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ORIGINAL PAPER

Demography of the threatened endemic shrub, *Arbutus pavarii*, in the Al-Akhdar mountainous landscape of Libya

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

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Abstract We sampled twenty populations of the vulnerable endemic shrub or tree, *Arbutus pavarii* Pampan., at different elevations and aspects within the Al-Akhdar mountainous region of Libya. Our sampling sites were at elevations ranging from 285 to 738 m above sea level, and several different habitats: vallies (locally known as wadis), north- and south-facing slopes, and mountaintops. All individuals within each quadrat were studied. Population size and structure, and plant functional traits were assessed. None of the populations had a stable distribution of size classes. Some consisted mostly of small plants, with little or no fruit production; others consisted only of mid-sized and large plants, with high fruit production, but no juvenile recruitment. There was a significant increase in percent cover with increasing elevation; reproductive output (the number of fruits per branch and total number of fruits per individual) also generally increased with elevation. In some of these populations the lack of recruitment, and in others the failure to produce fruit, together constituted serious demographic threats. In light of these results, recommendations are made for conservation of this vulnerable endemic species.

Keywords Al-Akhdar mountains · Conservation · Demography · Elevation · Functional traits · Vulnerable species

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Introduction

Effective conservation plans require information on population ecology and genetics, climatology, geology and human activities. Several authors have studied the ecology of narrow endemic Mediterranean species and have developed appropriate conservation plans (e.g., Martinell et al. 2011; Fenu et al. 2011). Here we characterize population structure, plant size and reproductive traits in *Arbutus pavarii* Pampan. (Family: Ericaceae), a narrow endemic perennial shrub in northeastern Libya. This study was intended as a first step toward developing an effective conservation management program for the species.

Northeastern Libya is a mountainous region rising to 878 m above sea level. It has a Mediterranean climate with significant spatial heterogeneity; this in turn is associated with a botanically diverse flora (El-Tantawi 2005; Hegazy et al. 2011). *A. pavarii* is a large shrub or small tree, long recognized as an important endemic (Gimingham and Walton 1954; Keith 1965). The species is globally threatened and categorized as vulnerable by the International Union for Conservation of Nature IUCN) (IUCN 2013). The IUCN Redlist and the "Global Biodiversity

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Information Facility-GBIF", as well as the "Encyclopedia of life" recognize *A. pavarii* as a distinct species endemic to Libya. However the Taxonomic database "Catalog of Life" suggests that *A. pavarii* is a synonym for the widespread Mediterranean species, *A. unedo*. In case the taxonomy should change in the future, we include as Fig. 1, photographs of the study species growing in the wild.

Flowering occurs in late spring and fruits mature in late summer (Jafri and El-Gadi 1977/1993). The fruit is globose, a many-seeded berry, yellow to orange in colour, turning red when fully ripe—hence the common name for the genus of "strawberry tree" and locally known as "*Shmeri*". *A. pavarii* is reported to grow at elevations above 230 m. Plants appear to grow more sparsely and have fewer branches in the southern part of the region.

The species is widely used as a fuel plant, and its flowers are a significant source of nectar and pollen for bees. The leaves, fruits and bark are used in tanning and as animal fodder, and the fruits are consumed locally. Fruits are a good source of nutrients, minerals and antioxidants, especially vitamin C (85 mg/g fresh weight), and are high in carbohydrate and caloric content (Hegazy et al. 2013). The species is used as a herbal remedy for gastritis and renal infections (El-Darier and El-Mogaspi 2009; Hamad et al. 2011; Louhaichi et al. 2011; Hegazy et al. 2013), and is also being assessed as a potential source of new antimicrobial and anticancer compounds (Alsabri et al. 2013).

Materials and methods

Study sites

Twenty study sites were selected within the mountainous landscape and numbered in order of increasing elevation

Fig. 1 Individual tree of *Arbutus pavarii* (about 4 m height) at the *left side* with inserted in mature fruits, vegetative branches at the *lower right side*, and branches with immature *yellow* fruits above

with the lowest first (Fig. 2; Table 1). Average temperature per month and total rainfall per month across the region were calculated from climate data collected at three permanent weather stations: Al Marj, at 325 m elevation, Shahat at 355 m, and Al Bieda at 646 m. (LNMC 2012; in Fig. 2 for locations).The climate does not follow a simple elevational gradient, due to other factors such as distance from the influence of the Mediterranean Sea. Thus sites at lower elevation, but adjacent to the Mediterranean (the northern part of the study region) such as Shahat (at 355 m elevation), experienced lower monthly temperatures and higher rainfall than sites at higher elevations and further inland, like Al Bieda (at 646 m), located on a south-facing slope (Fig. 3).

Population structure and trait analysis

A total of twenty stands representing the different study sites, where within each stand five quadrats (each 10×10 m) were demarcated within the study area (see Kabiel et al. 2016). The density of shrubs was recorded at each quadrat. Shrubs were categorized into size classes according to their estimated volume (calculated as $\pi/6$ $R_1R_2R_3$, where R_1 = the height, and R_2 and R_3 represent the major and minor dia/meters of the crown). Plants were grouped according to their volume: size class A ≤ 0.5 m^3, size class B = 0.5–2 m^3 and size class C ≥ 2 m^3. The percentage contribution of each size class to each population was calculated.

In addition to these measures of plant size, persistence and recruitment were estimated at each location. Persistence was represented by the height of the trees, in meters, plant cover per m^2, and the number of secondary branches (branches coming off the main trunk) per individual. Recruitment was represented by the presence of members of the smallest size class, including any seedlings observed. Reproductive potential was represented by the number of fruits per branch, total number of fruits per individual, and the percentage of plants at a site that were fruiting. Relationships among traits, and elevation were examined. The relative standard deviation or coefficient of variation (CV), defined as the ratio of the standard deviation to the mean, was estimated in order to evaluate the variability of each trait within populations. To evaluate the effect on traits of increasing elevation along the same mountain slope, five sub-regions were identified: (A) Wadi El Akar (sites 2, 4 and 5); (B) Wadi El Kouf (sites 3, 9 and 10); (C) Ras El Hilal (sites 1, 11 and 13); (D) Labrag (sites 15, 17 and 18); and (E) Slonta (sites 16, 19 and 20). The remaining sites (sites 6, 7, 8, 12 and 14) were more widely distributed across the region.

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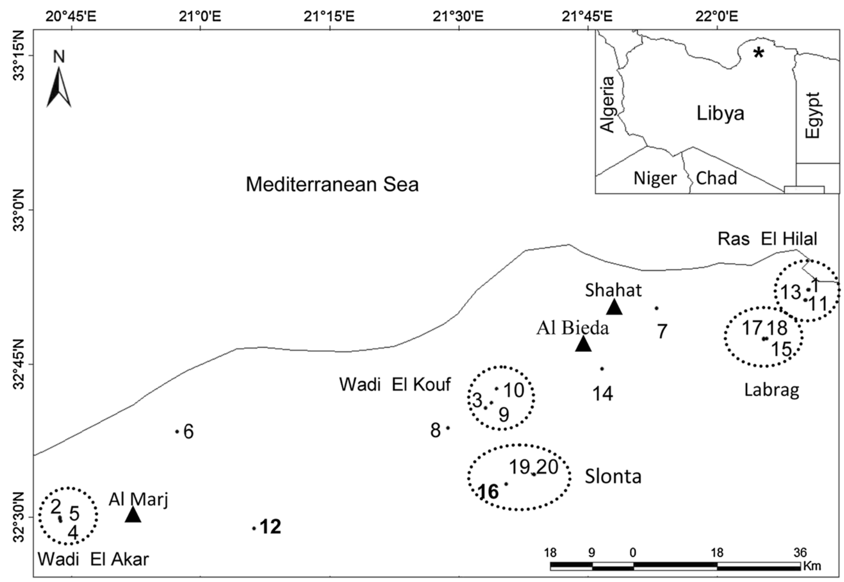

Fig. 2 Map of the study area and site locations within Al-Akhdar mountainous landscape. The numbers assigned to each site correspond to their relative elevation above sea level, with site 1 being at the lowest, and site 20 being at the highest elevation. Sites with a south-facing aspect (#12 and 16) are indicated in bold. See Table 1 for more detailed information on each site. The three weather stations where environmental data were collected are indicated with triangles (Al Marj, Shahat and Al Bieda)

Table 1 Location, elevation, and habitat type or aspect of study sites of *Arbutus pavarii* in the Al-Akhdar mountainous landscape

Population	E	D	Location	Site	Habitat or aspect
1	285	1.5	32° 52′ 16.6″N 22° 10′ 40.7″E	Ras El Hilal (a)	North-facing slope
2	302	11	32° 30′ 04.1″N 20° 43′ 40.4″E	Wadi El Akar (a)	Wadi
3	310	15	32° 41′ 15.0″N 21° 33′ 48.6″E	Wadi El Kouf (a)	Wadi
4	317	13	32° 29′ 40.1″N 20° 43′ 48.4″E	Wadi El Akar (b)	Wadi
5	325	12	32° 29′ 55.0″N 20° 43′ 41.7″E	Wadi El Akar (c)	Wadi
6	350	8	32° 38′ 24.5″N 20° 57′ 19.6″E	Derissia	North-facing slope
7	355	6	32° 50′ 29.1″N 21° 53′ 03.9″E	Shahat -Susa Road	North-facing slope
8	376	18	32° 38′ 46.4″N 21° 28′ 48.0″ E	Qasr Libya	North-facing slope
9	391	17	32° 40 42.6″N 21° 33′ 09.7″E	Wadi El Kouf (b)	Wadi
10	440	15	32° 42′ 36.8″N 21° 34′ 28.9″E	Wadi El Kouf (c)	Wadi
11	442	4	32° 51′ 15.5″N 22° 10′ 22.5″E	Ras El Hilal (b)	North-facing slope
12	448	30	32° 28′ 59.0″N 21° 06′ 19.4″E	Taknis	South-facing slope
13	452	4	32° 51′ 16.2″N 22° 10′ 20.8″E	Ras El Hilal (c)	North-facing slope
14	580	18	32° 44′ 31.5″N 21° 46′ 41.5″E	Wadi El Gharega	Wadi
15	673	12	32° 47′ 29.4″N 22° 05′ 51.8″E	Labrag (a)	North-facing slope
16	675	30	32° 33′ 19.3″N 21° 35′ 32.3″E	Slonta (a)	South-facing slope
17	685	11	32° 47′ 29.3″N 22° 05′ 29.3″E	Labrag (b)	North-facing slope
18	687	11	32° 47′ 28.1″N 22° 05′ 29.4″E	Labrag (c)	North-facing slope
19	713	28	32° 34′ 13.9″N 21° 38′ 48.1″E	Slonta (b)	Mountain top
20	738	31	32° 34′ 14.6″N 21° 38′ 46.2″E	Slonta (c)	Mountain top

E elevation (meter a.s.l), *D* distance from the sea in kilometers

Results

Population structure

Overall, *A. pavarii* populations had relatively few recent recruits. Only about 15 % of individuals were <0.5 m^3 in volume, whereas 21.5 % were in the 0.5–1 m^3 range (Fig. 4a). Nearly half of the individuals were between 0.5 and 2 m^3 in size, and a third were >2 m^3 (Fig. 4a, b).

Populations 7, 12, 14 and 16, located in different parts of the region, at various elevations, habitats and aspects (all <675 m elevation), had many plants in the smallest size class (A), constituting 92–100 % of individuals (Fig. 4c). In contrast the smallest size class was entirely absent at sites 2, 10, 11, 15, 17, 18, 19 and 20. Plants in size class B

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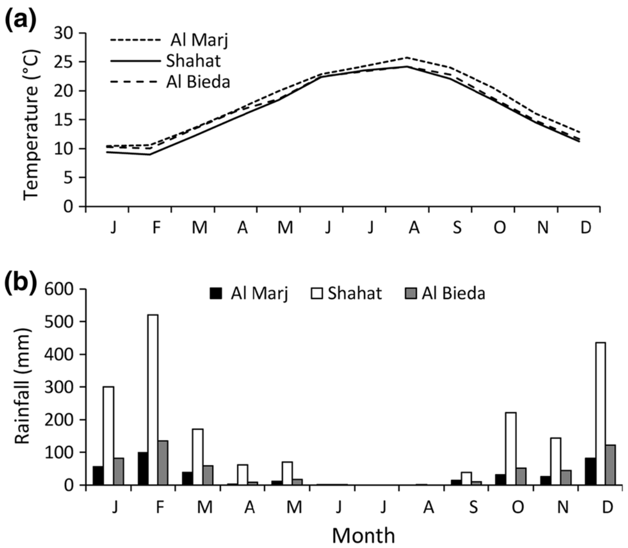

Fig. 3 Average monthly temperature (**a**) and total amount of rainfall (**b**) along an altitudinal gradient in the Al-Akhdar mountainous region. Al Marj is at 325 m, Shahat is at 355 m, and Al Bieda is at 646 m a.s.l. For locations of these sites see Fig. 2

contributed >50 % of individuals at Populations 1, 3, 5, 6, 8, 9, 10, 13 and 15. Three of these populations were located in wadis; the others were on north-facing slopes (Fig. 4c). Large mature plants in size class C made up >50 % of populations on north-facing sites and mountaintops at elevations ≥685 m. At lower elevations these large plants also made up >50 % of the population, for example in Wadi El Akar (populations 2 and 4) at elevations <317 m, and at site 13 (Ras El Hilal-c) near the Mediterranean coast, on the north-facing slopes at 442 m elevation (Fig. 4c).

The greatest population density, of about 40 individuals per 100 m^2, was recorded at sites 13 and 17: Ras El Hilal and Labrag-b, at 452 and 685 m, respectively (Fig. 4d). Very low densities of fewer than 10 individuals per 100 m^2 were recorded on sites of southerly aspect [sites 4, 7, 12, 14 and 16—namely, Wadi El Akar-b (317 m), Shahat-Susa Road (355 m), Taknis (448 m), Wadi El Gharega (580 m) and Slonta (675 m)]. At elevations ≥685 m, plant density decreased, with 16 individuals per 100 m^2 recorded at 738 m, at the top of the mountain range (Fig. 4d).

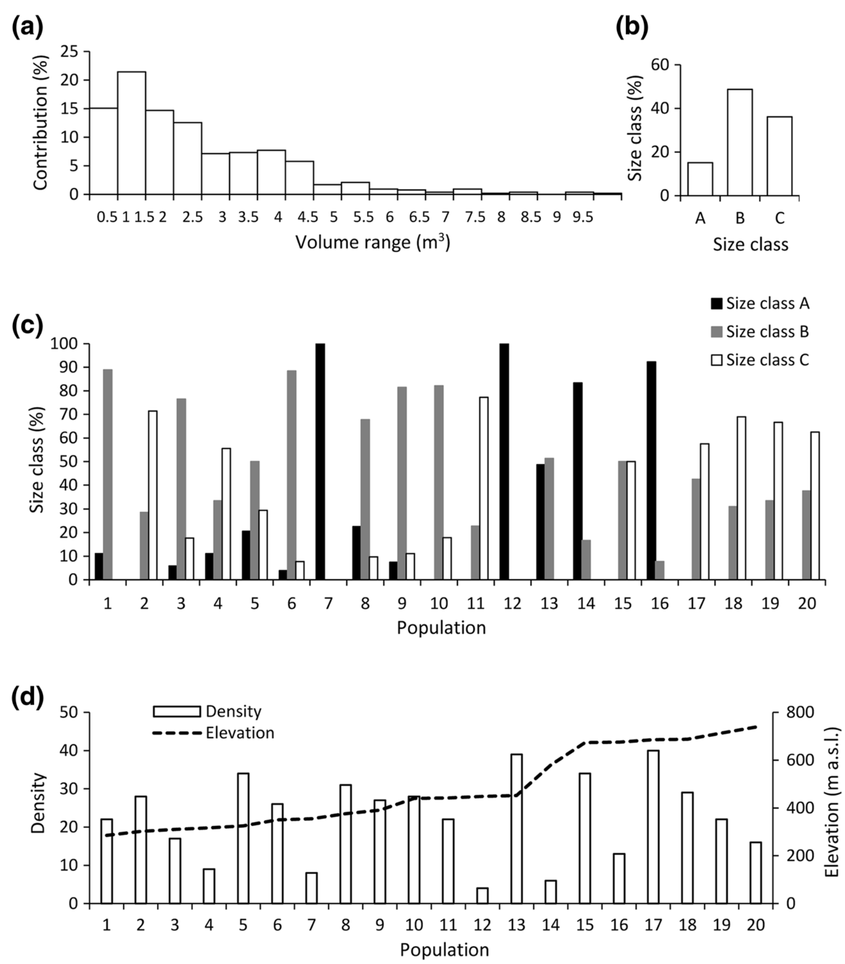

Fig. 4 **a** Overall size-frequency distribution of *A. pavarii* plants in the Al-Akhdar region. **b** Overall relative abundance of the three major size classes where A ≤ 0.5 m^3, B = 0.5–2 m^3, C ≥ 2 m^3. **c** Relative abundance of the three size classes in each of the 20 populations studied; **d** density of *A. pavarii* individuals per 100 m^2 in each of the 20 populations studied. Note sites are numbered along an elevation gradient, with one being at the lowest elevation and 20 being at the highest

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Functional variability

There was no clear relationship between plant height and elevation (Fig. 5; Table 2). The tallest plants (3.58 m ± 0.55) were found at Ras El Hilal-b (site 11) east of the Al Akhdar Mountains (at 442 m elevation, about 5 km from the sea). The shortest plants (0.99 m ± 0.15) were found at Taknis (site 12) to the west (448 m elevation, about 40 km from the sea, see Figs. 5a, 7b). The lowest-elevation site (Ras El Hilal-a, site 1 at 285 m) and the highest-elevation site (Slonta-c, site 20, 738 m) had plants of similar height (1.91 m ± 0.43 and 1.62 m ± 0.24 respectively, Figs. 5a, 7b). The trend in terms of the CV was not statistically significant, with similar values at low and high elevations, ranging from 1.19 m at 685 m elevation at Labrag (b) to 12.09 m at 355 m elevation at Shahat-Susa Road (Fig. 5a).

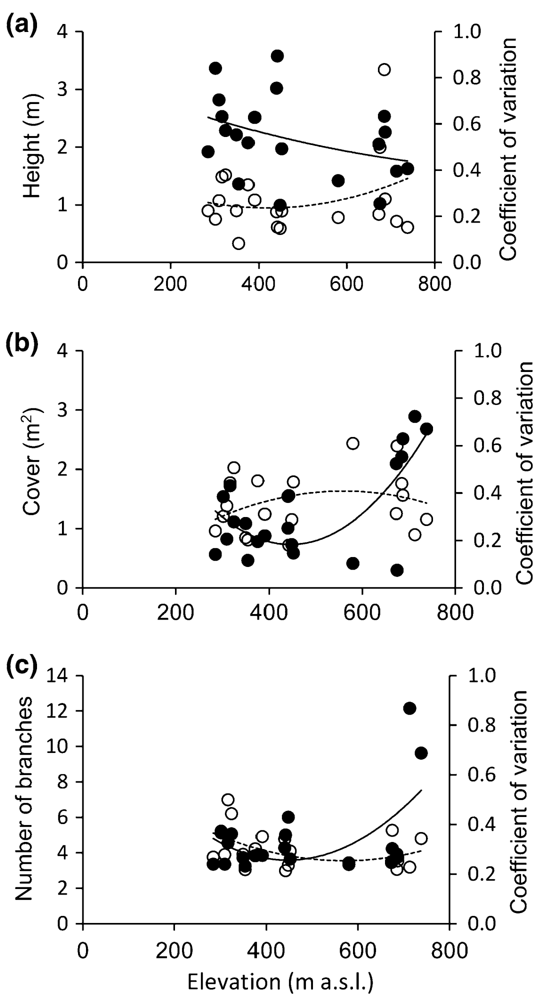

Fig. 5 Vegetative traits (*closed circles*) and magnitude of the coefficient of variation (*open circles*) in *A. pavarii* populations at different elevations within the Al-Akhdar region; **a** plant height in meters; **b** plant cover per square meter; **c** number of branches per individual. See Table 2 for equations

Shrub cover was significantly and positively correlated with elevation ($R^2 = 0.522$, $p < 0.01$, Fig. 5b; Table 2). Greatest cover values were recorded at the highest elevations (between 685 and 735 m). The CV for this trait did not show a significant trend ($R^2 = 0.076$, $p > 0.05$). No significant relationship was seen between the number of branches per shrub and elevation, or the CV for this trait with elevation (Fig. 5c; Table 2). However the greatest intensity of branching (9–12 branches per shrub) was recorded at sites above 700 m, in Slonta (sites 19 and 20; Slonta-b and Slonta-c).

The number of fruits per branch generally increased with elevation ($R^2 = 0.56$, $p < 0.01$) up to 685 m where it reached about 40 fruits per branch. It then decreased to <15 fruits per branch at elevations above 700 m (Fig. 6a; Table 2). Total fruits per individual showed a strong positive relationship with elevation ($R^2 = 0.92$, $p < 0.001$) reaching a maximum of 147 fruits per individual at 713 m (Fig. 6b; Table 2). The increase in number of fruits per branch and total number of fruits per individual is coupled with negative relationship with the increased elevation ($R^2 = 0.67$, $p < 0.01$ and $R^2 = 0.73$, $p < 0.01$, respectively. The percent of plants that were fruiting generally increased with elevation, but due to the several sites where no fruiting plants were observed (sites 1, 7, 13, 14, 16) the trend was not statistically significant; almost all of the plants were fruiting at elevations above 673 m (Fig 6c; Table 2).

Few significant differences in trait values were recorded with changing elevation for populations occurring close together, that is the groups corresponding to Wadi El Akar (sites 2, 4 and 5), Wadi El Kouf (sites 3, 9 and 10), Slonta (sites 16, 19 and 20), Labrag (sites 15, 17 and 18) and Ras El Hilal (sites 1, 13 and 11) (Fig. 7). An exception was the three sites at Ras El Hilal (sites 1, 11 and 13), all of which were on the north-facing slope near the coastal plain (Fig. 7b, c). There, trees at mid-level elevations (Ras El Hilal site 11) were significantly taller and had significantly greater cover than trees at either lower or higher elevations in the region. Another significant pattern was seen at Slonta, where the cover and degree of branching of trees on the (south-facing) slope (site 16, Slonta-a) were significantly lower than on the mountain top sites (sites 19, 20 Slonta-b and Slonta-c) (Fig. 7c, d).

Discussion

Elevation was not the sole or even necessarily the most important variable governing the density and size structure of *A. pavarii* populations; populations at similar elevations within the regional landscape often had different population characteristics. Five of our twenty study populations

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Table 2 Relationship between vegetative and reproductive traits in *A. pavarii* populations, in relation to elevation

Plant traits	Equation	R^2	P value	Statistical significance
Height (m)	$y = 1E - 06x^2 - 0.003x + 3.286$	0.143	0.101	NS
Coefficient of variation	$y = 1E - 06x^2 - 0.001x + 0.461$	0.067	0.332	NS
Cover (m^2)	$y = 2E - 05x^2 - 0.019x + 5.073$	0.522	0.007	**
Coefficient of variation	$y = -2E - 06x^2 + 0.001x - 0.087$	0.076	0.417	NS
Number of branches per individual	$y = 5E - 05x^2 - 0.041x + 12.81$	0.299	0.053	NS
Coefficient of variation	$y = 1E - 06x^2 - 0.001x + 0.699$	0.181	0.166	NS
Number of fruits per branch	$y = -5E - 05x^2 + 0.102x - 23.79$	0.555	0.004	**
Coefficient of variation	$y = 6E - 06x^2 - 0.007x + 2.961$	0.667	0.001	**
Number of fruits per individual	$y = 0.000x^2 - 0.369x + 76.02$	0.924	0.000	***
Coefficient of variation	$y = 6E - 06x^2 - 0.008x + 3.251$	0.731	0.003	**
Percentage of fruiting plants	$y = 0.119x + 17.93$	0.558	0.078	NS

In each case the variable was plotted against elevation and its coefficient of variation was also plotted against elevation. R^2 values are tabulated and statistical significance is indicated as follows: *NS* not significant; * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$

were not fruiting, at sites 1, 7, 12, 14 and 16. They were distributed at elevations from 285 to 675 m, and were not restricted to a specific aspect or to a particular habitat type, but rather were scattered throughout the region.

Perhaps the most striking observation is that the sites where none of the trees were fruiting (sites 1, 7, 13, 14, 16) did not correspond to the sites that showed no juvenile recruitment. Rather, these were the sites where the largest size class, of plants (>2 m^3) was missing. A better explanation for the absence of fruiting at these sites is the simple fact that plants in the population were smaller and pre-reproductive. In contrast, some of the sites with no juveniles such as sites 15, 17, 18, 19 and 20, were particularly successful in terms of fruit production (both in terms of fruits per branch and fruits per individual). This suggests that failed recruitment was not attributable to failed sexual reproduction (cf. Hegazy 1994). Instead the absence of plants in the smaller size classes at many sites might have been due to the greater percentage cover (Fig. 7c) or tree height (Fig. 7b) recorded at these sites, which might limit or prevent seedling establishment. It is possible that sites dominated by larger plants simply have no more suitable sites for seedling establishment (e.g. Ping et al. 2003). It would be useful to follow up with studies on the regeneration niche including light and moisture availability, and intraspecific competition as factors affecting seedling establishment at these sites.

Large plants (>2 m^3), were found in a variety of habitats across the region. Notably, the four highest-elevation sites all showed high proportions of large (volume) trees and no juveniles. This seems contrary to the generally observed trend of reduced tree size at higher elevations that has been reported by several authors (e.g. Barrera et al. 2000), but these trends are usually stated in terms of height rather than tree volume and the height of *A. pavarii* at these sites was lower, even though tree volume was greater.

In a stable and potentially self-sustaining population, there are typically more of the smaller size- or age classes, and progressively fewer of the larger size- and age classes, a "pyramidal" structure indicating ongoing recruitment. In *A. pavarii*, stable size structures, indicating successful juvenile recruitment, were not found at any of the sites. As stated earlier, most sites had no juveniles at all (sites 2, 10, 11, 15, 17, 18, 19, and 20). Sites 1, 7, 12, 14 and 16 supported predominately or only juveniles (size class A) and few if any fruiting individuals, indicating these populations were relatively recently established. In contrast, sites showing high fruit production were typically those with more, larger individuals. They were characterized by dominant mid- and large size classes (B and C), and few (or none) of size class A, indicating low juvenile recruitment. This presents a special challenge for the species in the region; none of the populations was characterized by a stable size structure, and fruiting was absent at the sites where there were juveniles, and juveniles were absent from the sites where plants were fruiting.

Spatial and temporal variations in fruit production and vegetative growth at small ecological scales have been observed in other tree species of limited distribution or at the edge of their ranges (Wiegand et al. 2006; Vilà-Cabrera et al. 2014). In the present situation it would be predicted that tradeoffs between vegetative growth and sexual reproduction (via fruit production), would be seen in the populations dominated by the larger size classes, where cover values and plant density would be greatest, as has been reported for other tree species (e.g. Acharya et al. 2011). However, in the present study high vegetative production and large plant size were accompanied by high fruit production.

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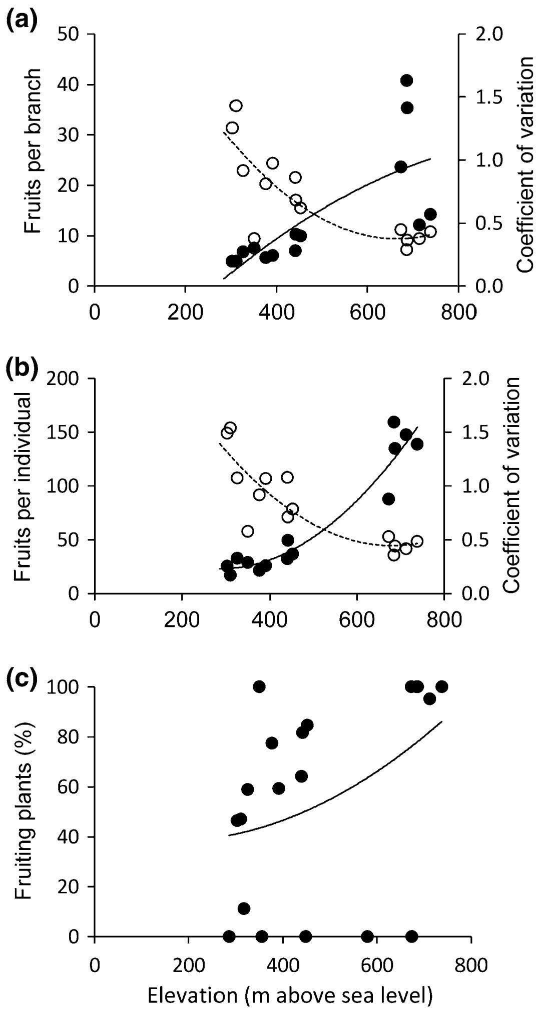

Fig. 6 Reproductive traits (*closed circles*) and coefficient of variation (*open circles*) in *A. pavarii* populations at different elevations within the Al-Akhdar region; **a** number of fruits per branch; **b** number of fruits per individual; **c** percentage of fruiting plants. Populations that lacked fruiting individuals were excluded from Fig. 5a, b

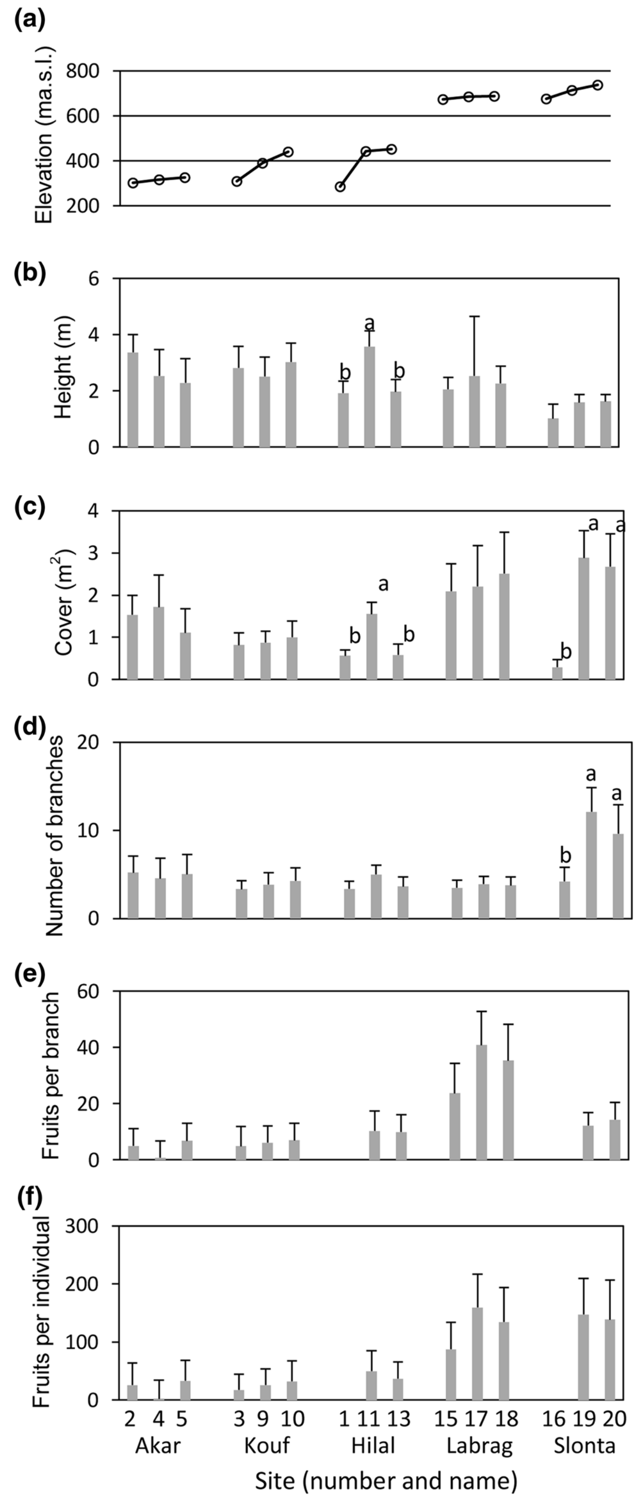

Fig. 7 Vegetative and reproductive traits in populations of *A. pavarii* in five study regions selected to represent increasing elevation within the Al-Akhdar region. Differences among trait values between sites within the same region were not significant at P ≤ 0.05 unless otherwise indicated. See Fig. 2 for site locations and Table 1 for more details on each site. The specific numbers identifying sites within regions are indicated

The significance of elevation as a driver of variation in growth, mediated by climatic effects is well documented (Hegazy et al. 2008; Galván et al. 2014). We have shown in recent studies of another Mediterranean shrub, *Juniperus phoenicia*, that elevation alone may not explain variation in plant traits (Hegazy 2001; Hegazy et al. 2011 and Kabiel et al. 2016). Rather there may be contributions from other factors that affect microclimate, such as aspect and distance from the sea, or exposure to onshore (marine) winds. These in turn directly affect moisture levels and temperature as key factors for plant growth and reproduction.

However in the present study, site type, aspect, elevation, and biotic factors such as plant density, did not provide a simple explanation of the variation between sites. The history of each site might be more important, with

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recently established populations showing no sexual reproduction (due to the predominance of pre-reproductive juveniles), and established sites showing no juvenile recruitment despite high levels of fruit production (perhaps because there were no suitable sites for establishment). It is possible that *A. pavarii* populations go through a cycle of establishment of juveniles, followed by aging and senescence of the population. As this proceeds, it may be followed by periods when suitable sites again become available for successful seedling establishment.

Conservation considerations

Several of our study populations merit particular attention from the conservation perspective. The two populations, on southerly aspects at sites 12 and 16, had low plant density, low vegetative growth (in terms of plant cover and number of branches), and did not produce fruits (they were almost entirely made up of small plants in the <0.5 m^3 category). The same was true of site 7, the Shahat-Susa Road site on a north-facing slope. The predominance of small plants may mean that these populations were only recently established, and none of the plants had yet reached reproductive maturity. It would be valuable to track these populations to determine if they develop stable size structures or are temporary and ultimately die out. Clearly, south-facing slopes located far from the maritime influence of the Mediterranean will experience lower precipitation and higher temperatures; these factors may limit growth and reproduction of *A. pavarii* even where seedlings may have germinated and established successfully. It would be useful to confirm the age of these trees to clarify whether they are young, or simply slow growing.

It may be necessary to reintroduce the species in populations lacking fruit production or evidence of juvenile recruitment. The preliminary findings of El Shatshat et al. (2009) are encouraging as they suggested in situ seed propagation might offer a suitable method for re-establishment of the species. The germination potential of seeds in stressed environmental conditions has not yet been studied. El Shatshat et al. (2009) based their suggestion on the observed high seed production coupled with high germination potential in this species, where seeds germinated immediately after harvest with no evidence of dormancy. However it is worth noting that fruits had spent about eight months ripening on the trees prior to those germination trials, and the study did not provide the opportunity for seeds to acquire dormancy. A more intensive study of non-fruiting populations is needed in order to identify the causes of the failure to fruit and set seed, as this may be due to a variety of causes including simply temporal (or intermittent) variability in seed production, or a high size threshold for initiation of reproduction. It is also possible that, in this insect-pollinated species, pollinator abundance may vary between sites.

Since *A. pavarii* is endemic to Libya's Al-Akhdar mountainous region, it is possible that genetic factors including reproductive isolation, a limited gene pool, population bottlenecks, small effective population size or inbreeding depression may be relevant to conservation efforts. In order to design an effective conservation and management program we also recommend the investigation of spatial genetic patterns in the species. It is likely, for example, that the complex topography of the region may limit gene flow among populations. Wang et al. (2014) reported for *Castanopsis chinensis* and Hegazy et al. (2008) for *Moringa peregrina* that tree populations located in mountains with complex topographic features had distinct genetic composition, even when sites were close. A sound understanding of the spatial genetic pattern of the species will aid in the choice of appropriate source populations for any "genetic rescue" initiatives, if it is found that local populations cannot reproduce successfully due to inbreeding depression or related effects.

The present study illustrates the need for more detailed studies and effective conservation management. The failure of juvenile recruitment in many populations and absence of fruit production in others present a serious demographic threat to the species.

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