Plant communities and reproductive phenology in mountainous regions of northern Libya

Ahmad K. Hegazy, Hanan F. Kabiel, Saud L. Al-Rowaily, Lesley Lovett-Doust & Abd El-Nasser S. Al Borki

Journal of Forestry Research

ISSN 1007-662X
Volume 28
Number 4

J. For. Res. (2017) 28:741-761
DOI 10.1007/s11676-016-0345-8

J. For. Res. (2017) 28(4):741–761
DOI 10.1007/s11676-016-0345-8

ORIGINAL PAPER

Plant communities and reproductive phenology in mountainous regions of northern Libya

Ahmad K. Hegazy[1] · Hanan F. Kabiel[1] · Saud L. Al-Rowaily[2] · Lesley Lovett-Doust[3] · Abd El-Nasser S. Al Borki[4]

Received: 22 November 2015 / Accepted: 18 July 2016 / Published online: 16 December 2016

Abstract Within the semi-desert landscape of northern Libya, two sub-humid escarpments occur: Al-Akhdar in the east and Nafusa (Jabal Al-Gharbi) in the west. This study compares plant communities in the two regions, which are along an elevation gradient, in terms of species composition and diversity, frequency of different Raunkiaer life forms, and reproductive phenology. The two regions differed in species composition and life-form frequency between regions and between elevation zones within each region. Patterns were associated with the lower rainfall and lower moisture-holding capacity of soils at Nafusa, resulting in more xeric conditions. Only 13% of species were shared between the two regional landscapes. Species diversity, life-form frequency, and duration of the flowering–fruiting phenophase were all affected by elevation above sea level. The duration of flowering and fruiting in spring and fall was associated with environmental conditions, although there were different thresholds in the two regions. There was both a spring and fall episode of flowering at Nafusa, but only spring flowering at Al-Akhdar. It is anticipated that there will be a gradual shift of plant communities to higher elevations and loss of certain sensitive species in response to ongoing climate change.

Keywords Altitudinal gradient · Raunkiaer life forms · Reproductive phenology · Southern Mediterranean

Project funding: The project was funded by Libyan Missions Department and Cairo University.

The online version is available at http://www.springerlink.com.

Corresponding editor: Hu Yanbo

✉ Ahmad K. Hegazy
hegazy@sci.cu.edu.eg

1 Department of Botany and Microbiology, Faculty of Science, Cairo University, Giza 12613, Egypt

2 Department of Plant Production, College of Food and Agricultural Sciences, King Saud University, Riyadh, Saudi Arabia

3 Department of Biology and Chemistry, Nipissing University, North Bay, ON, Canada

4 Department of Botany, Faculty of Sciences and Arts, University of Benghazi, Agdabia, Libya

Introduction

More than 90% of Libya is an arid desert ecosystem. Two elevated regions, approximately 1200 km apart, occur inland of the Mediterranean coastal plain: The Al-Akhdar mountains in the east and the Nafusa mountains in the west (Al-Idrissi et al. 1996). These two limestone escarpments lie within a sub-humid climatic zone where Saharo-Arabian and Mediterranean phytogeographic elements contribute most of the local flora (Brullo and Furnari 1981; Feng et al. 2013). Ben-Mahmoud et al. (2000) have described a pattern of increasing desertification since the last half of the twentieth century where soils and vegetation cover have become degraded due to climate change. One goal of the present study was to characterize the present vegetation and environmental conditions in each of these regional landscapes as a baseline for tracking vegetation responses to climate change in the future.

Raunkiaer (1934) developed a system for characterizing plant life forms in terms of where dormant buds are located relative to the surface of the soil during the season with adverse conditions. Although earlier applications were in the context of Northern Europe, where the adverse season was winter, with low solar irradiance and temperatures often below 0 °C, the approach is also readily applied in other climatic zones where the adverse season might be the time when conditions are particularly hot and dry (e.g., Hegazy and Lovett-Doust 2016). Raunkiaer also recognized that the same species, if it had a wide distribution, might be classified as different life forms in different parts of its range. Lovett-Doust (1981a, b) showed that detailed structure of a particular life form (in this case in terms of the length of internodes in the "stoloniferous" hemicryptophyte and common European weed, *Ranunculus repens*) might also differ between locally adapted ecotypes.

The major life forms present in a plant community reflect the adaptation and/or response of species to environmental constraints, and may be used to track environmental change (Arnold 1955). Hadar et al. (1999) suggested that classification of vegetation into particular functional groups, based on phylogeny and life forms can also be used to demonstrate plant community responses to anthropogenic disturbance. Likewise, Lavorel et al. (1997, 1999) showed that species composition and life-form patterns were sensitive to disturbance. These authors focused on within-species variations in life-form and functional traits, such as plant height and seed weight, in interpreting responses to disturbance. In the present study, we consider community-level patterns and characterize the relative abundance of different life forms in different elevation zones.

The timing of flowering and reproduction is one of the most significant phenological indicators of sensitivity to climatic change (Spano et al. 1999; Hegazy and Lovett-Doust 2016), which is the time when individual plant species flower, which is determined by both genetic and environmental factors (Fitter et al. 1995; Liu et al. 2014). Climatic factors play a major role in flowering, especially in temperate and cool climates (Walkovszky 1998; Tyler 2001). Three factors known to initiate onset of flowering include temperature, photoperiod, and rainfall (e.g., Rathcke and Lacey 1985; Hegazy et al. 2012). Studies on projected climate change predict progressively warmer and drier conditions in the Mediterranean basin over the next few decades (IPCC 2001; Hegazy et al. 2008). These seem likely to induce further changes in flowering phenology. As a result, species lacking phenological flexibility may experience greater stress, even local extinction because of the changing climate (Bradley et al. 1999).

Plant-community composition is the result of various abiotic and biotic processes acting on individuals within plant populations (Lavorel and Garnier 2002; Sundqvist et al. 2013; Kichenin et al. 2013). In a changing environment, environmental variables may act as selective filters on species composition and life-form patterns, and may explain particular local species assembly, selected from the regional species pool (Bradley et al. 1999; Lavorel and Garnier 2002; Read et al. 2014). Such changes begin at the species level, where phenotypic plasticity may be sufficient for one species to cope with a changing environment, while other species may be subject to strong directional selection for traits that allow persistence; some species may even go extinct (Valladares et al. 2007; Matesanz et al. 2010; Bellard et al. 2012).

In the present study, we explore variation in plant-community composition and reproductive phenology in the eastern and western mountainous landscapes of northern Libya, emphasizing the similarities and differences between the two landscapes. Our goal is to characterize the community context within a warming environment as a reference point for future studies. We will: (1) compare the plant communities in Al-Akhdar and Nafusa at the level of species composition and diversity, life-form frequency, and reproductive phenology; (2) study the relationship between soil and climate, and community structure and reproductive phenology; and (3) evaluate the effect of elevation and distance from the sea on these plant communities.

Materials and methods

Study sites

The two study regions, Al-Akhdar and Nafusa, are in northern Libya, close to the coastal plain. They are steep escarpments cut by deep wadis flowing toward the sea that are quite prone to landslides (Al-Idrissi et al. 1996). The Al-Akhdar region, also known as "The Green Mountain" or Al-Jabal Al-Akhdar, in Arabic, is in the northeast, and is composed of marine limestone sediments dating to the Paleozoic and Neogene. The Nafusa region, also known as The Western Mountain or Al-Jabal Al-Gharbi, in Arabic, is located in the northwest, and is composed of older marine sediments including limestone and sandstone from the Mesozoic.

A total of 32 stands in Al-Akhdar, and 17 in Nafusa, each 300 m × 300 m, were investigated (Fig. 1; Table 1). Within each stand, the vegetation was investigated using five randomly placed quadrats (each 10 m × 10 m). Sites in each region were classified as being in one of three elevation zones: the lower zone (zone A) = <200 m above sea level (a.s.l.); a middle or intermediate zone (zone B) = 200–400 m a.s.l.; and an upper zone (zone C) = >400 m a.s.l. (Fig. 1; Table 1).

Soil and climate

Physical and chemical properties of the soil in each stand were investigated by taking three replicate cores from the top 20 cm of the soil profile. The pooled samples from each stand were air dried and then sieved through a 2 mm screen prior to further analysis (Jackson 1973; Allen et al.

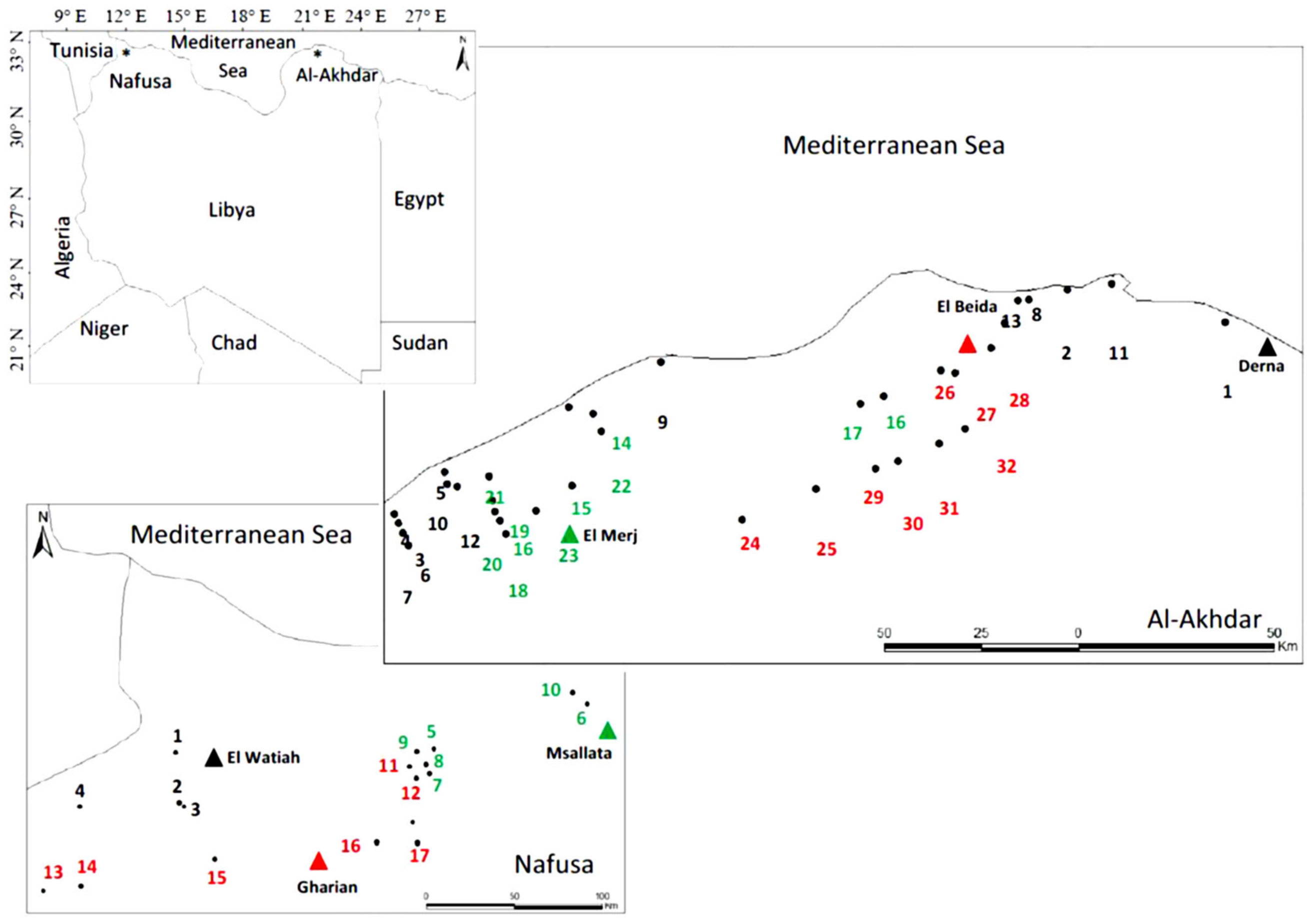

Fig. 1 Locations of the study sites in the Al-Akhdar and Nafusa regions. See Table 1 for further details. Sites are indicated as follows: *black numbers* indicate elevation zone A (<200 m a.s.l.), *green numbers* indicate elevation zone B (200–400 m a.s.l.), and *red numbers* indicate elevation zone C (>400 m a.s.l.). The locations of corresponding climate stations are indicated by *solid triangles*, with *black* for zone A, *green* for zone B and *red* for zone C

1974). Soil texture was determined by matching a sample to the Soil Texture Triangle. Mineral ion concentrations were determined using atomic absorption spectrophotometry (Varian, spectra AA220, Palo Alto, California, USA). Soil organic matter (OM) was determined by the loss of mass on ignition method.

Climate data were obtained from six weather stations, chosen to match with the three elevation zones (A, B, and C, described above), and located across the two study regions (see Fig. 1 for locations). In Al-Akhdar, these were at: Derna (30 m a.s.l.), El Merj (325 m a.s.l.), and El Beida (593 m a.s.l.). In Nafusa, the weather stations were at: El Watiah (88 m a.s.l.), Msallata (213 m a.s.l.) and Gharian (694 m a.s.l.). Mean values for monthly temperatures and rainfall recorded over a 7-year period (2006–2012) were used (LNMC 2012).

Species composition

A species list was developed for each stand following Jafri and El-Gadi (1977–1993) and Boulos (1999–2005, 2009) to confirm identifications. Voucher specimens of all recorded plant species were collected, identified, and deposited in the Cairo University Herbarium (CAI), and at Bani Ghazi (Benghazi) University. For each species, its presence or absence in each of the three elevation zones within a region was noted. The density, frequency, and percentage of individuals in each species were recorded, and the importance value (relative density + relative frequency + relative cover) for each species and for each site were calculated. These data were used to calculate the mean importance value for each species for each elevation zone (see too Hegazy et al. 2011).

Raunkiaer life forms

In each study site, each plant species found in the quadrats in each elevation zone. In each region, they were recorded as belonging to one of the following life forms: phanerophyte, chamaephyte, hemicryptophyte, geophyte, and therophyte. The relative contribution of each life form, at each site, was calculated.

Table 1 Locations of the study sites within the Al-Akhdar and Nafusa mountainous regions, along an elevation gradient

Stand	Zone	E	D	GPS locations		Site
Al-Akhdar						
1	A	2	1.47	32°51′24.9″N	22°24′14.4″E	Susa–Derna
2	A	3	0.74	32°54′19.9″N	22°02′12.0″E	Susa–Derna
3	A	6	5.88	32°32′57.2″N	20°41′13.0″E	Barce
4	A	7	4.41	32°27′12.3″N	20°42′59.5″E	Barce
5	A	11	2.94	32°31′16.2″N	20°44′50.4″E	Tocra–Al Bakur
6	A	33	8.82	32°31′13.5″N	20°43′52.7″E	Barce
7	A	36	11.76	32°32′14.9″N	20°43′35.0″E	Barce
8	A	36	2.21	32°53′11.6″N	21°56′54.8″E	Shahat–Susa
9	A	48	1.47	32°45′51.2″N	21°05′48.4″E	Derisia (Talmeta)
10	A	74	5.88	32°31′12.9″N	20°40′39.1″E	Tocra–Al Bakur
11	A	96	2.21	32°55′01.4″N	22°08′20.3″E	Susa–Derna
12	A	160	7.35	32°32′14.9″N	20°41′35.6″E	Tocra–Al Bakur
13	A	193	2.21	32°53′01.9″N	21°55′20.2″E	Shahat–Susa
14	B	237	7.35	32°39′50.2″N	20°56′22.3″E	Derisia (Talmeta)
15	B	287	20.59	32°31′19.9″N	20°53′29.5″E	El Merj
16	B	302	20.59	32°30′04.1″N	20°43′40.4″E	Wadi El Akar
17	B	310	19.12	32°41′15.0″N	21°33′48.6″E	Wadi El Kouf
18	B	317	23.53	32°42′24.0″N	21°34′38.4″E	Wadi El Kouf
19	B	317	13.24	32°29′40.1″N	20°43′48.4″E	Wadi El Akar
20	B	325	19.12	32°29′55.0″N	20°43′41.7″E	Wadi El Akar
21	B	325	7.35	32°29′45.9″N	20°43′44.8″E	Wadi El Akar
22	B	325	13.24	32°31′18.5″N	20°45′38.8″E	Tocra–Wadi El Akar
23	B	350	19.12	32°38′24.5″N	20°57′19.6″E	Derisia (Talmeta)
24	B	371	39.71	32°29′42.9″N	20°46′04.1″E	Wadi El Akar–El Merj
25	C	435	33.82	32°27′02.7″N	21°17′08.4″E	Marawa–El Merj
26	C	448	23.53	32°28′59.0″N	21°06′19.4″E	Marawa–El Merj
27	C	529	38.24	32°30′55.8″N	21°27′20.1″E	Slonta
28	C	551	14.71	32°44′36.5″N	21°45′53.5″E	Wadi El Gharega
29	C	567	35.29	32°44′32.1″N	21°46′39.0″E	Wadi El Gharega
30	C	646	36.76	32°47′28.7″N	21°51′04.0″E	El Beda–Shahat
31	C	675	44.12	32°33′19.3″N	21°35′32.3″E	Slonta
32	C	738	35.29	32°34′14.6″N	21°38′46.2″E	Slonta
Nafusa						
1	A	89	135	32°20′23.7″N	11°45′34.7″E	Wadi El Watiah
2	A	142	162.5	32°07′34.3″N	11°46′31.3″E	Wadi El Watiah
3	A	149	170	32°07′04.4″N	11°46′28.2″E	Wadi El Watiah
4	A	199	210	32°06′26.8″N	11°16′05.8″E	Nalut–Teji
5	B	289	95	32°17′31.5″N	13°01′48.4″E	Abu Ghilan (Gharian)
6	B	289	40	32°36′41.6″N	13°50′07.4″E	El–Shaffine (Msallata)
7	B	329	115	32°16′51.7″N	13°02′02.3″E	Abu Ghilan (Gharian)
8	B	354	105	32°16′42.2″N	13°02′07.4″E	Abu Ghilan (Gharian)
9	B	380	90	32°17′35.1″N	13°01′29.4″E	Abu Ghilan (Gharian)
10	B	380	35	32°36′35.4″N	13°50′07.1″E	El–Shaffine (Msallata)
11	C	402	105	32°16′28.3″N	13°02′09.8″E	Abu Ghilan (Gharian)
12	C	589	115	32°15′15.1″N	13°02′08.5″E	Abu Ghilan (Gharian)
13	C	592	295	31°45′10.6″N	11°04′55.5″E	Gharian–Nalut
14	C	636	290	31°46′24.8″N	11°16′30.6″E	Gharian–Nalut

Table 1 continued

Stand	Zone	E	D	GPS locations		Site
15	C	657	200	31°53′21.3″N	11°57′20.8″E	Gharian–Nalut
16	C	754	170	31°57′31.4″N	12°46′41.8″E	Gharian–Nalut
17	C	756	170	31°57′22.1″N	12°59′19.7″E	Gharian–Mizda

Low elevation (zone A) = <200 m a.s.l.; mid-elevation (zone B) = 200–400 m a.s.l.; high elevation (zone C) = >400 m a.s.l

E elevation in meters above sea level; *D* distance in km from the Mediterranean

Reproductive phenology

Seasonal and spatial patterns of reproductive phenology, from the beginning of flowering to the start of seed dispersal, were recorded in different elevation zones and in the two regions. At the community level, the duration and timing of the flowering–fruiting phenophase in each elevation zone and in each region was recorded. The proportion of species that were flowering or fruiting was noted each month so that it could be examined in light of the corresponding monthly rainfall and temperature patterns at the appropriate reference weather station (located in the same region and in the same elevation zone). The length of the flowering–fruiting stage was classified as short (<3 months), medium (3–6 months) or long (>6 months).

Data analysis

The mean importance value for each species, in each of the elevation zones, was calculated. The Shannon diversity index (H-index) was also calculated for each elevation zone (Wang et al. 2002; Hegazy et al. 2011). To investigate the possible influence of elevation, distance from the sea, and the location of the two mountain regions on the study parameters, a five randomly placed quadrats a generalized linear model were constructed. The independent variables identified were elevation above sea level (low, mid, and high elevation zones); distance from the sea (classified into two categories, d = ≤35 km from the sea and D = >35 km from the sea); and region (1 = Al-Akhdar and 2 = Nafusa). The latter two variables were used only for overall analysis of pooled data from both regions. The effect of interactions among independent variables was not assessed due to insufficient data, but it might be anticipated that sites that were farther from the sea might tend to be at higher elevations. Within each region, the effect of elevation was also considered.

To test the effect of independent variables on the distribution of life forms (number of species belonging to each life form and the percentage contribution of each life form in each altitudinal zone), a generalized linear models (GLMs)—assuming a Poisson distribution and using a log link function (Zuur et al. 2010)—were used because of the nature of the data (count data with a lot of zero values). Because there were very few examples of the "geophyte" life form (there were only five geophyte species at Al-Akhdar, and they were absent entirely from the quadrats at Nafusa) this life form was excluded from the model. Spearman's rank correlation coefficient was used to explore correlations between life forms and both soil and climate parameters.

Results

Soil and climate variables

Soil texture in the Al-Akhdar region showed more silt (33.3–39.7%), clay (24.5–38.9%) and fine-grained sands (15.3–48.7%), and less coarse sands than were seen in the Nafusa region (6.03–9.2% Fig. 2a). Looking at each site individually, most of the Al-Akhdar sites were in the range of loam to clay loam (see Fig. 3). In contrast, soils in the Nafusa region were almost all sandy loams (with silt comprising 17.8–20.06%, clay at 12.07–14.5%, fine sands at 45.8–49.8%, and coarse sand at 15.4–20.2%, Figs. 2d, 3). The differences in soil texture are most marked at low and high elevations (Zones A and C, Fig. 2a, d). Within a region, the only significant difference was at Al-Akhdar, where there was significantly less fine sand in zone C (15.35) compared to other zones (36.5 and 48.7% in zones A and B respectively, Figs. 2a, d, 3).

Soil organic matter (OM) content was more than five times greater at Al-Akhdar than Nafusa, in all elevation zones. The highest recorded OM content (6.64%) was in zone C at Al-Akhdar, whereas the highest value noted in Nafusa was 1.19% in elevation zone B (Fig. 2b, e). At Nafusa, zone A had a significantly lower OM content than the other zones in that region, but at Al-Akhdar the OM content did not change significantly with elevation.

Chemical analysis of the soil showed that iron content at Al-Akhdar ranged from 12.7 ± 4.9 to 14.2 ± 4.9 ppm. This was significantly greater than that at Nafusa, where iron content ranged from 2.24 ± 0.44 to 3.84 ± 0.97 ppm) in the three elevation zones (Fig. 2c, f). Significantly greater values of calcium in zone B (93.2 ± 24.11 ppm), and sodium in zone A (41.4 ± 11.91 ppm) were noted at

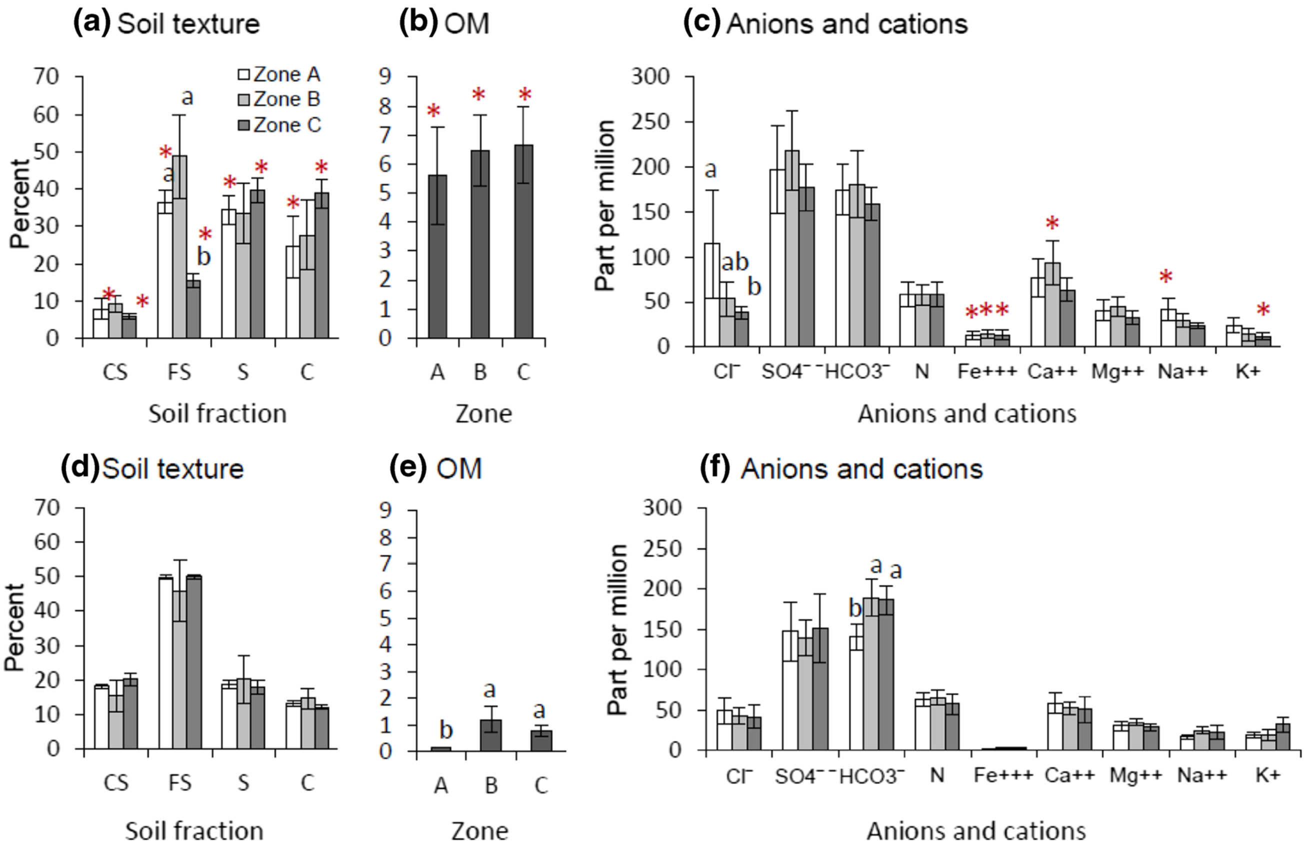

Fig. 2 Soil analysis for different altitudinal zones within the Al-Akhdar (**a**, **b**, and **c**) and Nafusa (**d**, **e**, and **f**) regions. Altitudinal zones are: *A* <200 m a.s.l.; *B* 200–400 m a.s.l.; *C* >400 m a.s.l. Soil fractions are: *CS* coarse sand; *FS* fine sand; *S* silt; C = clay. *OM* organic matter. The anions and cations assessed were: Cl^- = Chloride; SO_4^{2-} = Sulphate, HCO_3^- = Bicarbonate, N = Nitrogen = , Fe^{3+} = Iron, Ca^{2+} = Calcium, Mg^{2+} = Magnesium, Na^+ = Sodium, K^+ = Potassium. Differences among zones for the same parameter are not significant at P ≤ 0.05 unless otherwise indicated. A *star* above a histogram bar (**a**, **b**, or **c**) would indicate a significant difference between regions for the same parameter at P ≤ 0.05

Al-Akhdar, compared to Nafusa. Meantime, significantly higher values of potassium (32.06 ± 9.33 ppm) were found in zone C at Nafusa, than in zone C at Al-Akhdar (11.73 ± 3.91). With these exceptions (above), anion and cation content did not differ significantly between elevation zones within a region. Exceptions include chloride, which is significantly higher in concentration at lower elevations, closer to the sea, at Al-Akhdar; and bicarbonate, which is significantly lower at lower elevations, at Nafusa.

In both regions, rainfall increases significantly, and average temperatures decrease with elevation. The Al-Akhdar region receives a greater total annual rainfall (266–490 mm) with less variation between elevation zones (CV = 0.12–0.25) than in Nafusa, which has 124–287 mm rainfall with a CV of 0.31–0.43 (Fig. 4a). At Al-Akhdar, mid-elevations were more variable in terms of rainfall, whereas at Nafusa both low and higher elevations showed more variability (Fig. 4a). At matched elevations, slightly lower monthly temperatures were recorded at Al-Akhdar (16.69–20.02 °C) compared to Nafusa (ranging from 18.95 to 20.72 °C), but the coefficient of variation at Al-Akhdar was greater at high elevations (Fig. 4b).

Species composition and distribution

Only 16 species (of 76 at Al-Akhdar, and 64 at Nafusa) were shared by the two regions: *Cistus parviflorus*, *Avena barbata*, *Cichorium spinosum*, and *Pinus halepensis,* which were more widely distributed at Al-Akhdar, and *Retama raetam*, *Thymus capitatus*, *Periploca angustifolia* and *Stipa arabica*, which had greater importance values and wider elevational distribution at Nafusa (Tables 2, 3). The shared species belong to each of the Raunkier life form groups except the following geophytes: six phanerophytes, four chamaephytes, three hemicryptophytes, and three therophytes.

The species list for each region can be divided into three categories: (1) locally common species recorded at all three elevations, (2) species restricted to two of the three elevation zones; and (3) species restricted to one elevation zone (Tables 2, 3).

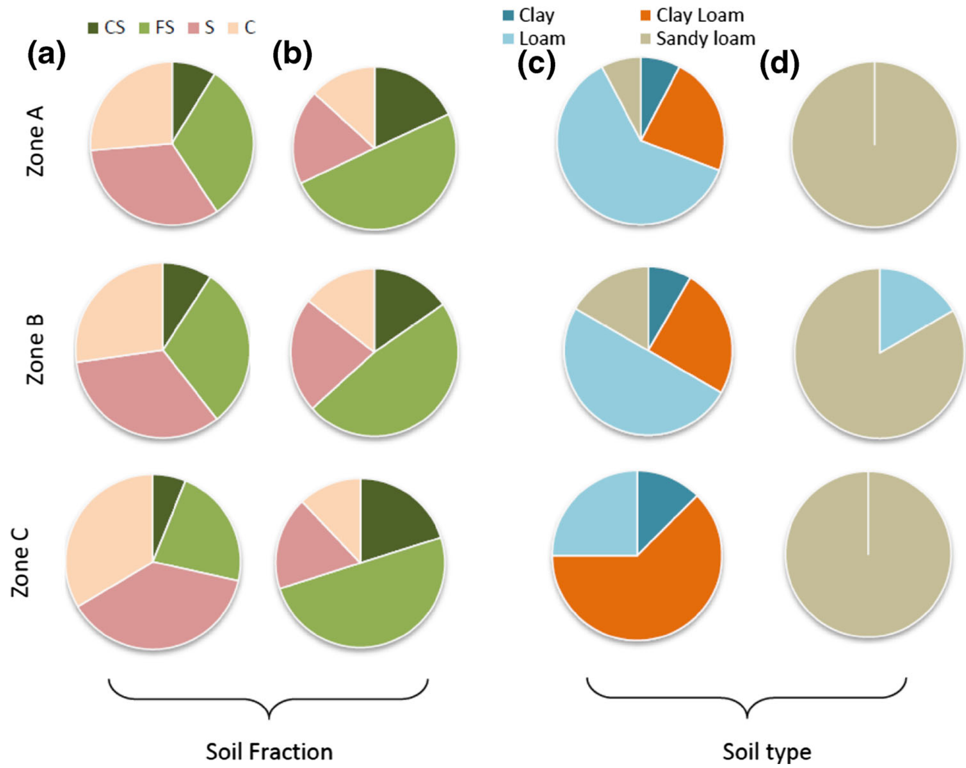

Fig. 3 Percent contribution of soil fractions (**a** and **b**) and percent contribution of soil types (**c** and **d**) in the study sites at different altitudinal zones within Al-Akhdar (a and c) and Nafusa (b and d) mountains. Altitidinal zone: *A* lower than 200 m a.s.l.; *zone B* between 200 and 400 m a.s.l.; *zone C* = higher than 400 m a.s.l

The importance values of species in each zone are as follows: *Juniperus phoenicea*, *Phillyrea angustifolia*, *Phlomis floccosa* and *Pistacia lentiscus* L.; all of these are phanerophytes (Table 2). *Carthamus lanatus* (chamaephyte) and *Ceratonia siliqua* (phanerophyte) are among the most important species present in zones A and B. Zone C shared one species, the phanerophyte *Pinus halepensis*, with zone A and three species (*Ballota pseudodictamnus* (therophyte), *Satyreja thymbra* (chamaephyte), and *Scarcopoterium spinosum* (chamaephyte) with zone B. The importance values of these species are more than five times greater in zone C than they are in zone B. Among the most important species reported only from zone A are: *Suaeda vermiculata*, *Stipa capensis*, *Limoniastrum monopetalum*, *Arthrocnemum macrostachyum*, *Sarcocornia perennis*, and *Juniperus oxycedrus* (three phanerophytes, two chamaephytes and one hemicryptophyte). The most important species found only in zone B are: *Plantago amplexicaulis, Centaurea alexandria*, *Eryngium campestre*, *Hypericum triquetrifolium, Silene cyrenaica*, and *Acacia karroo* (representing one phanerophyte, one chamaephyte, two hemicryptophytes and two therophytes). Only three species were restricted to zone C: the most important was *Cupressus sempervirens*, while the other two, *Thymus capitatus* and *Rubus sanctus* have low importance values. All three are phanerophytes.

Common species at Nafusa include: *Retama raetam*, *Haloxylon scoparium*, *Stipa tenacissima*, and *Thymus capitatus,* representing three phanerophytes and one hemicryptophyte (Table 3). Zone A at Nafusa had four species (*Carlina lanata, Periploca angustifolia*, *Rosmarinus officinalis*, and *Stipa barbata*) in common with zone B (representing two phanerophytes, one hemicryptophyte and one therophyte), and two species, both phanerophytes, (*Seriphidium herba-album* and *Ephedra alata*) were shared with zone C. Zones B and C shared eight species: the most important in both zones was the phanerophyte, *Thymelaea hirsuta*. Two phanerophytes (*Calotropis procera* and *Iphiona mucronata*) and one hemicryptophyte (*Peganum harmala*) were restricted to zone A. Some 15 species were restricted to zone B at Nafusa, and 27 species were restricted to zone C. The most important species found only in zone B were: *Oryzopsis miliacea*, *Cistus parviflorus*, *Anarrhinum fruticosum*, *Avena barbata*, *Pinus halepensis*, and *Ziziphus lotus*. Meanwhile, the most important species restricted to zone C included: *Pituranthos denudatus*, *Stipa parviflora*, *Sporobolus spicatus*, *Salsola tetragona*, *Matthiola fruticulosa*, *Medicago polymorpha,* and *Salsola tetrandra.*

Species diversity

Noting that the H-index measures overall diversity, without regard to the actual species present, the H-index showed non-significant differences, both between the corresponding elevation zones at the two mountain ranges (Fig. 5a) and between the two regions overall (Table 5b). The number of species at Al-Akhdar was greater overall than

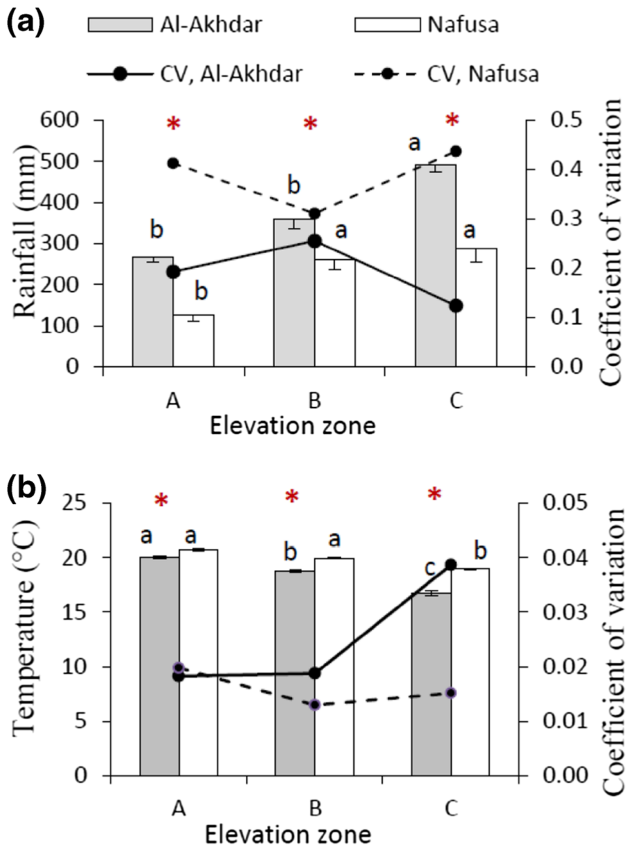

Fig. 4 Climate variables in the Al-Akhdar and Nafusa regions, at different elevations. Comparisons are made of mean values (*error bars* indicate the SE for means) and coefficients of variation (CV) of **a** the total amount of rainfall per year, and **b** the temperature each month. *Elevation zones* are indicated as follows: *A* <200 m a.s.l.; *B* 201–400 m a.s.l.; *C* >400 m a.s.l. The significance (at P $\leq$ 0.05) of differences within each group is indicated by *letters* where *different letters* indicate a significant difference. Significant differences between regions, for the corresponding elevation zone are indicated by a *star*

that at Nafusa, with three times more species in elevation zone A, one and half times more in zone B, but only one-third as many in zone C (Fig. 5b). Species diversity at Al-Akhdar was significantly greater at mid-elevations in zone B, with 51 species (Fig. 5a, b; Table 4b). In Nafusa, there was greater variation in the value of the H-index within elevation zones, so there were no significant differences in H-index between zones. The number of species at Nafusa increased with elevation, reaching a list of 42 species in zone C. Distance from the sea had no significant effect on species diversity.

Life form pattern and distribution

Overall, phanerophytes were the most common life form in the two regions. At Al-Akhdar, the percentage distribution of all life forms across elevation zones showed a significant effect of elevation ($P < 0.001$). At Nafusa, there were significant changes with elevation only in terms of the percentage contribution of chamaephytes and hemicryptophytes.

Figure 6 shows the relative abundance of each Raunkiaer life form in each elevation zone in each of the two regions. Overall, phanerophytes predominate, constituting 42% of life forms at Al-Akhdar, and 30% at Nafusa, but they are followed, in rank order by chamaephytes (19%), therophytes (18%), hemicryptophytes (14%), and geophytes (7%) at Al-Akhdar, and followed by hemicryptophytes (26%), therophytes (25%) and chamaephytes (19%) at Nafusa. This amounts to 86% more hemicryptophytes and 39% more therophytes at Nafusa relative to Al-Akhdar; the percent contribution of chamaephytes does not differ between regions. There is little correspondence in life form composition between sites at comparable elevations in the two regions.

When the data from the two regions were pooled for overall analysis, the percent contribution of life forms differed significantly between regions in relation to elevation and distance from the sea (Table 5a). For therophytes, both the number of species and their percent contribution differed significantly with elevation above sea level and the percent contribution of life forms significantly affected by distance from the sea.

Results of the generalized linear model analysis showed significant variation of the H-index along an elevation gradient, but only at Al-Akhdar ($P < 0.01$, Table 4b). When data from both regions were pooled, the effect of elevation was significant ($P < 0.01$), but the effect of region, and distance from the sea, were not (Table 5b).

Life forms and environmental conditions

At Al-Akhdar, results of the Spearman's Rank correlation showed that both phanerophytes and chamaephytes were significantly associated with habitats containing a high percent of silt and clay (with less sand) and higher rainfall (Table 6). Chamaephytes were also associated with soils containing higher levels of organic matter. At Nafusa, phanerophytes were significantly associated with higher levels of chlorides and calcium and higher temperatures and relative humidity, while chamaephytes were associated with higher levels of organic matter, nitrogen, iron, and sodium.

Hemicryptophytes were associated with coarse and fine sands in both regions; at Al-Akhdar, they were also associated with higher levels of most ions (chlorides, sulphates, bicarbonates, iron, calcium, magnesium, sodium, and potassium), but only with potassium and sulphates at Nafusa (Table 6). Therophytes and geophytes at Al-Akhdar were associated with higher percentages of coarse and fine sands, and certain ions

Table 2 Species lists and importance values of each species at different elevations in the Al-Akhdar region

Species	Family	Elevation zone			Life form
		A	B	C	
Zone: A, B and C					
Arbutus pavarii Pump.	Ericaceae	1.35	15.34	10.1	Ph
Cistus parviflorus Lam.*	Cistaceae	7.52	4.97	13.4	Ph
Cistus salvifolius L.	Cistaceae	8.24	3.75	4.84	Ch
Juniperus phoenicea L.	Cupressaceae	28.97	42.23	44.5	Ph
Phillyrea angustifolia L.	Oleaceae	22.41	21.30	23.5	Ph
Phlomis floccosa D. Don	Lamiaceae	15.81	14.40	17.2	Ph
Pistacia lentiscus L.	Anacardiaceae	9.49	5.31	30.2	Ph
Rhamnus lycioides L.	Rhamnaceae	6.53	8.64	11.8	Ph
Zone: A and B					
Amaranthus viridis L.	Amaranthaceae	1.11	6.89	–	Th
Avena barbata Pott ex Link*	Poaceae	2.54	3.13	–	Th
Carthamus lanatus L.*	Asteraceae	18.15	10.64	–	Ch
Ceratonia siliqua L.	Caesalpinaceae	9.94	14.04	–	Ph
Cichorium spinosum L.*	Asteraceae	1.82	17.22	–	Th
Cistus incanus L.	Cistaceae	6.54	1.12	–	Ph
Erica sicula Guss.	Ericaceae	0.39	7.06	–	Ch
Olea europaea L.	Oleaceae	3.72	4.38	–	Ph
*Ononis hispida*Desf.	Fabaceae	2.21	0.86	–	Ph
Phillyrea latifolia L.	Oleaceae	8.29	4.26	–	Ph
Rhamnus lycioides L. subsp. *oleoides* (L.) Jahand & Maire	Rhamnaceae	2.38	6.18	–	Ph
Rhus tripartita (Ucria) Grande	Anacardiaceae	22.33	1.61	–	Ph
Rosmarinus officinalis L.*	Lamiaceae	3.19	0.64	–	Ph
Zone: A and C					
Pinus halepensis Mill.*	Pinaceae	3.11	–	30.00	Ph
Zone: B and C					
Ballota pseudodictamnus (L.) Benth	Lamiaceae	–	5.48	28.2	Th
Satureja thymbra L.	Lamiaceae	–	2.46	13.8	Ch
Scarcopoterium spinosum (L.) Spach	Rosaceae	–	6.40	47.4	Ch
Zone: A					
Allium ampeloprasum L.	Alliaceae	0.56	–	–	Ge
Arthrocnemum macrostachyum (Moric.) K. Koch	Chenopodiaceae	8.92	–	–	Ph
Asparagus acutifolius L.	Liliaceae	0.35	–	–	Ge
Asphodelus fistulosus L.	Liliaceae	4.20	–	–	Th
Dactylis glomerata L.	Poaceae	5.07	–	–	He
Geranium robertianum L.	Geraniaceae	0.49	–	–	Th
Juniperus oxycedrus L.	Cupressaceae	7.23	–	–	Ph
Kickxia acerbiana (Boiss.) Täckh. & Boulos*	Scrophulariaceae	2.01	–	–	He
Limnium oleifolium Mill.	Plumbaginaceae	2.07	–	–	He
Limoniastrum monopetalum (L.) Boiss.	Plumbaginaceae	10.1	–	–	Ch
Mesembryantheum nodiflorum L.	Aizoaceae	1.82	–	–	Th
Oryzopsis miliacea (L.) Asch. & Schweinf.*	Poaceae	0.85	–	–	He
Periploca angustifolia Labill.*	Asclepiadaceae	2.11	–	–	Ph
Retama raetam (Forssk.) Webb & Berthel.*	Fabaceae	0.84	–	–	Ph
Rhamnus alaternus L. subsp. *alaternus*	Rhamnaceae	3.63	–	–	Ph
Salsola tetragona Del.*	Chenopodiaceae	1.17	–	–	Ch
Sarcocornia perennis (Mill.) A. J. Scott	Chenopodiaceae	8.16	–	–	Ch

Table 2 continued

Species	Family	Elevation zone			Life form
		A	B	C	
Suaeda palestina L.	Chenopodiaceae	1.65	–	–	Ch
Suaeda vermiculata Forssk.	Chenopodiaceae	25.2	–	–	Ph
Stipa arabica Trin & Rupr.*	Poaceae	5.43	–	–	He
Stipa capensis Thunb.	Poaceae	16.7	–	–	He
Zone: B					
Acacia karroo Hayne	Mimosaceae	–	5.33	–	Ph
Allium erdelii Zucc.	Alliaceae	–	3.93	–	Ge
Ammi majus L.	Apiaceae	–	3.19	–	Th
Arum cyrenaicum Hruby	Araceae	–	0.77	–	Ge
Asparagus stipularis Forssk.	Liliaceae	–	0.77	–	Ph
Asparagus aphyllus L.	Liliaceae	–	3.93	–	Ge
Beta vulgaris L. subsp. *vulgaris*	Chenopodiaceae	–	4.09	–	Th
Calicotome spinosa (L.) Link	Fabaceae	–	2.93	–	Ph
Capparis spinosa L.var*inermisTurra*	Capparaceae	–	2.47	–	Ph
Centaurea alexandria Del.	Asteraceae	–	8.21	–	Ch
Conyza aegyptiaca (L.) Dryland.	Asteraceae	–	3.78	–	Th
Cynara cornigera Lindl.	Asteraceae	–	1.00	–	He
Echium angustifolium Mill.	Boraginaceae	–	4.76	–	Ch
Eryngium campestre L.	Apiaceae	–	6.49	–	He
Fagonia cretica L.*	Zygophyllaceae	–	0.79	–	Ch
Genista acanthoclada DC	Fabaceae	–	0.99	–	Ph
Gymnocarpus decandrus Forssk.*	Caryophyllaceae	–	0.57	–	Ch
*Hypericum triquetrifolium*Turra	Gutterae	–	6.20	–	He
Lathyrus aphaca L.	Fabaceae	–	0.59	–	Th
Linum trigynum L.*	Linaceae	–	1.41	–	Th
Plantago amplexicaulis Cav.	Plantaginaceae	–	8.77	–	Th
Reaumuria vermiculata L.	Tamaricaeae	–	3.38	–	Ph
Silene cyrenaica Maire & Weiller	Caryophyllaceae	–	5.38	–	Th
Sorgumhalepense (L.) Pers.	Poaceae	–	4.34	–	He
Stachys tournefortil Poiret	Lamiaceae	–	2.65	–	Ch
Thapsia garganica Lag.	Apiaceae	–	3.79	–	He
Viburnum tinus L.	Caprifoliaceae	–	1.21	–	Ph
Zone: C					
Cupressus sempervirens L. var. *horizontalis*	Cupressaceae	–	–	21.0	Ph
Rubus sanctus shreb.	Rosaceae	–	–	1.56	Ph
Thymus capitatus (L.) Link*	Lamiaceae	–	–	3.23	Ph

The elevation zone where each species is present is indicated with the headings *A* zone A, <200 m a.s.l.; *B* zone B, 200–400 m a.s.l.; *C* zone C, >400 m a.s.l. Within a category of zonal distribution, species are listed in alphabetical order. Life forms are abbreviated as follows: *Ph* phanerophytes; *Ch* chamaephytes; *He* hemicryptophytes; *Ge* geophytes; *Th* therophytes

* Species that occur in both the Al-Akhdar and Nafusa regions

(sulphates, nitrogen, iron, calcium, magnesium, and sodium). At Nafusa, therophytes were associated with more organic matter, nitrogen, and iron content (Table 6). While the proportion of phanerophytes and chamaephytes at Al-Akhdar is clearly associated with greater rainfall, the contribution of other life forms there appears to be associated with higher temperatures. In contrast, at Nafusa, rainfall seems to be positively associated with hemicryptophytes, and higher temperature and relative humidity are associated with the distribution of phanerophytes.

Table 3 Species lists and importance values of each species at different elevations in the Nafusa region

Species	Family	Elevation zone			Life form
		A	B	C	
Zone: A, B and C					
Haloxilon scoparium Pomel	Chenopodiaceae	41.12	5.19	2.33	Ph
Retama raetam (Forssk.) webb & Berthel.*	Fabaceae	76.96	26.6	44.11	Ph
Stipa tenacissima L.	Poaceae	27.29	21.9	17.14	He
Thymus capitatus (L.) Link*	Lamiaceae	17.51	24. 6	14.97	Ph
Zone: A and B					
Carlina lanata L.	Asteraceae	3.01	2.58	–	Th
Periploca angustifolia Labill.*	Asclepiadaceae	9.35	7.61	–	Ph
Rosmarinus officinalis L.*	Lamiaceae	5.83	14.0	–	Ph
Stipa arabica Trin & Rupr.*	Poaceae	11.14	2.74	–	He
Zone: A and C					
Ephedra alata Decne.	Ephedraceae	21.67	–	7.37	Ph
Seriphidium herba-album (Asso) Soják	Asteraceae	44.23	–	12.63	Ph
Zone: B and C					
Artemisia campestris L.	Asteraceae	–	1.38	24.69	Ch
*Atractylis serrata*Pomel	Asteraceae	–	2.57	14.42	Th
Atractylis serratuloides Sieber ex Cass.	Asteraceae	–	3.87	2.91	Ch
Carthamus lanatus L.*	Asteraceae	–	3.44	19.58	Ch
Erodium glaucophyllum (L.) ĹHér	Geraniaceae	–	9.44	1.56	He
Fumana arabica (L.) Spach	Cistaceae	–	1.69	1.14	Ph
Lygeum spartum Loefl. ex L.		–	5.11	7.61	He
Tamarix nilotica (Ehrenb.) Bunge	Tamaricaeae	–	21.4	4.09	Ph
Thymelaea hirsuta (L.) Endl.	Thymelaeaceae	–	16.3	16.06	Ph
Zone: A					
Calotropis procera (Aiton) W. T. Aiton	Asclepiadaceae	19.54	–	–	Ph
Iphiona mucronata (Forssk.) Asch. & Schweinf	Asteraceae	15.77	–	–	Ph
Peganum harmala L.	Zygophyllaceae	9.558	–	–	He
Zone: B					
Anarrhinum fruticosum Desf.	Scrophulariaceae	–	18.6	–	Ch
Asteriscus hierochunticus (Michon) Wiklund	Asteraceae	–	6.06	–	Th
Atractylis cancellata L.	Asteraceae	–	3.79	–	Th
Avena barbata Pott ex Link*	Poaceae	–	9.30	–	Th
Cichorium spinosum L.*	Asteraceae	–	4.29	–	Th
Cistus parviflorus Lam.*	Cistaceae	–	20.9	–	Ph
Fagonia arabica (L.) var. *membranacea* Ghafoor.	Zygophyllaceae	–	1.43	–	Ch
Ifloga spicata (Forssk.) Sch. Bip.	Asteraceae	–	4.03	–	Th
Linum trigynum L.*	Linaceae	–	2.55	–	Th
Melica minuta L.	Poaceae	–	3.10	–	He
Oryzopsis miliacea (L.) Asch. &Schweinf.*	Poaceae	–	39.1	–	He
Pinus halepensis Mill.*	Pinaceae	–	8.23	–	Ph
Rosmarinus officinalis L.	Lamiaceae	–	14.0	–	Ph
Teucrium polium L.	Lamiaceae	–	2.45	–	Ch
Ziziphus lotus (L.) Lam.	Rhamnaceae	–	7.84	–	Ph
Zone: C					
Anagallis arvensis var.*caerulea* (L.) Gouan	Primulaceae	–	–	1.00	Th
Argyrolobium uniflorum (Decne.) Jaub. & Sparch	Fabaceae	–	–	4.91	Ch
Astragalus caprinus L. subsp. *lanigerus* (Desf.) Maire	Fabaceae	–	–	0.91	He

Table 3 continued

Species	Family	Elevation zone			Life form
		A	B	C	
Brassica tournefortii Gouan	Brassicaceae	–	–	1.93	Th
Erodium crassifolium ĹHér	Geraniaceae	–	–	2.66	He
Fagonia cretica L.*	Zygophyllaceae	–	–	1.40	Ch
Genista microcephala Coss. & Dur.	Fabaceae	–	–	2.09	Ph
Gymnocarpus decandrus Forssk.	Caryophyllaceae	–	–	1.01	Ch
Hypochoeris glabra L.	Asteraceae	–	–	0.91	Th
Kickxia acerbiana (Boiss.) Täckh. & Boulos*	Scrophulariaceae	–	–	0.80	He
Launaea mucronata subsp. *Mucronata* (Forssk.) Muschl.	Asteraceae	–	–	0.76	Th
Launaea nudicaulis (L.) Hook. F.	Asteraceae	–	–	1.44	He
Lotus glabra Mill.	Fabaceae	–	–	1.15	He
Malva sylvestris L.	Malvaceae	–	–	2.16	Th
Matthiola fruticulosa (L.) Maire	Brassicaceae	–	–	8.09	He
Medicago polymorpha L.	Fabaceae	–	–	7.63	Th
Ononis angustissima L.	Fabaceae	–	–	3.54	Th
Onopordu marenarium (Desf.) Pomel	Asteraceae	–	–	2.78	He
Pituranthos denudatus ssp. *Battandieri* (Maire) Jafri	Apiaceae	–	–	18.8	Ch
Polygonum equisetiforme Sm.	Polygonaceae	–	–	1.15	He
Pulicaria undulata subsp. *undulata* (L.) C. A. Mey.	Asteraceae	–	–	1.18	Ph
Salsola tetragona Del.*	Chenopodiaceae	–	–	8.86	Ch
Salsola tetrandra Forssk.	Chenopodiaceae	–	–	6.28	Ch
Scabiosa arenaria Forssk.	Dipsacaceae	–	–	2.61	Th
Sporobolus spicatus (Vahl) Kunth	Poaceae	–	–	13.7	He
Stipa parviflora Desf.	Poaceae	–	–	18.1	He
Thymelaea microphylla Coss.ex Dr	Thymelaeaceae	–	–	3.97	Ph

The elevation zone where each species is present is indicated with the headings *A* zone A, <200 m a.s.l.; *B* zone B, 200–400 m a.s.l.; *C* zone C, >400 m a.s.l. Within a category of zonal distribution, species are listed in alphabetical order. Life forms are abbreviated as follows: *Ph* phanerophytes; *Ch* chamaephytes; *He* hemicryptophytes; *Ge* geophytes; *Th* therophytes

* Species that occur in both the Al-Akhdar and Nafusa regions

Representation of life forms at different elevations in the two regions

Tables 2 and 3 provide a listing of the species present in each region, at each elevation. The following section summarizes patterns of distribution, for each life form.

Phanerophytes

Among the phanerophytes shared by both regions were: *Cistus parviflorus*, *Rosmarinus officinalis*, *Pinus halepensis*, *Periploca angustifolia*, *Retama raetam*, and *Thymus capitatus*—four shrubs and two trees. At Nafusa, *Retama raetam* was common, with high importance values at all three elevations, and but at Al-Akhdar it had only low importance values, and was only found in zone A. This may be related to the lower rainfall and higher temperatures there, compared to the other elevation zones.

Chamaephytes

At Al-Akhdar, the distribution of chamaephytes is mostly associated with silt and clay soils, higher organic matter content, and higher rainfall. At Nafusa, while chamaephytes are also associated with high organic matter, they are also associated with higher levels of nitrogen, iron, and sodium. The percent contribution of chamaephytes differed between elevation zones in both regions (Table 4a), and pooled data from the two regions showed a significant effect of both elevation and distance from the sea. The relative abundance of chamaephytes is significantly greater at Al-Akhdar than at Nafusa. The most abundant chamaephytes in both regions are: *Carthamus lanatus*, *Salsola tetragona*, *Fagonia cretica*, and *Gymnocarpus decandrus*. At Al-Akhdar, *Cistus parviflorus* is another common chamaephyte, while at Nafusa, additional common chamaephytes are *Artemisia campestris*, *Atractylis*

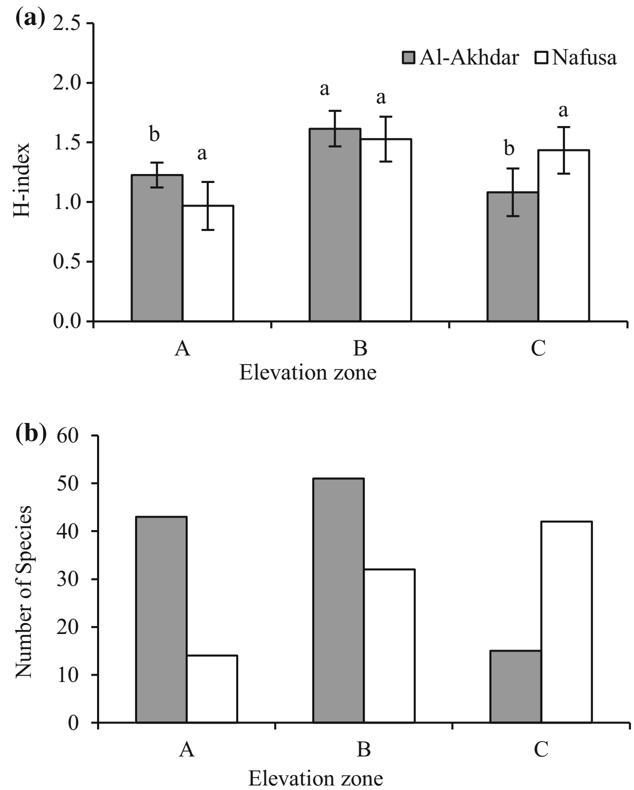

Fig. 5 **a** Shows the Shannon Diversity Index (H-index), SE are indicated; **b** shows the total number of species at each elevation, in each region. In **a**, the significance (at $P \leq 0.05$) of differences is indicated with different letters for means that differ significantly. No significant differences were found between regions at the corresponding elevation zone. Elevation zone: *A* lower than 200 m a.s.l.; *zone B* between 200 and 400 m a.s.l.; *zone C* higher than 400 m a.s.l

serratuloides, and *Carthamus lanatus,* but these species are found only in zones B and C.

Hemicryptophytes

Hemicryptophytes were more abundant at Nafusa than at Al-Akhdar. At Nafusa, their representation was positively associated with greater rainfall, sandy soils, sulphate, and potassium. At Al-Akhdar, they were associated with higher temperatures, more sandy soils, and greater concentrations of chloride, sulphate, bicarbonate, iron, calcium, magnesium, sodium, and potassium ions. Their relative abundance varied with elevation in both regions (Table 4a). Pooled data from both regions showed significant effects of both elevation and distance from the sea on the relative abundance of hemicryptophytes. Common hemicryptophytes in both regions are: *Kickxia acerbiana*, *Oryzopsis miliacea*, *and Stipa arabica*. At Al-Akhdar, hemicryptophytes are found in elevation zones A (*Stipa capensis*, *Stipa arabica*, and *Dactylis glomerata*) and B (*Eryngium campestre* and *Hypericum triquetrifolium*). At Nafusa, additional common hemicryptophytes include: *Stipa tenacissima, Stipa arabica, Erodium glaucophyllum*, and *Lygeum spartum*.

Geophytes

At Al-Akhdar, geophytes were associated with higher temperatures, more sandy soils, sulphates, iron, calcium, magnesium, and sodium. Geophytes found in zone A were: *Allium ampeloprasum,* and *Asparagus acutifolius;* in zone B, *Allium erdelii*, *Arum cyrenaicum*, and *Asparagus aphyllus* were present, but no geophytes were found in zone C. A few geophytes,—e.g., *Allium* and *Asparagus* spp.—were observed at Nafusa, but none were found in the sample quadrats at any of the study sites in that region.

Therophytes

Overall, the relative contribution of therophytes in terms of number of species and percent of species did not differ significantly between the two regions; however there were significant effects of both elevation and distance from the sea (Table 5). Therophyte abundance did not differ significantly among elevation zones at Nafusa, although the lowest contribution was seen in zone A, but at Al-Akhdar the percent contribution of therophytes was significantly lower in zone C (Fig. 6). At Al-Akhdar, therophytes were associated with sandy soils and elevated sulphates, nitrogen, iron, calcium, and magnesium, as well as higher temperatures and relative

Table 4 Results of applying a General Linear Model (GLM) to test the effect of elevation (three elevation zones, where zone A = <200 m a.s.l.; b = 200–400 m a.s.l.; and C = >400 m a.s.l) on (a) the life form; (b) the H-index; and (c) the length of the flowering–fruiting period in the Al-Akhdar and Nafusa regions

	Akhdar			Nafusa		
	Chi Square	df	P value	Chi Square	df	P value
(a) Life form						
Percent of contribution						
Ph	71.28	2	**<0.001**	4.50	2	0.105
Ch	12.89	2	**<0.001**	14.80	2	**<0.001**
He	11.19	2	**<0.001**	20.11	2	**<0.001**
Th	17.02	2	**<0.001**	1.97	2	0.160
Number of species						
Ph	3.58	2	0.167	2.21	2	0.331
Ch	8.92	2	**<0.050**	2.62	2	0.269
He	0.17	2	0.679	2.46	2	0.292
Th	4.81	2	0.090	5.14	2	0.077
(b) Species diversity						
H-index	10.21	2	**<0.010**	4.06	2	0.131
(c) Phenological duration						
Percent of contribution						
Short	84.452	2	**<0.001**	33.431	2	**<0.001**
Mid	93.563	2	**<0.001**	8.933	2	**<0.050**
Long	8.098	1	**<0.010**	5.754	1	**<0.050**
Number of species						
Short	6.513	2	**<0.050**	3.066	2	0.216
Mid	6.727	2	**<0.050**	4.074	2	0.130
Long	3.705	2	0.157	1.011	2	0.603

A normal distribution was assumed in the case of the H-index and a Poisson distribution was assumed for the number of species and percent contribution of species belonging to each life form. The geophytes (category "Ge") were excluded from the analysis due to the low number of cases at Al-Akhdar and the absence of this life form in the samples fromNafusa. Life forms were abbreviated as follows: *Ph* phanaerophytes; *Ch* chamaephytes; *He* hemicryptophytes; *Th* therophytes

Significant effects are indicated in bold face, and are designated as $P < 0.001$, $P < 0.01$, and $P < 0.05$

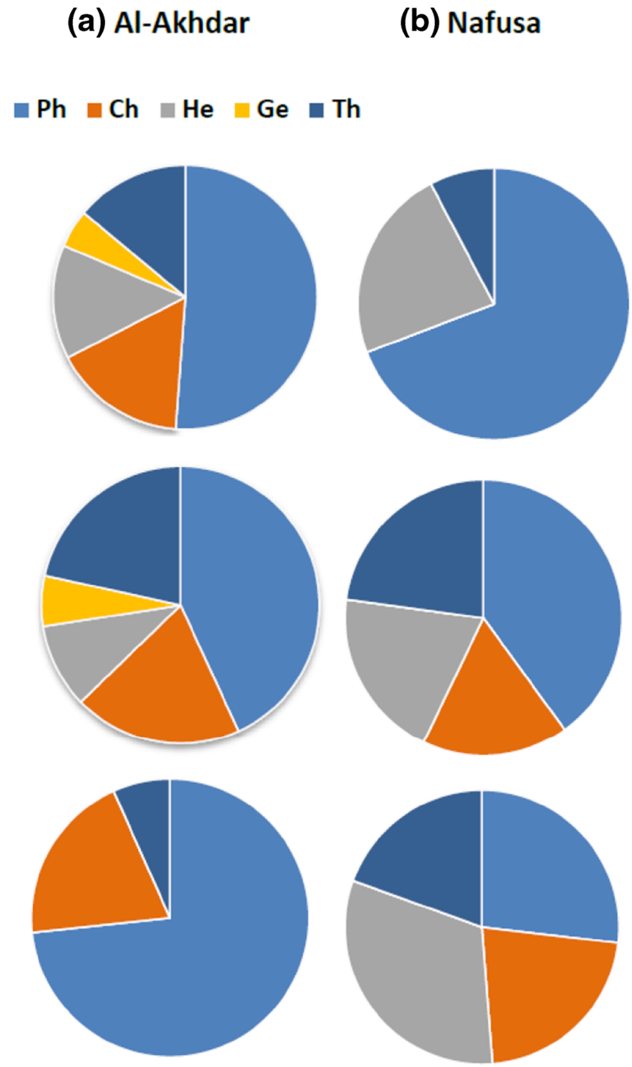

Fig. 6 Relative abundance of Raunkiaer Life Forms in each region, and at each elevation. *Zone A* <200 m a.s.l.; *zone B* 200–400 m a.s.l.; *zone C* >400 m a.s.l; *Ph* phanerophytes; *Ch* chamaephytes; *He* hemicryptophytes; *Ge* geophytes; *Th* therophytes (annuals). *Note* Geophytes were not recorded in the Nafusa sites, and were absent from the high-elevation sites at Al-Akhdar. Chamaephytes were absent from Nafusa at low-elevation sites

humidity. At Nafusa, therophytes were associated with higher soil organic matter, nitrogen, iron, and sodium. The most common therophytes at Al-Akhdar were *Amaranthus viridis* and *Avena barbata,* found in elevation zones A and B, and *Ballota pseudodictamnus* found in zones B and C (Table 2). At Nafusa, *Carlina lanata* is found in zones A and B, and *Atractylis serrata* is important in zones B and C.

Reproductive phenology

At Al-Akhdar, the proportion of species that were reproductive (in the flowering–fruiting stage) peaked in spring, as temperatures increased and rainfall decreased. The peak occurred in mid-March in zones A and B, but was delayed, to mid-April, in zone C. The fraction of species that were reproducing then declined in summer, when temperatures are higher, and there is little rainfall. Even fewer species were flowering or fruiting in fall and winter where temperatures are lowest, and rainfall is greatest (Fig. 7a, c). The proportion of flowering or fruiting species decreased in fall more rapidly in zone C than in zones A and B; there was no second round, or extension of flowering in zone C at Al-Akhdar.

At Al-Akhdar, in general, the lowest proportion of species recorded flowering or fruiting were found in zone

Table 5 Results of applying a General Linear Model (GLM) to test the effect of region (Al-AkhdarorNafusa), elevation (three elevation zones where zone A = <200 m a.s.l.; B = 200–400 m a.s.l.; and C = >400 m a.s.l.) and distance from the sea (less than and greater than 35 km from the coast) on (a) the life form, (b) the H-index, and (c) the duration of the flowering–fruiting period in pooled data from the two regions

	Number of species			Percent contribution		
	Chi Square	df	P value	Chi Square	df	P value
(a) Life form						
Phanerophytes						
Region	0.71	1	0.400	18.88	1	**<0.001**
Elevation	3.34	2	0.188	60.08	2	**<0.001**
Distance from the sea	0.05	1	0.816	4.99	1	**<0.050**
Chaemaephytes						
Region	0.05	1	0.822	44.521	1	**<0.001**
Elevation	1.41	2	0.494	72.572	2	**<0.001**
Distance from the sea	0.74	1	0.389	36.209	1	**<0.001**
Hemicryptophytes						
Region	0.16	1	0.687	15.97	1	**<0.001**
Elevation	3.04	2	0.219	51.61	2	**<0.001**
Distance from the sea	1.08	1	0.300	27.18	1	**<0.001**
Therophytes						
Region	0.82	1	0.364	0.24	1	0.626
Elevation	9.95	2	**<0.010**	33.65	2	**<0.001**
Distance from the sea	0.03	1	0.873	20.12	1	**<0.001**
(b) H-index						
Region	0.05	1	0.816			
Elevation	10.28	2	**<0.010**			
Distance from the sea	0.17	1	0.685			
(c) Duration of flowering–fruiting period						
Short						
Region	1.231	1	0.267	1.509	1	0.219
Elevation	4.716	2	0.095	94.832	2	**<0.001**
Distance from the sea	0.186	1	0.666	0.097	1	0.756
Mid						
Region	1.350	1	0.245	54.111	1	**<0.001**
Elevation	10.004	2	**<0.01**	10.539	2	**<0.01**
Distance from the sea	2.838	1	0.092	0.286	1	0.593
Long						
Region	1.188	1	0.276	4.666	1	**<0.05**
Elevation	0.865	2	0.649	0.477	2	0.788
Distance from the sea	0.160	1	0.689	3.003	1	0.083

A normal distribution was assumed in the case of the H-index, and a Poisson distribution was assumed for the number of species and percent contribution of species belonging to each life form. The geophytes (category "Ge") were excluded from the model due to the low number of cases at Al-Akhdar and the absence of this life form in the samples from Nafusa. Life forms were abbreviated as follows: *Ph* phanaerophytes; *Ch* chamaephytes; *He* hemicryptophytes; *Th* therophytes

Significant effects are indicated in bold face, and are designated as $P < 0.001$, $P < 0.01$, and $P < 0.05$

C, which had the lowest temperatures and greatest rainfall. The exception was the period from late spring to mid-summer when the number of species that were flowering or fruiting in zone C peaked, about a month later than at lower elevations. This delayed peak coincided with a more rapid drop in flowering and fruiting at lower elevations (Fig. 7a, c). Peak flowering and fruiting reached 0.6–0.7 (60–70% of species) with values of 0.63 in zone A, and 0.69 in zone B in mid spring, and 0.72 in zone C in late spring, when temperatures ranged from 16.63–18.90 °C. More than 50% of species were in the flowering–fruiting phenophase from early spring to early summer in zone A, from mid spring to early summer in zone B, and from mid spring to mid-summer in zone C. This reflects a pattern of earlier flowering in warmer zones (Fig. 7a, c).

Table 6 Spearman's rank correlation coefficient showing the positive (and negative) associations between life form, and soil and climate parameters along an elevation gradient in the Al-Akhdar and Nafusa regions

Parameters	Akhdar					Nafusa				
	Ph	Ch	He	Th	Ge	Ph	Ch	He	Th	Ge
Soil										
CS (%)	−0.99	−0.42	**0.74**	**0.99**	**0.97**	−0.07	−0.09	**0.87**	−0.23	–
FS (%)	−1.00	−0.49	**0.79**	**0.98**	**0.99**	0.33	−0.47	**0.61**	−0.60	–
S (%)	**0.99**	**0.67**	−0.90	−0.92	−1.00	0.09	0.06	−0.89	0.21	–
C (%)	**0.88**	**0.89**	−1.00	−0.72	−0.92	0.12	0.04	−0.90	0.18	–
OM (%)	0.39	**0.98**	−0.83	−0.13	−0.46	−0.84	**0.92**	0.01	**0.96**	–
Cl^- (ppm)	−0.42	−0.99	**0.85**	0.16	0.49	**0.99**	−0.99	−0.54	−0.96	–
SO_4^{2-}	−0.97	−0.35	**0.68**	**0.99**	**0.95**	0.03	−0.19	**0.82**	−0.33	–
HCO_3^- (ppm)	−0.39	−0.98	**0.83**	0.13	0.46	0.34	−0.19	−0.97	−0.04	–
N (ppm)	−0.47	0.46	−0.08	**0.69**	0.40	−0.84	**0.91**	0.01	**0.96**	–
Fe^{3+} (ppm)	−1.00	−0.59	**0.86**	**0.95**	**0.99**	−0.98	**0.99**	0.36	**0.99**	–
Ca^{2+} (ppm)	−0.95	−0.27	**0.62**	**0.99**	**0.92**	**0.99**	−0.96	−0.64	−0.91	–
Mg^{2+} (ppm)	−1.00	−0.52	**0.81**	**0.98**	**0.99**	−0.14	0.29	−0.75	0.43	–
Na^+ (ppm)	−0.56	−1.00	**0.92**	0.32	**0.63**	−0.86	**0.93**	0.05	**0.97**	–
K^+ (ppm)	−0.39	−0.98	**0.83**	0.12	0.46	−0.58	0.44	**0.99**	0.31	–
Climate										
R (mm)	**0.76**	**0.97**	−0.99	−0.55	−0.81	0.41	−0.55	**0.54**	−0.67	–
T (°C)	−0.71	−0.98	**0.98**	**0.49**	**0.76**	**0.92**	−0.84	−0.84	−0.75	–
RH (%)	−0.48	0.46	−0.08	**0.70**	0.41	**0.80**	−0.88	0.07	−0.94	–

Life forms were abbreviated as follows: *Ph* phanaerophytes; *Ch* chamaephytes; *He* hemicryptophytes; *Th* therophytes; *Ge* geophytes. Soil parameters were: Texture in terms of *CS* % of coarse sand; *FS* % of fine sand; *S* % silt; *C* % clay. Soil *OM* organic matter, and ion concentrations, measured in ppm, were designated as: Cl^- = chloride, SO_4^{2-} = sulfate, HCO_3^- = bicarbonate, N = nitrogen = , Fe^{3+} = iron, Ca^{2+} = calcium, Mg^{2+} = magnesium = , Na^+ = sodium, andK^+ = potassium. Climate parameters were abbreviated as: *R* rainfall; *T* air temperature; *RH* relative humidity

Values of the correlation coefficient that are greater than +0.5 are indicated in bold

At Nafusa, flowering peaked in all three elevation zones in mid-March. There was a marked increase in the proportion of flowering–fruiting species as temperatures increased and rainfall decreased from early to late spring, then reproductive activity decreased again in summer. A second round of flowering began in fall, as temperatures decreased and rainfall increased (Fig. 7b, d). In spring, the proportion of species that were flowering–fruiting peaked in late September in zone C when temperatures were comparatively low and rainfall was greater than at lower elevations. The fall flowering period was most pronounced in zone C (when zone C was experiencing both lower temperatures and lower rainfall), followed by zone A. The temperatures associated with the highest proportion of species that were flowering or fruiting are, for zones A, B and C, respectively, 19.3, 19.2, and 17.9 °C in the spring flowering period, compared to 22.3, 21.7, and 20.4 °C in the fall flowering period.

More than half of the species at Nafusa are in the flowering–fruiting phenophase during the spring, in zones A and B; this extends to early summer in Zone C. Peak flowering and fruiting occurred in mid-spring in the three zones, with values of 0.71, 0.75, and 0.95 in zones A, B, and C, respectively, while temperatures ranged from 17.95 to 19.2 °C (Fig. 7b, d).

When the length of the flowering–fruiting periods is considered using the GLM, results showed significant variation in the length of the flowering–fruiting period according to elevation in both study regions. Meanwhile, when the number of species belonging to particular phenological duration categories is considered, the GLM results indicated significant variation with elevation, but only at Al-Akhdar, for the short and mid durations (Table 4c). The pooled data for all sites at both locations showed that the number of species with mid-length flowering–fruiting periods was significantly affected by elevation.

When the percent contribution of species belonging to each phenological duration was considered, the distribution of both short- and mid-duration flowering–fruiting periods was significantly affected by elevation (Table 5c). The distribution of mid-length and long flowering–fruiting

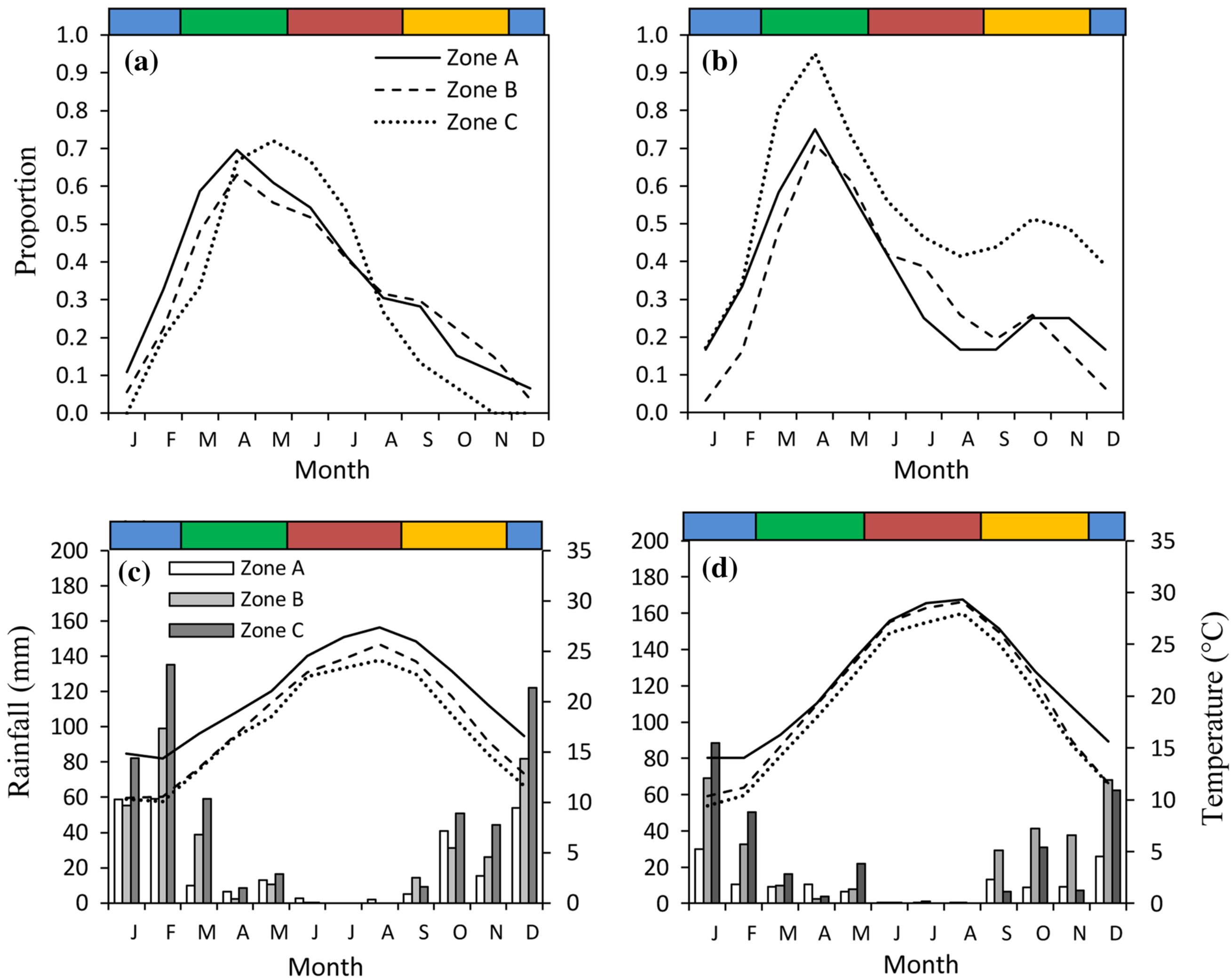

Fig. 7 In all **a**, **b**, **c**, and **d** a *solid line* indicates data for elevation zone A (<200 m a.s.l.), *dashed line* indicates zone B (200–400 m a.s.l.), and a *dotted line* indicates zone C (>400 m a.s.l.). Proportion of species that were flowering or fruiting at different elevations in Al-Akhdar (**a**) and Nafusa (**b**). **c**, **d** Show the corresponding mean total annual rainfall (histograms), and average temperatures (lines, where a *solid line* indicates data for elevation zone A (<200 m a.s.l.), dashed line indicates zone B (200–400 m a.s.l.), and a *dotted line* indicates zone C (>400 m a.s.l.) each month. **c** corresponds to conditions at Al-Akhdar, and **d** characterizes Nafusa. *Colored bars* along the upper *x*-axis of each figure indicate the seasons as follows: *blue* winter; *green* spring; *red* summer; *yellow* fall

periods differed significantly between regions in that there were more mid-length and fewer long-term flowering species at Al-Akhdar (42.8 and 10.5% in Al-Akhdar as compared to 29.1 and 22.1% respectively in Nafusa). However, distance from the sea had no significant effect on the duration of the flowering–fruiting period for any of the sites studied.

Discussion

Soils

Soil organic matter at levels <1% are associated with desert conditions; upland soils are typically somewhere between 1 and 6% (Troeh and Thompson 2005). In the present study, Nafusa soils are very low in organic matter, and will therefore have low moisture-holding capacity compared to the more typically upland soils of Al-Akhdar. The soils of Al-Akhdar are more weathered, with greater silt and clay (predominately loam, and clay loam), which will add to their moisture-holding capacity (Fig. 3). In contrast, the sandy loam soils of Nafusa will be -drain more freely, so this, combined with the lower organic matter and lower rainfall in the region will make sites at all three elevations at Nafusa much drier for the plants living there. This effect will be accentuated in the height of the summer (in August) when peak temperatures are slightly higher at Nafusa (27.9–29.3 °C) than they are at Al-Akhdar (24.1–27.4 °C).

Community structure and diversity

The considerable differences in substrate texture and moisture availability between the two regions explain why they share only 13% of their plant species, despite being located near the Mediterranean coastal zone, at similar latitudes. Similarly, in other systems, the species composition and life-form patterns of plant communities have been shown to be significantly influenced by the physical and chemical properties of soils (Hegazy et al. 2004, 2007; Spehn et al. 2000; Wang et al. 2002; Rodríguez-Loinaz et al. 2008; Brady and Weil 2010; McCain and Colwell 2011).

Al-Akhdar is generally closer to the sea, with all sites being within 50 km of the Mediterranean coast, so the lower slopes (zone A) will be more subject to onshore breezes, which explains the elevated levels of chloride and sodium in the soils at these sites. The elevated iron levels at Al-Akhdar are associated with the *terra rossa* –red earth soils for which the region is noted.

In general, greater species diversity is associated with greater community stability (Johnson et al. 1996; Hooper and Vitousek 1997; Loreau et al. 2001). There are somewhat more species found at Al-Akhdar (76) than at Nafusa (64), so this would suggest that the vegetation of Al-Akhdar may be more stable and resilient in the face of climate change (Fitzjarrald et al. 2001; Kessler et al. 2011). Environmental data showed that the variability of rainfall at Nafusa was greater than that at Al-Akhdar, so again conditions are less predictable and therefore more challenging for plants to respond to at Nafusa.

It is generally inferred that a high proportion of annual plantss in a system indicates a higher level of disturbance (McIntyre et al. 1995; Sternberg and Shoshany 2001). Overall, annuals are more abundant at Nafusa (25%) than at Al-Akhdar (18%). We noted low representation of annuals, and the greatest level of phanerophytes (mostly trees and shrubs) at high elevations in Al-Akhdar, where the phanerophyte-dominated vegetation is 60% evergreen trees (six of the ten phanerophyte species). In contrast, low levels of annuals, and high numbers of phanerophytes occur at low elevations at Nafusa where the phanerophytes are almost entirely bushes and shrubs. It would be useful to add studies of land use, including assessment of the relative intensity of herbivory in the two regions, at each elevation, as disturbance may be a consequence of grazing, or natural (landslides) or anthropogenic (agricultural) soil disturbance.

The major difference between chamaephytes and hemicryptophytes is that the aerial perennating buds are more exposed to desiccation in chamaephytes, whereas they are close to the ground in hemicryptophytes. In both regions, the relative abundance of chamaephytes increases with elevation, most likely in response to increasing moisture availability due to orographic effects (increased precipitation as moist air rises and cools over mountain ranges) and condensation of water on plant surfaces as the air cools at night. The contrasting conditions at Nafusa and Al-Akhdar are underscored by the predominance of the more drought-resistant hemicryptophytes in Nafusa, relative to the number of chamaephytes.

In other studies, contrasting environmental conditions have been associated with differences in functional traits and flowering phenology, in some species even at the microhabitat level (Hegazy 1994, 2001; Llorens and Peñuelas 2005; Sundqvist et al. 2011; Read et al. 2014). If environmental conditions change, it is therefore reasonable to predict that there will be changes in species composition and the array of life forms present (Llorens and Peñuelas 2005; Hegazy et al. 2011; Read et al. 2014).

Species diversity measures do not take in account which species are present; nor do they address aspects of community structure and function (see too Díaz et al. 1999). The values of the H-index, and tallies of the number of species did not differ significantly between the two regions. In both, the highest H-index values were found at mid elevations (zone B, between 200 and 400 m a.s.l., Fig. 5), but variability in H-index values were generally greater at Nafusa, suggesting that microhabitat heterogeneity, particularly at mid elevations, may be greater there (Hegazy 1994, 2001; Llorens and Peñuelas 2005; Rahbek 2005; Read et al. 2014).

Reproductive phenology

The period of flowering and fruiting in both regions seems to be associated with changes in temperature and rainfall, although the thresholds for these conditions differ between the regions, and, indeed, between the spring and the fall pulses of reproduction at Nafusa. Increasing temperatures and decreasing rainfall in the spring were associated with flowering and fruiting. Hot and dry conditions develop in summer, with average temperatures ranging from 23.3 to 25.7 °C in Al-Akhdar, and 26.1 to 28.4 °C in Nafusa, while at that time average rainfall is between 0.0 and 0.9 mm in Al-Akhdar, and 0.1 and 0.4 mm in Nafusa. These xeric conditions induce most species to stop flowering and fruiting. Posé et al. (2013) have pointed out that temperature is an important environmental signal regulating flowering at the molecular level, emphasizing that flowering and fruiting are generally a response to increased temperatures and decreasing rainfall.

The Al-Akhdar region has a more mesic climate, so flowering and fruiting peak in mid-March, extend into the summer, and decline in the fall. At Nafusa, the March peak is more pronounced, and species have shorter flowering and fruiting periods as xeric conditions develop more rapidly in the summer. Then, a second wave of flowering and fruiting is noted in the fall (Fig. 7). A species-by-species examination of the data showed that plant species at Nafusa showed greater phenological diversity than those at Al-Akhdar; indeed, the species list at Nafusa can be split into two groups. The first group shows peak flowering and fruiting in spring associated with increasing temperatures (from 17.95 to 19.2 °C) at that time. The second group shows peak flowering and fruiting in fall and early spring, when temperatures range between 20.42 and 22.35 °C.

These distinct patterns suggest an alternative explanation to temperature as the cue that triggers flowering in each case. The late spring/early summer-flowering species may be long-day plants, while those flowering and fruiting in fall and early spring are short-day plants (e.g., see Mauseth 2003). Of the 13 species that are flowering or fruiting in fall and spring, the majority (9) are found at Nafusa; this difference in terms of the particular species present would be sufficient to explain the apparent "second period" at Nafusa in contrast to Al-Akhdar. This issue, of the relative occurrence of short-day and long-day species, would merit confirmation through physiological studies.

This kind of phenological diversity or temporal dispersion in phenology among species in response to the same environmental cues has been reported by several authors (e.g., Rathcke and Lacey 1985; Hooper and Vitousek 1997; Cleland et al. 2007). Diversity of plant phenology, including reproductive periods, may promote coexistence in plant communities by influencing relative demands on ecosystem processes, such as nutrient capture and productivity. This would be a form of niche partitioning whereby different species would make peak demands on soil and water resources at different times of the year. Timing of flowering and fruiting may also be related to co-evolution with specialized pollinators and seed-dispersers; reduced overlap between closely related species would reduce the frequency of (unsuccessful) interspecific pollinations. The absence of a second Al-Akhdar flowering and fruiting period in the fall may simply be a function of the different species list and contrasting contributions of different life forms, as Al-Akhdar receives comparable or even higher amounts of rainfall in the fall, with similar temperatures at that time.

Conclusions

It was surprising in many ways to see how different the plant communities were at Al-Akhdar and Nafusa, two escarpment regions in Northern Libya that are only 1200 km apart. While there were some species in common, most were restricted to one region or the other.

In theory, higher species diversity, and the presence of several species of similar life forms, together promote ecosystem efficiency and stability (Díaz and Cabido 2001; Johnson et al. 1996; Hooper and Vitousek 1997). The idea of this "ecological redundancy" would be that loss of one or a few species would not cause a niche or particular life form to be lost altogether. Overall, in the present study, there appears to be a more efficient and stable ecosystem in place at Al-Akhdar than at Nafusa. There, environmental conditions are less predictable and have higher variance, the effects of drought are accentuated by characteristics of the soil substrate, and rainfall, as a critical limiting factor for plant growth and reproduction, is significantly lower.

Differences in the timing of flowering and fruiting may simply reflect differences in the particular species list (and therefore the relative abundance of short-day and long-day flowering species) in each region. There is no satisfactory alternative explanation in terms of temperature, rainfall, or relative humidity, for the (second) fall round of flowering that occurs at Nafusa.

Although conditions for plant growth would seem to be better at Al-Akhdar, the percentage of plants that are flowering peaks at 63–70%, depending on elevation. In contrast, at Nafusa, the first peak is at 75–95%, and the second peak is at 27–50%, depending on elevation. This would suggest that more flowering is occurring at Nafusa, the more xeric region. This may be due to the greater representation of annuals (where all individuals will flower and complete their life cycle that year) as well as shrubs at Nafusa, while the tree species at Al-Akhdar would typically require several years of (pre-reproductive) vegetative growth prior to beginning flowering and seed production. It is interesting that the spring flowering peak is in March for five of the six study areas, but is delayed until April, and ends more abruptly in the cooler, high elevation sites at Al-Akhdar.

Over the coming decades, there will be a gradual change in these plant communities, based on predicted meteorological changes. The more moist, cooler climate in the Al-Akhdar range may be replaced by drier and warmer conditions, more like those of the Nafusa region (see Llorens and Peñuelas 2005). At Al-Akhdar, the decline of species, such as *Arbutus pavarii*, a vulnerable endemic shrub (see Kabiel et al. 2016a), and common keystone species like *Juniperus phoenicea,* an evergreen tree that is, in many areas, showing low juvenile recruitment and dieback of vegetative branches (Kabiel et al. 2016b), will intensify.

Some have suggested (e.g., Gritti et al. 2006; Hegazy et al. 2008) that the accelerating effects of climate change, and overuse of environmental resources through water diversion and overgrazing, will shift plant communities toward those currently found in more xeric sites. It may be the case that the vegetation of Al-Akhdar will become more like that of Nafusa, but the fact that there is only a 16% overlap in the species lists of these areas suggests that the new or empty niches may instead be filled by new invasive species. It will be valuable to use the baseline provided by the present study to track the rate and direction of community change, and to include not only recognition of shifts in the representation of different plant species and life forms, but also to track shifts in physiology and genetic composition of the populations that persist as conditions become more xeric.

References

Al-Idrissi M, Sbeita A, Jebriel A, Zintani A, Shreidi A, Ghawawi H, Tazi M (1996) Libya: Country report to the FAO international technical conference on plant genetic resources. Tripoli, Libya

Allen S, Grimshaw H, Parkinson J, Quarmby C, Roberts J (1974) Chemical analysis of ecological materials. Blackwell, Oxford

Arnold JF (1955) Plant life-form classification and its use in evaluating range conditions and trends. J Range Manag 8:176–181

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377

Ben-Mahmoud R, Mansur S, Al-Gomati A (2000) Land degradation and desertification in Libya. Land Degradation and Desertification Research Unit, Libyan Center for Remote Sensing and Space Science, Tripoli

Boulos L (1999-2005) Flora of Egypt, vol 4. Al Hadara Publishing, Cairo

Boulos L (2009) Flora of Egypt checklist, Revised Annotated Edition. Al Hadara Publishing, Cairo

Bradley NL, Leopold AG, Ross J, Huffaker W (1999) Phenological changes reflect climate change in Wisconsin. Proc Natl Acad Sci USA 96:9701–9704

Brady NC, Weil RR (2010) Elements of the nature and properties of soils, 3rd edn. Prentice-Hall, Boston

Brullo S, Furnari F (1981) Phytogeographical considerations on the coastal vegetation of Cyrenaica. Anales Jardín Botánico De Madrid 37:765–772

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22:357–364

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655

Díaz S, Cabido M, Zak M, Carretero EM, Araníbar J (1999) Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. J Veg Sci 10:651–660

Feng Y, Lei JQ, Xu XW, Pan BR (2013) Composition and characteristics of Libyan flora. Arch Biol Sci Belgrad 65:651–657

Fitter AH, Fitter RS, Harris ITB, Williamson MH (1995) Relationships between first flowering date and temperature in the flora of a locality in central England. Funct Ecol 9:55–60

Fitzjarrald DR, Acevedo OC, Moore KE (2001) Climatic consequences of leaf presence in the Eastern United States. J Clim 14:598–614

Gritti ES, Smith B, Sykes MT (2006) Vulnerability of Mediterranean Basin ecosystems to climate change and invasion by exotic plant species. J Biogeogr 33:145–157

Hadar L, Noy-Meir I, Perevolotsky A (1999) The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. J Veg Sci 10:673–682

Hegazy AK (1994) Trade-off between sexual and vegetative reproduction of the weedy *Heliotropium curassavicum* L. J Arid Environ 27:209–220

Hegazy AK (2001) Reproductive diversity and survival of the potential annual *Diplotaxis harra* (Forssk.) Boiss. (Brassicaceae) in Egypt. Ecography 24:403–412

Hegazy AK, Lovett-Doust J (2016) Plant ecology in the Middle East. Oxford University Press, Oxford

Hegazy AK, Fahmy GM, Ali MI, Gomaa NH (2004) Vegetation diversity in natural and agro-ecosystems of arid lands. Community Ecol 5:163–176

Hegazy AK, Lovett-Doust J, Hammouda O, Gomaa NH (2007) Vegetation distribution along the altitudinal gradient in the northwestern Red Sea region. Community Ecol 8:151–162

Hegazy AK, Medany MA, Kabiel HF, Maez MM (2008) Spatial and temporal projected distribution of four crop plants in Egypt. Nat Resour Forum 32:316–324

Hegazy AK, Boulos L, Kabiel HF, Sharashy OS (2011) Vegetation and species altitudinal distribution in *Al-Jabal Al-Akhdar* landscape. Pak J Bot 43:1885–1898

Hegazy AK, Alatar AA, Lovett-Doust J, El-Adawy HA (2012) Spatial and temporal plant phenological niche differentiation at the Wadi Degla ecosystem (Egypt). Acta Bot Croat 71:261–277

Hooper DU, Vitousek PM (1997) Effects of plant composition and diversity on nutrient cycling. Ecol Monogr 68:121–149

IPCC (2001) Climate change: the scientific basis. Third assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Jackson M (1973) Soil chemical analysis. Prentice-Hall, Englewood Cliffs

Jafri SM, El-Gadi A (1977-1993) Flora of Libya. Al Fatteh University, Tripoli

Johnson KH, Vogt KA, Clark HJ, Schmitz OJ, Vogt DJ (1996) Biodiversity and the productivity and stability of ecosystems. Trends Ecol Evol 11:372–377

Kabiel HF, Hegazy AK, Lovett-Doust L, Al-Rowaily SL, Al-Borki AE (2016a) Demography of the threatened endemic shrub, *Arbutus pavarii,* in the Al-Akhdar Mountainous Landscape of Libya. J For Res. doi:10.1007/s11676-016-0263-9

Kabiel HF, Hegazy AK, Lovett-Doust L, Al-Rowaily SL, Al-Borki AE (2016b) Ecological assessment of populations of *Juniperus phoenicea* L. in the Al-Akhdar Mountains of Libya. Arid Land Res Manag 30:269–289

Kessler M, Kluge J, Hemp A, Ohlemüller R (2011) A global comparative analysis of elevational species richness patterns of ferns. Glob Ecol Biogeogr 20:868–880

Kichenin E, Wardle DA, Peltzer DA, Morse CW, Freschet GT (2013) Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. Funct Ecol 27:1254–1261

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16:545–556

Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general functional groups to specific groups of response to disturbance. Trends Ecol Evol 12:474–478

Lavorel S, McIntyre S, Grigulis K (1999) Plant response to disturbance in a Mediterranean grassland: how many functional groups? J Veg Sci 10:661–672

Liu J, Tan YH, Slik JWF (2014) Topography related habitat associations of tree species traits, composition and diversity in a Chinese tropical forest. For Ecol Manag 330:75–81

Llorens L, Peñuelas J (2005) Experimental evidence of future drier and warmer conditions affecting flowering of two co-occurring Mediterranean shrubs. Int J Plant Sci 166:235–245

LNMC (2012) Libyan National Meteorological Center, Climate Research Unit, Tripoli (source for data on temperature and rainfall representing means for years 2006-2013)

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808

Lovett-Doust L (1981a) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. J Ecol 69:743–755

Lovett-Doust L (1981b) b. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). II. The dynamics of leaves and reciprocal transplant–replant experiment. J Ecol 69:757–768

Matesanz S, Gianoli E, Valladares F (2010) Global change and the evolution of phenotypic plasticity in plants. Ann N Y Acad Sci 126:35–55

Mauseth JD (2003) Botany: an introduction to plant biology, 3rd edn. Jones and Bartlett, Sudbury, pp 422–427

McCain CM, Colwell RK (2011) Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecol Lett 14:1236–1245

McIntyre S, Lavorel S, Tremont RM (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. J Ecol 83:31–44

Posé D, Verhage L, Ott F, Yant L, Mathieu J, Angenent GC, Immink RGH, Schmid M (2013) Temperature-dependent regulation of flowering by antagonistic FLM variants. Nature 503:414–417

Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecol Lett 8:224–239

Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. Annu Rev Ecol Syst 16:179–214

Raunkiaer C (1934) Plant life forms (trans: Gilbert-Cater H). Clarendon Press, Oxford

Read QD, Moorhead LC, Swenson NG, Bailey JK, Sanders NJ (2014) Climate convergent effects of elevation on functional leaf traits within and among species. Funct Ecol 28:37–45

Rodríguez-Loinaz G, Onaindia M, Amezaga I, Mijangos I, Garbisu C (2008) Relationship between vegetation diversity and soil functional diversity in native mixed-oak forests. Soil Biol Biochem 40:49–60

Spano D, Cesaraccio C, Duce P, Snyder RL (1999) Phenological stages of natural species and their use as climate indicators. Int J Biometeorol 42:124–133

Spehn EM, Joshi J, Schmid B, Alphei J, Körner C (2000) Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. Plant Soil 224:217–230

Sternberg M, Shoshany M (2001) Influence of slope aspect on Mediterranean woody formations: comparison of a semiarid and an arid site in Israel. Ecol Res 16:335–345

Sundqvist MK, Giesler R, Graae BJ, Wallander H, Fogelberg E, Wardle DA (2011) Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. Oikos 120:128–142

Sundqvist MK, Sanders NJ, Wardle DA (2013) Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Annu Rev Ecol Evol Syst 44:261–280

Troeh FR, Thompson LM (2005) Soils and Soil Fertility, 6th edn. Blackwell, Ames

Tyler G (2001) Relationships between climate and flowering of eight herbs in a Swedish deciduous forest. Ann Bot 87:623–630

Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. New Phytol 176:749–763

Walkovszky A (1998) Changes in phenology of the locust tree (*Robinia pseudoacacia* L.) in Hungary. Int J Biometeorol 41:155–160

Wang G, Zhou G, Yang L, Li Z (2002) Distribution, species diversity and life-form spectra of plant communities along an altitudinal gradient in the northern slopes of Qilianshan Mountains, Gansu, China. Plant Ecol 165:169–181

Zuur AF, Leno EL, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14