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ABSTRACT

Jebel Marra, a volcanic complex in western Sudan, is an important site of early settled agriculture, with high plant diversity, supported by orographic rainfall. Vegetation types were examined in relation to habitat, altitude, soils, and land management. In 52 sites, 274 species, predominantly Fabaceae and Poaceae, were recorded (with 17 new records). Sites were clustered using TWINSPAN, and Detrended Correspondence Analysis (DCA), generating eight vegetation types, six new since the 1970s. Changes in the dominant species show that the savanna has become sparser, with annuals displacing perennials. Soils were mostly "sandy clay loams," so vegetation types did not directly correspond to soil types, although Type VIII vegetation grew in soils with a higher clay content. The sand fraction that predominated in soils of all other vegetation types was, mainly (87%) "soft" or aeolian sand. Canonical Correspondence Analysis (CCA) separated communities and species along a first axis, associated with finer soil textures, higher Fe, and lower elevations. The second axis was positively associated with elevated phosphorus, and negatively with sandy loams. CCA showed that rainfall alone was less pertinent than soil texture, which determines plant-available water capacity. The region's vegetation was not uniformly diverse; instead, a mosaic of patches of diverse terrain, associated with different vegetation "types," collectively generates a diverse flora. Besides climate change, overgrazing and increasing human pressures due to conflict, local population growth and an influx of refugees place these (already stressed) plant resources at risk. Our survey provides a baseline to track changes and develop adaptive management strategies.

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Chorotype; climate change; Darfur; environmental factors; more sparse (diffuse) savanna; ordination; overgrazing; plant communities; refugees; soil moisture; Sudan

Introduction

There is a strong association between vegetation type and soil type, and many early soil maps were inferred from the observed surface vegetation, rather than through systematic soil sampling and analysis, particularly at the local scale. Each plant species often has a recognized range of optimal soil conditions, so this approach has worked quite

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well, although it relies on circular reasoning. Factors such as parent material have also been considered for mid-scale, and topography for large-scale, soil mapping. Generally, today, multi-scale approaches that consider a combination of vegetation, parent material and topography, supported by direct soil sampling, are used to develop soil maps (Miller and Schaetzl 2016).

In arid regions where rainfall, though low and variable in timing, is an annual event, perennials are often restricted to habitats where water is available for longer periods such as wadis, depressions and montane valleys where some soil has accumulated (a "restricted" vegetation type, *sensu* Walter 1979). In less arid areas, perennials may be more widespread, although stands vary in density giving a more diffuse, "sparse" savanna vegetation. In the most arid areas, we see "opportunistic" plant communities that include ephemerals and annuals (therophytes) and perennials that grow only during (often unpredictable), occasional moist periods; these may use stored moisture reserves to prolong active growth, but then the plant may dry up and enter an extended (sometimes multi-year) dormancy period (Hegazy and Lovett-Doust 2016). These three perennial vegetation strategies (diffuse, restricted, and opportunistic) are taken to represent points along a wetter-to-drier continuum although most studies do not directly confirm soil moisture or other soil characteristics when assigning these interpretations.

Most of Sudan is "semi-arid," vulnerable to degradation or desertification (Aziz, Chen, and Gong 2008; Hegazy et al. 2018). There is significant evidence that the current trend is toward drier conditions (Abdul-Jalil 2008). Climate ranges from continental desert (rainfall of 20 mm/year) in the north, through dry shrub savanna in the center, to tropical savanna with rainfall of 1,600 mm/year in the far south (Elagib and Mansell 2000).

The Jebel Marra region is a volcanic range reaching 3,057 m; it is geologically distinct, as it is the result of volcanic activity since the Miocene, up to historic times; it is also a site of early human habitation with stone tools dating back 500,000 years (Williams 2016). The soils are distinctive, as they are not simply sandy, but include material from the weathering of lava, ejecta and volcanic ash; these Andisols have a distinctive low bulk density, and are typically dominated by glass and colloidal weathering products such as allophane, imogolite, and ferrihydrite (minerals). As a result, these soils have "andic" properties that include high water-holding capacity and the ability to retain, and make available to plants, many essential plant nutrients including Fe, Ca, Mg, Na, K, P, S, and Si; their fine particles have a high affinity for organic matter, retaining it in the soil (Neill 2006). Combined with the benefits of orographic rainfall (Hegazy et al. 2020), this makes Andisols valuable for agriculture, although a challenge for soil management is their tendency to "mineralize" phosphorus, making that macronutrient less available.

In their textbook on "Plants of the Middle East," Hegazy and Lovett-Doust (2016) characterized the flora of Jebel Marra, as being among the richest floristic regions in the Middle East, with nearly a thousand species of vascular plants (Wickens 1976a). Many of these species are endemic, although Wickens (1976a) suggested they are largely relicts of formerly more widespread species. Some species are more typical of distant centers of diversity, such as the Ethiopian Highlands, the western Saharan Massifs, the Mediterranean coast, and southern Africa, and some (presumably naturalized) fruit tree species are native to India. This is at first surprising in such an (apparently) isolated flora, in the middle of an arid area, far from other areas of high plant diversity, but it reflects the early trading and naturalization of crops in the early millennia of agriculture (see Elsiddig 2007) and the fertility of volcanic soils (Neill 2006). Other plants in Jebel Marra include trees typical of mixed savannas such as *Faidherbia albida, Afzelia abyssinica, Albizia zygia, Boswellia papyrifera, Khaya senegalensis*, and *Sterculia setigera* (Wickens 1976a; Elsiddig 2007). Trees such as *Azanza garckeana, Vitex doniana, Combretum mole, Cussonia arborea,* and the figs, *Ficus palmata* and *F. sur*, are also present, but perhaps some of these, too, were actively introduced from other parts of Africa by early agricultural communities starting as much as 10,000 YBP. The flora of Jebel Marra is also unusual for a Middle Eastern montane region in that it has very few conifers.

The vegetation of Jebel Marra is often classified and zoned according to altitude and topography, but many endemic species are found in all altitudinal zones (Elsiddig 2007). Near the summit, shrubs predominate (Wickens 1976a, 1976b; Hegazy and Lovett-Doust 2016; Hegazy et al. 2018). In contrast, savanna vegetation is seen at elevations <1,500 m, with trees at a range of densities and size classes, and ground vegetation dominated by grasses (Elsiddig 2007). Today, the effects of climate change and decreasing rainfall are aggravated by increasing anthropogenic disturbance, due to localized overgrazing on the agricultural lowlands, and the challenges of regional conflicts and an influx of refugees (El Amin 1990; Hegazy et al. 2018, 2019). Some researchers, particularly those advocating the establishment of government-run forestry plantations in the region have criticized the rotational agriculture that has been practiced by the local Fur farmers for millennia (Ahmed 1983; Babikir 1988). They argued that the duration of "bush fallow" between periods of 3 and 7 years of tillage is becoming shorter; more recently we found that extensive lowland agricultural areas were only fallowed for a few months; essentially resulting in continuous cultivation (Hegazy et al. 2020), so trees and shrubs are declining in abundance, resulting in periodic crises in terms of the supply of fuelwood.

This study tests the hypothesis that the whole region of Jebel Marra is uniformly rich in terms of biodiversity; the alternate hypothesis is that regional biodiversity is simply the "sum" of distinct patches of contrasting vegetation types corresponding to "fine-scale" heterogeneity of soils and land use. If the latter is the case, distinct vegetation types will match local heterogeneity in soils and/or land use and management, rather than presenting a uniformly diverse flora. A second hypothesis that is being tested is the proposition that introduced and weedy species will be more frequent at lower elevations – the plains and terraced lower slopes of Jebel Marra, where farming and overgrazing are more intensive.

This region is one of the early sites of established agriculture, going back at least 7,000 years; this is evidenced by the fact that contoured terraces with stone wall retainers cover all accessible slopes of the Jebel Marra massif up to an altitude of 2,750 m (Ahmed 1982). Some naturalized species that are now collected "from the wild" were first introduced as crops, timber or grazing and fodder species (Hegazy et al. 2020). Terraced farmland requires intensive labor and management; at the same time, it provides several benefits in terms of the conservation of soil and water. Terraces reduce both the amount and velocity of water moving across the soil surface, which greatly reduces soil erosion. Terracing thus permits more intensive cropping than would otherwise be possible on these slopes (see Wheaton and Monke 2001; Dorren and Rey 2012). It also allows farmers to benefit from, and "trap" orographic rain. Based on the area under terraced cultivation, Ahmed (1983) inferred that the local population would have been much greater before the Mahadiya period (1881–1898); however, the population was severely impacted over that period by taking of people as slaves, warfare, and epidemics, resulting in a sharp decline in terraced cultivation. This is reflected in the observation by FAO investigators that *Acacia albida* trees on the terraced slopes were remarkably uniform in age, dating to the Mahadiya period at the end of the nineteenth century (FAO (United Nations) 1968).

In an experimental study of indigenous practices intended to support soil conservation, Ahmed et al. (2020) found that the ancient Fur practices of building contour ridges with stone bonds (terracing) and zero tillage were significantly more effective in preventing soil erosion and loss than practices like chisel plowing, cross slope tied bonding, and cross slope bonding. The challenge is that from 2003 to the present, ongoing "Tribal Conflicts" have meant that it is too dangerous for Fur farmers to be far from their homes in the lowlands, so the upland terraced farmland has largely reverted to wild vegetation (Hegazy et al. 2020).

Another potential contributing factor to the changing vegetation is the recent, severe pressure on local resources due to growth of the local population, and the influx of refugees, both from within Sudan (termed Internally Displaced Persons or IDPs), and migrants from adjacent countries such as Chad. The population of Darfur increased from 1.3 million in 1973–9.3 million in 2017 (CIA World Factbook 2019). A 2008 survey indicated 53% of the population was 16 or younger, so this trend of population growth is likely to continue. Many Darfuris had sheltered in refugee camps in Eastern Chad since 2003, but recently returned, to populate the IDP camps. Additional IDPs have arrived from South Sudan (estimated at about 130,000 as of July 2020 (UNHCR 2020). The refugees' needs for food and firewood, combined with a young and growing local indigenous (Fur) population, add pressures to already-strained resources. As a result, there has been a significant increase in collection of wild "famine foods" and firewood (Ali 2013; Hegazy et al. 2020). This was vividly demonstrated in a recent study based on satellite imagery (Spröhnle et al. 2016); these authors tested two possible explanations of severe declines in forest cover in the Zalingei area from 2003 to 2008; first variability in precipitation, and, second, changes in the size of the local population. The results showed that deforestation was directly associated with the locations of the several IDP refugee camps, as refugees were harvesting nearby forest areas for fuelwood, rather than a decline in local rainfall over that period.

Materials and methods

Study area

The study area of about 9,000 km^2 lies between 11°32′ 20″–13°00′ N, and 23″ 24′–24° 10′ E, in the watershed of Wadi Azum, draining the western slopes of Jebel Marra into the endorheic basin of Lake Chad (Figure 1). Three major regions were

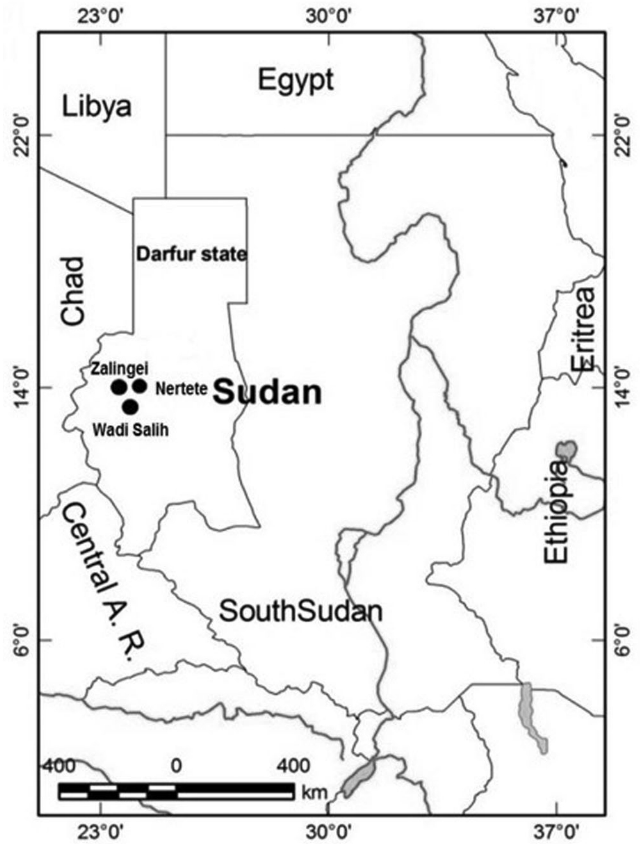

Figure 1. Map of Jebel Marra, Darfur, Sudan. Survey plots were in the vicinity of each of the three towns indicated (Zalingei, Nertete, and Wadi Salih), on the Western slopes of the Jebel Marra.

surveyed: Zalingei, Wadi Salih and Nertete, with elevations from 750 m a.s.l. in Wadi Salih to 1,265 m a.s.l. in Nertete (Appendix I, and see Hegazy et al. 2018, 2019). The region has been described as semi-arid savanna, with thorny shrubs and broad-leaved deciduous trees, and short-to medium-height annual grasses (Elsiddig 2007). Earlier studies divided the soils of Jebel Marra, specifically Zalingei, into (1) soils of the flood plain and lower terrace, (2) soils of the upper terrace, and (3) gray cracking clay (Hunting Technical Services Ltd. 1958). As part of their study designed to assess the potential of various parts of Jebel Marra for forestry plantations, Hunting Technical Services Ltd. (1958) described textures ranging from sandy clay to clayey sand (which is no longer a recognized texture type), with the latter restricted to an area near Wadi Aribo in Zalingei. Climate, based on 10-year averages (2001–2010) is very similar in the three study areas (Hegazy et al. 2018), with annual rainfall of 520 mm in Zalingei, 672.02 mm in Nertete and 692.43 mm in Wadi Salih, generating a regional average of 628.15 mm, peaking in July and August. All three areas have long, hot rainy summers (June–October) and short, mild, dry winters, with peak monthly temperatures (27.8 °C) in April, and relative humidity ranging from 34% in March, to 93% in August.

Sampling sites and species composition

Sampling was stratified within each of three study regions; Appendix I lists the 52 sampling plots and their coordinates, with plots 1–30, and 42–45 in Zalingei, 31–41 in Wadi Salih, and 46–52 in Nertete. For each plot, the altitude and altitude zone (in 100 m increments for zones 1–5), habitat type and location were noted. Sampling was in summer of 2011 when most species were actively growing, and readily collected and identified. Plots were chosen to represent the range of environmental conditions in each study region. Within each of the three regions, distinct, relatively homogeneous areas were identified based on the dominant species, using the presence/absence relevé method (Mueller-Dombois and Ellenberg 1974). Applying this method, first, distinct contiguous patches of vegetation that appear homogeneous, with the same dominant species, are identified. This is a relevé. In each study region, there could be several different kinds of relevé, depending on the dominant species. Within each relevé, a randomly selected plot (10 m × 10 m) was surveyed. This plot size was chosen because it was necessary to ensure all species present were tallied, and because homogeneous relevés within the vegetation mosaic were sometimes not much bigger than 10 m^2. In each plot, all species present were listed, and specimens collected. The density, frequency, and % cover for each species were recorded, and the importance value (relative density + relative frequency + relative cover), in each plot, calculated. These data were used to calculate the mean importance value for each species, following Hegazy, Lovett-Doust, et al. (2011) and Hegazy, Boulos, et al. (2011). Plant identifications were verified by comparison with the Cairo University Herbarium (CUH) collection; our voucher specimens are now in CUH with duplicates deposited in the herbarium at Al Fashir University, Sudan.

Soil characterization and analyses

Given their volcanic origin, the soils of this region are broadly described as "Andisols" in the USDA system, or Andosols in the IUSS (International Union of Soil Sciences) World Reference Base for Soil Resources (2015). These are "highly porous, dark-colored soils developed from parent material of volcanic origin, such as volcanic ash, tuff, and pumice" (Miehe 1986). Typically, such young soils are relatively fertile (IUSS 2015), and are often used for intensive agriculture. This general volcanic background is modified by the input of windblown sand from surrounding desert areas, and the development of clay (erosion) plains in the lowlands where Alfisols (soils rich in aluminum and iron) can form (El-Mobarak 2003). Since the soils of Jebel Marra are "young," horizons are generally poorly developed so soil pits were not dug. In each sampling plot, at three random points, soil cores were collected from the top 25 cm of the profile, providing a total of 156 soil samples altogether. Samples were air dried, sieved (2 mm mesh) to remove gravel and debris, and analyzed (Allen et al. 1998). Texture was determined using the hydrometer method (Ashworth et al. 2001). In this region, close to desert expanses, but also with orographic rainfall on the slopes of Jebel Marra, sand-sized particles in the soil are either aeolian ("soft," wind-abraded and rounded) or fluvial ("hard," water-worked, angular). Therefore, in addition to separating particles into the standard three categories according to size (sand, silt and clay), following the USDA classification system, the sand fraction of each soil sample was also examined microscopically, to estimate the proportion of sand in each of the aeolian and fluvial categories (Powers 1953; Sweeney, McDonald, and Markley 2013).

Soil constituents, such as Na, K, Ca, Mn, Mg, and Fe were determined in a 1:5 soil-water extract using a GBC model 1100B atomic absorption spectrophotometer, and reported as ppm; levels of total nitrogen and total phosphorus were measured (ppm) following Jackson (1962).

Raunkiaer life forms, growth forms, and floristic categories

Species were categorized by life span (growth form) and Raunkiaer life form (Raunkiaer 1934), describing the position of buds during the adverse season (here, the cooler, dry winter). Following Wickens (1976a, 1976b) and Good (1974), the origin (biogeographic region or sub-region, or "chorotype") of each was noted.

Vegetation data analysis

Each sample plot was first tabulated in terms of the cover values for each of the species present; a second table was then developed, with plots and cover values for each of the species, in relation to the soil type in each plot. Multivariate analyses allowed classification and ordination of each plot's vegetation. The first matrix was subjected to a numerical classification using Two-Way INdicator SPecies ANalysis, or "TWINSPAN" (Hill 1979a). This simultaneously classifies both stands and species, generating an ordered two-way table showing the relationship between them and providing a hierarchical classification of vegetation groups (i.e., plant communities). These in turn were characterized in terms of their respective dominant species. A "Detrended Correspondence Analysis," or DCA (Hill 1979b) was also applied to the first data matrix, generating a graphical plot of relationships among the vegetation groups already identified using TWINSPAN. To explore relationships between the identified vegetation "types" and environmental factors including soils, Canonical Correspondence Analysis, "CCA" was then conducted (ter Braak and Smilauer 2002). Using the second matrix described above, species cover for each plot was examined in relation to environmental factors. Relationships between the ordination axes and environmental variables were tested using Pearson's simple linear correlation coefficient (r). One-way analyses of variance (ANOVA, SAS 1989–1996) examined environmental attributes of sample plots in relation to each identified plant community.

Results

Floristic diversity, life forms, growth forms, and biogeographic affinities

Altogether, 274 flowering plant species (139 annuals, 125 perennials, and 10 biennials), in 179 genera and 57 families, were found (Appendix II). The most common families were: Fabaceae (51 species, contributing 18.6%), Poaceae (40 species, 16.4%); Asteraceae (5.8%); Convolvulaceae (4.5%); Rubiaceae (4%); and Acanthaceae (3.6%). Wickens (1976a, 1976b) provided the most thorough inventory of the region, and he found several species that were new listings for the region (Wickens 1971; Wickens and Mathew 1971). We found 17 additional new species, mostly annuals, in 10 families, not previously reported in the flora of Jebel Marra (see Appendix III). Indeed, three of these (annual) species have already become dominant species in their respective vegetation types (Table 1). In terms of life span (Figure 2a), annuals predominated (49%), followed by herbaceous perennials (22%); trees and shrubs together made up only 22% of species, and several families (23) were represented by a single species. Similarly, in terms of Raunkiaer life forms (Figure 2b), most (54.4%) species were therophytes (annuals and ephemerals), followed by phanerophytes, typically woody trees and shrubs, with aerial resting buds (24.5%). The rest were hemicryptophytes, with buds at or near ground level (9%), chamaephytes, woody plants with buds on persistent shoots near the ground (6.2%), geophytes, with underground resting buds, often on rhizomes, tubers or bulbs (4.7%), and a few (1.5%) were epiphytes and parasitic species. The biogeographic affinities ("chorotypes") of the species were quite diverse; 88 species (32%) were Sudano-Zambezian; 34 species (12.5%) Pantropical, 33 species (11.9%) Palaeotropical, 27 species (9.7%) Sudanian, and 22 species (8.03%) were multi-regional (Figure 2c).

Multivariate analysis of plant communities

A TWINSPAN analysis, using the 100 most dominant species, identified eight vegetation types, labeled Types I–VIII, at level 4 (Table 1). A Detrended Correspondence Analysis (DCA) of sites (Figure 3a) also separated the same eight vegetation groupings (Figure 3b), placing them along two primary axes. In Table 1, dominant species are listed for these eight communities; vegetation Type III is subdivided into three subtypes; on (1) sandy plains, (2) wadis and (3) south-facing slopes. Dominant species noted in both the TWINSPAN and the DCA analyses are shown in bold, in shaded boxes (Table 1). Species that are collected from the wild by the indigenous Fur community are indicated with an asterisk.

Relationships among plant communities, altitude, and soil types

In Table 2, using analysis of variance, the eight vegetation groups are compared in terms of the statistical significance of their associations with altitude zones, soil texture types, and soil concentrations of nitrate-nitrogen (NO_3), phosphorus, Fe and Mn. Vegetation types differed significantly ($p < 0.01$), in terms of the mean altitude where they were found, with Types I and VI being associated with higher altitudes. Types V and VII were mostly seen in zone 1, Types IV and VIII in zone 2, and Types I and VI were at higher altitudes in zone 5. No vegetation type was limited to a single soil texture type. For all vegetation types, "sandy clay loam" was the predominant soil texture; it was accompanied, usually at a much lower frequency, by one or more of the other five soil types. There were statistically significant differences in terms of presence (or absence) of loamy-sand (highest in Type VI, $p < 0.01$) and clay (noted only in Types II and IV, $p < 0.01$). In all sites, the sand fraction was predominantly made up of aeolian (soft, or rounded) sand as opposed to fluvial (water-worked) sand, ranging from 80.1% of the sand in vegetation Type VI, to 93.1% of the sand in vegetation type VIII.

Table 1. Vegetation types (I–VIII) and their respective dominant species in the Jebel Marra Region.

Vegetation type									
I	II	IIIa (SP)	IIIb (W)	IIIc (SS)	IV	V	VI	VII	VIII
Aristida adscendionis	*****Commiphora africana***	*Dactyloctenium aegyptium*	**Asparagus africanus*	**Albizia amara*	**Acacia seyal*	*****Faidherbia albida***	***Monechma ciliatum***	***Sesbania rostrata***	*****Acacia nilotica***
Cleome monophylla	*Acanthospermum hispidum*	*Zornia glochidiata*	**Diospyros mespiliformis*	**Grewia flavescens*	*Oxygonum sinuatum*	*Crotalaria podocarpa*	**Terminalia brownii*	*Crotalaria naragutensis*	*Senna occidentalis*
*****Cordia africana***	**Acacia senegal*	*Pennisetum pedicellatum*	*Cassia obtusifolia*	***Crotalaria laburnifolia***	*Heteropogon contortus*	*Chloris pilosa*	***Tithonia rotundifolia***	*Blainvillea acmella*	***Zornia glochidiata***
Euphorbia heterophylla	**Anogeissus leiocarpus*	*Aristida adscendionis*	*Monechma ciliatum*	*Panicum maximum*	*Verbascum sinaiticum*	*Merremia pinnata*	*Polycarpaea eriantha*	*Phragmites australis*	*Sesamum angustifolium*
Justicia striata	*****Lannea fruticosa***	**Ficus sycomorus*	**Capparis sepiaria*	**Dalbergia melanoxylon*	*Asteracantha longifolia*	*Amaranthus hybridus*	***Alysicarpus glumaceus***	*****Cordia africana***	***Ipomoea obscura***
	**Combretum glutinosum*	*Justicia striata*	*Rothia hirsuta*	*Tetrapogon cenchriformis*	*****Acacia senegal***	*Sida ovata*	**Grewia villosa*	*Sida alba*	
	Farsetia stenoptera				***Pennisetum pedicellatum***	**Acacia tortilis*	*Cassia absus*	*Echinochloa colona*	
	**Ziziphus spina-christi*				**Albizia amara*	*Achyranthes aspera*	*Sesbania rostrata*	**Bauhinia thonningii*	
					*****Grewia flavescens***	**Balanites aegyptiaca*	**Albizia amara*	*Cassia mimosoides*	
						Triumfetta rhomboidea		*Digitaria ciliaris*	
						**Anogeissus leiocarpus*		*Cleome monophylla*	
						Pennisetum pedicellatum		**Anogeissus leiocarpus*	
								Pennisetum pedicellatum	

Note: vegetation Type III is essentially three different habitats with non-overlapping dominant species distinguished as IIIa, IIIb, and IIIc. SP: sandy plain; SS: south-facing slope; W: Wadi. Species in bold, in shaded boxes were identified as dominant species in both the TWINSPAN and the DCA analysis. Dominant species marked with an asterisk were identified as plants collected from the wild (wildcrafted) by the "Fur," indigenous people of Darfur, Sudan. These (wildcrafted) species are all used for five or more of the following list of 8 categories of use: traditional medicines, livestock forage, human food, firewood, research and education, construction, beekeeping, and "other uses" (Hegazy et al. 2020).

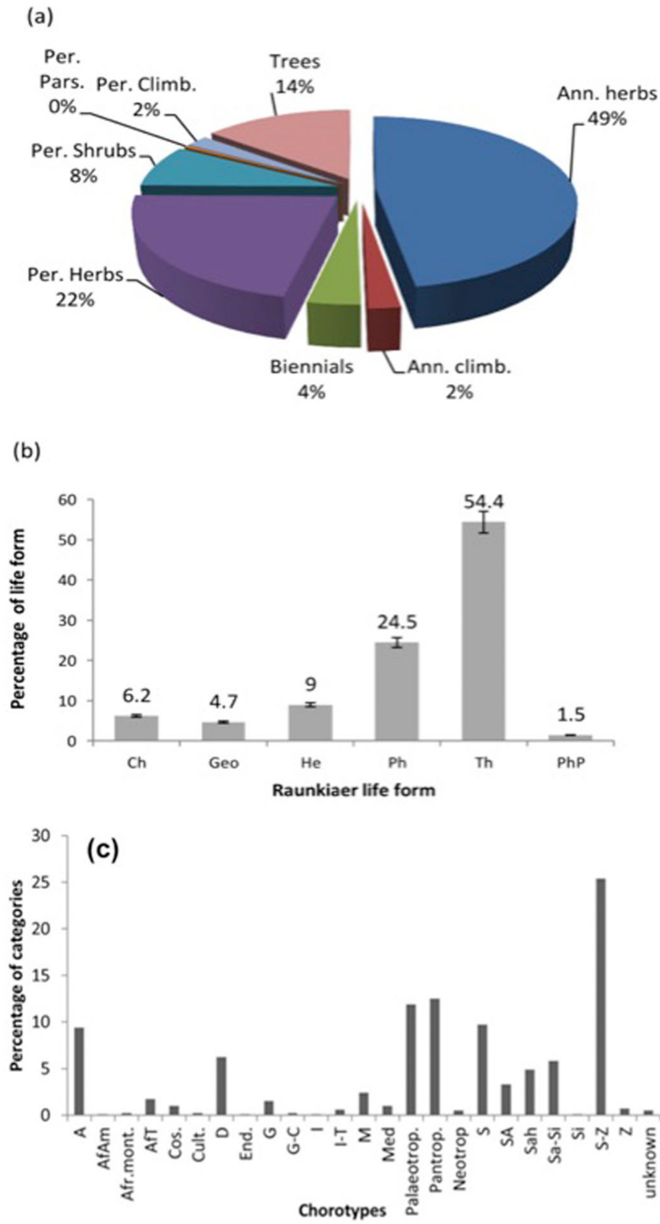

Figure 2. Allocation of species according to various categories. (a) Pie chart showing the relative number of species in each of the following "life history" categories: annual herbaceous plants, annual climbing plants (epiphytes), biennials, perennial herbaceous plants, perennial shrubs, perennial parasitic plants, perennial climbing plants (epiphytes) and trees. (b) The relative frequency of species belonging to each of the following Raunkier life forms based on the position of the persistent living bud during the adverse season: Ch (Chamaephyte); Geo (Geophyte); He (Hemicryptophyte); Ph (Phanerophyte); Th (Therophyte) and PhP (Epiphyte). (c) The proportion of species originating from each biogeographic origin or "Chorotype." Categories, from left to right across the *X*-axis are: A (African); AfAm (Afro-Arabian, meaning the domain including southern Arabia and SW Yemen as well as adjacent Africa); Afr-Mont (Afro-Montaine); AfT (Afro-Tropical); Cos. (Cosmopolitan); Cult. (Cultivar); D (Deccan Domain); End. (Endemic); G (Guinea); G-C (Guineo-Congo); I (Iranian); I-T (Irano-Turanian); M (Madagascan); Med (Mediterranean); Paleotrop. (Paleotropical); Pantrop. (Pantropical); Neotrop (Neotropical); S (Sudanian); SA (Saharo-Arabian); Sah (Sahelian); Sa-Si (Saharo-Sindian); Si (Sindian); S-Z (Sudano-Zambesian); Z (Zambesian); Unknown (Unknown origin).

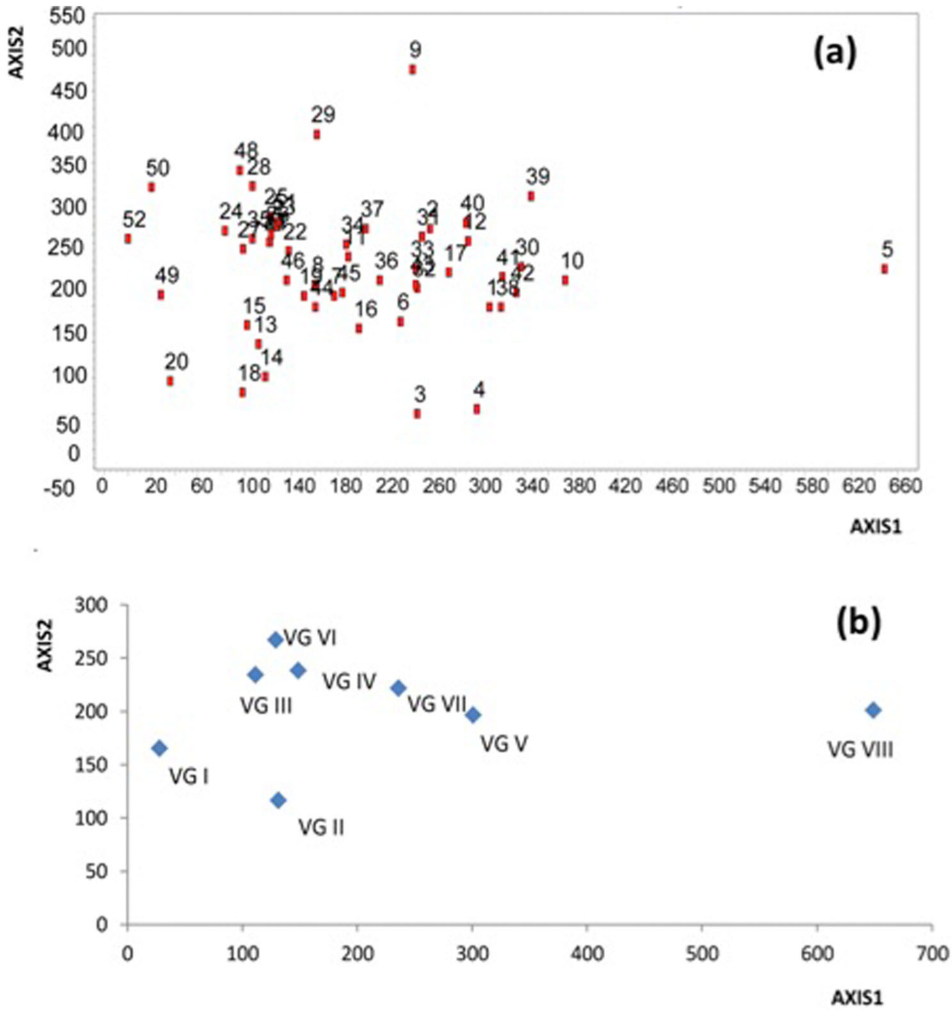

Figure 3. Detrended Correspondence Analysis (DCA). (a) An ordination of the 52 sites in the Jebel Marra region, Darfur, Sudan. (b) An Ordination of the mean scores of each of the eight vegetation types identified using DCA. Dominant species in each of the vegetation types are: I = *Aristida adscensionis* – *Justicia striata* – *Cordia africana*; II = *Commiphora africana* – *Lannea fruticosa*; III = *Crotalaria laburnifolia* – *Anogeissus leiocarpus*; IV = *Acacia senegal* – *Grewia flavescens* –*Pennisetum pedicellatum*; V = *Albizia amara* – *Faidherbia albida* – *Cassia obtusifolia*; VI = *Monechma ciliatum* – *Alysicarpus glumaceus* – *Tithonia rotundifolia*; VII = *Sesbania rostrata* – *Cordia africana*; and VIII = *Acacia nilotica* – *Ipomoea obscura* – *Zornia glochidiata*.

Note that the % for soil fractions do not always add up to 100% because the table shows the average of three subsamples in all quadrats belonging to a particular vegetation type, with varying numbers of quadrats representing each vegetation type; also, a vegetation type was typically found on two or more distinct soil textures (Table 2).

Higher levels of phosphorus were associated with Type II vegetation. Higher concentrations of Fe ($p < 0.01$) and Mn ($p < 0.05$) were associated with Type VIII vegetation. Soils with Type VIII vegetation tend to have an elevated percent clay (40.2 ± 9.9) and

Table 2. Results of one-way ANOVAs summarizing the attributes of each of the eight vegetation types according to various environmental variables.

Variable	VG I	VG II	VG III	VG IV	VG V	VG VI	VG VII	VG VIII	*F*-value
Elevation									
(m.a.s.l.)	1,230.0	990.5	996.6	949.4	834.0	1,207.0	848.6	912.0	3.89**
	±117.6	± 39.2	± 52.6	± 27.7	± 31.4	± 117.6	± 67.9	± 117.6	
# Soil samples	3	27	54	12	39	6	9	6	
Texture									
Loamy sand	0.0	0.0	0.80	0.17	0.29	1.00	0.67	0.0	3.14**
	± 0.0	± 0.0	± 0.2	± 0.1	± 0.1	± 0.4	± 0.2	± 0.4	
Clay loam	0.0	0.11	0.20	0.06	0.07	0.0	0.0	1.0	1.69
	± 0.0	± 0.09	± 0.12	± 0.02	± 0.01	± 0.0	± 0.0	0.28	
Sandy loam	0.0	0.11	0.0	0.0	0.14	0.0	0.0	0.0	0.54
	± 0.0	± 0.0	± 0.0	± 0.0	± 0.06	± 0.0	± 0.0	± 0.0	
Sandy clay loam	17.6	12.11	9.94	9.70	12.23	8.2	13.6	22.8	1.32
	± 5.4	± 1.8	± 2.4	± 1.3	± 1.4	3.4	± 3.1	± 5.4	
Loamy clay	0.0	0.67	0.0	0.17	0.0	0.0	0.0	0.0	4.11**
	± 0.0	± 0.1	± 0.0	± 0.07	± 0.0	± 0.0	± 0.0	± 0.0	
Loamy clay sand	1.00	0.11	0.0	0.06	0.14	0.0	0.33	0.0	1.63
	± 0.3	± 0.05	± 0.0	± 0.01	± 0.08	± 0.0	± 0.17	± 0.0	
Particle size/type									
Hard sand	7.5	9.98	12.28	7.94	8.7	16.2	6.8	2.5	1.56
(fluvial)	± 4.2	± 1.4	± 1.9	± 1.0	± 1.1	± 4.2	± 2.4	± 0.2	
Soft sand	49.7	57.12	57.54	65.71	60.71	65.2	55.7	33.9	0.98
(aeolian)	± 15.2	± 5.0	± 6.7	± 3.6	± 4.0	± 15.2	± 8.8	± 12.2	
Silt	17.6	12.11	9.94	9.70	12.23	8.20	13.56	22.8	1.32
	± 5.4	± 1.8	± 2.4	± 1.2	± 1.4	± 5.4	± 3.1	± 5.4	
Clay	25.2	17.52	15.92	12.97	18.25	9.5	20.06	40.2	1.44
	± 9.9	± 3.3	± 4.4	± 2.3	± 2.7	± 1.9	± 5.7	± 9.9	
Elements									
N	97.44	66.12	78.9	64.45	79.17	101.7	96.08	60.9	0.74
	± 32.9	± 10.9	± 14.7	± 7.7	± 8.8	± 32.9	± 19.0	± 32.9	
P	10.06	18.3	12.39	7.43	8.1	8.1	5.28	9.5	3.70**
	± 5.8	± 1.9	± 2.6	± 1.4	± 1.5	± 5.8	± 3.3	± 5.8	
Fe	73.4	52.05	44.88	32.68	28.72	53.05	66.56	173.2	3.55**
	± 31.7	± 10.5	± 14.2	± 7.4	± 8.4	± 31.7	± 18.3	± 31.7	
Mn	19.7	44.63	33.26	36.96	19.18	31.0	17.07	99.2	2.68*
	± 22.4	± 7.4	± 10.0	± 5.3	± 6.0	± 22.4	± 12.9	± 22.4	

Variables include: mean elevation, and soil attributes based on three replicate samples per quadrat, and various numbers of quadrats that matched each vegetation type. Soil attributes assessed were: texture, average proportion of hard sand, soft sand, silt and clay, and concentrations of (total) N, (total) P, Fe, and Mn in ppm. Statistical analyses were carried out using SAS. For each attribute, the first line presents the mean and second line is the Standard Error (± S.E.). The overall level of significance of differences among sites is shown by the *F*-value, $^{**}p \leq 0.01$ and $^{*}\ p \leq 0.05$. *F*-values with no stars are not statistically significant (NS).

were associated with clay loam soils as well as the more common sandy clay loams, and elevated Fe (173.2 ppm) and Mn (99.2 ppm).

A Canonical Correspondence Analysis (CCA) depicts associations between major environmental factors and the 62 most abundant species (Figure 4a) or vegetation types (Figure 4b). Vector arrows represent gradients of various parameters, and help separate (or cluster) sites according to the match between environmental conditions and species. The positive end of the first (X) axis is associated with fine soil particles (clay and silt), higher concentrations of Fe and Mn and low elevations (Zones 1 and 2); the negative end corresponds to sandy textures and higher elevations. The positive end of the second (Y) axis denotes elevated phosphorus concentration. As was the case for the DCA plot of vegetation types in Figure 3b, Type VIII was very distinct from the others, placed on the high positive end of the X-axis, in soils with a higher % of silt and clay, that were rich in Fe and Mn. Vegetation Types I and II are at the positive end of the Y-axis, and Type II is particularly associated with elevated phosphorus concentration, supporting the results of the ANOVA in Table 2.

A correlation analysis matrix (Table 3) confirms the association between sites at the positive end of the first (X) axis of Figure 4a and finer soils (with higher % silt and clay, $p < 0.01$), and elevated iron ($p < 0.01$), and the negative association with sandy soils ($p < 0.01$) and higher elevations ($p < 0.05$). The positive end of the second (Y-axis) is associated with elevated phosphorus ($p < 0.001$) and sandy loams ($p < 0.05$), conditions usually found on the north-facing slopes of Nertete, and Sermi (in the Zalingei area). The negative end is associated with sandy clay loams ($p < 0.001$). Other significant positive correlations included: clay content with (each of) silt content, clay loams ($p < 0.001$), concentrations of Fe ($p < 0.01$) and Mn ($p < 0.05$); loam with elevated NO_3^- ($p < 0.001$); silt with clay ($p < 0.001$); and Fe with Mn ($p < 0.001$). Significant correlations are also seen between: silt content and elevated N, Fe, and Mn ($p < 0.01$); and clay and silt content and levels of Fe ($p < 0.01$).

Discussion

Plant diversity

Overall, Fabaceae and Poaceae predominate, supporting earlier reports on Jebel Marra (Wickens 1976a, 1976b) and findings in nearby Saudi Arabia and Libya (Hegazy, El-Demerdash, and Hosni 1998; Al-Turki and Al-Qlayan 2003; Hegazy et al. 2007; El-Ghanim et al. 2010; Hegazy et al. 2017). The frequency and distribution of annuals and ephemerals (therophytes) and perennial shrubs (phanerophytes), with just over half of the species being therophytes, is typical of vegetation in arid regions, and patterns represent predictable responses to topography, aridity and human impacts seen in the desert, semi-desert, and dry woodland savannas that constitute about 50% of Sudan, where annuals provide much of the ground cover (cf. Hegazy and Lovett-Doust 2016). However, the present dominance of therophytes represents a significant change in the region since the surveys by Wickens (1976a, 1976b), who reported that phanerophytes were predominant. In other words, since the 1970s, perennial trees, some shrubs and herbs have been replaced by annuals (see, also Abusuwar and Mohammed 2011). Reinforcing this point, the new species recorded are mostly annuals (see Appendix III),

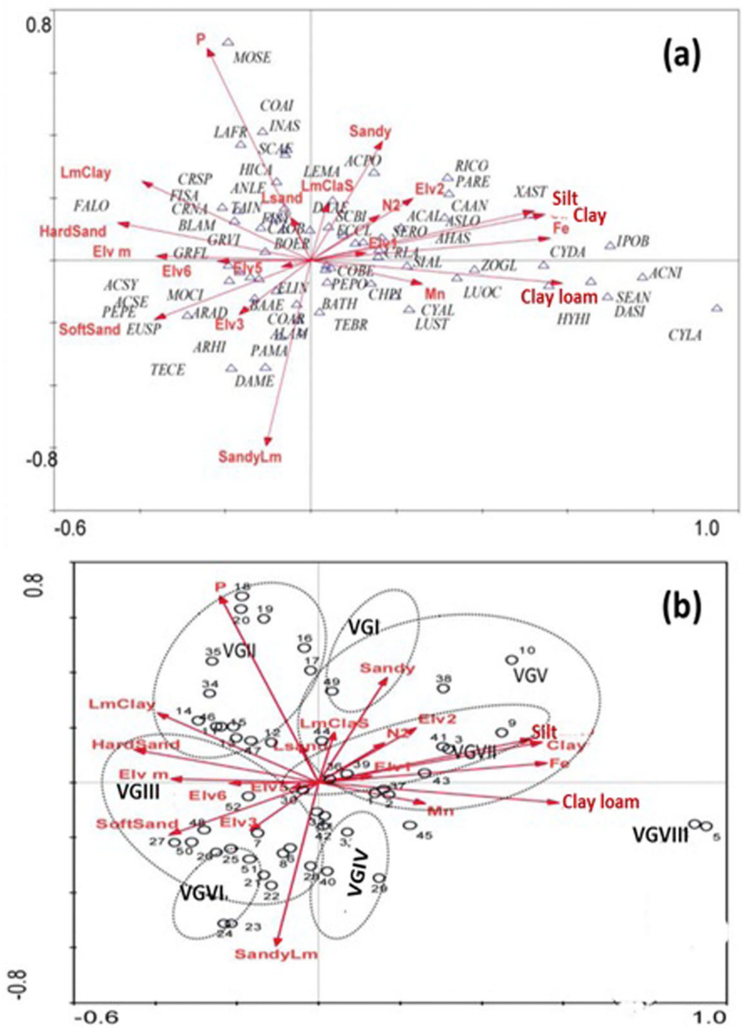

Figure 4. Canonical Correspondence Analysis (CCA). (a) A bi-plot ordination of the 62 most common plant species according to environmental variables. Species names are abbreviated to four letters; for a list of their full names, see Appendix II. (b) Using the same vectors for soil attributes and altitudes, a bi-plot ordination of stands matching the eight distinct categories (I–VIII) according to environmental variables. Elevation zones (Elv) are: Elv 1 = 750–850 m.a.s.l., Elv 2 = 850–950 m.a.s.l., Elv 3 = 950–1,050 m.a.s.l., Elv 4 = 1,050–1,150 m.a.s.l., and Elv 5 = >1,150 m.a.s.l. Soil textures are distinguished, following the USDA classification system as: LS: loamy-sand; CL: clay loam; SL: sandy loam; SCL: sandy clay loam; C: clay. Additional axes correspond to other attributes of soils; Soft Sand = proportion of rounded aeolian (wind eroded) sand; Hard Sand = proportion of water-worked, angular sand; Silt = proportion of silt-sized particles, and clay = proportion of clay-sized particles. Gradients of various nutrients are indicated as corresponding to increasing concentrations of total phosphorus (P); total nitrogen (N); Mn = manganese, and Fe = iron. Note sand particles are defined as 0.05–2.00 mm diameter; silt particles as 0.002–0.05 mm; and clay particles as <0.002 mm diameter.

Table 3. Correlation analysis (Pearson correlation coefficient, "*r*") between environmental variables and first and second DCA axes.

	AX1	AX2	Elev.	Loamy Sand	Clay Loam	Sandy Loam	Sandy Clay Loam	Loamy clay	Loamy Clay sand	Hard Sand	Soft Sand	Silt	Clay	N	P	Fe	Mn
Elev.	−0.36*	0.01	1.00														
Loamy Sand	−0.05	0.14	−0.17	1.00													
Clay Loam	0.59**	−0.07	−0.07	−0.18	1.00												
Sandy Loam	0.17	0.38*	0.019	−0.14	−0.08	1.00											
Sandy Clay Loam	−0.10	−0.60***	−0.02	−0.39*	−0.22	−0.17	1.00										
Loamy Clay	−0.40*	0.25	0.19	−0.28	−0.17	−0.11	−0.33*	1.00									
Loamy Clay Sand	0.04	0.18	0.09	−0.18	−0.10	−0.07	−0.21	−0.15	1.00								
Hard Sand	−0.45**	0.12	0.21	0.03	−0.49**	0.34*	−0.11	0.15	0.16	1.00							
Soft Sand	−0.37*	−0.19	0.12	0.03	−0.64***	0.15	0.57**	−0.01	−0.44**	0.15	1.00						
Silt	0.53**	0.16	−0.11	−0.11	0.59**	−0.17	−0.44**	−0.08	0.52**	−0.37*	−0.91	1.00					
Clay	0.55**	0.15	−0.20	−0.01	0.71***	−0.24	−0.47**	−0.05	0.33*	−0.43**	−0.92***	0.93***	1.00				
N	0.16	0.15	−0.05	−0.11	0.04	−0.08	−0.14	−0.16	0.63***	0.05	−0.32*	0.38**	0.28	1.00			
P	−0.24	0.68***	0.06	0.20	−0.10	0.09	−0.40**	0.33*	−0.08	0.31*	0.01	−0.14	−0.12	−0.16	1.00		
Fe	0.56**	0.07	0.19	−0.09	0.66***	−0.15	−0.20	−0.06	−0.01	−0.38*	−0.41**	0.48**	0.49**	−0.04	0.20	1.00	
Mn	0.26	−0.08	0.24	−0.37*	0.69***	−0.07	−0.05	0.06	−0.09	−0.32*	−0.38*	0.42**	0.38*	−0.08	0.15	0.81***	1.00

Axis 1 (AX1) and Axis 2 (AX2) are distinguished, then Elevation (m.a.s.l.) as "Elev." Soil texture categories are distinguished, relative proportions of hard or soft sand, silt and clay, and concentrations of elements, in ppm (Total N, Total P, Fe, and Mn), in soil are indicated. The significance level is indicated as $^{***}p \le 0.001$; $^{**}p \le 0.01$; $^{*}p \le 0.05$ and no star indicates the correlation was not significant (NS). Boxes are shaded from darkest to lightest gray to correspond to these three levels of significance. Positive correlations are indicated by a positive *p*-value, inverse correlations by a negative *p*-value.

and three of these have already become dominant in three different vegetation types; *Rothia hirsuta, Asteracantha longifolia,* and *Blainvillea acmella* (see Table 1). The shift noted from perennial trees and shrubs to annuals is a typical consequence of reduced water availability, increased grazing pressure, harvesting of wild tree species for firewood and other uses (see Hegazy et al. 2020), and conversion of savanna to cultivated land.

The earliest accounts of the flora of Jebel Marra were vague, alluding to "fair numbers" of various species (Browne 1799 cited in Wilson 2012). More recent studies described the woody vegetation as dominated by *Anogeissus leiocarpus*, various species of *Acacia*, and other desert trees (Wickens 1976a, 1976b; Ahmed 1982; Hegazy and Amer 2003). The present study offers a more nuanced, and explicitly quantitative picture, in that it identifies, and explains, distinct patches of vegetation corresponding to contrasting soils set in a heterogeneous landscape. Today *Anogeissus leiocarpus* (Combretaceae) is a dominant species only in vegetation Types II, V and VII; other species, especially members of the Fabaceae such as *Acacia* species dominate in vegetation Types IV, V, and VIII. The abundance of endemic species from the Sudano-Zambezian and Sudanian regions (32% and 9.7%) is not surprising given that the study area lies at the center of that region (Wickens 1976a, 1976b). Eleven species are endemic to Jebel Marra (Elsiddig 2007), and we encountered three of these in our surveys (*Vernonia amygdalina, Kickxia aegyptiaca* and *Cyperus spp*. (in our survey we found five species of *Cyperus,* see Appendix II). Paleotropical species represent the earlier Gondwana flora; some species, such as *Acacia seyal* and *Ziziphus spina-christi*, are shared with India (Saharo-Sindian Chorotype), while others such as *Oldenlandia herbacea* and *Pupalia lappacea* are known to have been introduced from Madagascar, the Mediterranean, and India (they belong to the Deccan Chorotype). This reflects the long history of agriculture and cultural exchange, going back millennia (see Khalid et al. 2012; Hegazy et al. 2020), as well as, potentially, long distance seed dispersal by birds (Wickens 1976b).

Vegetation types

The general agreement between the "TWINSPAN" analysis of plant associations and the DCA plots in Figure 3 supports the identification of eight vegetation groups. Type VIII is a clear outlier, with a list of dominant species unique to that vegetation type (Table 1). Figure 3b shows that vegetation Type VI placed highest on Axis 2; it, too had a relatively distinctive species list, except that it shares *Albizia amara* with vegetation Types IV (in more rocky sites) and III (specifically, Type IIIc) on south-facing slopes. Vegetation Type I has the lowest value along Axis 1; it shares two species (*Aristida adscensionis* and *Justicia striata)* with the sandy plains subgroup (Type IIIa) of vegetation Type III, which is closest to it along Axis 1 (Figure 3b). Species are not exclusive to a vegetation type; rather the lists may overlap to varying degrees. It is important to note that niche breadth is a *species* characteristic that is not necessarily shared by all species that are members of a given "vegetation type," thus, some species are likely to emerge as dominants in more than one vegetation type (e.g., *Pennisetum pedicellatum* is one of the dominant species in Types IIIa, IV, V, and VII; and *Anogeissus leiocarpus* is a dominant in Types II, V, and VII).

Soils

All vegetation types were predominantly growing on soils of "sandy clay loam" texture, with relatively low occurrence on an additional one to four other soil texture types, depending on the vegetation type (see Table 2). In terms of particle size distribution in the three standard size classes, the sand fraction (aeolian plus fluvial, or "soft + hard" sand) was predominant for all vegetation types except one; Type VIII, where the clay fraction was greatest at an average of 40.2% (Table 2). Silt fractions were relatively low, ranging from 8.2% in vegetation Type VI, to 22.8% in Type VIII) and they never exceeded either the clay or sand fractions. While not strictly part of the standard international soil texture system, it is interesting to note the predominance of "soft" sand, over "hard" sand (Table 2). This suggests that the sand of the lowland sandy plains originated in nearby desert regions, and was brought in by wind, rather than being formed through local water erosion and weathering of the largely volcanic, surface parent material.

Associations among vegetation, altitude, and soils

The CCA ordination considers the environmental factors (particularly soil texture and elevation) that may explain patterns in the distribution of species (Figure 4a), and the eight vegetation types (Figure 4b). The three regions of Jebel Marra that were studied (Zalingei, Wadi Salih and Nertete) do not have distinctive vegetation types; all three regions are heterogeneous in terms of the kinds of soils and range of elevations and varied topography that they include. This kind of patchy vegetation distribution is common in arid and semi-arid regions where differences in soil texture and gradient significantly affect local moisture retention, and moisture stress experienced by plants during the dry winter months (Kassas and Batanouny 1984). Some of the dominant vegetation types we identified were previously recorded. For example, Type V, found around wadis, and on alluvial plains with clay soils was first recorded by Wickens (1976a), specifically around Wadi Azum and Wadi Aeba, where the lower terraces were dominated by pure stands of *Faidherbia albida*. However, in these sites Wickens also found some *Cordia africana* (which we only found dominant in vegetation Types I and VII), and *Ficus* spp. (we only found *Ficus sycomorus* dominant in Type IIIa, on the sandy plains). He also noted two *Acacia* species that we did not see as dominant species in any of our vegetation types (*Acacia sieberiana* and *A. polyacantha*), and *Acacia* (now *Senegalia*) *mellifera,* recognized as a dominant species in four of his vegetation types, was recorded, but was not dominant in any of the vegetation types we found, so plant communities have clearly changed significantly since the 1970s.

The "outlier" vegetation type evident in Figures 3b and 4b (Type VIII) found in the heavily overgrazed clay plains, was dominated by weedy and invasive species, naturalized cultivars, or species associated with overgrazing by herbivores, such as the invasive *Acacia nilotica*, a Sudanian (S) chorotype, often called the "gum arabic tree," or in India, "Amaravati gum." It produces a gummy exudate that resembles the more usual commercial sources of gum arabic, namely *Acacia senegal* and *Acacia seyal*, also in the Fabaceae family. Others have noted that *Acacia nilotica* is associated with clay soils including alluvium and smectites with >35% clay (Holm et al. 1979), and is often spread by livestock, as seeds remain viable after passing through the gut of cattle, but not sheep (Mackey 1997). We note that *Acacia nilotica* was not seen as a dominant at all by Wickens in 1973, nor was it reported 10 years later, according to the vegetation "sketch maps" developed by Ahmed (1983). At the time of his survey, Ahmed (1983) reported the rainfall around Nertete as being 922 mm/year; this was significantly (27%) higher than the more recent average of 672.02 mm/year reported for the period 2001–2010.

Other dominant species in Type VIII vegetation include two other Fabaceae species (*Zornia glochidiata,* used as a food and medicine, and *Senna occidentalis*, "coffee senna," a species introduced from the Americas that is often used as a coffee substitute), as well as *Sesamum angustifolium*, a relative of pearl millet, introduced originally from Kenya. Seeds and leaves of *S. angustifolium* are used as food, and as a source of medicines (see Hegazy et al. 2020). Human agricultural activities in terms of planting introduced species, and disturbance, including the deliberate cycle of "brush fallow," where local trees and shrubs, including "introduced species," can re-colonize abandoned fields, are contributing determinants of this vegetation type.

Agriculture, with terracing of lower slopes, and alternating periods of tillage and return to natural vegetation, combined with pastoralism has been under way in this region for millennia (Ahmed 1982; Cayrol et al. 2000; Loeser, Sisk, and Crews 2007). The "brush fallow" period restores nutrient levels, particularly nitrates, thanks to the many species of Fabaceae in the flora, and ground vegetation combined with the deeper rooting of trees and shrubs allows restoration of organic matter and nutrients in soil. Unfortunately, due to the conflict in the region, the dangers of moving with livestock to the upper slopes have increased significantly in recent decades, so livestock have become more restricted to pastures on the lower slopes, which now show the effects of over-grazing, as reported by local Fur farmers and cited in Hegazy et al. (2018, 2020). Besides the direct effects of over-grazing on lowland pastures, driven by selective herbivory of preferred species, and farmers supplementing pasture species with branches cut from surrounding leguminous trees and shrubs, semi-arid regions, especially those with clay soils, are more vulnerable to trampling by domestic livestock; this causes soil compaction, inhibits water percolation, reduces plant cover, and promotes soil erosion (Oztas, Koc, and Comakli 2003; Connolly et al. 1997).

Changes in vegetation over time

Earlier authors (Jenny 1941; Obeid and Mahmoud 1971) proposed that the presence, distribution, and density of vegetation in semi-arid regions of Sudan were determined by physical factors including wind (force and direction), water supply, topography, soil types, and sometimes the presence of a tree canopy (e.g., *Acacia nilotica*, see Hegazy and Lovett-Doust 2016). Our results show, more specifically, that although soil texture "category" in terms of the standard USDA texture triangle was predominantly "Sandy Clay Loam" for all vegetation types, the % clay in soil was a useful indicator of vegetation composition, most likely through its effect on soil moisture retention, with a higher % clay being associated with greater moisture retention and more phosphorus release. White (1983) described the Jebel Marra vegetation as part of the Sahelian semi-desert, where annual grasses and scattered bush steppe transition gradually into the Sudanian savannas, with communities dominated by perennial grasses and scattered trees. This description, broadly speaking, matches our vegetation Type I, which today is usually found in uplands (elevation Zone 4) on the northern slopes of Jebel Nertete, in the north-eastern part of the study area. This part of Jebel Marra is less densely populated, so that may explain why there has been less change in vegetation in that relatively remote region. Lebon (1965) reported a more diverse tree cover in sites on the lower slopes around Zalingei, corresponding to our vegetation type VII, which is still found in more moist sites in the sandy and clay plains of Zalingei (in Garash and Wadi Aeba) and Wadi Salih (in Segergerah).

Beginning with the surveys by the FAO (United Nations) (1968) and Wickens (1976a) vegetation types were usually characterized in terms of 1–2 dominant species, and a general description of the soil in that area. A striking finding is that the eight vegetation types we identified were not readily related to the 15 vegetation types listed by Wickens (1976a) as corresponding to topography and soil type (soil in Wickens' study was characterized in a general descriptive sense, rather than through soil texture assessment or chemical analysis). Although Wickens usually listed one, and sometimes two dominant species in each case, only two of his classes corresponded (partially) to any of our vegetation categories. His type 2 (with *Faidherbia albida* and *Balanites aegyptiaca* as dominants), which he saw on "alluvial soils," corresponded to our Type V vegetation, at least in having these two species among the dominants. However, our "Type V" vegetation also had high frequencies of ten additional characteristic species (see Table 1). Also, we have shown the fallacy of the assumption that soils in plains and wadis are, by definition, a product of fluvial processes (Wickens 1976a); instead soil particles, specifically sand particles that can be viewed and classified under the microscope, are predominantly the product of wind-erosive processes rather than water erosion. Wickens' Types V and VI vegetation roughly corresponded to our Type II vegetation, in that *Commiphora africana* was a dominant species, but the other dominant species he cited in these vegetation types was *Senegalia mellifera* (at the time known as *Acacia mellifera*), which we did not encounter as a dominant species in any of the vegetation types we identified, although it was recorded in quadrats (see Appendix II). Some other species that Wickens (1976a) identified as characteristic dominant species in his various vegetation types were not recorded at all in our survey, namely, *Boswellia papyrifera* ("Sudanese Frankincense") and *Terminalia laxiflora*. This illustrates the value of surveying vegetation more systematically, as relevés within discernable areas of homogeneous vegetation, and assessing entire quadrats in terms of parameters such as % cover, and presence of each species, assigning an importance value for each species. It also shows the value of the more "hands-off" approach of ordination, and CCA analysis, which tends to remove the "expert bias" effect of early methods of mapping of vegetation, and categorization of vegetation "types." The loss of several former dominants illustrates the major changes in vegetation over the past 50 years, and the urgency of addressing the loss of species that were of economic importance in the past.

So, looking back at these earlier studies (e.g., Lebon 1965; FAO (United Nations) 1968; Wickens 1976a), most of the other vegetation types that we identified using TWINSPAN, confirmed using DCA and explained in terms of soil type and elevation using CCA, had not been identified by earlier researchers. This illustrates three things: first, the rapid rate of change in the composition of plant communities over the past 50–60 years, second the important impacts of human activities on vegetation, and third, the value of using more "dispassionate" methods of vegetation assessment such as TWINSPAN, DCA, and CCA, where quantified assessments of species' representation (and in the case of CCA, environmental conditions) in quadrats, within recognized relevés, are used as a data source, rather than empirical adjudication of vegetation types based on perceived canopy dominants and "observer expertise."

Jebel Marra lies northwest of the "Eastern Afromontane Hotspot" (EAH), one of 35 regions recognized globally as deserving special management protection, as it has at least 0.5% or 1,500 plant species as endemics, and has lost at least 70% of the primary vegetation (Myers et al. 2000). Given its proximity to the EAH, and some shared attributes, (e.g., the region is montane, lowlands have been farmed since an early point in human history, and it is currently a site of regional conflict and severe human pressures), it would be valuable to assess Jebel Marra in terms of the "hotspot" criteria. This would require significant follow-up study, including assessing the extent of loss of primary vegetation and quantification of the evidence for overgrazing. Our identification of eight distinct vegetation types in contrast to the two (roughly corresponding to our Types II and V) that were previously described may directly reflect the consequences of overgrazing, and, perhaps, as Babikir (1988) suggested, the impacts of shorter periods of "bush fallow" between periods of tillage in the rotation system practiced in the region.

An obvious consequence is the increased representation of weedy and (introduced) agricultural species that differ in different soil types. This effect was most obvious in the case of vegetation Type VIII, which was dominated by introduced species, but some of the other vegetation types were also, at least in part, shaped by human land management practices. For example, in grazing land on the plains, farmers often leave "useful" trees growing among the herbs and forage grasses. Examples of these are *Acacia nilotica, Cordia africana, Albizia amara, and Ziziphus spina-christi*, all species with multiple uses including medicine, livestock forage, wood, and beekeeping (as nectar sources) (Hegazy et al. 2020). In our recent study investigating subtle differences in plant phenology in different parts of Jebel Marra, we found that, for 5 months of the year, from December to May, most plants showed very little active growth (Hegazy et al. 2018). In wadis, however, where surface water may be available for longer, phanerophytes (trees and shrubs) still made up most of the vegetation, and provided animals can reach their branches, the accumulated biomass of these plants would be available. Traditionally, farmers also cut off upper branches, and provide them as fodder to livestock during the dry season (Hegazy et al. 2020); a popular species for this is *Acacia seyal*, dominant in vegetation Type IV.

Human impacts and changes in management

The human population of this region has fluctuated significantly over time; it lies almost at the center of North Africa, in that Jebel Marra is equidistant from the Atlantic and the Indian Ocean, the Mediterranean and the Red Sea, and would have been a natural focal point for human migration, evidenced by Paleolithic art in the north (Wadi Howar) and early development of sophisticated, settled agriculture in the Neolithic (Ahmed 1982); indeed, as mentioned above, archaeological finds include stone tools dating back 500,000 years (Williams 2016). The regional population dropped nearly 50% between 1881 and 1894 due to warfare, slave-raiding, famine and epidemics (Gleichen 1905). Ahmed (1982) makes the point that the region has experienced continuous disturbance of the woody vegetation; the most striking evidence of previous land use, he shows, is the fact that nearly all the accessible slopes of the massif, from the base to 2,750 m.a.s.l., are terraced with the Neolithic Tora (Fur) technique of drystone walling and bench terracing (Balfour-Paul 1955). In many areas, this is no longer obvious as most of the upland terraces have been abandoned, and recolonized by local tree species (Barbour 1961). In the lowlands, large paddocks, several hectares in area, and bounded by drystone walls, correspond to lands set aside for livestock grazing. There is also evidence of active irrigation of farmland from surface waters in the perennial wadis, dating back, at least, to the Neolithic (Balfour-Paul 1955).

There have been periods in the recent history of Jebel Marra when the supply of fuelwood has been critically depleted. The government's approach was, in 1958, to establish a Forest Reserve on the SW slopes of Jebel Marra, where harvesting by local people was explicitly prohibited (Babikir 1988). Most of the 2,594 hectares set aside were planted with exotic softwoods such as *Cupressus* spp.; apparently, plantings of local species were not very successful, so emphasis remained on these introduced species, particularly the conifer, *Cupressus lusitanica,* which is native to Mexico and Central America (Ahmed 1983). Clearly this kind of "forest reserve" is not a conservation tool, but rather a wood production system (Idris and Osman 2014). The patchy vegetation of Jebel Marra has long been shaped by human agricultural practices. In a review of vegetation, soil and land use changes in the Jebel Marra, Babikir (1988) concluded that the practice of terracing of slopes, and rotational agriculture, 3–7 successive years of tillage followed by a rotation to "scrub vegetation" was the norm (Ahmed 1983). He also suggested that this form of agriculture was responsible for a decline in the amount of timber available in the region. Specifically, Ahmed (1983) argued that the problem may have developed because the period of fields laying fallow was being shortened, such that the natural ("climax") tree- and shrub-dominated vegetation was becoming more and more restricted in its distribution. Another anticipated consequence of the loss of this vegetation was increased soil erosion. Babikir (1988) pointed out that the topography of the region means that there is a lot of soil creep and gullying under way such that soil profile development is limited. However, we would argue that the recent loss of tree and shrub vegetation is not attributable to terraced farming, which prevents soil erosion and gullying, but rather to the fact that today it is more difficult for Fur farmers to access more remote terraced fields, so these are no longer cultivated and have become more susceptible to erosion. Given that the severity of droughts began to increase in the early 1970s, it would be more appropriate to look at the loss of tree cover as a multifactorial issue; a nexus that includes confluence of a significant increase in the regional population, conflict, and disruption of traditional practices, well-intentioned, but sometimes detrimental activities by relief agencies, large-scale Forestry Reserve initiatives and a trend of lower annual rainfall, rather than insisting that any single factor is responsible for the loss of tree and shrub cover in Darfur.

This region has long been sensitive to changes in rainfall; Wilson (2012) offers an interesting historical overview of biological exploration and land management in Darfur. About 11,500 YBP, he infers, regional rainfall was significantly greater, based on the Neolithic rock paintings in Wadi Howar and the Tagabo Hills, north of Jebel Marra which show giraffes, elephants, lions and hyenas – species that are today only found to the south-east of Darfur, where annual rainfall is higher. The Sultanate of Darfur was independent for 800 years, then annexed by Egypt in the 1870s. Governance varied until 1916, when Darfur became part of "Anglo-Egyptian Sudan." From 1916 to 1955, Sudan Political Service (SPS) officers gathered local information on wildlife and plant products. Larger animals like lions, hyenas, jackals and foxes were eliminated partly due to European hunters, and wildlife poisoning by the colonial "Veterinary Department" (Wilson 2012). When Sudan regained independence in 1956, the impacts of intense rural development became a growing concern. Studies of local resources, sponsored by the United Nations Development Program (UNDP), included the field surveys carried out by Wickens (1971, 1976a, 1976b); and Wickens and Mathew (1971). National parks were established; Radom National Park in 1979, in the South, and Wadi Howar (or Wadi Howa) National Park in 2002, in the North, but Wilson (2012) noted that researchers' access to the region has been relatively limited since then, with little new information on Jebel Marra since the 1980s.

Today the influx of refugees to Radom National Park and Jebel Marra has placed increased pressure on wildlife and plants, as demonstrated by Spröhnle et al. (2016) who used satellite imagery to examine the Zalingei region, and concluded that growing populations in the Zalingei IDP camps were associated with a significant decrease in woody vegetation (deforestation) in the immediate vicinity of the camps – essentially any areas within walking distance of the camp boundaries were being harvested for fuel. Wilson (2012) concluded that more extensive cultivation, greater use of timber, firewood and charcoal, more livestock, and reduced and less predictable rainfall were likely the principal drivers of vegetation change. Our study offers a useful update in that we have documented a switch from dominant perennials to dominant annuals, we have recognized five new vegetation "types," and we have recorded the establishment of previously unreported species. The fact that 14 of the 17 new species records were annuals matches the trend we see toward more annuals and fewer perennials, and supports our decision to survey in the middle of the growing season, reducing the chance of missing such species (Call and Roundy 1991; Hosni and Hegazy 1996).

Conclusions

There has been much discussion of the crisis in Darfur, where there is a confluence of population increase, conflict, and changes in climate and vegetation. Some have suggested that the conflict in Darfur represents a clear case of civil war that was directly caused by climate change (Gore 2006; Sachs 2006). However, others have countered that the decline in rainfall was already under way, and occurred over 30 years before the current conflict erupted in 2003, so Sachs' (2006) "cause-and-effect" theory is not supported by the evidence (Kevane and Gray 2008). Some authors have argued that the (ancient) traditional practice of shifting tillage (alternating with extended periods of brush fallow) is no longer working well because the length of the period of fallow has become shorter (Ahmed 1983; Babikir 1988); indeed, the lowland fields are now essentially continuously cultivated (Hegazy et al. 2020). The findings of Spröhnle et al. (2016) suggest that at least some of the decline in perennial trees and shrubs has been driven by the increasing demand for firewood, largely used for cooking in the refugee camps. This additional (destructive) harvesting process places the refugees in direct competition with local (Fur) residents who normally harvest, sustainably, cuttings from upper branches from these same shrubs and trees as supplemental livestock forage during dry seasons. The *combined* effects of an increase in the human population, increasing aridity, and, potentially, deterioration in soil quality have contributed to the decline of dominant perennial species. It would be a stretch to call the current pattern of land use the result of a "Management Policy" of any kind; rather it is the consequence of multiple social and climatic stressors. Traditional land use patterns such as the combination of cultivation of plains, and lowland terraces, and upland seasonal pastoralism have been disrupted. For Fur farmers, the collapse of terraced farming activities, and decline in seasonal pastoralism due to the dangers of being away from their main (lowland) homes, mean overgrazing of lowland pastures is an inevitable result.

By using, simultaneously, several different techniques including TWINSPAN, DCA, and CCA to characterize the flora of the Jebel Marra region, alongside more ecological and evolutionary analyses of the flora in terms of plant families, life history strategies, life forms, soils, and regions of origin, we have identified the key determinants of the vegetation types present today. The regional flora certainly is very diverse, but not because all sites are similar, and highly diverse. Rather, the eight vegetation types reflect the heterogeneity of soils, elevations, and intensity of human impacts in the region. We, therefore, reject the first hypothesis, that Jebel Marra is home to a uniformly diverse flora, and instead adopt the alternate hypothesis, that the high regional biodiversity is due to heterogeneity of soil conditions and land management (including terracing of hillsides) at a relatively small scale, largely attributable to the long-standing traditional practice of the "bush fallow" rotation. The fact that many of the local trees and shrubs are members of the Fabaceae is no doubt important to the enhancement of soil nitrates, and in the recent past, the vegetation that developed during the fallow period also enhanced the overall level of soil organic matter. In our study, site-to-site variation in current rainfall and climate were not significant contributing factors (see Hegazy et al. 2018, 2019). Instead, soil texture, as a determinant of plant-available water capacity (PAWC), and different stages (for each patch) in terms of time elapsed since last cultivation, were key factors.

The second hypothesis proposed that introduced and weedy species would be found in heavily farmed lowlands; this is accepted with some "qualifications." The key driver for the weedy species in vegetation type VIII is a high % clay in the soil (Figure 4a), but this is only one of the three major lowland soil types, the others being sandy plains and wadis. The "Type VIII" species were not found in sandy soils, even though, located on the lowlands near settlements, intensive agriculture and grazing also occur there. We relied on general observation of the thinly vegetated lowland pasture and local (Fur) farmers' accounts of the challenges of overgrazing, but it would be valuable to undertake further study to assess, directly, the degree to which overgrazing is altering the vegetation of the lowland pastures. According to local reports, a contributing factor is the danger of pursuing the traditional practice of seasonal upland pastoralism, given the current conflict in the area, so livestock are now more likely to be kept close to the Fur farmers' main habitations, on the lowland slopes.

Annuals are among the dominant species in several of the vegetation types, and most of the "new" species records were annuals, reinforcing the point that we have identified a shift from the dominance of perennial trees and shrubs to annuals. At a larger scale, none of the three study regions were homogeneous; except for vegetation type VIII, in the weed-dominated, overgrazed clay soils of Garas, in Zalingei, all vegetation types were found in at least two, and often all three, study regions. Each distinct community is a product of specific combinations of soil type and altitude resulting from the region's heterogeneous topography and surface geology, and for lands in rotation, the time elapsed since the last tillage (which is a direct function of distance from the permanent settlements, and/or the issue of whether the farmer and his family are still living at home, or have been moved to an IDP camp) is likely a factor. These combinations, combined with the introduction of some plants by humans, and the recent surge in the regional population, help explain current plant biodiversity in the region.

The TWINSPAN and DCA analyses were useful for identifying groups of associated species, but the CCA provided a more useful level of explanation, highlighting soil texture (particularly clay and silt content) as a determinant of the most critical limiting factor for species growing in a semi-desert region, namely soil moisture availability under drought conditions. Although the standard "texture classes" were too crude to distinguish soils associated with each vegetation type, the measured sand, silt and clay percentages were more informative. Soil texture is a key determinant of water stress, which in turn is more relevant than a simple "rainfall-based" assessment of aridity. In conclusion, CCA, as well as (or instead of) TWINSPAN and DCA, was a superior approach for identifying and explaining vegetation types. This supports the conclusions of Zhou et al. (2015) in their vegetation studies of Inner Mongolia. From a management perspective, the establishment of Parks in Jebel Marra has the potential to offer some "formal" protection of vegetation and wildlife, but this does not necessarily protect the local flora and fauna – especially when the tree plantations are of introduced species. The pressures of displaced refugees and a growing local population present an ongoing challenge, as addressing famine will, of necessity, take precedence over conservation initiatives. Finally, our methodology, especially the CCA approach, provides a solid quantitative baseline that can be used to track future patterns in vegetation, and we recommend that this method be applied, and that a monitoring survey be carried out at least every decade as a tool to guide adaptive land management policies and approaches.

Colonial, and later international interventions have had major impacts on the lives of the indigenous peoples of Darfur. The maintenance of upland terraces for agriculture was largely abandoned as forest reserves and forest plantations, established in the 1970s, often using non-native species, were created at the expense of bush-fallowed, terraced lands. In addition, farmers were persuaded to grow more cash crops on the piedmont and lowland valleys, rather than the staple food plants previously grown on the terraces (Ahmed 1982). More recently, a report by the United Nations Environment Program (UNEP 2007) pointed out the irony of the fact that the demand for building materials to create quarters for peacekeeping bases, displacement shelters and accommodation for UN staff has meant that valuable clay soils around the towns were dug up to make bricks for these dwellings, and over 52,000 trees a year have been harvested (the brick-making kilns are wood-fueled). Such observations illustrate the multifaceted local, national and international policy implications of the situation.

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Appendix I. Locations of the study sites in Western Darfur, Sudan, west of the Jebel Marra. Sites are grouped within each of three sample regions (Nertete, Zalingei, and Wadi Salih), indicated as N, Z and WS under "Region" in the table below. The sites occur along an elevation gradient classified in 100 m increments as follows; elevation zones are: 1 = 750–850 m.a.s.l.; 2 = 850–950 m.a.s.l.; 3 = 950–1,050 m.a.s.l.; 4 = 1,050–1,150 m.a.s.l. and 5 = >1,150 m.a.s.l. The sites also identified in terms of corresponding to different habitat types: SP: sandy plain; CP: clay plain; W: wadi; NS: North-facing slope; SS: south-facing slope (see Hegazy et al. 2019).

Site number	Location	Region	Habitat	longitude	latitude	Elevation	Zone
1	Gerei	Z	CP	12.80°N	23.32° E	842	1
2	Gerei	Z	CP	12.75°N	23.29° E	859	2
3	Garash	Z	CP	12.96°N	23.53° E	897	3
4	Garas	Z	W	12.95°N	23.48° E	904	2
5	Garas	Z	CP	13.00°N	23.54° E	912	2
6	Jebel Karadito	Z	SS	12.99°N	23.46° E	935	2
7	Jebel Karadito	Z	SS	13.01°N	23.44° E	950	2
8	Jebel Karadito	Z	SS	13.05°N	23.50° E	974	3
9	Wadi Aeba	Z	W	12.92°N	23.47° E	897	2
10	Wadi Aeba	Z	W	12.88°N	23.50° E	889	2
11	Sermi	Z	W	12.85°N	23.52° E	924	2
12	Sermi	Z	W	12.82°N	23.47° E	938	2
13	Jebel Sermi	Z	NS	12.82°N	23.54° E	964	3
14	Jebel Sermi	Z	NS	12.79°N	23.55° E	984	3
15	Jebel Sermi	Z	NS	12.78°N	23.57° E	1,009	3
16	Jebel Sermi	Z	SS	12.73°N	23.59° E	1,069	4
17	Jebel Sermi	Z	SS	12.70°N	23.61° E	1,084	4
18	Jebel Sermi	Z	SS	12.78°N	23.72° E	1,112	4
19	Jebel Sermi	Z	SS	12.81°N	23.69° E	1,126	4
20	Jebel Sermi	Z	NS	12.88°N	23.60° E	1,109	4
21	Jebel Banjadeed	Z	NS	12.63°N	23.30° E	924	2
22	Jebel Banjadeed	Z	NS	12.61°N	23.36° E	962	3
23	Jebel Banjadeed	Z	SS	12.50°N	23.42° E	940	2
24	Jebel Banjadeed	Z	SS	12.53°N	23.42° E	950	2
25	Jebel Banjadeed	Z	SS	12.61°N	23.43° E	966	3
26	Jebel Banjadeed	Z	SS	12.59°N	23.47° E	946	2
27	Jebel Banjadeed	Z	SS	12.58°N	23.52° E	940	2
28	Ghor Abundoboba	Z	W	12.59°N	23.58° E	911	2
29	Ghor Abundoboba	Z	W	12.62°N	23.57° E	902	2
30	Ghor Abundoboba	Z	W	12.65°N	23.56° E	887	2
31	Angeria	WS	SP	11.91°N	23.52° E	766	1
32	Angeria	WS	SP	11.82°N	23.42° E	775	1
33	Angeria	WS	SP	11.73°N	23.36° E	791	1
34	Jebel Karto	WS	SS	11.71°N	23.47° E	897	2
35	Jebel Karto	WS	SS	11.64°N	23.36° E	825	1
36	Segergerah	WS	CP	11.55°N	23.35° E	752	1
37	Segergerah	WS	CP	11.56°N	23.49° E	755	1
38	Segergerah	WS	CP	11.64°N	23.57° E	756	1
39	Segergerah	WS	CP	11.70°N	23.63° E	758	1
40	Brango	WS	SP	11.57°N	23.64° E	761	1
41	Brango	WS	SP	11.54°N	23.77° E	757	1
42	Gerei	Z	CP	12.81°N	23.26° E	829	1
43	Jebel Gerei	Z	SS	12.86°N	23.27° E	845	1
44	Jebel Gerei	Z	SS	12.90°N	23.30° E	873	2
45	Jebel Gerei	Z	SS	12.94°N	23.22° E	906	2
46	Jebel Nertete	N	NS	12.96°N	23.84° E	1,255	5
47	Jebel Nertete	N	NS	12.95°N	23.92° E	1,249	5
48	Jebel Nertete	N	NS	12.91°N	23.94° E	1,244	5
49	Jebel Nertete	N	NS	12.86°N	23.95° E	1,230	5
50	Jebel Nertete	N	NS	12.99°N	23.96° E	1,265	5
51	Jebel Nertete	N	SS	12.94°N	23.22° E	1,207	5
52	Jebel Nertete	N	SS	13.04°N	23.92° E	1,196	5

Appendix II. List of species recorded in the study of Jebel Marra.
Species are listed in Alphabetic order. Species featuring as dominants in one or more of the eight vegetation types that were distinguished are shaded. Species that are new records for the region are indicated with an asterisk. For more details on these new records, see Appendix III.

Acacia (now *Senegalia*) *mellifera* (Vahl) Benth.
Acacia nilotica (L.) Willd.
Acacia polyacantha Willd.
Acacia senegal (L.) Willd.
Acacia seyal Delile
Acacia sieberiana DC.
Acacia tortilis (Forssk.) Hayne
Acanthospermum hispidum DC.
Achyranthes aspera L.
Adansoni adigitata L.
Aeschynomene uniflora E. Mey.
**Ailanthus excelsa* Roxb.
Albizia antunesiana Harms
Albizia amara (Roxb.) Boivin
**Alternanthera sessilis* (L.) R.Br. ex DC.
Alysicarpus glumaceus (Vahl) DC.
Alysicarpus rugosus (Willd.) DC.
Alysicarpus vaginalis (L.) DC.
Amaranthus graecizans L.
Amaranthus hybridus L.
Amaranthus spinosa L.
Ammannia senegalensis Lam.
Ampelocissus africana (Lour.) Merr.
Andropogon gayanus Kunth
Andropogon schirensis Hochst. A Rich.
Anogeissus leiocarpus (DC.) Guill&Perr.
Aristida adscensionis L.
Aristida hordeacea Kunth
Arachis hypogaea L.
Asparagus africanus Lam.
Aspilia kotschyi (Sch. Bip. ex Hochst.) Oliv.
**Asteracantha longifolia* (L.) Nees
Azanza garckeana (F.Hoffm.) Exell & Hillc.
Balanites aegyptiaca L.
Bauhinia rufescens Lam.
Bauhinia thonningii (Schumach.) Milne-Redh.
Bidens bipinnata L.
Bidens pilosa L.
Bidens schimperi Sch. Bip. ex Walp.
**Blainvillea acmella* (L.) Philipsons
Blepheris linariifolia Pers.
Blepheris maderaspatensis (L.) B. Heyne ex Roth
**Boerhavia erecta* L.
Boscia senegalensis (Pers.) Lam.
Brachiaria deflexa (Schumach.) C. E. Hubb. ex Robyns
Brachiaria ramosa (L.) Stapf
Bulbostylis coleotricha (Hochst. ex A.Rich.) C.B.Clarke
Cadaba farinose Forssk.
Capparis sepiaria L.
Cardiospermum halicacabum L.
Carica papaya L.
Cassia absus L.
Cassia angustifolia Vahl
Cassia mimosoides L.
Cassia nigricans Valh
Cassia obtusifolia L
Cassia occidentalis (L.) Link.
Celosia argentea L.
Celosia trigyna L.

(*continued*)

Chloris gayana Kunth
Chloris pilosa Schumach. &Thonn.
Chloris virgata Swartz.
Cissus quadrangularis L.
Citrullus lanatus (Thunb) Mansf.
Clematis hirsute Perr. &Guill.
Cleome monophylla L.
Coccinia adoensis (A. Rich.) Cogn
Coccinia grandis (L.) Voigt
Combretum glutinosum Perrot. ex DC
Combretum molle R. Br. ex G. Don
Commelina africana L.
Commelina benghalensis L.
Commelina forskaolii Vahl.
Commelina kotschyi Hassk.
Commicarpus africanus Dandy
Commiphora africana (A. Rich.) Engl.
Conyza stricta Willd.
Corallocarpus schimperi (Naudin.)Hook. F.
Corchorus trilocularis L.
Corchorus olitorius L.
Cordia africana Lam.
Coriandrum sativum L.
Crotalaria atrorubens Hochst. Ex Benth.
Crotalaria goreensis Guill. &Perr
Crotalaria laburnifolia L.
Crotalaria naragutensis Hutch.
Crotalaria podocarpa DC.
Crotalaria spinosa Hochst. exBenth.
Croton lobatus L.
**Ctenolepis cerasiformis* (Stocks) Hook. f.
**Cucumis prophetarum* L.
Cucurbita moschata Duchesne
Cymbopogon caesius (Hook&Arn.) Stapf
Cynodon dactylon (L.) Pers.
Cyperus alopecuroides Rottb.
Cyperus laevigatus L.
Cyperus longus var. *pallidus* Boeckeler
Cyperus rotundus L.
Cyperus sulcinux Chake.
Cyphostemma serpens (Hochst. ex A.Rich.) Desc.
Dactyloctenium aegyptium (L.) Willd.
Dalbergia melanoxylon Guill. &Perr.
**Dalbergia sissoo* Roxb.ex DC.
Datura stramonium L.
**Desmodium ospriostreblum* Steud ex A. Rich.
Dichrostachys cinerea var. africana Brenan &Brummitt
Digitaria ciliaris (Retz.) Koeler
Diospyros mespiliformis Hochst.ex A. DC.
Dolichos trilobus L.
Echinochloa colona (L.) Link
Echinochloa pyramidalis (Lam.) P. Beauv.
Eleusine indica (L.) Gaertn.
Emilia abyssinica (Sch. Bip. ex A. Rich.) C. Jeffrey
Eragrostis tremula (Lam.) Hochst. ex Steud.
Eragrostis aspera (Jacq.) Nees
Eragrostis viscosa (Retz.) Trin.
Eruca sativa L.
Ethulia conyzoides L.
Eucalyptus camaldulensis Dehuh.
Euphorbia heterophylla L.
Euphorbia hirta L.
**Euphorbia tircucalli* L.
Evolvulus alsinoides (L.) L.

(*continued*)

Faidherbia albida (Delile) A.Chev.
Farsetia longistyla Baker. F.
Farsetia stenoptera Hochst.
Ficus salicifolia Vahl
Ficus sycomorus L.
Gardenia ternifolia subsp. *jovis-tonantis* (Welw.) Verdc.
Grewia bicolor Juss.
Grewia flavescens Juss.
Grewia villosa Willd.
Guizotia scabra (Vis.) Chiov.
Gynandropsis gynandra (L) Briq.
Heteropogon contortus (L.) P. Beauv.
Hibiscus cannabinus L.
Hibiscus diversifolius Jacq.
Hibiscus micranthus L.f.
Hibiscus sabdariffa L.
Hyparrhenia hrita (L.) Stapf
Hypoestes forskalei (Vahl) Sol. ex Roem. &Schult.
Hyptis pectinata (L.) Poit.
Indigofera arrecta Hochst. ex A. Rich.
**Indigofera astragalina* DC.
Indigofera hochstetteri Baker
**Indigofera nummulariifolia* (L.) Livera. ex Alston
Indigofera parviflora Heyne ex Wight & Arm.
Indigofera stenophylla Guill. &Perr.
Ipomoea aquatica Forssk.
Ipomoea dichroa Hochst. ex Choisy
Ipomoea carnea Jacq.
Ipomoea coscimosperma Hochst. ex Choisy
Ipomoea eriocarpa R. Br.
Ipomoea obscura (L.) Ker Gawl.
Ipomoea biflora (L.) Pers**.**
Ipomoea vagans Baker
**Justicia heterocarpa* T. Anderson
Justicia striata (Klotzsch) Bullock
**Justicia flava* (Vahl) Vahl
Khaya senegalensis (Desr.) A. Juss.
Kedrostis gijef (J. F. Gmel.) C. Jeffrey.
Kickxia aegyptiaca (L.) Nābélck.
Kohautiaca espitosa Schinzl.
Kyllinga ferniifolius (Hend.) Dandy
Kyllinga monocephala Rottb.
Lagenearia siceraria (Molina) Standley.
Lannea fruticosa (Hochst. ex A. Rich.) Engl.
Lantana camara L.
Leonotis nepetifolia (L.) Aiton f.
Leucas martinicensis (Jacq.) Aiton f.
Ludwigia stolonifera (Guill. &Perr.) P.H.Raven
Ludwigia octovalvis (Jacq.) P.H.Raven
Luffa cylindrica L.M.Roem.
Malus sylvestris Mill.
Malva verticillata L.
Mangifera indica L.
Melhania velutina Forssk.
Melothria puntata (Thunb.) Cogn.
Merremia aegyptia (L.) Urb.
Merremia pinnata (Hochst. ex Choisy) Hallier f.
Mirabilis jalapa L.
Mitracarpus scaber Zucc.
Monechma ciliatum (Jacq.) Milne-Redh.
Monsonia senegalensis Guill. &Perr.
Newbouldia laevis (P. Beauv.) Seem.
Nicandra physalodes (L.) Gaertn.
Ocimum bacilicum L.

(*continued*)

Ocimum gratissimum L. subsp. *gratissimu*m
Oldenlandia corymbosa L.
Oldenlandia echinulosa K. Schum.
Oldenlandia herbacea (L.) Roxb.
Oxygonum sinuatum (Meisn) Dammer
Panicum maximum Jacq.
Panicum repens L.
Pavetta gardeniifolia Hochst ex A. Rich. var. *gardeniifo*lia
Pennisetum glaucum (L.) R. Br.
Pennisetum pedicellatum Trin.
Pennisetum polystachion (L.) Schult.
Pennisetum sieberianum Stapf & C.E. Hubb.
Peristrophe paniculata (Forssk.) Brummitt
Phragmates australis Trin. ex Steud.
Phyllanthus maderaspatensis L.
Phyllanthus reticulatus Poir.
Physalis angulata L.
**Plectranthus candelabriformis* Launert
Plumbago zeylanica L.
Polycarpaea eriantha Hochst. ex A. Rich.
Polygala erioptera DC.
Polygonum salicifolium Willd.
Psidium guajava L.
Pulicaria crispa (Forssk.) Benth. & Hook. f. Oliv. &Hiern.
Punica granatum L.
Pupalia lappacea (L.) Juss.
Reichardia tingitata (L.) Roth.
Rhynchelytrum repens (Willd.) C. E. Hubb.
Rhynchosia malacophylla (Spreng.) Bojer
Ricinus communis L.
Rogeria adenophylla J. Gay ex Delile
**Rothia hirsuta* (Guill. &Perr.) Baker
Schizachyrium exile (Hochst.) Pilger
Schoenefeldia gracilis Kunth
Sclerocarpus africanus Jacq.
Sclerocarya birrea (A. Rich.) Hochst.
Scoparia dulcis L.
Senna occidentalis (L.) Link
Sesamum alatum Thonn.
Sesamum angustifolium (Oliv.) Engl.
Sesamum indicum L.
Sesbania rostrata Bremek. &Oberm.
Setaria pumila (Poir.) Roem. &Schult.
Setaria verticillata (L.) P. Beauv.
Sida alba L
Sida ovata Forssk.
Solanum incanum L.
Solanum nigrum L.
Sorghum dura L.
Sorghum sudanense (Piper) Stapf
Spermacoce chaetocephala DC.
Spermacoce radiata (DC.) Hiern.
Spermacoce stachydea DC.
Sporobolus cordofanus (Hochst. ex Steud.) Coss.
Sporobolus pyramidalis P. Beauv.
Sporobolus welwitschii Rendle
Striga hermonthica (Delile) Benth.
Stylosanthes fruticosa (Retz.) Alston
Tamarindus indica L.
Tapinanthus globifer (A.Rich.) Tiegh
Tephrosia bracteolata Guill. &Perr.
Tephrosia uniflora Pers.
Teramnus labialis (L.f.) Spreng.
Terminalia brownii Fresen.

(*continued*)

Tetrapogon cenchriformis (A. Rich.) W. D. Clayton
Tithonia rotundifolia (Mill.) S. F. Blake
**Trichodesma africanum* (L.) Lehm.
Triumfetta annua L.
Triumfetta rhomboidea Jacq.
Urginea altissima (L.f.) Baker.
Urginea indica (Roxb.) Kunth.
Vangueria venosa (Hochst.) Sond.
Verbascum sinaiticum Benth.
Vernonia amygdalina Delile
Vetiveria nigritana (Benth.) Stapf
Vigna senensis (L.) Endl.
Waltheria indica L.
Wissadula rostrata (Schumach.) Planch.
Withania somnifera (L.) Dunal.
Xanthium pungens Waller.
Xanthium strumarium L.
Xanthosoma violaceum Schott.
Zaleya pentandra (L.) Jeffrey
Ziziphus abyssinica Hochst.ex A. Rich.
Ziziphus spina-christi (L.) Desf.
Zornia glochidiata Rchb ex DC.

Appendix III. Species identified that represent new records for the flora of the study area.
The species family, life form, bioregion of origin (chorotype) and known uses are also noted. Species already established as dominant species in one of our eight vegetation types are shaded, and the vegetation type is indicated in parentheses. For more details on indigenous uses of wild-collected plants see Hegazy et al. (2020).

Species	Family	Life Form	Bioregion (origin)	Uses
Ailanthus excelsa Roxb	Simaroubaceae	Perennial	India	Animal fodder
Alternanthera sessilis (L.) R.Br. ex DC	Amaranthaceae	Annual	South America	Food, medicine, weed of sugar cane
Asteracantha longifolia (L.) Nees (IV)	Acanthaceae	Annual	India	Food, medicine
Blainvillea acmella (L.) Philipson. (VII)	Asteraceae	Annual	Paleotropical	Medicine, dyes
Boerhavia erecta L.	Nyctaginaceae	Annual	Tropical America	Eaten, grazed
Ctenolepis cerasiformis (Stocks) Hook. F.	Cucurbitaceae	Annual	Africa	Medicine
Dalbergia sissoo Roxb.ex DC.	Papilionoideae	Perennial	S. Iran and India	Timber
Desmodium ospriostreblum Chiov.	Papilionoideae	Annual	Tropical	Livestock forage and cover crop
Indigofera astragalina DC	Papilionoideae	Annual	Paleotropical	Fodder, medicine
Indigofera nummulariifolia (L.) Livera.	Papilionoideae	Annual	Paleotropical	Forage, medicine, dye
Justicia flava (Vahl.) Vahl.	Acanthaceae	Annual or Perennial	Pan-African	Medicine
Justicia heterocarpa T. Anderson	Acanthaceae	Annual	Afro-Tropical	Food (leaves)
Plectranthus candelabriformis Launert.	Lamiaceae	Perennial	Zambia-Namibia	Food, Medicine
Rothia hirsuta (Guill. & Perr.) Baker (IIIb)	Papilionoideae	Annual	Paleotropical	Medicine
Trichodesma africanum (L.) Lehm.	Boraginaceae	Annual or short-lived Perennial	Ethiopia	Medicine
Cucumis prophetarum L.	Cucurbitaceae	Perennial	Tropical Africa	Food, medicine
Euphorbia tircucalli L.	Euphobiaceae	Perennial		Medicine, hedge (stabilizing sandy soils), fuel