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Classification and distribution patterns of plant communities on Socotra Island, Yemen

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Nomenclature
Miller & Morris (2004)

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Abstract

Question: What are the main plant communities and vegetation zones on Socotra Island in relation to climatic, geological and topographic factors?

Location: Socotra Island (Yemen).

Methods: A total of 318 relevés were sampled along an altitudinal gradient. Floristic and environmental (topographic, geological and climatic) data were collected and analysed using numerical classification and NDMS ordination; an analysis of the correlation between plant communities and environmental factors was also performed.

Results: Eight types of woody vegetation, seven of shrubs, six of herbaceous and seven of halophytic vegetation were identified. Ordination revealed the importance of altitudinal and climatic gradients, as well as of geological substrata.

Conclusions: Four vegetation zones were identified. The first three are located in the arid region with altitude ranging from 0 to 1000 m and the fourth in the semi-arid region from 1000 to 1500 m a.s.l. Specifically they are: (1) an arid coastal plain mainly located on an alluvial substratum between 0 and 200 m, characterized by shrubland and grassland communities; (2) a transition zone from 200 to 400 m, between the alluvial substratum and the upper limestone area; (3) an arid limestone zone between 400 and 1000 m, interspersed with hills and plateaus; and (4) a semi-arid upper zone of the Haghier Mountains from 1000 to 1500 m on a granitic substratum.

Introduction

The Socotra archipelago is located 380 km south of Ras Fartak on the Gulf of Aden, along the coast of Yemen, and 230 km east of Cape Guardafui in Somalia (Fig. 1). It stands on a broad undersea plateau, the Socotra Platform, and comprises Socotra Island, the smaller islets of Abd-al Kuri, Samha and Darsa and a few rocky outcrops. The Socotra archipelago is of continental origin and was joined to the Arabian plate in the region of present-day Dhofar and Al-Mahra, prior to the rifting of the Gulf of Aden, no <15 Myr (at most 35 Myr) ago (Richardson et al. 1995; Samuel et al. 1997). Its long geographical isolation is responsible for the high level of endemism: according to the inventory of Miller & Morris (2004) and Kilian & Hein (2006), Socotra archipelago hosts 837 species of vascular plants, of which 308 (37%) are endemic.

Rapid changes in land use and the effect of climate change are increasing the pressures on plant species, many of which are now threatened with extinction according to an assessment carried out by Miller & Morris (2004) based on the IUCN classification system and criteria (IUCN 2001, 2010).

The existing literature on the vegetation of Socotra is rather heterogeneous. The island received much attention from collectors at the end of the 19th and early 20th century, when several expeditions were made. Several studies increased scientific knowledge of the local flora (Balfour 1888; Forbes 1903; Vierhapper 1907), but they contained only general and synthetic descriptions of the vegetation without attempting to classify the plant communities and analyse their distribution pattern. Descriptions of vegetation can be found in the works of Engler (1910) and Von Wettstein (1906), while Pichi-Sermolli (1955) made a

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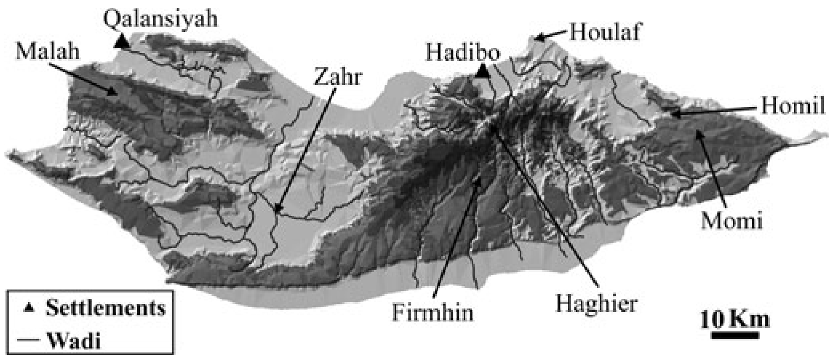

Fig. 1. Location of study area.

synthesis of all the information available regarding the vegetation of Socotra in a review of the plant ecology of arid and semi-arid zones of East Africa. More recently attempts have been made to describe the vegetation of Socotra Island both physiognomically (Popov 1957; Hemming 1966; Gwynne 1968; White 1983; Friis 1992; Mies & Zimmer 1993; Miller & Morris 2004; Kràl & Pavliš 2006) and phytosociologically (Knapp 1968; Mies 1999, 2001; Kürschner et al. 2006). These studies, however, are difficult to compare due to the different approaches and scales used. The present study is aimed at providing a first comprehensive phytosociological analysis of the plant communities and vegetation zones of Socotra Island and their relationships with environmental factors, including geological features and altitudinal and climatic gradients.

Methods

Study area

Socotra is characterized by an undulating plateau, with altitude ranging from 300 to 900 m a.s.l. This plateau is composed of thin strata of Cretaceous and Tertiary limestone overlying igneous and metamorphic basement (Socotra Platform), which is exposed in three areas (Beydoun & Bichan 1970). The most scenic of these are the peaks of the Haghier Mountains, which rise up to 1500 m, the summit of the island. On the coastal plains and in the inner depressions, Quaternary and recent deposits of marine, fluvial and continental origin overlie the older substrata. In these areas the decomposition of granites has led to the formation of rich, red and fertile soils (Popov 1957).

The island lies on the margin of the sub-equatorial and northern tropical climate belts. The local climate is influenced by large-scale weather phenomena characteristic of this area, particularly the seasonally reversing monsoon: the NE (winter) monsoon, which lasts from November to March, and the SW (Indian or summer) monsoon, which blows from May to September. The most reliable rains fall during the winter (November–January), while the summer monsoon winds are stormy and generally produce less rainfall. Mean annual rainfall and temperature are 216 mm and 28.9 °C, respectively, but the former varies across the island according to exposure and elevation: on the coastal plains the annual precipitation may be as little as 125 mm or even absent altogether (Scholte & De Geest 2010); while in the mountains it can reach exceptional levels of 1000 mm, of which preliminary measurements suggest that fog-derived moisture may constitute over two-thirds of the total (Scholte & De Geest 2010).

Data set

Phytosociological investigation was performed according to Westhoff & van der Maarel (1978) and Braun-Blanquet (1964). Data on the vegetation were obtained from relevés made between 2007 and 2009. In total, 318 relevés (including 417 vascular plant taxa) were obtained. At each site the relevés were selected in relation to the homogeneity of physical features, vegetation structure and species dominance. Plot sizes ranged from 200 m^2 to 4 m^2 (Table 4) depending on the plant community. Cover/abundance data for all vascular plants were recorded in the field using the Braun-Blanquet (1964) scale. A database was created in TURBOVEG (Hennekens & Schaminée 2001) and data were then exported as percentages for further analyses.

Environmental data included altitude, slope, climate and geological features. Climate data (annual precipitation and mean annual temperature) were interpolated from a network of ten meteorological stations using universal kriging, with a trend function defined on the basis of a set of covariates (altitude, slope, aspect and distance from the coast). This interpolation method produces reliable climatic and bioclimatic raster maps at a regional scale when complex topographical effects are present (Attorre et al. 2007b). In addition a moisture index was used (UNEP 1992), based on:

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$$MoI = P/ETp \tag{1}$$

where P is mean annual precipitation and ETp is potential evapotranspiration. ETp was calculated according to Jensen & Haise (1963).

$$ETp = (RS/2450) \times (0.025T + 0.08) \tag{2}$$

where RS is annual potential solar radiation (kJ) and T is mean annual temperature. MoI was used to classify Socotra into three climatic regions: hyper-arid, arid and semi-arid.

Geological data were obtained from Beydoun & Bichan (1970) and included four main types: volcanic rocks, limestone, alluvial sediments and sand deposits. Geological data were used as surrogate of soil data since a complete soil map of the island is still lacking.

Data analysis

The data collected were used to create a plots-vs-species matrix (using the percentage values of each species) for each main physiognomic form of vegetation: woodland, shrubland, grassland and halophytic vegetation.

A multivariate analysis was applied to these matrices using the program Syn-Tax v. 5.0. A hierarchical agglomerative clustering was used, with Euclidean distance as the similarity coefficient and complete linkage as the method for group formation. The data were log transformed (base 10) in order to reduce skewness and kurtosis (see e.g. Johnson & Wichern 2007). For each vegetation community identified, we calculated the total number of species, average species richness, total number and percentage of endemism, and average Shannon diversity index.

Diagnostic species of plant communities were determined using the fidelity coefficient of Tichý & Chytrý (2006). To avoid phi being dependent on the size of the target site group, group size was standardized to equal the average size of all groups present in the data set (Tichý & Chytrý 2006). The phi values vary independently of the concentration of species occurrence in the relevés of individual clusters. Statistical significance was obtained by a simultaneous calculation of Fisher's exact test in the JUICE program. Species with phi values higher than 0.35 and Fisher's exact test significance lower than 0.05 were deemed to be diagnostic.

To support results of the hierarchical classification and to analyse relationships between environmental factors and the distribution pattern of plant communities (except for halophytic and hygrophilous vegetation, which respond to smaller-scale gradients than those available in this study) non-metric multidimensional scaling (NMDS) analyses were performed using the vegan package of R statistical environment (R Foundation for Statistical Computing, Vienna, AT). The NMDS procedure was applied with default options that included use of the Bray–Curtis dissimilarity index and a maximum of 20 random starts in search of the stable solution. The Bray–Curtis dissimilarity for ordination, instead of the Euclidean distance, was used because we were interested in the compositional dissimilarity between the sites rather than in raw differences in abundance of one species or another. In addition, Wisconsin double standardization and square-root transformation, default options for large samples, were used. To evaluate the ordination, R^2 between fitted vectors and ordination values (R) was calculated using the stress-plot function of *vegan* together with the stress index. The fitted environmental vectors and centroids were overlaid using the *envfit* function. To further investigate relationships between the distribution pattern of vegetation communities and environmental variables, these variables were overlaid on the NMDS ordination using the *ordisurf* function. *Ordisurf* fits smooth surfaces on the ordination using generalized additive models (GAM) with thin plate splines (Wood 2000).

Results

The results are presented separately for each main physiognomic type of vegetation identified in the field. Moreover, a synoptic table (Appendix S1) was prepared in order to compare our vegetation classification with some of the most important previous studies (Pichi-Sermolli 1955; Popov 1957; Mies 1999, 2001; Miller & Morris 2004; Kràl & Pavliš 2006; Kürschner et al. 2006).

Woodlands and forests

Species composition and classification

The analysis of classification identified seven types of woodland (Table 1): *Sterculia africana* woodland (SaW), *Commiphora ornifolia* woodland (CoW), *Boswellia elongata* woodland (BeW), *Boswellia ameero* woodland (BaW), *Dracaena cinnabari* woodland (DcW), *Leucas hagghierensis–Pittosporum viridiflorum* woodland (LhPvW) and *Ficus cordata–Ziziphus spina-christi* woodland (FcZsW). An eighth woody vegetation type dominated by *Avicennia marina* and classified as forest (AvmarF) was identified in the field but excluded from the classification analysis because it is always represented by monospecific coenoses. The NMDS ordination (Appendix S2), which was performed without the azonal hygrophilous vegetation (represented only by the FcZsW, which can be found along wadis), confirmed the classification (r = 0.87, stress = 17.1), as the groups appear in specific areas of the scatter diagram together with their diagnostic species.

Table 1. Synoptic table showing percentages of diagnostic species occurrence (bold values) in the woody vegetation communities identified by cluster analysis. The diagnostic species have phi values > 0.50 and Fisher's exact test significance < 0.05 and are presented in descending order of indicator value. The full list of species, mean values of environmental variables and of cover vegetation layers are presented in Appendix S3.

Cluster No.	4(SaW)	16(CoW)	20(BeW)	19(BaW)	12(DcW)	7(LhPvW)	21(FcZsW)
No. of relevé	19	10	6	10	8	15	2
Sterculia africana	**84**	40	0	0	0	0	0
Cordia obovata	**47**	0	0	0	0	0	0
Eureiandra balfourii	**42**	0	0	10	0	0	0
Cissus subaphylla	**47**	20	0	0	0	0	0
Commiphora ornifolia woodland							
Trichocalyx obovatus	63	**100**	17	10	0	0	0
Commiphora ornifolia	53	**90**	17	20	0	0	0
Trichodesma microcalyx	5	**80**	0	0	38	27	0
Boswellia elongata woodland							
Boswellia elongata	21	20	**100**	0	0	0	0
Plantago amplexicaulis	11	10	**83**	0	0	0	0
Trachyspermum pimpinelloides	0	0	**67**	0	13	0	0
Lycium sokotranum	16	0	**67**	0	0	0	0
Anagallis arvensis	16	20	**83**	10	0	0	0
Boswellia ameero woodland							
Boswellia ameero	0	0	0	**80**	0	0	0
Acridocarpus socotranus	42	10	0	**90**	0	0	0
Rhus thyrsiflora	11	10	0	**100**	25	53	0
Ruellia insignis	0	10	0	**50**	0	0	0
Gnidia socotrana	16	30	0	**70**	0	0	0
Maerua angolensis	5	0	0	**40**	0	0	0
Anisotes diversifolius	5	0	0	**40**	0	0	0
Dracaena cinnabari woodland							
Apluda mutica	11	0	0	0	**63**	0	0
Cissus hamaderohensis	0	0	0	0	**50**	0	0
Dracaena cinnabari	0	10	0	30	**100**	80	0
Ballochia amoena	0	0	0	0	**38**	0	0
Asystasia gangetica	0	0	0	0	**38**	0	0
Kalanchoe farinacea	0	0	0	0	**38**	0	0
Leucas hagghierensis–Pittosporum viridiflorum woodland							
Leucas hagghierensis	0	0	0	0	13	**73**	0
Oplismenus compositus	0	0	0	10	13	**80**	0
Croton sulcifructus	11	0	0	10	0	**73**	0
Pittosporum viridiflorum	0	0	0	0	13	**67**	0
Dichondra repens	0	0	0	0	13	**60**	0
Coelocarpum haggierensis	0	0	0	0	13	**60**	0
Asplenium schweinfurthii	0	0	0	0	0	**47**	0
Pteris quadriaurita	0	0	0	0	0	**40**	0
Sideroxylon discolor	0	0	0	0	0	**33**	0
Asplenium aethiopicum	0	0	0	0	0	**33**	0
Pteridium aquilinum	0	0	0	0	25	**53**	0
Ficus cordata–Ziziphus spina-christi woodland							
Ficus cordata	0	0	0	0	0	0	**100**
Pergularia tomentosa	0	0	0	0	0	0	**100**
Ziziphus spina-christi	5	10	0	0	0	0	**100**

Sterculia africana woodland (SaW)

This woodland is widespread in the central–west part of Socotra, at altitudes between 100 and 500 m, on slopes facing the sea or inside wadis protected from the strong summer monsoon. Diagnostic species are *Sterculia africana*, *Cordia obovata*, *Eureiandra balfourii* and *Cissus subaphylla*; constant species are *Jatropha unicostata*, *Commiphora socotrana*, *Ballochia amoena* and *Adenium obesum* (Photo S1).

Commiphora ornifolia woodland (CoW)

This type replaces SaW in some areas at higher altitude (250–550 m). Diagnostic species are *Commiphora ornifolia*,

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Trichocalyx obovatus and *Trichodesma microcalyx*; constant species are *Ipomea sinensis*, *Cryptolepis volubilis*, *Zygocarpum coeruleum*, *Diodia aulacosperma* and *Carphalea obovata.* Floristically and ecologically CoW and SaW are very similar, as can be seen from the NMDS ordination diagram (Appendix S2): they develop in hot, dry, low-lying areas, generally on alluvial substrates (Photo S2).

Boswellia elongata woodland (BeW)

Boswellia elongata woodland is found on the limestone plateau between 300 and 450 m, on stony (35%) soils. It is an open formation and the herbaceous layer has high values of cover because of the fertility and high water retention of the karst soils. It lacks typical nemoral herbaceous species and has many diagnostic species in common with the *Panicum atrosanguineum* grassland: *Plantago amplexicaulis, Trachyspermum pimpinelloides, Lycium sokotranum* and *Anagallis arvensis.* It is difficult to tell if this woodland is a natural formation that has been degraded by overgrazing or if is a remnant of former plantations for gum production, since *Boswellia elongata*, among the seven endemic frankincense species of Socotra, is the species producing the most valuable incense (Attorre et al. 2011). The degradation and/or the anthropogenic origin of these formations are also evident in the scarcity of endemic species (32%) (Photo S3).

Boswellia ameero woodland (BaW)

This formation replaces the *Commiphora ornifolia* woodland at about 600 m. It is a closed formation, sometime classifiable as forest, with a dense shrub layer, growing mainly on granite. Diagnostic species are *Boswellia ameero*, *Acridocarpus socotranus, Rhus thyrsiflora, Ruellia insignis, Gnidia socotrana, Maerua angolensis* and *Anisotes diversifolius.* Constant species are *Adiantum balfourii, Rhus thyrsiflora, Ageratum conyzoides* and *Commiphora socotrana*. In February this woodland is recognizable from a long distance, thanks to the showy red blooms of *Boswellia ameero*. The high number of endemic species (58%) is also of note, including the rare, white-flowered *Dirachma socotrana*, the only member of the regional (restricted to Somalia and Socotra) subendemic Dirachmaceae family (Photo S5).

Dracaena cinnabari woodland (DcW)

Dracaena cinnabari woodland is located on limestone between 300 and 750 m on thin and dry soils with a large quantity of protruding rocks (48%) and stones (37%). Generally, it is an open formation with a reduced herbaceous layer, however at least in one area (Firmhin) it can be classified as forest due to higher canopy closure. Diagnostic species are *Apluda mutica, Cissus hamaderohensis, Dracaena cinnabari, Ballochia amoena, Asystasia gangetica* and *Kalanchöe farinacea*. This woodland represents the largest and most impressive formation on the island, dominated by *Dracaena cinnabari*, one of the Socotra's flagship species (Photo S4).

Leucas hagghierensis-Pittosporum viridiflorum woodland (LhPvW)

This woodland is located in the highest parts of the island (1300–1520 m) in the granitic summit area of the Central Haghier. It is a scattered closed formation with a very dense shrub layer, and develops on deep soils with few protruding rocks. Diagnostic species are *Leucas hagghierensis, Oplismenus compositus, Croton sulcifructus, Pittosporum viridiflorum, Dichondra repens, Coelocarpum haggierensis, Sideroxylon discolor* and several ferns, such as *Asplenium schweinfurthii, Pteris quadriaurita, Asplenium aethiopicum* and *Pteridium aquilinum.* The numerous ferns are an indicator of the high humidity of these areas. In fact, the highest mountains are frequently covered with clouds and mist, and dew is common. Constant species are *Dracaena cinnabari*, *Euclea divinorum* and *Rhus thyrsiflora.* Where pressure from grazing is higher, overgrazing indicators such as *Achyranthes aspera, Bidens chinensis, Oxalis corniculata, Urtica urens* become more abundant, and the woodland tends to be replaced by shrublands dominated by *Coelocarpum haggierensis* and *Hypericum scopulorum* (Photo S6).

Ficus cordata–Ziziphus spina-christi woodland (FcZsW)

This formation is the only azonal woodland identified on the island. It develops mainly in the basal area along open wadis on large flood plains on a substrate of coarse sediment. This hygrophilous formation is very rare on the island; in fact, in general, only scattered individuals of *Ficus* and *Ziziphus* can be found. The woodland has a closed canopy with a very poor herbaceous layer. The diagnostic species are the dominant trees *Ficus cordata* and *Ziziphus spina-christi* and the herbaceous species *Pergularia tomentosa*. It has the lowest number of endemic species (26%), richness (average: 10) and diversity (Shannon index: 1.2) (Photo S7).

Avicennia marina forest (AvmarF)

Today, due to heavy timber harvesting for building, making tools and as a source of charcoal, only two large monospecific stands of *Avicennia marina* are left in the western part of the island. They can be found behind the dunes, parallel to the coastline, in muddy and salty depressions (Photo S8).

Gradient analysis

The axes of the NMDS analysis explain 87% of the variation in the data set (s-stress: 17.71). Axis 1 (Fig. 2a) separates woody communities along a climatic (r MOI = 0.78; r PRE = 0.87; r TEM = 0.84) and topographic (r ALT = 0.89) gradient. In particular LhPvW (cluster 7), SaW (4) and CoW (16) overlap with these factors. Axis 2 is correlated to geological substrata (r Granite = 0.23; r Limestone = 0.22) and to solar radiation and potential evapotranspiration (r RAD = 0.62; r EPT = 0.2); BaW (cluster 19) overlaps with granitic substrata and DcW with high solar radiation.

Shrubland

Species composition and classification

The cluster analysis identified seven shrubland communities (Table 2): *Croton socotranus* shrubland (CsocS), *Pulicaria stephanocarpa* dwarf shrubland (PsDS), *Jatropha unicostata–Adenium obesum* shrubland (JuAoS), *Croton sarcocarpus* shrubland (CsarS), *Buxanthus pedicellatus* shrubland (BpS), *Trichodesma scottii–Cephalocroton socotranus* shrubland (TsCsS) and *Coelocarpum haggierensis–Hypericum scopulorum* shrubland (ChHsS). The NMDS ordination (Appendix S4) resulted in a clear differentiation of only five groups, as CsocS proved to be very similar to PsDS, and TsCsS to ChHsS; however, differences that justify their division into separate groups are presented below.

Croton socotranus shrubland (CsocS)

This is the most common type of vegetation in the dry basal areas. It develops from the coast up to an altitude of 500 m on stony sedimentary soils. The only diagnostic species is the endemic and dominant shrub *Croton socotranus*; frequent species are the herbaceous *Corchorus erodioides*, *Aristida adscensionis* and *Indigofera nephrocarpa*. Physiognomically it is sometimes characterized by other nanophanerophytes such as *Cissus subaphylla*, *Trichocalyx obovatus*, *Ballochia amoena* and *Carphalea obovata*. Hemicryptophytes and therophytes are rare in the understorey during the dry season, but can become rapidly abundant after rain. In this period, several grasses, including *Aristida adscensionis*, *Cenchrus pennisetiformis* and *Eragrostis ciliaris*, and herbs or subshrubs, such as *Indigofera nephrocarpa*, *Crotalaria leptocarpa* and *Indigofera pseudointricata*, appear. This community has a low level of plant species richness (average: 17) and endemics (39%), probably due to the fact that, being located in the basal alluvial plains, it is strongly affected by human activities such as grazing and timber harvesting. The frequent presence of species such as *Tephrosia apollinea*, *Aerva javanica* and *Aizoon canariense* is a clear indicator of overgrazing (Photo S9).

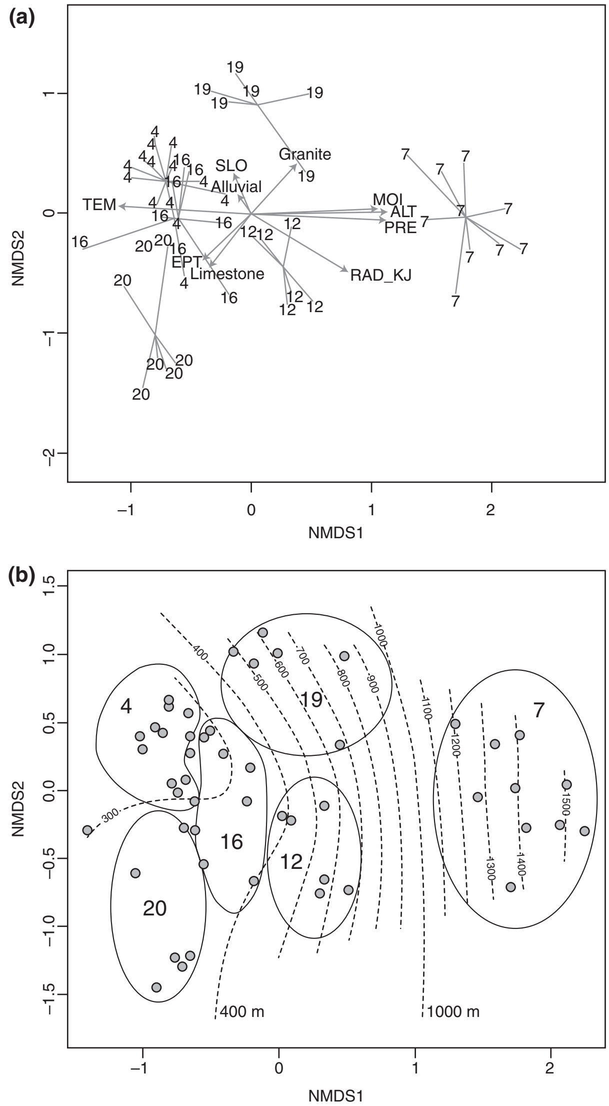

Fig. 2. (**a**) NMDS ordination of woody vegetation relevés, with environmental factors indicated with arrows. TEM is mean annual temperature, EPT potential evapotranspiration, SLO slope, RAD solar radiation, MOI moisture index, PRE annual precipitation, ALT altitude and granite, limestone and alluvial are geological substrata of the island. The arrows point to the direction of most rapid change in the environmental variable. (**b**) ordination diagram of relevés overlapped by the altitudinal contour lines. In both (a) and (b) diagrams the numbers represent clusters resulting from the classification analysis: 4 is *Sterculia africana* woodland, 16 *Commiphora ornipholia* woodland, 20 *Boswellia elongata* woodland, 19 *Boswellia ameero* woodland, 12 *Dracaena cinnabari* woodland, 7 *Leucas hagghierensis–Pittosporum viridiflorum* woodland.

Pulicaria stephanocarpa dwarf shrubland (PsDS)

This community develops in coastal areas and can be considered a degraded form of CsocS, caused by overgrazing and excessive timber harvesting, which have an impact especially on the shrub layer. PsDS is dominated by several

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Table 2. Synoptic table showing percentages of diagnostic species occurrence (bold values) in the shrub communities identified by cluster analysis. The diagnostic species have phi values > 0.50 and Fisher's exact test significance < 0.05 and are presented in descending order of indicator value. The full list of species, mean values of environmental variables and of cover vegetation layers are presented Appendix S5.

Cluster No.	14(CsocS)	5(PsDS)	8(JuAoS)	15(CsarS)	18(BpS)	2(TsCsS)	17(ChHsS)
No. of relevé	53	4	15	21	12	5	7
Croton socotranus shrubland							
Croton socotranus	**100**	50	33	0	25	0	0
Pulicaria stephanocarpa dwarf shrubland							
Pulicaria stephanocarpa	32	**100**	20	0	0	0	0
Indigofera cordifolia	2	**100**	0	5	0	0	0
Cleome brachycarpa	23	**100**	40	5	8	0	0
Jatropha unicostata–Adenium obesum shrubland							
Cissus subaphylla	55	0	**73**	0	0	0	0
Senna holosericea	38	25	**67**	5	0	0	0
Jatropha unicostata	77	50	**100**	33	33	0	0
Tephrosia apollinea	40	75	**80**	0	0	0	0
Placopoda virgata	4	25	**47**	5	0	0	0
Adenium obesum	21	50	**60**	0	17	0	0
Trichocalyx orbiculatus	9	0	**33**	5	0	0	0
Croton sarcocarpus shrubland							
Croton sarcocarpus	0	0	0	**67**	8	0	0
Cryptolepis volubilis	4	0	0	**71**	42	0	0
Hibiscus diriffan	0	0	0	**19**	0	0	0
Heteropogon contortus	2	0	7	**71**	42	60	14
Allophylus rubifolius	2	0	0	**57**	25	40	14
Buxanthus pedicellatus shrubland							
Buxanthus pedicellatus	2	0	0	38	**100**	0	0
Ballochia atro-virgata	0	0	0	0	**50**	0	0
Leucas virgata	2	0	0	0	**50**	0	0
Cissus hamaderohensis	8	0	0	33	**75**	0	0
Trichocalyx obovatus	32	0	0	24	**75**	0	0
Solanum incanum	0	0	13	5	**50**	0	0
Trichodesma scottii–Cephalocroton socotranus shrubland							
Trichodesma scottii	0	0	0	0	0	**71**	0
Croton sulcifructus	0	0	0	0	0	**83**	43
Cephalocotron socotranus	0	0	0	19	0	**79**	14
Sideroxylon discolor	0	0	0	0	0	**57**	0
Oplismenus compositus	0	0	0	0	0	**100**	14
Coelocarpum haggierensis–Hypericum scopulorum shrubland							
Coelocarpum haggierensis	0	0	0	0	0	20	**86**
Lotus ononopsis	0	0	0	0	0	20	**86**
Eragrostis papposa	0	0	0	0	0	0	**57**
Launaea socotrana	0	0	0	5	0	0	**71**
Micromeria remota	0	0	0	5	8	0	**71**
Pteridium aquilinum	0	0	0	0	0	20	**57**
Hypericum scopulorum	0	0	0	5	0	100	**100**
Oldenlandia balfourii	0	0	0	10	8	80	**86**

dwarf shrub species, such as *Pulicaria stephanocarpa*, *Indigofera cordifolia* and *Justicia rigida*, the latter being locally abundant where the soil becomes less sandy and more silty. It is the shrubland community with the lowest number of endemic species (34%) (Photo S10).

While the NMDS ordination analysis does not differentiate between CsS and PsDS (Appendix S4), we have chosen to keep them separate according to results of the classification due to their different physiognomy and because it is important to identify them separately for rangeland management purposes.

Jatropha unicostata–Adenium obesum shrubland (JuAoS)

This formation seems to replace the *Croton socotranus* shrubland on escarpments bordering the basal plains, on more rocky substrata and generally at higher altitude. It has many diagnostic species in common with this community: *Cissus subaphylla*, *Senna holosericea*, *Jatropha unicostata*, *Tephrosia apollinea*, *Trichocalyx orbiculatus* and *Adenium obesum*. For this reason, Kürschner et al. (2006) considered the division between these two communities, suggested previously by Mies (1999), to be largely unjustified. Conversely, our analysis seems to confirm this separation, as also highlighted by the NMDS ordination (Appendix S4) (Photo S11).

Croton sarcocarpus shrubland (CsarS)

This community is typical of the limestone plateau at an altitude between 300 and 1000 m, and it is found on thin and rocky soil. In the absence of disturbances (grazing and timber harvesting), it would probably evolve towards DcW, with which it shares floristic composition and ecological characteristics. The abundance of species such as *Ageratum conyzoides, Achyranthes aspera* and *Tragia balfouriana* is an indicator of overgrazing. Diagnostic species are the dominant shrub *Croton sarcocarpus*, other nanophanerophytes such as *Cryptolepis volubilis*, *Hibiscus diriffan*, *Allophylus rubifolius* and the grass *Heteropogon contortus*. Species found in higher mountain areas characterized by a granitic substratum, such as *Rhus thyrsiflora*, *Euryops arabicus* and *Adiantum balfourii*, are also common in this shrubland, which is characterized by a high number of endemics (50%) (Photo S12).

Buxanthus pedicellatus shrubland (BpS)

This vegetation is widespread in sub-mountain areas (400–800 m) on limestone slopes with a high level of bare rock. It can also be found at lower altitudes, but only along wadis with a high level of humidity, as required by many characteristic species: *Commelina albescens*, *Anagallis arvensis* and *Panicum atrosanguineum*. Diagnostic species are mainly shrubs such as *Buxanthus pedicellatus* (dominant), *Ballochia atro-virgata*, *Leucas virgata*, *Cissus hamaderohensis, Trichocalyx obovatus* and *Solanum incanum* (Photo S13).

Trichodesma scottii–Cephalocroton socotranus shrubland (TsCsS)

This is located in the Haghier Mountains at an average altitude of just above 1000 m, immediately below ChHsS. It has already been described by Kürschner et al. (2006) as a woodland of the mountain belt (*Trichodesmo scottii–Cephalocrotonetum socotrani* woodland). However, we have chosen to include this community among the shrublands because of the very low cover of tree species such as *Dracaena cinnabari, Pittosporum viridoflorum, Euphorbia socotrana, Euclea divinorum* and *Vernonia cockburniana*. Diagnostic species are the dominant shrubs *Cephalocroton socotranus* and *Croton sulcifructus*, other shrubs such as *Trichodesma scottii, Sideroxylon discolor* and the herb *Oplismenus composites*; common species are *Dichondra repens*, *Helichrysum paulayanum*, *Oxalis corniculata* and *Hypoestes pubescens* (Photo S14).

Coelocarpum haggierensis–Hypericum scopulorum shrubland (ChHsS)

This is the highest elevation shrubland on the island (900–1450 m, with an average altitude of 1338 m), and it has already been described by Kürschner et al. (2006) as the *Hypericum scopulorum* community. It is a very closed formation that develops on gentle slopes or small plateaus with a deep soil and a high level of precipitation. It substitutes for the *Leucas hagghierensis–Pittosporum viridiflorum* woodland when grazing and timber cutting and collection hamper the development of tree cover. Diagnostic species are the shrubs *Coelocarpum hagghierensis* and *Hypericum scopulorum* (which dominates) and the herbs *Lotus onopsis*, *Eragrostis papposa*, *Launea socotrana*, *Micromeria remota, Oldenlandia balfourii* and *Pteridium aquilinum*. It is the community with the highest percentage of endemics (54%) (Photo S15).

Gradient analysis

The NMDS ordination analysis explains 88% of the variation in the data set (s-stress: 17.46). Axis 1 follows a climatic (r MOI = 0.88, r PRE = 0.87, r TEM = 0.84) and topographic (r ALT = 0.84) gradient, where temperature and evapotranspiration increase while rainfall, humidity and altitude decrease (Fig. 3a). The high mountain communities (ChHsS, TsCsS), the hilly shrubland of CsarS and BpS and the lowland communities of CsocS, PsDS and JuS can be identified along this gradient from left to right. Axis 2 mainly represents a geological gradient (r Granite = 0.49, r Limestone = 0.34, r Alluvial = 0.2). This axis shows a clear separation of shrub communities growing on a granitic substratum (ChHsS and TsCsS) and those growing on limestone (CsarS and BpS) and alluvial (CsocS, PsDS and JuAoS) substratum.

Grasslands

Species composition and classification

The cluster analysis (Table 3) identified six main types of herbaceous vegetation: *Aristida adscensionis–Tephrosia apollinea* grassland (AaTaG), *Dactyloctenium robecchii* grassland (DrG), *Panicum atrosanguineum* grassland (PaG), *Heteropogon contortus–Chrysopogon serrulatus* grassland (HcCsG), *Eragrostis papposa–Arthraxon micans* grassland (EpAmG) and *Juncus socotranus* marshland (JsM). The NMDS

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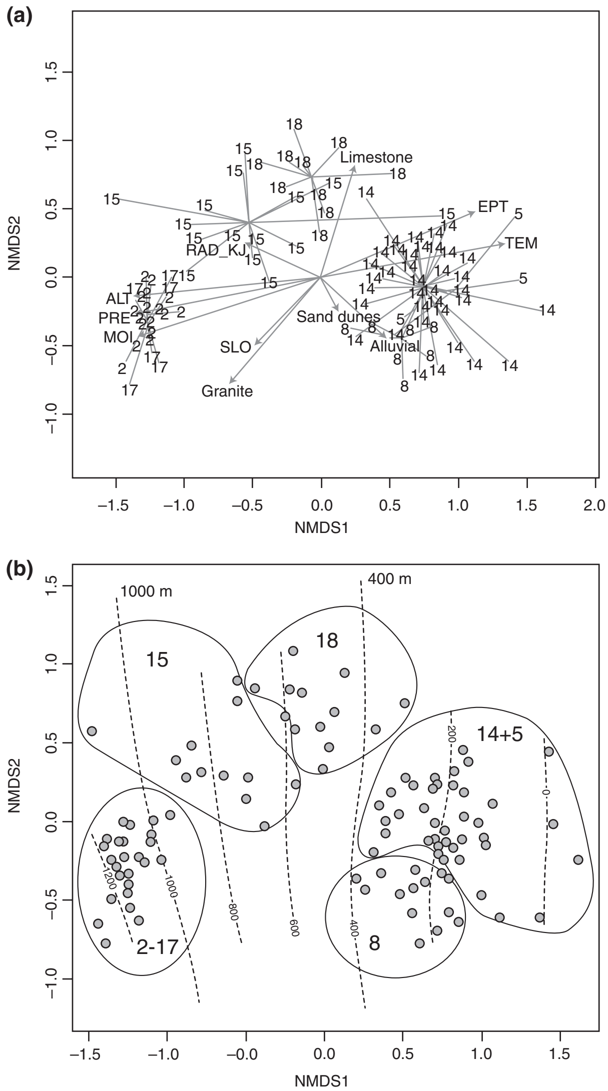

Fig. 3. (**a**) NMDS ordination of shrub vegetation relevés, with the environmental factors indicated with arrows. TEM is mean annual temperature, EPT potential evapotranspiration, SLO slope, RAD solar radiation, MOI moisture index, PRE annual precipitation, ALT altitude and granite, limestone, alluvial and sand are geological substrata of the island. The arrows point to the direction of most rapid change in the environmental variable. (**b**) ordination diagram of relevés overlapped by the altitudinal contour lines. In both (a) and (b) diagrams the numbers represent the clusters resulting from the classification analysis: 14 is *Croton socotranus* shrubland, 5 *Pulicaria stephanocarpa* dwarf shrubland, 8 *Jatropha unicostata–Adenium obesum* shrubland, 18 *Buxanthus pedicellatus* shrubland, 14 *Croton sarcocarpus* shrubland, 2 *Trichodesma scottii–Cephalocroton socotranus* shrubland, 17 *Coelocarpum haggierensis–Hypericum scopulorum* shrubland.

ordination analysis, from which the azonal JsM marshland was excluded, confirms the identification of five different groups (Appendix S6). JsM should be discussed in a separate section, but being the only freshwater community, we preferred it to be included here due to the structural similarity.

Aristida adscensionis–Tephrosia apollinea grassland (AaTaG)

This is the most common grassland on the coastal plains, as is the case under similar environmental conditions in northern Africa and on the Arabian Peninsula (Kilian & Hein 2006). Due to high grazing pressure, it is dominated by *Tephrosia apollinea*, which is an indicator of overgrazing and disturbance. Other diagnostic species are *Aristida adscensionis* and *Melanocenchris jaquemontii*; good fodder species such as *Indigofera nephrocarpa, Crotalaria leptocarpa* and *Cenchrus pennisetiformis* are also very frequent (Photo S16).

Dactyloctenium robecchii grassland (DrG)

This particular type of grassland was found in small, scattered patches only on the Zahr plain, a very dry, sandy and salty plain located at the centre of the island at an altitude of 100 m, and formed by Pleistocene fluvial and continental deposits. In periods of drought it represents an important source of food for livestock, and inside the almost monospecific *Dactyloctenium* tussock several other diagnostic species can be found: *Euphorbia schimperi, Eragrostis lepida, E. minor, Cissus subaphylla, Pulicaria stephanocarpa, Trachyspermum pimpinelloides, Cleome brachycarpa* and *Indigofera pseudointricata* (Photo S17).

Panicum atrosanguineum grassland (PaG)

This community is typical of the hilly and low-mountain limestone areas (400–600 m), and develops on karst plateaus on deep soils with high water retention capacity. The best examples can be found in the Momi and Malah plateaus, respectively located in the western and eastern part of the island. This grassland type is one of the most important pastures of the island and a nodal point of the transhumance system. Diagnostic species are *Asphodelus fistulosus, Commelina forskalaei, Panicum atrosanguineum* and *Helichrysum gracilipes*. In this community, *Panicum atrosanguineum* is the most frequent species, while *Asphodelus fistulosus* is becoming more abundant due to overgrazing (Photo S18).

Heteropogon contortus–Chrysopogon serrulatus grassland (HcCsG)

This is the grassland of lower parts of the granitic mountain belt (average altitude 900 m). It represents a transition form between the *Panicum atrosanguineum* grassland and the *Eragrostis papposa–Arthraxon micans* grassland and, with these, shares several frequent or diagnostic species: *Anagallis arvensis, Corchorus erodioides* and *Haya obovata* with the

Table 3. Synoptic table showing percentages of diagnostic species occurrence (bold values) in the grassland communities identified by cluster analysis. The diagnostic species have phi values > 0.50 and Fisher's exact test significance < 0.05 and are presented in descending order of indicator value. The full list of species, mean values of environmental variables and of cover vegetation layers are presented in Appendix S7.

Cluster No.	3(AaTaG)	13(DrG)	6(PaG)	11(HcCsG)	10(EpAmG)	8(JsM)
No. of relevé	6	4	9	13	10	4
Aristida adscensionis-Tephrosia apollinea grassland						
Tephrosia apollinea	**100**	0	0	0	0	0
Aristida adscensionis	**90**	22	10	15	0	0
Melanocenchris jacquemontii	**67**	0	0	0	0	0
Dactyloctenium robecchii grassland						
Dactyloctenium robecchii	0	**100**	0	0	0	0
Euphorbia schimperi	0	**75**	0	0	0	0
Eragrostis lepida	0	**75**	0	0	0	0
Cissus subaphylla	0	**75**	0	0	0	0
Pulicaria stephanocarpa	33	**100**	0	0	0	0
Eragrostis minor	17	**75**	0	0	10	0
Trachyspermum pimpinelloides	33	**75**	0	0	0	0
Cleome brachycarpa	50	**75**	0	0	0	0
Indigofera pseudointricata	17	**100**	0	8	0	0
Panicum atrosanguineum grassland						
Asphodelus fistulosus	0	0	**50**	0	0	0
Commelina forskalaei	0	0	**44**	0	0	0
Panicum atrosanguineum	17	0	**83**	18	22	0
Helichrysum gracilipes	0	0	**39**	31	31	0
Heteropogon contortus–Chrysopogon serrulatus grassland						
Oxalis corniculata	0	0	0	**31**	0	0
Chrysopogon serrulatus	0	0	11	**85**	5	0
Heteropogon contortus	0	0	11	**100**	40	0
Themeda triandra	0	5	0	**51**	0	0
Eragrostis papposa–Arthraxon micans grassland						
Eragrostis papposa	0	0	0	0	**90**	0
Arthraxon micans	0	0	0	46	**90**	0
Digitaria velutina	0	0	0	38	**80**	0
Helichrysum paulayanum	0	0	0	69	**90**	0
Oldenlandia balfourii	0	0	0	62	**90**	0
Setaria pumila	0	0	11	38	**80**	25
Romulea fischeri	0	0	0	8	**40**	0
Juncus socotranus marshland						
Juncus socotranus	0	0	11	0	0	**100**
Exacum affine	0	0	11	0	0	**50**

first mentioned and *Helichrysum paulayanum*, *Oldenlandia balfourii* and *Arthraxon micans* with the second. Diagnostic species of this community are *Oxalis corniculata, Chrysopogon serrulatus, Heteropogon contortus* and *Themeda triandra*. Among the grasslands, this community has the highest number of endemic species (36%) (Photo S19).

Eragrostis papposa–Arthraxon micans grassland (EpAmG)

This is the herbaceous community typical of the Haghier Mountains, where it grows on deep, fertile red soils formed from the erosion of hematized granite, which are normally found inside stone-walled enclosures or in woodland clearings. Diagnostic species are the grasses *Arthraxon micans, Digitaria velutina, Eragrostis papposa, Setaria pumila* (all important as fodder for livestock), *Helichrysum paulayanum*, *Oldenlandia balfourii* and *Romulea fisheri* (Photo S20).

Juncus socotranus marshland (JsM)

This formation is scattered along permanent streams and in flat areas with small springs, generally between 200 and 900 m. It is characterized by few species (average: eight) and a low level of endemism (total: five); diagnostic species are *Juncus socotranus* and *Exacum affin*e (Photo S21).

Gradient analysis

In the NMDS ordination analysis ($r = 0.88$, s-stress = 16.39), Axis 1 (Fig. 4a) reflects the variation in topography

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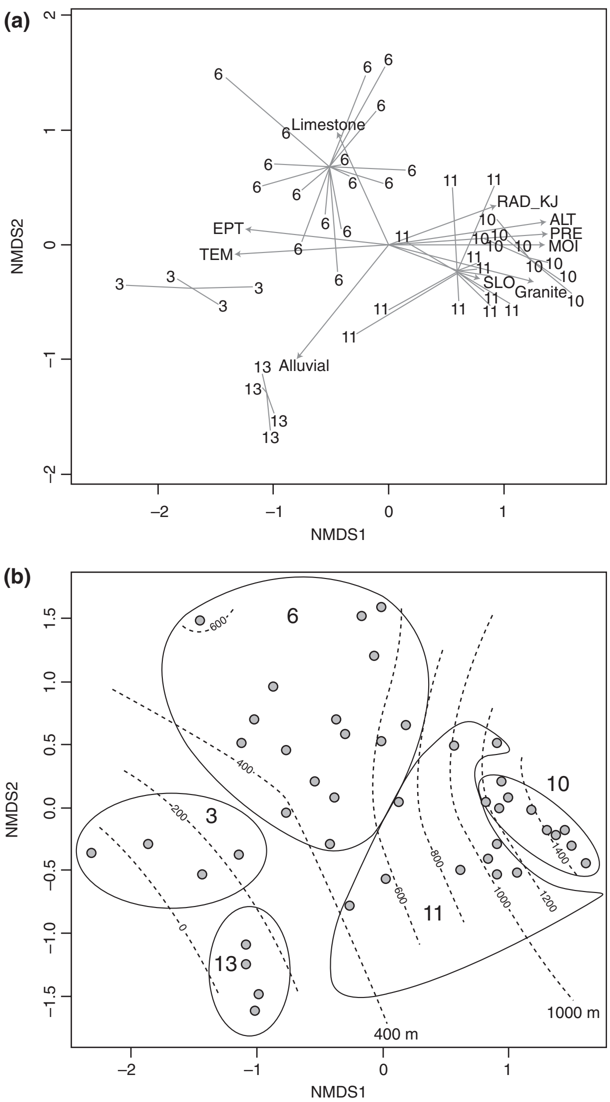

Fig. 4. (**a**) NMDS ordination of grass vegetation relevés, with the environmental factors indicated with arrows. TEM is mean annual temperature, EPT potential evapotranspiration, SLO slope, RAD solar radiation, MOI moisture index, PRE annual precipitation, ALT altitude and granite, limestone and alluvial are geological substrata of the island. The arrows point to the direction of most rapid change in the environmental variable. (**b**) ordination diagram of relevés overlapped by the altitudinal contour lines. In both (a) and (b) diagrams the numbers represent the clusters resulting from the classification analysis: 3 is *Aristida adscensionis –Tephrosia apollinea* grassland, 13 *Dactyloctenium robecchii* grassland, 6 *Panicum atrosanguineum* grassland, 11 *Heteropogon contortus–Chrysopogon serrulatus* grassland, 10 *Eragrostis papposa–Arthraxon micans* grassland.

(r ALT = 0.85), climate (r PRE = 0.86; r MOI = 0.82; r TEM = 0.84; r EPT = 0.68) and geology (r Granite = 0.76). This axis shows a gradient ranging from the dry AaTaG to the mountain communities of EpAmG and HcCsG that prevail on granitic substrata. Axis 2 identifies a geological gradient ranging from *Dactyloctenium* on an alluvial substratum, to PaG characteristic of a calcareous substratum.

Halophytic vegetation

The cluster analysis (Table 4) identified seven groups of halophytic vegetation: *Atriplex griffithii* community (AgC), *Urochondra setulosa* community (UsC), *Limonium sokotranum* community (LsC), *Arthrocnemum macrostachyum* community (ArmacC), *Acacia edgeworthii* community (AeC), *Tamarix nilotica* community (TnC) and *Limonium paulayanum* community (LpC).

Atriplex griffithii community (AgC)

This community is found only on the southwest coast of the island, where *Atriplex griffithii* is an important colonizer of the foredune and is often accompanied by *Cistanche phelipaea* (Orobanchaceae), an obligate root parasite that depends totally on its host for water, minerals and organic nutrients. In the more disturbed areas, other species from inland communities can be found, such as *Pulicaria stephanocarpa, Cissus subaphylla, Aizoon canariensis, Eragrostis minor, Tribulus terrestris, Launaea massauensis, Justicia rigida* and *Dactyloctenium hackelii* (Photo S22).

Urochondra setulosa community (UsC)

This perennial halophytic coenosis develops on the top of the foredune and in the first portion of the backdune on sandy soils. Diagnostic species are the perennial rhizomatous grass *Urochondra setulosa* (important in the stabilization of mobile dunes) and the succulents *Zygophyllum simplex* and *Z. qatarense* (Photo S23).

Limonium sokotranum community (LsC)

This community colonizes the backdune bordering perennial hyperhaline communities of *Arthrocnemum macrostachyum* or the *Avicennia marina* forest. The only diagnostic species is *Limonium sokotranum*, which is often accompanied by other typical dune species such as *Zygophyllum simplex* and *Z. qatarense* (Photo S24).

Arthrocnemum macrostachyum community (ArmacC)

This is one of the most widespread types of halophytic vegetation, being found all around the island. It colonizes the salt marshes of the backdune, which can remain flooded for long periods during the rainy monsoon season and form a salt crust during the dry season. The diagnostic species is *Arthrocnemum macrostachyum*, which is occasionally

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Table 4. Synoptic table showing percentages of diagnostic species occurrence (bold values) in the halophytic communities identified by cluster analysis. The diagnostic species have phi values > 0.50 and Fisher's exact test significance <0.05 and are presented in descending order of indicator value. The full list of species, mean values of environmental variables and of cover vegetation layers are presented in Appendix S8.

Cluster No.	1(AgH)	6(UsH)	2(LsH)	4(ArmaH)	3(AeH)	5(TnH)	7(LpH)
No. of relevé	5	6	11	3	4	5	6
Atriplex griffithii community							
Atriplex griffithii	**100**	0	0	0	0	20	0
Cistanche phelipaea	**40**	0	0	0	0	0	0
Urochondra setulosa community							
Urochondra setulosa	0	**100**	18	0	0	0	0
Zygophyllum simplex	40	**80**	55	0	0	20	40
Zygophyllum qatarense	40	**80**	45	33	0	20	40
Limonium sokotranum community							
Limonium sokotranum	0	40	**100**	67	0	0	0
Arthrocnemum macrostachyum community							
Arthrocnemum macrostachyum	0	0	9	**100**	0	0	0
Acacia edgeworthii community							
Acacia edgeworthii	0	0	0	0	**100**	0	0
Sporobolus spicatus	0	0	9	0	**75**	0	0
Oldenlandia pulvinata	0	0	9	0	**75**	0	0
Dactyloctenium aristatum	0	0	27	0	**75**	0	0
Tamarix nilotica community	0	0	0	0	0	0	0
Tamarix nilotica	0	0	9	0	0	**100**	20
Limonium paulayanum community							
Limonium paulayanum	0	0	0	0	0	20	**100**
Indigofera nephrocarpa	0	0	0	0	50	0	**60**
Trachyspermum pimpinelloides	0	0	9	0	0	0	**60**
Capparis cartilaginea	0	0	9	0	0	0	**40**
C orchorus erodioides	20	0	0	0	25	0	**60**

accompanied by other suffrutex species of the genera *Zygophyllum* and *Suaeda* (Photo S25).

Acacia edgeworthii community (AeC)

This community was found in only one location, along the northern coast. It is difficult to explain this limited distribution: Popov (1957) suggested that it might depend on the 'unexpected thickness of deposits of soft sands' above other coarser alluvial substrata present in the area. Probably it is not a strictly halophyte community, but we decided to include it in this section because of the distribution of *Acacia edgeworthii*, that grows only on sands close to the sea, and the presence of other typical species of these coenoses (*Sporobolus spicatus, Suaeda monoica*). Diagnostic species are *Acacia edgeworthii*, *Sporobolus spicatus, Oldenlandia pulvinata* and *Dactyloctenium aristatum*. The high frequency of *Tephrosia apollinea* and *Senna holosericea* is due to overgrazing (Photo S26).

Tamarix nilotica community (TnC)

Tamarisk formations are scattered along the coastal plain of the island on the salty, sandy soils of the highest dunes, which they help to stabilize, and at the mouth of several wadis. They host few species and *Tamarix nilotica* is the only diagnostic species (Photo S27).

Limonium paulayanum community (LpC)

This community is spread all along the coast on soils characterized by a mixture of sand and stones. *Limonium paulayanum* grows on soils with lower levels of salinity than those of *L. sokotranum*. It is often accompanied by non-halophytic species, such as *Indigofera nephrocarpa, Trachyspermum pimpinelloides, Capparis cartilaginea* and *Corchorus erodioides* (Photo S28).

Discussion

The results of the gradient analysis of the four main types of vegetation (woodlands, shrublands, grasslands and halophytic communities) were used for identification of the geo-altitudinal zonation.

For woodland vegetation, three main zones can be identified. In particular, *Leucas hagghierensis–Pittosporum viridiflorum* woodland can be found in the semi-arid region at the top of higher mountains, while all other communities

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are located in the arid region (Appendix S2). Inside this latter region, a further altitudinal gradient can be identified: *Boswellia ameero* and *Dracaena cinnabari* woodlands are located between 400–1100 m (Fig. 2b) and are differentiated by their respective substrata, the former being characterized by granite and the latter by limestone (Fig. 2a). Between 200 and 400 m, *Sterculia africana*, *Commiphora ornifolia* and *Boswellia elongata* woodlands can be found. Within this altitudinal range, they are differentiated by a geological gradient, ranging from an alluvial substratum to limestone.

Shrublands and grasslands showed three main vegetation zones, starting from the basal areas where woody vegetation is absent and only scattered trees can be found. In particular, the hot and dry basal alluvial plain from 0 to 400 m hosts xeric communities (Fig. 3b) of *Croton socotranus*, *Pulicaria stephanocarpa* and *Jatropha unicostata–Adenium obesum* shrublands and *Aristida adscensionis–Tephrosia apollinea* and *Dactyloctenium robecchii* grasslands (Fig. 4b). In the limestone hills and plateaux from 400 to 1000 m the shrublands of *Buxanthus pedicellatus* and *Croton sarcocarpus* and the herbaceous communities of *Panicum atrosanguineum* can be found. Above 1000 m the semi-arid mountain belt on a granitic substratum is characterized by the *Trichodesma scottii–Cephalocroton socotranus* and *Coelocarpum haggierensis–Hypericum scopulorum* shrublands and the *Heteropogon contortus–Chrysopogon serrulatus* and *Eragrostis papposa–Arthraxon micans* grasslands.

By integrating the results it is possible to identify four main vegetation zones (Fig. 5) and their main biogeographic, evolutionary, ecological and conservationist aspects are discussed below.

An arid coastal plain, mainly located on an alluvial substratum between 0 and 200 m

In this zone two different environments can be distinguished. Along the coastline, the series of distinctive and sharply zoned halophytic formations can be found. The nature of the zonation and species composition of these formations depends on several factors, e.g. soil salinity, waterholding capacity and available water in the soil, height above sea level and inundation by high tide, distance from the shore and texture deposits. Key species in these saline habitats are generally perennial. The predominant life forms are succulent semi-woody dwarf shrubs belonging to Chenopodiaceae, Zygophyllaceae and Plumbaginaceae, and hemicryptophytes of the Poaceae. Annual succulents, such as *Zygophyllum simplex*, are exceptions. Coastal species are either obligate halophytes, e.g. representatives of the Chenopodiaceae and Plumbaginaceae, or salt-tolerant genera from unspecialized families, such as *Urochondra* and *Sporobolus* (Poaceae), or salt-secreting species such as *Avicennia marina* (Verbenaceae). Due to the harsh and very limiting environmental conditions, these halophytic communities and their spatial sequence are very similar to those identified along coasts of the Arabian peninsula (Kürschner 1998) and Iran (Akhani & Ghorbanli 1993). In fact, from our field observations, it was possible to identify an ideal sequence of plant communities colonizing the dune system, from the foredune characterized by *Atriplex griffithii* and *Urochondra setulosa* communities, to the top and backdune with *Limonium sokotranum* community and the interior salt marshes with *Arthrocnemum macrostachyum* community and *Avicennia marina* forest. Today, these communities are scattered along the coast due to the interaction of several disturbance factors, e.g. wind, erosion and human activities, such as timber harvesting and grazing. In particular *Arthrocnemum macrostachyum, Limonium sokotranum* and *Urochondra setulosa* communities are heavily grazed because they are considered an important rangeland providing a healthy amount of salt to small livestock and camels (Miller & Morris 2004).

In the inner areas of the coastal plain, the vegetation is characterized by the dynamically linked *Croton socotranus* shrubland, *Pulicaria stephanocarpa* dwarf shrubland and *Aristida adscensionis–Tephrosia apollinea* and *Dactyloctenium robecchii* grasslands, according to the level of disturbance. Only scattered trees, mainly *Boswellia socotrana*, *Commiphora ornifolia, Euphorbia arbuscula* and *Dendrosycios socotrana*, can

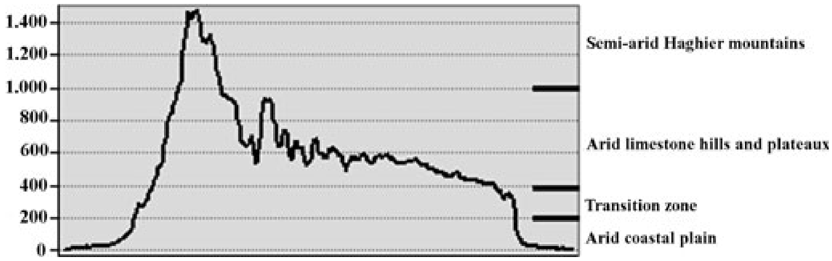

Fig. 5. North (left)–South (right) profile diagram of Socotra Island and the main vegetation zones. Profile diagram was drawn using the 'Profile tool' of ArcMap 9.3 (ESRI Inc., Redlands, CA, US).

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be found. The last species is one of the few tree species of the Cucurbitaceae family and is characterized by a noticeable swollen, succulent trunk capable of storing water to resist drought, and shares this adaptive strategy with *Adenium obesum*, which is more abundant in the next vegetation zone.

The *Croton socotranus* community is one of the most studied plant communities on Socotra and has been described in various ways (Appendix S1): 'Croton short grass community' (Popov 1957), 'subdesert shrub and grass' (Pichi-Sermolli 1955), 'grass steppe with shrubs and trees' (Gwynne 1968) or 'Somali-Masai semi-desert grassland and shrubland' (White 1983). Popov (1957) had already noted is uniqueness, in fact it is not found in surrounding regions of Africa and the Arabian peninsula. Conversely, the *Pulicaria stephanocarpa* dwarf shrubland resembles an association of xeromorphic dwarf shrubs characterized by *Pulicaria hadramautica* and *Zygophyllum amiense* described in Al-Gifri & Gabali (2002) for the Hadramaut coast of Yemen, and the herbaceous communities dominated by *Tephrosia apollinea,* an indicator of overgrazing, are quite frequent in northern Africa and the Arabian peninsula in ecologically comparable areas (Kürschner et al. 2006; Zahran 2010).

A transition zone from 200 to 400 m, between the alluvial substratum and the upper limestone area

In this zone, on the steeper escarpments, *Sterculia africana* and *Commiphora ornifolia* woodlands are dynamically linked to the *Jatropha unicostata–Adenium obesum* shrubland, while the flatter areas are characterized by *Boswellia elongata* woodland, *Croton socotranus* shrubland and *Aristida adscensionis–Tephrosia apollinea* grassland. These formations show the strong xero-tropical African influence on the flora of the low hills of Socotra, which belongs to the Somalia-Masai regional centre of endemism (including the Eritreo-Arabian province of the Sudanian region, *sensu* Zohary 1973), as proposed by Leonard (1989) in his phytogeographic subdivision of the Arabian peninsula. An example of this strong link was provided by Kürschner et al. (2006), who identified a woodland formation on the Arabian Peninsula that is physiognomically nearly identical and floristically closely related to *Sterculia africana* woodlands of Socotra and the African mainland. Here, as on Socotra, this woodland characterizes the lower mountain slopes of the Jabal Arays and other southern coastal mountains, and shows many closely-related, vicarious species belonging to corresponding genera particularly diverse in the centre of endemism, such as *Acacia, Adenium, Anisotes, Asparagus, Boswellia, Cissus, Commiphora, Euphorbia* and *Jatropha,* strong indicators of the common floristic history of the whole region.

An arid limestone zone from 400 to 1000 m, interspersed with hills and plateaus

Here, a sequence formed by *Dracaena cinnabari* woodland, *Croton sarcocarpus, Buxanthus pedicellatus* shrublands, *Panicum atrosanguineum* and *Heteropogon contortus–Chrysopogon serrulatus* grasslands can be identified. In particular, *Dracaena* woodland represents one of the most important and peculiar plant communities of the island, being likely remnants of the Mio-Pliocene Laurasian subtropical forests (Quézel 1978; Mies 1996). In the past, this unique ecosystem was present over large areas of the former Tethys, but in the Pliocene it was disrupted by climate change causing the desertification of North Africa. Today, *Dracaena cinnabari* represents together with another five *Dracaena* tree species (*D. serrulata, D. ombet, D. schizantha, D. draco* and *D. tamaranae*; see Marrero et al. 1998) a well-known example of the biogeographic disjunction between East and West Africa caused by this process.

According to Beyhl (1996), the above species share their typical dracoid growth form (characterized by a single stem with tips that successively ramify at the ends) with another 15 unrelated species. They are found in regions with a similar climate, such us the Canary Islands, Cape Verde Islands, Yemen, Oman and countries around the Mediterranean, which were also part of the Laurasian subtropical forest. It has been suggested (Beyhl 1996) that this growth form has evolved in arid environments with a high level of atmospheric humidity, such as the Socotra archipelago.

Dracaena woodland is today threatened: its population structure and the lack of regeneration due to grazing, especially by goats, have led several authors to hypothesize its future disappearance in the absence of appropriate management and conservation strategies (Adolt & Pavlis 2004; Habrova et al. 2009; Scholte & De Geest 2010). At present, regeneration is limited only to higher mountain areas (Attorre et al. 2007a), where the woodland vegetation has been classified in another group (see *Leucas hagghierensis–Pittosporum viridiflorum* woodland). In these areas, the availability of water, due to the precipitation regime and atmospheric humidity, and the steep escarpments, which are less accessible to livestock, allow seedlings and saplings of *Dracaena cinnabari* to become established.

The strong biogeographic link with East Africa is highlighted by the species composition of the dry grassland of this vegetation zone. The *Heteropogon contortus* and *Chrysopogon serrulatus* grassland has numerous species in common (e.g. *Arthraxon micans, Heteropogon contortus, Setaria pumila, Themeda triandra*) with the *Themedo–Hyparrhenietea*, which includes tall, perennial herbaceous communities

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widespread in southern and East Africa. In fact, the relatively late separation of Arabia from Africa and Asia, some 10–18 million years BP, allowed for the migration of plants between tropical Africa, southern Arabia and the Indo-Malayan region (Raven & Axelrod 1974; Mandaville 1984; White & Léonard 1991; Kürschner 1998). During the Miocene, when today's separate landmasses were still connected, Arabia supported palaeotropical vegetation with swamps and open savanna grassland (Hamilton et al. 1978; Whybrow & Mc Clure 1981; Mandaville 1984). During the late Tertiary, this vegetation was progressively replaced by more drought-adapted vegetation. Mesic elements of the palaeo-African and palaeo-Indo-Malayan stock could only survive in climatically favourable refugia (Lioubimtseva 1995; Kürschner 1998). These refugia in southern Arabia and Socotra Island developed during the late Tertiary and early Quaternary through a strong enhancement of the monsoon (Mandaville 1984; Jolly et al. 1998).

Within this vegetation zone, the *Boswellia ameero* woodland is noteworthy, which occupies a specialized environmental niche between 500 and 900 m on the granitic substratum. Together with the other six endemic *Boswellia* spp., *Boswellia ameero* is considered one of the most peculiar examples of adaptive radiation processes (Turelli et al. 2001), which gave the relatively small island the highest concentration of frankincense tree species in the world (Thulin & Al-Gifri 1998). In fact, *Boswellia* spp. of Socotra have been classified into two distinct growth forms (Mies et al. 2000; Miller & Morris 2004): the so-called cliff-rooted species (*B. bullata, B. dioscorides, B. nana, B. popoviana*) and the ground-rooted species (*B. ameero, B. elongata, B. socotrana*), and they rarely overlap, being segregated geographically or ecologically (Attorre et al. 2011).

The semi-arid upper zone of the Haghier Mountains on a granitic substratum

Here *Leucas hagghierensis–Pittosporum viridiflorum* woodland, two types of shrubland, *Trichodesma scottii–Cephalocroton socotranus* and *Coelocarpum haggierensis–Hypericum scopulorum*, and two of grassland, *Heteropogon contortus–Chrysopogon serrulatus* and *Eragrostis papposa–Arthraxon micans*, are found.

In this area, fog and mist brought by sea winds can more than double the moisture available for plants, as indicated by the presence of several ferns (Scholte & De Geest 2010). For this reason, the Haghier Mountains can be considered an island-like refugium of Afromontane vegetation, floristically and ecologically similar to those of northeast Africa (Kürschner 1998), from which they separated only recently, as described above. In particular, species such as *Euclea divinorum*, *Sideroxylon discolor* and other evergreen Afromontane vicariants of the genera *Croton*, *Hibiscus*, *Hypericum* and *Rhus* indicate the strong floristic, biogeographic and physiognomic relationships of this association to similar vegetation types of the Ethiopian and East African mountains (Pichi-Sermolli 1955; White 1983; Friis 1992).

Despite the unstable and changeable climate of the last 55 000 years, and the abrupt change over the last 6000 years, that characterized the island (Fleitmann et al. 2004; De Geest 2006), the Haghier Mountains showed relative climatic stability. This, in turn, also allowed a wet refugium for several endemic species (e.g. *Euclea divinorum, Dracaena cinnabari*, *Dirachma socotrana*), which have been hypothesized to have evolved through an anagenetic process, being the single representatives of families and genera (Banfield et al. 2011).

Due to the peculiar environmental characteristics, even in the future the Haghier Mountains may represent potential refugia for *Dracaena cinnabari* and many other endemic species threatened by increasing drought caused by climate change, and, for this reason, they are of special importance from a conservation point of view (Attorre et al. 2007a). Moreover, traditional land practices including rotational grazing inside stone-fenced areas (the 'zeribah' system) have allowed this plant community to survive, and the collapse of transhumance seems to favour the regeneration of this vegetation, especially in areas less accessible to livestock.

In conclusion, the vegetation of Socotra hosts an extraordinary heritage of endemic species that have originated from adaptive radiation processes within the archipelago, or phyletic evolution from Paleo-African, African-mesic and mesic-tropical Asian taxa. These species are now aggregated in plant communities displaced along a geo-altitudinal gradient. The identification of Socotra's main vegetation zones and the environmental factors that determine the distribution patterns of the plant communities represents important information for the development of conservation strategies and management actions in such an important biodiversity hotspot.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Comparison between current and previous descriptions of the vegetation of Socotra Island.

Appendix S2. NMDS ordination diagrams of woody vegetation: relevés–species (A) and relevés–isolines of moisture index (B).

Appendix S3. Synoptic table of the relevés of woodland vegetation.

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Appendix S4. NMDS ordination diagrams of shrubland vegetation: relevés–species (A) and relevés–isolines of moisture index (B).

Appendix S5. Synoptic table of the relevés of shrubland vegetation.

Appendix S6. NMDS ordination diagrams of grassland vegetation: relevés–species (A) and relevés–isolines of moisture index (B).

Appendix S7. Synoptic table of the relevés of grassland vegetation.

Appendix S8. Synoptic table of the relevés of halophytic vegetation.

Photo S1–S8. The main types of woodland community of Socotra Island.

Photo S9–S15. The main types of shrubland community of Socotra Island.

Photo S16–S21. The main types of grassland community of Socotra Island.

Photo S22–S28. The main types of halophytic community of Socotra Island.

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