Drivers and patterns of vascular plant diversity in the arid mountain Gebel Elba, Egypt

Dissertation

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Submitted by

Maged Mohamed Mohamed Ali Abutaha

from Egypt

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The following evaluators recommended the admission of the dissertation:

Prof. Dr. Norbert Jürgens (First reviewer)

Prof. Dr. Udo Schickhoff (Second reviewer)

Members of the examination commission:

Prof. Dr. Jörg Ganzhorn (Chairman)

Prof. Dr. Norbert Jürgens

Prof. Dr. Udo Schickhoff

Prof. Dr. Kathrin Dausmann

Dr. Jens Oldeland

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Preface

This thesis is based on three published papers:

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To increase the readability of the thesis, all figures, tables and supporting information have been renumbered in a consecutive manner. Moreover, one combined reference section is provided and one section containing all supporting information is given at the end of the thesis.

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Summary

The arid mountain Gebel Elba is situated in the south-east corner of Egypt, nearly 15 km west of the Red Sea coast. Although this mountain is surrounded by a hyper arid desert, orographic precipitation on its northern slopes provides favourable climatic conditions for a richer growth of Afrotropical species than any similar region in Egypt. Meanwhile, a phytosociological classification of the vegetation was lacking, and its environmental drivers were mostly unknown. Additionally, plant diversity patterns for this arid mountain were not completely evaluated. Thus, this thesis aimed to provide scientific data to increase the knowledge on diversity patterns and vegetation distribution in an arid mountain ecosystem (Gebel Elba).

The thesis combined ecological classification and ordination analyses with ecological modelling based on different environmental parameters. It presented an extensive and quantitative account of the vegetation composition and plant diversity of wadi systems on north-western slopes of Gebel Elba for the first time. The established vegetation-plot database covered the open desert plains and the mountainous area. It contained standardised vegetation plots along elevational gradients of four wadies, i.e., Yamib, Marafai, Acow and Kansisrob. In **Chapter Two**, an uncommon elevation-richness pattern was described for wadi systems of Gebel Elba. The thesis also provided the first phytosociological classification of the vegetation in Gebel Elba (**Chapter Three**). The vegetation classification in this study contained detailed species lists. Thus, a coherent base for future work on the Afrotropical vegetation of Gebel Elba was established and made available. Furthermore, ground truth data combined with remotely sensed information were used to produce the first model-based plant diversity maps for the arid mountain Gebel Elba (**Chapter Four**).

The thesis focused on the Afrotropical vegetation of Egypt and filled a knowledge gap on woodlands distribution and diversity patterns in Gebel Elba region. The presented thesis indicated the high importance to conserve mountainous wadi systems of Gebel Elba especially at higher elevations.

Zusammenfassung

Die aride Gebirgskette des Djebel Elba liegt im Südosten Ägyptens, circa 15 km westlich vom Roten Meer. Obwohl dieser Berg von einer hyperariden Wüste umgeben ist, bietet der orografische Niederschlag an seinen Nordhängen klimatische Bedingungen, die ein ausgiebiges Wachstum afrotropischer Pflanzenarten erlaubt und in dieser Hinsicht jede ähnliche Region in Ägypten übertrifft. Bisher fehlte eine phytosoziologische Klassifizierung der Vegetation, Informationen zu den steuernden Umweltfaktoren waren größtenteils unbekannt. Darüber hinaus wurden die räumlichen Muster der Pflanzendiversität für dieses Gebirge nicht vollständig bewertet. Das Ziel der vorliegenden Arbeit ist es, Vegetationsdaten zu analysieren, um das Wissen hinsichtlich der Diversitätsmuster und der Vegetationsverteilung in diesem trockenen Gebirgsökosystem (Djebel Elba) zu erweitern.

Diese Arbeit kombiniert ökologische Klassifizierungs- und Ordinationsanalysen mit räumlichen Vorhersagemodellen, basierend auf verschiedenen Umweltparametern. Erstmals wird eine umfassende und quantitative Darstellung der Vegetationszusammensetzung und Pflanzenvielfalt von Wadi-Systemen an den nordwestlichen Hängen des Djebel Elba präsentiert. Eine erstellte Vegetationsdatenbank deckt die offene Wüste und die Gebirgshänge ab. Es wurden standardisierte Vegetationsaufnahmen entlang von Höhengradienten in vier Wadis erstellt. Die Wadis heißen Yahmib, Marafai, Acow und Kansisrob. **Kapitel Zwei** beschreibt ein Diversitäts-Höhenmodell welches ein ungewöhnliches Muster aufweist und hier für die Wadi-Systeme des Djebel Elba beschrieben wird. Diese Arbeit liefert auch die erste phytosoziologische Klassifikation der Vegetation des Djebel Elba (**Kapitel Drei**). Die Vegetationsklassifikation in dieser Studie enthält detaillierte Artenlisten und Standortbeschreibungen. Damit wird eine kohärente Basis für zukünftige Arbeiten zur afrotropischen Vegetation des Djebel Elba geschaffen und verfügbar gemacht. Darüber hinaus wurden die Vegetationsdaten in Kombination mit Satellitendaten und aus einem digitalen Höhenmodell abgeleiteten Informationen verwendet, um die ersten modellbasierten Karten der Pflanzendiversität für die aride Gebirgskette des Djebel Elba zu erstellen (**Kapitel Vier**).

Diese Arbeit konzentrierte sich auf die afrotropische Vegetation Ägyptens und füllte eine Wissenslücke hinsichtlich der räumlichen Verbreitung der Vegetationseinheiten und deren Diversitätsmuster in der Region des Djebel Elba. Diese Arbeit zeigt auch auf, wie wichtig es ist, die Wadi-Systeme an den Hängen des Djebel Elba, insbesondere in höheren Lagen, aufgrund der Pflanzenvielfalt zu schützen.

ملخص

يقع جبل علبة في الركن الجنوبي الشرقي من مصر، على بعد حوالي ١٥ كم غرب ساحل البحر الأحمر. على الرغم من أن هذا الجبل محاط بصحراء شديدة الجفاف ، إلا أن هطول الأمطار على منحدراته الشمالية يوفر ظروفًا مناخية مواتية لنمو أكثر ثراءً للأنواع الأفرواستوائية من أي منطقة مماثلة في مصر. ومع ذلك، لا يوجد تقسيم واضح للغطاء النباتى والمعلومات حول العوامل البيئية المؤثرة على توزيع وثراء الغطاء النباتى في الغالب غير معروفة. بالإضافة إلى ذلك، لم يتم تقييم أنماط التنوع النباتي لهذا الجبل القاحل بشكل كامل. و لذلك، تهدف الأطروحة المقدمة إلى توفير بيانات علمية لزيادة المعرفة بأنماط التنوع وتوزيع الغطاء النباتي في النظام البيئي للجبل القاحل (جبل علبة).

تجمع الأطروحة بين التصنيف البيئي وتحليلات التنسيق والنمذجة البيئية بناءً على عوامل بيئية مختلفة. قدمت هذه الرسالة لأول مرة عرضا كميا واسعا لتكوين الغطاء النباتي والتنوع النباتي لنظم الأودية على المنحدرات الشمالية الغربية لجبل علبة. تشمل قاعدة البيانات الغطاء النباتى فى المناطق الجبلية والصحراوية المفتوحة. وتحتوي على بيانات نباتية معيارية على طول التدرجات الارتفاعية لأربعة أودية وهى أودية: يحميب، معرفاى، أكاو وكانسيسروب. في **الفصل الثاني**، تم وصف نمط غير مألوف للثراء على طول التدرجات الارتفاعية لأنظمة الوديان بجبل علبة. كما قدمت الأطروحة أول تصنيف للغطاء النباتي في جبل علبة (**الفصل الثالث**). يحتوي تصنيف الغطاء النباتي في هذه الدراسة على قوائم تفصيلية للأنواع. وبذلك، تم إنشاء قاعدة بيانات للغطاء النباتي الأفرواستوائي لجبل علبة وإتاحتها للدراسات المستقبلية. علاوة على ذلك ، تم استخدام بيانات الغطاء النباتي المتاحة من خلال هذه الرسالة جنبًا إلى جنب مع معلومات الاستشعارعن بعد لإنتاج خرائط التنوع النباتي القائمة بناءاً على نماذج احصائية أولية لجبل علبة (**الفصل الرابع**).

ركزت الأطروحة على الغطاء النباتي الأفرواستوائي في مصر وسدت فجوة معرفية حول توزيع الغطاء النباتي الشجرى، وأنماط التنوع في منطقة جبل علبة. أشارت الأطروحة المقدمة إلى الأهمية القصوى لصون أنظمة الوديان بجبل علبة خاصة في المرتفعات العالية.

Chapter One

General Introduction

Biodiversity in arid environments

Arid environments represent about one-third of the earth’s land surface, and they are usually characterized by a shortage of rainfall, high temperatures and a general scarcity of vegetation in terms of species abundance and cover (Tchakerian, 2015; Pfadenhauer & Klötzli, 2020). Arid environments are mostly considered to be ecosystems with poor biodiversity. However, recent studies pointed at relatively high levels of biodiversity, high rates of endemism and many species of conservation concern in certain arid regions (Brito et al., 2014; Razgour et al., 2018; Carrasco-Puga et al., 2020). Spatial patterns of diversity derive from the interaction of multiple environmental factors, biotic and disturbances across the ecosystem (García-Gutiérrez et al., 2018; Ramos et al., 2020). However, species abundance and density in arid environments is lower than in more humid environments; species distribution is not homogenous and often scattered or restricted to specific microhabitats.

Limited water availability, high temperature, and strong solar radiation exert high pressure on living organisms of arid environments (Carrasco-Puga et al., 2020). Thus, desert biota exhibit a wide range of morphological and physiological adaptations to cope with the extreme conditions (Solbrig & Orians, 1977; Abutaha, 2010; Eldemirdash, 2016). Such adaptations allow xerophytes to dominate arid environments. In relation to water supply, two types of vegetation can be recognized in arid regions; (1) ephemeral or annual vegetation growing after rainfall and (2) perennial vegetation, which either scattered or restricted to water accumulation areas such as wadis, depressions and runnels in open plains and mountain ranges (Solbrig & Orians, 1977; Batanouny, 1983).

Diversity in arid mountains

Mountain ranges in arid regions represent a home for many species with different ecological requirements. Due to their topographic roughness, they offer suitable habitats for adapted and unadapted species to xeric conditions across their environmental gradients (Garcia-Porta et al., 2017; Zizka & Antonelli, 2018; Ramos et al., 2020). Arid mountains provide great reservoirs and represent species pumps, as species disperse into their surrounding areas (Garcia-Porta et al., 2017; Zhang & Zhang, 2017). This is because of the high variation of ecosystem types and microhabitats found within relatively small areas, influenced by changes in elevation, microclimate and complex topography (McNeely, 2003; Rahbek et al., 2019; Van Staden et al., 2020). Therefore, Mountain ranges are often focal points for biodiversity management and conservation planning in arid regions such as the Hajar mountains at the south-eastern corner of the Arabian Peninsula (Brinkmann et al., 2011; Garcia-Porta et al., 2017), the Tianshan Mountains in Central Asia (Zhang & Zhang, 2017) and the Saint Katherine mountains in Egypt (Coals et al., 2018).

Environmental drivers of plant diversity in arid mountains

Mountains can differ greatly in their environmental gradients, depending on factors like their geological formations, steepness, and local climatic conditions (Zizka & Antonelli, 2018; Perrigo et al., 2020). The great variety of habitat types along elevational gradients is offering suitable environmental conditions for plant communities to be isolated from the harsher environments (Quintero & Jetz, 2018). Several studies realized the importance of environmental heterogeneity including variations along elevational gradients for mountains biodiversity (Stein & Kreft, 2015; Hoorn et al., 2018).

Grytnes and McCain (2013) reviewed hypotheses for diversity patterns along elevational gradients and classified them into four main hypothesis; climatic, spatial, biotic and historic hypotheses. The most common explanations for diversity patterns are related to climatic variables, habitat diversity, soil nutrients and moisture content. Climatic variables such as temperature and rainfall are the most cited causes for broad-scale diversity patterns (Grytnes & McCain, 2013). In arid regions, high temperature and low precipitation were recognized as limiting factors for plant growth and diversity (Zahran & Willis, 2009; Coals et al., 2018). Hence, it seems that changes in the water availability and thermal regime are the main drivers of diversity patterns along elevational gradients of arid mountains.

Mountain's climates are considerably differing from the surrounding lowlands. Temperature decreases gradually with increasing elevation and water is more available on higher slopes (Houze, 2012). The complex topography of mountains offers the chance for orographic precipitation, which is more recognized on the coastal mountains, when aggregation of clouds and wind direction support mist and fog formation on higher slopes. The effect of orographic rains is leading to a high plant diversity on slopes and drainage systems of arid mountains such as the arid valleys of the Himalaya (Panthi et al., 2007), the Mongón mountain in Peru (Muenchow et al., 2013a, b), the mountain ranges of Serra de Bodocongó and Serra da Arara in Brazil (Ramos et al., 2020) and the Jabal Al-Akhdar in Oman (Ghazanfar, 1991; Brinkmann et al., 2011).

Diversity patterns along elevational gradients

Elevational gradients in mountain regions provide unique opportunities for studying the effects of abiotic features such as, edaphic properties, topographic, temperature and available moisture (Guo et al., 2013). Many types of elevation-richness relationships have been identified for plants (Rahbek, 2005; Grytnes & McCain, 2013). The most documented patterns for plant species richness were hump-shaped (Vetaas & Grytnes, 2002; Wohlgemuth et al., 2008; Dubuis et al., 2011; Baniya et al., 2012; Lee et al., 2013; Lee & Chun, 2016) and linear decrease in richness with increasing elevation (Fosaa, 2004; Trigas et al., 2013). Also, several studies found an increase in richness with elevation (Lovett et al., 2006, Hoppe et al., 2016; Coals et al., 2018). A less common diversity pattern, which is an increase in richness followed by a plateau of species richness at higher elevations, was reported only by Panthi et al., (2007) for a dry valley in the Nepal Himalaya and was visible in the study by Ghazanfar (1991) for vascular plants on the Jabal Shams in Oman. The high plateau pattern could be common in arid mountains, but little has been done in arid regions to test such hypothesis (Guo et al., 2013).

Although many studies described the species richness-elevation relationships in temperate and tropical mountains, arid mountains were severely understudied especially in North Africa and the Arabian Peninsula (see Figure 1; from (Guo et al., 2013). In some arid mountain systems, favourable climatic conditions were found at intermediate elevations where climatic conditions provide an environmental optimum for plant growth and diversity (Hegazy & Lovett-Doust, 2016). However, many studies were mainly focused on wadi (dry valley) systems, which consider just one of the most important desert ecosystems (Abd El-Ghani & Abdel-Khalik, 2006; Panthi et al., 2007).

The rugged topography of mountains offers variation of solar insolation and different landform classes such as slopes, ridges, plains, streams, and valleys (wadis). Accumulations of water in drainage systems (wadis and streams) support growth of richer and more vigorous vegetation than on higher slopes or open desert plains at the foot of the arid mountains (Gomaa, 2014; Hegazy & Lovett-Doust, 2016).

Beside hydrologically favoured landforms in mountainous areas, steepness of slopes increases shaded areas in comparison to open desert plains. Edaphic factors are another aspect which helps to explain diversity patterns in arid mountains. Heterogeneity of nutrient availability and soil water retention for plants can be reflected by the species richness and structure of plant communities along altitudinal gradients (Muenchow et al., 2013a; Ramos et al., 2020). Hence, patterns of diversity can be related to climatic stress and environmental heterogeneity hypotheses along the elevation gradients of mountains (Grytnes & McCain, 2013; Sabatini et al., 2018).

Figure 1: The global distribution of 443 studies on species richness-elevation relationships examined by Guo et al., (2013).

Using remote sensing for monitoring diversity

Topography of arid mountains plays an important role in determining diversity patterns, at the same time it causes a research challenge for observing biodiversity. Inaccessibility of arid mountains and lack of information on environmental parameters are two main obstacles for management and conservation (Brinkmann et al., 2011). Remote sensing can offer information for monitoring and predicting patterns of plant diversity (Wang & Gamon, 2019). Environmental parameters such as topography, edaphic parameters, climatic variables and productivity can be derived from remote sensing data (Turner et al., 2003). With the rapid rise of statistical techniques and data generation, e.g., digital photogrammetry, remote sensing can be used more efficiently for biodiversity assessments (Merganic et al., 2012). It increasingly represents a helpful and powerful technology for assessment of plant diversity using spectral data (Nagendra, 2001; Turner et al., 2003; Peng et al., 2018; Fundisi et al., 2020). Remote sensing can provide cost efficient spatial digital data which is more accurate than before (Merganic et al., 2012). Recently, very high-resolution remote sensing can provide information on primary productivity and environmental parameters that was previously not available on an appropriate scale (Wang & Gamon, 2019).

Studies on arid mountains revealed that remote sensing data have been successfully used for predicting habitat, species distribution and diversity mapping (Brinkmann et al., 2011; Hüttich et al., 2011; Muenchow et al., 2013a; Vanselow & Samimi, 2014). The relationship between environmental parameters derived from remote sensing data and species diversity has usually a unimodal pattern (Brinkmann et al., 2011; Muenchow et al., 2013a). However, no general predictive model has been derived yet to explain this relationship for arid mountains. So far, there are still few studies that apply remote sensing in arid regions.

Arid mountains of Egypt

Arid mountains in Egypt exhibiting a high plant diversity and different plant communities than those found in the open desert habitats of the country (Zahran & Willis, 2009; Hegazy & Lovett-Doust, 2016). According to the Nature Conservation Sector (NCS, 2006), twenty-four protected areas were declared in Egypt (Figure 2). Mountain ranges are the core of the protected areas in the south of the Sinai Peninsula and the Eastern Desert of Egypt such as the Wadi El Gemal – Hamata protected area and the Gebel Elba National Park in south of the Eastern Desert, and the Saint Katharine protectorate in South Sinai. Furthermore, arid mountains, i.e. St. Katharine and Elba ranges, represent the most diverse ecosystems in two (Gebel Elba and Sinai) of the seven main phytogeographical regions of Egypt (Boulos, 2009).

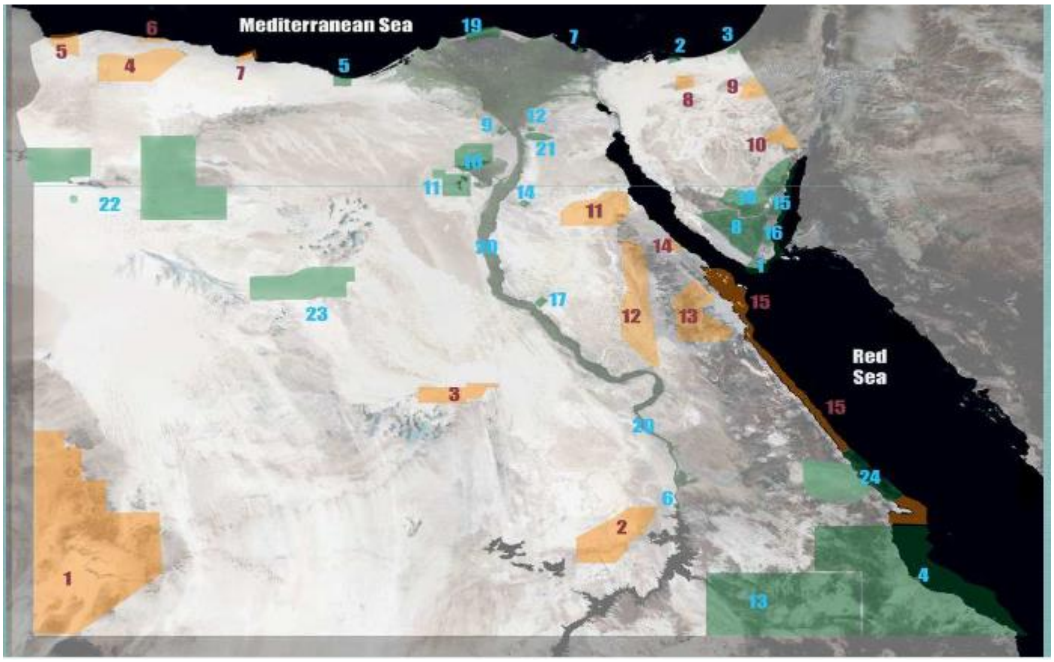

Figure 2: Map of Egypt showing the distribution of protected areas in Egypt according to the Nature Conservation Sector, Egyptian Environmental Affairs Agency, Ministry of Environment, Egypt (NCS, 2006). Green colour refers to protected areas and orange colour to newly proposed areas. Gebel Elba National Park is located at the south-eastern corner of Egypt (No. 4 in green).

The arid mountain Gebel Elba

Geology and climate

Gebel Elba National Park (GENP) is the largest protected area in south-eastern Egypt, covering 36,000 km^2. It is encompassing many habitats, from mangroves, coral reefs, coastal wetlands to sand dunes, desert wadis and coastal mountains (NCS, 2006). The mountain range comprises a cluster of six granite mountains overlooking the Red Sea coast, near to the political border with Sudan (Kamel et al., 2015), which include Gebel Shellal (1409 m), G. Elba (1435 m), G. Shendodai (1526 m) and G. Shendib (1901 m). Wadis (drainage systems) are deeply cut through the mountain range and flow towards the Nile Valley or the Red Sea coast. The Elba range is the southernmost of Egypt's coastal mountains running parallel to the Red Sea near the borders with Sudan.

Gebel Elba is the most northerly peak of the group (Figure 3). It is located approximately 20-25 km west of the seacoast and facing a wide coastal plain of the Red Sea (Zahran & Willis, 2009). Gebel Elba receives more orographic precipitation than any other mountain in the range. This is due to its closeness to the coast and its position facing moisture-laden north-easterly winds (Kamel et al., 2015). This orographic precipitation creates a mist oasis at the top of the mountain that is found nowhere else in Egypt (Zahran & Willis, 2009). The orographic precipitation provides climatic conditions that are favourable for rich plant growth (Hegazy and Lovett-Doust 2016), especially in the wadis (Abd El-Ghani & Abdel-Khalik, 2006; Al-Gohary, 2008a; Zahran & Willis, 2009). The relative high moisture content allows for a diverse fauna and flora to exist on Gebel Elba.

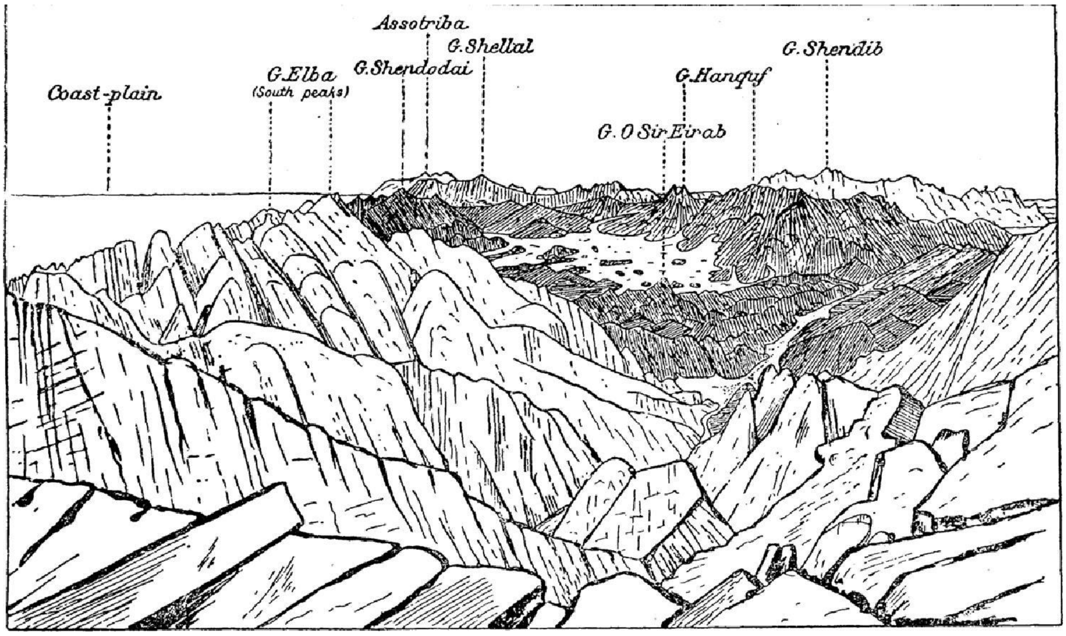

Figure 3: Historical view from the summit of Gebel Elba range. It was drawn by John Ball during the geology and geography survey for South-Eastern Egypt according to a request from the Egyptian government (Ball, 1912).

Biogeography and species diversity

The biodiversity of GENP is incomparable to any other region of Egypt and comprises a unique flora and fauna. Many Afrotropical species have their northern limits at the park of Elba (Schweinfurth, 1864; Zahran and Willis 2009). In total, 458 plant species representing almost 21% of the Egyptian flora occur in GENP (Boulos 2008; Zahran and Willis 2009). Also, the different ecosystems harbour several birds, mammals, amphibians, reptiles, corals, and fish species (NCS, 2006; BirdLife International, 2020). Many globally near threatened, vulnerable or endangered species are found in GENP like the Dragon tree (*Dracaena ombet*), rare mammals like *Gazella dorcas* and *Capra nubiana*, and birds of prey like *Gypaetus barbatus* (IUCN, 2020).

The Gebel Elba Mountain is the core area of GENP, and its species richness is related to its favourable climatic conditions. The vegetation is comparable to similar ecosystems in Erkwit, Sudan, and the southern part of the Arabian Peninsula (Kassas 1956; Kürschner et al. 2004; Hegazy and Lovett-Doust 2016). Thus, Gebel Elba represents the northern limit of Eritreo-Arabian vegetation in East Africa (Zohary 1973). The Eritreo-Arabian vegetation on Gebel Elba is continuous and changes from deciduous *Vachellia* woodlands at lowlands (Figure 4) to evergreen *Olea* woodlands at higher elevations (Figure 5). Zahran and Willis (2009) found three elevational zones of vegetation on the northern slopes of Gebel Elba: two belts (zones) from low to middle elevations, dominated by xerophytes such as *Vachellia tortilis* (synonym: *Acacia tortilis*), *Euphorbia cuneata* and *E. nubica* and a higher zone dominated by evergreen species such as *Carissa spinarum* and *Olea europaea* subsp. *cuspidata*. Previous studies on Gebel Elba focused on the floristic composition and only qualitatively described the vegetation zonation (Zohary, 1973: Zahran & Willis, 2009).

Figure 4: *Vachellia* woodland at the foot of Gebel Elba. Photo credit: Maged Abutaha

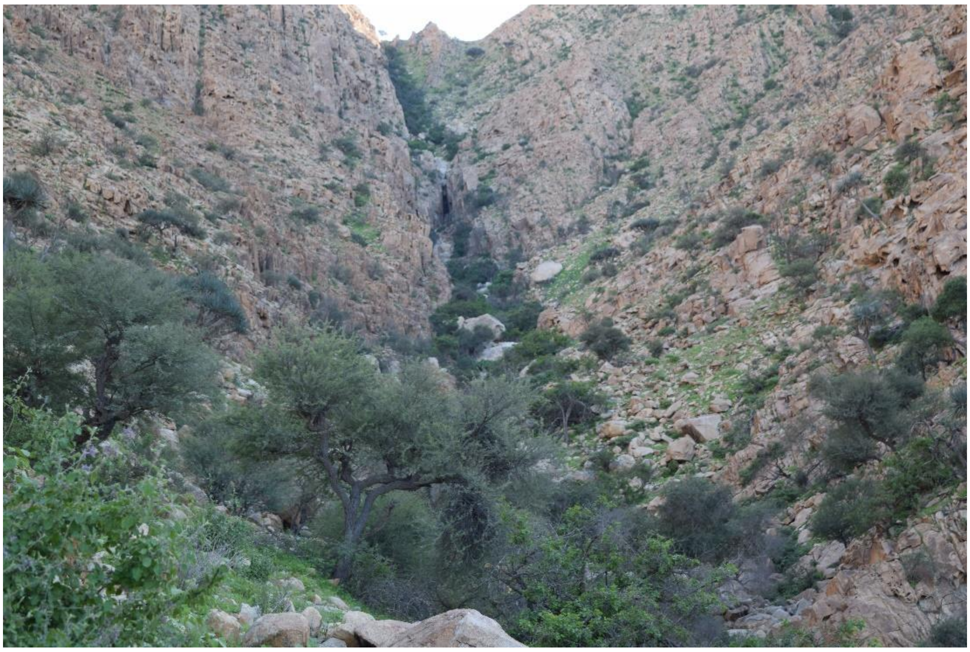

Figure 5: *Olea* woodland at higher elevations of Gebel Elba. Photo credit: Maged Abutaha

Knowledge gaps on the Gebel Elba and aims of my thesis

Previous studies on Gebel Elba have been mainly focused on wadi systems, where vegetation is rich and continuous (Ahmed 1999; Zahran & Willis 2009; Abd El-Ghani & Abdel-Khalik, 2006; Al-Gohary, 2008a). These studies have been based on a small number of vegetation plots or compiled vegetation lists. A systematic study of elevation-richness relationships of the wadi systems for this arid mountain has not yet been completed. Furthermore, a classification of the wadi vegetation is still lacking. The elevational range of the main plant communities is unknown and information on environmental drivers are mostly unavailable. For conservation management, it is urgently needed to identify the vegetation units of Gebel Elba and the environmental drivers controlling their distributions. To better understand the biodiversity pattern in Gebel Elba using appropriate methods and tools applying theoretical considerations in the description of these patterns.

In my thesis, I aimed to identify elevation-richness relationships for vascular plants along elevational gradients of the wadi systems of Gebel Elba **(Chapter Two)**. I hypothesised that plant species richness will show a humped shape pattern for the wadi system as proposed by Abd El-Ghani and Abdel-Khalik (2006) and El-Keblawy et al. (2016). In **Chapter Three**, I aimed to describe the plant communities, their compositions, and the relations to environmental factors. I also aimed to analyse the distribution patterns of trees along the elevational gradient to identify a transition zone between deciduous and evergreen trees. In **Chapter Four**, I aimed to explore predictive mapping of alpha and beta plant diversity based on remotely sensed information. I hypothesized that the mountainous areas are more diverse than the surrounding desert plains. I further hypothesized the importance of topography, plant productivity and soil parameters in determining the diversity patterns along the elevational gradients of Gebel Elba.

Chapter Two

Elevation-richness pattern of vascular plants in wadis of the arid mountain Gebel Elba, Egypt

Maged M. Abutaha, Ahmed A. El-Khouly, Norbert Jürgens, Amal A. Morsy and Jens Oldeland

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Abstract

Mountains provide a unique opportunity to study drivers of species richness across relatively short elevation gradients. However, few studies have reported elevational patterns for arid mountains. We studied elevation-richness pattern along an elevational gradient at the arid mountain Gebel Elba, south-east of Egypt, expecting a unimodal richness pattern. We sampled 133 vegetation plots (10 m × 10 m) in four wadis along an elevational gradient from 130 m to 680 m which represents the transition from desert to mountain wadi systems. We used generalized additive models to describe the relationship between elevation and plant species richness. We found a strong increase in species richness and Shannon diversity at low elevations followed by a plateau at mid to high elevations. When we analyzed each tributary as a single gradient, no pattern was found. The analyzed elevational gradient seems to be a major stress gradient in terms of temperature and water availability, exhibiting a trend of increasing species richness that changes to a plateau pattern; a pattern rarely observed for wadi systems in arid mountains. We discuss the observed pattern with the climatic-stress hypothesis and the environmental heterogeneity hypothesis as possible explanations for the pattern.

Keywords: arid mountain; altitude; stress; plant diversity; GAM; Gebel Elba.

Introduction

Elevational gradients often show strong elevation-richness relationships, i.e., species richness varies with elevation. Three main types of elevation-richness relationships have been identified for plants (Rahbek, 1995, 2005; Grytnes & McCain, 2013): (1) a linear decrease of richness, (2) a high richness plateau at lower elevations followed by a linear decrease, and (3) a hump-shaped or unimodal pattern. In temperate and tropical mountains, studies have found that plant species richness decreases monotonically with elevation, e.g., in Crete Island (Trigas, Panitsa, & Tsiftsis, 2013) and in the Faroe Islands (Fosaa, 2004).

Most studies have documented hump-shaped relationships between plant species richness and elevation including Nepal (Vetaas & Grytnes, 2002), South Korea (Lee, Chun, Um, & Cho, 2013; Lee & Chun, 2016), Switzerland (Wohlgemuth, Nobis, Kienast, & Plattner, 2008; Dubuis et al., 2011), and Tibet (Baniya, Solhøy, Gauslaa, & Palmer, 2012). Grytnes (2003) found both, monotonic decreasing and hump-shaped relationships for vascular plants in Norway. Hence, the prevailing pattern for wet mountains seems to be either a hump-shape or a decreasing pattern.

A fourth pattern, i.e., an increase in richness with elevation, has also been reported several times, e.g., in Tanzania (Lovett, Marshall, & Carr, 2006), in Kyrgyzstan (Hoppe, Zhusui Kyzy, Usupbaev, & Schickhoff, 2016), and in Egypt (Coals, Shmida, Vasl, Duguny, & Gilbert, 2018). A fifth pattern, which is rarely observed, is an increase in richness followed by a plateau of species richness at higher elevations. This pattern was reported only by Panthi, Chaudhary, and Vetaas (2007) for a dry inner valley of the Himalayas in Nepal and was visible in the study by Ghazanfar (1991) for plants in the arid mountain Jebel Shams, Oman.

Although elevation is merely a proxy measure for parameters being physically tied to altitude, such as air temperature or air pressure (Körner, 2007), many studies analyze taxonomic richness pattern along elevation gradients. Grytnes and McCain (2013) reviewed hypotheses for elevation-richness relationships and classified them into climatic, spatial, biotic, and historic hypotheses. Common explanations for richness patterns along such gradients relate to environmental variables such as rainfall, temperature, habitat diversity, soil nutrients, and moisture content. Climatic variables like temperature and rainfall are probably the most commonly cited causes for broad-scale patterns in species richness and elevation patterns. Land use such as livestock grazing is also known to affect elevation patterns of plant diversity (Speed, Austrheim, & Mysterud, 2013). However, no real consensus has been reached on which of these hypotheses holds for temperate, tropical, or arid mountains. While the number of studies for temperate and tropical mountains is still increasing, arid mountain systems remain severely understudied.

For arid mountains, many studies found high plant species richness in intermediate elevations, which are often related to favorable climatic conditions where the interaction of precipitation and temperature provides optimum hygrothermal conditions for plant growth and diversity (Ghazanfar, 1991; Hoppe, Zhusui Kyzy, Usupbaev, & Schickhoff, 2016). For desert mountains of the Middle East, several studies reported a hump-shaped pattern in the higher arid mountains, e.g. in the Red Sea region of Saudi Arabia and Egypt (Hegazy, El-Demerdash, & Hosni, 1998; Hegazy, Lovett-Doust, Hammouda, & Gomaa, 2007), and in Oman (Brinkmann, Patzelt, Dickhoefer, Schlecht, & Buerkert, 2009).

A unimodal pattern was even described along short elevation gradients with a mid-elevation peak near 400 m in Wadi Yahmib, Gebel Elba, Egypt (Abd El-Ghani & Abdel-Khalik, 2006) and in Wadi Helo, Hajar Mountains, the United Arab Emirates (El-Keblawy, Khedr, & Khafaga, 2016). Short gradients have often been subject to similar studies also for wet mountains (Grytnes, 2003; Fosaa, 2004). Although Egypt has many arid mountain ranges, few studies have explicitly tested them for elevation-richness relationships (Abd El-Ghani & Abdel-Khalik, 2006; Hegazy, Lovett-Doust, Hammouda, & Gomaa, 2007; Coals, Shmida, Vasl, Duguny, & Gilbert, 2018). Most of the mountain ranges in Egypt remain unstudied.

The most important arid mountains in Egypt exhibiting high plant diversity are Saint Katherine in South Sinai, Gebel Uweinat at the Egyptian-Libyan-Sudanese border, and Gebel Elba in the south of the Eastern Desert near the Sudanese border. Some studies have described the vegetation of Gebel Elba and it´s diversity (Ahmed, 1999; Abd El-Ghani & Abdel-Khalik, 2006; Al-Gohary, 2008a; Zahran & Willis, 2009). These studies were mainly confined to wadis, which represent one of the most prominent desert ecosystems.

A wadi is a drainage system, collecting water from often extensive catchments and consists of several microhabitats depending on the surface of the local topography (Gomaa, 2014). The water supply of the wadi is greater than that of the surrounding slopes, which is reflected by its typically rich vegetation (Hegazy & Lovett-Doust, 2016). However, studies on Gebel Elba have been based on a small number of vegetation plots or compiled vegetation lists (Abd El-Ghani & Abdel-Khalik, 2006; Al-Gohary, 2008a). A systematic study of elevation-richness relationships of the diverse wadi systems for this iconic arid mountain has not yet been completed.

In this study, we examined elevation-richness relationships for vascular plants along an elevation gradient constrained to the wadi systems of Gebel Elba, Egypt. Using data from 133 vegetation plots, we analyzed the elevation-richness pattern along the complete elevation gradient of Wadi Yahmib and its tributaries on Gebel Elba. We hypothesized that plant species richness will show a unimodal pattern for the wadi system as described by the previous studies (Abd El-Ghani & Abdel-Khalik, 2006; El-Keblawy, Khedr, & Khafaga, 2016). Besides total species richness, we were further interested whether any other subgroups of species, e.g. perennials vs. annuals, would show similar relationships. Furthermore, we investigated whether the elevation-richness pattern differs for each single wadi. Here, we hypothesized that in the more arid wadis, the increase in richness with elevation will be steeper than that for the upper wadis due to the higher climatic stress in the desert plains.

Material and methods

Study area

The arid mountain Gebel Elba is a part of Gebel Elba National Park (declared in 1986) which covers nearly 35,600 km² with different ecosystems such as mangroves, coral reefs, coastal wetlands, desert plains, and coastal mountains. Gebel Elba is located in the extreme southeast corner of Egypt, between longitudes 36° and 36.5° and approximately, at 22° northern latitude (Figure 6); it is the most northerly of a mountain range consisting of six granite mountains. This mountain is situated approximately 20-25 km west of the Red Sea coast.

Gebel Elba receives coastal mist throughout the year, which creates a “mist oasis” on the highest peaks (Ball, 1912; Zahran & Willis, 2009). This moisture is sufficient to allow the growth of a rich flora of 350 species (Ghabbour, 1997), which are 76% of the 458 species reported for Gebel Elba National Park (Zahran & Willis, 2009). The proportion of tree and shrub species is much higher than in any other region of Egypt. Most of them are included in the red data book on woody plants of Egypt (El Hadidi, Abd El-Ghani, & Fahmy, 1992).

According to global climate datasets (Harris, Jones, Osborn, & Lister, 2014) Gebel Elba has a hyper-arid climate with a mean annual temperature of 26.1 °C and rainfall of 37 mm per year (Appendix 1). However, Gebel Elba receives precipitation up to 400 mm of rain per year from orographic precipitation (Kamel, Ghazaly, & Callmander, 2015). The moist air is brought from the sea by the east winds and thus supports dense vegetation growth on the north and northeast flanks of Gebel Elba, while the south and southwest sides are sheltered from the wind and thus are more arid and sparse in vegetation (Zahran & Willis, 2009).

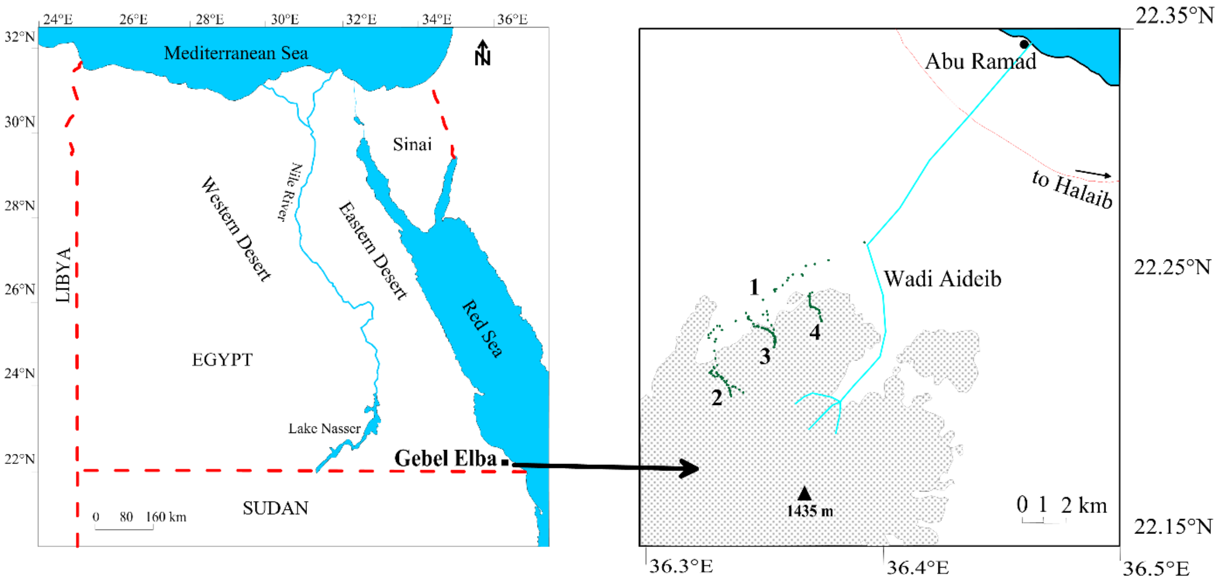

Figure 6. Map showing the location of Gebel Elba in Egypt (left), and the distribution of plots in Wadi Yahmib and its tributaries at the north flank of Gebel Elba (right); Wadi Yahmib (1), Wadi Marafai (2), Wadi Acow (3), and Wadi Kansisrob (4).

The highest peak of Gebel Elba reaches 1.435 m above sea level. The mountain is dissected by many drainage lines (wadis) radiating in all directions. The principal and richly vegetated wadi that drains the northern slopes of Gebel Elba is Wadi Yahmib (Zahran & Willis, 2009). Wadi Yahmib is locally divided into two wadis; the mountainous part is called Marafai while the part in the sandy plains at the foot of the mountain is called Yahmib.

Wadi Yahmib also receives water from two other feeders, i.e. Wadi Acow and Wadi Kansisrob. Both drain the north faces of the mountain, and unite with Wadi Aideib, which drains the northeastern flanks (Figure 6).

The elevational gradient of Wadi Yahmib increases towards the northwestern slopes. Substrates of the wadi bed vary with elevation; fine sand at the foot of the mountain, coarse gravel in Kansisrob and big granite boulders at higher elevations in Acow and Marafai. Furthermore, the granite rocks are particularly favorable for water accumulation from rainfall (Abu All-Izz, 1971), which supports dense vegetation between rocks in the wadi beds of Acow and Marafai. On the other hand, at lower elevations, Kansisrob is the narrowest wadi and the vegetation grows mainly near the side slopes, while Yahmib is sandy plain with scattered vegetation dominated by *Acacia tortilis* trees and *Zygophyllum simplex* at the ground layer.

Field sampling

Gebel Elba National Park is difficult to access, as it is partly a military area; thus, access to the mountain requires special permission which usually is restricted to only a few days. We conducted five field visits during the years 2013, 2015 and 2016. The three years were comparable in winter rainfall, which is most relevant for annual species. Visits were always made at the same time of the year, i.e., in January and March. We sampled the altitudinal gradient from 130 m to 680 m covering all main Wadis, i.e. Yahmib, Marafai, Acow, and Kansisrob. In order to assess the plant diversity, a total of 133 vegetation plots (10 m × 10 m) were distributed along the altitudinal gradient. It was difficult to take fixed intervals between sampling plots due to rugged topography. So, plots were randomly positioned within altitudinal intervals of 100 m in the main wadi and 50 m in the smaller wadis.

Vegetation plot coordinates (Geodetic datum: WGS 84) were recorded in the center using a GPS, model Garmin eTrex 30x (Appendix 2). For each plot, a complete species inventory with presence and absence information was assembled. We further noted growth form (woody and herbaceous), and life form (perennial and annual). For perennial species we recorded the number of individuals. Identification and nomenclature were according to Boulos (1999, 2000, 2002, 2005, 2009). Voucher specimens were deposited in the Herbarium of Desert Research Center (CAIH).

Data analysis

For the analysis of the elevation-richness relationships, we calculated the species richness per plot based on the species lists. We also calculated species richness for species subgroups, i.e. for woody, herbaceous, annual, perennial, common, and rare species. Common and rare species were defined according to a study on the vegetation of Gebel Elba National Park by Ahmed (1999). We also calculated the Shannon index for perennial species per plot based on the abundance.

Studies of elevation-richness relationships commonly use ordinary least-squares regression or Generalized Linear Models using polynomials to identify linear or unimodal relationships. However, patterns including a plateau as described by Grytnes and McCain (2013) are difficult to identify due to the low flexibility of these models. Hence, in order to be as flexible as possible, we applied Generalized Additive Models (GAM) with a Poisson distribution to describe the relationship between elevation and species richness for all single wadis and different wadi combinations, i.e. Marafai and Yahmib, mountain wadis, as well as all wadis together. We checked the residuals of the GAM models for spatial autocorrelation using a Moran´s I correlogram but no effects were detected. We fitted all GAMs using the *mgcv* package (Wood, 2011) in the statistical software R 3.5.0 (R Core Team, 2018).

Results

In total, we recorded 157 plant species (102 perennials and 55 annuals) belonging to 52 families (Appendix 3). The most common families were Fabaceae (9%), Poaceae (8%) and Asteraceae (8%). Of all recorded species, 41% were woody species such as *Acacia mellifera*, *Ephedra ciliata* and *Lycium shawii,* while 59% of the total recorded species were herbs such as *Forsskaolea tenacissima*, *Rumex vesicarius* and *Zygophyllum simplex*. Few species of the total recorded taxa were common species (36 species), while 121 species were rare among them *Grewia tembensis, Jasminum fluminense* and *Viola cinerea*. Most of the recorded plant species were found in the three mountain Wadis (155 species).

The numbers of species varied between the three wadis Marafai, Acow and Kansisrob (131, 98 and 71 plant species, respectively). The lowest number of plant species was recorded in Wadi Yahmib (26 plant species). It was noticed that deciduous trees like *Acacia tortilis* and *Balanites aegyptiaca* dominate the lower wadis, i.e., Yahmib and Kansisrob, while evergreen trees as *Ficus cordata* and *Olea europaea* grow in the higher wadis (> 300 m), i.e., Acow and Marafai.

The elevation-richness relationship for all combined wadis showed an increase between 130 m and 350 m in elevation and then remained at a plateau until 680 m in elevation (Figure 7e). The combination of Wadi Marafai and Wadi Yahmib showed a strong increase and then a pattern of levelling off to a plateau above 400 m in elevation (Table 1). The mountain wadis showed a linear pattern with estimated degrees of freedom (edf) value of 1.00 (Table 1).

A strong variation in richness was observed for the mountain wadis Wadi Marafai the richest, with an average of 15 species (Figure 7a). However, the single wadis did not show a significant pattern, except Wadi Yahmib which revealed a strong linear increase in species richness with elevations (Figure 7a-d). The linear pattern is demonstrated by an edf =1, as shown in Table 1, which means that a linear pattern instead of a more complex pattern best fits the data in the GAM (Wood, 2011). It is apparent from Table 1 and Figure 8 that GAM regression for all species subgroups increased significantly at lower altitudes and showed non-linear patterns, often similar to the overall elevation-richness pattern observed.

Rare species showed the strongest increase with the elevation, although with an edf of 2.84 hence being more complex than a linear pattern. Annual species showed a low average of species number per plot (5 species). Meanwhile, it is noticed that in Wadi Yahmib with its three main tributaries, woody, herbaceous, common, and perennial species showed high plateau patterns comparable to the total species richness. Shannon diversity for perennials reached its maximum at 350-400 m and then remained at a plateau until 680 m in elevation. The presence of monodominant species caused many zero valued points at lower elevations (Figure 7f). The variation in the Shannon diversity was reduced when compared to the pattern for species richness (Figure 8a).

Table 1. Regression results of species richness obtained from GAM. GAM models were done for single wadis, combinations thereof and all wadis, different species subgroups, and perennial Shannon index for all wadis. edf = estimated degrees of freedom (1 = linear pattern, 2 = unimodal pattern, > 2 = complex pattern), Chi² = Chi² test statistic, p-value for the Chi² test.

Wadi	**Plant type**	**No. of species**	**Plots**	**R^2**	**edf**	**Chi^2**	**P-value**
Marafai		131	56	-0.01	1.00	1.31	0.25
Acow		118	28	-0.04	1.00	0.07	0.80
Kansisrob		67	21	-0.05	1.00	0.17	0.68
Yahmib		25	28	0.47	1.00	21.38	<0.001
Marafai+Yahmib		137	84	0.41	2.91	124.90	<0.001
Mountain wadis		155	70	-0.001	1.00	1.92	0.17
All wadis		157	84	0.27	2.91	79.79	<0.001
	Perennial (P)	102	84	0.28	2.94	59.30	<0.001
	P Shannon index	102	84	0.47	2.81	17.09	<0.001
	Annual	55	84	0.14	2.17	24.32	<0.001
	Woody	64	84	0.35	2.85	51.96	<0.001
	Herbaceous	93	84	0.11	2.81	32.24	<0.001
	Rare	121	84	0.29	2.84	66.12	<0.001
	Common	36	84	0.18	2.88	32.91	<0.001

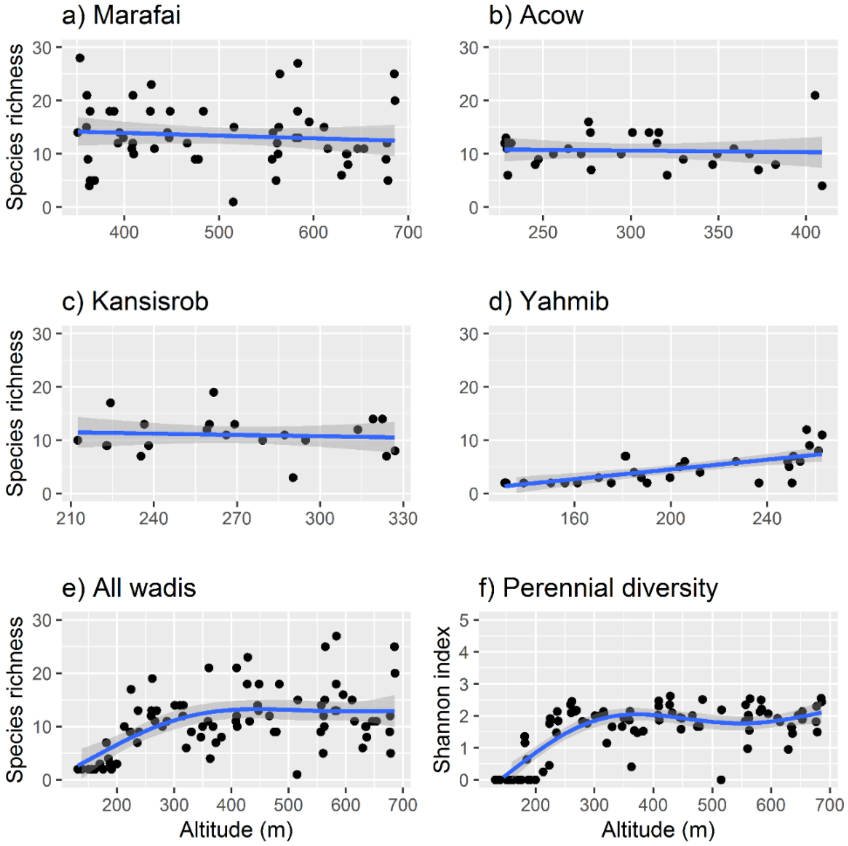

Figure 7. Elevation-richness pattern for vascular plants in Wadi Yahmib and its tributaries, Gebel Elba. (a-d) The GAM models for each single wadi do not show significant pattern except for the Wadi Yahmib. (e) GAM model for all wadis together exhibiting an increase at lower elevations and a plateau in species richness at higher elevations. (f) Shannon index of perennial species for all wadis.

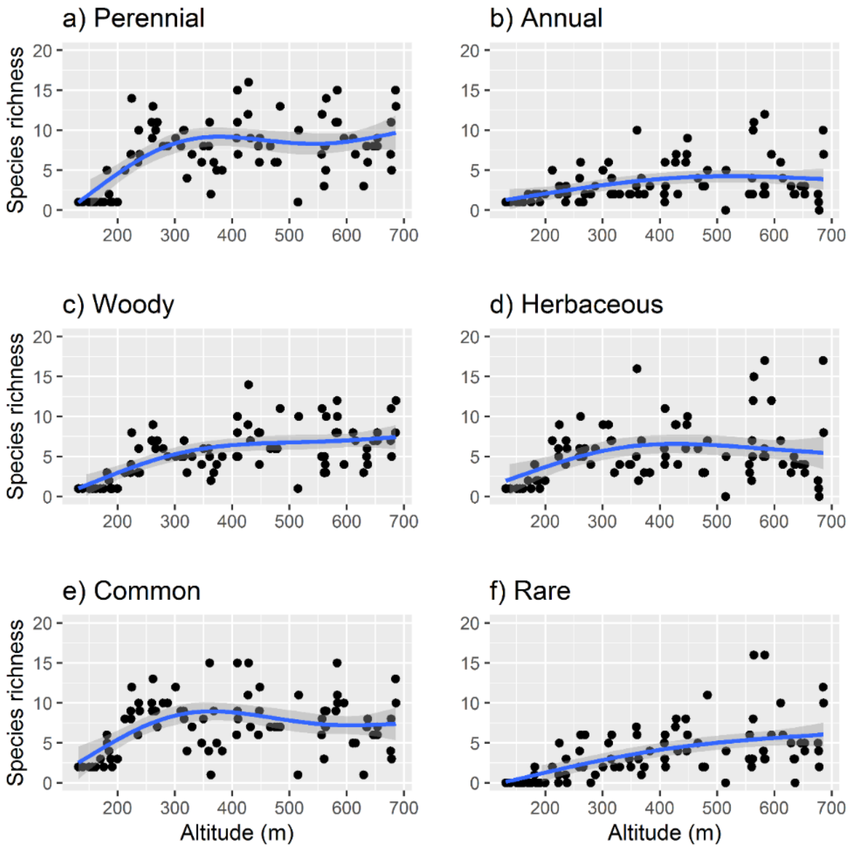

Figure 8. Elevation-richness pattern for different subgroups of vascular plants in Wadi Yahmib and its tributaries, Gebel Elba. Life form "perennial species (a), annual species (b)", growth form "woody species (c), herbaceous species (d)", "common species (e), and rare species (f)".

Discussion

A unimodal pattern with a high species richness at intermediate elevations has often been considered to be a general pattern for plants in high arid mountains (e.g. Hegazy, El-Demerdash, & Hosni, 1998; Hegazy, Lovett-Doust, Hammouda, & Gomaa, 2007; Brinkmann, Patzelt, Dickhoefer, Schlecht, & Buerkert, 2009). This pattern has been also reported for wadis in arid mountains with short altitudinal gradients, i.e. less than 1000 m (Abd El-Ghani & Abdel-Khalik, 2006; El-Keblawy, Khedr, & Khafaga, 2016). These studies related the high species richness at intermediate elevations to probably be more climatically preferential for plant growth and diversity than at either lower or higher altitudes. However, our results indicated that plant species richness did not follow a unimodal pattern for wadi drainage systems of Gebel Elba.

We found a strong increase in species richness from low to medium elevations followed by a plateau for medium to high elevations. Similar observations of a high elevation plateau in species richness were found only in two other studies so far; at Gebel Shams, Oman, between 1000 m and 3000 m (Ghazanfar, 1991) and in the dry inner valley of the Himalayas in Nepal between 3000 m and 4000 m (Panthi, Chaudhary, & Vetaas, 2007). However, the plateau we observed occurred at a much lower elevation (100-700m) on the low, arid mountain Gebel Elba (1400 m) in south east Egypt.

This elevation pattern could be related to specific species subgroups, i.e., life forms, life history types, or being a cause of the commonness and rarity of plants, which would imply that only specific plants have an impact on the actual observed pattern. Studies that test elevational patterns of different life forms, e.g., therophytes, chamaephytes or phanerophytes, often find divergent patterns between the life forms (Pavón, Hernández-Trejo, & Rico-Gray, 2000; Mahdavi, Akhani, & Van der Maarel, 2013; Moradi, Attar, & Oldeland, 2017).

In our study area, all species subgroups increased significantly along the gradient and showed non-linear patterns. Most of the rare species are the least resistant to drought and are confined to the highest zones of the north slopes of Gebel Elba. The higher elevations are less stressful and contain diverse microhabitats support the growth of many rare species (Zahran & Willis, 2009). Most of herbaceous and annual species are often rare in the area. Annual species showed a low average of species number, i.e. five per 100 m^2, as is common in arid regions; annuals grow for a short period after occasional winter precipitation (El-Keblawy, Khedr, & Khafaga, 2016). Meanwhile, it is noticed that perennial and woody species are common in Gebel Elba. Woody perennial species showed a strong increase in species richness from low to medium elevations followed by a plateau for medium to high elevations comparable to the total species richness. This is remarkable as tree and shrub diversity in Gebel Elba is much higher than in any other region of Egypt (Boulos, 2008). However, it is clear that the different species sub groups all behave similarly and thus all contribute to the observed pattern.

The environmental heterogeneity hypothesis is one the more recent hypotheses that try to explain elevational richness pattern. Indeed, the variation in species richness in the upper wadis seems to be connected to a change in topography. In contrast, the lower part of the gradient consists of open sandy plains with little variation in topography, thus offering lower diversity in habitats and less ecological niches species can dwell in (Zahran & Willis, 2009).

The mountain wadis cover a variety of microhabitats such as wadi beds, side slopes, cliffs, and soil pockets (Gomaa, 2014; Hegazy & Lovett-Doust, 2016). Furthermore, the topography strongly changes in the upper wadis, e.g. the wadis become narrower, valley slopes become steeper, offering more shaded areas where tree growth is supported. Such a high diversity in habitats promotes species richness. Hortal et al. (2013) described that local richness will monotonically increase with habitat diversity and level off but not decline when approaching the regional richness. Also, Stein, Gerstner, and Kreft (2014) described environmental heterogeneity, and in particular habitat diversity, as an important driver of species richness.

In relation to elevational gradients, Grytnes and McCain (2013) found it difficult to generalize habitat heterogeneity as a driver in elevation-richness studies as the effects might depend too much on the life form and the scale of the study. Yet, as we showed with this study, the life forms all behave similar and the small scale of the study actually should decrease the impact of strong climatological gradients.

Hence, the environmental heterogeneity hypothesis, in form of a higher diversity in microhabitats could explain our observed pattern. As we did not measure the heterogeneity of habitats but only observed the obvious differences in the environment, further studies should specifically focus on measuring habitat diversity along the wadi system in Gebel Elba.

Another hypothesis that could explain our pattern is the climatic stress hypothesis (Grytnes & McCain, 2013). Climatic harshness often acts as a filter and reduces the species pool and thus species richness. In Wadi Yahmib and its tributaries, the lower wadis (W. Yahmib and W. Kansisrob) are the most stressful due to strong evapotranspiration and species richness is reduced. An increase in elevation is then accompanied by a reduction in stresss caused by topography and the strong differences between the open plains and the mountain wadis.

Complex topography may provide refugia, allowing species to remain in areas of suitable microclimate where regional climatic conditions become less suitable (Bennie, Huntley, Wiltshire, Hill, & Baxter, 2008; Stewart & Lister, 2001). After splitting the dataset into single wadi subsets; the desert wadi showed a linear increase in plant species richness, while the mountain wadis did not show any significant pattern. On the other hand, all mountain wadis taken together showed a non-significant linear effect. Thus, it seems that the observed plateau pattern represents the transition from desert to mountain wadi systems.

However, increase in richness in mountain wadis with comparable topography remains low, and has a high variation effectively producing a plateau. Hence, we see the climatic harshness at the lower end of the gradient to be responsible for low number of species and the steep increase in species richness to be the effect of stress-release when reaching the mountain wadis. The relatively long plateau (i.e. from 350 – 680 m) then could be explained by similar climatic conditions throughout the mountain wadi system. There is no data on temperature or relative humidity for the wadis, which could demonstrate the change in the evapotranspiration pattern. We encourage further studies at Gebel Elba to focus on quantifying this environmental gradient with temperature and relative humidity data loggers.

The most important parameter controlling plant abundance and distribution in arid regions is water availability or moisture (Jürgens, Burke, Seely, & Jacobsen, 2003). Körner (2003) stated that moisture increase, and evapotranspiration decrease with elevation in mountain regions. In our study area, water availability increases with elevation while temperature and solar irradiance are considerably lower in the higher elevations. However, Gebel Elba receives low amount of water after winter rainfall, big granite boulders at higher elevations increase water accumulation between rocks and the forming of springs in wadi beds. In addition, the higher elevations of Gebel Elba receive orographic precipitation in the form of dew, mist and clouds (Hegazy & Lovett-Doust, 2016).

In total, higher elevations of Gebel Elba could receive precipitation up to 400 mm of rain per year (Kamel, Ghazaly, & Callmander, 2015), providing the favorable conditions for dense vegetation growth, especially evergreen tress such as *Ficus cordata*, *Olea europaea* and *Rhus flexicaulis*. On the other hand, growth of scattered vegetation dominated by more xeric trees such as *Acacia tortilis* and *Balanites aegyptiaca*, with deep root system to reach the ground water, occurring in the wide desert plain downstream of Wadi Yahmib indicate that these areas are the most stressful. Our findings also concur with the elevational climate model for dry mountains proposed by Grytnes and McCain (2013; their Figure 1b) which states that water availability shows a unimodal pattern. Due to the short elevational gradient studied, it seems likely that we might have reached the peak of a truncated unimodal curve. Future studies should try to extend the gradient, if possible, to the peak at 1400m, in order to better understand the overall plant species richness pattern at this important mountain range of south east Egypt.

Conclusion

In this study, we analyzed the plant richness pattern in four connected wadis of the arid mountain Gebel Elba in Egypt. Several studies reported the general unimodal pattern of plant species richness for arid mountains. However, we found a rare elevation-richness pattern for a low, arid mountain. The pattern is characterized by an increase in species richness followed by a plateau of species richness at higher elevations. It was independent of life forms, growth forms or abundance pattern. When single wadis were analyzed, only the lowermost desert wadi showed a linear increasing trend in species richness. We explain this increase in species richness as a result of reduced climatic stress and an increase in water availability. Furthermore, specific to our study area, orographic precipitation, greater habitat diversity in the mountain wadis and decreasing irradiance might also have contributed to the observed pattern. Thus, we support the climatic stress hypothesis and the environmental heterogeneity hypothesis in shaping the observed pattern of plant species richness for this arid mountain.

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Chapter Three

Plant communities and their environmental drivers on an arid mountain, Gebel Elba, Egypt

Maged M. Abutaha, Ahmed A. El-Khouly, Norbert Jürgens & Jens Oldeland

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Abstract

Aims: Gebel Elba is an arid mountain range supporting biological diversity that is incomparable to any other region of Egypt. This mountain has a vegetation structure and floristic community similar to the highlands of East Africa and the southwestern Arabian Peninsula. We aimed to provide the first classification of the vegetation units on Gebel Elba and identify the environmental factors controlling their distribution. **Study area:** Wadi Yahmib and its tributaries, which drain the north-western slopes of Gebel Elba, south-eastern Egypt. **Methods:** On the basis of 169 relevés, we used TWINSPAN to classify the perennial vegetation. We calculated separate GAMs for the deciduous and evergreen species to describe the patterns for each leaf strategy type with elevation. We used CCA to quantify the relationship between the perennial vegetation and the studied environmental factors. To estimate diversity and our sampling strategy, we used rarefaction curves for species richness. **Results:** We identified seven communities along the elevational gradient of Wadi Yahmib and its tributaries. We found that each community was restricted to a confined habitat depending on its drought resistance ability. Deciduous *Vachellia* woodland was the main vegetation type on Gebel Elba, while evergreen *Olea* woodland appeared in small fragments at higher elevations. We analysed the distribution patterns of deciduous and evergreen trees along the elevational gradient. We found a turnover at 500 m, indicating a potential ecotone between the *Vachellia* and *Olea* woodlands that was occupied by a *Ficus* community. CCA revealed the importance of altitude and soil quality in determining the vegetation structure of Gebel Elba. The species richness increased with elevation as a result of reduced stress and increased water availability at the upper wadis. **Conclusions:** This study identified seven vegetation units in the study area and showed the importance of orographic precipitation, soil quality and the complex topography in determining the habitats.

Taxonomic reference: Boulos (2009); names updated according to Plants Of the World Online (POWO 2019).

Abbreviations: CCA = Canonical Correspondence Analysis; GAM = Generalized Additive Model; TWINSPAN = Two Way Indicator Species Analysis.

Keywords: *Acacia*, Afromontane forest, classification, ecotone, Eritreo-Arabian, soil, vegetation, woodland

Introduction

The Eastern Desert of Egypt is characterized by coastal mountain ranges running parallel to the Red Sea. The most biodiverse mountain range in the region is the Gebel Elba in the south-eastern corner of Egypt, on the border between Egypt and Sudan (Kassas and Zahran 1971; Abd El-Ghani and Abdel-Khalik 2006). The flora of the Gebel Elba range is much richer than those of other coastal mountain ranges. In total, 458 plant species have been collected within the area of Gebel Elba, representing almost 21% of the Egyptian flora (Boulos 2008; Zahran and Willis 2009). The other mountain ranges overlooking the Red Sea are less rich in plant diversity, with less than 130 species recorded in total (Zahran and Willis 2009).

The proportion of Afrotropical elements on the Gebel Elba is much higher than those in any other region of Egypt (Abd El-Ghani and Abdel-Khalik 2006; Al-Gohary 2008a). This range represents the northern limit of the Eritreo-Arabian province and the Sahel regional transition zone in Africa (Zohary 1973; White 1983), including the Somalia-Masai regional centre of endemism (White 1983; White and Léonard 1991; Boulos 2008). Thus, the Gebel Elba is considered one of the seven main phytogeographical regions of Egypt (Boulos 2009).

The biodiversity of the Gebel Elba region is unique to Egypt, and many globally threatened species are found there (IUCN 2019). In 1986 this area was declared the Gebel Elba National Park, covering nearly 36,000 km^2. Gebel Elba Mountain is the core part of this protected area. The richness of vegetation on Gebel Elba is related to its orographic precipitation. The proximity of Gebel Elba to the sea and its windward position create a unique ecosystem, known as a “mist oasis”, that is found nowhere else in Egypt, but is comparable to similar ecosystems in Erkwit, Sudan, and the southern part of the Arabian Peninsula (Kassas 1956; Kürschner et al. 2004; Hegazy and Lovett-Doust 2016). Because of moisture-laden north-eastern winds, the vegetation is much richer on the northern slopes of Gebel Elba than on the southern slopes (Zahran and Willis 2009). Thus, both species richness and abundance are much higher on the mountain than in the exposed open desert (Abutaha et al. 2019). On the foothills of the mountain, *Vachellia tortilis* (synonym: *Acacia tortilis*) forms an extensive natural woodland landscape (Zahran and Willis 2009).

Gebel Elba has a unique phytogeographic position and a floristic composition that is more complex than the total floral composition of the rest of Egypt. This arid granite mountain bears floristic similarities and shares common vegetation with the neighbouring mountains of East Africa and the southwestern Arabian Peninsula (Kassas 1956; Hegazy et al. 1998). Gebel Elba and the southwestern Arabian highlands represent the northern limit of Eritreo-Arabian vegetation (Zohary 1973). The vegetation of the Eritreo-Arabian province is continuous and changes from deciduous *Vachellia-Commiphora* woodland at lower elevations to evergreen Afromontane forest of *Juniperus procera* at elevations above 2000 m (Zohary 1973; Kürschner et al. 2008; Deil 2014; Berhanu et al. 2018).

The evergreen woodland dominated by *Olea europaea* subsp. *cuspidata* represents a transition zone between the lower montane *Vachellia-Commiphora* woodland and the upper montane *Juniperus procera* forest (White 1983; Kürschner et al. 2008). Comparably, Zohary (1973) recognized three altitudinal zones of Afrotropical vegetation in Gebel Elba: a lower zone of *Vachellia-Ziziphus* (pseudo-savanna vegetation), a middle zone of *Vachellia-Commiphora* (savanna vegetation), and a montane zone of *Olea-Ficus* forest fragments. Zahran and Willis (2009) found three altitudinal belts of vegetation on the northern slopes of Gebel Elba: a lower zone of *Euphorbia cuneata*, a middle zone of *E. nubica* and a higher zone of moist habitat vegetation. Within this higher zone, many evergreen species were recorded, such as *Euclea racemosa*, *Dodonaea viscosa*, *Carissa spinarum* and *Olea europaea* subsp. *cuspidata* (White 1983). The vegetation of Gebel Elba changes from *Vachellia tortilis* woodland at lower elevations to forested vegetation at middle and higher elevations (Abd El-Ghani and Abdel-Khalik 2006; Zahran and Willis 2009). The elevational gradient of Gebel Elba is known to harbour a relatively large number of tree species. Two prominent leaf strategy types occur (deciduous and evergreen). However, these types do not occur evenly across the elevational gradient; evergreen trees are prominent in the upper altitudes, while deciduous species are more common in the lower, arid parts of the gradient (Abutaha et al. 2019). The ecotone between evergreen woodland at higher elevations and deciduous woodland at lower elevations has not been studied (White 1983; Berhanu et al. 2018).

Most of the previous studies on Gebel Elba have mainly focused on wadis, which are temporary waterways that collect run-off water from the surrounding slopes and contain several microhabitats (Zohary 1973; Gomaa 2014), where vegetation is rich and continuous (Ahmed 1999; Zahran and Willis 2009; Abutaha et al. 2019). While the lower elevations of wadis show recognizable features of zonal communities, the vegetation on the higher slopes is more variable due to minor differences in habitat and recognizing clearly defined zonal communities is difficult (Zahran and Willis 2009). A classification of wadi vegetation is still lacking. Additionally, no agreement has been reached regarding the vegetation zonation of the northern wadis of Gebel Elba (Al-Gohary 2008a; Zahran and Willis 2009). The altitudinal range of plant communities and information on environmental drivers are mostly unavailable. Thus, there is a need to identify the vegetation units of Gebel Elba and the environmental drivers controlling their distributions.

In this study, we aimed to describe the altitudinal zonation of the defined plant communities, their compositions and the relations to environmental factors in wadis on the northern slopes of Gebel Elba. This classification was based on 169 relevés which have not been previously sampled on this mountain. We also aimed to analyse the distribution patterns of deciduous and evergreen trees along the elevational gradient to identify a transition zone between the two different leaf strategy types representing different phytoregions. Finally, we also compared our findings on the diversity between the different vegetation communities with previous studies.

Materials and Methods

Study area

Gebel Elba Mountain (1435 m) is located at 22.25° N and ranges from 36.25° to 36.43° E, nearly 15 km west of the Red Sea coast, south-eastern Egypt (Figure 9). The mountain itself is formed of a group of granite peaks in the shape of a square with sides of approximately 15 km by 15 km. From the central peak, drainage lines (wadis) radiate in all directions (Ball 1912). The principal wadi on the northern slopes of Gebel Elba is Wadi Yahmib (Zahran and Willis 2009). Yahmib is located at the foothills of the mountain and receives water mainly from three mountainous tributaries: Wadis Marafai, Acow, and Kansisrob, which drain the western-northern flanks of Gebel Elba (Figure 9). The substrates of the wadis vary with an elevation gradient which increases from east to west; the substrate of Wadi Yahmib is fine sand, that of Wadi Kansisrob is coarse gravel, and Wadis Acow and Marafai, at higher elevations, have large granite boulder substrates (Abutaha et al. 2019).

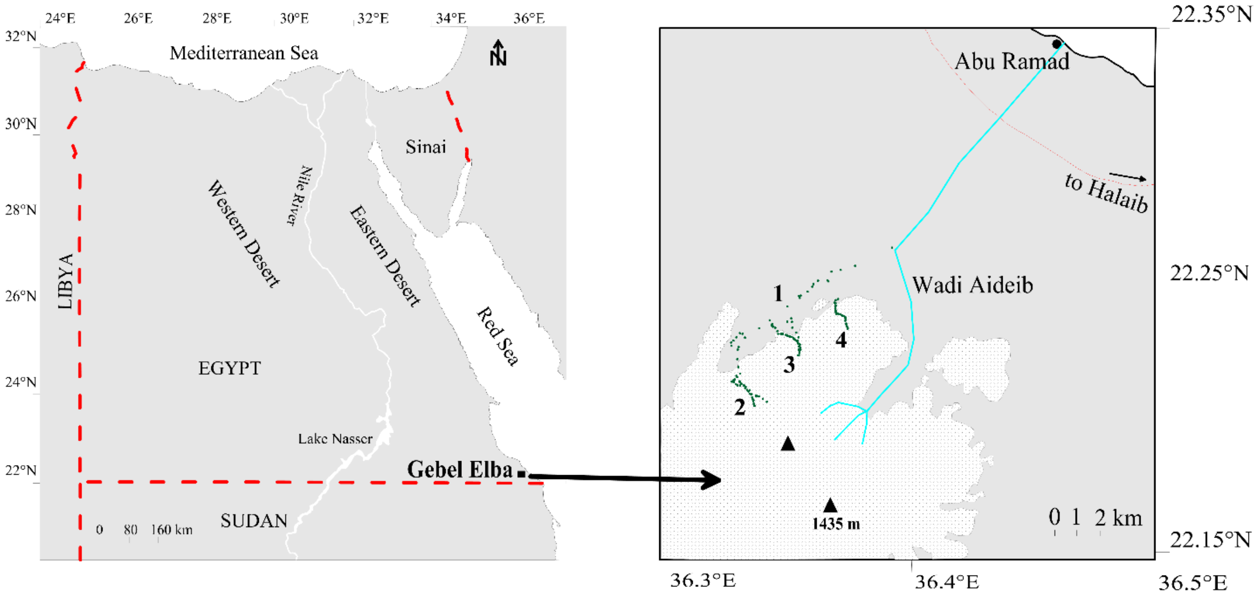

Figure 9. The location of Gebel Elba in Egypt (left) and the distribution of the vegetation relevés (green dots) surveyed for this study in Wadi Yahmib and its tributaries at the northern slopes of Gebel Elba (right); Wadi Yahmib (1), Wadi Marafai (2), Wadi Acow (3) and Wadi Kansisrob (4).

Gebel Elba has a hyper-arid climate (Harris et al. 2014). The climatic aridity of the region is expressed in the climate diagram between 1985-2015 (Figure 10) adopted from Walter and Lieth (1967). The temperature ranges between 15.3 °C and 38.1 °C, with a mean annual temperature of 26.1 °C. The area received less than 40 mm of rainfall per year, mainly from winter rainfall and light summer rainfall (Figure 10). However, Gebel Elba receives up to 400 mm of orographic precipitation per year (Goodman et al. 1989; Kamel et al. 2015). Gebel Elba is influenced by winter rain and summer monsoons, dew falls regularly, clouds and mist shrouds the mountain (see Figure 13A-B). Although this mountain is surrounded by an extremely arid desert, orographic precipitation provides a climatic condition that is favourable for rich plant growth (Ball 1912; Hegazy and Lovett-Doust 2016).

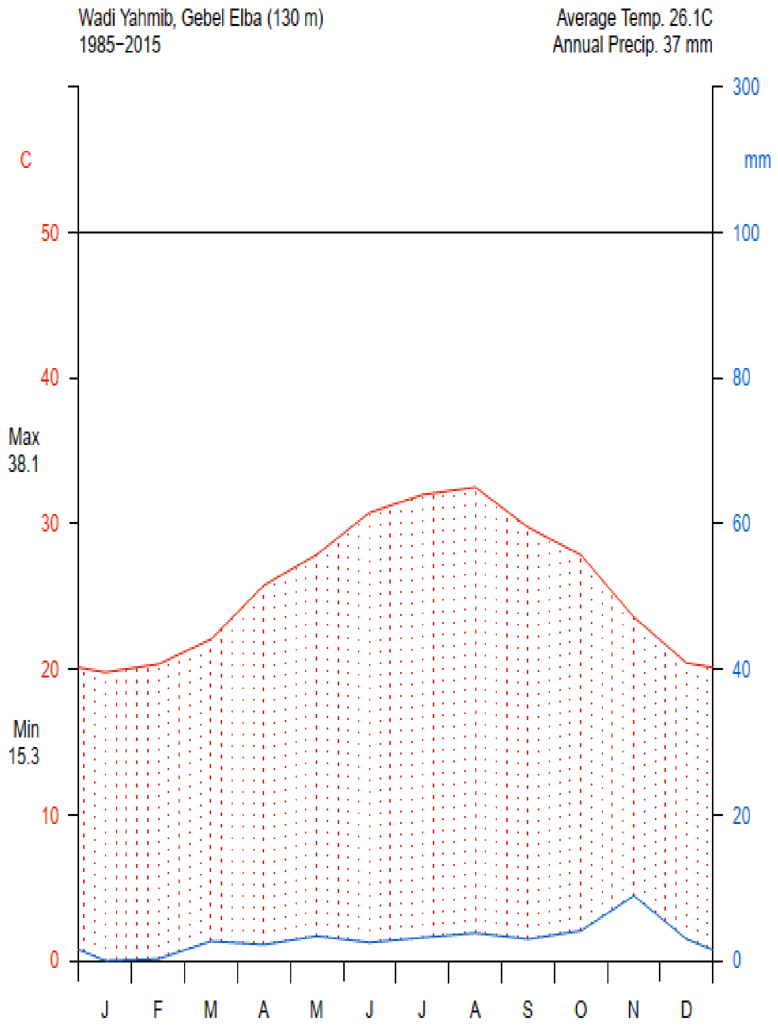

Figure 10. Climate diagram of Wadi Yahmib, Gebel Elba based on CRU datasets TS 4.01. Data is for the period from 1985 to 2015. The upper red line stands for mean monthly temperature of 26.1°C (left axis); numbers beside the axis are the mean monthly maximum and minimum temperatures. The lower blue line stands for precipitation (right axis). Area shaded with dots (dotted area), above the precipitation line, and below the temperature line, indicates a dry period.

Vegetation sampling

We conducted vegetation sampling on five visits; two in 2013, two in 2015 and one in 2016. The visits were made in January or March after the rainy season. We sampled 169 geo-referenced vegetation relevés that were marked with a GPS device (Garmin eTrex 30x). The relevés (10 m × 10 m) were distributed along transects in the four studied wadis, i.e., Yahmib, Marafai, Acow, and Kansisrob (see Abutaha et al. 2019). Locations of the relevés were selected randomly during the field work. For each relevé, we assembled a list of all vascular plant species that were present. We noted the growth forms of the listed species and identified the life forms according to Raunkiaer's system of classification (Raunkiaer 1934). Furthermore, we visually estimated the percentage cover of perennial species in each relevé. Owing to the arid climatic conditions of the study area, annual species were only noted as being present/absent. The nomenclature of the plant species followed Boulos (1999, 2000, 2002, 2005, 2009). We updated the list of taxonomic names according to Plants Of the World Online (POWO 2019) provided by the Royal Botanic Gardens, Kew. Voucher specimens were deposited in the Herbarium of Desert Research Center (CAIH) and the Herbarium Hamburgense (HBG).

Soil sampling and analysis

We took mixed soil samples from the surface layer (0 - 10 cm) of each relevé. We air-dried and analysed the samples to determine the physical and chemical soil properties. First, we determined soil texture by sieving with successively finer meshes (Estefan et al. 2013; AG Boden 2005). Second, we prepared soil suspensions by the addition of distilled water in a 1:1 ratio and stirring continuously for 2 hours, then measured the pH and electrical conductivity (EC) of the suspensions with a pH meter (Jenway 3510) and conductivity meter (Jenway 4510), respectively (Hendershot et al. 2008; Miller and Curtin 2008). We then filtered the soil suspensions and used the extracts to determine the soluble mineral contents.

The analyses of major constituents in the soil extracts (calcium, magnesium, sodium, potassium, sulfate and chloride) were determined using an ion chromatography system, IC (Dionex, ICS-1100). Carbonate and bicarbonate ions were estimated with the titrimetric method (Jackson 1967; Estefan et al. 2013). Finally, we estimated the organic matter content by the weight loss-on-ignition method (Schulte and Hopkins 1996; Combs and Nathan 1998) and determined $CaCO_3$ volumetrically using a Collin's calcimeter (Piper 1950).

Data analysis

Multivariate analysis procedures

For the floristic classification of the relevés, we imported a vegetation matrix, including the percentage cover values of perennial species, into the software Juice, version 7.0 (Tichý 2002), and used the TWINSPAN classification (Hill 1979). We set the minimum group size to 3, and used percentage cover values of 0, 5 and 50 as cut levels. As a fidelity measure, we used the phi value (De Cáceres and Legendre 2009). The calculations of the phi values were adjusted for equal group sizes. If the phi value exceeded 0.25, a species was considered diagnostic, and if the phi value was > 0.50, the species was considered highly diagnostic; the p-value of Fisher's exact test was 0.05. Species with a frequency higher than 70% were considered as constant.

To measure correlations between the perennial species and relevant environmental drivers, we used canonical correspondence analysis (CCA) for the ordination (Ter Braak and Prentice 1988). We selected altitude and edaphic factors after the exclusion of collinear variables (anions and cations were highly correlated with EC). We applied biplot scaling and the species were centred. Only perennials with significant phi values > 0.25 are shown in the ordination. We performed CCA using CANOCO, version 5.0 (Ter Braak and Šmilauer 2012).

To better describe and interpret the results of the classification, we used analysis of variance (ANOVA) and Tukey's post hoc tests for the pairwise comparisons to test for differences in the soil physical and chemical parameters between the identified plant communities. Before the statistical tests, each soil parameter was logarithmically or square root transformed in cases where the data did not follow a normal distribution. The analyses were carried out using R software (R Development Core Team 2018).

Diversity

To evaluate diversity and our sampling strategy, we used rarefaction and extrapolation sampling curves for species richness to estimate the completeness of our vegetation samples (Chao et al. 2014). We performed all calculations for the complete datasets (perennial and annual species) of the four wadis (transects) and for the identified plant communities. We constructed the rarefaction curves with the R-based interactive online programme *iNEXT* (Chao et al. 2016).

Distribution of deciduous and evergreen trees along the elevational gradient

We wanted to determine the altitude at which the change from deciduous to evergreen species occurred. To that end, we first classified each tree species as either deciduous or evergreen and determined the relative percentage of each leaf strategy type (LST) for the estimated plant cover per vegetation relevé along the elevation gradient from 130 to 680 m (14 relevés / 100 m). Then, we calculated separate generalized additive models (GAM) for each LST using the *mgcv* package (Wood 2017) with a binomial distribution and a cubic regression spline for elevation to model the relationship between the percentage of respective LST per relevé and elevation in metres. We plotted the respective models using the *ggplot2* package (Wickham 2016) in R 3.5.0 statistical software (R Development Core Team 2018).

Results

Floristic pattern

We recorded 162 vascular plant species (104 perennials and 58 annuals) belonging to 53 families (Appendix 4). The most common families were Fabaceae (9%), Poaceae (9%), Asteraceae (7%) and Malvaceae (7%). Poaceae is one of the species rich families in the study area. However, the grasses were less abundant (frequent) and were represented by many annual species (Appendix 5; Tables S1-S7 in Supplementary material 1). In total, 84% of the recorded species were found in the mountain tributaries feeding Wadi Yahmib.

The number of species varied among the three tributaries: in Marafai, Acow and Kansisrob, there were 131, 99 and 76 species, respectively. The lowest number of plant species (n=26) were recorded in Wadi Yahmib itself, located in the open sandy plain. The dominant life forms were therophytes (36%), phanerophytes (27%) and chamaephytes (24%). Of all perennial species, 63% were woody species, including *Vachellia tortilis, Balanites aegyptiaca* and *Dodonaea viscosa*, while 37% were herbs, such as *Forsskaolea tenacissima*, *Cucumis prophetarum* and *Senna italica*. We recorded 21 tree species in Wadi Yahmib and its tributaries (Appendix 4).

Pattern of deciduous-evergreen trees

The response of the two LSTs, i.e., deciduous and evergreen, showed two clear decreasing and increasing patterns along the altitudinal gradient from 130 to 680 m (Figure 11). While there was a slight change below 400 m, the deciduous-evergreen ratio changed from 75/25 to 25/75 between 450 m and 600 m, indicating a potential ecotone; the switch between both LSTs was at 500 m. The smoothness of both GAMs was highly significant, demonstrating a clear pattern in the data. While there were very few evergreen species in the lower parts of the gradient (e.g., *Maerua crassifolia*), deciduous species did occur in low numbers at higher elevations, such as *Vachellia etbaica* (synonym: *Acacia etbaica*) and *V. tortilis*.

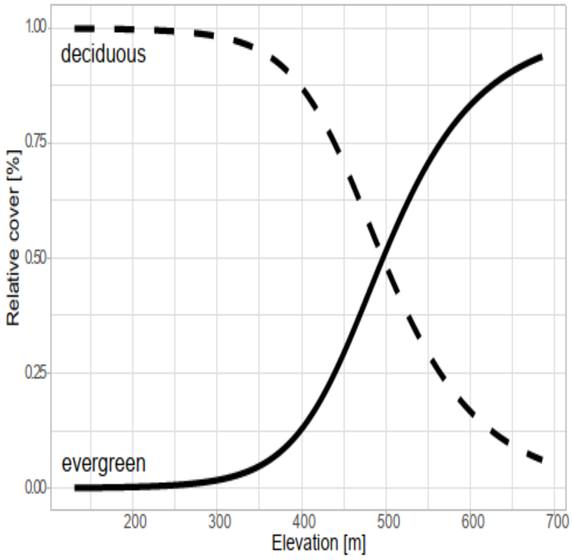

Figure 11. The relative proportions of deciduous and evergreen trees per vegetation relevé along the elevational gradient at the northern slopes of Gebel Elba. The pattern for deciduous tree species is shown as a dashed line while the evergreen tree species are represented by a solid line. The lines are the resulting smoothers of a cubic-regression GAM.

Classification

Seven woodland communities were described on Gebel Elba (Figure 12; Table 2). The first two communities (I-II) contained relevés from middle to higher elevations and were mainly composed of evergreens, while the communities (III-VII) in the lower part of the elevational gradient included relevés from low to middle elevations and were inhabited by deciduous trees (Tables 2, 3; Tables S1-S7 in Supplementary material 1). The observed communities were classified as follows.

Table 2. Synoptic table of the seven communities showing percentage constancy values of the diagnostic species and non-diagnostic species with high constancy (> 70%). Diagnostic species are highlighted in light grey and highly diagnostic species in dark grey.

Community	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**
No. of plots	20	17	36	24	15	23	34
Total no. of species	80	73	84	84	48	68	72
Perennials	50	44	55	53	25	45	40
Annuals	30	29	29	31	23	23	32
No. of diagnostic species	8	4	1	1	2	3	2
Dracaena ombet - Olea europaea **subsp.** ***cuspidata*** **community**							
Olea europaea subsp. *cuspidata*	90	12	-	-	-	-	-
Vachellia etbaica	45	-	-	-	-	4	-
Dracaena ombet subsp. *ombet*	40	-	3	-	-	-	-
Carissa spinarum	35	-	-	-	-	-	-
Searsia flexicaulis	55	35	-	-	-	-	-
Jasminum grandiflorum subsp. *floribundum*	30	-	-	-	-	-	-
Pistacia khinjuk var. *glabra*	30	6	-	-	-	-	-
Triumfetta flavescens	75	41	25	29	-	-	6
Solanum incanum - Ficus salicifolia **community**							
Ficus salicifolia	10	47	14	-	-	-	-
Solanum incanum	55	76	17	-	7	-	15
Ficus palmata	-	18	-	-	-	-	-
Diceratella elliptica	-	18	3	-	-	-	-

Vachellia tortilis **subsp.** ***tortilis*** **community**							
Vachellia tortilis subsp. *tortilis*	10	29	100	79	53	70	44
Euphorbia nubica **community**							
Euphorbia nubica	-	-	17	88	33	57	24
Forsskaolea tenacissima	25	47	19	75	53	65	21
Aerva javanica - Abutilon pannosum **community**							
Abutilon pannosum	-	24	8	8	100	48	9
Aerva javanica	-	18	11	4	67	35	6
Lycium shawii	-	18	50	50	73	39	26
Euphorbia cuneata **community**							
Euphorbia cuneata	-	6	6	17	7	87	6
Tephrosia purpurea subsp. *apollinea*	-	-	11	67	87	83	26
Delonix elata	-	6	-	-	7	30	-
Balanites aegyptiaca – Vachellia tortilis **subsp.** ***raddiana*** **community**							
Balanites aegyptiaca	-	-	11	38	13	-	85
Vachellia tortilis subsp. *raddiana*	-	-	3	8	13	9	44

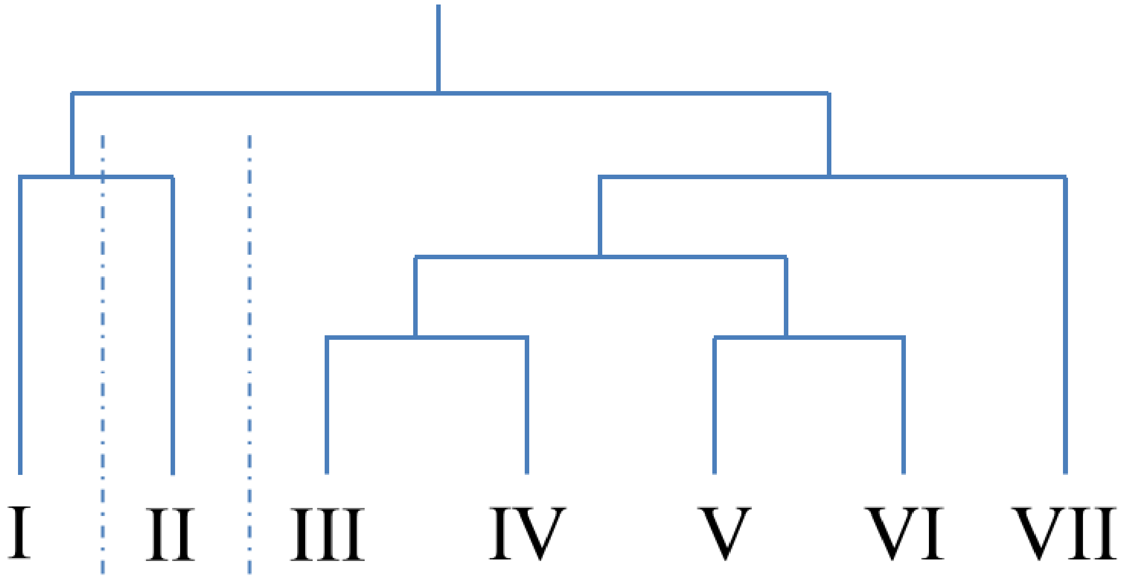

Figure 12. Showing the seven communities resulted from TWINSPAN classification.

I) *Dracaena ombet* - *Olea europaea* subsp. *cuspidata* community

This evergreen community was confined to the high elevations of Wadi Marafai, from 560 to 680 m. This community supported a high coverage of evergreen species and was characterized by six diagnostic evergreen species in total, including *Olea europaea* subsp. *cuspidata* and *Carissa spinarum* and two deciduous tree species, *Pistacia khinjuk* and *Vachellia etbaica*. The wadi bed was dominated mainly by *O. europaea* subsp. *cuspidata* (Figure 13C). The slopes were characterized by the growth of *V. etbaica* and *Dracaena ombet*. The vegetation in the wadi bed was dense and more vigorous than that occurring at lower elevations. In this community, many liana species, such as *Pergularia daemia*, *Jasminum fluminense* and *J. grandiflorum*, were climbing on olive trees. The soils of this community were often loamy sand on the side slopes and sandy loam in the wadi bed. The presence of large granite boulders increases water run-off to the main channels.

II) *Solanum incanum* - *Ficus salicifolia* community

This community was located mainly in moist habitats near flowing water or in the water courses of the high-elevation wadis, Wadis Acow and Marafai, at elevations from 346 to 550 m (Figure 13D). The vegetation consisted of two diagnostic fig trees (*Ficus salicifolia* and *F. palmata*) and two small shrubs (*Solanum incanum* and *Diceratella elliptica*). A characteristic species, *Searsia flexicaulis* (synonym: *Rhus flexicaulis*) from the former community, was also recorded in this community. The soil supporting this community was mainly loamy sand, and the organic matter content was the highest (0.41%, Table 4) of all seven communities. The organic matter content was related to the leaf litter of fig trees.

III) *Vachellia tortilis* subsp. *tortilis* community

This community was the most widespread one in the study area. The deciduous tree *Vachellia tortilis* subsp. *tortilis* was the only characteristic species (Figure 13E). This community occurred in a variety of habitats from low to middle elevations (130 to 383 m). The most common habitats of *V. tortilis* were the water channels of the wadis and gravelly terraces. This species was also abundant at the foot of Gebel Elba. The soil in this community was always sandy. The substrate deposits varied from fine sand in Wadi Yahmib to coarse sand deposits with gravel and rock detritus in the mountainous tributaries.

IV) *Euphorbia nubica* community

This community usually occurred on run-off slopes and the delta of Wadi Marafai. It was located in rocky habitats at middle elevations from 264 m to 379 m. The succulent shrub *Euphorbia nubica* was the only diagnostic species (Figure 13F). The tree layer was mainly absent on the run-off slopes, and *E. nubica* was the dominant succulent shrub, whereas *Forsskaolea tenacissima* grew on the lower run-off slopes of Wadi Kansisrob. Downward in the delta of Wadi Marafai, *E. nubica* grew in rocky outcrops between trees. We recorded the liana species *Cocculus pendulus* climbing on unhealthy trees of *Vachellia tortilis* and *Balanites aegyptiaca* in shady localities in the delta of Marafai. The soil texture was mainly loamy sand. This community had the highest silt (20.74%) and EC (1.59 mS/m) values.

V) *Aerva javanica - Abutilon pannosum* community

This community was located along the main channel of the tributary Wadi Kansisrob and occasionally downstream of Wadi Acow. It usually occurred in gravelly habitats near slopes at low elevations, from 237 to 275 m (Figure 13G). The two diagnostic species of this community were *Abutilon pannosum* and *Aerva javanica*. In this community, trees were less common, and the vegetation mainly consisted of shrubs and herbs, such as *Cucumis prophetarum*, *Tephrosia purpurea* and *Lycium shawii*. The soil was shallow, and the ground texture consisted of medium sand mixed with gravel and rock detritus. This community had the highest medium sand and pH values (38.46% and 7.73, respectively).

VI) *Euphorbia cuneata* community

This community occurred in the midstream areas of Wadi Kansisrob and was less frequent in Wadi Acow. It was often located in rocky habitats at elevations from 241 to 320 m (Figure 13H). Three diagnostic species characterized this community: two trees, *Euphorbia cuneata* and *Delonix elata*, and one herb, *Tephrosia purpurea*. The soil of this community had a high pH (7.63) and was similar to the soil of community V.

VII) *Balanites aegyptiaca* - *Vachellia tortilis* subsp. *raddiana* community

This community was located in Wadi Yahmib and in the deltas of its tributaries at elevations ranging from 196 to 361 m. It was represented mainly by patches in Wadi Yahmib (Figure 13I) and some patches in the midstream areas of its tributaries. *Balanites aegyptiaca* and *Vachellia tortilis* subsp. *raddiana* were the two diagnostic species of this community. Unlike the *V. tortilis* subsp. *tortilis* community, which occurred in several habitats, this community was usually restricted to water channels. The soil supporting this community was usually pure sand with fine soil deposits.

Table 3. Distribution of relevés, communities in the studied wadis, and the elevational gradients of the studied wadis and the seven communities (I-VII).

Communities		**Localities**				**relevés per community**
		Yahmib	**Kansisrob**	**Acow**	**Marafai**	
	Elevation	**(130 – 263 m)**	**(210 – 327 m)**	**(228 – 410 m)**	**(350 - 680 m)**	
I	**(560 - 680 m)**	--	--	--	20	20
II	**(346 - 550 m)**	--	--	9	8	17
III	**(130 - 383 m)**	11	1	16	8	36
IV	**(264 - 379 m)**	--	5	10	9	24
V	**(237 – 275 m)**	--	10	5	--	15
VI	**(241 – 320 m)**	--	17	6	--	23
VII	**(196 – 361 m)**	14	1	10	9	34
Total of relevés		**25**	**34**	**56**	**54**	**169**

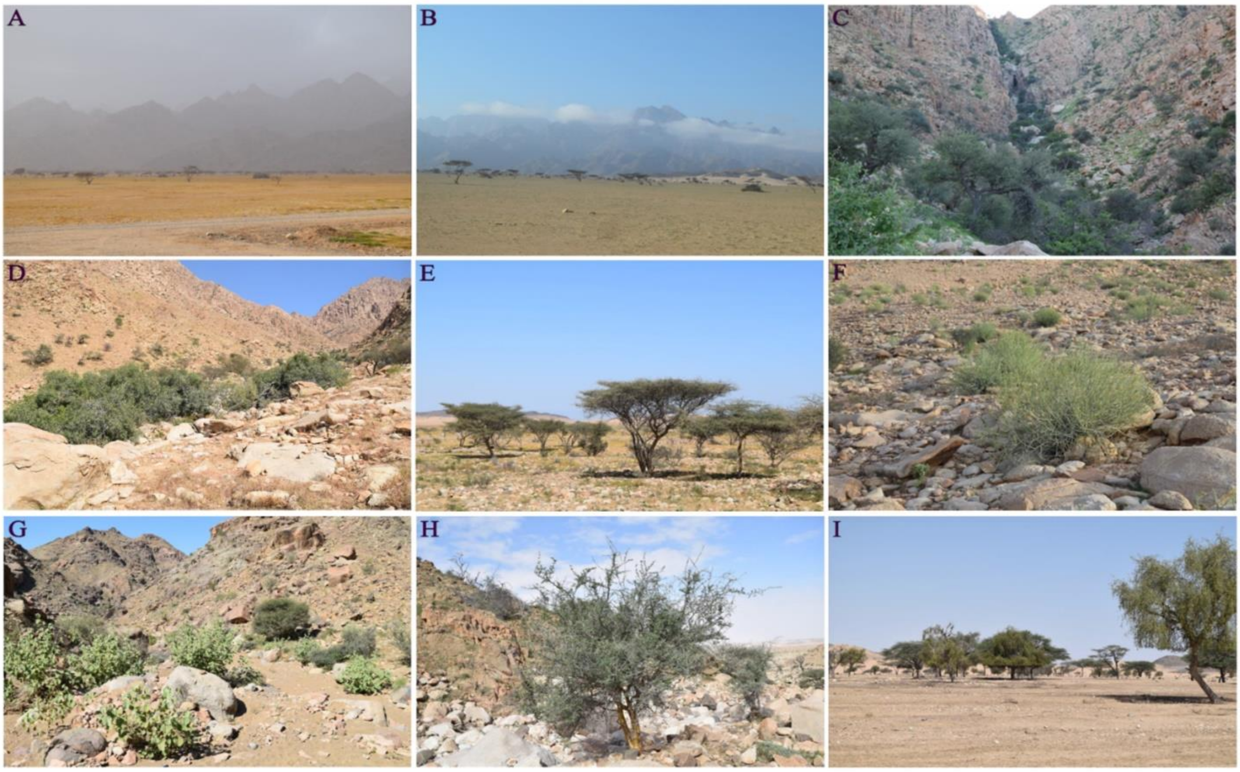

Figure 13. Representative photos showing Gebel Elba shrouded in mist (**A**) and clouds (**B**) accumulation on the Gebel Elba, and the leading species of the seven derived plant communities; *Olea europaea* subsp. *cuspidata* (**C**), *Ficus salicifolia* (**D**), *Vachellia tortilis* subsp. *tortilis* (**E**), *Euphorbia nubica* (**F**), *Abutilon pannosum* (**G**), *Euphorbia cuneata* (**H**), and *Balanites aegyptiaca* (**I**).

Environmental drivers

The soils of the study area were characterized as neutral to slightly alkaline, with the mean pH value ranging from 7.26 to 7.73 (Table 4). The soil texture was pure sand on the desert plain and changed to sandy loam at higher elevations. The EC (0.74-1.59 mS/m) and mineral contents were low. The $CaCO_3$ content was less than 3% (0.54-1.21%), and the organic matter content ranged from 0.11 to 0.41% (Table 4), which is considered very low but typical for arid ecosystems.

Table 4. Means and standard deviations for elevation and soil properties of the seven communities (I-VII). ANOVA test is for original, sqrt, or log data values, where values are not normally distributed. F-value and P-value refer to the ANOVA. Small letters denote the statistically different groups as identified by ANOVA post-hoc test.

Parameter		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**F-value**	**P-value**
	Altitude$_{.log}$	^{a} 617.45 (57.72)	^{b} 450.49 (104.09)	^{c} 285.92 (96.63)	^{c} 321.51 (57.33)	^{c} 255.13 (19.43)	^{c} 280.51 (39.37)	^{c} 278.39 (82.94)	42.33	<0.001
Soil separates	**Coarse sand.$_{sqrt}$**	^{a} 22.88 (15.63)	^{ab} 14.25 (4.81)	^{b} 10.00 (7.09)	^{ab} 12.84 (4.94)	^{b} 11.13 (8.35)	^{ab} 15.48 (7.83)	^{ab} 14.39 (8.72)	5.073	<0.001
	Medium sand.$_{sqrt}$	^{bc} 27.75 (9.71)	^{abc} 32.80 (9.02)	^{ab} 36.10 (12.59)	^{c} 27.47 (8.06)	^{a} 38.46 (9.36)	^{a} 37.73 (8.64)	^{a} 37.92 (12.37)	4.997	<0.001
	Fine sand	^{b} 26.36 (10.58)	^{ab} 33.09 (5.46)	^{a} 37.76 (6.80)	^{a} 37.69 (6.12)	^{a} 36.78 (8.81)	^{ab} 32.82 (8.54)	^{ab} 32.88 (8.05)	5.997	<0.001
	Sand.$_{sqrt}$	^{b} 76.99 (15.41)	^{ab} 80.14 (9.33)	^{ab} 83.87 (9.39)	^{ab} 78.00 (7.80)	^{a} 86.37 (7.69)	^{a} 86.03 (7.49)	^{a} 85.19 (8.16)	3.823	<0.01
	Silt.$_{sqrt}$	^{ab} 20.06 (12.63)	^{ab} 18.75 (8.32)	^{ab} 15.28 (8.62)	^{a} 20.74 (6.86)	^{ab} 13.07 (7.31)	^{ab} 13.47 (7.18)	^{b} 14.04 (7.70)	2.968	<0.01
	Clay.$_{sqrt}$	^{a} 2.62 (3.27)	^{ab} 0.95 (1.20)	^{b} 0.77 (1.00)	^{ab} 1.21 (1.29)	^{b} 0.47 (0.57)	^{b} 0.36 (0.50)	^{b} 0.57 (0.91)	4.145	<0.001
Soil chemistry	**pH**	^{b} 7.26 (0.24)	^{b} 7.36 (0.24)	^{b} 7.35 (0.23)	^{b} 7.30 (0.20)	^{a} 7.73 (0.24)	^{a} 7.63 (0.26)	^{b} 7.26 (0.26)	12.41	<0.001
	EC$_{.log}$	^{c} 0.74 (0.35)	^{abc} 0.80 (0.20)	^{abc} 1.19 (0.98)	^{a} 1.59 (1.54)	^{bc} 0.84 (0.66)	^{abc} 1.12 (1.00)	^{ab} 1.20 (0.56)	4.199	<0.001
	$CaCO_{3.log}$	^{a} 1.05 (1.06)	^{ab} 1.21 (1.56)	^{c} 0.55 (0.39)	^{abc} 0.61 (0.31)	^{c} 0.54 (0.58)	^{abc} 0.71 (0.50)	^{bc} 0.57 (0.35)	4.096	<0.001
	$CO_{3.sqrt}$	^{a} 0.03 (0.02)	^{a} 0.04 (0.03)	^{a} 0.03 (0.01)	^{a} 0.04 (0.02)	^{a} 0.03 (0.02)	^{a} 0.03 (0.02)	^{a} 0.04 (0.04)	1.541	0.168
	$HCO_{3.log}$	^{b} 0.29 (0.17)	^{a} 0.63 (0.62)	^{ab} 0.35 (0.16)	^{a} 0.47 (0.20)	^{b} 0.24 (0.10)	^{b} 0.29 (0.14)	^{ab} 0.39 (0.19)	5.045	<0.001
	Organic matter.$_{sqrt}$	^{c} 0.11 (0.08)	^{a} 0.41 (0.30)	^{c} 0.20 (0.17)	^{ab} 0.35 (0.27)	^{c} 0.15 (0.12)	^{abc} 0.23 (0.16)	^{bc} 0.21 (0.19)	6.113	<0.001
	Ca.$_{log}$	^{b} 0.05 (0.02)	^{a} 0.09 (0.05)	^{a} 0.10 (0.08)	^{a} 0.14 (0.21)	^{ab} 0.07 (0.05)	^{ab} 0.08 (0.08)	^{a} 0.09 (0.05)	5.154	<0.001
	Mg.$_{log}$	^{b} 0.03 (0.02)	^{ab} 0.07 (0.07)	^{ab} 0.04 (0.02)	^{a} 0.06 (0.04)	^{b} 0.02 (0.01)	^{ab} 0.03 (0.02)	^{ab} 0.05 (0.03)	4.038	<0.001
	Na.$_{log}$	^{b} 0.04 (0.03)	^{ab} 0.04 (0.03)	^{a} 0.07 (0.05)	^{ab} 0.06 (0.06)	^{ab} 0.04 (0.04)	^{ab} 0.05 (0.05)	^{a} 0.06 (0.03)	3.652	<0.01
	K.$_{log}$	^{c} 0.04 (0.03)	^{ab} 0.09 (0.06)	^{ab} 0.09 (0.11)	^{a} 0.12 (0.11)	^{bc} 0.05 (0.05)	^{bc} 0.07 (0.10)	^{a} 0.09 (0.07)	7.485	<0.001
	SO_4	^{a} 0.02 (0.05)	^{a} 0.02 (0.02)	^{a} 0.08 (0.12)	^{a} 0.17 (0.55)	^{a} 0.08 (0.12)	^{a} 0.08 (0.14)	^{a} 0.07 (0.07)	1.06	0.389
	Cl.$_{log}$	^{c} 0.04 (0.04)	^{bc} 0.05 (0.05)	^{ab} 0.15 (0.20)	^{ab} 0.22 (0.43)	^{abc} 0.08 (0.13)	^{abc} 0.13 (0.20)	^{a} 0.13 (0.10)	5.194	<0.001

The CCA results revealed that the edaphic factors changed with the elevational gradient (Figure 14). At the foot of Gebel Elba, the soil texture was defined primarily by fine and medium sands. High proportion of sands at low elevations led to poor water holding capacity, and thus, the EC of the surface layer increased. The vegetation in the sandy part of the gradient consisted mainly of deep-rooted tree species, e.g., *Vachellia tortilis* and *Balanites aegyptiaca*. At higher elevations on Gebel Elba, the silt and clay contents increased, thus supporting the growth of less drought-resistant species, such as *Ficus salicifolia*, *Olea europaea* subsp.

cuspidata, *Carissa spinarum* and *Pistacia khinjuk* (Figure 14). Mountain communities at lower elevations, mainly in Wadi Kansisrob, contained plant species suited to higher soil pH values i.e., *Abutilon pannosum* and *Euphorbia cuneata*. Overall, Wadi Kansisrob was the driest and the least diverse among the studied mountainous wadis.

Plant diversity (species richness)

The plant diversity in the study area clearly differed between the four sampled wadis and the seven observed communities. Generally, Wadi Marafai was the most diverse wadi, with 131 species, while W. Yahmib was the least diverse, with only 26 species. When the sampling size was fixed at 24 relevés (Figure 15; Table 5), we expected the wadis to be ranked as Marafai > Acow > Kansisrob > Yahmib, which reflected the same order as the altitude gradient. The lower and upper bounds of the extrapolated species richness curve did not overlap, although there was some overlap between Acow and Kansisrob, yet there was still a significant difference in the lower bound of species richness (Figure 15; Table 5).

Interestingly, these two wadis showed greater differences when the sampling rate was lower (Figure 15). When we compared the upper vs the lower bounds of species richness for the communities (Table 5), we recognized two main groups. The first group contained the communities with high species richness (I, II, and IV) from the higher wadis, i.e., Acow and Marafai. The communities located in the lower wadis, i.e., Kansisrob and Yahmib (III, V, VI, and VII) belonged to the second group, with significantly reduced species richness (significant because the upper confidence value did not overlap with the lower value of the other group).

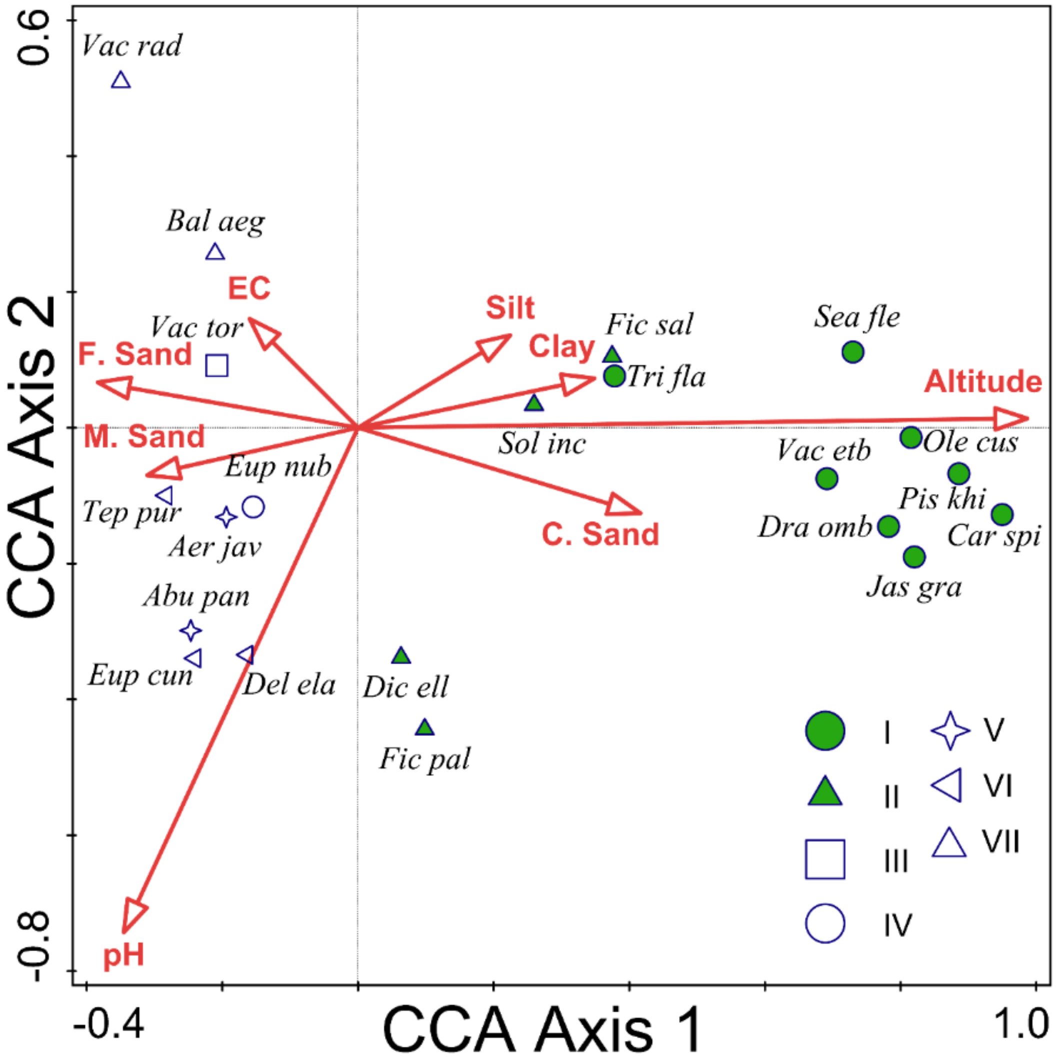

Figure 14. CCA ordination showing the relation between perennial species with phi coefficient > 0.25 and environmental factors represented by altitude and seven soil parameters. Variation is mostly explained by elevation (Alt), soil texture and pH. The lower left part contains species from Wadi Kansisrob. The upper part contains species of the open sandy plain, Wadi Yahmib. The right part contains evergreen species from mid to higher elevations. Eigenvalues for biplot scaling are 0.60 for axis 1 and 0.16 for axis 2 and the adjusted explained variation is 11.54%. The legend is placed at the lower right part of the figure. The diagnostic species for each community are represented by different symbols; solid symbols for communities of higher elevations and hollow symbols for communities from low to middle elevations. For species and sand fractions abbreviations see tables 2 and 4.

Table 5. Sample based rarified richness for the four studied wadis and the seven studied communities at sample size equal 24 relevés for wadis and 13 for communities.

		t	Richness	Lower	upper
Wadi	**Marafai**	24	100.15	94.30	106.00
	Acow	24	74.02	69.65	78.38
	Kansisrob	24	63.62	56.94	70.30
	Yahmib	24	25.64	20.11	31.17
Community	**I**	13	68.11	62.97	73.25
	II	13	65.15	58.88	71.43
	III	13	52.35	47.51	57.20
	IV	13	63.73	57.82	69.64
	V	13	44.07	37.58	50.56
	VI	13	51.54	45.51	57.57
	VII	13	46.26	41.87	50.65

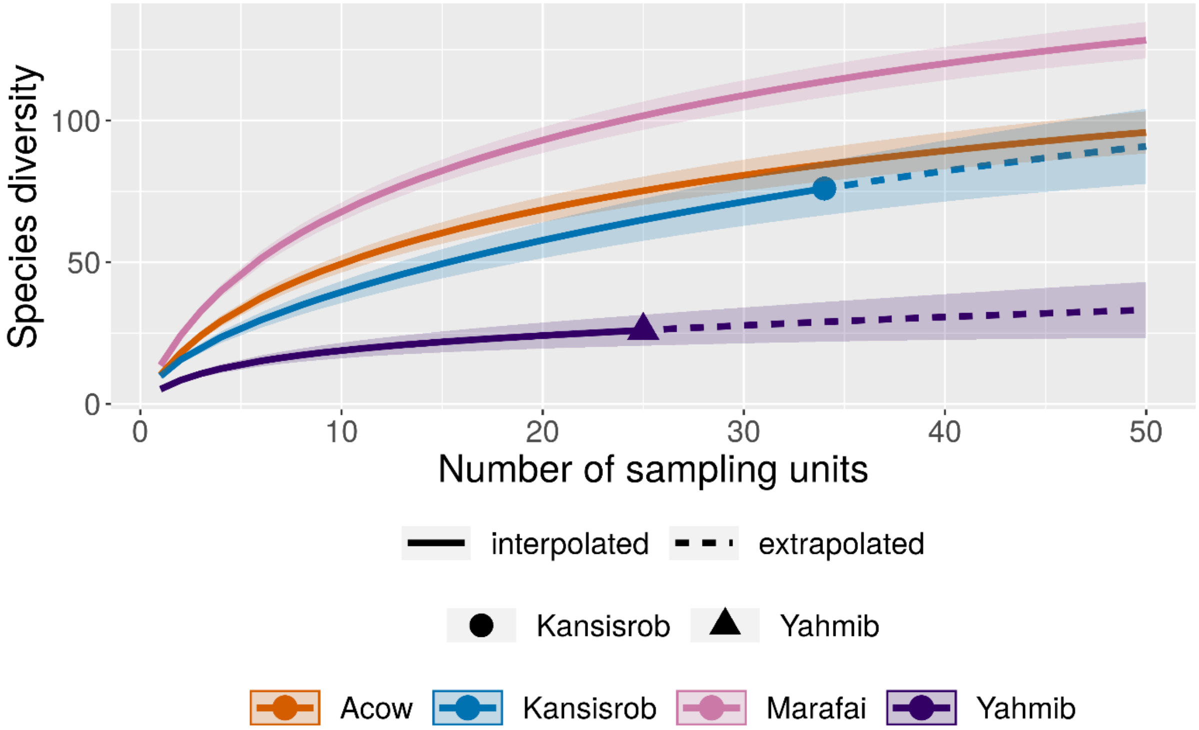

Figure 15. Sample-size-based rarefaction and extrapolation sampling curve for the four studied wadis.

Discussion

Floristic pattern

The location of Gebel Elba offers a lush “mist oasis” ecosystem where the sea-facing slopes are blanketed by moisture-laden clouds (Hegazy and Lovett-Doust 2016). Gebel Elba Mountain acts as a refuge for tropical flora in an otherwise arid regional climate. While the flora of Gebel Elba is found across south Egypt, the floristic composition is similar to that of neighbouring mountains, such as Jebel Marra, Sudan, and the Asir Mountains, Saudi Arabia (Wickens 1976; Hegazy et al. 1998).

Fabaceae, Poaceae and Asteraceae have previously been reported as the most common families on Gebel Elba and in the arid mountains of East Africa and the southern Arabian Peninsula (Abd El-Ghani and Abdel-Khalik 2006). We found that therophytes, phanerophytes and chamaephytes were the dominant life forms in Gebel Elba. Similar results for life forms were observed in the Eastern desert of Egypt and in south-western Saudi Arabia (Abd El-Ghani and Abdel-Khalik 2006).

The flora of East Africa and southwest Asia is influenced by Somalia-Masai elements. The Somalia-Masai regional centre of endemism is covered by deciduous and evergreen bushlands, while grasses are represented by a few annual and short-lived perennial species (White 1983; White and Léonard 1991). According to Zohary (1973), Gebel Elba and southwestern Arabia harbour Sudanian floras and represent the northern boundaries of the Eritreo-Arabian province. This area comprises a belt of savanna vegetation in East Africa and extends through tropical Arabia (Zohary 1973; Zahran and Willis 2009). The Sudanian flora of Gebel Elba is characterized by a large proportion of tropical shrub and tree species (Zohary 1973; Abd El-Ghani and Abdel-Khalik 2006; Al-Gohary 2008b). The number of tree species we recorded (n=21) was greater than other studies found in similar regions in Egypt (e.g. Boulos 2008). The most abundant species were deciduous trees at lower elevations, e.g., *Vachellia tortilis* subsp. *tortilis*, *V. tortilis* subsp. *raddiana* and *Balanites aegyptiaca*, while evergreen trees characterized the higher elevations, such as *Searsia flexicaulis* and *Olea europaea* subsp. *cuspidata*. It is misleading to describe the vegetation as savanna depending on the floristic list only, because Gebel Elba is characterized by deciduous bushland and grasses contribute little to the plant biomass (White 1983).

Classification

Many Saharo-Arabian vegetation types grow in Egypt, and Sudanian vegetation is represented only in the southern part of Egypt. The Sudanian vegetation is divided into Nubo-Sindian vegetation, mainly in desert wadis and depressions, and Eritreo-Arabian vegetation, which is restricted to the Gebel Elba region (Zohary 1973). According to White and Léonard (1991) and Boulos (2008), vegetation of the Gebel Elba represents a satellite of the Somalia-Masai region, and the southern part of the Arabian Peninsula is an extension of this region into southwest Asia. However, Gebel Elba is lower than the tropical mountain ranges in the area (Ghazanfar 1991; Hegazy et al. 1998).

The vegetation showed altitudinal zonation that was comparable to the patterns in East Africa and tropical Arabia. Two main climatic zones were observed, both of which are typical for East Africa and tropical Arabia. Palaeotropical *Vachellia-Commiphora* woodland was present from the foothills of Gebel Elba to the middle elevations, and the mist zone showed fragments of Afromontane forest dominated by *O. europaea* subsp. *cuspidata* (Zohary 1973; Zahran and Willis 2009).

Our classification results for the northern slopes of Gebel Elba accorded with the observation of Zahran and Willis (2009). According to Zohary (1973), the lower elevations of Gebel Elba were classified as Acacietea sudano-arabica. This class comprises the bulk of the xerotropical vegetation on Gebel Elba from low to middle elevations. In this study, we described six communities within deciduous *Vachellia-Commiphora* woodland and one community within evergreen *Olea* woodland. However, the fine resolution of this study allowed us to characterize specific habitats within each community, thereby providing a more exact zonation of the plant communities along the altitudinal gradients.

Only two communities represented the desert plains and foothills to the mid elevations of Gebel Elba, forming an open woodland; *Balanites aegyptiaca* - *Vachellia tortilis* subsp. *raddiana* and *Vachellia tortilis* subsp. *tortilis*, although the former was restricted to the main water channels. The *V. tortilis* subsp. *tortilis* community is more drought resistant and occurred in several habitats, e.g., channels, terraces and gentle slopes. *V. tortilis* subsp. *raddiana* is much more widespread in the Eastern Desert and Sinai Peninsula (Zohary 1973; Abutaha 2010; Morsy et al. 2010), whereas *V. tortilis* subsp. *tortilis* communities are mostly confined to the southern part of Egypt, Sudan and tropical Arabia (Kassas 1957; Ghazanfar 1991; Zahran and Willis 2009).

In the mountain wadis, the lower part of the elevation gradient (210 - 350 m) was more arid than the higher part (350 - 680 m). Three communities were recorded in rocky habitats (stony, rocky outcrops and run-off slopes) from low to middle elevations. Stony habitats near run-off slopes were occupied by *Aerva javanica* - *Abutilon pannosum* community. This community was characterized by frutescent vegetation. The characteristic species were shrubs and herbs, whereas the tree layer was less established. *Aerva* communities are more common in stony wadis and the southern slopes of Gebel Elba (Ahmed 1999; Zahran and Willis 2009).

Additionally, *Aerva javanica* and *Abutilon pannosum* are frequent in the frutescent communities of the Hijaz Mountains, Saudi Arabia (Abd El-Ghani 1996). Rocky outcrop habitats are more favourable for plants than habitats with shallow soil containing stones in the upper layer, because rainwater can accumulate in rock crevices, leading to well-developed soil. In addition, rocks offer shade for herbs (Zohary 1973). We found that the *Euphorbia cuneata* community dominated this habitat in the lower parts of the northern slopes of Gebel Elba. While this community is found on the northern slopes of Gebel Elba and is common in the arid zones of Erkwit, the species *Euphorbia cuneata* has occasionally been recorded in the runnels of the southern slopes of Gebel Elba (Kassas 1956; Zahran and Willis 2009).

At middle elevations, the succulent species, *Euphorbia nubica*, grows on run-off slopes and rocky outcrops. *Euphorbia cuneata* community is replaced by *Euphorbia nubica* community on rocky outcrops as the elevation increases. This distribution pattern of the two *Euphorbia* communities on Gebel Elba was comparable to that of the coastal mountains of Sudan (Kassas 1960; Zahran and Willis 2009). While rainwater is well preserved between boulders in wadi beds, run-off slopes are dry habitats, and rainfall is less available for plants (Deil 2014). Thus, the succulent *E. nubica* community is the pedoclimax community on the run-off slopes of Gebel Elba, whereas *Vachellia*-*Commiphora* woodland is the climax community on wadi beds. This distribution pattern is comparable to the pattern of succulent vegetation in Yemen; however, we did not record any similar communities (Deil 2014).

The higher elevations of Gebel Elba are influenced relatively by monsoon clouds more than the lowlands. The vegetation in this moist zone is less resistant to drought and is represented by fragments of *Ficus* and *Olea* forest (Zohary 1973). Similarly, to Zohary, we identified two communities, *Solanum incanum* - *Ficus* *salicifolia* which is found lower down than *Dracaena ombet - Olea europaea* subsp. *cuspidata*; the former represents the *Ficus* community, whereas the latter represents the *Olea* community. *Ficus* is a typical wadi species that grows on water run-on habitats in *Vachellia-Commiphora* woodlands (Zohary 1973; Ghazanfar 1991). *Vachellia tortilis* subsp. *tortilis* is frequent in this community, which also contains characteristic species of *Olea* communities. In our view, this community represents an ecotone (transitional plant community) between the *Vachellia* and *Olea* woodlands.

Dracaena ombet - Olea europaea subsp. *cuspidata* was found in the mist zone of Gebel Elba. Many characteristic species from the evergreen *Olea* woodland can be observed here, such as *Dodonaea viscosa*, *Euclea racemosa* and *Maytenus senegalensis*. The wadi bed was dominated mainly by evergreen trees, such as *O. europaea* subsp. *cuspidata* and *Searsia flexicaulis*, which may form forest-like growth (Abd El-Ghani and Abdel-Khalik 2006). Plant individuals were crowded in patches (Zahran and Willis 2009) due to the presence of many liana species on olive trees, such as *Pergularia daemia*, *Jasminum fluminense* and *J. grandiflorum*.

The olive community contained many vascular species that are the least resistant to drought and are thus confined to the highest elevations of the northern slopes of Gebel Elba (Zahran and Willis 2009). The mountain slopes were characterized by rich *Vachellia etbaica* growth, which was also recorded on the northern slopes of three coastal mountains in the Elba range but not on the inland mountains (Zahran and Willis 2009). Most of these species were also very abundant in the wettest zone of the Erkwit mist oasis, Sudan (Kassas 1956). Additionally, healthy populations of *Dracaena ombet* were observed at higher elevations on the northern slopes of Gebel Elba (Kamel et al. 2015; Elnoby et al. 2017). *Dracaena ombet* is usually associated with *O. europaea* subsp. *cuspidata* on Gebel Elba, and scattered populations extend southward from Sudan to Somalia along the African hills that face the Red Sea (Marrero et al. 1998; Kamel et al. 2015).

According to White (1983) and Kürschner et al. (2008) the evergreen '*Olea* woodland' is in close association with the *Vachellia*-*Commiphora* woodland sensu Zohary (1973), which characterize the lower slopes and also to the montane forest communities of *Juniperus procera* forest. Because of the lower topography of Gebel Elba (1435 m), we encountered the *Olea* woodland but not the upper montane *Juniperus procera* woodland which occured above ca. 2000 m in the Asir mountains, Saudi Arabia and the Yemen highlands (Kürschner et al. 2008). Also, the *Dracaena ombet* - *Olea europaea* subsp. *cuspidata* community here is found at lower elevations (560 – 680 m) than the community of *Tarchonanthus camphoratus* - *Olea europaea* subsp. *cuspidata* (1600 – 2000 m) in the Arabian Peninsula (Kürschner et al. 2008).

Environmental drivers

The water supply for plants strongly depends on soil structure, rainfall, and plant cover. The capacity of soil to store moisture, in turn, depends on the depth and quality of soil supporting plant growth (Körner 2012). Sandy soils at low elevations exhibited poor water storage capacities in our study. The sandy plain mainly supported the growth of drought-tolerant trees, e.g., *Vachellia tortilis* subsp. *tortilis*, *V. tortilis* subsp. *raddiana* and *Balanites aegyptiaca* (Zahran and Willis 2009). However, soils in rocky habitats at higher elevations often have higher water holding capacities. Fine soil material accumulates in rock crevices, and rainwater is well protected against evaporation (Zohary 1973; Deil 2014).

The sandy loamy soils support a dense growth of *Olea* trees (Ahmed et al. 2016). Furthermore, water droplets from mist and clouds increase the moisture content of soils and reduce plant transpiration rates (Hegazy and Lovett-Doust 2016). The drought stress has a stronger effect on species richness than physiological stress associated with extreme soil pH values (Palpurina et al. 2017).

The elevational gradient of the studied wadis could mirror an inversed stress gradient (Abutaha et al. 2019). In arid climates, water evaporates quickly, leading to an increase in the alkalinity and EC of soil (Knapp 1973; Abutaha 2010). At higher elevations, orographic precipitation decreases the pH and EC. This negative relationship between precipitation and soil pH results in favourable soil conditions for plant growth at higher wadis. Although we did not determine the soil moisture content, orographic precipitation and the soil quality at higher elevations seem to support the growth of moist vegetation.

Plant diversity (species richness)

In the wadi systems of Gebel Elba, the species richness increased from low to mid elevation, followed by a plateau pattern from mid to high elevation (Abutaha et al. 2019). This pattern represented the transition from desert to mountain wadi systems. The increase in species richness was the result of reduced climatic stress and increased water availability. The high species richness from mid to higher elevations was related to more climatically suitable conditions for plant growth and diversity (Ghazanfar 1991; El-Keblawy et al. 2016; Hoppe et al. 2018). However, there are many other factors that may affect plant species richness, particularly mountain topography.

A complex topography results in relatively greater habitat diversity. Cliffs, crevices and large boulders offer more favourable conditions to plants (Zohary 1973; Hegazy and Lovett-Doust 2016). For example, rocky habitats collect water run-off, supporting dense tree populations. Furthermore, the topography offers more shade for herbs and shrub species.

Plant growth is commonly less constrained by soil moisture shortages at high elevations than at low elevations. Precipitation often increases with increasing elevation, and the evaporation/precipitation ratio decreases (Körner 2007). The increase in richness on Gebel Elba could thus be the result of reduced stress and an increase in water availability due to orographic precipitation at higher elevations (Abutaha et al. 2019).

Deciduous / evergreen trees pattern with elevation

The tree limit in arid mountains is mainly determined by drought resistance (Gieger and Leuschner, 2004; Karger et al. 2018). The natural vegetation of Gebel Elba includes deciduous and evergreen woodlands (Zohary 1973). The studied elevational gradient (130 – 680 m) seems to be a major stress gradient in terms of water availability and temperature.

The lower elevations are more arid and thus support the growth of scattered drought-deciduous species such as *Vachellia* trees. However, the orographic precipitation at higher elevations exhibit a trend of increasing evergreen species richness that are less resistant to drought (Zahran and Willis 2009). Hence, we can confirm that deciduous species prevail in the more arid parts of the total elevational gradient and occur in the upper parts as they also can cope with the humid conditions.

Nevertheless, drought-resistant deciduous trees appear to be outcompeted by evergreen species with continuous increasing elevation. Above 500 m, evergreen species continuously dominate the vegetation relevés. This confirms our findings from the vegetation classification, i.e. evergreen *Olea* and *Ficus* communities compared with identified deciduous vegetation units *Vachellia* and *Balanites*.

Local tree limits can also be greatly altered by fine-scale topography (Case and Duncan 2014; Karger et al. 2018). Up to 400 m, the slopes of Gebel Elba mainly comprise of open sandy plain or stony habitats. From 500 m upward, the mountain slopes of Wadi Marafai become steeper and narrower, thus providing more shadow, and the rockier slopes increase water runoff to wadi beds (Abutaha et al. 2019).

Conclusion

In this study, we identified seven communities along the elevational gradients of four wadis in the northern slopes of Gebel Elba. These communities show an altitudinal zonation and represent the core of the Eritreo-Arabian (tropical) vegetation in the Gebel Elba National Park, Egypt. Two main woodland types are observed in Gebel Elba; first, a deciduous *Vachellia* woodland, appearing in the desert plain and foothills to the mid-elevations of Gebel Elba (communities III-VII). Second, an evergreen *Olea* woodland, at the upper moisture altitudes (community I). The lower limit of the evergreen vegetation in Gebel Elba is found to be lower than in the higher mountains of East Africa and tropical Arabia.

The studied elevational gradient mirrors a typical stress gradient. We found that each plant community within the *Vachellia* woodland is restricted to a definite habitat depending on its ability to adapt to drought stress, while the climatically more favourable habitats are occupied by the *Olea* community. The *Ficus* community (II) represents a transition zone between deciduous and evergreen communities. In sum, orographic precipitation, soil quality and complex topography are the main factors that affect the vegetation structure and species richness of Gebel Elba.

Author contributions

Maged M. Abutaha (MMA) carried out fieldwork and soil analysis. MMA and Jens Oldeland performed the statistical analyses and wrote the first draft of the manuscript, while all authors contributed to the final version.

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Chapter Four

Predictive mapping of plant diversity in an arid mountain environment (Gebel Elba, Egypt)

Maged M. Abutaha, Ahmed A. El-Khouly, Norbert Jürgens & Jens Oldeland

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Abstract

Aim: This study aimed to predict the alpha and beta plant diversity of an arid mountain based on environmental variables derived from remotely sensed and ground truth data.

Location: Gebel Elba, Egypt

Methods: Based on 133 vegetation plots of 100 m², we calculated alpha (Shannon index) and beta [the first ordination axis of nonmetric multidimensional scaling (NMDS1)] plant diversity. Generalized additive models (GAMs) were used to map alpha and beta diversity based on various environmental variables derived from a digital elevation model, the SoilGrids dataset, and very high resolution PlanetScope satellite imagery. The predictive models for alpha and beta diversity were mapped within the northern slopes of Gebel Elba. An ANOVA *post hoc* test was used to compare Shannon index and NMDS1 values among plant communities.

Results: The selected models revealed the importance of altitude, landforms, solar insolation, catchment area, and modified soil-adjusted vegetation index for Shannon diversity and NMDS1. The GAMs explained 54.9% of Shannon diversity and 80.6% of NMDS1. The predicted diversity maps showed that the mountainous area was more diverse and substantially different from the open desert. The post-hoc test revealed a clear separation of mountain and desert vegetation.

Conclusions: Employing remotely sensed variables combined with ground truth data offers great opportunities for exploring spatial patterns of biodiversity. By mapping alpha and beta diversity, it was possible to determine the spatial distribution of plant diversity in Gebel Elba; the results highlighted the importance of the wadi systems and higher slopes of this mountain area. We expect our findings can be generalized to similar arid mountains in the region.

Keywords: *Acacia*, floristic gradient, Gebel Elba National Park, satellite imagery, predictive mapping, protected area, remote sensing, woodland, alpha diversity, beta diversity

Introduction

Mapping regional biodiversity is necessary for conservation planning and delimiting biodiversity hotspots in arid mountain areas (von Wehrden *et al.*, 2009; Brinkmann *et al.*, 2011; Muenchow *et al.*, 2013a); however, the inaccessibility of these areas and the lack of available information on environmental drivers of diversity are important challenges for conservation management. Remote sensing can potentially overcome these challenges as it can provide basic information required for modeling and predicting patterns of diversity (Ferrier, 2002; Hüttich *et al.*, 2011; Levanoni *et al.*, 2011).

For example, topography, edaphic parameters, climate variables, and productivity can be determined by remote sensing (Turner *et al.*, 2003); such parameters can be used to model species diversity along environmental gradients and predict species distribution patterns (Ferrier, 2002; Hüttich *et al.*, 2011; Levanoni *et al.*, 2011). Both the availability of remotely sensed data and new powerful statistical techniques are already supporting the production of predictive diversity maps (Levin *et al.*, 2007; Muenchow *et al.*, 2013a; Vanselow and Samimi, 2014; Hein, Löffler, and Feilhauer, 2019). However, such maps are often not prepared for arid ecosystems.

Predictive mapping of alpha (diversity within sampling units) and beta diversity (variation in species composition between habitats) (Whittaker, 1972) can help identify areas of high local diversity caused by species turnover along environmental gradients (Botta-Dukát, 2018; Ochoa-Franco *et al.*, 2019). Oldeland *et al.* (2010) demonstrated that using the Shannon index improves the ability to estimate alpha diversity with hyperspectral remotely sensed data: R^2 values were up to fivefold higher than those obtained when considering species richness only. The Shannon index is useful in this context because it is less affected than species richness by the presence of rare species (Rocchini *et al.*, 2016). Estimation of beta diversity begins with the use of distance matrices, which are designed to quantitatively describe multivariate gradual transitions in the species composition of sampled sites. Measuring the distance between two sampling sites in multidimensional ordination space is an effective method for representing species turnover (Rocchini *et al.*, 2018). When this measure is related to the environmental distance between the sampled sites, beta diversity at this scale can be estimated (Rocchini *et al.*, 2018).

The spatial patterns of alpha and beta diversity reflect species representation in various habitats; such pattern depend on specific environmental parameters, which can strongly influence species persistence (Domisch *et al.*, 2019). In general, patterns of species diversity are influenced by parameters, including climatic variation, anthropogenic activities, dispersal limitation, and habitat heterogeneity (Sabatini *et al.*, 2018; Gebrehiwot *et al.*, 2019). Studies in arid mountains have also explored the influence of topography, vegetation indices, climate, and soil parameters on the distribution of plant species and communities; the rugged topography of mountains offers many niches, wherein specialized plant species can thrive in arid environments (Brinkmann *et al.*, 2011; Vanselow and Samimi, 2014; Abutaha *et al.*, 2020).

The arid mountain Gebel Elba is one of the most important conservation areas in Egypt (Abutaha *et al.*, 2019). Mist oases provide a unique ecosystem on the mountain tops of Gebel Elba (Zahran and Willis, 2009); however, there is little information on the spatial distribution of plant diversity for this mountain. Previous studies have reported on patterns of plant diversity on Gebel Elba (Abutaha *et al.*, 2019, 2020); they have shown how a combination of elevation and soil factors shape the species diversity and distribution of plant communities in the wadi systems, but the high elevations of the mountain have received less attention. Cartographic representations of plant diversity on Gebel Elba are currently lacking; these could provide important information for conservation management.

In this study, we aimed to map alpha and beta plant diversity in the wadi systems and inaccessible higher slopes of Gebel Elba based on remotely sensed information. Based on our previous work, we hypothesized that the mountainous areas would be more diverse than the surrounding plains of the desert. Moreover, we expected the dissimilarity between sites to increase with elevation. We further hypothesized that topography, plant productivity, and soil parameters would be important for determining patterns of diversity along the altitudinal gradients on the northern slopes of Gebel Elba, from the open desert to the mist oases.

Material and Methods

Study area

The Gebel Elba range is a group of six granite mountains situated near the Red Sea in the extreme south-east corner of Egypt at 22° N and between 36° and 37° E (Al-Gohary, 2008a). Gebel Elba is the most northern mountain of the range with the highest peak at 1,435 m above sea level (asl) (Ball, 1912). From another more central peak (1,428 m asl), drainage lines radiate in all directions (Ball, 1912). Our study area was located on the northern slopes of Gebel Elba (Figure 16). Wadi Aidieb and Wadi Yahmib are the principal wadis that drain these slopes. The topography varies from open sandy plains to complex mountain drainage systems. The Gebel Elba region has a hyperarid climate wherein precipitation is <50 mm/year and a mean annual temperature is approximately 26.1ºC (Abutaha *et al.*, 2020). The mid and high elevations of the mountain receive coastal mist, which creates “mist oases”. This orographic precipitation supports woody vegetation that is more diverse than in any other region of Egypt (Zahran and Willis, 2009).

Floristically, Gebel Elba contains elements of the Afrotropical flora and is dominated by two woodland types: *Vachellia* and *Olea* woodlands. While *Vachellia* woodland is dominant from low to mid elevations, *Olea* woodland is restricted to higher elevations (Abutaha *et al.*, 2020). Seven plant communities have been identified in the area, one (I) was described within the *Olea* woodland and six (II–VII) were within the *Vachellia* woodland (see Table 2 in Abutaha *et al.*, 2020). These identified communities show an altitudinal zonation and occupy different habitats along the elevational gradient from the open plain to the higher mountain elevations.

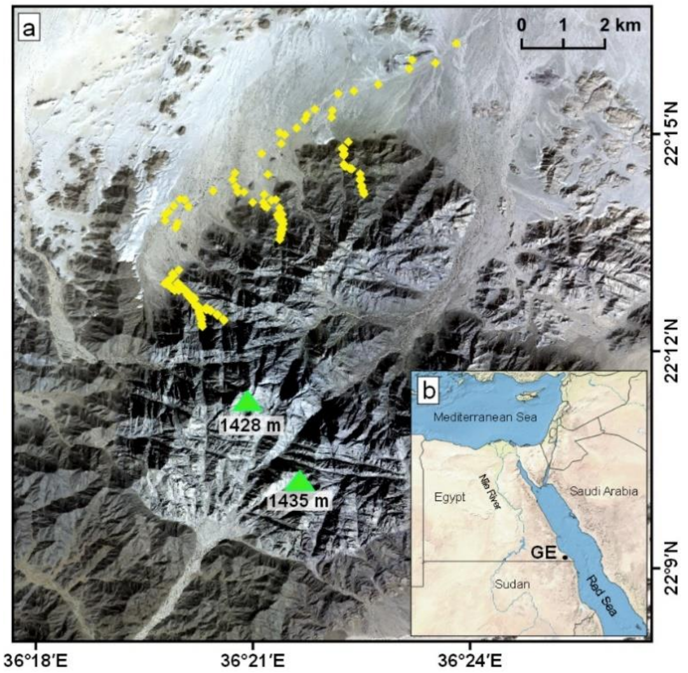

FIGURE 16 PlanetScope image (March 22, 2019; Planet Team, 2017) showing the study area. Yellow dots represent the distribution of the vegetation plots on Gebel Elba (a). A map of Egypt (derived from https://www.naturalearthdata.com/) shows the location of Gebel Elba in Egypt (b)

Field sampling and variable assessment

The Gebel Elba National Park is inaccessible as it is partly a military area. Permission is required to access the mountain area, which is usually restricted to a few days per field visit. Hence, only five field visits were made in January or March after the rainy season (i.e., from October to December) during 2013, 2015, and 2016. To assess plant diversity, 133 vegetation plots (10 m × 10 m) distributed along the elevational gradient of the northern slopes of Gebel Elba were studied. We sampled across the altitudinal gradient from 130 to 680 m; this area covered four wadis: Yahmib, Marafai, Acow, and Kansisrob. Ensuring that the intervals were fixed between sampling plots was difficult due to the rugged topography; therefore, plots were randomly positioned within altitudinal intervals of 100 m or 50 m in the main wadi or smaller wadis, respectively.

Vegetation plot coordinates (geodetic datum: WGS 84) were recorded in the center using a GPS device (Garmin eTrex 30x). For each plot, a complete species list was assembled, and the percentage cover of perennial species was estimated. The taxonomical identification of plant species followed Täckholm (1974) and Boulos (1999, 2000, 2002, 2005, 2009). However, we updated the nomenclature according to Plants of the World Online (POWO, 2019).

We have previously shown that altitude and soil properties were important in determining the vegetation structure and diversity patterns on Gebel Elba (Abutaha *et al.*, 2019, 2020). In addition, the availability of water has been related to the rugged topography and orographic precipitation on the higher northern slopes of Gebel Elba, which support dense vegetation (Zahran and Willis, 2009). Based on these studies, we tested 14 environmental parameters as predictors (see Appendix S6 for a description).

We extracted the altitude, catchment slopes, catchment area, openness, solar insolation (the increase in shadow), and landforms (four classes: plains, streams, valleys, and slopes and ridges) from a digital elevation model (DEM: ASTER DEM 30 m, derived from https://lpdaac.usgs.gov/). Moreover, we used very high-resolution PlanetScope satellite data (3 m) from March 2019 to calculate a vegetation index representing living green plant biomass. The satellite data were already geometrically and atmospherically pre-processed by the data provider. The satellite data were provided as a level 3A PlanetScope Ortho Tile Product in units of spectral reflectance with four spectral bands covering infra-red (780-860nm), red (590-670nm), green (500-590nm) and blue (455-515nm). The imagery was atmospherically pre-processed using the 6S algorithm (Vermote et al. 1997). Besides that, the images also were geometrically corrected, and final product was delivered in UTM projection (Planet Team, 2017).

Due to the hyperarid conditions of the study area, it was necessary to calculate a modified soil-adjusted vegetation index ($MSAVI_2$) according to Qi *et al.* (1994) from the four-band (RGB-NIR) PlanetScope satellite images. SAGA-GIS version 7.2.0 (Conrad *et al.*, 2015) and QGIS version 3.4.2 (QGIS Development Team, 2019) were used to prepare the raster data. For soil parameters, i.e., cation exchange capacity, pH, organic carbon, coarse fragments, silt, sand, and clay, we used soil layers (depth: 0–5 cm) from the SoilGrids dataset at a spatial resolution of 250 m (Hengl *et al.*, 2017) and used a raster package (Hijmans, 2020) in R (R Development Core Team, 2020) to crop all 14 environmental raster layers to the extent of the study area. We then resampled all raster layers to the same resolution of the DEM, e.g., 30 m × 30 m. Finally, we extracted the values from these raster layers for each vegetation plot at its center coordinate.

We calculated alpha and beta diversity from the vegetation plot data. For alpha diversity, we chose the Shannon index (Magurran, 2004) over species richness because information on abundance was important for differentiating among communities. We compared our results to those from richness-based models; however, as the Shannon index produced better results, we reported the Shannon index results only (see Appendix S7 for richness-based models).

To quantify beta diversity as an increase in dissimilarity between vegetation plots, we performed nonmetric multidimensional scaling (NMDS) to represent the floristic gradient using a reduced number of dimensions that could easily be visualized (Lovelace, Nowosad, and Münchow, 2019). Using the Bray–Curtis dissimilarity distance, the best NMDS solution reached a stress value of 0.107. The NMDS ordination identified altitude as the most important predictor in explaining the turnover of species. Moreover, we found that the first axis of NMDS (denoted “NMDS1”) clearly captured the main floristic gradient. Thus, we used NMDS1 to model beta diversity. We rotated the NMDS axes (as this improves interpretation of the axes) so that NMDS1 contained the largest variance in ordination space (Schmidtlein *et al.*, 2007; Lovelace, Nowosad, and Münchow, 2019). NMDS was performed using the vegan package (Oksanen *et al.*, 2020).

Data analysis

The relationship between vegetation and environment is often complex and difficult to capture with linear or unimodal models (Dobrowski *et al.*, 2008; Song, Huang, and Liu, 2013; Matus-Hernández, Hernández-Saavedra, and Martínez-Rincón, 2018). Generalized additive models (GAMs; Wood, 2006) are more flexible than generalized linear models; they can model both linear and nonlinear relationships between response and predictor variables. Furthermore, we previously found that a GAM effectively described the nonlinear and linear diversity patterns of the wadi systems of Gebel Elba (Abutaha *et al*., 2019). Given the continuous nature of the normally distributed Shannon values and the negative and positive continuous values centered at zero for the NMDS axis, we used GAMs with a Gaussian distribution to model alpha (Shannon index) and beta (NMDS1) diversity with the selected environmental parameters. The catchment area was log10 transformed to adjust data to a normal distribution. Moreover, we tested correlations between the environmental predictor variables to avoid multicollinearity problems in GAM regression analysis (Performance Analytics package; Peterson and Carl, 2020). Consequently, we excluded all soil variables, catchment slopes, and openness due to high correlations ($r > 0.7$) with altitude or with each other (Appendix S8).

After removing the correlated predictors, only five parameters remained: altitude, landforms, solar insolation, catchment area, and $MSAVI_2$. These parameters were used to model alpha (Shannon index) and beta diversity (NMDS1). As smoothing terms, we used thin-plate regression splines with shrinkage-to-zero for the numeric variables (altitude, catchment area, solar insolation, and $MSAVI_2$) and a simple random effect for the factor variable (landforms). We fitted all GAMs using the mgcv package in R (Wood, 2011).

The residuals of the GAMs were checked with diagnostic plots to identify deviations from an expected random pattern. Furthermore, the residuals for spatial autocorrelation were analyzed using a Moran's I correlogram with the spdep package (Bivand *et al.*, 2013); however, effects were not detected in this analysis. The Akaike information criterion was used to compare a set of candidate models containing all possible models without interaction. Model selection was performed with the MuMIn package (Barton *et al.* 2020). The best models were subsequently used to produce diversity maps via their application to the raster data. To assess the usefulness of the models, we related observed and predicted values for the vegetation plots and used the R^2 value as an indicator of model quality (Piñeiro *et al.*, 2008).

To verify the findings of our previous study (Abutaha *et al.*, 2020), we used the scores along the first and second axes of NMDS to describe the floristic gradient on Gebel Elba in ordination space. ANOVA *post hoc* tests (Tukey's HSD test) were used to test for differences in Shannon index and NMDS1 values between the seven plant communities using the multcompView package (Graves *et al.*, 2019). Preparation of diversity parameters and all statistical analyses for predictive modeling and mapping were conducted in R version 4.0.3.

Results

Diversity–environment models

Of 32 candidate models, the best model selected for alpha diversity (Shannon index) required all five parameters, i.e., the vegetation index $MSAVI_2$ and four topographical parameters (altitude, solar insolation, landforms, and catchment area; Table 6); this model explained 54.9% of the variation. The accuracy of the alpha diversity model as obtained by comparing predicted and observed Shannon values reached a fit of $R^2 = 0.55$. Altitude showed a nonlinear pattern, whereas catchment area and $MSAVI_2$ were linear, and the landforms parameter was a factor (Appendix S9). The most diverse landforms class was "streams" in the mountainous area; the least diverse class was "plains" (Figure 17a).

The best model selected for beta diversity (NMDS1) was the full model, which again comprised all five parameters; this model explained 80.6% of the spatial variability (Table 6). Altitude showed a nonlinear pattern, catchment area showed a complex pattern, and solar insolation and $MSAVI_2$ showed a linear pattern (Appendix S10). The accuracy of the beta diversity model was rather high ($R^2 = 0.81$). However, it should be noted that for both models no independent evaluation was possible given the low number of vegetation plot data and the strong environmental heterogeneity.

TABLE 6 Selected parameters applied to model the alpha and beta diversity to produce predictive maps

Diversity model	**R^2 (adj.)**	**Deviance explained**	**Parameters**	**EDF**	**F**	**P value**
Alpha (Shannon index)	0.53	54.9%	Altitude	2.44	7.82	<0.001
			Landforms	2.25	6.82	<0.001
			Solar insolation	0.39	0.08	0.18
			Catchment area	0.51	0.16	0.09
			$MSAVI_2$	0.81	0.86	<0.01
Beta (NMDS1)	0.79	80.6%	Altitude	2.14	13.00	<0.001
			Landforms	2.80	6.78	<0.001
			Solar insolation	0.79	0.77	<0.01
			Catchment area	5.47	1.94	0.02
			$MSAVI_2$	0.64	0.26	0.07

EDF: estimated degrees of freedom (≤1 = linear pattern; ≤2 = nonlinear/unimodal pattern; >2 = complex pattern)

Diversity maps

The GAMs were extrapolated for the whole study area and predictive maps of alpha and beta diversity were produced as shown in Figure 17. Both maps could discriminate between open desert and mountainous areas. In the alpha diversity map, the change in diversity strongly depended on topography. The predicted Shannon diversity map corresponded to the pattern of alpha diversity observed in the field at Gebel Elba. The Shannon index strongly increased from low to mid elevations toward the mountain; it reached a plateau from the mid to high elevations in the mountainous wadi systems. Alpha diversity was higher in the main streams of the drainage systems (wadis) than on the slopes (Figure 17a).

The beta diversity map showed increasing dissimilarity according to elevational gradient, with mountainous areas being very different from the plain in terms of species composition (Figure 17b). A Shannon value of 1 and NMDS1 of 0 marked the beginning of the mountain, representing a clear change in the floristic gradient of the study area. NMDS1 values <0 marked the deciduous *Vachellia* woodland at the foot of the mountain, whereas values >1 represented the evergreen *Olea* woodland at higher elevations. The area with NMDS1 values between 0 and 1 represented a transition between *Vachellia* and *Olea* woodlands, and it was occupied by a *Ficus* community; thus, we interpret this area as an ecotone from the open desert plain to the mountain habitats (Figure 17b and Appendix S11).

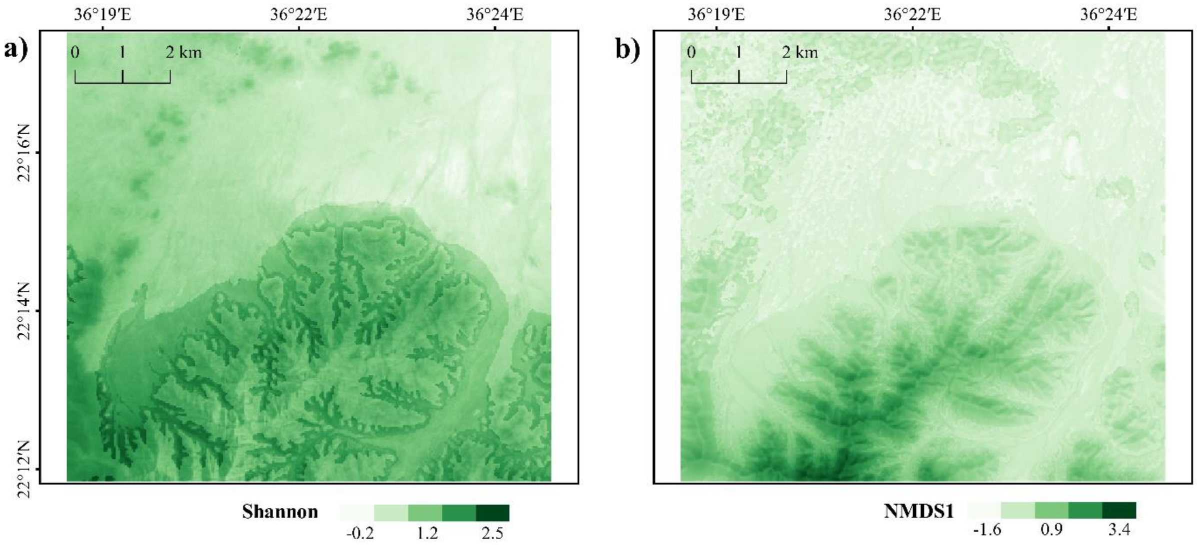

FIGURE 17 Predictive diversity mapping of alpha (a) and beta diversity (b). Alpha diversity map represents the predicted Shannon index, whereas beta diversity was predicted from the first axis of a Bray–Curtis nonmetric multidimensional scaling (NMDS) ordination

Diversity gradients

The Shannon diversity and NMDS1 values highlighted the differences in plant diversity between the *Olea* and *Vachellia* woodlands. These parameters were moderately correlated ($r = 0.53$); thus, they provide slightly different perspectives on diversity (or its components). Using Tukey's *post hoc* test, we clarified the differences in Shannon index and NMDS1 between the seven identified communities (Table 7). The communities along the elevational gradient of Gebel Elba were classified into two groups according to alpha and beta diversity. The first group was more diverse and contained communities from the mid to high elevations, while the second group contained communities that occupied the lower part of the elevational gradient. Specifically, three communities were recorded from mid to high elevations: *Euphorbia nubica*, *Solanum–Ficus*, and *Dracaena–Olea* (which showed the highest Shannon index values; Table 7). The most common community in Gebel Elba, the *Vachellia tortilis* community, had the widest range of Shannon indices (Table 7). We observed small differences between the communities from low to mid elevations.

The dissimilarity of the floristic composition strongly changed with elevation. NMDS ordination (axes 1 and 2) showed that the vegetation communities changed from deciduous to evergreen (Appendix S11). The first axis of NMDS explained the change in floristic gradient, whereas the second axis explained the variation within the deciduous plant communities at the foot of the mountain. According to Tukey's *post hoc* tests, there were significant differences among the NMDS1 values of the seven communities (Table 7).

The highest mean NMDS1 value (1.19) was found in the *Dracaena–Olea* community, which occupied higher elevations, with the next highest value for the *Solanum–Ficus* community (0.70). The *Vachellia tortilis* and *Balanites–Vachellia raddiana* communities on the open desert plain showed the lowest mean values (−0.47 and −0.55, respectively). Furthermore, communities found from the low to mid elevations (III–VII) differed from each other with a low level of significance (Table 7).

TABLE 7 NMDS1 (first ordination axis of nonmetric multidimensional scaling) and Shannon index for the identified communities in the study area (according to Abutaha *et al.*, 2020). See also Appendix S11

Community No.	**Community name**	**Altitude range (m)**	**No. of species/plot**	**Shannon index (mean ± SD)**	**NMDS$_1$ (mean ± SD)**
I	*Dracaena ombet–Olea europaea* subsp. *cuspidata*	560–680	9 ± 4	(1.97 ± 0.42)^{a}	(1.19 ± 0.34)^{a}
II	*Solanum incanum–Ficus salicifolia*	346–550	8 ± 4	(1.71 ± 0.61)^{abc}	(0.70 ± 0.36)^{b}
III	*Vachellia tortilis* subsp. *tortilis*	131–383	5 ± 4	(1.10 ± 0.95)^{c}	(-0.47 ± 0.45)^{de}
IV	*Euphorbia nubica*	264–379	9 ± 4	(1.79 ± 0.59)^{ab}	(-0.16 ± 0.26)^{cd}
V	*Aerva javanica–Abutilon pannosum*	237–275	7 ± 2	(1.49 ± 0.59)^{abc}	(-0.25 ± 0.25)^{cde}
VI	*Euphorbia cuneata*	241–320	9 ± 2	(1.79 ± 0.27)^{ab}	(-0.08 ± 0.29)^{c}
VII	*Balanites aegyptiaca–Vachellia tortilis* subsp. *raddiana*	196–361	5 ± 3	(1.35 ± 0.59)^{bc}	(-0.55 ± 0.42)^{e}

Different lowercase letters denote statistical differences between groups (ANOVA *post hoc* test: Tukey's HSD)

Discussion

Diversity modeling

Remotely sensed data is a valuable source for modeling spatial biodiversity patterns in mountains with complex and diverse topography (Liu *et al.*, 2018; Lazarina *et al.*, 2019). In arid mountains, changes in topography and altitude constitute a proxy for the gradient of water availability, the most important factor in determining species composition and distribution (Muenchow *et al.*, 2013a; Dorji *et al.*, 2014; Vanselow and Samimi, 2014). The elevational gradients of Gebel Elba mirror an inverse environmental stress gradient (Abutaha *et al.*, 2019), as indicated by the upper and lower vegetation belts visibly dominated by evergreen and deciduous trees, respectively (Abutaha *et al.*, 2020). To date, altitude has been described as the major factor explaining the change in species diversity and floristic composition in Gebel Elba (Abd El-Ghani and Abdel-Khalik, 2006; Abutaha *et al.*, 2019, 2020). However, several studies have shown that more environmental variables resulted in more accurate models (Feilhauer and Schmidtlein, 2009; Vanselow and Samimi, 2014; Brun *et al.*, 2020).

The best models for alpha and beta diversity reported in this study included multiple remotely sensed environmental parameters. Our findings support previous studies (von Wehrden *et al.*, 2009; Muenchow *et al.*, 2013a; Vanselow and Samimi, 2014) showing that the use of combined environmental variables in addition to altitude is beneficial than using only altitude as a predictor of plant alpha and beta diversity. Thus, the predicted patterns of alpha and beta diversity on Gebel Elba reported in this study are likely to be robust since they are based on multiple remotely sensed environmental parameters and ground truth data.

The predictive models presented here show that remotely sensed environmental data can explain the pattern of alpha and beta diversity on arid mountains. Models in which a vegetation index and topographical parameters were combined indicated that both variable groups were required for modeling, which is in agreement with other studies on arid mountains (Brinkmann *et al.*, 2011; Vanselow and Samimi, 2014). In contrast to temperate mountains (Leathwick, Burns, and Clarkson, 1998; García-Gutiérrez *et al.*, 2018), favorable climatic conditions are found at higher elevations in arid mountains (Abutaha *et al.*, 2019). In our study area, productivity and moisture availability increased with elevation, whereas temperature and solar insolation were notably lower at higher elevations.

Patterns of diversity can also be related to the environmental heterogeneity hypothesis, and structural predictors (not used in this study) might likely enhance the Shannon diversity model (Hernández-Stefanoni *et al.*, 2014; Sabatini *et al.*, 2018). Indeed, the variation in diversity in the mountainous area seems to be connected to changes in topography, as is visible in the predicted diversity maps. Mountainous wadis cover a variety of microhabitats, such as wadi beds, side slopes, cliffs, and soil pockets (Abutaha *et al.*, 2019). Such high diversity in habitats promotes the growth of dense vegetation. In contrast, the open desert consists of sandy plains with little variation in topography; thus, it contains lower diversity in habitats and supports the growth of scattered vegetation only (Zahran and Willis, 2009; Abutaha *et al.*, 2020).

In previous studies (de la Estrella *et al.*, 2012; Tukiainen *et al.*, 2019), including environmental predictors that capture run-off water enhanced the predictive power of diversity modeling. In our study, moist landforms, such as streams in the mountainous area and U-shaped valleys at the foot of the mountain, had higher plant diversity than that in the open desert plain. Less abundant evergreen species such as *Olea europaea* subsp. *cuspidata*, *Ficus salicifolia*, and *Searsia flexicaulis* were found in water courses at higher elevations, whereas trees that were more drought resistant, such as *V. tortilis* and *Balanites aegyptiaca*, dominated the open desert at lower elevations (Abutaha *et al.*, 2020). The environmental predictors used in our models reflected water availability, changes in topography, and microclimatic conditions along the environmental gradient of Gebel Elba.

Predictive mapping

The predictive mapping of alpha and beta diversity quantified the spatial changes in Shannon diversity (alpha diversity) and species composition (beta diversity) in our study area. This approach offers information on areas in which conservation efforts should be focused (de la Estrella *et al.*, 2012). Topographic gradients regulate species diversity and distribution in mountainous ecosystems (Dirnböck *et al.*, 2003; Brinkmann *et al.*, 2011); although altitude is the major factor controlling the predictive mapping of alpha and beta diversity (von Wehrden *et al.*, 2009; Muenchow *et al.*, 2013a), we cannot neglect the importance of landforms in determining species diversity patterns. Our predictive mapping of alpha diversity clearly showed that species diversity in the wadi systems was higher than on the slopes of the mountain. On the other hand, the predictive mapping of beta diversity reflected the floristic gradient and dissimilarity between the communities in the plains and at higher elevations. The turnover (roughly NMDS1 > 0) between the two main woodland communities occurred at mid elevations.

The change in topography from open desert to mountain habitat regulated species diversity and distribution at Gebel Elba. Thus, our predictive diversity maps show where conservation efforts should be focused, e.g., the wadi areas at higher elevations of Gebel Elba. Mapping the alpha and beta diversity of Gebel Elba highlights the importance of topographic variables, especially altitude and landforms, when mapping diversity in arid mountains. Similar to the work of von Wehrden *et al.* (2009), the small scale of our study area was not a limitation as we identified a change in primary productivity ($MSAVI_2$) along the examined gradient. Soil quality in mountainous areas is known to differ from that at the foot of the mountain (Abutaha *et al.*, 2020); however, we found that soil parameters extracted from SoilGrids were highly correlated with elevation ($r > 0.70$) (obviously because altitude was used to model the SoilGrids data). Therefore, we removed soil parameters from our predictive model to avoid issues with collinearity.

Another possible limitation may be unmeasured microclimatic parameters along the elevational gradient. Gebel Elba is characterized by mist oases at higher elevations (Zahran and Willis, 2009); however, data on moisture content along the environmental gradient was not available. In addition, due to the mismatch between the coarse resolution of the climatic research unit (CRU) data ($0.5^{o} \times 0.5^{o}$) and the fine-scale heterogeneity of our study area, we decided not to use climatic parameters in our predictive modeling. Nevertheless, altitude is often a proxy for soil and microclimatic variables (Muenchow *et al.*, 2013a). Future studies, in which improved fine-scale predictors are used along the environmental gradient, could improve the power of predictive diversity modeling for mountainous study systems.

Conclusion

In this study, we have created the first model-based plant diversity maps for the arid mountain Gebel Elba. Specifically, we mapped alpha and beta diversity on the northern slopes of Gebel Elba based on remotely sensed information combined with ground truth data. We found that topographical parameters and plant productivity ($MSAVI_2$) played important roles in explaining the predictive models of alpha and beta diversity in the study area. Our predictive mapping showed that the change in topography at Gebel Elba from an open desert to a mountain ecosystem regulated species diversity and distribution. Furthermore, the floristic composition changed from deciduous woodland at low elevations to evergreen woodland at higher elevations, and the turnover between the two woodlands occurred at mid elevations. Future studies setting out to generate plant diversity maps for arid mountains adjacent to Gebel Elba could verify our approach. As remote sensing products are globally available in high quality, we recommend that more effort should be made on sampling high quality vegetation data.

Acknowledgments

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Author contributions

J.O. conceived of the research idea; M.A. collected data and performed statistical analyses; M.A. wrote the first draft of the manuscript with a contribution from J.O.; all authors discussed the results and commented on the manuscript.

Data availability statement

The data that support the findings of this study and the R script used to generate the analyses presented in this paper are available in Zenodo.org at http://doi.org/10.5281/zenodo.4662118

Chapter Five

General Discussion

Research highlights of the three published studies

In this thesis, I worked on diversity patterns of vascular plants, vegetation structure and their environmental drivers in wadi systems of Gebel Elba. In this chapter, I will summarize and discuss the key findings of this thesis according to the main objectives, which are:

1- Identifying elevation-richness relationships for vascular plants along different elevational gradients on the northern slopes.
2- Providing a first classification of the vegetation units on the mountain.
3- Identifying the environmental drivers controlling distribution of plant communities on Gebel Elba.
4- Predicting maps of alpha and beta plant diversity in wadi systems and inaccessible higher slopes based on remotely sensed and ground truth data.

1. Species richness - elevation relationships

In **Chapter 2**, I focused on the relationship between elevation and species richness for all single wadis and different wadi combinations to identify the main pattern of species richness along the elevational gradient of Wadi Yahmib with its tributaries. The observed pattern showed an increase in total species richness in the open desert towards the foot of the mountain followed by a plateau pattern in mountainous wadis. Also, different species subgroups (woody versus herbaceous; annual versus perennial; rare versus common plant species) had high plateau patterns comparable to the total species richness, meaning that the found pattern was the main pattern for wadis in Gebel Elba. In this thesis, I reported an unusual pattern compared to the hump–shaped pattern which was commonly observed in almost of 50% of literature studies examined elevational richness patterns for plants (Rahbek, 2005).

In **Chapters 3** and **4**, I clarified that the mountainous area was more diverse and substantially different from the open desert in Gebel Elba region, and species diversity was higher in the wadi systems than on the slopes. The mountainous wadis of Gebel Elba were less stressful for plants than the surrounding hyper arid desert habitats, also a dense vegetation could be observed at higher elevations, as the climatic conditions continue to be favourable for species richness and growth at higher elevations (Zahran and Willis, 2009).

The identified richness-pattern in Gebel Elba could also be related to a change in habitat heterogeneity along the elevational gradient from an open desert to diverse microhabitats in mountainous area. This is in line with Hortal et al. (2013) who described that local species richness will monotonically increase with habitat diversity and level off (plateau) but not decline when approaching the regional richness. So, the observed plateau pattern in Gebel Elba from middle to high elevations might be related to suitable climatic conditions and diverse microhabitats in mountainous wadis.

Gebel Elba offered suitable conditions for plant growth and diversity along the environmental gradients of wadi systems and a small variation in species richness could be observed. In this content, Panthi et al. (2007) reported a plateau pattern of species richness along the elevational gradient of a dry valley in Nepal. Thus, the high plateau pattern I found on the northern slopes of Gebel Elba was interpreted as a common pattern for wadi systems in arid mountains. This was consistent with the elevational-climate model for dry mountains proposed by Grytnes and McCain (2013; their Figure 1b) which stated that water availability showed a unimodal pattern with a wide peak. It seemed likely that the higher wadis of Gebel Elba were in the peak of a truncated unimodal curve, and this could be explained by the availability of water at higher elevations of Gebel Elba.

Only few studies were published on the distribution patterns of species richness in relation to altitudinal gradient in arid mountains (see Figure: 1 in Guo et al., 2013). Most of the previous studies on the arid mountains of the Middle East reported a unimodal (hump-shaped) pattern (e.g.: Ghazanfar, 1991; Hegazy et al., 1998; Abd El-Ghani and Abdel-Khalik, 2006; El-Keblawy et al., 2016). However, it seemed that the main pattern was not well described.

For example, Hegazy et al. (1998) reported a unimodal pattern for Asir mountains, Saudi Arabia. However, the highest species richness showed a plateau pattern from 500-2000 m along an altitudinal gradient from 0 to 3000 m. Similar observation of a plateau pattern was found between 1000 m and 3000 m in the study of Ghazanfar (1991) on Gebel Shams, Oman. Moreover, Brinkmann et al. (2009) reported a unimodal pattern with a mid-peak around to 1700 m in high arid mountains. As Gebel Elba is a low mountain (1435 m), the high-plateau pattern could be valid for this arid mountain. Still, more studies need to be proceeded for the whole mountain range focusing on the complete elevational gradients, to better understand the overall plant species richness pattern for arid mountains.

2. Floristic composition and vegetation classification

Previous studies on vascular plants of Gebel Elba National Park were mainly based on floristic lists that described only distributions of species among wadi systems (Ahmed, 1999; Abd El-Ghani and Abdel-Khalik, 2006; Al-Gohary, 2008a; Zahran and Willis, 2009). More details regarding common and rare species were identified by Täckholm (1974) and Ahmed (1999). Täckholm recorded the rare species in the whole Park, while Ahmed focused more on wadis vegetation. Previous studies noted that Wadi Yahmib was one of the most diverse wadis in Gebel Elba region (Ahmed, 1999; Abd El-Ghani and Abdel-Khalik, 2006; Al-Gohary, 2008a).

In this thesis, I reported that the Wadi Yahmib is locally divided into two wadis which even carry two different names; the part in the mountainous area is called Marafai while the part at the foot of the mountain is called Yahmib. Also, I clarified that Marafai was more diverse than Yahmib itself (**Chapters 2** and **3**). Due to the location of Gebel Elba in South-East Egypt, Saharan as well as Sudanian tropical influences were noted in the floristic composition (Täckholm, 1974; Al-Gohary, 2008b; Boulos, 2009). In **Chapter 3**, I reported that the Saharo-Arabian vegetation was mostly found in the open desert, while the Afrotropical vegetation was usually confined to the mountainous area. Moreover, the vegetation of the open desert not only differed from that on the mountain in its species composition, but also exhibited a distinct scattered vegetation structure dominated by drought resistant trees (**Chapters 3**).

Few studies described the vegetation zonation on Gebel Elba and focused on the vegetation for each wadi as a single transect (Ahmed, 1999; Zahran and Willis, 2009). A phytosociological classification of the vegetation was lacking. Thus, there was a need to classify the vegetation units of Gebel Elba and the environmental drivers controlling their distribution. In **Chapter 3,** I presented an overview of the vegetation on the northern slopes of Gebel Elba.

In this study, I provided the first classification of the woodland vegetation units and identified the environmental factors controlling their distribution. This classification was based on 169 vegetation plots (relevés) which have not been previously sampled on this mountain. Based on a TWINSPAN classification, the vegetation relevés were assigned to seven new communities. These communities were distributed along the elevational gradient and each community was restricted to a confined habitat depending on its drought resistance ability.

The fine scale of this study allowed to characterize specific habitats within each community, thereby providing a more exact zonation of the plant communities along the altitudinal gradients rather than that described by Zahran & Willis (2009) for Gebel Elba. Moreover, I clarified that the identified communities included many of characteristic species with a wide distribution range in East Africa and the southwestern Arabian Peninsula.

In **Chapter 3**, seven woodland communities were described along the elevational gradients on the northern slopes of Gebel Elba. The first five communities inhabited by deciduous trees and represented the perennial vegetation in the arid zone from low to middle elevations, while the last two communities were mainly composed of evergreens and represented the vegetation in the moist zone from middle to high elevations.

Arid zone vegetation:

a- Open desert communities

I identified two communities: namely the community of *Balanites aegyptiaca*–*Vachellia tortilis* subsp. *raddiana* and the community of *Vachellia tortilis* subsp. *tortilis* in wadis at foot of the mountain to the mid elevations of Gebel Elba. The *V. tortilis* subsp. *tortilis* community was mostly confined to the Afrotropical region (Kassas, 1957; Ghazanfar, 1991; Zahran & Willis, 2009), whereas *V. tortilis* subsp. *raddiana* was represented much more in the Sahara region (Zohary, 1973; Abutaha, 2010; Morsy et al., 2010, 2015; Eldemirdash, 2016; Abd El-Ghani et al., 2017). Moreover, the community of *V. tortilis* subsp. *tortilis* was found in several habitats in the open desert and mountainous wadis, while the community of *Balanites aegyptiaca*–*V. tortilis* subsp. *raddiana* was usually restricted to main water courses of the wadis throughout the Saharo-Sudanian area (Zohary, 1973; Zahran & Willis, 2009).

b- Mountainous wadis communities

I recorded two communities: namely the *Aerva javanica–Abutilon pannosum* community and *Euphorbia cuneata* community, in rocky habitats of wadi beds from low to middle elevations. These two communities were associated with the community of *V. tortilis* subsp. *tortilis*. The lower wadis of Gebel Elba were gravely in texture and the community of *Aerva javanica–Abutilon pannosum* was usually found near side slopes. The two characteristic species of this community, *Aerva javanica* and *Abutilon pannosum*, were very common all over the Saharo-Sudanian area and were frequent in the frutescent communities of the gravely deserts in tropical Arabia and East Africa (Abd El-Ghani, 1996; Ahmed, 1999; Zahran & Willis, 2009; Abd El-Ghani et al., 2014).

The rocky outcrop habitat in the mountainous wadis was dominated by the community of *Euphorbia cuneata*, at lower parts of Gebel Elba. This habitat was characterized by accumulation of rainwater in rock crevices. In addition, big rocks offered shade for herbs (Zohary, 1973; Zahran & Willis, 2009). The soil of this community was well-developed and more favourable for tree species than the previous community. Similarly, *Euphorbia cuneata* community was also common on the lower arid slopes of Erkwit in Sudan (Kassas, 1956).

c- The succulent community on the slopes

I described one community on run-off slopes and rocky outcrops of mountainous wadis. This community was characterized by the succulent species *Euphorbia nubica*, which was adapted to dry conditions on the run-off slopes (Deil, 2014). At middle elevations, this community replaced the community of *Euphorbia cuneata* in wadi beds.

Most communities from the *Vachellia–Commiphora* woodland on Gebel Elba were found in the wadi beds, whereas the succulent *E. nubica* community was found on the run-off slopes of Gebel Elba. This distribution pattern was comparable to the pattern of vegetation from low to middle elevations on the highlands in Sudan, Saudi Arabia, Yemen, and Oman (Kassas, 1960; Ghazanfar, 1991; Kürschner et al., 2008; Deil, 2014).

Moist zone vegetation:

d- Evergreen communities

The vegetation in the moist zone on Gebel Elba was mostly represented relatively by evergreen woody vegetation (Abd El-Ghani & Abdel-Khalik, 2006; Zahran & Willis, 2009). I identified two communities in the moist zone from middle to higher elevations: namely the *Solanum incanum–Ficus salicifolia* community and *Dracaena ombet–Olea europaea* subsp. *cuspidata* community. Comparably, Zohary (1973) mentioned the presence of *Ficus* and *Olea* fragments vegetation on higher slopes of Gebel Elba.

The *Ficus* community was found lower down along the elevational gradient than the *Olea* community. The higher mist zone on Gebel Elba was occupied by *Dracaena ombet–Olea europaea* subsp. *cuspidata* community. The olive community contained many diagnostic species that were confined to the fog zone of tropical Arabia and the mist zone of Erkwit, Sudan (Kassas, 1956; Boulos, 2008; Kürschner et al., 2008). Moreover, the population of *Dracaena ombet* was found on the most northern limit of its distribution range, and its population was scattered southward of Gebel Elba from Sudan to Somalia (Marrero et al., 1998; Kamel et al., 2009). Additionally, the olive community was characterized by a rich *Vachellia etbaica* growth, which was also recorded on the northern slopes of three coastal mountains in the Elba range but not on the inland mountains (Zahran & Willis 2009).

Vegetation pattern in Gebel Elba

The vegetation of Gebel Elba is incomparable to any other region in Egypt but comparable to the highlands of East Africa and the southwestern Arabian Peninsula (Kassas,1956; Bussmann, 2006; Kürschner et al., 2008; Deil, 2014; Berhanu et al., 2018). The identified communities were mostly not recorded elsewhere in Egypt and the proportion of trees was higher than any similar areas in Egypt (e.g., Boulos, 2008; Abd El-Ghani et al., 2014, 2017). The classification proposed in **Chapter 3** accorded with the observation of Zohary (1973) and Zahran & Willis (2009).

The deciduous *Vachellia-Commiphora* woodland was the most common in Gebel Elba National Park, and it was represented by six plant communities in the open desert to the middle elevations. While the evergreen *Olea* woodland was only represented by one plant community at the higher elevations. I determined the distribution patterns of deciduous and evergreen trees along the elevational gradient, and I identified the *Ficus* community as a potential ecotone (a transition zone) between the two major vegetation units at middle elevations. The phytosociological classification presented in **Chapter 3** could be a baseline for future studies on Afrotropical woodlands with detailed information on vegetation composition and structure in south-eastern Egypt.

The Acacietea sudano-arabica sensu Zohary (1973) was described as the main vegetation class in the lower mountain zones in south Arabia and south Egypt. This class comprised the bulk of the xerotropical vegetation on Gebel Elba from low to middle elevations. However, I found that most of the names of the syntaxa described by Zohary were invalid since neither a sufficient original diagnosis nor a reference to such diagnosis was included (see Léonard, 1993).

The identified woodland communities in **Chapter 3** could be classified within the Boscio-Commiphoretalia abyssinicae, Boscio-Commiphoretea abyssinicae Knapp (1965) for the *Vachellia-Commiphora* woodland, and the Pistacio-Eucleetalia schimperi, Hyperico-Rhamnetea Knapp (1968) for the *Olea* woodland. This communities could be classified as new phytosociological associations. But the phytosociological data was insufficient as there was no single relevés or comparative constancy tables for this region. The description of the associations would be based on a regionally very limited sample within a radius of few kilometres. Most of the associations might occur also outside the Gebel Elba area as many of the characteristic species had a wide distribution range. Future studies should check the literature for relevés from a supra-regional level, to delimit these new associations from others already described ones based on a larger set of samples (e.g., Kürschner et al., 2008; Boucheneb & Benhouhou, 2012; Mahdjoubi & Guendouz-Benrima, 2017).

3. Environmental drivers of vegetation patterns

Previous studies generally discussed vegetation patterns in Gebel Elba region considering altitude and water availability (Abd El-Ghani and Abdel-Khalik, 2006; Al-Gohary, 2008a; Zahran and Willis, 2009). However, they did not determine the altitudinal ranges of vegetation belts or the location of mist oases on Gebel Elba. Also, there was very few information about soil properties in the region (Zaki, 2000). In this thesis, I studied the contribution of environmental variables to better understand the effects of environmental parameters on species diversity and vegetation composition in Gebel Elba (**Chapters 2, 3** and **4**).

For more details, these environmental parameters were discussed in the following sections:

3.1. Altitude:

Altitude is the major environmental driver in mountains regarding the species diversity and composition change along altitudinal gradients (Körner; 2007; Muenchow et al., 2013a). In **Chapter 2**, I discussed changes in diversity along the altitudinal gradients of wadi systems based on the elevational-climate model for arid mountains proposed by Grytnes and McCain (2013; their Figure 1b). Also, I clearly identified the altitudinal zonation of the plant communities and the location of a mist oasis on the north-western slopes of Gebel Elba (**Chapter 3**). Altitude is a proxy for other parameters such as soil moisture content and evapotranspiration (Körner & Spehn, 2019). In wadi systems, water availability increases with altitude while solar irradiance and temperature are considerably lower at higher altitudes. As a result, evergreen plants only grew very well in high altitudes, whereas deciduous plants dominated in low to middle altitudes (**Chapters 3** and **4**).

3.2. Climate:

Change in climatic conditions represented an important environmental driver along elevational gradients of Gebel Elba. Plants in lower elevations were more affected by high temperature and drought, compared to plants in higher elevations (Hegazy and Lovett-Doust, 2016). In **Chapter 3**, I stated the climate of Wadi Yahmib and its tributaries (Marafai, Acow and Kansisrob) based on the climatic research unit (CRU) datasets. The mean annual temperature at lower elevations was nearly 26 ºC while it decreased by five degrees along the elevational gradient. In addition, the location of Gebel Elba formed the highest topographical structure near the Red Sea coast and thereby increased the chance to receive more rainfall from orographic precipitation (Zharan and Willis, 2009). Yahmib plain at the foot of the mountain was the most stressful area for plant life, while Marafai at higher elevations had the most favourable climatic conditions among the studied wadis. So, the highest number of plant species was found in Marafai and less drought resistant species were confined to the mist zone.

3.3. Soil:

In **Chapter 3**, the vegetation survey was associated with a soil sampling approach, soil properties changed along the studied elevational gradient. On the one hand, soil at lower elevations was mostly sandy and it had lower content of organic matter with higher mineral content. Sandy soil in the open desert had a low water holding capacity, thus, the vegetation was usually scattered and dominated by deep-rooted species to reach underground water. On the other hand, soil at higher elevations was sandy loam with lower salinity and higher content of organic matter. Increasing silt and clay content with elevation caused a higher water holding capacity in mountainous wadis, hence herbs and shrubs had a better chance to grow than at lower elevations. So, the change in the soil properties along the studied elevational gradient was a determining factor of species richness and turnover in Gebel Elba.

3.4. Topography:

The rugged topography of mountains allowed species to survive in habitats of suitable microclimate where the surrounding area was less suitable (Stewart & Lister, 2001; Bennie et al., 2008; Hegazy and Lovett-Doust, 2016). In **Chapter 3**, I found that the mountainous areas acted as a refuge for Afrotropical flora in an otherwise hyper arid regional climate. Moreover, I described different microhabitats for plant species in the mountainous wadis such as side slopes for

Euphorbia nubica and *Vachellia etbaica*, and wadi beds for *Olea europaea* subsp. *cuspidata* and *Ficus salicifolia*. The topography strongly changed at higher elevations, offering a high variety in microhabitats which promoted species diversity in Gebel Elba (**Chapter 2**). At higher elevations, wadis (Marafai and Acow) became narrower and side slopes became steeper, offering more shaded areas for many herbaceous species. Moreover, the change in topography reflected water availability and its accumulation in wadi systems. As the presence of big granite boulders increased water accumulation between rocks and forming springs in wadi beds (**Chapters 2** and **3**). Thus, water availability in mountainous wadis and the change in topography from an open sandy desert to a rocky mountain ecosystem affected species richness and distribution in Gebel Elba region.

4. Using remotely sensed data to predict plant α- and β-diversity

The rugged topography and the inaccessibility of Gebel Elba region were the main obstacles to assess its diversity (Abutaha et al., 2019). Therefore, using remote sensing could be helpful to predict the diversity for this unique mountain. As shown in **Chapter 4**, topographic and remotely sensed data combined with ground truth data played a notable role to generate data for spatial conservation planning and management in Gebel Elba region. In this study, I used data derived from using very high-resolution PlanetScope satellite image and a digital elevation model (DEM) to model alpha and beta diversity calculated from the vegetation-plots datasets of Gebel Elba.

The predictive models showed that the use of modified soil-adjusted vegetation index ($MSAVI_2$) and topographic variables (i.e., altitude, landforms, catchment area and solar insolation) were important to explain spatial diversity patterns in arid mountains. So far, elevation was considered as the main environmental factor explaining the change in species richness and floristic composition on

Gebel Elba (Al-Gohary, 2008a; Abd El-Ghani et al., 2017). My findings in **Chapter 4** support previous studies on arid mountains (von Wehrden et al., 2009; Brinkmann et al., 2011; Muenchow et al., 2013a; Vanselow & Samimi, 2014) showing that the use of combined environmental variables in addition to elevation was more beneficial than using only elevation as a predictor of plant diversity.

In **Chapter 4**, I provided the first model-based plant diversity maps for the arid mountain Gebel Elba. Mapping alpha and beta diversity revealed that the change in topography from an open desert to a mountain ecosystem regulated species diversity and distribution. The predictive mapping clearly reflected that species diversity in mountainous wadi systems was higher than at the foot of the mountain. Also, the maps clearly showed that species diversity in mountainous wadi beds was higher than that on the run–off slopes, and the turnover between the deciduous and evergreen woodlands occurred at mid elevations. These differences were mainly related to the altitudinal gradient being a major stress gradient and vegetation being mostly restricted to wadi systems. Thus, my predictive diversity maps showed that it is important to focus conservation efforts on wadi areas at higher elevations of Gebel Elba as these were the most diverse ecosystems. I expect that my findings can be generalized to neighbouring mountains in the region.

Although soil was an important driver for plant diversity, its parameters were removed from the predictive models to avoid high collinearity with altitude. Another possible limitation might be the unmeasured microclimatic parameters along the elevational gradient, which could enhance the predictive power of diversity modeling in the study. I encourage further studies at Gebel Elba to focus on quantifying this environmental gradient with temperature and relative humidity data loggers.

Conclusion

The presented thesis provided the first extensive description of plant species composition and plant diversity of the arid mountain Gebel Elba. I identified an uncommon richness-elevation relationship for wadi systems in arid mountains. The identified pattern was mainly related to the elevational gradient being a major stress gradient. Also, I added knowledge to the Afrotropical woodlands of Egypt and established the first phytosociological classification of the vegetation units of Gebel Elba. Moreover, I contributed to the knowledge of vegetation-environment relationships for wadis in a mountain ecosystem and revealed the importance of elevation, change in topography and soil quality in determining the vegetation structure.

Furthermore, I explored the usefulness of spatial predictive models based on remotely sensed data to map plant diversity components in inaccessible mountainous areas. Given the global availability of remote sensing products, I recommend that emphasis should be put on sampling high quality vegetation data to serve as ground truth. The identified patterns in this thesis highlighted the importance of wadis for plant growth and diversity in arid environments and showed clear differences between the desert and mountain ecosystems. The current work will help local conservation efforts in the Gebel Elba region, and it can serve as a case study for adjacent arid mountains.

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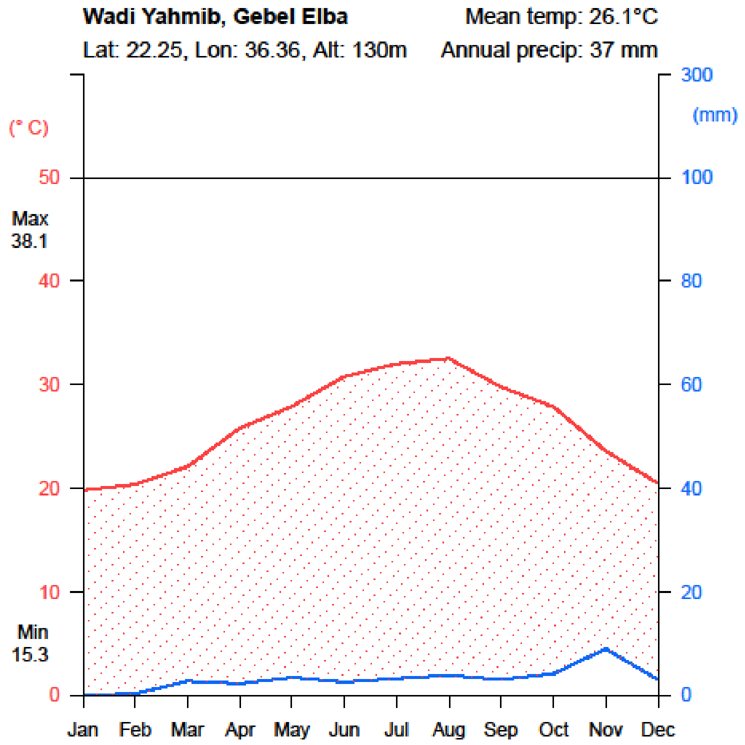
SUPPORTING INFORMATION



Appendix 1: Walter & Lieth (1967) Climate diagram for Wadi Yahmib, Gebel Elba, Egypt. Data was extracted from the high-resolution gridded datasets developed by Climatic Research Unit (CRU TS v. 4.01), University of East Anglia (Harris, Jones, Osborn, & Lister, 2014) for the period 1985 to 2015. The upper red line stands for mean monthly temperature of 26.1°C (left axis); numbers beside the axis are the mean monthly maximum and mean monthly minimum temperature. The lower blue line stands for precipitation (right axis). Area shaded with red dots (dotted area), above the precipitation line, and below the temperature line, indicates a dry period.

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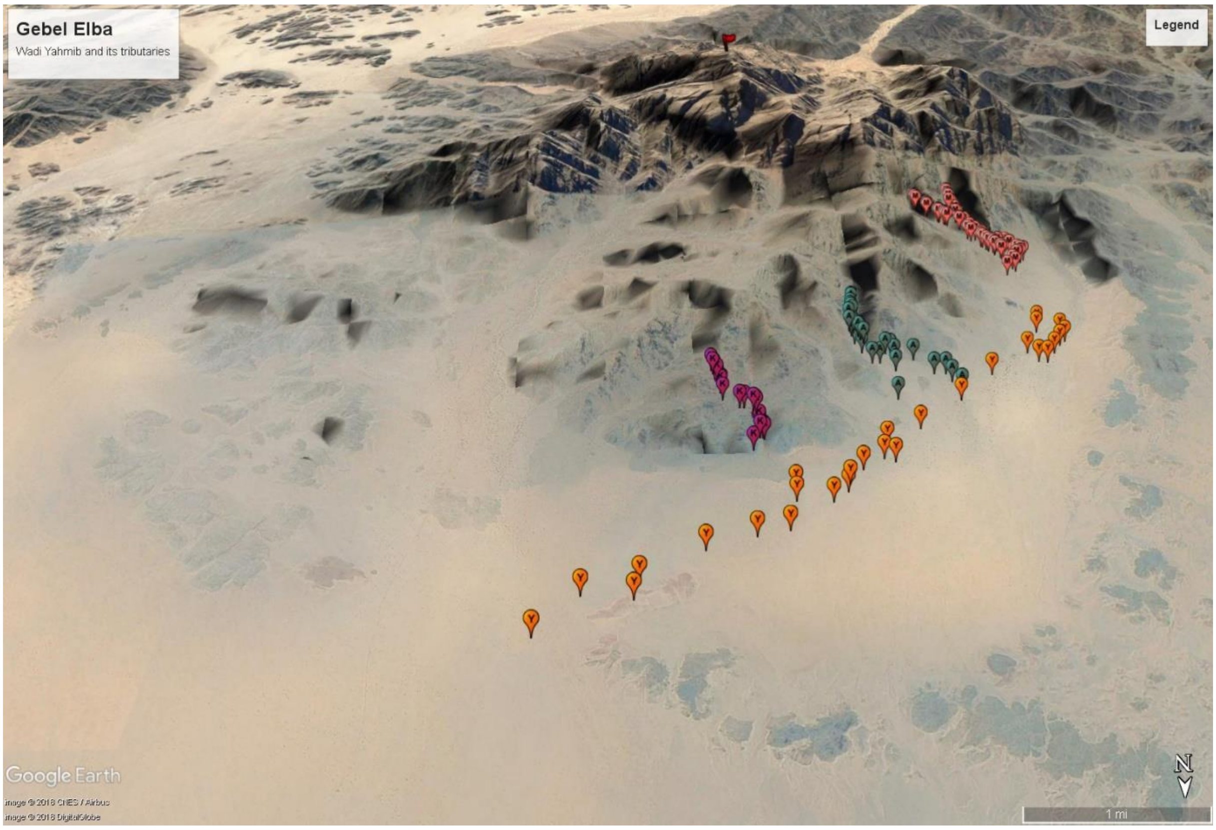

Appendix 2: Location map showing the distribution of the 133 sampling plots in Wadi Yahmib and its mountain tributaries, Gebel Elba.

Appendix 3: Species list including family names, information on life form (P = perennial, A = annual), growth form (W = woody, H = herbaceous), rarity (R = rare, C = common), and the distribution of species in the studied Wadis (M = Marafai, A = Acow, K = Kansisrob, and Y = Yahmib).

Notes:

- Rarity was based on a study on the vegetation of Gebel Elba National Park by Ahmed (1999). Five classes were defined: very rare (rr), rare (r), common (c), very common (cc), and abundant (ab).
- The main wadi gradient is known as Wadi Yahmib, which we locally divided into two wadis; the mountainous part is called Marafai while the part in the sandy plains at the foot of the mountain is called Yahmib. Wadi Yahmib also receives water from two other tributaries, i.e. Wadi Acow and Wadi Kansisrob.

	Family	Species incl. author	Life form	Growth form	Rarity	Wadi			
						M	A	K	Y
1	Acanthaceae	***Barleria hochstetteri*** Nees	P	W	R	rr			
2		***Blepharis edulis*** (Forssk.) Pers.	P	H	R	r	r	c	
3		***Peristrophe paniculata*** (Forssk.)	A	H	C	c	c	c	
4	Adiantaceae	***Onychium divaricatum*** (Poir.) Alston	P	H	R	r			
5	Aizoaceae	***Aizoon canariense*** L.	A	H	C	cc	cc	cc	c
6	Amaranthaceae	***Achyranthes aspera*** L. var. ***sicula*** L.	P	H	R	rr		r	
7		***Aerva javanica*** (Burm. f.) Juss. ex Schult. in Roem. & Schult. var ***javanica***	P	H	C	cc	c	cc-ab	
8		***Aerva lanata*** (L.) Juss. ex Schult.	P	H	R	r	r		
9		***Amaranthus graecizans*** L. subsp. ***graecizans***	A	H	R	rr	r	r	
10		***Psilotrichum gnaphalobryum*** (Hochst.) Schinz	P	H	R	rr			
11		***Pupalia lappacea*** (L.) Juss.	P	H	R	rr			
12	Amaryllidaceae	***Pancratium tortuosum*** Herb.	P	H	R	rr	r	rr	
13	Anacardiaceae	***Pistacia khinjuk*** Stocks var. ***glabra*** Schweinf. ex Engl.	P	W	R	r			
14		***Rhus abyssinica*** Hochst. ex Oliv.	P	W	R	rr			
15		***Rhus flexicaulis*** Baker	P	W	C	c			
16		***Rhus tripartita*** (Ucria) Grande	P	W	R	rr			
17	Apiaceae	***Pimpinella etbaica*** Schweinf.	A	H	R	rr	rr		

18	Apocynaceae	***Carissa spinarum*** L.	P	W	R	r			
19	Asclepiadaceae	***Calotropis procera*** (Aiton) W. T. Aiton	P	W	R		rr		r
20		***Leptadenia pyrotechnica*** (Forssk.) Decne.	P	W	R		r		r
21		***Pergularia daemia*** (Forssk.) Chiov.	P	H	R	r			
22		***Periploca aphylla*** Decne. subsp. ***laxiflora*** Browicz	P	W	R	r	rr		
23	Asphodelaceae	***Asphodelus tenuifolius*** Cav.	A	H	C	c	c	r	rr
24	Asteraceae	***Bidens bipinnata*** L.	A	H	R	r			
25		***Bidens schimperi*** Sch. Bip.	A	H	R	r	r		
26		***Echinops hussonii*** Boiss.	P	H	C	cc	c	r	
27		***Launaea nudicaulis*** (L.) Hook. f.	P	H	R		rr		
28		***Osteospermum vaillantii*** (Decne.) Norl.	P	H	R	rr		rr	
29		***Pegolettia senegalensis*** Cass.	A	H	R	rr	rr		
30		***Phagnalon schweinfurthii*** Sch. Bip. ex Schweinf.	P	H	R	rr			
31		***Pulicaria petiolaris*** Jaub. & Spach	P	H	R	rr			
32		***Pulicaria undulata*** (L.) C. A. Mey.	P	W	R	r	rr	rr	
33		***Reichardia tingitana*** (L.) Roth	A	H	R	r	c		
34		***Senecio flavus*** (Decne.) Sch.Bip.	A	H	R	r			
35		***Urospermum picroides*** (L.) F. W. Schmidt	A	H	R	r	r	rr	
36	Boraginaceae	***Arnebia hispidissima*** (Lehm.) DC.	A	H	R		r		
37		***Heliotropium bacciferum*** Forssk. subsp. ***bacciferum*** var. ***bacciferum***	P	H	R				r
38		***Heliotropium supinum*** L.	A	H	R				r
39		***Heliotropium zeylanicum*** (Burm. f.) Lam.	P	H	R	r		rr	
40		***Trichodesma africanum*** (L.) R. Br. var. ***africanum***	P	H	R	r	r		
41		***Trichodesma ehrenbergii*** Schweinf.	A	H	C	c	c	c	
42	Brassicaceae	***Diceratella elliptica*** (DC.) Jonsell	P	H	R	rr	r		
43		***Farsetia longisiliqua*** Decne.	P	W	R	r	c	r	
44		***Sisymbrium erysimoides*** Desf.	A	H	C	cc	cc	c	
45	Capparaceae	***Boscia senegalensis*** Poir.	P	W	R	rr			
46		***Capparis decidua*** (Forssk.) Edgew.	P	W	R	rr		rr	

47		**_Cleome amblyocarpa_** Barratte & Murb.	A	H	R		rr		rr
48		**_Maerua crassifolia_** Forssk.	P	W	R	r	r	r	r
49		**_Maerua oblongifolia_** (Forssk.) A. Rich.	P	W	R			r	
50	Caryophyllaceae	**_Cometes abyssinica_** R. Br.	A	H	R	r	rr	r	
51		**_Spergula fallax_** (Lowe) E. H. L. Krause	A	H	R	r		r	rr
52	Celastraceae	**_Maytenus senegalensis_** (Lam.) Exell	P	W	R	rr			
53	Chenopodiaceae	**_Chenopodium murale_** L.	A	H	C	cc	c	c	r
54	Commelinaceae	**_Commelina benghalensis_** L.	P	H	C	c	c		
55		**_Commelina forsskaolii_** Vahl	A	H	C	cc	c	c	
56	Convolvulaceae	**_Convolvulus hystrix_** Vahl	P	W	R	r		rr	
57		**_Cuscuta chinensis_** Lam.	A	H	R	r	r	rr	
58		**_Cuscuta pedicellata_** Ledeb.	A	H	R		r		
59		**_Ipomoea sinensis_** (Desr.) Choisy subsp. **_blepharosepala_** (A. Rich.) Meeuse	A	H	R	rr	rr	rr	
60	Cucurbitaceae	**_Citrullus colocynthis_** (L.) Schrad.	P	H	R	r	r	r	
61		**_Cucumis prophetarum_** L. subsp. **_dissectus_** (Naudin) C. Jeffrey	P	H	R	rr			
62		**_Cucumis prophetarum_** L. subsp. **_prophetarum_**	P	H	C	c	c	cc	r
63		**_Kedrostis gijef_** (J. F. Gmel.) C. Jeffrey	P	W	R	rr	rr		
64	Cyperaceae	**_Cyperus laevigatus_** L. **_laevigatus_**	P	H	R	rr			
65	Dracaenaceae	**_Dracaena ombet_** Kotschy & Peyr.	P	W	R	c			
66	Ebenaceae	**_Euclea racemosa_** Murray subsp. **_schimperi_** (A. DC.) F. White	P	W	R	rr			
67	Ephedraceae	**_Ephedra ciliata_** Fischer & C. A. Mey	P	W	R	r	r	r	
68	Euphorbiaceae	**_Andrachne aspera_** Spreng.	P	H	R	r			
69		**_Chrozophora oblongifolia_** (Delile) Spreng.	P	H	R	r		r	
70		**_Chrozophora tinctoria_** (L.) Raf.	A	H	R	r	r		
71		**_Euphorbia consobrina_** N. E. Br.	P	W	C	cc	cc	c	
72		**_Euphorbia cuneata_** Vahl	P	W	C	r	c	cc	
73		**_Euphorbia granulata_** Forssk.	A	H	R	r		r	
74		**_Euphorbia_** sp.	A	H	R			rr	
75	Fabaceae	**_Acacia etbaica_** Schweinf.	P	W	R	r	rr		

76		***Acacia laeta*** R. Br. ex Benth.	P	W	R	rr			
77		***Acacia mellifera*** (Vahl) Benth.	P	W	C	c	r	c	
78		***Acacia oerfota*** (Forssk.) Schweinf. var. ***oerfota***	P	W	R			rr	
79		***Acacia*** sp.	P	W	R		r		
80		***Acacia tortilis*** (Forssk.) Hayne subsp. ***raddiana*** (Savi) Brenan	P	W	C	r	c	r	c
81		***Acacia tortilis*** (Forssk.) Hayne subsp. ***tortilis***	P	W	C	cc-ab	cc-ab	cc-ab	cc-ab
82		***Crotalaria impressa*** Nees ex Walp.	A	H	R			rr	
83		***Crotalaria senegalensis*** (Pers.) DC.	A	H	R			rr	
84		***Delonix elata*** (L.) Gamble	P	W	R		rr	r	
85		***Indigofera spinosa*** Forssk.	P	W	R	*	*	*	*
86		***Rhynchosia minima*** (L.) DC. var. ***memnonia*** (Delile) Cooke	P	H	R	rr			
87		***Senna italica*** Mill.	P	H	C	c	c	r	r
88		***Tephrosia purpurea*** (L.) Pers., subsp. ***apollinea*** (Delile) Hosni & El-Karemy	P	H	C	cc	c	cc-ab	c
89	Geraniaceae	***Erodium neuradifolium*** Delile ex Godr.	A	H	R	r	rr		
90		***Geranium trilophum*** Boiss.	A	H	R	r	rr	rr	
91	Lamiaceae	***Lavandula coronopifolia*** Poir.	P	W	C	c	c	r	
92		***Leucas neuflizeana*** Courbai	A	H	R	rr			
93		***Ocimum forsskaolii*** Benth.	P	W	R	c	r		
94		***Otostegia fruticosa*** (Forssk.) Penz. subsp. ***fruticosa***	P	W	R	r	rr		
95		***Salvia aegyptiaca*** L.	P	W	R	c	r		
96	Loranthaceae	***Plicosepalus acaciae*** (Zucc.) Wiens & Polhill	P	W	R	r	rr		
97		***Plicosepalus curviflors*** (Benth. ex Oliv.) Tiegh	P	W	R	r	rr		
98	Malvaceae	***Abutilon bidentatum*** A. Rich.	P	W	R	r			
99		***Abutilon fruticosum*** Guill. & Perr.	P	W	C	cc	cc	cc	
100		***Abutilon pannosum*** (G. Forst.) Schltdl.	P	W	C	cc	cc	cc	
101		***Hibiscus micranthus*** L.f.	P	W	R	r	r	rr	
102		***Hibiscus vitifolius*** L.	P	W	R	r	r		
103		***Malva parviflora*** L.	A	H	R		rr		
104		***Pavonia triloba*** Guill. & Perr.	P	H	R	rr			

105	Menispermaceae	***Cocculus pendulus*** (J. R. & G. Forst) Diels	P	W	C	c	c	c	c
106	Moraceae	***Ficus cordata*** Thunb. subsp. ***salicifolia*** (Vahl) C. C. Berg	P	W	C	c	c		
107		***Ficus palmata*** Forssk.	P	W	R		r		
108	Moringaceae	***Moringa peregrina*** (Forssk.) Fiori	P	W	R	rr	r		
109	Nyctaginaceae	***Commicarpus helenae*** (Schult.) Meikle	P	H	R	rr		rr	
110	Oleaceae	***Jasminum fluminense*** Vell. subsp. ***gratissimum*** (Deflers) P. S. Green	P	W	R	rr			
111		***Jasminum grandiflorum*** L. subsp. ***floribundum*** (R. Br. ex Fresen.) P. S. Green	P	W	R	r			
112		***Olea europaea*** L. subsp. ***cuspidata*** (Wall. ex G. Don) Ciferri	P	W	C	cc-ab			
113	Oxalidaceae	***Oxalis anthelmintica*** A. Rich.	P	H	R	rr	rr		
114	Plantaginaceae	***Plantago afra*** L.	A	H	R	c		rr	rr
115		***Plantago ciliata*** Desf.	A	H	R		rr		
116	Poaceae	***Brachypodium distachyum*** (L.) P. Beauv.	A	H	R		rr		rr
117		***Bromus fasciculatus*** C. Presl	A	H	R	r			
118		***Cenchrus ciliaris*** L.	P	H	C	cc	cc	r	rr
119		***Cenchrus pennisetiformis*** Hochst. & Steud.	A	H	R	rr	rr	r	rr
120		***Centropodia forskaolii*** (Vahl) Cope	P	H	R		r		
121		***Cynodon dactylon*** (L.) Pers.	P	H	R		rr	rr	
122		***Digitaria nodosa*** Parl.	P	H	R			rr	
123		***Eragrostis cilianensis*** (All.) Vignolo ex Janch.	A	H	R	r	rr		
124		***Melanocenchris abyssinica*** (R. Br. ex Fresen.) Hochst.	A	H	R	r	rr		
125		***Panicum turgidum*** Forssk.	P	H	R	rr	rr		
126		***Stipagrostis ciliata*** (Desf.) De Winter	P	H	R			rr	
127		***Tragus racemosus*** (L.) All.	A	H	R		rr		
128	Polygonaceae	***Rumex simpliciflorus*** Murb.	A	H	R	rr			
129		***Rumex vesicarius*** L.	A	H	C	cc	c	c	
130	Portulacaceae	***Portulaca oleracea*** L. subsp. ***oleracea***	A	H	R	rr	rr		
131	Primulaceae	***Anagallis arvensis*** L.	A	H	R		rr		
132	Resedaceae	***Caylusea hexagyna*** (Forssk.) M. L. Green	A	H	R		r	rr	
133		***Ochradenus baccatus*** Delile	P	W	R	rr	rr	rr	

134	Rubiaceae	***Galium spurium*** L.	A	H	R	r			
135	Salvadoraceae	***Salvadora persica*** L.	P	W	R	rr		rr	
136	Sapindaceae	***Dodonaea viscosa*** (L.) Jacq.	P	W	R	r			
137	Scrophulariaceae	***Kickxia hastata*** (R. Br. ex Benth.) Dandy in Andrews	A	H	R	r	rr	rr	
138		***Scrophularia arguta*** Sol.	A	H	R	rr	rr		
139		***Lindenbergia indica*** (L.) Vatke	P	W	R	rr	rr		
140	Solanaceae	***Lycium shawii*** Roem. & Schult. var ***shawii***	P	W	C	c	c	c	c
141		***Solanum forsskaolii*** Dunal	P	W	C	c	c	r	
142		***Solanum incanum*** L.	P	W	C	c	c		
143		***Solanum nigrum*** L. var. ***elbaensis*** Täckh. & Boulos	A	H	R	r	r		
144		***Solanum villosum*** Mill. Subsp. ***villosum***	A	H	R	rr	rr		
145	Tiliaceae	***Grewia tenax*** (Forssk.) Fiori	P	W	R	rr			
146		***Grewia tembensis*** Fresen.	P	W	R	rr			
147		***Grewia villosa*** Willd.	P	W	R	rr			
148		***Triumfetta flavescens*** Hochst. ex A. Rich.	P	W	C	cc	c	r	rr
149		***Triumfetta rhomboidea*** Jacq.	P	W	R	c			
150	Urticaceae	***Forsskaolea tenacissima*** L.	P	H	C	c	c	cc	r
151		***Forsskaolea viridis*** Webb	A	H	C	c	c	rr	
152		***Parietaria debilis*** G. Forster	A	H	R	rr	r	c	
153	Verbenaceae	***Lantana viburnoides*** **(**Forssk.) Vahl	P	W	R	rr			
154	Violaceae	***Viola cinerea*** Boiss. var. ***stocksii*** (Boiss.) Becker	A	H	R	rr			
155	Zygophyllaceae	***Balanites aegyptiaca*** (L.) Delile	P	W	C	ab	ab	r	c
156		***Tribulus terrestris*** L.	A	H	C	cc	c	r	
157		***Zygophyllum simplex*** L.	A	H	C	cc-ab	cc-ab	cc-ab	cc-ab

Appendix 4. Updated species list including information on growth form and the distribution of species in the studied Wadis (M = Marafai, A = Acow, K = Kansisrob, and Y = Yahmib).

	Family	Species incl. author	Life cycle	Life form	Growth form	Wadi			
						M	A	K	Y
1	Acanthaceae	***Barleria hochstetteri*** Nees	P	Ch	shrub	*			
2		***Blepharis edulis*** (Forssk.) Pers.	P	Ch	herb	*	*	*	
3		***Dicliptera paniculata*** (Forssk.) I. Darbysh.	A	Th	herb	*	*	*	
4	Aizoaceae	***Aizoon canariense*** L.	A	Th	herb	*	*	*	*
5	Amaranthaceae	***Achyranthes aspera*** L. var. ***sicula*** L.	P	H	herb	*		*	
6		***Aerva javanica*** (Burm. f.) Juss. ex Schult. in Roem. & Schult. var ***javanica***	P	Ch	herb	*	*	*	
7		***Aerva lanata*** (L.) Juss. ex Schult.	P	Ch	herb	*	*		
8		***Amaranthus graecizans*** L. subsp. ***aschersonianus*** (Thell.) Costea, D. M. Brenner & Tardif	A	Th	herb	*	*	*	
9		***Chenopodiastrum murale*** (L.) S. Fuentes, Uotila & Borsch	A	Th	herb	*	*	*	*
10		***Psilotrichum gnaphalobryum*** (Hochst.) Schinz	P	Ch	herb	*			
11		***Pupalia lappacea*** (L.) Juss.	P	Ch	herb	*			
12	Amaryllidaceae	***Pancratium tortuosum*** Herb.	P	G	herb	*	*	*	
13	Anacardiaceae	***Pistacia khinjuk*** Stocks var. ***glabra*** Schweinf. ex Engl.	P	Ph	tree	*			
14		***Searsia flexicaulis*** (Baker) Moffett	P	Ph	tree	*			
15		***Searsia glutinosa*** subsp. ***abyssinica*** (Hochst. ex Oliv.) Moffett	P	Ph	tree	*			
16		***Searsia tripartita*** (Ucria) Moffett	P	Ph	tree	*			
17	Apiaceae	***Pimpinella etbaica*** Schweinf.	A	Th	herb	*	*		
18	Apocynaceae	***Calotropis procera*** (Aiton) W. T. Aiton	P	Ph	tree		*		*
19		***Carissa spinarum*** L.	P	Ph	shrub/liana	*			
20		***Leptadenia pyrotechnica*** (Forssk.) Decne.	P	Ph	shrub		*		*

21		***Pergularia daemia*** (Forssk.) Chiov.	P	Ch	liana	*			
22		***Periploca aphylla*** Decne. subsp. ***laxiflora*** (Bornm. ex Drar) Browicz	P	Ph	shrub	*	*		
23	Asparagaceae	***Dracaena ombet*** Heuglin ex Kotschy & Peyr. subsp**. ombet**	P	Ph	tree	*			
24	Asphodelaceae	***Asphodelus tenuifolius*** Cav.	A	Th	herb	*	*	*	*
25	Asteraceae	***Bidens bipinnata*** L.	A	Th	herb	*			
26		***Bidens schimperi*** Sch. Bip. ex Walp.	A	Th	herb	*	*		
27		***Echinops hussonii*** Boiss.	P	H	herb	*	*	*	
28		***Launaea nudicaulis*** (L.) Hook. f.	P	H	herb		*		
29		***Osteospermum vaillantii*** (Decne.) Norl.	P	H	herb	*		*	
30		***Pegolettia senegalensis*** Cass.	A	Th	herb	*	*		
31		***Phagnalon schweinfurthii*** Sch. Bip. ex Schweinf.	P	Ch	herb	*			
32		***Pulicaria petiolaris*** Jaub. & Spach	P	H	herb	*			
33		***Pulicaria undulata*** (L.) C. A. Mey.	P	Ch	shrub	*	*	*	
34		***Reichardia tingitana*** (L.) Roth subsp. ***tingitana***	A	Th	herb	*	*		
35		***Senecio flavus*** (Decne.) Sch. Bip.	A	Th	herb	*			
36		***Urospermum picroides*** (L.) Scop. ex. F. W. Schmidt	A	Th	herb	*	*	*	
37	Boraginaceae	***Arnebia hispidissima*** (Sieber ex Lehm.) A. DC.	A	Th	herb		*		
38		***Heliotropium bacciferum*** Forssk.	P	Ch	herb				*
39		***Heliotropium supinum*** L.	A	Th	herb				*
40		***Heliotropium zeylanicum*** (Burm. f.) Lam.	P	Ch	herb	*		*	
41		***Trichodesma africanum*** (L.) R. Br. var. ***africanum***	A	Th	herb	*	*		
42		***Trichodesma ehrenbergii*** Schweinf.	P	H	herb	*	*	*	
43	Brassicaceae	***Diceratella elliptica*** (DC.) Jonsell	P	H	herb	*	*		
44		***Farsetia longisiliqua*** Decne.	P	Ch	shrub	*	*	*	
45		***Sisymbrium erysimoides*** Desf.	A	Th	herb	*	*	*	

46	Burseraceae	***Commiphora gileadensis*** (L.) C. Chr.	P	Ph	shrub			*	
47	Capparaceae	***Boscia senegalensis*** (Pers.) Lam. ex Poir.	P	Ph	shrub	*			
48		***Capparis decidua*** (Forssk.) Edgew.	P	Ph	tree	*		*	
49		***Maerua crassifolia*** Forssk.	P	Ph	tree	*	*	*	*
50		***Maerua oblongifolia*** (Forssk.) A. Rich.	P	Ch	liana			*	
51	Caryophyllaceae	***Cometes abyssinica*** R. Br. ex Wall.	A	Th	herb	*	*	*	
52		***Paronychia argentea*** Lam.	A	Th	herb			*	
53		***Spergularia flaccida*** (Madden) I. M. Turner	A	Th	herb	*		*	*
54	Celastraceae	***Gymnosporia senegalensis*** (Lam.) Loes.	P	Ph	shrub	*			
55	Cleomaceae	***Cleome amblyocarpa*** Barratte & Murb.	A	Th	herb		*		*
56	Commelinaceae	***Commelina benghalensis*** L.	A	Th	herb	*	*		
57		***Commelina forskaolii*** Vahl	A	Th	herb	*	*	*	
58	Convolvulaceae	***Convolvulus hystrix*** Vahl subsp. ***hystrix***	P	Ch	shrub	*		*	
59		***Cuscuta chinensis*** Lam.	A	Th	liana	*	*	*	
60		***Cuscuta pedicellata*** Ledeb.	A	Th	liana		*		
61		***Ipomoea biflora*** (L.) Pers.	A	Th	herb	*	*	*	
62	Cucurbitaceae	***Citrullus colocynthis*** (L.) Schrad.	P	H	herb	*	*	*	
63		***Cucumis prophetarum*** L. subsp. ***dissectus*** (Naudin) C. Jeffrey	P	H	herb	*			
64		***Cucumis prophetarum*** L. subsp. ***prophetarum***	P	H	herb	*	*	*	*
65		***Kedrostis gijef*** (Forssk. ex. J. F. Gmel.) C. Jeffrey	P	Ch	liana	*	*		
66	Cyperaceae	***Cyperus laevigatus*** L. subsp. ***laevigatus***	P	H	sedge	*			
67	Ebenaceae	***Euclea racemosa*** Murray subsp. ***schimperi*** (A. DC.) F. White	P	Ph	tree	*			
68	Ephedraceae	***Ephedra foliata*** Boiss. ex C. A. Mey.	P	Ph	shrub	*	*	*	
69	Euphorbiaceae	***Chrozophora oblongifolia*** (Delile) A. Juss. ex Spreng.	P	Ch	herb	*		*	
70		***Chrozophora tinctoria*** (L.) Raf.	A	Th	herb	*	*		

71		***Euphorbia cuneata*** Vahl subsp. ***cuneata***	P	Ph	tree	*	*	*	
72		***Euphorbia nubica*** N. E. Br.	P	Ch	shrub	*	*	*	
73		***Euphorbia granulata*** Forssk.	A	Th	herb	*		*	
74		***Euphorbia*** sp. L.	A	Th	herb			*	
75	Fabaceae	***Crotalaria impressa*** Nees ex Walp.	A	Th	herb			*	
76		***Crotalaria senegalensis*** (Pers.) Bacle ex DC.	A	Th	herb			*	
77		***Delonix elata*** (L.) Gamble	P	Ph	tree		*	*	
78		***Indigofera spinosa*** Forssk.	P	Ch	shrub	*	*	*	*
79		***Rhynchosia minima*** (L.) DC. var. ***memnonia*** (Delile) T. Cooke	P	Ch	liana	*			
80		***Senegalia laeta*** (R. Br. ex Benth.) Seigler & Ebinger	P	Ph	tree	*			
81		***Senegalia mellifera*** (Benth.) Seigler & Ebinger	P	Ph	shrub	*	*	*	
82		***Senna italica*** Mill.	P	Ch	herb	*	*	*	*
83		***Tephrosia purpurea*** (L.) Pers. subsp. ***apollinea*** (Delile) Hosni & El-Karemy	P	Ch	herb	*	*	*	*
84		***Vachellia etbaica*** (Schweinf.) Kyal. & Boatwr.	P	Ph	tree	*	*		
85		***Vachellia oerfota*** (Forssk.) Kyal. & Boatwr. var. ***oerfota***	P	Ph	shrub			*	
86		***Vachellia*** sp. Wight & Arn.	P	Ph	tree		*		
87		***Vachellia tortilis*** (Forssk.) Galasso & Banfi subsp. ***raddiana*** (Savi) Kyal. & Boatwr.	P	Ph	tree	*	*	*	*
88		***Vachellia tortilis*** (Forssk.) Galasso & Banfi subsp. ***tortilis***	P	Ph	tree	*	*	*	*
89	Geraniaceae	***Erodium neuradifolium*** Delile ex Godr.	A	Th	herb	*	*		
90		***Geranium trilophum*** Boiss.	A	Th	herb	*	*	*	
91	Lamiaceae	***Lavandula coronopifolia*** Poir.	P	Ch	shrub	*	*	*	
92		***Leucas neuflizeana*** Courbon	A	Th	herb	*			
93		***Ocimum forskoelei*** Benth.	P	Ch	shrub	*	*		

94		***Otostegia fruticosa*** (Forssk.) Schweinf. ex Penzig subsp. ***fruticosa***	P	Ch	shrub	*	*		
95		***Salvia aegyptiaca*** L.	P	Ch	shrub	*	*		
96	Loranthaceae	***Plicosepalus acaciae*** (Zucc.) Wiens & Polhill	P	Ph	shrub	*	*		
97		***Plicosepalus curviflorus*** (Benth. ex Oliv.) Tiegh.	P	Ph	shrub	*	*		
98	Malvaceae	***Abutilon bidentatum*** Hochst. ex A. Rich.	P	Ch	shrub	*			
99		***Abutilon fruticosum*** Guill. & Perr.	P	Ch	shrub	*	*	*	
100		***Abutilon pannosum*** (G. Forst.) Schltdl.	P	Ph	shrub	*	*	*	
101		***Grewia tenax*** (Forssk.) Fiori	P	Ph	shrub	*			
102		***Grewia tembensis*** Fresen.	P	Ph	shrub	*			
103		***Grewia villosa*** Willd.	P	Ph	shrub	*			
104		***Hibiscus micranthus*** L. f.	P	Ch	shrub	*	*	*	
105		***Hibiscus vitifolius*** L.	P	Ch	shrub	*	*		
106		***Malva parviflora*** L.	A	Th	herb		*		
107		***Pavonia triloba*** Guill. & Perr.	P	Ch	herb	*			
108		***Triumfetta flavescens*** Hochst. ex A. Rich.	P	Ch	shrub	*	*	*	*
109		***Triumfetta rhomboidea*** Jacq.	P	Ch	shrub	*			
110	Menispermaceae	***Cocculus pendulus*** (J. R. & G. Forst.) Diels	P	Ch	liana	*	*	*	*
111	Moraceae	***Ficus palmata*** Forssk.	P	Ph	tree		*		
112		***Ficus salicifolia*** Vahl	P	Ph	tree	*	*		
113	Moringaceae	***Moringa peregrina*** (Forssk.) Fiori	P	Ph	tree	*	*		
114	Nyctaginaceae	***Commicarpus helenae*** (Roem. & Schult.) Meikle	P	Ph	shrub	*		*	
115	Oleaceae	***Jasminum fluminense*** Vell. subsp. ***gratissimum*** (Deflers) P. S. Green	P	Ph	liana	*			
116		***Jasminum grandiflorum*** L. subsp. ***floribundum*** (R. Br. ex Fresen.) P. S. Green	P	Ph	liana/shrub	*			
117		***Olea europaea*** L. subsp. ***cuspidata*** (Wall. ex G. Don) Ciferri	P	Ph	tree	*			

118	Orobanchaceae	***Lindenbergia indica*** (L.) Vatke	P	Ch	shrub	*	*		
119	Oxalidaceae	***Oxalis anthelmintica*** A. Rich.	P	G	herb	*	*		
120	Phyllanthaceae	***Andrachne aspera*** Spreng.	P	Ch	herb	*			
121	Plantaginaceae	***Nanorrhinum hastatum*** (R. Br. ex Benth.) Ghebr.	A	Th	herb	*	*	*	
122		***Plantago afra*** L.	A	Th	herb	*		*	*
123		***Plantago ciliata*** Desf.	A	Th	herb		*		
124	Poaceae	***Brachypodium distachyon*** (L.) P. Beauv.	A	Th	grass		*		*
125		***Bromus fasciculatus*** C. Presl	A	Th	grass	*			
126		***Cenchrus ciliaris*** L.	P	H	grass	*	*	*	*
127		***Cenchrus pennisetiformis*** Hochst. & Steud.	A	Th	grass	*	*	*	*
128		***Cenchrus setiger*** Vahl	P	G	grass			*	
129		***Centropodia forskalii*** (Vahl) Cope	P	H	grass		*		
130		***Cynodon dactylon*** (L.) Pers.	P	G	grass		*	*	
131		***Digitaria nodosa*** Parl.	P	H	grass			*	
132		***Eragrostis cilianensis*** (All.) Vignolo ex Janch.	A	Th	grass	*	*		
133		***Melanocenchris abyssinica*** (R. Br. ex Fresen.) Hochst.	A	Th	grass	*	*		
134		***Panicum turgidum*** Forssk.	P	G	grass	*	*		
135		***Stipagrostis ciliata*** (Desf.) De Winter	P	H	grass			*	
136		***Tragus racemosus*** (L.) All.	A	Th	grass		*		
137		***Urochloa deflexa*** (Schumach.) H. Scholz	A	Th	grass		*	*	
138	Polygonaceae	***Rumex simpliciflorus*** Murb.	A	Th	herb	*			
139		***Rumex vesicarius*** L.	A	Th	herb	*	*	*	
140	Portulacaceae	***Portulaca oleracea*** L. subsp. ***oleracea***	A	Th	herb	*	*		
141	Primulaceae	***Lysimachia arvensis*** (L.) U. Manns & Anderb.	A	Th	herb		*		
142	Pteridaceae	***Onychium divaricatum*** (Poir.) Alston	P	H	herb	*			

143	Resedaceae	***Caylusea hexagyna*** (Forssk.) M. L. Green	A	Th	herb		*	*	
144		***Ochradenus baccatus*** Delile	P	Ph	shrub	*	*	*	
145	Rubiaceae	***Galium spurium*** L.	A	Th	herb	*			
146	Salvadoraceae	***Salvadora persica*** L.	P	Ph	shrub	*		*	
147	Sapindaceae	***Dodonaea viscosa*** Jacq.	P	Ph	shrub	*			
148	Scrophulariaceae	***Scrophularia arguta*** Sol. ex Aiton	A	Th	herb	*	*		
149	Solanaceae	***Lycium shawii*** Roem. & Schult.	P	Ph	shrub	*	*	*	*
150		***Solanum forskaolii*** Dunal	P	Ch	shrub	*	*	*	
151		***Solanum incanum*** L.	P	Ch	shrub	*	*		
152		***Solanum nigrum*** L. var. ***elbaensis*** Täckh. & Boulos	A	Th	herb	*	*		
153		***Solanum villosum*** Mill. subsp. ***villosum***	A	Th	herb	*	*		
154		***Withania somnifera*** (L.) Dunal	P	Ch	shrub			*	
155	Urticaceae	***Forsskaolea tenacissima*** L.	P	H	herb	*	*	*	*
156		***Forsskaolea viridis*** Webb	A	Th	herb	*	*	*	
157		***Parietaria debilis*** G. Forst.	A	Th	herb	*	*	*	
158	Verbenaceae	***Lantana viburnoides*** (Forssk.) Vahl	P	Ch	shrub	*			
159	Violaceae	***Viola cinerea*** Boiss. var. ***stocksii*** (Boiss.) Becker	A	Th	herb	*			
160	Zygophyllaceae	***Balanites aegyptiaca*** (L.) Delile	P	Ph	tree	*	*	*	*
161		***Tribulus terrestris*** L.	A	Th	herb	*	*	*	
162		***Zygophyllum simplex*** L.	A	Th	herb	*	*	*	*

Appendix 5 (Supplementary material 1)

Supplementary tables showing the percentage cover and the distribution of perennial species in the studied relevés for each community. Wadi Marafai (M), W. Acow (A), W. Kansisrob (K), and W. Yahmib (Y).

Link: https://10.3897/VCS/2020/38644.suppl1

Table S1: The individual relevés for community I: *Dracaena ombet* - *Olea europaea* subsp. *cuspidata*

Species	**Relevés**																			
	M26	M29	M30	M31	M32	M33	M34	M35	M36	M37	M38	M39	M40	M43	M49	M50	M51	M52	M53	M54
Abutilon bidentatum	-	-	-	2.96	1.16	-	-	-	-	-	-	-	5.28	-	-	-	-	-	-	-
Abutilon fruticosum	-	7.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aerva lanata	2.64	-	-	6.08	-	5.47	-	-	7.08	-	-	6.52	-	-	-	-	-	-	-	-
Andrachne aspera	-	-	-	-	-	-	-	-	-	-	-	6.06	-	-	-	-	-	-	-	-
Barleria hochstetteri	2.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Boscia senegalensis	-	-	-	-	-	-	-	-	-	10.98	-	-	-	-	-	-	-	-	-	-
Carissa spinarum	-	-	-	-	-	-	16.41	6.13	11.12	7.15	-	-	12.85	-	-	-	-	14.27	3.61	-
Cenchrus ciliaris	-	-	-	-	-	8.94	-	-	-	12.15	-	-	-	-	-	-	-	-	-	-
Chrozophora oblongifolia	-	-	-	-	0.60	-	-	-	-	-	-	5.84	-	-	-	-	-	-	-	-
Cocculus pendulus	-	21.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.58	-	11.24	-
Commicarpus helenae	2.44	-	-	-	-	-	-	-	-	-	-	-	-	-	6.45	-	-	-	-	-
Cucumis prophetarum subsp. ***prophetarum***	-	-	18.44	-	-	4.59	-	-	-	-	-	5.00	-	-	-	-	-	-	-	-
Dodonaea viscosa	-	-	-	8.74	-	-	-	-	-	-	-	7.94	-	-	-	11.67	-	-	-	-
Dracaena ombet	-	-	34.01	7.51	6.55	-	-	18.27	-	-	19.50	-	10.84	54.13	-	-	-	-	-	22.37
Echinops hussonii	-	-	-	-	6.10	-	-	-	-	-	18.35	10.12	-	-	19.01	19.09	7.11	-	-	-

Ephedra ciliata	2.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euclea racemosa subsp. ***schimperi***	-	-	-	-	-	-	-	-	-	-	15.14	-	-	-	-	-	-	-	9.36	-
Ficus salicifolia	29.32	-	-	-	-	-	-	-	43.07	-	-	-	-	-	-	-	-	-	-	-
Forsskaolea tenacissima	-	-	-	11.48	-	-	-	-	-	-	-	-	11.94	-	3.85	6.32	11.41	-	-	-
Grewia villosa	-	-	-	-	-	-	-	-	-	-	-	9.24	-	-	-	-	-	-	-	-
Hibiscus vitifolius	-	-	-	-	-	-	-	-	5.43	-	-	-	-	-	-	-	-	-	-	-
Jasminum fluminense subsp. ***gratissimum***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.36	-	-	-	-
Jasminum grandiflorum subsp. ***floribundum***	10.40	-	-	-	-	-	-	17.97	5.10	6.43	-	-	-	-	3.69	-	-	7.77	-	-
Lavandula coronopifolia	-	-	-	5.62	3.56	-	-	-	-	-	-	5.18	4.92	-	-	-	-	-	6.85	-
Lindenbergia indica	-	-	-	-	-	-	5.80	-	-	-	-	-	-	-	-	-	-	-	-	-
Maytenus senegalensis	-	-	-	-	-	-	9.76	-	-	13.20	-	-	-	-	-	-	-	-	-	-
Olea europaea subsp. ***cuspidata***	10.6	18.35	-	16.58	16.49	21.41	13.61	15.88	15.74	25.09	31.21	12.48	7.68	-	19.64	31.23	30.76	36.12	14.11	36.87
Onychium divaricatum	-	-	-	4.92	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Osteospermum vaillantii	-	-	-	-	-	-	-	-	-	-	-	2.20	-	-	-	-	-	-	-	-
Otostegia fruticosa	-	-	-	-	-	-	-	5.49	-	-	-	-	7.42	-	-	-	-	-	-	-
Oxalis anthelmintica	-	-	6.32	-	-	-	-	-	-	-	-	4.56	-	-	-	-	-	-	-	-
Pancratium tortuosum	-	-	-	-	3.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pergularia daemia	-	-	-	-	6.04	8.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Periploca aphylla	6.55	-	-	-	-	-	10.52	-	-	-	4.94	-	-	-	-	-	-	-	-	-
Phagnalon schweinfurthii	-	-	-	-	3.12	-	6.43	-	-	-	-	-	-	-	-	-	-	-	-	-
Pistacia khinjuk var. ***glabra***	6.45	-	-	-	-	-	-	-	-	14.43	-	4.18	6.44	-	-	-	-	13.41	10.41	-
Plicosepalus acaciae	-	-	-	-	-	-	-	-	-	-	-	-	6.72	-	-	-	-	-	-	-
Plicosepalus curviflors	-	9.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salvadora persica	-	5.52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salvia aegyptiaca	-	-	-	8.12	-	-	5.10	-	-	-	-	-	-	-	-	-	-	12.54	-	-
Searsia flexicaulis	10.50	-	-	-	15.47	18.13	-	13.84	-	-	-	6.14	7.24	-	35.04	12.52	9.32	13.57	9.30	-
Searsia glutinosa subsp. ***abyssinica***	-	-	-	-	6.42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Searsia tripartita	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.11	5.60	-	-	-	-
Senegalia mellifera	7.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21.33	-

Solanum forskaolii	-	1.85	9.21	1.86	-	-	-	-	-	5.74	4.12	-	-	-	-	-	-	-	1.01	11.16
Solanum incanum	6.11	-	-	11.01	10.15	13.33	21.16	-	4.21	4.83	3.17	8.43	5.22	-	-	-	-	-	9.71	-
Triumfetta flavescens	2.72	4.97	-	6.41	9.18	-	-	-	8.25	-	3.57	6.11	3.39	29.77	6.21	10.21	25.82	2.32	3.07	15.98
Triumfetta rhomboidea	-	8.89	-	8.71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia etbaica	-	13.21	32.02	-	9.85	19.28	11.21	22.42	-	-	-	-	10.06	16.10	-	-	-	-	-	13.62
Vachellia tortilis* subsp. *tortilis	-	9.87	-	-	2.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table S2: The individual relevés for community II: *Solanum incanum - Ficus salicifolia*

Species	**Relevés**																
	M21	M28	M42	M44	M45	M46	M47	M48	C32	C33	C47	C51	C52	C53	C54	C55	C56
Abutilon pannosum	-	-	5.35	-	-	-	-	-	-	-	-	32.21	-	45.25	15.82	-	-
Aerva javanica	5.96	-	-	-	-	7.15	4.70	-	-	-	-	-	-	-	-	-	-
Aerva lanata	-	-	-	-	7.80	-	-	-	10.16	-	-	-	-	-	5.51	-	-
Andrachne aspera	-	-	-	1.55	-	-	-	-	-	-	-	-	-	-	-	-	-
Barleria hochstetteri	-	-	0.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cenchrus ciliaris	-	-	-	-	-	-	-	-	-	-	-	4.23	-	-	3.83	-	-
Cocculus pendulus	4.49	-	-	-	-	-	4.33	6.10	-	-	-	-	-	-	-	-	-
Cucumis prophetarum* subsp. *prophetarum	-	-	-	-	2.60	2.96	4.74	3.53	-	-	-	-	-	-	4.21	6.20	-
Delonix elata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25.77
Diceratella elliptica	-	-	-	-	-	-	-	-	-	-	11.08	4.95	-	-	-	-	36.14
Dodonaea viscosa	-	-	-	-	-	5.08	3.50	-	-	-	-	-	-	-	-	-	-
Echinops hussonii	-	-	-	-	-	-	7.13	-	-	-	11.48	-	3.87	-	9.72	-	12.14
Euclea racemosa* subsp. *schimperi	-	-	-	-	-	6.88	-	-	-	-	-	-	-	-	-	-	-
Euphorbia cuneata	-	-	-	-	-	-	-	-	-	-	-	6.39	-	-	-	-	-
Ficus palmata	-	-	-	-	-	-	-	-	-	-	-	-	54.11	-	32.21	31.92	-
Ficus salicifolia	41.98	100.00	-	64.14	28.61	28.97	15.52	32.12	-	48.06	-	-	-	-	-	-	-
Forsskaolea tenacissima	-	-	2.24	3.97	-	1.00	-	1.85	11.73	-	-	7.62	-	-	6.00	10.64	-
Grewia villosa	-	-	-	-	-	14.4	9.46	-	-	-	-	-	-	-	-	-	-

Kedrostis gijef	-	-	1.05	-	-	-	-	-	-	20.07	-	-	-	-	-	-	-
Lantana viburnoides	-	-	-	1.95	-	-	-	-	-	-	-	-	-	-	-	-	-
Launaea nudicaulis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.35	-
Lavandula coronopifolia	-	-	-	-	-	-	2.86	-	-	-	-	-	-	-	-	-	-
Leptadenia pyrotechnica	-	-	-	-	-	-	-	-	-	-	14.88	-	-	-	-	-	-
Lindenbergia indica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.03	-
Lycium shawii	-	-	-	-	-	-	-	-	43.85	12.60	-	-	-	8.63	-	-	-
Maytenus senegalensis	7.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Moringa peregrina	-	-	-	-	-	-	-	-	-	-	6.10	-	-	-	-	-	25.95
Ocimum forskoelei	-	-	30.30	-	-	6.48	-	6.10	-	-	-	-	-	-	-	-	-
Olea europaea subsp. ***cuspidata***	-	-	4.85	-	-	-	-	5.73	-	-	-	-	-	-	-	-	-
Osteospermum vaillantii	-	-	-	1.25	1.00	-	-	-	-	-	-	-	-	-	-	-	-
Otostegia fruticosa	-	-	-	-	-	-	3.91	-	-	-	-	-	3.94	-	-	-	-
Pancratium tortuosum	2.69	-	-	-	-	-	-	-	-	-	-	-	-	-	8.01	-	-
Periploca aphylla	10.89	-	-	-	-	-	-	11.68	-	-	-	-	-	9.23	-	-	-
Pistacia khinjuk var. ***glabra***	-	-	3.45	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pulicaria undulata	-	-	1.70	-	-	-	-	-	12.99	-	-	-	-	-	-	-	-
Rhynchosia minima	-	-	-	-	5.05	-	-	-	-	-	-	-	-	-	-	-	-
Searsia flexicaulis	5.96	-	21.53	16.21	29.66	-	24.14	17.82	-	-	-	-	-	-	-	-	-
Senegalia mellifera	-	-	-	-	-	4.71	2.67	-	-	-	-	-	-	-	-	-	-
Solanum forskaolii	-	-	-	6.29	-	-	4.23	-	-	-	-	-	5.91	-	-	-	-
Solanum incanum	11.84	-	12.43	4.64	15.18	-	2.50	5.47	21.27	19.27	-	44.60	32.17	23.96	13.21	39.17	-
Trichodesma africanum var. ***africanum***	-	-	-	-	-	-	-	3.09	-	-	-	-	-	-	1.48	1.80	-
Triumfetta flavescens	-	-	2.21	-	10.10	14.29	4.11	6.51	-	-	18.04	-	-	-	-	3.89	-
Vachellia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	12.93	-	-	-
Vachellia tortilis subsp. ***tortilis***	9.12	-	14.14	-	-	8.08	6.20	-	-	-	38.42	-	-	-	-	-	-

Table S3: The individual relevés for community III: *Vachellia tortilis* subsp. *tortilis*

Species	**Relevés**																				
	M10	M15	M17	M18	M19	M20	M27	M41	C1	C4	C13	C18	C19	C20	C23	C27	C29	C31	C34	C37	C39
Abutilon fruticosum	-	2.34	-	18.48	-	5.48	4.04	-	-	-	-	-	-	-	-	12.06	-	-	-	11.21	9.12
Abutilon pannosum	1.77	-	-	-	-	-	-	-	-	-	11.64	-	-	-	-	-	-	-	-	6.60	-
Aerva javanica	-	-	3.14	3.64	-	-	-	-	-	-	15.05	-	34.46	-	-	-	-	-	-	-	-
Aerva lanata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.20
Balanites aegyptiaca	-	11.18	-	-	14.84	6.86	-	-	-	-	-	-	-	-	-	-	-	-	-	-	33.21
Barleria hochstetteri	-	-	0.71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Blepharis edulis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.10	-	-	-	-	-	-
Calotropis procera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19.70	-	-	-	-	-	-
Cenchrus ciliaris	0.95	-	-	-	-	-	-	5.70	-	-	-	-	-	-	-	-	-	-	15.81	2.15	-
Cocculus pendulus	6.90	7.21	15.01	-	2.57	1.63	-	-	-	-	-	-	-	-	10.04	14.4	-	10.71	13.93	-	-
Cucumis prophetarum subsp. ***prophetarum***	2.83	6.68	-	-	-	2.66	-	-	-	-	11.60	-	-	-	-	-	-	-	-	-	-
Diceratella elliptica	-	-	-	-	1.53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dodonaea viscosa	-	-	-	-	-	-	-	22.40	-	-	-	-	-	-	-	-	-	-	-	-	-
Dracaena ombet	-	-	-	-	-	-	-	29.92	-	-	-	-	-	-	-	-	-	-	-	-	-
Echinops hussonii	-	-	-	-	-	5.29	-	-	-	-	-	-	-	-	-	-	-	-	-	3.12	-
Ephedra ciliata	2.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.21	-	11.78
Euphorbia cuneata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.15	-	-	-	-	-	-
Euphorbia nubica	-	11.51	-	-	6.37	8.37	-	-	-	-	-	-	-	-	-	11.57	44.85	-	-	-	-
Ficus salicifolia	-	5.94	-	-	12.52	10.95	26.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Forsskaolea tenacissima	2.75	9.47	-	-	-	-	-	10.54	-	-	-	16.08	-	-	4.25	-	-	-	-	-	1.19
Grewia tembensis	-	-	-	-	-	-	6.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Grewia tenax	-	-	-	-	4.48	2.31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heliotropium zeylanicum	1.91	0.28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hibiscus micranthus	-	0.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hibiscus vitifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.01	-	5.50	-

Indigofera spinosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.18	-	-	-	-	-	-
Launaea nudicaulis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.00	-	-	-	-	-
Lavandula coronopifolia	-	-	3.09	-	-	8.85	0.96	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lycium shawii	12.94	4.43	13.03	19.81	-	-	2.16	-	52.82	32.54	10.90	32.76	-	-	20.37	16.54	13.01	37.69	-	-	-
Maerua crassifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18.33	-
Moringa peregrina	-	-	-	-	-	-	-	6.68	-	-	-	-	-	-	-	-	-	-	-	-	-
Ocimum forskoelei	-	2.97	-	-	4.56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Onychium divaricatum	-	-	-	-	-	-	1.80	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Otostegia fruticosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.21	-
Pancratium tortuosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.85	-	-	-	-
Pergularia daemia	-	-	10.66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plicosepalus acaciae	-	-	-	-	-	2.56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psilotrichum gnaphalobryum	-	-	-	-	1.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pulicaria petiolaris	1.06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salvia aegyptiaca	-	-	-	-	-	2.86	-	-	-	-	-	-	-	-	-	-	-	-	-	10.09	-
Senegalia laeta	-	-	4.23	-	-	3.36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Senegalia mellifera	4.05	-	-	-	4.26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solanum forskaolii	-	-	-	-	-	16.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solanum incanum	-	1.23	5.41	13.67	-	3.86	-	-	-	-	-	8.24	-	5.60	-	-	-	-	-	-	-
Tephrosia purpurea subsp. ***apollinea***	-	-	7.75	-	0.58	-	-	-	-	-	-	-	-	38.20	-	-	-	-	-	-	-
Trichodesma africanum var. ***africanum***	-	-	-	3.44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Triumfetta flavescens	-	12.81	6.51	14.42	14.59	7.43	-	5.65	-	-	-	-	-	-	-	-	14.61	-	-	3.21	-
Vachellia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22.52
Vachellia tortilis subsp. ***raddiana***	-	-	-	-	-	-	-	-	28.05	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia tortilis subsp. ***tortilis***	62.77	23.2	30.46	26.54	32.68	11.49	58.08	19.11	19.13	67.46	50.81	42.92	65.54	56.20	28.21	43.43	19.68	42.59	59.05	30.58	15.98

Table S3 cont.: The individual relevés for community III: *Vachellia tortilis* subsp. *tortilis*

Species	**Relevés**														
	C44	C46	C48	K2	Y4	Y5	Y7	Y12	Y17	Y18	Y19	Y21	Y22	Y24	Y25
Abutilon fruticosum	22.2	10.72	-	-	-	-	-	-	-	-	-	-	-	-	-
Calotropis procera	-	-	-	-	-	-	35.67	-	-	-	-	-	-	-	-
Cenchrus ciliaris	-	2.40	-	-	2.78	-	-	-	-	-	-	-	-	-	-
Cocculus pendulus	-	-	9.28	-	-	-	-	-	-	-	-	-	-	-	-
Cucumis prophetarum **subsp.** ***prophetarum***	-	-	-	-	4.87	-	-	-	-	-	-	-	-	-	-
Ephedra ciliata	-	-	10.96	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia cuneata	-	9.80	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia nubica	-	20.14	-	-	-	-	-	-	-	-	-	-	-	-	-
Farsetia longisiliqua	-	2.75	-	-	-	-	-	-	-	-	-	-	-	-	-
Ficus salicifolia	-	-	16.96	-	-	-	-	-	-	-	-	-	-	-	-
Forsskaolea tenacissima	-	-	2.41	-	-	-	-	-	-	-	-	-	-	-	-
Heliotropium bacciferum	-	-	-	-	-	1.99	-	-	-	-	-	-	-	-	-
Indigofera spinosa	10.52	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptadenia pyrotechnica	-	-	-	-	18.75	-	25.37	-	5.41	-	-	-	-	-	-
Lycium shawii	-	-	-	19.21	51.64	-	12.01	11.65	16.24	-	-	-	-	-	-
Maerua crassifolia	-	-	-	-	-	63.48	-	22.17	-	-	-	-	-	-	-
Oxalis anthelmintica	11.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plicosepalus acaciae	-	-	13.68	-	-	-	-	-	-	-	-	-	-	-	-
Salvia aegyptiaca	-	-	9.88	-	-	-	-	-	-	-	-	-	-	-	-
Senna italica	-	-	-	-	-	-	3.83	-	1.62	-	-	-	-	-	-
Solanum forskaolii	-	4.72	-	-	-	-	-	-	-	-	-	-	-	-	-
Tephrosia purpurea **subsp.** ***apollinea***	-	-	-	8.50	-	-	-	-	3.71	-	-	-	-	-	-
Triumfetta flavescens	-	6.92	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia **sp.**	-	-	10.10	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia tortilis **subsp.** ***tortilis***	56.04	42.55	26.73	72.29	21.96	34.53	23.12	66.18	73.02	100.00	100.00	100.00	100.00	100.00	100.00

Table S4: The individual relevés for community IV: *Euphorbia nubica*

Species	**Relevés**																							
	M1	M2	M3	M8	M11	M12	M13	M14	M16	C3	C11	C12	C30	C35	C38	C40	C41	C42	C43	K1	K13	K28	K31	K34
Abutilon fruticosum	-	-	-	2.30	-	-	-	-	-	-	-	-	-	-	6.21	-	-	-	-	-	-	-	2.97	-
Abutilon pannosum	-	-	-	-	1.52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.31	-	-	-
Achyranthes aspera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.06	-	-	-
Aerva javanica	-	-	-	-	-	-	-	-	-	-	-	-	-	17.10	-	-	-	-	-	-	-	-	-	-
Aerva lanata	-	-	-	-	1.86	-	-	-	-	-	-	-	-	-	-	-	7.36	-	-	-	-	-	-	-
Balanites aegyptiaca	-	-	-	36.92	-	-	46.11	29.53	-	-	-	-	-	29.37	13.24	55.15	38.94	8.84	-	-	37.94	-	-	-
Barleria hochstetteri	-	0.39	-	0.75	0.66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Blepharis edulis	-	0.57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.66	-	-
Capparis decidua	-	-	-	-	-	-	-	2.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cenchrus ciliaris	-	-	1.45	-	0.44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Citrullus colocynthis	1.59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cocculus pendulus	5.68	-	-	-	4.71	-	-	5.17	14.83	-	18.52	-	8.21	11.11	-	-	7.93	-	15.72	-	6.54	-	-	-
Commicarpus helenae	-	1.53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.74	-	-	-
Convolvulus hystrix	-	0.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cucumis prophetarum subsp. ***dissectus***	-	-	-	-	-	-	-	0.35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cucumis prophetarum subsp. ***prophetarum***	1.00	2.51	-	2.81	2.20	-	-	2.13	-	-	-	-	13.16	-	-	-	-	-	4.51	-	-	-	-	-
Echinops hussonii	-	-	-	-	-	-	-	-	-	-	-	-	-	19.20	-	-	6.85	-	-	-	-	-	1.86	-
Ephedra ciliata	-	1.44	-	1.86	-	-	-	-	6.00	-	-	-	-	-	-	-	-	10.30	-	-	-	-	-	-
Euphorbia cuneata	-	2.59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12.85	-	-	-	-	33.85	26.82
Euphorbia nubica	26.18	13.87	50.16	18.49	14.24	49.85	26.13	24.15	25.04	24.96	23.15	-	21.99	-	23.65	9.40	8.06	-	16.44	5.80	9.15	13.63	22.32	24.32
Farsetia longisiliqua	-	2.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.66	-	-	2.07
Forsskaolea tenacissima	0.59	1.15	2.57	-	-	3.96	12.42	-	-	34.10	5.21	18.04	15.14	-	6.12	6.96	1.65	5.77	7.32	44.10	6.56	26.33	12.38	10.51
Heliotropium zeylanicum	0.80	-	1.97	-	-	1.24	1.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.12
Hibiscus micranthus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.82	-	-	1.02	-	-	-
Hibiscus vitifolius	-	-	-	-	-	-	-	-	-	-	11.67	-	-	-	-	-	-	-	-	-	-	-	-	-

Indigofera spinosa	-	1.26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kedrostis gijef	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.68	-	-	-	-	-
Launaea nudicaulis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.20	5.02	-	-	-	-	-	-
Lavandula coronopifolia	-	1.32	-	1.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lycium shawii	10.81	12.64	8.02	-	8.68	-	-	12.39	-	-	-	15.20	15.24	-	6.45	6.55	-	9.50	-	15.2	11.96	-	-	-
Maerua crassifolia	-	-	-	-	3.54	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Moringa peregrina	-	-	-	-	-	-	-	2.61	-	-	-	-	-	-	-	-	-	9.94	-	-	-	-	-	-
Ochradenus baccatus	-	-	-	-	-	-	2.14	-	-	-	-	-	-	-	-	-	-	-	8.20	-	-	-	-	-
Pancratium tortuosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.91	-	-	-	-	-	-	-	-	-
Panicum turgidum	-	-	-	-	-	-	-	-	-	9.70	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pavonia triloba	-	-	-	-	-	-	-	-	0.84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Periploca aphylla	-	4.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plicosepalus acaciae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.99	-	-	-	-	-	-	-
Pulicaria petiolaris	-	-	-	-	-	-	-	-	0.96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pulicaria undulata	-	-	1.31	-	-	-	-	-	-	-	8.45	-	-	-	-	-	-	-	-	-	-	-	-	-
Pupalia lappacea	-	-	-	-	-	-	-	-	1.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salvadora persica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	45.86	-	-
Salvia aegyptiaca	-	-	-	0.93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Senegalia mellifera	-	-	-	18.64	4.36	-	-	7.41	-	-	-	-	-	-	-	13.70	-	-	-	-	1.23	-	-	-
Senna italica	1.59	-	-	-	-	-	-	-	-	11.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solanum forskaolii	-	2.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tephrosia purpurea subsp. ***apollinea***	1.00	-	3.64	11.51	7.72	16.99	-	-	9.25	20.14	13.05	20.3	-	5.10	11.27	-	2.30	10.62	-	2.30	3.98	-	-	13.05
Trichodesma africanum var. ***africanum***	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Triumfetta flavescens	-	2.45	-	4.47	3.21	-	-	6.19	8.07	-	-	-	12.01	-	-	-	-	-	-	-	-	12.52	-	-
Triumfetta rhomboidea	-	-	-	-	2.37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.24	-	17.34	-	-	-	-	-	-
Vachellia tortilis subsp. ***raddiana***	7.41	6.86	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia tortilis subsp. ***tortilis***	43.35	42.43	30.88	-	44.47	27.96	11.91	7.40	33.69	-	19.95	46.46	14.25	18.12	28.15	-	13.72	-	42.13	32.6	5.85	-	26.62	22.11

Table S5: The individual relevés for community V: *Aerva javanica - Abutilon pannosum*

Species	**Relevés**														
	C2	C22	C25	C28	C36	K3	K6	K7	K8	K9	K10	K11	K12	K18	K27
Abutilon fruticosum	-	23.84	-	-	-	-	-	-	-	-	-	-	-	-	-
Abutilon pannosum	14.25	11.07	12.10	17.60	12.16	3.50	51.65	53.18	35.21	41.17	32.21	34.30	5.46	11.65	22.69
Aerva javanica	9.10	-	17.02	15.10	10.14	6.35	1.02	-	2.70	-	2.50	5.60	-	-	37.12
Balanites aegyptiaca	19.25	-	-	-	20.45	-	-	-	-	-	-	-	-	-	-
Cenchrus ciliaris	-	-	-	-	-	-	-	3.26	-	-	-	-	-	-	-
Citrullus colocynthis	8.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cucumis prophetarum subsp. ***prophetarum***	-	-	8.51	-	-	13.20	1.60	5.50	10.20	-	-	4.90	-	-	-
Delonix elata	-	-	-	-	-	-	-	-	-	-	-	-	-	6.90	-
Digitaria nodosa	-	-	-	-	-	-	-	-	0.84	-	-	-	-	-	-
Echinops hussonii	-	-	-	-	-	-	-	4.58	-	-	-	-	-	-	-
Ephedra ciliata	13.60	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia cuneata	-	-	-	-	-	-	-	-	5.02	-	-	-	-	-	-
Euphorbia nubica	-	-	22.66	-	15.80	-	-	6.04	5.70	-	-	-	-	2.85	-
Farsetia longisiliqua	-	-	-	-	-	-	-	-	-	-	-	5.24	-	-	-
Forsskaolea tenacissima	32.10	24.30	-	13.20	1.11	4.10	-	-	-	-	10.22	-	8.75	33.32	-
Indigofera spinosa	-	-	-	-	-	-	-	-	-	-	-	-	6.04	-	-
Lycium shawii	-	-	29.21	54.10	10.21	16.14	5.32	18.54	6.21	8.47	6.75	15.75	24.23	-	-
Maerua oblongifolia	-	-	-	-	-	-	-	-	-	-	-	-	7.46	-	-
Senegalia mellifera	-	-	-	-	-	-	-	-	4.88	-	-	-	3.12	-	-
Senna italica	-	-	-	-	-	-	-	-	-	3.46	-	-	-	-	-
Solanum incanum	-	5.69	-	-	-	-	-	-	-	-	-	-	-	-	-
Tephrosia purpurea subsp. ***apollinea***	3.65	-	10.50	-	11.21	15.30	18.50	8.90	8.60	8.91	1.92	4.67	4.06	10.63	40.19
Vachellia oerfota var. ***oerfota***	-	-	-	-	-	-	-	-	-	-	-	-	14.14	-	-
Vachellia tortilis subsp. ***raddiana***	-	35.10	-	-	18.92	-	-	-	-	-	-	-	-	-	-
Vachellia tortilis subsp. ***tortilis***	-	-	-	-	-	41.41	21.91	-	20.64	37.99	46.40	29.54	26.74	34.65	-

Table S6: The individual relevés for community VI: *Euphorbia cuneata*

Species	**Relevés**																						
	C5	C8	C26	C45	C49	C50	K4	K5	K14	K16	K17	K19	K20	K21	K22	K23	K24	K25	K26	K29	K30	K32	K33
Abutilon fruticosum	-	-	9.80	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Abutilon pannosum	-	-	-	13.68	-	-	2.10	-	6.80	-	-	6.36	11.65	5.32	4.82	-	7.23	-	9.12	2.22	-	1.89	-
Aerva javanica	-	-	7.02	-	-	-	-	-	-	-	4.20	-	-	4.01	-	-	-	-	2.04	1.16	2.92	1.40	12.21
Blepharis edulis	-	-	-	-	-	-	-	-	-	-	-	3.20	5.10	-	-	-	-	-	-	0.51	-	-	-
Capparis decidua	-	-	-	-	-	-	6.80	-	-	-	12.26	-	-	-	-	-	-	-	-	-	-	-	-
Cenchrus ciliaris	-	4.22	-	3.52	-	9.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cenchrus setiger	-	-	-	-	-	-	-	-	2.66	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Centropodia forskalii	8.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chrozophora oblongifolia	-	-	-	-	-	-	1.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Citrullus colocynthis	-	-	-	-	-	-	-	1.15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cocculus pendulus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.42	-	-	-	-	3.03	-
Commiphora gileadensis	-	-	-	-	-	-	-	-	-	-	-	-	-	28.25	-	-	-	-	-	-	-	-	-
Convolvulus hystrix	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.55	-	-	-	-	-	-	-	-
Cucumis prophetarum subsp. ***prophetarum***	-	9.43	7.30	4.21	-	-	-	7.80	10.24	8.30	5.12	3.05	1.80	-	-	8.27	-	-	-	1.74	1.71	-	2.53
Cynodon dactylon	-	-	-	-	11.88	-	-	-	-	5.04	-	-	-	-	-	-	-	-	-	-	-	-	-
Delonix elata	-	-	-	-	10.96	-	-	-	-	14.36	-	-	7.30	-	-	-	-	-	9.24	5.12	4.60	2.94	-
Echinops hussonii	-	-	-	-	-	-	4.40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ephedra ciliata	-	-	-	-	-	-	-	-	-	-	-	-	2.45	-	-	-	-	-	-	-	0.69	1.11	-
Euphorbia cuneata	-	-	23.16	20.08	-	12.64	5.14	5.85	17.74	11.11	11.24	16.94	16.39	26.02	29.65	42.13	25.31	45.36	36.32	29.41	24.03	21.12	38.57
Euphorbia nubica	-	-	-	8.54	-	-	15.10	14.60	-	13.12	-	-	-	-	4.30	21.35	7.02	40.76	26.36	17.21	8.15	16.21	30.78
Farsetia longisiliqua	-	-	-	8.21	-	-	-	-	-	-	-	-	6.30	-	-	-	-	-	-	-	-	-	-
Forsskaolea tenacissima	-	26.65	-	-	8.02	5.41	2.20	-	-	12.05	-	1.21	2.35	-	33.32	5.36	4.52	13.88	6.32	-	26.02	10.83	7.62
Heliotropium zeylanicum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.51	-
Indigofera spinosa	-	-	-	-	-	-	-	-	3.90	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lavandula coronopifolia	-	7.09	-	-	6.08	5.40	-	-	-	-	-	-	1.10	-	-	-	-	-	-	-	-	-	-

Lycium shawii	28.49	-	39.70	-	-	-	2.21	6.60	15.92	9.46	14.7	6.80	-	-	-	-	-	-	-	1.62	-	-	-
Maerua crassifolia	-	-	-	-	-	-	-	-	-	2.84	-	-	-	-	-	-	-	-	-	-	-	-	-
Maerua oblongifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.29	-	-
Moringa peregrina	-	-	-	-	6.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ochradenus baccatus	-	-	-	-	-	-	-	-	-	-	-	2.85	-	-	-	-	-	-	-	-	-	-	-
Ocimum forskoelei	-	-	-	-	10.76	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Osteospermum vaillantii	-	-	-	-	-	-	-	-	-	-	-	-	-	1.05	-	-	-	-	-	-	-	-	-
Pancratium tortuosum	-	-	-	-	-	-	1.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plicosepalus curviflors	-	-	-	-	-	12.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pulicaria undulata	-	-	-	-	-	-	-	-	-	-	3.04	-	-	-	-	-	-	-	-	-	-	-	-
Salvia aegyptiaca	-	-	-	7.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Senegalia mellifera	-	-	-	-	-	-	-	-	-	-	6.21	13.30	-	-	-	-	-	-	-	1.83	-	-	-
Solanum forskaolii	-	-	-	-	-	10.36	1.20	-	-	-	-	-	-	-	-	3.21	1.04	-	1.81	-	-	-	-
Stipagrostis ciliata	-	-	-	-	-	-	0.70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tephrosia purpurea subsp. ***apollinea***	21.55	34.21	13.02	-	-	-	2.60	3.90	6.25	3.15	9.65	16.05	20.24	14.12	9.82	19.68	9.32	-	8.79	7.22	13.63	15.45	8.29
Vachellia etbaica	-	-	-	-	25.90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia sp.	-	-	-	-	20.30	19.20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia tortilis subsp. ***raddiana***	-	-	-	-	-	-	11.70	60.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia tortilis subsp. ***tortilis***	41.21	18.40	-	34.52	-	25.19	42.95	-	36.49	20.57	17.54	30.24	25.32	21.23	15.54	-	35.14	-	-	31.96	16.96	24.51	-
Withania somnifera	-	-	-	-	-	-	-	-	-	-	16.04	-	-	-	-	-	-	-	-	-	-	-	-

Table S7: The individual relevés for community VII: *Balanites aegyptiaca* - *Vachellia tortilis* subsp. *raddiana*

Species	**Relevés**																		
	M4	M5	M6	M7	M9	M22	M23	M24	M25	C6	C7	C9	C10	C14	C15	C16	C17	C21	C24
Abutilon fruticosum	-	-	-	-	2.85	-	-	-	3.96	-	-	-	-	-	-	-	-	-	-
Abutilon pannosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	39.40	-	6.10
Achyranthes aspera	-	-	-	-	-	0.54	-	-	-	-	-	-	-	-	-	-	-	-	-
Aerva javanica	-	-	3.93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Balanites aegyptiaca	95.72	67.58	19.54	55.57	53.08	86.32	58.94	45.71	16.80	25.21	35.91	51.65	15.95	35.5	100.00	-	-	-	27.26
Barleria hochstetteri	-	-	-	-	-	-	0.45	-	-	-	-	-	-	-	-	-	-	-	-
Blepharis edulis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.06
Cenchrus ciliaris	-	-	-	-	1.64	-	-	-	-	5.11	13.42	-	-	-	-	-	-	-	-
Centropodia forskalii	-	-	-	-	-	-	-	-	-	-	-	9.55	-	-	-	-	-	-	-
Citrullus colocynthis	-	-	-	-	-	-	-	-	-	-	-	-	8.35	-	-	-	-	-	-
Cocculus pendulus	-	4.02	-	16.39	19.49	-	-	-	-	-	28.95	-	-	-	-	-	-	-	-
Convolvulus hystrix	4.28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cucumis prophetarum subsp. ***prophetarum***	-	-	-	-	4.47	-	-	-	-	9.25	-	12.92	-	-	-	-	-	-	-
Cyperus laevigatus	-	-	-	-	-	0.33	-	-	-	-	-	-	-	-	-	-	-	-	-
Dodonaea viscosa	-	-	-	-	-	-	-	2.01	-	-	-	-	-	-	-	-	-	-	-
Echinops hussonii	-	-	-	-	-	-	0.39	-	-	-	-	-	-	-	-	-	-	-	-
Ephedra ciliata	-	-	-	-	-	-	-	1.42	-	-	-	-	-	-	-	-	-	-	-
Euphorbia cuneata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.11
Euphorbia nubica	-	13.84	16.20	10.20	-	2.21	4.51	-	25.40	-	-	-	-	-	-	-	-	-	19.89
Farsetia longisiliqua	-	-	-	-	-	-	0.63	-	-	-	-	-	-	-	-	-	-	-	-
Forsskaolea tenacissima	-	-	-	-	-	-	-	-	-	22.26	-	-	12.14	19.05	-	-	-	-	6.75
Hibiscus micranthus	-	-	-	-	-	-	-	-	0.56	-	-	-	-	-	-	-	-	-	-
Hibiscus vitifolius	-	-	-	-	-	-	-	1.14	-	-	-	-	-	-	-	-	-	-	-
Indigofera spinosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.80
Lavandula coronopifolia	-	-	-	-	-	-	2.94	-	-	7.12	-	12.68	-	-	-	-	-	-	-

Lycium shawii	-	-	-	-	-	8.82	-	-	-	-	-	-	-	30.20	-	-	-	-	17.93
Ocimum forskoelei	-	-	-	-	-	1.78	-	4.10	-	-	-	-	-	-	-	-	-	-	-
Panicum turgidum	-	-	-	-	1.91	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salvia aegyptiaca	-	-	-	-	-	-	-	-	-	4.10	-	8.10	-	-	-	-	-	-	-
Senegalia laeta	-	-	-	-	-	-	3.68	4.27	-	-	-	-	-	-	-	-	-	-	-
Senegalia mellifera	-	-	-	17.84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Senna italica	-	-	-	-	-	-	-	-	-	5.10	-	5.10	-	-	-	-	-	-	-
Solanum incanum	-	-	-	-	-	-	-	1.47	5.00	-	-	-	-	15.25	-	45.81	-	38.30	-
Tephrosia purpurea subsp. ***apollinea***	-	-	-	-	16.56	-	-	-	-	9.64	-	-	29.59	-	-	-	-	-	-
Trichodesma africanum var. ***africanum***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20.49	-
Triumfetta flavescens	-	-	-	-	-	-	8.42	-	-	-	-	-	-	-	-	-	-	-	-
Triumfetta rhomboidea	-	-	6.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia tortilis subsp. ***raddiana***	-	-	25.15	-	-	-	-	-	-	12.21	21.72	-	15.97	-	-	54.19	60.6	41.21	-
Vachellia tortilis subsp. ***tortilis***	-	14.56	29.11	-	-	-	20.04	39.88	48.28	-	-	-	18.00	-	-	-	-	-	5.10

Table S7 cont.: The individual relevés for community VII: *Balanites aegyptiaca* - *Vachellia tortilis* subsp. *raddiana*

Species	**Relevés**														
	K15	Y1	Y2	Y3	Y6	Y8	Y9	Y10	Y11	Y13	Y14	Y15	Y16	Y20	Y23
Abutilon pannosum	3.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aerva javanica	4.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Balanites aegyptiaca	25.31	63.52	53.34	5.51	16.39	83.84	-	100.00	62.85	64.42	54.12	100.00	-	89.21	60.37
Blepharis edulis	3.34	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cenchrus ciliaris	-	5.96	-	-	-	1.87	-	-	-	-	-	-	-	-	-
Cocculus pendulus	-	-	10.82	-	-	-	-	-	-	-	-	-	-	-	-
Cucumis prophetarum subsp. ***prophetarum***	-	2.06	4.20	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia cuneata	17.21	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia nubica	8.21	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Forsskaolea tenacissima	4.46	1.15	2.81	-	-	-	-	-	-	-	-	-	-	-	-

Indigofera spinosa	-	4.10	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptadenia pyrotechnica	-	-	-	-	-	-	-	-	6.67	-	-	-	-	-	-
Lycium shawii	17.19	-	-	2.79	-	-	-	-	3.65	-	10.78	-	7.58	10.79	-
Senegalia mellifera	2.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Senna italica	-	-	3.44	-	-	-	-	-	-	-	-	-	1.21	-	-
Tephrosia purpurea subsp. ***apollinea***	1.24	3.43	4.51	-	-	-	-	-	-	4.01	1.47	-	1.01	-	-
Triumfetta flavescens	-	4.54	-	-	-	-	-	-	-	-	-	-	-	-	-
Vachellia tortilis subsp. ***raddiana***	-	-	14.48	31.34	60.42	14.29	100.00	-	26.83	-	33.63	-	52.26	-	-
Vachellia tortilis subsp. ***tortilis***	13.43	15.24	6.40	60.36	23.19	-	-	-	-	31.57	-	-	37.94	-	39.63

Supporting information to the paper
Abutaha, M. M. et al. Predictive mapping of plant diversity in an arid mountain environment (Gebel Elba, Egypt). *Applied Vegetation Science*.

Appendix S6. Environmental factors derived from a digital elevation model (DEM), SoilGrids data, and PlanetScope images. Out of 14 environmental parameters, the best models selected for alpha and beta diversity comprised only five parameters, i.e., four topographical parameters (altitude, solar insolation, landforms, and catchment area) and the Modified soil-adjusted vegetation index ($MSAVI_2$)

Environmental variable	Unit	Spatial resolution	Description
Topography		30 m	Extracted from the DEM, the elevational gradient represents an inverse stress gradient, which can determine changes in temperature, water availability, and diversity in microhabitats
Altitude	m		The elevational gradient of the study area is ca. 90–1435 m asl
Log (catchment area)	Log(m^2)		Water accumulation area
Catchment slope	--		Water capture slope
Openness	Radian (rad or º)		Positive openness; increases with elevation. At the foot of the mountain, a homogenous open desert plain exists, whereas openness varies in the drainage systems of the mountainous areas
landforms	--		Includes four different landforms: streams, valleys, plains, and slopes and ridges
Solar insolation	W/m^2		Shadow in the study area increases with elevation toward the northwestern slopes
Primary productivity		3 m	We used red and infrared bands of a PlanetScope image to measure reflectance and assess the presence/absence of vegetation
Modified soil-adjusted vegetation index ($MSAVI_2$)	--		$MSAVI_2$ is applied to areas with arid conditions. We resampled $MSAVI_2$ raster according to the DEM
Edaphic factors		250 m	We used SoilGrids data (depth 0–5 cm) and compared it with the result of the sampled soil analyses from the study area (Abutaha *et al.*, 2020). We resampled the SoilGrids data according to the DEM
Sand content	g/kg		Pure sand in the open desert plain. Purity decreases with elevation, but the soil remains sandy in the mountainous area
Silt content	g/kg		Increases with elevation
Clay content	g/kg		Increases with elevation
Coarse fragments content	cm^3/dm^3		Increases in the mountainous area
Organic carbon content	dg/kg		Increases with elevation
Cation exchange capacity	mmol(c)/kg		Increases with elevation
pH water	pH*10		Decreases with elevation

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Appendix S7. Results of Shannon index and richness-based models (total species richness and perennials richness)

Alpha diversity model	R^2 (adj.)	Deviance explained	Parameters	EDF	F	P value
Shannon index	0.53	54.9%	Altitude	2.44	7.82	<0.001
			Landforms	2.25	6.82	<0.001
			Solar insolation	0.39	0.08	0.18
			Catchment area	0.51	0.16	0.09
			$MSAVI_2$	0.81	0.86	<0.01
Total species richness	0.37	40.6%	Altitude	1.77	2.70	<0.001
			Landforms	2.19	4.31	<0.001
			Solar insolation	2.76	0.60	0.13
			$MSAVI_2$	0.74	0.56	0.02
Perennial species richness	0.46	48.7%	Altitude	0.98	2.06	<0.001
			Landforms	2.40	10.35	<0.001
			Solar insolation	3.28	1.84	<0.01
			Catchment area	0.00	0.00	0.63
			$MSAVI_2$	0.80	0.79	0.01

EDF: estimated degrees of freedom (≤1 = linear pattern; ≤2 = nonlinear/unimodal pattern; >2 = complex pattern)

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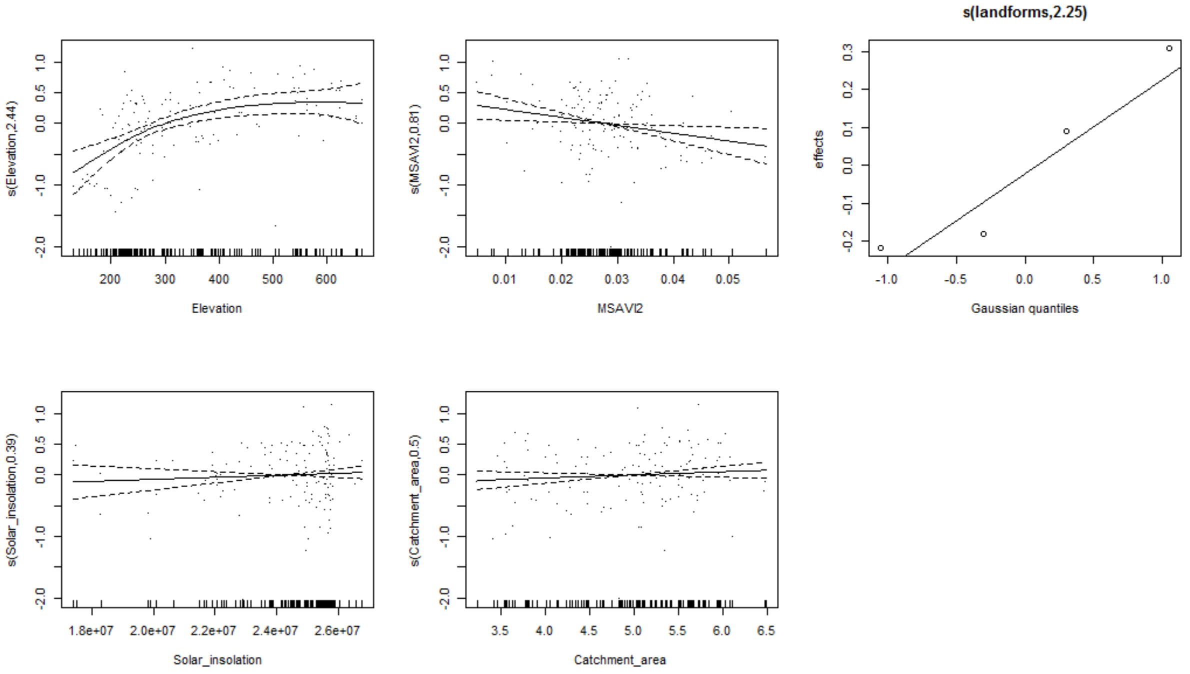
Appendix S8. Correlation matrix of the 14 environmental predictors used to select variables for predictive modeling of diversity

	Altitude	MSAVI$_2$	Clay	Silt	Sand	Organic carbon	Coarse fragments	EC	pH	Solar insolation	Openness	Landforms	Catchment area	Catchment slope
Altitude	0	ns	***	***	***	***	***	***	***	***	***	***	***	***
MSAVI$_2$	−0.052	0	**	***	***	**	***	*	ns	*	***	**	ns	**
Clay	**0.73**	−0.23	0	***	***	***	***	***	***	***	***	***	**	***
Silt	0.43	−0.53	0.54	0	***	***	***	***	***	**	***	***	**	***
Sand	−0.67	0.41	**−0.91**	**−0.84**	0	***	***	***	***	***	***	***	***	***
Organic carbon	**0.86**	−0.24	**0.73**	0.63	**−0.77**	0	***	***	***	***	***	***	***	***
Coarse fragments	**0.72**	−0.30	**0.90**	0.62	**−0.89**	**0.79**	0	***	***	***	***	***	**	***
EC	**0.86**	−0.18	**0.87**	0.49	**−0.80**	**0.80**	**0.89**	0	***	***	***	***	**	***
pH	**−0.78**	−0.0012	**−0.70**	−0.32	−0.60	**−0.73**	**−0.77**	**-0.85**	0	***	***	***	***	***
Solar insolation	−0.65	0.21	−0.62	−0.26	0.53	−0.51	−0.63	−0.68	0.56	0	***	***	ns	***
Openness	**−0.80**	0.29	**−0.82**	−0.53	**0.79**	**−0.76**	**−0.88**	**-0.94**	**0.80**	0.67	0	***	**	***
Landforms	−0.59	0.28	**−0.75**	−0.46	**0.72**	−0.59	**−0.81**	**−0.81**	**0.70**	0.49	**0.86**	0	**	***
Catchment area	0.31	0.0094	0.27	0.24	−0.30	0.42	0.27	0.27	−0.30	0.016	−0.26	−0.23	0	***
Catchment slopes	**0.82**	−0.24	**0.82**	0.64	**−0.84**	**0.85**	**0.81**	**0.84**	**−0.73**	−0.58	**−0.79**	−0.66	0.45	0

Predictors were highly correlated if $r > 0.70$. asterisk indicates a significant correlation (* low, ** medium, *** high); ns = not significant

Supporting information to the paper

Abutaha, M. M. et al. Predictive mapping of plant diversity in an arid mountain environment (Gebel Elba, Egypt). *Applied Vegetation Science*.



Appendix S9. Generalized additive model (GAM) plots showing the partial effects of selected explanatory variables on the Shannon index of perennial species in Gebel Elba. The tick marks on the x-axis show observed data points. The y-axis represents the partial effect of each variable. The areas between the dashed lines indicate the 95% confidence intervals

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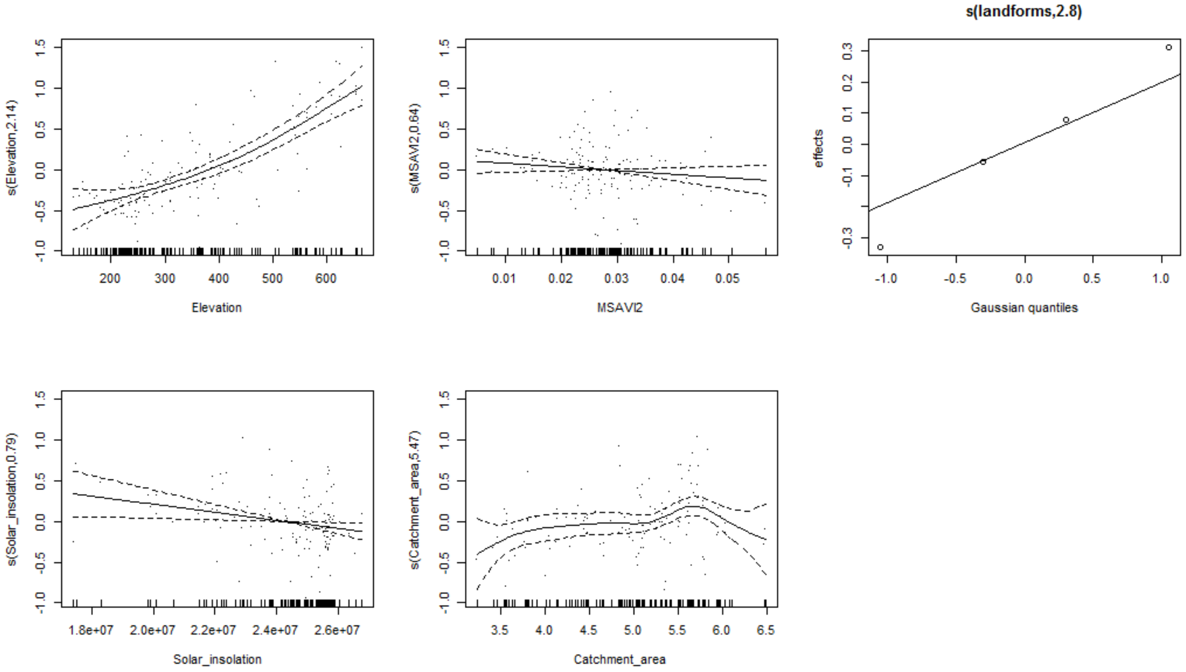

Appendix S10. Generalized additive model (GAM) plots showing the partial effects of selected explanatory variables on the first ordination axis of nonmetric multidimensional scaling (NMDS1) for perennial species in Gebel Elba. The tick marks on the x-axis show observed data points. The y-axis represents the partial effect of each variable. The areas between the dashed lines indicate the 95% confidence intervals

Supporting information to the paper
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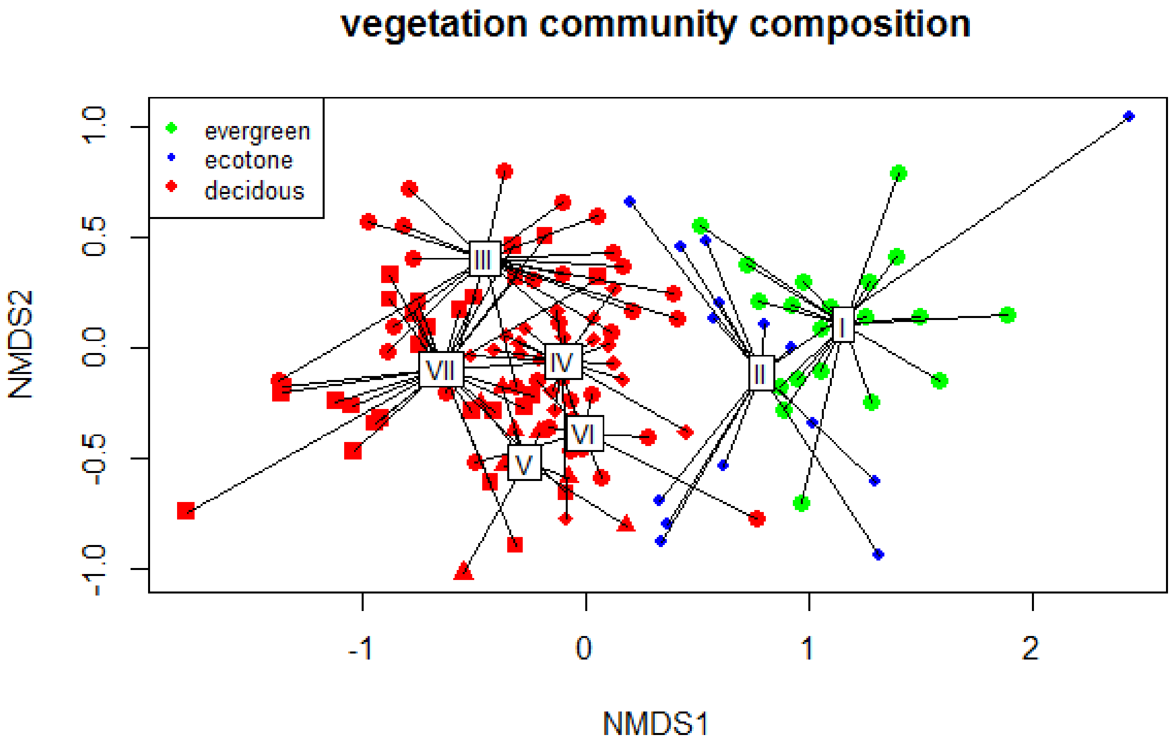

Appendix S11 Distribution of seven vegetation communities along the nonmetric multidimensional scaling (NMDS) axes 1 and 2 (based on Abutaha *et al.*, 2020). The NMDS ordination shows two main woodlands: evergreen (I) and deciduous (III–VII). The *Ficus* community (II) represents a transitional ecotone between these two woodlands

References

Abutaha, M. M., El-Khouly, A. A., Jürgens, N. and Oldeland, J. (2020) Plant communities and their environmental drivers on an arid mountain, Gebel Elba, Egypt. *Vegetation Classification and Survey*, 1, 21–36. https://doi.org/10.3897/VCS/2020/38644

Author contributions

Chapter One	I wrote this chapter.
Chapter Two	The study was conceived together with Jens Oldeland. I carried out field work and performed the statistical analysis. I wrote the first draft of the manuscript. All authors discussed the results and contributed to the manuscript.
Chapter Three	I had the initial idea of the study, carried out field work and soil analysis. I performed the statistical analysis and wrote the first draft of the manuscript with a contribution from Jens Oldeland, while all authors contributed to the final version.
Chapter Four	Jens Oldeland conceived of the research idea. I collected data and performed statistical analyses. I wrote the first draft of the manuscript with a contribution from Jens Oldeland. All authors discussed the results and commented on the manuscript.
Chapter Five	I wrote this chapter. All findings are based on my research and data analysis in chapters 2–4.

Co-author affiliations

Ahmed A. El-khouly: Department of Plant Ecology and Range Management, Desert Research Center, Cairo, Egypt

Amal A. Morsy: Botany Department, Faculty of Science, Ain Shams University, Cairo, Egypt

Norbert Jürgens: Biodiversity, Evolution and Ecology of Plants, Institute of Plant Sciences and Microbiology, Hamburg University, Hamburg, Germany

Jens Oldeland: Biodiversity, Evolution and Ecology of Plants, Institute of Plant Sciences and Microbiology, Hamburg University, Hamburg, Germany

Declaration on oath

I hereby declare, on oath, that I have written the presented dissertation by my own and have not used other than the acknowledged resources and aids.

Eidesstattliche Versicherung

Hiermit erklare ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Abutaha

Hamburg, den 20.05.2021 Maged Abutaha