have the potential of higher productivity in comparison to ecologically similar and co-occurring C3 plants (Still et al. 2003).

C4 proportion and climatic parameter

While the number of studied regions was limited we observed a general increasing trend in richness and cover of C4 species with increasing aridity (lower value of aridity index) (Table 1). C Iran, the driest and warmest study region (highest mean temperature, lowest precipitation and lowest aridity index) has the highest proportion of C4 species, indicating that regional climate affects the proportion of C4 plants.

Among climatic parameters, temperature is strongly positively correlated with C4 species richness and biomass (Sage et al. 1999). Bremond et al. (2012) showed that mean annual temperature is the best predictor of C4 grass proportion in Neotropical Andes. The same result has been reported to explain the distribution of C4 species in Europe (Collins & Jones 1985). In the more recent work, Pyankov et al. (2010) indicated that the total abundance of C4 species in Europe is positively correlated with aridity. Furthermore, they showed that different groups of C4 species respond differently in respect to temperature and precipitation; e.g. the abundance of total C4 monocots were correlated with temperature whereas C4 dicots with precipitation. Even grasses of different biochemical subtypes of C4 photosynthesis (NAD-ME, NADP-ME or PCK) may have different distribution patterns (Ehleringer et al. 1997), whereby NAD-ME C4 grasses dominate drier regions. Duffy & Chown (2016) correlated the relative abundance of C4 species with the urban warming and showed that local increased temperature in cities of Europe favors C4 species.

Competitive advantage of C4 plants and their higher diversification in warm, dry and open environments was shown in previous studies (Long 1999; Bouchenak-Khelladi et al. 2014). However, the current distribution of C4 plants in warm and dry climates is not only due to the evolution of the photosynthetic type but could be the heritage of their C3 ancestors and subfamilies (Taub 2000; Edwards & Still 2008). It has been shown that the distribution of C3 and C4 grasses in Hawaii is linked with the distribution pattern of Pooideae (only C3 species) and the more thermophilous PACMAD lineage (both C3 and C4 species) and it is not only due to photosynthetic pathway as the latter lineage preferred warmer climates (Edwards & Still 2008). Nevertheless, they suggest that the C4 pathway may fix the ecological role of C4 plants as warm climate specialist. These findings emphasize that considering C4 plants as one group, without taking into consideration their phylogeny and functional variation (e.g. monocots vs. dicots, C4 subtypes, etc.) may lead to misinterpretation of the observed patterns.

Conclusion

Mediterranean, Hyrcanian and Irano-Turanian sand ecosystems with high summer temperature, intensive light, nutrient poor soils and dry condition are suitable places for inhabiting C4 plants. Physiological and morphological advantages of C4 plants lead to C4 plant dominance in mobile dunes, saltmarshes and disturbed sandy grounds. We found that C4 plants are more prominent in dry regions and that the regional climate may affect the proportion of C4 plants. The contribution of C4 species to total vegetation cover is shown to be important in ecological studies of C4 distribution as the number of species alone may not fully explain the role of C4 plants in a given area. We suggest including other plant traits in addition to the photosynthetic pathway. Joint ecological, physiological and evolutionary approaches will be fruitful for a comprehensive understanding of C4 plants.

Acknowledgment

We would like to thank the Reinhold-und-Johanna-Tüxen-Stiftung for funding the field work in Iran for P.M. Special thanks to Dr. Inga Schmiedel for her help for producing the map of the study area.

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Chapter 5

Synthesis

Key findings and implications

Sand dunes as assemblages of functional groups

Using the functional trait approach for studying sand ecosystems revealed that this ecosystem can be defined by sets of functional groups despite their regional climatic and species pool differences. Functional groups (species with similar sets of traits) obtained by cluster analysis of the species-trait matrix gave comparable results when performed for separate climatic regions. Such repeatable patterns are crucial for global-scale application (Gitay and Noble 1997). Thus our results further support the feasibility of functional group concept across regions (Wright et al. 2004; Sasaki et al. 2011) and add a step towards generalization in biogeography and ecology. Examining functional traits instead of individual species or their composition allows the combination of the three regional datasets in one matrix. Three regions are so different in terms of species composition that it is not possible to analyze them in a meaningful way as one dataset based on the species. This is the advantage of using functional traits to study areas with no species in common.

Classification of species based on their traits, reduced the total number of species from 309 to 7 main functional groups. We found that cluster analysis is a simple but an effective method for defining functional groups. Based on our results, adaptive strategies of plants in sand dune are revealed in three groups of perennial: FG1 Non-graminoid perennials; FG2 Shrubs; FG3 Graminoid perennials; and four groups of annuals: FG4 Annual ruderals; FG5 Insect-pollinated (entomophilous) annuals; FG6 Annual (non-ruderal) grasses; FG7 Annual succulents.

Specifically, we found that plant traits in sand ecosystems are grouped reflecting habitat affiliation rather than regional belonging. Ordination analysis of the trait composition of plots shows that functional traits of the same habitat assembled together irrespective of their regions. Therefore, habitats can be described by sets of traits and functional groups reflecting the adaptive strategy of plants to the environmental conditions of that habitat. Community weighted trait means revealed the dominant traits in each sand dune habitats. For instance, insect-pollinated species with dense indumentum and thick storage stems/roots were found chiefly in stabilized dunes. In terms of functional group, ordination analysis indicated that for example perennial grasses (subgroup of FG3) and entomophilous annuals (FG5) were more associated with mobile dunes.

Observed patterns of traits and functional groups were similar across three regions and even between littoral and inland dunes. It reveals the filtering effect of habitats and supports the hypothesis that functional groups are more shaped by niche characteristic than by biogeographic regions (Cornwell et al. 2006; Lebrija-Trejos et al. 2010; Maire et al. 2012). Salinity and dryness were considered as main factors in shaping the trait assemblages and habitat characteristic.

Is habitat similarity reflected in vegetation similarity across regions?

Habitat similarity of sand ecosystems across four climatic regions was investigated in chapter 3 to find out to what extent sand habitats are azonal with respect to taxonomic (species and genera), syntaxonomic and functional similarity.

The concept of azonality in a broader sense, refers to habitats where environmental conditions have prevailing influence on composition and structure of the vegetation over macroclimate (Mucina et al. 2006). We found by changing the focus from species to community and to functional level, sand habitats of same kind represent more similarity across regions. At the same time different sand habitats of one region have no or low similarity at all levels. It indicates that by going beyond species to the functional aspect of habitat, the vegetation becomes more independent from the regional climate and biogeography. On the other hand, the vegetation is azonal at the functional level. The lowest degree of azonality was observed at taxonomic level. Both at species and at genus level, very low similarity was found within a habitat across regions as well as across habitats within a region. It indicates that floristic composition of sand habitats highly depends on the biogeographical region.

Salt marshes and drift lines show in particular a high degree of azonality at syntaxonomic level. It is explained by particular high salinity (at least temporarily) and high disturbance rates in case of drift lines. The narrow ecological niche acts as environmental filter and thus only few tolerant species with specific adaptation to the habitat can occur and shape the communities (Gallego-Fernández & Martínez 2011; Bermúdez & Retuerto 2013). This explains considerable syntaxon similarities between regions as well as very low species richness recorded for these habitats, e.g. 4-6 species per plot in salt marshes. In contrast, mobile and stabilized dunes of different regions have less degree of stress and very few syntaxa in common. Therefore, the more stress-prone a habitat, the more is its vegetation habitat-related and the less dependent on the biogeographic region.

The highest similarity among habitats of the same kind but of different regions was observed at functional level. In this context, all habitats including mobile and stabilized dunes form azonal vegetation as they are independent from the climatic region. Mobile dunes of different regions are very different in plant communities and species composition; however, they show similar functional composition and physiognomy across regions and share highest proportions of graminoid perennials (FG3). They are characterized mainly by rhizomatous clonal grasses with CS/CSR strategy, pollinated and dispersed by wind. Plant communities on stabilized dunes, similarly, show common adaptation to dry conditions and thus consist of comparable functional groups across regions.

Functional aspects of the vegetation can be applied to compare plant communities across different regions. They are useful to understand and describe plant communities as they are reflecting habitat and ecosystem conditions. The functional approach adds a new aspect to classical phytosociology in defining high-rank syntaxa in addition to species composition and diagnostic species. Trait characters together with morphological characters of vegetation can be used to describe plant communities. We applied functional traits for defining vicariant syntaxa in sand dune habitats and to discuss their syntaxonomic position communities. For example, plant communities of *Kalidietea foliaty* and *Salicornietea fruticosae* dominated by species of similar function (FG2) and have very similar ecological needs and trait characteristics as response to similar environmental stress even though they are geographically distinct. These two ecological counterparts might even be combined into a single class.

Despite of the large area of sand deserts and coastal sands in Iran and Greece, the Phytosociological knowledge for both countries is still far from sufficient. Thus, field surveys and vegetation classification are of particular interest. Sand dune plant communities were defined and assigned to the high-rank syntaxa. Synoptic tables and the detailed syntaxonomic overview of the vegetation are provided.

Sand dunes as a habitat for C4 plants

By studying functional traits in sand dunes (chapter 2) we found that C4 photosynthetic type is represented in three functional groups including shrubs, graminoid perennials and annual succulents. Plant communities dominated by C4 plant communities were surveyed in the field. We looked at distribution of C4 plants in sand habitats of different regions are discussed (chapter 4). Improved ecological knowledge on C4 plants may be useful for understanding the global distribution pattern of C4 species. The key findings are described in the following sections.

Considerable contribution of C4 plants to vegetation cover C4 plants have notable presence in sand habitats in terms of vegetation cover despite of quite low contribution to the richness in comparison to C3 species. It indicates that environmental conditions (at least in some sand habitats) favor C4 plants, which then form dominant vegetation. Intensive light, high summer temperature and dryness are features of sand ecosystems which make C4 photosynthesis more efficient than the C3 pathway. According to crossover temperature hypothesis, at a given pCO_2 and the temperature of ca. 22° C, C3 and C4 plants have equal quantum yield of carbon fixation. C4 plants have higher quantum yield of carbon fixation at temperatures above 30° C in contrast to C3 plants which are more efficient at low temperatures (below 22° C) (Ehleringer 1978; Ehleringer et al. 1997). Therefore, C4 plants in hot conditions are competitive and may dominate the area. In this respect, sand dunes of Mediterranean, Irano-Turanian and Hyrcanian regions are of particular interest as the average temperature in summer is above the crossover temperature. High vegetation cover of C4 plants can be explained by improved water and nitrogen use efficiency of C4 plants which may increase biomass allocation (Ehleringer & Monson 1993, Long 1999).

Salt marshes, mobile dunes and disturbed sandy sites as preferred habitats of C4 plants We found notable presence of C4 plants in terms of vegetation cover in mobile dunes (N and C Iran), saltmarshes (C Iran) and disturbed sandy ground (NE Greece), despite of their low number of species. There is a general trend for C4 plants to occur in hot, arid, saline and disturbed habitats (Ehleringer & Monson 1993). Nitrogen and water use efficiency of C4 plants is well reflected in dry shifting dunes of C Iran, where dominated by diverse C4 plant communities of shrubs and grasses. Salinity stress which is also associated with drought adaptation, may have promoted the evolution of C4 halophytes (Sage 2005; Kadereit et al. 2012). Plants in disturbed habitats grow rapidly and have short life histories to withstand unfavorable conditions. In this context, the nitrogen use efficiency of C4 plants and the potential of high biomass production is an advantage in disturbed habitats.

We found that C4 abundance differed in the same habitat of different regions and common distribution patterns among habitats were not observed. Different habitat preference of C4 plants across regions may be partly due to climatic differences between regions and partly due to variation in C4 groups including different biochemical subtypes, anatomical types, monocots vs. dicots and different lineages of C4 plants. These variations are reflected in ecophysiological response to regional environmental conditions and could affect the habitat preference of different groups. For example, biomass allocation is greater in NADP-ME subtype of C4 grasses than in other subtypes and C3 species (Taylor et al. 2010); NAD-ME C4 grasses dominate drier regions (Ehleringer et al. 1997) and the total abundance of C4 monocots is correlated with temperature whereas C4 dicots with precipitation (Pyankov et al. 2010).

Higher presence of C4 plants in arid regions We observed a general increasing trend in richness and cover of C4 species with increase of aridity. The highest proportion of C4 species occurred in C Iran, the driest and warmest study region. Our result is inconsistent with effect of aridity on total abundance of C4 species in Europe (Pyankov et al. 2010).

Competitive advantage of C4 plants and their higher diversification in warm, dry and open environments was shown in previous studies (Long 1999) (Bouchenak-Khelladi et al. 2014). However, the current distribution of C4 plants in warm and dry climates is not only due to the evolution of the photosynthetic pathway but could be the heritage of their C3 ancestors and subfamilies (Taub 2000; Edwards & Still 2008). Considering the fact that C4 plants have evolved many times independently (Christin et al. 2013; Sage 2016), it is difficult to estimate the influence of phylogenetic bias on C4 plant distribution.

General conclusions

In conclusion, the results of this thesis show that the functional trait approach provides the possibility to generalize the ecosystem which is useful for the investigation of ecosystem properties, dynamics and functions. In this study, we objectively approached classification of functional traits through multivariate analysis. We have defined sets of functional groups applicable in different biogeographic regions with different floristic composition. We proved sand ecosystems of different regions have similar functional groups and thus sand habitats may respond in a same way to environmental drivers and disturbances. This similarity may allow a transfer of ecological findings and principles among sand ecosystems. Restoration, management and conservation actions developed in one region may thus be comprehensively applied.

As already mentioned in the key findings, results of the first two studies pointed out that functional affiliation of sand species is shaped by habitat characteristic rather than climatic regions. In the first study, sand habitats were defined as group of species with similar traits and described as sets of traits similar in one habitat. The second study compared the functional composition of the plant communities across regions. Both studies revealed that functional groups are rather independent from the regional climate and biogeography and more influenced by niche conditions. In contrast, floristic composition of sand habitats highly depends on the biogeographical region.

Sand dune habitats show a variable degree of azonality considering taxonomic, syntaxonomic and functional aspect of vegetation. The highest habitat similarity was observed at functional level, for which in this framework, all habitats are considered to belong to azonal vegetation. We found out at community level, the more stress-prone a habitat, the more is its vegetation habitat-related and independent from the region. However, species composition of habitats shows more region-related patterns. In this case, biogeographical distance prevails over environmental similarity.

The functional approach provides a new aspect to classical phytosociology as functional composition of the communities in addition to species composition can be applied to understand community ecology and to define high-rank syntaxa and vicariant communities. Description of communities based on functional traits extends the ecological aspect of the communities especially for across regions comparison in order to make syntaxonomic classification more applicable at global scale. We conclude that functional groups are an effective tool for comparison of ecosystem functions and processes and a good complementary method in classical phytosociology.

Functional trait classification also showed that in sand dune habitats assemblages of plants with C4 photosynthetic type are presented. Based on the results of the third study, salt marshes, mobile dunes and disturbed sandy grounds are specifically dominated by C4 vegetation and considered as preferred habitats of C4 plants. C4 plants have notable contribution to the vegetation cover in sand habitats despite of quite low contribution to the richness in comparison to C3 species. The patterns of C4 species distribution among habitats differed across regions. Phylogenetic bias and/or limited number of regions may be a reason for that. However, a generally increasing trend in richness and cover of C4 species with increased aridity was observed. C4 plants tend to be more tolerant in dry, saline sites under high temperature where water and nutrient availability are limiting factors for most C3 species.

Open questions, challenges and future perspectives

Even though in this study we showed that functional groups are an effective tool to compare ecosystems across regions with different species pool, however, the application of functional groups at global scale depends on standardized methods. This requirement has been considered in recent years and foundation works started. Nevertheless further reliable standardized attribute data need to be collected. Comprehensive trait databases for a large number of species are essential for future trait studies. Trait classification needs to be refined in order to achieve the finer assessment on response of functional groups to ecological changes. Another challenge will be to define more accurate groups which are representative of particular ecosystems, vegetation structures and plant biodiversity. Our study suggests that functional approaches are especially appropriate for ecosystems with extreme environmental conditions and distinct vegetation zonation.

There are further aspects in sand ecosystems which can be explored using functional trait approaches. They could partly be answered with the database of this thesis by further analysis and partly need a new study design and method. One analysis could reveal the influence of environmental conditions on functional groups; another could model habitat response to ecological changes when habitats are considered as units of functional groups. Open questions are for instance: 1) How do functional groups respond to environmental stress such as salinity and dryness? 2) How are environmental variables (e.g. temperature, precipitation, soil pH) correlated with functional groups across different regions? 3) Which factors influence the functional diversity of sand habitats? Are they affected by climatic condition? Do they show different pattern across different regions?

The second important aspect will be to implement the functional traits and groups in conservation and management. In this context, the degree of human impact and the effect of disturbing factors on target functional groups of endangered habitats could be evaluated, to identify conservation priorities and suitable management actions. This aspect is of particular importance considering that sand dunes and salt marshes are among the most endangered and sensitive ecosystems worldwide.

Another approach is the exploration of C4 plant ecology and distribution patterns. Some questions were not fully answered in our study due to the limited number of study regions. For example, How do climatic parameters affect the distribution of C4 plants across regions? Do different subtypes of C4 plants (monocots and dicots) respond similarly to climatic conditions? Is current distribution of C4 pants in sand/saline habitats reflected in climatic conditions or habitat features? Which trait combination is used by C4 plants in disturbed habitats? To answer these questions, the study area needs to be extended to other biogeographic and climatic regions and phylogenetic analysis need to be combined with ecological analysis in order to capture the variation of C4 groups in response to environmental variables. It will help to better interpret and understand the notable contribution of C4 plants in sand vegetation which we observed in this study.

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Acknowledgements

I would like to particularly thank my supervisor Prof. Erwin Bergmeier for his helpful advises and support throughout this thesis and for giving me the opportunity to work at his department which positively influenced my scientific life. Furthermore, I would like to thank Prof. Christoph Leuschner as well as Prof. Hermann Behling, Prof. Thomas Friedl, Prof. Matthias Waltert and Prof. Holger Kreft for being part of my thesis committee and for taking the time to evaluate my work.

Sincere thanks to all my colleagues in the department of Vegetation and Phytodiversity Analysis for their help, support, discussions, their scientific and social company and all the nice times that we had together. Special thanks go to Florian Goedecke and Friedemann Goral for the nice team work experience during the monitoring project, botanical excursion and intensive fieldwork on Crete. I would like to thank Inga Schmiedel, Oliver Fried, Ricarda Pätsch and Nina Kirchhoff whom I could freely ask questions and for giving me warm responds.

I would like also to thank my parents ‘Parvaneh and Farhad’, my sister ‘Parisa’, my brother ‘Nariman’ and his family ‘Fatemeh and Raha’ as they are always there for me. Their unconditional love is a great support and gave me the strength on my way. With their help and encouragement I could finish this thesis.

Many thanks to my good friends Madina, Mandana, Rita, Waad, Roksana and Fatemeh for their company through the ups and downs of my life. Thank you for a nice feeling that you give me, when you are around. You are making my life more beautiful and colorful.

Thanks to the nature and amazing life of plants that inspired me since long.

Appendix

Appendix A The data sheet as used for the vegetation survey

Name(s): Date:

Relevé No.	Field No.
Loc.:	
Relevé area:	Distance to last relevé:
Lat.:	Alt.:
Long.:	Slope and aspect:
Total cov.(%):	Soil number and depth:
Shrub cov.(%):	Shrub height(m):
Herb cov.(%):	Herb height(cm):
Soil & substrate type:	
Community:	
Note:	

	Species		1
			2
			3
			4
			5
			6
			7
			8
			9
			10
			11
			12
			13
			14
			15
			16
			17
			18

Br.-Bl. cover-abundance scale:
r = <1 % [1, little plant]
+ = >1 % [1-5 small plants]
1 = <5 % [or over 50 small plants or 1-5 large plants]
2 = 5-25 %
3 = 25-50 %
4 = 50-75 %
5 = 75-100 %

Appendix B Alphabetical list of species for plant functional groups resulted from cluster analysis. Plants exceptional from the general plant character composition of the groups exist in small proportions.

FG1		
Non-graminoid perennials		
Mediterranean		**Irano-Turanian**
Achillea maritima	*Lactuca serriola*	*Alhagi maurorum*
Alkanna tinctoria	*Limonium gmelinii*	*Allium kotschyi*
Allium guttatum	*Lolium perenne*	*Artemisia sieberi*
Anchusa undulata	*Lomelosia argentea*	*Convolvulus chondrilloides*
Artemisia campestris	*Pancratium maritimum*	*Convolvulus dorycnium*
Artemisia santonicum	*Petrorhagia illyrica*	*Cressa cretica*
Asperula tenella	*Polygonum maritimum*	*Echinops sp.*
Astragalus sp.	*Sarcopoterium spinosum*	*Frankenia hirsuta*
Calystegia soldanella	*Scabiosa atropurpurea*	*Gymnarrhea micrantha*
Carduus sp.	*Scabiosa webbiana*	*Heliotropium arguzioides*
Centaurea diffusa	*Seseli tortuosum*	*Heliotropium dasycarpum*
Centaurea grisebachii	*Silene frivaldszkyana*	*Lactuca sp.*
Chondrilla juncea	*Silene otites*	*Peganum harmala*
Chrysopogon gryllus	*Silene supina*	*Prosopis farcta*
Cichorium intybus	*Stipa capensis*	*Schumannia karelinii*
Convolvulus arvensis	*Teucrium capitatum*	*Smirnovia turkestana*
Crithmum maritimum	*Thymbra capitata*	
Cynanchum acutum	*Thymus sibthorpii*	
Dianthus gracilis	*Trifolium physodes*	
Dianthus monadelphus	*Verbascum blattaria*	
Dittrichia graveolens	*Verbascum pinnatifidum*	
Dittrichia viscosa		
Dorycnium herbaceum	**Hyrcanian**	
Eryngium campestre	*Alhagi maurorum*	
Eryngium maritimum	*Allium subnotabile*	
Euphorbia paralias	*Argusia sibirica*	
Fumana procumbens	*Artemisia tschernieviana*	
Fumana scoparia	*Calystegia sepium*	
Glaucium flavum	*Chondrilla juncea*	
Goniolimon collinum	*Convolvulus cantabrica*	
Haplophyllum suaveolens	*Convolvulus persicus*	
Hypericum montbretii	*Cynanchum acutum*	
Hypericum olympicum	*Frankenia hirsuta*	
	Petrosimonia brachiata	

FG2	**FG3**	
Shrubs	**Graminoid perennials**	
Mediterranean	**Mediterranean**	**Hyrcanian**
Arthrocnemum macrostachyum	*Aeluropus littoralis*	*Calamagrostis epigejos*
Aster tripolium	*Agrostis stolonifera*	*Carex otrubae*
Atriplex portulacoides	*Ammophila arenaria*	*Carex sp.*
Ephedra distachya	*Bolboschoenus maritimus*	*Cynodon dactylon*
Halocnemum strobilaceum	*Bothriochloa ischaemum*	*Equisetum arvense*
Osyris alba	*Calamagrostis epigejos*	*Imperata cylindrica*
Sarcocornia fruticosa	*Carex acuta*	*Juncus acutus*
Sarcocornia perennis	*Carex divisa*	*Juncus heldreichianus*
Tamarix hampeana	*Carex extensa*	*Juncus inflexus*
Tamarix smyrnensis	*Cynodon dactylon*	*Juncus littoralis*
	Cyperus capitatus	*Paspalum distichum*
Hyrcanian	*Cyperus rotundus*	*Phragmites australis*
Ephedra procera	*Elytrigia elongata*	*Plantago lanceolata*
Lycium shawii	*Elytrigia bessarabica*	*Saccharum ravennae*
Punica granatum	*Elytrigia juncea*	*Saccharum spontaneum*
Rubus anatolicus	*Imperata cylindrica*	*Schoenus nigricans*
	Juncus acutus	*Scirpoides holoschoenus*
Irano-Turanian	*Juncus gerardii*	
Astragalus squarrosus	*Juncus heldreichianus*	**Irano-Turanian**
Calligonum crinitum	*Juncus littoralis*	*Aeluropus littoralis*
Calligonum polygonoides	*Juncus maritimus*	*Aeluropus lagopoides*
Ephedra strobilacea	*Leymus racemosus ssp. sabulosus*	*Centropodia forskalii*
Halothamnus subaphyllus	*Melica ciliata*	*Cynodon dactylon*
Haloxylon ammodendron	*Paspalum paspalodes*	*Cyperus eremicus*
Nitraria schoberi	*Phragmites australis*	*Juncus maritimus*
Seidlitzia rosmarinus	*Plantago lanceolata*	*Phragmites australis*
Suaeda fruticosa	*Puccinellia convoluta*	*Stipagrostis karelinii*
Tamarix hispida	*Puccinellia intermedia*	*Stipagrostis pennata*
Zygophyllum eichwaldii	*Saccharum ravennae*	*Stipagrostis plumosa*
	Scirpoides holoschoenus	
	Sorghum halepense	
	Sporobolus pungens	

FG4		**FG5**
Annual ruderals		**Entomophilous annuals**
Mediterranean		**Mediterranean**
Althaea sp.	*Vicia lutea*	*Alyssum strigosum*
Amaranthus albus	*Vicia villosa*	*Alyssum umbellatum*
Amaranthus retroflexus	*Xanthium spinosum*	*Anthemis tomentosa*
Anthoxanthum aristatum	*Xanthium strumarium*	*Blackstonia acuminata*
Avena sterilis		*Cakile maritima*
Bassia hirsuta	**Hyrcanian**	*Centaurium pulchellum*
Bituminaria bituminosa	*Anagallis arvensis*	*Centaurium spicatum*
Bupleurum tenuissimum	*Astragalus tribuloides*	*Daucus guttatus*
Cenchrus incertus	*Avena sp.*	*Erodium cicutarium*
Chenopodium album	*Bromus danthoniae*	*Erysimum calycinum*
Cistus creticus	*Medicago sativa*	*Euphorbia peplis*
Digitaria sanguinalis	*Phleum paniculatum*	*Filago gallica*
Echinochloa crus-galli	*Polypogon monspeliensis*	*Hedypnois rhagadioloides*
Eragrostis minor	*Tragus racemosus*	*Helianthemum salicifolium*
Galium verum	*Tribulus terrestris*	*Hordeum marinum*
Heliotropium europaeum	*Xanthium strumarium*	*Hypecoum procumbens*
Herniaria hirsuta		*Jasione heldreichii*
Hibiscus trionum	**Irano-Turanian**	*Linum trigynum*
Hordeum murinum subsp. glaucum	*Centaurea bruguierana*	*Lotus halophilus*
Hordeum murinum subsp. murinum	*Chrozophora tinctoria*	*Malcolmia nana*
Hypericum perforatum	*Glycyrrhiza glabra*	*Matthiola tricuspidata*
Juncus hybridus	*Haplophyllum sp.*	*Medicago disciformis*
Kochia laniflora	*Hyoscyamus sp.*	*Medicago littoralis*
Malva neglecta	*Polygonum luzuloides*	*Medicago marina*
Melilotus albus	*Polypogon monspeliensis*	*Medicago minima*
Melilotus indicus	*Sonchus oleraceus*	*Nigella arvensis*
Papaver dubium	*Tribulus terrestris*	*Oenothera laciniata*
Phleum exaratum		*Onobrychis caput-galli*
Polygonum albanicum		*Portulaca oleracea*
Polygonum arenarium		*Pseudorlaya pumila*
Polypogon monspeliensis		*Sideritis montana*
Secale sylvestre		*Silene conica*
Setaria verticillata		*Silene dichotoma*
Solanum nigrum		*Silene gallica*
Sonchus asper		*Silene grisebachii*
Sonchus oleraceus		*Spergularia bocconei*
Tribulus terrestris		*Spergularia maritima*
Trifolium tomentosum		*Spergularia rubra*
Urtica dioica		*Trifolium arvense*

FG5 continue	**FG6**	
Entomophilous annuals	**Annual grasses**	
Trifolium echinatum	**Mediterranean**	**Irano-Turanian**
Trifolium lappaceum	*Apera intermedia*	*Bromus scoparius var. villiglumis*
Tuberaria guttata	*Briza maxima*	
Xeranthemum inapertum	*Bromus diandrus*	*Bromus tectorum*
	Bromus intermedius	*Cornulaca aucheri*
Hyrcanian	*Bromus japonicus*	*Cutandia dichotoma*
Brassica tournefortii	*Bromus tectorum*	*Halimocnemis rarifolia*
Cakile maritima	*Corispermum nitidum*	*Kochia stellaris*
Centaurium pulchellum	*Corynephorus divaricatus*	*Salsola praecox*
Daucus guttatus	*Cynosurus elegans*	*Scabiosa olivieri*
Senecio sp.	*Dasypyrum villosum*	*Schismus barbatus*
Silene conica	*Lagurus ovatus*	*Tribulus longipetalus*
Sonchus asper	*Lolium rigidum ssp. rigidum*	
Spergularia bocconei	*Milium vernale*	
Spergularia diandra	*Mollugo cerviana*	**FG7**
	Parapholis filiformis	**Annual succulents**
Irano-Turanian	*Plantago arenaria*	**Mediterranean**
Acantholepis orientalis	*Plantago coronopus*	*Hainardia cylindrica*
Aphanopleura breviseta	*Plantago lagopus*	*Petrosimonia brachiata*
Camelina rumelica subsp. rumelica	*Polypogon maritimus*	*Salicornia procumbens*
Eremopyrum bonaepartis	*Trifolium angustifolium*	*Salsola tragus*
Erodium cicutarium	*Vulpia ciliata*	*Salsola soda*
Fortuynia bungei	*Vulpia fasciculata*	*Suaeda maritima*
Isatis minima		*Suaeda splendens*
Koelpinia linearis	**Hyrcanian**	
Lappula sp.	*Briza minor*	**Hyrcanian**
Launea acanthodes	*Bromus diandrus*	*Petrorhagia saxifraga*
Malcolmia africana	*Bromus racemosus*	*Salicornia iranica*
Matthiola chenopodiifolia	*Bromus tectorum*	*Salsola kali*
	Corynephorus divaricatus	*Suaeda crassifolia*
	Coryspermum sp.	
	Cutandia memphitica	**Irano-Turanian**
	Henrardia persica var. persica	*Salsola kali*
	Parapholis incurva	*Suaeda arcuata*
	Plantago psyllium	
	Trisetaria linearis	

Appendix C List of distinguished syntaxa in the study areas

Drift lines

Cakiletea maritimae **Tx. et Preising in Tx. ex Oberdorfer 1952**

- *Atriplicetalia littoralis* Sissingh in Westhoff et al. 1946
  - *Salsolo-Minuartion peploidis* Tx. in Br.-Bl. et Tx. 1952
    - *Cakiletum maritimae* Nordhagen 1940
  - *Atriplicion littoralis* Nordhagen 1940
    - *Atriplicetum littoralis* Feekes 1936
- *Thero-Atriplicetalia* Pignatti 1953
  - *Euphorbion peplidis* Tx. ex Oberd. 1952
    - *Salsolo kali-Cakiletum maritimae* Costa et Mansanet 1981 corr. Rivas-Martinez, Costa & Loidi 1992
- ?
  - ?
    - *Cakile maritima-Arguzia* sibirica comm.

Mobile dunes

Ammophiletea **Br.-Bl. et Tx. ex Westhoff et al. 1946**

- *Ammophiletalia* Br.-Bl. et Tüxen ex Westhoff et al. 1946
  - *Elymion arenarii* Christiansen 1927
    - *Elymo arenarii-Ammophiletum arenariae* Br.-Bl. et Dee Leeuw 1936
  - *Ammophilion* Br.-Bl. 1921
    - *Medicagini maritimae-Ammophiletum australis* Br.-Bl. 1921
  - *Elymion gigantei* Morariu 1957
    - *Elymetum sabulosi* Babalonas 1979

Artemisietea lerchianae **Golub 1994**

- *Artemisietalia tschernievianae* Golub 1994
  - Euphorbion seguierianae Golub 1994
    - *Artemisia tschernieviana* comm.

Stipagrostietea pennatae **Zohary 1963**

- *Stipagrostietalia pennatae* Asri 2003
  - *Stipagrostion pennatae* Asri 2003
    - *Centropodia forsskalii* comm.
    - *Stipagrostis karelinii* comm.
  - ?
    - *Cyperus eremicus* comm.

Stabilized dunes

Koelerio-Corynephoretea **Klika in Klika et Novák 1941**

- *Corynephoretalia canescentis* Klika 1934
  - *Corynephorion canescentis* Klika 1931
    - *Caricetum arenariae* Christiansen 1927
- *Thero-Airetalia* Rivas Goday 1964
  - *Thero-Airion* Tx. ex Oberdorfer 1957
    - *Airo -Festucetum* Sommer 1971

Helichryso-Crucianelletea maritimae **Géhu et al. in Sissingh 1974**

- *Crucianelletalia maritimae* Sissingh 1974

- *Crucianellion maritimae* Rivas Goday et Rivas-Mart. 1958
    - *Ephedro distachyae-Silenetum subconicae* Oberd. 1952
    - *Artemisietum campestris* Babalonas 1979

Artemisietea sieberi Zohary 1973

- *Artemisietalia sieberi* Zohary 1973
    - *Artemision sieberi* Asri 2003
        - *Artemisietum sieberi* Asri 2003
    - *Prosopidion farctae* Asri 2003
        - *Prosopidetum farctae* Asri 2003
    - *Ephedrion strobilaceae* Asri 2003
        - *Ephedretum strobilaceae* Asri 2003
    - ? *Stipagrostis plumosa* comm.

Haloxyletea ammodendri Asri 2003

- *Haloxyletalia ammodendri* Asri 2003
    - *Haloxylion ammodendri* Asri 2003
        - *Haloxyletum ammodendri* Zohary 1973
        - *Calligonum crinitum* comm.

Salt marshes

Thero-Salicornietea Tx. in Tx. et Oberd. 1958

- *Thero-Salicornietalia* Pignatti 1952
    - *Thero-Salicornion* Br.-Bl. 1933
        - *Salicornia procumbens* comm.
    - *Salicornion dolichostachyo-fragilis* Gehu et Rivas-Mart. in Gehu et Gehu-Franck 1984
        - *Salicornietum strictae* Christiansen ex Tx. 1974
    - *Salicornion ramomissimae* Tx. 1974
        - *Salicornietum ramosissimae* Christiansen 1955
        - *Suaedetum maritimae* (Conard 1935) Pignatti 1953
    - ? *Salicornia iranica* comm.

Saginetea maritimae Westhoff et al. 1962

- *Frankenietalia pulverulentae* Rivas-Mart. ex Castroviejo et Porta 1976
    - *Frankenion pulverulentae* Rivas-Mart. ex Castroviejo et Porta 1976
- ? ? *Hordeum marinum* comm.
- ? ? *Psylliostachys spicata* comm.
- ? ? *Frankenia hirsuta* comm.

Salicornietea fruticosae Br.-Bl. et Tx. ex A. Bolòs et O. de Bolòs in A. Bolòs 1950

- *Salicornietalia fruticosae* Br.-Bl. 1933
    - *Salicornion fruticosae* Br.-Bl. 1933
        - *Halimionetum portulacoidis* Kuhnholtz-Lordat 1927
        - *Statico bellidifoliae-Salicornietum fruticosae* Br.-Bl. 1933
        - *Sarcocornio perennis-Puccinellietum convolutae* J.C. Costa in Costa et al. 1997
    - *Arthrocnemion glauci* Rivas-Mart. et Costa 1984
        - *Arthrocnemum macrostachyum* comm.
        - *Arthrocnemo glauci-Halocnemetum strobilacei* Oberdorfer 1952

Kalidietea foliati Mirkin et al. ex Rukhlenko 2012

- *Kalidietalia foliati* Golub et al. 2001
    - *Kalidion caspici* Golub et al. 2001
        - *Halocnemum strobilaceum* comm.
        - *Alhagietum pseudalhagi* Asri 2003
        - *Halostachys belangeriana* comm.
        - *Petrosimonia brachiata* comm.
    - *Seidlitzion rosmarini* Asri 2003
        - *Seidlitzietum rosmarini* Asri 2003

Aeluropodetea littoralis **Golub et al. 2001**

- *Aeluropodetalia littoralis* Golub et al. 2001
    - *Aeluropodion littoralis* Asri 2003
        - *Aeluropodetum littoralis* Asri 2003

Juncetea maritimi **Br.-Bl. in Br.-Bl. et al. 1952**

- *Puccinellio maritimae-Salicornietalia* Br.-Bl. et De Leeuw 1936
    - *Armerion maritimae* Br.-Bl. et De Leeuw 1936
        - *Juncetum gerardii* Christiansen 1927
    - *Festucion maritimae* Christiansen 1927
        - *Limonietum vulgaris* Christiansen 1927
    - ?
        - *Tripolium pannonicum-Salicornia iranica* comm.
- *Juncetalia maritimi* Br.-Bl. ex Horvatić 1934
    - *Juncion maritimi* Br.-Bl. ex Horvatić 1934
        - *Juncus maritimus* comm.

Phragmito-Magnocaricetea **Klika in Klika et Novák 1941**

- *Scirpetalia maritimi* Hejný in Holub et al. 1967
    - Scirpion maritimi Dahl et Hadač 1941
        - *Scirpetum maritimi* van Langendonck 1931

Festuco-Puccinellietea **Soó ex Vicherek 1973**

- Puccinellietalia Soó 1947
    - Puccinellion convolutae Micevski 1965
        - *Aeluropus littoralis* comm.

Unclassified plant communities: *Ephedra procera* comm., *Tamarix hispida* comm.

List of Publications

Mahdavi, P. & Bergmeier, E. Distribution of C4 plants in sand dune habitats of different region. *Folia Geobotanica.* Accepted.

Mahdavi, P., Isermann M. & Bergmeier, E. 2017. Sand habitats across biogeographical regions at species, community and functional level. *Phytocoenologia*. *Phytocoenologia*, 47: 139-165.

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Eigenständigkeitserklärung

Hiermit bestätige ich die vorliegende Dissertationsschrift eigenständig verfasst und keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet zu haben.

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Ort, Datum, Unterschrift