*Biodiversity Journal*, 2012, 3 (4): 331-336

# Vascular flora evolution in the Soqotra Archipelago (Indian Ocean)

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**ABSTRACT** The main floristic and vegetational features of the Soqotra Archipelago are outlined. The theories of vicariance and dispersal are commented with the support of examples suggesting the idea that both are complementary in the establishment and evolution of the flora of Soqotra. Finally the relation of alien vs natural elements of the flora is analyzed.

**KEY WORDS** Biogeography; Soqotra; alien plants.

Received 11.05.2012; accepted 7.12.2012; printed 30.12.2012
Proceedings of the 1st International Congress "Insularity and Biodiversity", May 11th-13th, 2012 - Palermo (Italy)

## INTRODUCTION

The Soqotra Archipelago is placed in the northern part of the Indian Ocean between 12° 06'-12°42'N and 52°03'-54°32'E and consists of four islands. Soqotra, the main one, rises up to 1500 m a.s.l., 240 Km from the African Coast and more than 400 from the Arabian peninsula. It is of continental origin in fact it was joined to the Arabian plate not less than 15 myr ago. The stratigraphy is characterized by an igneous and metamorphic basement complex that crops out in the Haghier mountains and is overlaid by a plateau ranging from 300 to 900 m composed of Cretaceous and Tertiary limestone. On the coastal plains, quaternary and recent deposits of marine and fluvial origin overlie the older limestone (Beydou & Bichan, 1970).

The existing literature on the vegetation of Soqotra is rather heterogeneous. Recent attempts to classify the plant communities and analyse their distribution pattern can be found in Kràl & Pavliš (2006), Kürschner et al. (2006) and De Sanctis et al. (2012). The latter recognizes a geo-altitudinal gradient divided in four main vegetation belts: Semi-arid Haghier mountain from 1000 to 1550 m a.s.l., Arid limestone hills and plateaux from 400 to 1000 m a.s.l., a transition zone from 200 to 400 m a.sl. and the Arid coastal plain from the sea level to 200 m of altitude (Fig. 1). These host eight woody vegetation types, seven scrubland communities, six main herbaceous vegetation types and seven groups of halophytic vegetation concentrated in the arid coastal plain. Due to its high levels of biodiversity Soqotra has been designated a UNESCO World Heritage Site, UNESCO Man and Biosphere Reserve, WWF Global 200 Ecoregion and Plantlife International Centre of Plant Diversity.

## MATERIALS AND METHODS

This contribution is the result of personal observations made in the island during the 2007 expedition by the members of the Department of Botany of the University of Palermo, exchanges of views with Ahmed Adeeb, Ahmed Eissa Ali Afraar, Fahmi

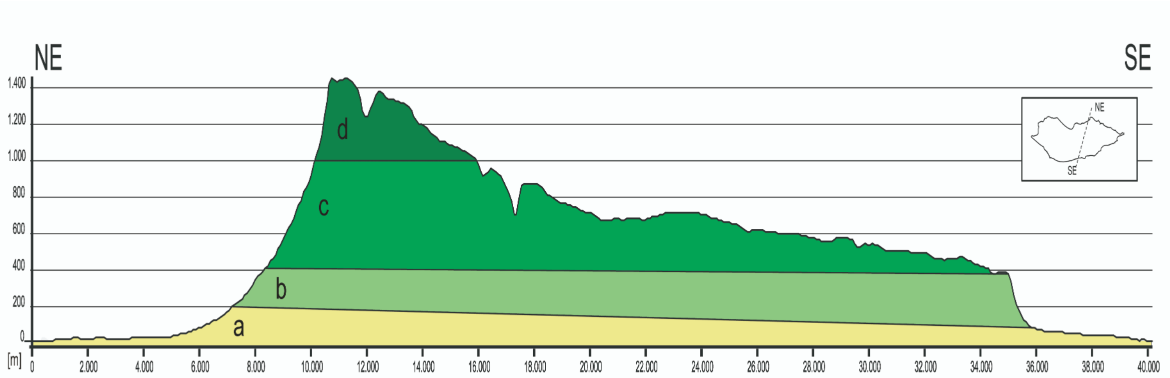


Figure 1. Section of the island of Soqotra along the dominant direction of the monsoon with the vegetation belts recognized by De Sanctis et al. (2012) (redrawn). a: Arid coastal plain; b: Transition zone; c: Arid limestone hills and plateaux; d: Semi-arid Haghier mountain.

Abdullah Mohamed Ba Ashwan from Soqotra and Lisa M. Banfield from Edinburgh hosted in 2009 and 2010 in the Botanical Garden of Palermo as far as from relevant literature.

## RESULTS AND DISCUSSION

The Soqotra Archipelago includes 837 vascular plants, 310 (37%) of which are endemic (Kilian & Hein, 2006; Domina & Raimondo, 2009; Raimondo & Domina, 2009). These species belong to 433 genera included in 114 families. The ferns consist of 30 species and there is a single gymnosperm (*Ephedra foliata* Boiss. ex C.A.Mey.). The family of Poaceae is the richest one (90 species), followed by Fabaceae (70) and Asteraceae, Euphorbiaceae, Apocynaceae, Acanthaceae and Rubiaceae with over 20 species each. Together these families total more than 40% of the flora (Miller & Morris, 2004). There are 15 endemic genera: 12 including only one species: *Angkalanthus* (Acanthaceae), *Nirarathamnos* and *Oreofraga* (Apiaceae), *Duvaliandra* and *Socotrella* (Asclepiadaceae) *Hemicrambe*, *Lachnocapsa* and *Nesocrambe* (Brassicaceae), *Haya* (Caryophyllaceae), *Dendrosicyos* (Cucurbitaceae) *Placopoda* and *Tamridaea* (Rubiaceae); two with 2 species each: *Trichocalyx* (Acanthaceae) (Fig. 2) and *Rughidia* (Apiaceae); one with 3 species: *Ballochia* (Acanthaceae).

Soqotra falls in an arid area that has experienced rainfall fluctuations over the last 150,000 years that caused widespread desertification in the region. The varied topography of the island and the moisture brought by ocean monsoons offered wet refugia for many plants that have otherwise been unable to survive to arid periods that affected the area (Miller & Morris, 2004). According to Takhtajan (1986) Soqotra belongs to the Eritreo-Arabian subregion which includes South Arabia, Somalia, Ethiopia, Kenya and Tanzania and is characterised by high levels of generic endemism (but not usually families unless mono-generic) and very high levels of species endemism. White (1983) includes the Soqotra Archipelago in the Somalai-Masai Regional Centre of Endemism and considers it as a local centre of endemism due to its exclusive endemics.

The flora of Soqotra Archipelago shows close relations with the floras of the neighbouring Southern Arabia and NE Africa. Soqotra and NE Somalia share a high number of near-endemics, e.g. *Dirachma soqotrana* Schweinf. ex Balf.f, *Caralluma soqotrana* (Balf.f.) N.E.Br. and *Erythroseris amabilis* (Balf.f.) N. Kilian & Gemeinholzer. Further biogeographic relations are with: NW Africa, Macaronesia, SW Africa, S Asia, Madagascar and N America.

The species of Soqotra shared with the Mediterranean are also spread in Tropical Africa, C and SW Asia e.g. *Dactyloctanium aegyptium* (L.) Willd., *Hyparrenia hirta* (L.) Stapf (Poaceae), *Juncus bufonius* L. (Juncaceae), *Silene apetala* Willd. (Caryophyllaceae), *Erodium cicutarum* (L.) (Geraniaceae), *Galium setaceum* Lamk. and *Valantia hispida* L. (Rubiaceae) or are weeds arrived in the last centuries, e.g. *Anagallis arvensis* L. (Primulaceae). Similarities concerning the Mediterranean-Soqotran geographical disjunction refer to genera with ally species: *Cleome*, *Teucrium*, *Dipcadi*, *Lepturus*, etc. (Balfour, 1898) and are often related to problematic taxa, e.g. *Convolvulus siculus* L. (Convolvulaceae) and *Valerianella affinis* Balf.f. (Valerianaceae) collected only in the 19th Century but not seen recently. Strongest relationships were observed for Highlands of Northern Somalia where 40 % of the genera are in common with the Mediterranean region and several taxa could represent real disjunctions (Fici, 1991).

Soqotra as all the oceanic islands attracted several botanists and biogegraphers that applied traditional theories to explain the evolution of its flora. A review of these theories is reported in Miller & Morris (2004) and Banfield et al. (2011). The main ones concern Vicariance: Tethyan fragments, Dry Pleistocene Corridor, Boreotropical Origin, and Dispersal: Colonisation, Adaptive Radiation. Both vicariance and dispersal look like complementary in the establishment and evolution of the flora of Soqotra.

### *Vicariance*

Vicariance implies barriers that restrict gene flow, the isolated populations evolve separately and become unlike enough to turn different species. This is suggested by disjunctions and anagenesys. The "Tethyan fragments" theory, supported by Bramwell (1976, 1985), Marrero et al. (1998), Miller et al. (2002), Andrus et al. (2004), Rodrigues-Sanchez & Arroyo (2008), etc., provides for a widespread vegetation around the Tethys Ocean, the continental Drift (Separation of populations) followed by aridification that caused widespread extinctions and left of relict populations. This theory is elucidated in Soqotra by endemic taxa that have unclear affinities/relationships with other more widespread ones, and are therefore assumed to be ancient relicts, e.g. *Punica protopunica* Balf.f. (Punicaceae) and *Dendrosicyos soqotranus* Balf.f. (Cucurbitaceae).

Other plants with a distribution split on both sides of the African continent that could have been generated by this phenomenon, are the arborescent *Dracaena* (Dracaenaceae) with *Dracaena draco* L. in Morocco and Macaronesia, *D. tamaranae* Marrero et al. in Gran Canaria, *D. serrulata* Baker in the Arabian peninsula, *D. cinnabari* Balf.f. in Soqotra, *D. ombet* Heuglin ex Kotschy et Peyr. and *D. schizantha* Sinet in E Africa; and *Campylanthus* (Scrophulariaceae) with 15 species that occur scattered in Soqotra, Canaries, Cape Verde Islands, NE Africa and Arabian peninsula.

Some taxa have distributions that support the hypothesis of a dry corridor during the Pleistocene (1.8 mya), linking SW Africa, Soqotra, Somalia, Ethiopia, and Arabia. Plants showing this distribution occur within: *Wellstedia* (6 species: Soqotra, Somalia, Ethiopia, South Africa, Namibia), *Graderia* (four species occurring in Soqotra, South Africa, Tanzania), *Camptoloma* (three species: Canary Islands, Somalia, Arabia, Namibia, Soqotra), *Chorisochora* (three species: Soqotra, South Africa).

Some taxa have widely disjunct distributions that stretch to the New World (America). During the Tertiary Period (65-2 myr), a warm, wet climate and tropical woodland vegetation covered large areas of N America, Europe and Asia (Eurasia). The little barriers to dispersal facilitated the spread of widely diffused taxa. Now some of these taxa have become separated because of: continental drift northwards, glaciation in northern areas, increased aridity in Northern Africa and the Middle East, severance of the Bering Land Bridge. These phenomena caused extinctions and barriers to dispersal and the populations remained isolated.

Plants showing a Boreotropical origin are: *Chapmannia* (Fabaceae) (seven species: four in Soqotra, one in Somalia and two in America), *Thamnosma* (Rutaceae) (six species: Soqotra, South Africa, Somalia, Yemen and Oman).

Molecular analyses done on *Echidnopsis* (Apocynaceae) proved that the four Soqotran endemics sampled were monophyletic and have evolved from a single colonising ancestor (Thiv & Meve, 2007). Divergence time older than 35 - 17.6 my is required to provide evidence for vicariance (Palaeo-endemics). Closest relationship should be between Soqotran and Arabian taxa. This was provided only for *Dendrosicyos soqotranus* that has an estimated age of 40 my that supports his vicariant history.

### *Dispersal*

Dispersal implies the occurrence of different colonization events that bring to adaptive radiation in a particular cladogenesis (the splitting of a species into two or more groups, which give rise to more new species) that can occur when a taxon colonises a new environments and rapidly evolves to fill available niches (Simpson, 1953). Adaptive radiation brings to genera with many species, often lightly morphologically different, with high levels of endemism.

Examples in Soqotran floras are: *Hibiscus* (Malvaceae) with 15 species, 9 endemic; *Heliotropium* (Boraginaceae) with 17 species, 10 endemic; *Helichrysum* with 13 species, 12 endemic, *Boswellia* (Burseraceae) and *Pulicaria* (Asteraceae) with 7 species, all endemic; *Echidnopsis* (Asclepiadaceae) and *Hypericum* (Clusiaceae) with 5 species, all endemic.

However, colonisation (or dispersal) was never considered the most important engine of differentiation of the Soqotran flora due to many genera and families with only one or two species that suggest vicariance to have the biggest influence. Divergence time younger than 35 - 17.6 myr indicates dispersal events producing neo-endemics. An example is represented by *Limonium guigliae* Raimondo et Domina and *L. paulayanum* (Vierh.) J.R. Edm. (Plumbaginaceae) and their affinities with other *Limonium* from Arabian peninsula (Raimondo & Domina, 2009). According to Thiv et al. (2006) three independent colonization lineages from the Eritreo-Arabian subregion of the Sudano-Zambesian Region were revealed in *Aerva* (Amaranthaeae) providing further support to colonization via dispersal, rather than a vicariance origin of the island elements. The same applies to *Exacum* (Gentianaceae) (Yuan et al., 2005). Phylogenetic patterns indicate several dispersal events from E Africa and/or Arabia in several other taxa such as *Thamnosma* (Rutaceae), *Echidnopsis* (Apocynaceae), *Kleinia* (Asteraceae), *Zygocarpum* (Fabaceae), *Polycarpaea* (Caryophyllaceae), *Reseda* (Resedaceae), *Camptoloma* (Scrophulariaceae), *Pulicaria* (Asteraceae) in contrast to more rare affinities to Madagascar, the Mascarenes, Southern Africa, and tropical Asia.

### *Aliens*

Recent changes in the flora that risk to have a deep impact both on endemic and non endemic elements are caused by aliens. Invasive alien species are widely recognized as one of the major threats to native biodiversity, particularly on oceanic islands (Denslow et al., 2009; Caujapé-Castells et al., 2010; Kueffer et al., 2010). Naturalization of aliens on islands is higher than in mainland environments (Stohlgren et al., 2008).

A recent survey on the alien flora of Soqotra (Senan et al., 2012) reports 88 taxa: 17 of them naturalized and four invasive: *Argemone mexicana* L., *Colotropsis procera* (Aiton) W.T. Aiton, *Leucaena leucocephala* (Lam.) de Wi and *Parkinsonia aculeata* L.). The remaining are cultivated for food, forage, medicine, or ornament but new naturalizations from this pool are to be expected also considering that several of them are included in the Global Invasive Species Database (http://www.issg.org/database).

Anyway these results are fortunately low if compared with other oceanic islands. This could be due to the fact that in Soqotra agriculture, which is the main source of alien species in oceanic islands, has always been limited to small tracts of ground near houses (Balfour, 1898); the same situation can be observed still nowadays. No large plantations have been realized with the single exception of date palm (*Phoenix dactylifera* L.) (Fig. 3) now naturalized and African finger millet (*Eleusine coracana* Gaertn.), now abandoned. Fruit, rice, vegetables and khat (*Catha edulis* Forssk.) consumed in Soqotra come almost totally from outside. The airport, opened in 2000, plays an important role in growth of trade and transport facilitations. Today there seems to be little awareness of the problem of invasive species, severe controls are done only on plants and plant propagules that are exported outside the island; on the contrary no security or pest check is done on the material that arrives.

## CONCLUSIONS

Biogeography of oceanic islands always attracted botanists attention. Soqotra represents an important case study of an ancient island not extremely isolated from the continents but with a rich and well differentiated flora that makes it an excellent world's hotspot of biodiversity. Its flora benefited of wet and dry refugia to survive geologic and climatic variations occurred in the area. A particular relevance has the diversity in some tropical genera such as *Boswellia* and *Commiphora* that have a high ethnobotanic interest. Its landscape is characterized by the representative occurrence of the endemic *Adenium obesum* subsp. *sokotranum* (Vierh.) Lav. (Fig. 4). Both traditional theories and molecular evidence tried to explain the origins and modifications of this flora using the vicariant as well as the dispersal approach. But there are some problematic taxa with unclear affinities and unclear relationships with known relatives (e.g. *Dendrosi-*

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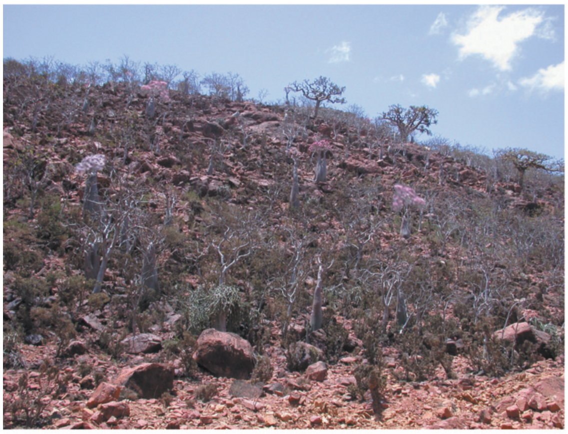

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Figure 2. *Trichocalyx obovatus* Balf.f. at Hom Hil. Figure 3. Date plantation near Di Lishah, in the background the massif of Haggeher. Figure 4. Hilly shrubland characterized by *Jatropha unicostata* and *Adenium obaesum* subsp. *sokotranus*. Figure 5. Centuries old tree of tamarind at Zam Hom used as shelter for livestock.

*cyos soqotranus* and *Punica protopunica*). However the molecular analysis cannot take into account wide-ranging extinctions that have been described for the region during aridification. More phylogenies are therefore needed of more obvious relictual species or those thought to be more ancient.

Considering the low impact of residential and agricultural activities and the total absence of industrial ones, the most severe threat to this unique flora is represented by the touristic development of the island that, as happened in other parts of the world, risks to provoke deep modifications in the environment damaging unequalled habitats. The millenary balanced relationship between man and nature as underlined by the occurrence of centuries old trees of tamarind (*Tamarindus indica* L.) (Fig. 5), used as meeting point for man and livestock, risks to be considerably altered.

In order to attain an overall protection of both human culture and biodiversity of the island, the local Administrations and the inter-governmental organizations need to elaborate a long time forecast planning addressed to an eco-sustainable development. In short time period a deeper control on new introductions in order to prevent pests and new undesired alien taxa is indispensable.

## ACKNOWLEDGEMENTS

Funding by Università degli Studi di Palermo (ex 60 %) and Prof. Attilio Carapezza for critical reading of the text are gratefully acknowledged. A special thanks to Dr. Luigi Guiglia a true lover of the island that guided us during our exploration.

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