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# Grazing pressure versus environmental covariates: Effects on woody and herbaceous plant biodiversity on a limestone mountain in northern Tunisia

**David Anthony Kirk** Corresp., [1] , **F. B. Goldsmith** [2]

[1] Aquila Conservation & Environment Consulting, Ottawa, Ontario, Canada

[2] Department of Biology, University College London, University of London, London, United Kingdom

Corresponding Author: David Anthony Kirk
Email address: david@aquilaecology.com

Mediterranean vegetation is characterized by high biodiversity and conservation value and grazing is controversial. We sampled woody and herbaceous plants on a limestone mountain with strong mesic-xeric gradients, ranked grazing pressure (on a scale of 1-4) and asked whether grazing had a significant effect on plant compositional abundance before and after controlling for environmental covariates. For woody species the shift in means among grazing classes was greater than for herbaceous species according to distance-based redundancy analysis (dbRDA). For herbaceous species differences in multivariate dispersion were greater among grazing classes. Both groups showed significant differences among grazing classes in multivariate location (permutational multivariate ANOVA), even after controlling for aspect. After taking into account biophysical covariates, grazing was not significant and the variation unique to grazing was small. According to best models in dbRDA, grazing was significant in two models for woody species, and all models for herbaceous species. For woody species, spatial variables were most important and confounded with grazing while for herbs, altitude, distance to road, slope, rock outcropping were important. Significant effects of grazing were found for forbs, Poaceae, and Geophytes but not woody and herbaceous legumes. We found a negative relationship between grazing intensity and beta diversity for herbs overall and especially Poaceae, but moderate grazing resulted in higher beta diversity for Geophytes and herbaceous legumes. Jebel Ichkeul provides a microcosm of similar conservation and management issues elsewhere in the Mediterranean. Carefully controlled grazing may enhance plant diversity and maintain the characteristics of maquis vegetation.

Running head: Effect of grazing on maquis vegetation

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David Anthony Kirk[1,2] and F. B. Goldsmith[1]

University College London, Department of Biology, Gower Street, London, United Kingdom WC1E 6BT

Present Address: Aquila Conservation & Environment Consulting, 75 Albert Street, Suite 300, Ottawa, Ontario, Canada, K1P 5E7

Send correspondence to: Dr. D. A. Kirk, Email: david@aquilaecology.com; telephone: (613) 290 7472

**Abstract.** Mediterranean vegetation is characterized by high biodiversity and conservation value and grazing is controversial. We sampled woody and herbaceous plants on a limestone mountain with strong mesic-xeric gradients, ranked grazing pressure (on a scale of 1-4) and asked whether grazing had a significant effect on plant compositional abundance before and after controlling for environmental covariates. For woody species the shift in means among grazing classes was greater than for herbaceous species according to distance-based redundancy analysis (*db*RDA). For herbaceous species differences in multivariate dispersion were greater among grazing classes. Both groups showed significant differences among grazing classes in multivariate location (permutational multivariate ANOVA), even after controlling for aspect. After taking into account biophysical covariates, grazing was not significant and the variation unique to grazing was small. According to best models in *db*RDA, grazing was significant in two models for woody species, and all models for herbaceous species. For woody species, spatial variables were most important and confounded with grazing while for herbs, altitude, distance to road, slope, rock outcropping were important. Significant effects of grazing were found for forbs, Poaceae, and Geophytes but not woody and herbaceous legumes. We found a negative relationship between grazing intensity and beta diversity for herbs overall and especially Poaceae, but moderate grazing resulted in higher beta diversity for Geophytes and herbaceous legumes. Jebel Ichkeul provides a microcosm of similar conservation and management issues elsewhere in the Mediterranean. Carefully controlled grazing may enhance plant diversity and maintain the characteristics of maquis vegetation.

## Introduction

Mediterranean shrublands are highly disturbed landscapes that have been subjected to anthropogenic influence for millennia (Mazzoleni et al. 2004; Papanastasis, 1998; Rundel, 1998; Vogiatzakis et al. 2006). Thus, balancing human use and disturbance with conservation of biodiversity in the Mediterranean region is an ongoing challenge (Falcucci, Maiorano, & Boitani, 2007; Rundel et al., 2016), but at the outset needs to recognize the historical and integrale role played by humans and their livestock (Blondel et al. 2010). Humans have coevolved with the Mediterranean landscape for millennia (Naveh 1990).

Historically, low intensity grazing by domestic livestock and fires set by shepherds may have provided a substitute for previously more abundant native herbivores in maintaining the floristically rich, spatially heterogeneous landscapes of Mediterranean maquis (Le Houérou, 1981; Papanastasis, 1998; Papanastasis, Kyriakakis, & Kazakis, 2002). The shrubland communities that result from this disturbance or those in various successional stages have been highly valued ecologically because of their rich diversity of annuals, and geophytes from the Orchidaceae, Iridaceae and Liliaceae (Pons 1981; Quézel 1981). However, these values have often been based on the belief that diversity begets stability or resilience, which is controversial (see de la Riva et al. 2016). Without such disturbance, many shrublands develop into forests, with concomitant loss of plant diversity, and a build up of organic matter over time, later rendering them susceptible to hot wildfires (Rackham & Moody 1996; Perevolotsky and Seligman 1998; Henkin 2011). Indeed it has been suggested that without management, many endemic species might become extinct (Gomez-Campo 1985). On the other hand, overgrazing and uncontrolled wood-cutting can also lead to loss of plant diversity, erosion and in some areas desertification (Hill et al. 1998; Papanastasis 1998; Papanastasis et al. 2002).

66 The effects of grazing on plant biodiversity are equivocal, being temporally and spatially
67 variable and dependent on many factors (Olff and Ritchie 1998; Olsvig-Whittaker et al. 2006). In
68 some cases, particularly on islands, intensive overgrazing by goats has devastated vegetation and
69 intensified threats to island endemics (Campbell and Donlan 2005). However, many Mediterranean
70 plant species have coevolved with livestock and developed strategies to resist grazing, including
71 spininess, chemical repulsion, prostrate growth, and their ability to grow on remote rocky cliffs
72 inaccessible to livestock (Papanastasis 1998).

73 Shrub formations in the Mediterranean region are dominated by woody, evergreen
74 sclerophyllous (leathery, drought resistant) vegetation (Di Castri 1981). Known variously as karri,
75 chaparral, fynbos, matorral, maquis or garrigue, these shrub communities are classified according to
76 height and structure (Tomaselli 1977). Because of the confusion over terminology of
77 Mediterranean vegetation types, (Tomaselli 1977) argued that the term ‘matorral’ was most
78 appropriate, being 'a stand of xerophilous evergreen woody plants of which the part above ground
79 cannot be clearly differentiated as between trunk and foliage, but whose foliage generally extends
80 to the base'. Such vegetation occurs in five widely separated distinct areas with Mediterranean
81 climates: California (United States), Chile, South Africa, Australia and the Mediterranean Basin in
82 southern Europe and North Africa (Cowling et al. 1996). Characterized by extremely high floristic
83 richness, the Mediterranean region holds about 10% of global plant species diversity (25,000
84 species) on only two percent of the land base and half of the plant species are endemic to the region
85 (Médail and Quézel, 1997; Radford et al. 2011). One of the main contributory factors to high
86 biodiversity in the Mediterranean Basin is believed to be the stability of climate across timescales,
87 including provision of Pleistocene refugia, thus preventing species’ extinctions and facilitating
88 speciation (Nogués-Bravo et al. 2008; Nogués-Bravo et al. 2012).

89 Only 4.7% of the Mediterranean basin has primary ‘natural’ vegetation (Geri et al. 2010)
90 and many of the remaining 'wildlands' of the Mediterranean are restricted to mountainous or
91 coastal regions with slopes too steep for cultivation. Given their long history of human use the
92 question of how to protect and manage these hotspots of biodiversity is a conservation dilemma
93 (Blondel et al. 2010). Prioritizing and setting aside protected areas such as National Parks or nature
94 reserves is one approach to conserving Mediterranean shrublands, but these constitute a relatively
95 small area, and even in these protected landscapes vegetation quality has declined (Wilson et al.
96 2007). With predicted high impacts of climate change, areas of high plant endemism in the
97 Mediterranean are a cause for concern and it has been forecasted that the frequency and intensity of
98 drought and desertification will lead increasingly to loss of plant biodiversity (Gauquelin et al.
99 2016) and this could influence functional heterogeneity (de la Riva et al. 2016). Thus, fundamental
100 to the conservation of Mediterranean flora is the question of intervention or protection to maintain
101 the diversity of plant communities and the challenge of integrating multiple uses of Mediterranean
102 landscapes in the face of climate change.
103 Although concern has been expressed about conservation of the Mediterranean wooded
104 landscape significant knowledge gaps in plant ecology still exist, particularly in North Africa
105 (Radford et al. 2011). About 11% of the 48.2 million ha of forests occurring in the Mediterranean
106 Basin occur within this region and in some areas deforestation and overgrazing has created serious
107 ecological disfunction, especially in high altitude forests (Quézel et al. 1999). This has resulted in
108 four consequences: 1) disruption of natural disturbance cycles; 2) homogenization of plant
109 assemblages in terms of structure and compostion; 3) loss of biodiversity in forest species; and 4)
110 increases in invasive plants (Quézel et al. 1999).

Jebel Ichkeul, a limestone mountain within Le Parc National de L'Ichkeul in the north of the Republic of Tunisia, represents a microcosm of many of the conservation issues and human threats facing Mediterranean vegetation including overgrazing, wood-cutting and invasive plant species. In a recent assessment of the threats to Important Plant Areas (IPAs) in the south and eastern Mediterranean, (Radford et al. 2011) identified overgrazing as the main threat to IPAs in Tunisia (see also Underwood et al. 2009). In the early 1980s when we conducted our study, the forests and maquis of Jebel Ichkeul provided nutritious grazing (graminoids and legumes) for livestock (goats, sheep and cattle), particularly during the autumn and winter months (Hollis 1977). The marshlands and wetlands of the National Park were a source of nutritious forage at other times of year and over 2,500 livestock grazed in the national park (Anon 1988). Combined with uncontrolled wood-cutting for firewood on the southern slopes of the mountain this grazing caused loss of vegetation cover, reduced species diversity, soil erosion and spread of invasive plants (Fay 1980). These impacts were most apparent in close proximity to gourbi village settlements and the Hammams (hot springs) located at the foot of the mountain. Illegal quarries, since closed, also mined limestone on the southern slopes of the Jebel, and contributed to the xeric conditions at these sites, and potentially dust pollution (Kirk 1983). One potentially ecologically sustainable use was ethnobotany; the mountain provided medicinal herb species for local people (Fay 1980), but the impact on plants was not monitored. Collection of plants for medicinal use has to be carried out sustainably otherwise it can lead to endangerment as in Syria (Radford et al. 2011).

In this paper we ask: 1) what is the impact of grazing on plant biodiversity of functional groups (woody and herbaceous as well as grasses, legumes and Geophytes) at Jebel Ichkeul and how much unique variation in species composition and abundance is explained by this factor; 2) is the impact of grazing on plant beta diversity still significant after controlling for the main

environmental drivers and 3) what is the effect of *Olea europaea* size and density on herbaceous or other woody plant species compared to abiotic natural features(Osem et al. 2007; Shachak et al. 2008; Agra and Ne'eman 2009). Our results can provide a framework for the conservation and sustainable use of the Jebel's forests and maquis and contribute to the broader question of the impact of grazing and the structure of woody vegetation on maquis vegetation elsewhere in the Mediterranean, both inside and outside protected areas. They also provide a baseline of plant species composition prior to the onset of climate change.

## Methods

*Study area*

Containing one of the last remaining permanent freshwater lakes in North Africa, Le Parc National de L'Ichkeul is an internationally important wetland and is listed as a World Heritage Site, Ramsar site and Biosphere reserve. Typically the lake held fresh water in the winter and saline water in the summer when the water level fell below that of Lac de Bizerte and the Oued Tindja reversed its flow. In the 1990s, dams constructed on the main rivers contributed to highly saline conditions and significant loss of biodiversity in the marshes of national park; however, the ecological functioning of the park and some of the wetland diversity was believed to be largely restored by heavy rainfall in 2003 /2004and 2005/2006 (Ghrabi-Gammar et al. 2006; Ouali et al. 2014) and its World Heritage status was restored (IUCN, 2003).

Set in the Mateur plain, Jebel Ichkeul is 25 km south-west of Bizerte in north-eastern Tunisia and 15 km south of the Mediterranean sea (37° 10' N, 09° 40' E; Figure 1). It is surrounded along the northern flanks by Garaet el Icheul, while south of the southern perimeter there is intensive arable farming, pasture and orchards (UNEP/WCMC 2003). Formerly an island within

Lac Ichkeul, the dolomitic massif covers an area of 1,363 ha (13.6 km$^2$); 690 ha of this was gazetted in the original declaration of the National Park in 1977 (Hollis 1977; Hollis 1986). Jebel Ichkeul was listed as an Important Plant Area (IPA) in 2000 (Radford et al. 2011), and is nationally important (Peterken and Radford, 1971). Of the 29 plant families listed for the Mediterranean region (Quézel 1981), 24 occur on the Jebel, including the rare Tunisian endemic *Teucrium schoenenbergeri* (Fay 1980). Managed as a hunting reserve in 1240 AD by the dynasty of the Hafsids, Jebel Ichkeul was acquired by the state government in 1890 (UNEP/WCMC 2003).

Jebel Ichkeul was listed in the European Red list of Habitats as one of the most typical examples of *Olea europaea* var *sylvestris* with *Ceratonia siliqua* and *Pistacia lentiscus* along with southern Andalusia, Menorca, Sardinia, Sicily, Calabria and Crete (European Environment Agency 2017) . It has extremely high vegetation heterogeneity because of its varied geology (dolomite, calc-schist and marble), dissected relief, high altitude (maximum 512 m.a.s.l.), adjacent Lac Ichkeul and spatially varying anthropogenic factors (Daoud-Bouattour et al. 2007). The northern slopes facing Lac Ichkeul are generally mesic with high spatial heterogeneity and often continuous vegetation cover. By contrast, the southern aspects of the mountain had illegal limestone quarries (now abandoned), contained most of the gourbi village settlements and as a consequence had xeric plant communities. A road running along the southern flanks of the mountain links the villages and quarries and is served by some secondary roads from the Mateur Plain (Figure 1). On the southern slopes of the mountain sites with high soil pH occur due to their calc-schist parent material, while the northern slopes are mostly dolomitic. Jebel Ichkeul occurs in the Mediterranean bioclimatic zone with a summer drought (Daget 1977). Mean monthly temperatures range from 11.3$^o$C in January (winter minimum 0$^o$C) to a mean of 25.2$^o$C in July (summer maximum 40$^o$C). The average annual rainfall is 625 mm, with only 4 per cent of this falling in summer (Hollis 1977).

180

181 *Plant surveys and sampling design*

182 We conducted this study between 18 June and 7 August 1983. To describe plant species
183 distribution and abundance, we located 78 quadrats on the Jebel, stratified using the data and
184 vegetation maps in Fay (Fay 1980) for guidance. Except for inaccessible crags and steep cliffs, we
185 sampled all vegetation types. At each location we threw a quadrat randomly to locate the centre of
186 the sampling site. We used a nested quadrat design with dimensions of 2 x 2m, 5 x 5m, 7.07 x
187 7.07m, 10 x 10m, and 14 x 14m (Bunce 1982). We estimated cover-abundance for herbaceous and
188 woody species within the 2 x 2m quadrat and the 10 x 10 m quadrat, respectively, using a modified
189 Braun Blanquet scale (e.g., <1%, 1-5%, 6-10%, 11-25%, 26-50%, 51-75%, >75%). In the
190 remaining quadrats we recorded presence-absence of species but here present only data from the 2 x
191 2 m and 10 x 10 m quadrats. On average three quadrats were surveyed during 8-10 hours of
192 fieldwork per day.

193

194 *Identifying plant species*

195 We collected and pressed any plants not identified in the field and compared them with specimens
196 at the herbarium in Tunis or the British Museum herbarium in the United Kingdom. Our study took
197 place towards the end of the flowering period for many herbaceous species (Daoud-Bouattour et al.
198 2007). Thus, families like the Liliaceae and Orchidaceae, which die back by early summer, were
199 probably under-recorded. Other species were difficult to identify in this condition. Leaves of
200 *Asphodelus ramosus* subsp. *ramosus* resemble those of *Moraea sisyrinchium*, and some other
201 Asphodelaceae had similar leaves. Among other groups, the following species pairs were combined
202 because they could not be easily distinguished: *Hypochoeris achyrophorus and H. saldensis;*

*Hyoseris radiata* and *H. scabra; Hippocrepis minor* and *H. unisiliquosa;* and *Sedum tuberosum* and *S. rubens*.

Since conducting our study plant nomenclature has changed substantially (Supplementary Tables 1 and 2). We updated all plant names using a combination of sources – the Euro-Med Plantbase (PlantBase 2017), or the Medchecklist (Medchecklist 2012). Plant names and occurrences in the national park were also verified by a plant ecologist at the University of Tunis (A. Daoud Bouattour, pers. comm. 2012), and the final names are based on a catalogue of plants of Tunisia (Le Floc'h et al. 2010), as well as a flora of the national park compiled since our study (Daoud-Bouattour et al. 2007).

*Measuring grazing intensity*

At each of the quadrat locations within the 10 x 10 m square, we recorded browsing by livestock on the principal woody plant species as: 1) unbrowsed; no evidence of grazing; (i.e. dense forests, forests with gaps or high altitude arborescent matorral); 2) lightly browsed; (i.e. dense middle or low matorral with trees showing signs of browsing on shrubs); 3) bushes clipped to a hedge-like shape; and 4) severely clipped to short stunted bushes; (i.e., scattered low matorral communities) as in Tomaselli (1977). We also recorded the activity of herbivorous mammals qualitatively by signs such as hair on tree trunks, droppings and feeding signs (e.g., Wild Boar *Sus scrofa* often left uprooted tubers and soil disturbance).

*Controlling for biophysical features*

It is critical to consider the effect of other environmental covariates on plant species compositional turnover as these are often confounded with grazing (Arévalo et al. 2011). We therefore measured a suite of biophysical variables at the centre of each quadrat (Table 1). Mediterranean maquis vegetation is strongly influenced by soil moisture (Sardans and Peñuelas 2013). At Jebel Ichkeul, prevailing westerly winds carry moisture from the lake and create a humidity gradient from northerly mesic vegetation to xeric southern vegetation (Fay 1980). We did not have estimates of humidity or soil moisture but because of the orientation of Jebel Ichkeul within the Mateur Plain (Figure 1), we could use the spatial coordinates of quadrats as a proxy for a moisture gradient. Thus we determined the spatial locations (latitude, longitude) of all quadrats in Google Earth (see Treatment of species data and environmental covariates).

We recorded altitude with a field altimeter. Because slope aspect plays an important role in the distribution of woody vegetation in the Mediterranean (Sternberg and Shoshany 2001) we also measured slope using an inclinometer (Abney Level - Eugene Dietzgen, Chicago, USA) and recorded compass aspect as a proxy for solar insolation. Soil depth and characteristics play a strong role in shaping Mediterranean shrub communities (Molina-Venegas et al. 2016), so we recorded the percentage of rock outcropping or rock cover at quadrats. Because soils on the Jebel were highly variable (ranging from deep loams to sandy substrates - Fay 1980), we collected soil samples at 50 sites for analysis. Soils were often very shallow and compacted, so we removed samples with a hand trowel from the A horizon. We placed soils in sealed plastic bags and refrigerated them for about six weeks before analysis. We measured pH by wetting soil to a paste-like consistency, and took the average of duplicate readings from different parts of the sample with a glass electrode. We also compared calcium-magnesium ratios for six contrasting sites, three on the degraded southern slopes and three on the relatively pristine northern slopes.

248

249 *Tree diameter measurements and relative abundance estimates*

250 Woody vegetation may shade out herbaceous species and thus be considered an environmental
251 modulator influencing the composition and abundance of herbaceous plant species (Agra and
252 Ne'eman 2009; Segoli et al. 2012). Woody vegetation, especially *Olea europaea*, is also a key
253 indicator and surrogate for the intensity of anthropogenic activities, including assessment of grazing
254 and wood-cutting activities. Therefore, we measured *Olea europaea* stems (> 4cm) in the 10 x 10
255 m quadrat at breast height (dbh; c 1.5m) and at 30 cm above ground level for 69 sites. The 30 cm
256 height measurement provided the most data because in shallow soils or heavily grazed sites most
257 trees were too small to obtain a breast height measurement. We then calculated *Olea* densities in 0-
258 5, 6-10, 11-15, 16-20 and >20 cm circumference size classes. Where trees bifurcated, all stems
259 were measured and the following calculation was used to provide a single diameter comparable with
260 a tree of the same surface area:

261 $$r_i = c_i/2\pi$$

262 $$A_i = \pi \times r_i^2$$

263 $$A = \Sigma A_i$$

264 $$r = \sqrt{(A/\pi)}$$

265 where $r_i$ = radius of stem i, $c_i$ = circumference of stem i, $\pi$ = 3.146; $A_i$ = surface area of stem i, A =
266 total surface area of all stems and r = equivalent radius.

267

268 *Spatial variation and other human footprint variables*

269 We predicted that proximity to human dwellings and roads would influence vegetation since
270 these are sources and conduits for livestock, respectively. Therefore, we used ArcGIS (version

10.5.1, ESRI 2017) to extract and download satellite imagery and calculate the distance from survey sites to the nearest road and the nearest settlement. For roads, the ArcGIS shapefile was extracted from CloudMade data (OpenStreetMap contributors 2015) collected in 1982. For settlements we manually dropped pins on buildings from the ArcGIS Google Earth Imagery basemap (imagery 2016, data from the 1980s were not available at sufficiently accurate resolution). Because distance to road and distance to settlement were highly correlated (Pearson R = 0.89), we included only one of these variables in separate models. To account for nonlinear plant responses to spatial location, we normalized latitude and longitude and derived trend surface variables (latitude$^2$, latitude$^3$ etc.) which we then included in models.

*Treatment of species data and environmental covariates*

All plant cover data were square-root transformed before creating a resemblance matrix to reduce the effect of high values; we used the Bray-Curtis distance similarity measure for all multivariate species analyses (Anderson et al. 2008). We also grouped species into functional groups that we predicted would have differing responses to grazing: these included Poaceae (Graminoids), herbaceous legumes, Geophytes, all herbaceous forbs (annual and perennial), shrub legumes and shrubs/trees (similar to those in Fernández-Lugo et al. 2013). For the 'all herbaceous forbs' functional group we retained ferns, cactuses, club mosses and some unidentified mosses. However, we did not differentiate between annual and perennial species as in Fernández-Lugo et al. (2013) because our study took place over a single season. We also calculated species richness (alpha), and Shannon diversity indices for overall woody and herbaceous functional groups.

For the environmental covariates we inspected draftsman plots to determine whether variable distributions were approximately linear. For example, untransformed altitude data showed

294 a quadratic (bell-shaped) relationship with latitude, which was improved by transformation. We
295 log-transformed altitude, distance to roads and settlements and olive diameters using natural
296 logarithms (+0.1 was added as a constant to the latter because of zero values) to reduce skewness
297 after examining draftsman plots (Anderson et al. 2008). Distributions of other variables were not
298 improved by transformation. Because it is a circular variable we also transformed aspect using a
299 trigonometric function (Roberts 1986) into two variables 'northness' (the cosine of aspect) and
300 'eastness' (the sine of aspect). Since these were not significant and not easily interpretable in
301 ordination models, we also created eight classes of aspect based on compass bearings: (1: 0-45$^{o}$
302 (NNE); 2: 46-90$^{o}$ (ESE); 3: 91-135$^{o}$ (SSE); 4: 136-180$^{o}$ (SSW); 5: 181-225$^{o}$ (WSW); 6: 226-270$^{o}$
303 (WNW); 7: 271-315$^{o}$ (NNW); 8: 316-360$^{o}$ (ENE). For alternate models we pooled the aspect
304 classes into 'north' and 'south' to simplify model structure. For the eight aspect classes we
305 grouped variables into an indicator group as this was a binary categorical variable; trend surface
306 variables were treated similarly as these were all derived from spatial coordinates. We explored
307 models treating grazing as a grouped categorical variable and as a semi-quantitative variable.
308
309 *What are the main patterns in plant species distribution and abundance and how do these relate to*
310 *environmental factors?*
311 Because the effects of grazing and other human activities could differentially affect plant species,
312 we subdivided plant species into woody and herbaceous categories and other functional groups (see
313 above; Appendix 1). We visualized woody and herbaceous species groups using non-metric multi-
314 dimensional scaling (*n*MDS) to investigate general patterns in plant species composition and
315 abundance for all 78 sites (Clarke and Gorley, 2014). Superimposing species and environmental
316 covariate vectors (Pearson correlations) on *n*MDS ordinations enabled us to identify indicator

317 species for grazing pressure and of different plant assemblages. Doing so allowed us to use all 78
318 sites and all variables in the ordination as these correlations were *post-hoc* (thus missing values, and
319 sites for which we did not have environmental data, such as soil pH, could be included in
320 exploratory analyses).

321 To statistically separate out the effects of grazing versus the other main factors driving variation in
322 plant species distribution and abundance we used distance-based redundancy analysis (*db*RDA -
323 Legendre & Anderson 1999). We first conducted models for the 50 sites with soil pH data to test if
324 the overall effect of soil pH was significant. Since soil pH had no effect we excluded this variable
325 from all further models, enabling us to maximize sample sizes (most of the 28 sites lacking soil pH
326 data were at high altitude, so omission of these sites would also have compromised the length of
327 environmental gradients investigated).

328 We then performed two *db*RDA models, first with all 78 sites and second with the 69 sites for
329 which data on size classes of *Olea europaea* were available. For each of these subsets we first ran a
330 *db*RDA model to identify the best 10 model solutions selected using Akaike's Information Criterion
331 corrected for small sample size ($AIC_c$). Because we were specifically interested in grazing and
332 human footprint (e.g., distance to road) we selected models containing these variables for ordination
333 plots. For each of the 10 best models, we then ran separate models using forward selection of
334 variables to obtain significance levels. For the woody species analysis we excluded *Olea europaea*
335 from the resemblance matrix since cover values for this species were confounded with the densities
336 of *Olea* by diameter size class.

337 We partitioned the variance among subsets of grazing classes, biophysical factors (altitude,
338 aspect, slope, rock outcrops), spatial variables (including trend surface variables, distance to road
339 and settlement) and *Olea* densities by size class to determine the amount of unique and shared

variance among these subsets. This also allowed us to assess the relative importance of variable subsets in driving woody and herbaceous assemblages, respectively. Variance partitioning was conducted following methods outlined by Legendre & Legendre (2012). We examined the variance explained by different subsets to factor out the effect of grazing versus spatial effect and biophysical features (see Table 1). All *db*RDA analyses were performed for woody species and herbaceous species separately but not for finer subdivisions (e.g., Graminoids, Geophytes etc.) within these groups.

*Effects of grazing on woody and herbaceous plant distribution and abundance*

First, to provide a visualization of the variability in the averages within each grazing group we calculated 95% bootstrapped averages (Anderson et al. 2008). Comparison of the relative sizes of these ellipses provided information on differences in the underlying variation in average values (beta diversity) within grazing classes. Second, we performed two tests to evaluate whether differences between grazing classes were due to variation in multivariate dispersion (test for the homogeneity of multivariate dispersions) or location in multivariate ordination space (permutational multivariate ANOVA), or both. The first test was performed using the routine PERMDISP, which provides a direct measure of beta diversity (Anderson et al. 2008). The second test was done using a one-way permutational multivariate ANOVA to ascertain whether there were differences in multivariate locations between grazing classes. This model was set up with grazing class as a fixed effect; we also conducted *post hoc* pairwise t-tests between grazing classes. We performed a second, two-way permutational multivariate ANOVA model including grazing as a fixed effect, and aspect (eight classes) as a random effect. We inspected P values for the two-way permutational multivariate ANOVA and removed the interaction term (grazing x

363 aspect) when P >0.8. We also pooled the aspect variable when P values were > 0.25 to avoid
364 Type II errors (Anderson et al. 2008). We ran a third one-way permutational multivariate
365 ANOVA to test if the effect of grazing was still significant after controlling for all biophysical
366 covariates. Because our design was unbalanced we used Type I sums of squares for our models
367 to partition the variation explained by different factors and when covariates were used in the
368 models. We performed these models for all functional groups. It is important to note that the
369 multivariate models that we used differentiated between location and dispersion in multivariate
370 space, which has been a criticism of these types of modeling platforms (Warton et al. 2012). We
371 also used Bray-Curtis and not Euclidean distances for resemblance matrices based on
372 compositional species data. Statistical modelling was performed using the software, Primer
373 (Clarke and Gorley 2006), PERMANOVA + (Anderson et al. 2008) and variance partitioning was
374 done in R (R. Core Development Team 2014).
375
376 **Results**
377 *Plant species*
378 We identified 219 of the 348 plant species recorded for Jebel Ichkeul (Fay 1980). Species
379 richness and diversity were highly variable; high altitude, northerly, ridge crest assemblages were
380 most species-rich, while species-poor sites were prevalent on the heavily grazed and cleared lower
381 southerly slopes, where invading ruderals were abundant. Overall, 21% of sites had more than 50
382 species, 32% had 40-50 species, 32% had 30-40 species, and the remainder had less than 30
383 species. The richest site contained 65 species (site 35) and was located near the summit at an
384 altitude of 352 m.a.s.l. Only 16 species were found in the most species-poor quadrat (site 57)
385 which comprised *Ceratonia siliqua* and *Olea europaea* forest. The influence of soil limitations,

386 exposure and grazing in high matorral created clearings rich in herbaceous species, while in deep
387 valleys subject to ephemeral winter flooding closed canopy climax forest had lower species
388 richness.
389
390 *Patterns in plant species distribution and abundance and relationship to environmental factors*
391 According to Tomaselli's criteria (Tomaselli 1977), 75% of the sites we examined comprised
392 forest or matorral with trees, while only 25% of sites had no arborescent individuals. The latter
393 included degraded matorral or 'potential natural vegetation' on ridge crests and valley sides.
394 Grazing had a large impact as shown by the woody species *n*MDS ordination which demonstrated a
395 gradient from low altitude sites with moderate to heavy grazing to high altitude sites with low
396 grazing pressure (Figure 2). Spatial location (latitude) represented a surrogate for a moisture
397 gradient from xeric sites on the southern slopes of the mountain to mesic sites on the northern slopes
398 adjacent to Lac Ichkeul (Figure 2). Similar patterns were evident in the herbaceous species *n*MDS
399 (Figure 3).
400 Woody species indicators associated with unbrowsed sites included *Ceratonia siliqua, Erica*
401 *multiflora, Erica arborea, Pistachia terebinthus* and *Phillyrea angustifolia* (Figure 2;
402 Supplementary Figure 1a, b). These species were associated with mesic sites on the northern slopes
403 of the mountain. By contrast, *Olea europaea* was indicative of heavily grazed sites (Figure 2;
404 Supplementary Figure 1c). A similar pattern was evident for herbaceous species with widespread
405 (often invasive) species - *Chenopodium murale* and *Urtica pilulifera* being indicative of heavily
406 grazed sites, whereas *Geranium robertianum* was typical of shaded locations under closed canopy
407 *Olea* on alluvial fans (Figure 3).

We compiled the best 10 *db*RDA models for all 78 sites for woody and herbaceous species (Tables 2 and 3, respectively). For woody species, spatial location was most important and occurred in all models. Grazing was clearly confounded with spatial location and other variables (Figure 4a) and occurred in two of the top 10 models (Table 2). This was demonstrated by the fact that the grazing index did not occur in models until five variables were included (altitude, slope, distance to road and spatial location). Biophysical variables such as slope, altitude and rock outcrop occurred in 4, 2 models each, respectively. In model 10, which included the grazing index, axis 1 explained 23.9% and axis 2 explained 6.2% of the total variation respectively (Figure 4a). In model 6, which included distance to roads, axis 1 explained 24.6% of the variation and axis 2, 6.2% of the variation. We also ran a second set of *db*RDA models to test the effect of using distance to settlement - detailed models are not reported as results were similar to distance from roads.

For the herbaceous species, the best *db*RDA model contained both the grazing index and distance to roads and explained much less of the total variation on axis 1 than for woody species (6.1%) and axis 2, 3.9% (Table 3, Figure 4c). In contrast to woody species, grazing featured in all models. While distance to roads occurred in four models, biophysical variables were much more important than was the case for woody species such as altitude (8), rock outcrop (5), and slope (5). Spatial location did not occur in any models (Table 3). As for woody species, inclusion of distance to settlements produced similar results to those from distance to road (Figure 4d) so we do not report these in detail.

*Effects of grazing*

We classified 71% of sites as grazing class 1 (unbrowsed, n = 55), 12.8% as grazing class 2 (10), 11.5% as grazing class 3 (9) and 5% as grazing class 4 (4). Heavily grazed sites were generally of low altitude with more rock outcropping and smaller-diameter olive trees (Supplementary Figure 2). According to the test for the homogeneity of multivariate dispersions based on 78 sites, we found a marginally significant difference in woody species beta diversity among the four grazing regimes ($F_{3,74}$ = 3.16, P = 0.0872; Figure 5a). Highest beta diversity for woody species was in grazing classes 2 and 1 followed by grazing classes 3 and 4 (Figure 5a). Pairwise comparisons for woody species demonstrated significant differences between grazing classes 1 and 4 and 2 and 4. The difference among grazing classes for herbaceous plant species beta diversity was highly significant ($F_{3,74}$ = 19.85, P < 0.0001). No difference was found among grazing classes for woody legumes (Figure 5b). For all forb species, beta diversity was highest in grazing class 1, and was similar in grazing classes 2 and 3 (though slightly higher in 3) and lowest in grazing class 4 (Figure 5c). Pairwise comparisons demonstrated significant differences between all grazing classes except between grazing class 2 and 3 (Figure 5c). These results relate to differences in dispersion in multivariate ordination space and suggested that effects of grazing were greater in this respect for herbaceous than for woody species (the opposite to what was found for the *db*RDA models). Separate models for Gramineae revealed similar results to those for forbs overall, except that grazing class 3 had lower beta diversity than class 2 (Figure 5d). However, results for Geophytes and Leguminosae differed, with beta diversity being higher at intermediate levels of grazing (Figures 5e and 5f respectively; tests of main effects overall were non-significant).

Significant differences among grazing classes were also found according to one-way permutational multivariate ANOVA for both woody (pseudo-$F_{3,74}$ = 3.80, P = 0.0001, 9981 unique permutations) and herbaceous plant species (pseudo-$F_{3,74}$ = 1.88, P = 0.0006, 9824 unique

permutations; see also Supplementary Figure 3 for species richness and Shannon index). The two-way permutational multivariate ANOVA demonstrated that grazing still had a significant effect for both woody (pseudo-$F_{3,57}$ = 2.08, P = 0.0555) and herbaceous species (pseudo $F_{3,57}$ = 1.73, P = 0.0218) even after controlling for aspect. However, aspect (8 classes) was not significant for either group (woody pseudo-$F_{3,57}$ = 1.01, P > 0.1; herbaceous pseudo-$F_{3,57}$ = 0.80, P > 0.1) and the interaction was also non-significant (Table 4a). Results differed when aspect was categorized as 'north' and 'south' and was significant for Graminoids, all herbs, all other shrubs and all shrubs/trees (Table 4b). When all biophysical parameters were controlled for as covariates in the one way permutational multivariate ANOVA, the effect of grazing was not significant for either woody or herbaceous species (pseudo-$F_{3,74}$ = 0.936 and 0.817, respectively, both Ps >0.1). This was not surprising because of the strong relationships between grazing, and biophysical factors (e.g., altitude, slope and some slope aspects - positively with SSW, negatively with NNW). We also conducted similar models for other functional groups and detailed results for Gramineae, Geophytes, forbs and shrubs are in Table 4a. However, no significant effect of grazing was found for either herbaceous or woody legume functional groups in the multivariate permutational ANOVA (Table 4a).

Separate *db*RDA models for grazing alone demonstrated that for woody plant species, grazing class 1 was positively loaded on axis 1 (11.8% of the total variation), and heavily browsed sites (index 4) were negatively loaded on axes 1 and 2 (0.9% of the fitted variation). For herbaceous species, grazing explained a smaller amount of the total variation on axis 1 (4.1%) but about the same amount as in woody species on axis 1 (1%).

According to variance partitioning, grazing accounted for a very small amount of variation in models for the 78 sites, and shared 8% and 3% of the variation with spatial and biophysical factors

for woody and herbaceous species separately (Figure 6). However, in the models for 69 sites including *Olea* densities, grazing explained 2% of the unique variation for woody species (see Figure 6).

*Olea size and density and herbaceous and woody species assemblages*

The best *db*RDA model for woody species with the reduced dataset for 69 sites contained trend surface variables and mean *Olea* diameters (Table 5): axes 1 and 2 explained 26.9% and 5.7% of the total variation, respectively (Figure 7a). Grazing did not occur in any of the top 10 models, but mean *Olea* diameter occurred in six models, densities of *Olea* in size classes 11-15 cm and 16-21 cm (3 each), rock outcrop in 4, and slope and aspect WNW in one model each (Table 5). As for the *db*RDA models for the 78 sites, far less variation was explained for the best model on axis 1 for herbaceous (7.3%) compared to woody species (Figure 7b). In terms of individual variables, rock outcrop and large *Olea* trees (16-21 cm) occurred in most models (7 each), and slope and altitude in five models each; grazing did not occur in any models (Table 6).

## Discussion

Our results demonstrated that grazing had a significant effect on plant beta diversity at Jebel Ichkeul, even after controlling for aspect. Some differences were found among functional groups with significant effects of grazing for woody shrubs, forbs, graminoids, and geophytes but not for herbaceous or woody legumes in terms of multivariate location. In relation to beta diversity (distance from centroids), the most striking difference among groups was a clear negative relationship between grazing intensity and woody shrubs, herbaceous forbs overall and especially graminoids. Our results support those from the Canary lslands, where woody shrubs also declined

499 strongly from abandoned to heavily grazed areas (Fernández-Lugo et al. 2013). However, we
500 found that beta diversity of graminoids was negatively impacted by grazing pressure, whereas they
501 found that annual grasses were more frequent in heavily grazed areas. We also found that low
502 intensity or intermediate grazing appeared to result in higher beta diversity for geophytes and
503 legumes, which supports the 'intermediate grazing' hypothesis (Gabay et al. 2006; Miguel-Ayanz et
504 al. 2010).

505 Our results also confirm the findings from other studies that depending on the scale of the
506 investigation, environmental covariates often play a more important role than grazing in explaining
507 species composition and diversity (e.g., Brinkmann et al. 2009; Arevalo et al. 2011). When all
508 biophysical covariates were controlled for in permutational multivariate ANOVA the effect of
509 grazing was no longer significant; other factors, especially spatial location (a proxy for moisture),
510 altitude, slope and rock outcropping were more important. This was confirmed by the variance
511 partitioning in *db*RDA which demonstrated that the variation unique to grazing was relatively small
512 (<1% to 3%). That grazing had a limited effect in our sample was perhaps not surprising since over
513 70% of sampled sites showed no visible signs of browsing on woody vegetation, though herbaceous
514 species were also likely grazed. In some respects our index of grazing intensity was confounded
515 with cover estimates for woody species.

516 Our second main finding was that spatial location was much more highly confounded with
517 grazing in woody than herbaceous species. The grazing index occurred in
518 all models for herbaceous species but in only two models for woody species. However, in terms of
519 a shift in means (i.e. variation explained in *db*RDA) far more variation was explained by the models
520 for woody species than herbaceous species. In terms of multivariate dispersion the effect of grazing
521 was greater for herbaceous species than woody species. Third, *Olea* size and density was strongly

522 related to the grazing gradient and *Olea* was also the woody species most affected by wood-cutting.
523 However, we could only record incidence of wood-cutting qualitatively; in most instances this was
524 strongly associated with heavily grazed sites.

525 We recorded a low incidence of wood cutting overall in our study partly because we
526 concentrated our sampling away from the denuded southern border of the mountain and
527 concentrated on areas that were more highly diverse and floristically rich (Figure 1). We found
528 that the diameter of large *Olea europea* was negatively correlated with the grazing gradient. This
529 was probably partly correlated with the level of cutting in heavily grazed sites. In the 1980s, Fay
530 (Fay 1980) reported that 45% of trees in all stands had been felled and 32% had been cut above
531 one metre on the south side of the mountain resulting in degraded vegetation. While most cutting
532 is for firewood, removal of high branches by shepherds for livestock is also practiced in the
533 Mediterranean (Morandini 1977) and this occurred at Ichkeul (Fay 1980, personal observations).
534 For example, *Pistacia lentiscus* had high cover close to the Hammams and above the visitor centre
535 and the Écomusée due to coppicing by visitors (Fay 1980). *Papaver rhoeas*, an annual invader
536 species also occurs in this area. According to Le Houérou (Le Houérou 1981) the minimum
537 subsistence level for firewood is 1.5 kg/day/person, but an extraction rate of 0.3 kg/day/person at
538 Jebel Ichkeul was estimated by Hollis (Hollis 1977). This level of cutting by the 120 families on
539 the Jebel, combined with overgrazing in some areas, may have been incompatible with the mean
540 annual production of olives estimated by Muller (1976) at 0.12 $m^3$ per year.

541 Jebel Ichkeul was grazed by goats, sheep and cattle (Hollis 1977), but striking spatial
542 differences occurred in intensity of use over the mountain as revealed by this study. These
543 different livestock have varying effects on vegetation structure and composition with goats
544 generally being considered the most destructive species (Tomaselli 1981). Plant species response

545 to grazing on Jebel Ickeul may be classified into: 1) species sensitive to increased grazing pressure;
546 2) species maintained by particular levels of grazing intensity; and 3) species indicative of
547 overgrazing. Examples of species in (1) include favoured woody browse species (e.g., *Ceratonia*
548 *siliqua, Coronilla valentina, Erica arborea, Erica multiflora* and *Rhamnus lycioides* - Le Houérou
549 1981) which were negatively correlated with the grazing gradient. The increased humidity on the
550 north side of the lake and deep valley soils allowed the development of closed canopy forest
551 dominated by *Olea europea, Ceratonia siliqua* and *Phillyrea angustifolia*. Typically, these
552 communities were species poor but nevertheless were of high ecological value because of their
553 intactness and the importance of this characteristic vegetation type in the park, in Tunisia, and in the
554 Mediterranean basin as a whole. Where these shrub species occurred on the southern slopes of the
555 mountain they grew at higher elevations beneath the ridge crest, outside the normal range of goat
556 herds. Closed canopy *Olea europea*, similar to some of the stands in the northern valleys, may have
557 represented 'potential natural vegetation' in valleys with deep soils and illuvial slopes on the lower
558 southern aspects of the mountain prior to pastoralism (Fay 1980). Elsewhere in the Mediterranean,
559 the *Olea-Ceratonion* formation is restricted to zones below 300m (Tomaselli 1977). However, it is
560 important to note that the concept of PNV is controversial and here is defined as "the plant
561 community that would become established if all successional sequences were completed without
562 interference by humans under the present climatic and edaphic conditions (including those
563 created by humans)" (Loidi et al. 2010). With ongoing climate change and the dynamic
564 successional changes that occur in Mediterranean vegetation it is no longer certain that closed
565 canopy *Olea-Ceratonia* forest would represent the potential natural vegetation.

566 Medium intensity grazing on some areas of Jebel Ichkeul may increase plant species
567 richness by maintaining openings between woody vegetation patches, removing competing plant

568 biomass and providing nutrients from livestock manure. Those species maintained by such
569 intermediate levels of grazing include most of the orchid species found growing in the
570 *Ampelodesma* stand at Saida Lalia Hadan, which also contains the largest *Olea europea* in the Park
571 (Fay 1980). For example, the resident herd of 45-60 cattle and numerous Wild Boar which forage in
572 this area (Fay 1980) created the open conditions needed by Orchidaceae and Liliaceae, as well as
573 various pasture grass species which have socio-economic importance (Noy-Meir and Oron 2001).
574 However, a high density of paths resulted in soil compaction and erosion.

575 Many grass species and annuals depend on dense matorral vegetation being opened up by
576 browsing livestock. Nevertheless, Gramineae, which include some valuable pasture species,
577 showed a negative correlation with heavy grazing pressure in this study. Some sites, characterized
578 by complex vertical stratification and open glades, were floristically rich and apparently maintained
579 by grazing. The level of grazing needed to maintain this vegetation in an equilibrium state is an
580 important area for further research.

581 In the vicinity of the gourbi villages, at the south-eastern perimeter, on the southern face
582 and the western end of the mountain, denuded xeric slopes are common and form scattered low
583 matorral. Herbaceous indicators of overgrazing in these areas included weedy species (Asteraceae)
584 like *Atractylis cancellata, Carthamus lanatus* and *Scolymus hispanicus*. In addition, there is a lack
585 of woody browse species in these areas (e.g., *Ceratonia siliqua, Coronilla valentina, Erica*
586 *arborea* and *Rhamnus lycioides*) and even species like *Pistacia lentiscus*, normally resistant to
587 grazing (Le Houerou 1981), had low cover values. These woody species do occur on the southern
588 slopes of the mountain but at higher elevations beneath the ridge crest, outside the normal range of
589 goat herds and their keepers. Overgrazing on the southern slopes of the mountain creates

590 inhospitable conditions for establishment of other protective vegetation and high insolation and
591 aridity (previously including limestone dust) may exacerbate this problem.

592 We did not collect quantitative information on the numbers of livestock grazing at Jebel
593 Ichkeul during our study, but it was estimated that there were 2,500 grazing animals in 1980 (Fay
594 1980; Anon 1988). While livestock fodder at Ichkeul is abundant in early spring it disappears
595 almost entirely by late summer; it is during this period and in the autumn and winter months that
596 extensive browsing of woody species occurs on the Jebel. According to Fay (Fay 1980) much of
597 the northern Jebel is under-grazed which led him to suggest that the main conservation and
598 management problem was related to the spatial unevenness of grazing. For example, if more woody
599 forage was utilized on the north side of the Jebel this could ease the pressure of overgrazing on the
600 southern slopes. However, this presupposes that grazing would be beneficial to all vegetation types
601 which may not be the case. Some areas of closed forest are of high value ecologically because
602 they may be representative of 'intact' vegetation and are also important educationally for visitors to
603 the national park and as a control study area for scientific research.

604 One question is how has the vegetation of Jebel Ichkeul changed over the the 35 year period
605 since the fieldwork for this study was done and what predictions can be made regarding vegetation
606 changes in relation to conservation and management? Four major changes have occurred since
607 1983. First, in the 1990s, dams were installed at all of the major rivers flowing into Lac Ichkeul,
608 resulting in a decline in lake water levels, and associated increasing salinity (UNEP/WCMC 2003).
609 However, this trend was reversed by substantial rainfall in 2003-2005/2006. Second, the gourbi
610 villages that occurred along the southern flanks of the Jebel within the national park boundaries
611 have been evacuated and their inhabitants evicted, together with their livestock. However, the
612 village that was present close to the limestone quarries is still inhabited (?) and agricultural land,

613 including pasture, still occurs along the southern flanks so livestock presumably continue to graze in
614 the national park. Third, the limestone quarries which were having a substantial local impact on
615 vegetation through dust deposition have been closed down (UNEP/WCMC 2003). Finally, ongoing
616 climate change has already occurred in Tunisia between the 1970s and 1999 (Paeth et al. 2009) and
617 compared with this earlier period it is predicted that precipitation will decrease by 20% and
618 temperatures increase by between 1$^{o}$ and 3$^{o}$ C by 2050 (Tramblay et al. 2013; Dakhlaoui et al.
619 2017).

620 Given the fact that that the spatial location of sites had a significant effect on woody vegetation
621 because of the humidity gradient, we would predict that the effects of the dams on water levels
622 could have had a detrimental effect on the vegetation of the northern slopes of the Jebel. Conditions
623 could have become more xeric over time; however, the effect was likely temporary and has
624 probably not resulted in substantial change in scerophyllous vegetation. One way to assess possible
625 changes would be to compare aerial photographs or satellite imagery from the 1980s with recent
626 imagery (see later).

627 When this study took place (Kirk 1983) suggested that the most effective measure which
628 could be taken at Jebel Ichkeul would be to reduce goat and sheep numbers, as was done elsewhere
629 in the Mediterranean in the 1970s (Tomaselli 1977). In Sardinia, this was achieved by a heavy tax
630 on goats, lifting taxes on sheep and providing financial incentives for the conversion. Where local
631 people were unwilling to replace their goat herds, an alternative to changing domestic livestock is
632 to employ more intensive animal husbandry (Tomaselli 1977). This could take the form of fencing
633 and provision of supplementary fodder in summer and winter (see Naveh 1968). When our study
634 was conducted and up until 2004, there were 1,000 people living in gourbi villages within the
635 boundaries of the national park. By 2008 numbers of inhabitants had been reduced to 400 and today

(2017) all of the gourbi villages have been abandoned, together with reductions in livestock (?). Similar removals of livestock took place over large areas of the Mediterranean in the 1980s and 1990s (Papanastasis 1998). It is not known the extent to which livestock still graze on the Jebel (?) but we recommend that surveys of livestock and their ongoing effects on vegetation be monitored. This is partly because cessation of long-term grazing can have unintended consequences - including continued degradation of vegetation, increased abundance of invasive species or succession into dense thickets or closed canopy forest (Mata et al. 2014; Fernández-lugo 2016). However, it has been argued that sustaining ecosystem goods and services by managing goat grazing is preferential to complete eradication of livestock (Fernández-lugo 2016; Lázaro et al. 2016). As well as maintaining biodiversity values this provides ecologically sustainable resource use for often impoversished rural communities.

## Conclusions

We have several management recommendations for controlling grazing at Jebel Ichkeul. First, it is important to monitor changes in vegetation, particularly woody species and rare herbaceous species. Maintaining the heterogeneity and diversiy of vegetation types and structure at Jbel Ichkeul is an important management goal (see Gabay et al. 2006; Miguel-Ayanz et al. 2010). We did not measure the spatial distribution and structure of woody vegetation (except for *Olea* diameters and density) which is a key step in achieving this goal. Monitoring effects of goats on landscape structural characteristics could include a combination of aerial photo classification (or landsat satellite imagery) and on-the-ground measurements of metrics such as patch size, patch density or edge density (Glasser et al. 2013). It is important to also include ground truthing because goat grazing is not fully quantifiable using 2D images, because much of it is below canopy (Glasser

et al. 2013), although LiDAR imagery may circumvent this problem. Among such measures are species composition, gap dimensions and height of vegetation.

Grazing and wood-cutting on the Jebel should be controlled and the recovery and restoration of woody vegetation cover on the eroded southern slopes facilitated. Maquis vegetation plays an important role in protecting watersheds and removal of vegetation can result in soil erosion, particularly on alluvial fans on the southern base of the mountain and cause sedimentation of adjacent marshland. This could be achieved by erecting fencing on the southern slopes of the mountain to allow restoration of *Olea europaea* and other woody species. Combined with restrictions on wood-cutting and provision of alternative sources of fuel (e.g., livestock manure), this could reduce degradation on the southern slopes of the mountain and enable vegetation cover to re-establish. An education programme could be implemented to operationalize changes in livestock practices and to enthuse the local inhabitants about the importance of vegetation cover, both in preventing erosion and as a source of fodder for their livestock. On the northern slopes, an investigation is needed of the role of native herbivores, like wild boar *Sus scrofa*, in maintaining a balance between herb-rich pasture and woody vegetation (see Dovrat et al. 2014).

Jebel Ichkeul provides representative seral stages in the degradation of forest and shrublands to arid grassland landscapes and this has a number of implications for conservation and management. Our study provides a useful baseline of the plant assemblages at Jbel Ichkeul with which to compare future vegetation changes. For example, using the spatial locations of survey sites it would be possible to re-survey plant assemblages and compare results over time. Monitoring what has happened to the vegetation since this study is also critical, and determining the current level of grazing which may have declined since the abandonment of the gourbi villages.

At the same time it is important to balance biodiversity goals with multiple uses, including traditional pastoralism which may be beneficial to plant biodiversity (Verdú et al. 2000; Perevolotsky 2005). For example, ecosystem services provided by the national park have recently been identified (Daly-Hassen 2017). One way to achieve this is to use a systematic conservation planning tool such as Marxan for zones, which could be used to prioritize areas within the national park by prioritizing the temporally spatial variation in plant assemblages (Levin et al. 2013). Such an approach could incorporate the goals of achieving spatially dynamic vegetation changes over time, as well as different zones for controlled grazing and setting biodiversity targets for specific vegetation types. Given the predicted effects of climate change in North Africa, which include decreasing precipitation and increasing aridity (Tramblay et al. 2013; Dakhlaoui et al. 2017), it is vital that areas of high endemism are protected and managed carefully as these may provide critical refugia for endemic plant species (Harrison and Noss 2017). The proximity of the Jebel to Lake Ichkeul may mean that the effects of climate change, at least on the northern aspects of the mountain are buffered and thus represent an hydrologic microrefugia for plants (McLaughlin et al. 2017). In addition its complex topography may provide multiple microclimates that increase the chances that local climate extremes will be buffered and plant species continue to survive. Its possible function as a climate refugium means that it is even more important that management of livestock and other anthropogenic factors are carefully monitored and controlled, and that special management plans be developed for rare and threatened species.

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## Table 1(on next page)

Biophysical variables measured at Jebel Ichkeul

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| Variable | Mean ± SE | Range | N |
|---|---|---|---|
| Altitude m.a.s.l. | 143.0 ± 12.7 | 6-404 | 78 |
| Aspect | | 20-360º | 78 |
| Slope | 23.0 ± 1.1 | 4.3-64.5 | 78 |
| Rock (% cover) | 36.9 ± 3.2 | 0-90 | 78 |
| pH | 7.36 ± 0.03 | 6.7-7.7 | 50 |
| Density Olive A (0-5cm) | | | |
| 30 cm | 1.48 ± 0.45 | 0-25 | 69 |
| DBH | 2.03 ± 0.63 | 0-32 | 69 |
| Density Olive B (6-10cm) | | | |
| 30 cm | 2.03 ± 0.42 | 0-15 | 69 |
| DBH | 1.81 ± 0.38 | 0-15 | 69 |
| Density Olive C (11-15cm) | | | |
| 30 cm | 1.41 ± 0.24 | 0-8 | 69 |
| DBH | 1.20 ± 0.21 | 0-7 | 69 |
| Density Olive D (16-21cm) | | | |
| 30 cm | 0.74 ± 0.18 | 0-8 | 69 |
| DBH | 0.39 ± 0.10 | 0-3 | 69 |
| Density Olive E (21cm+) | | | |
| 30 cm | 0.41 ± 0.11 | 0-4 | 69 |
| DBH | 0.20 ± 0.08 | 0-4 | 69 |

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## Table 2(on next page)

Best model solutions (based on $AIC_c$) according to *db*RDA for woody plant species on Jebel Ichkeul for 78 sites with distance to road. P values derived from sequential tests in forward selection of variables in each model (*** P = 0.0001; **

1

| Model | AICc | $R^2$ | RSS | N | Variables |
|---|---|---|---|---|---|
| 1 | 552.03 | 0.33553 | 73283 | 1 | Spatial*** (latitude, latitude$^2$, latitude$^3$, longitude,longitude$^2$, longitude$^3$, latitude x longitude) |
| 2 | 552.23 | 0.35530 | 71102 | 2 | Spatial***, slope* |
| 3 | 552.34 | 0.35436 | 71206 | 2 | Spatial***, log (distance to road) * |
| 4 | 552.57 | 0.37401 | 69038 | 3 | Spatial***, slope*, log (distance to road) * |
| 5 | 552.65 | 0.35179 | 71490 | 2 | Spatial***, rock outcrop* |
| 6 | 553.03 | 0.37029 | 69448 | 3 | Spatial***, log (distance to road) *,rock outcrop$^n$ |
| 7 | 553.28 | 0.34658 | 72064 | 2 | Spatial***, log (altitude) |
| 8 | 553.40 | 0.34553 | 72179 | 2 | Spatial***, grazing index |
| 9 | 553.59 | 0.36574 | 69951 | 3 | Spatial***, slope*, log (altitude) |
| 10 | 553.64 | 0.36539 | 69990 | 3 | Spatial***, slope*, grazing index |

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## Table 3(on next page)

Best model solutions (based on $AIC_c$) according to *db*RDA for herbaceous plant species on Jebel Ichkeul for 78 sites with distance to road. P values derived from sequential tests in forward selection of variables in each model (*** P = 0.000

| Model | AICc | | $R^2$ | RSS | N | |
|---|---|---|---|---|---|---|
| 1 | | 621.83 | 0.14190 | 1.9681E+05 | 4 | Grazing index$^{***}$, log (altitude) $^{**}$, rock outcrop$^{**}$, log (distance to road) $^{**}$ |
| 2 | | 621.98 | 0.11471 | 2.0305E+05 | 3 | Grazing index$^{***}$, log (altitude) $^{**}$, rock outcrop$^{**}$ |
| 3 | | 622.10 | 0.11331 | 2.0337E+05 | 3 | Grazing index$^{***}$, log (altitude) $^{**}$, log (distance to road) $^{**}$ |
| 4 | | 622.21 | 0.11206 | 2.0366E+05 | 3 | Grazing index$^{***}$, log (altitude) $^{**}$, slope$^{*}$ |
| 5 | | 622.23 | 0.13748 | 1.9783E+05 | 4 | Grazing index$^{***}$, Log (altitude) $^{**}$, log (distance to road) $^{**}$, slope$^{**}$ |
| 6 | | 622.27 | 0.13709 | 1.9792E+05 | 4 | Grazing index$^{***}$, log (altitude) $^{**}$, rock outcrop$^{**}$, slope$^{**}$ |
| 7 | | 622.30 | 0.16236 | 1.9212E+05 | 4 | Grazing index$^{***}$, log (altitude) $^{**}$, rock outcrop$^{**}$, log (distance to road) $^{**}$, slope$^{**}$ |
| 8 | | 622.47 | 0.08338 | 2.1023E+05 | 2 | Grazing index$^{***}$, log (altitude) $^{**}$ |
| 9 | | 622.65 | 0.08118 | 2.1074E+05 | 2 | Grazing index$^{***}$, rock outcrop$^{**}$ |
| 10 | | 622.67 | 0.08097 | 2.0374E+05 | 2 | Grazing index$^{***}$, slope$^{**}$ |

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## Table 4(on next page)

Results of permutational multivariate ANOVA tests for functional groups.

Mean abundance (% cover) and standard error (in parentheses) are given for main factors. Different letters indicate significant differences for grazing effect (pair-wise t-test, P < .(0.05 Column headings: Graminoids (22 spp.), Herbaceous legumes (22 spp.), Geophytes (16 spp.), Forbs (88 spp.), All herbaceous (144 spp.), Shrub legumes (5 spp.), All other shrubs (30 spp.), All shrubs/trees (35 spp.). Separate tests run for aspect in 8 classes, and aspect in 2 classes.

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| | Graminoids | Herbaceous legumes | Geophytes | All Forbs | Shrub Legumes | Non legume shrubs | All shrubs/trees |
|---|---|---|---|---|---|---|---|
| Grazing class (n) | | | | | | | |
| Grazing 4 (4) | 0.659 (0.347) | 0.068 (0.041) | 0.031 (0.031) | 0.208 (0.062) | 0.100 (0.100) | 1.525 (0.978) b | 1.321 (0.840) b |
| Grazing 3 (9) | 0.470 (0.232) b | 0.126 (0.030) | 0.146 (0.132) b | 0.232 (0.050) b | 0.178 (0.178) | 2.185 (1.158) b | 1.898 (0.998) b |
| Grazing 2 (10) | 0.786 (0.349) | 0.236 (0.078) | 0.206 (0.174) | 0.294 (0.067) | 0.880 (0.782) | 2.137 (1.104) b | 1.957 (0.953) b |
| Grazing 1 (55) | 0.820 (0.326) a | 0.221 (0.082) | 0.116 (0.043) a | 0.315 (0.060) a | 0.615 (0.415) | 2.719 (1.133) a | 2.419 (0.979) a |
| *P (Perm)* | **0.016** | 0.655 | **0.002** | **0.000** | 0.586 | **0.000** | **0.000** |
| Aspect (n) | | | | | | | |
| NNE (6) | 0.492 (0.195) | 0.114 (0.052) | 0.104 (0.040) | 0.285 (0.060) | 0.367 (0.226) | 2.967 (1.190) | 2.595 (1.030) |
| ESE (10) | 1.141 (0.494) | 0.254 (0.129) | 0.138 (0.064) | 0.377 (0.090) | 0.500 (0.247) | 2.697 (1.246) | 2.383 (1.074) |
| SSE (8) | 1.119 (0.628) | 0.273 (0.086) | 0.062 (0.028) | 0.332 (0.105) | 0.625 (0.461) | 2.071 (1.081) | 1.864 (0.930) |
| SSW (19) | 0.746 (0.434) | 0.266 (0.087) | 0.102 (0.078) | 0.281 (0.074) | 0.590 (0.413) | 2.419 (1.266) | 2.158 (1.089) |
| WSW (5) | 0.554 (0.300) | 0.109 (0.043) | 0.212 (0.200) | 0.212 (0.055) | 0.120 (0.120) | 1.887 (0.939) | 1.634 (0.810) |
| WNW (3) | 0.439 (0.220) | 0.121 (0.056) | 0.229 (0.174) | 0.322 (0.085) | 0.067 (0.067) | 1.922 (1.045) | 1.657 (0.900) |
| NNW (10) | 0.654 (0.196) | 0.246 (0.108) | 0.119 (0.065) | 0.278 (0.050) | 0.260 (0.189) | 2.600 (1.074) | 2.266 (0.929) |
| ENE (17) | 0.687 (0.307) | 0.123 (0.048) | 0.147 (0.052) | 0.288 (0.057) | 1.047 (0.948) | 2.835 (1.091) | 2.580 (0.947) |
| *P (perm)* | **0.014** | 0.111 | 0.311 | 0.118 | -- | 0.243 | 0.283 |
| Grazing x aspect | --- | -- | -- | -- | -- | -- | -- |

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Mean abundance (% cover) and standard error (in parentheses) are given for main factors. Different letters indicate significant differences for grazing effect (pair-wise t-test, $P < 0.05$). Column headings: Graminoids (22 spp.), Herbaceous legumes (22 spp.), Geophytes (16 spp.), Forbs (88 spp.), All herbaceous (144 spp.), Shrub legumes (5 spp.), All other shrubs (30 spp.), All shrubs/trees (35 spp.). Separate tests run for aspect in 8 classes, and aspect in 2 classes.

## Table 5(on next page)

Results of permutational multivariate ANOVA alternative with 2 aspect categories (north and south)

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| | Graminoids | Herbaceous legumes | Geophytes | All Forbs | Shrub Legumes | Non-legume shrubs | All shrubs/trees |
|---|---|---|---|---|---|---|---|
| Grazing | | | | | | | |
| Grazing 4 (4) | 0.659 (0.347) | 0.068 (0.041) | 0.031 (0.031) | 0.208 (0.062) | 0.100 (0.100) | 1.525 (0.978) b | 1.321 (0.840) b |
| Grazing 3 (9) | 0.470 (0.232) | 0.126 (0.030) | 0.146 (0.132) b | 0.232 (0.050) b | 0.178 (0.178) | 2.185 (1.158) b | 1.898 (0.998) b |
| Grazing 2 (10) | 0.786 (0.349) | 0.236 (0.078) | 0.206 (0.174) | 0.294 (0.067) | 0.880 (0.782) | 2.137 (1.104) b | 1.957 (0.953) b |
| Grazing 1 (55) | 0.820 (0.326) | 0.221 (0.082) | 0.116 (0.043) a | 0.315 (0.060) a | 0.615 (0.415) | 2.719 (1.133) a | 2.419 (0.979) a |
| *P(perm)* | **0.029** | 0.661 | **0.003** | **0.001** | -- | **0.000** | **0.000** |
| North (36) | 0.625 (0.214) | 0.155 (0.058) | 0.139 ( 0.052) | 0.288 ( 0.047) | 0.633 ( 0.463) | 2.716 (1.071) | 2.418 (0.926) |
| South (42) | 0.888 (0.454) | 0.246 (0.080) | 0.116 (0.059) | 0.306 (0.077) | 0.519 (0.332) | 2.356 (1.145) | 2.093 (0.986) |
| *P (perm)* | **0.002** | 0.084 | -- | **0.005** | -- | **0.012** | **0.016** |
| Grazing x aspect | -- | -- | -- | | -- | -- | -- |

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## Table 6(on next page)

Best model solutions (based on $AIC_c$) according to *db*RDA for woody plant species on Jebel Ichkeul for 69 sites (including *Olea* size and density and distance to road). P values derived from sequential tests in forward selection of vari

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| Model | AICc | $R^2$ | RSS | N | Variables |
|---|---|---|---|---|---|
| 1 | 509.22 | 0.40153 | 78377 | 3 | Spatial*** (latitude, latitude$^2$, latitude$^3$, longitude, longitude$^2$, longitude$^3$, latitude x longitude), rock outcrop**, log (# *Olea* 16-21 cm 30 cm) ** |
| 2 | 509.37 | 0.37592 | 81732 | 2 | Spatial*** , rock outcrop** |
| 3 | 509.46 | 0.39947 | 78647 | 3 | Spatial*** , rock outcrop**, mean *Olea* diameter 30 cm** |
| 4 | 509.84 | 0.37164 | 82292 | 2 | Spatial*** , log (# *Olea* 16-21 cm 30 cm) ** |
| 5 | 510.09 | 0.39395 | 79370 | 3 | Spatial*** , rock outcrop**, frequency *Olea* diameter 30 cm$^n$ |
| 6 | 510.19 | 0.36842 | 82714 | 2 | Spatial*** , mean *Olea* diameter 30 cm** |
| 7 | 510.20 | 0.39299 | 79496 | 3 | Spatial*** , rock outcrop**, log (# *Olea* 11-15 cm 30 cm) |
| 8 | 510.27 | 0.36774 | 82803 | 2 | Spatial*** , slope** |
| 9 | 510.32 | 0.39190 | 79638 | 3 | Spatial*** , rock outcrop**, log (# *Olea* > 20 cm at 30 cm ht) |
| 10 | 510.34 | 0.36712 | 82884 | 6 | Spatial*** , log (# *Olea* 11-15 cm 30 cm) ** |

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## Table 7 (on next page)

Best model solutions (based on $AIC_c$) according to *db*RDA for herbaceous plant species on Jebel Ichkeul for 69 sites (including *Olea* size and density). P values derived from sequential tests in forward selection of variables in each mo

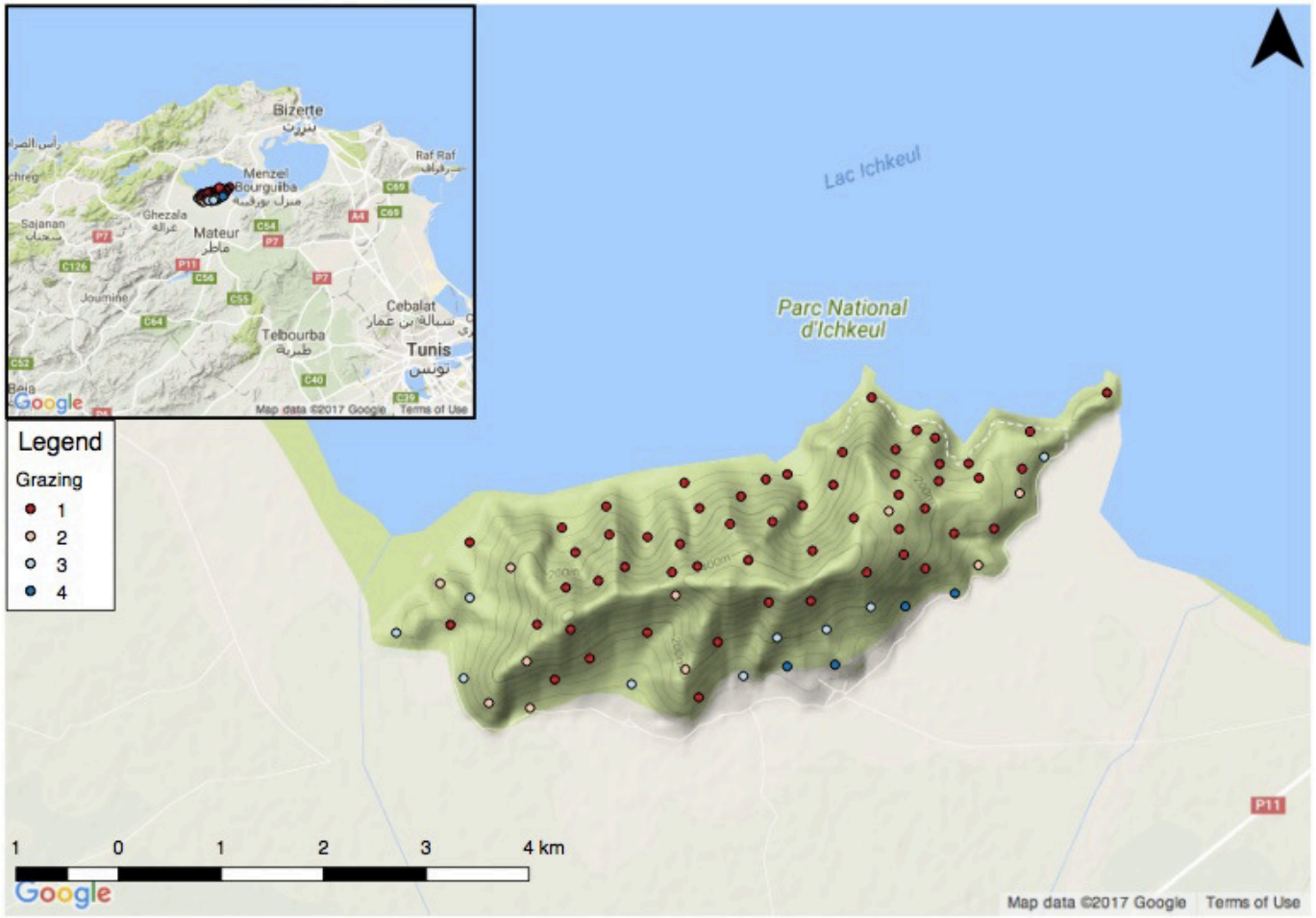
1

| Model | AICc | $R^2$ | RSS | N | Variables |
|---|---|---|---|---|---|
| 1 | 552.35 | 0.14593 | 1.7638E+05 | 4 | Log (distance to road) ***, log (altitude) **, rock outcrop**, log (# *Olea* 16-21 cm 30 cm height) ** |
| 2 | 552.47 | 0.11509 | 1.8275E+05 | 3 | Log (distance to road) ***, log (altitude) **, rock outcrop** |
| 3 | 552.66 | 0.11259 | 1.8327E+05 | 3 | Log (distance to road) ***, rock outcrop**, log (# *Olea* 16-21 cm 30 cm height) ** |
| 4 | 552.76 | 0.14078 | 1.7745E+05 | 4 | Log (distance to road) ***, log (altitude) **, rock outcrop**, mean *Olea* diameter at 30 cm* |
| 5 | 552.76 | 0.14078 | 1.7745E+05 | 4 | Log (distance to road) ***, log (altitude) **, rock outcrop**, grazing index* |
| 6 | 552.83 | 0.11047 | 1.8371E+05 | 3 | Grazing index**, log (# *Olea* 16-21 cm 30 cm height) **, rock outcrop** |
| 7 | 552.88 | 0.16880 | 1.7166E+05 | 5 | Log (distance to road) ***, log (altitude) **, rock outcrop**, log (# *Olea* 16-21 cm 30 cm height) **, grazing index* |
| 8 | 552.90 | 0.13911 | 1.7779E+05 | 4 | Grazing index**, log (# *Olea* 16-21 cm 30 cm height) **, rock outcrop**, log (altitude) ** |
| 9 | 552.91 | 0.10935 | 1.8394E+05 | 3 | Log (distance to road) ***, log (altitude) **, log (# *Olea* 16-21 cm 30 cm height) ** |
| 10 | 552.94 | 0.07939 | 1.9013E+05 | 2 | Log (distance to road) ***, log (altitude) ** |

2
3

## Figure 1(on next page)

Map showing location of study sites on Jebel Ichkeul within Le Parc National de L'Ichkeul and location within northern Tunisia (inset). Shown also are spatial locations of grazing classes.

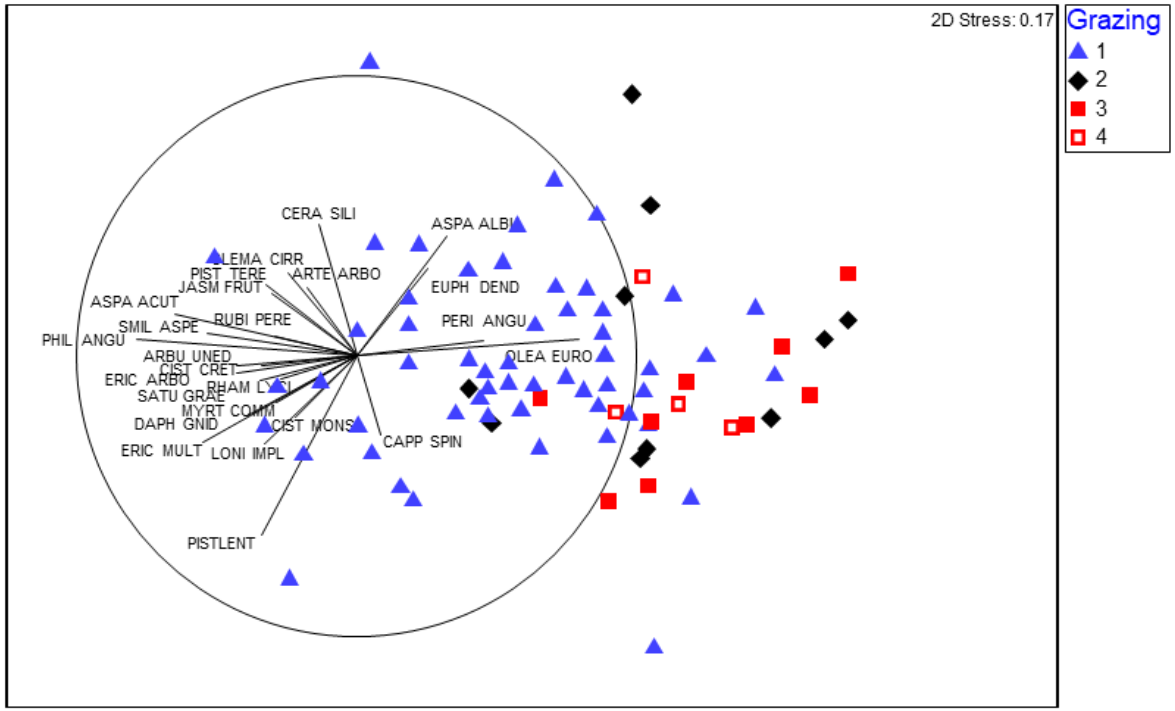



1035

## Figure 2(on next page)

*n*MDS ordination plot of woody species at 78 sites on Jebel Ichkeul showing species vectors with correlations of ≥ 0.3 with the axes (3D stress = 0.13 ).

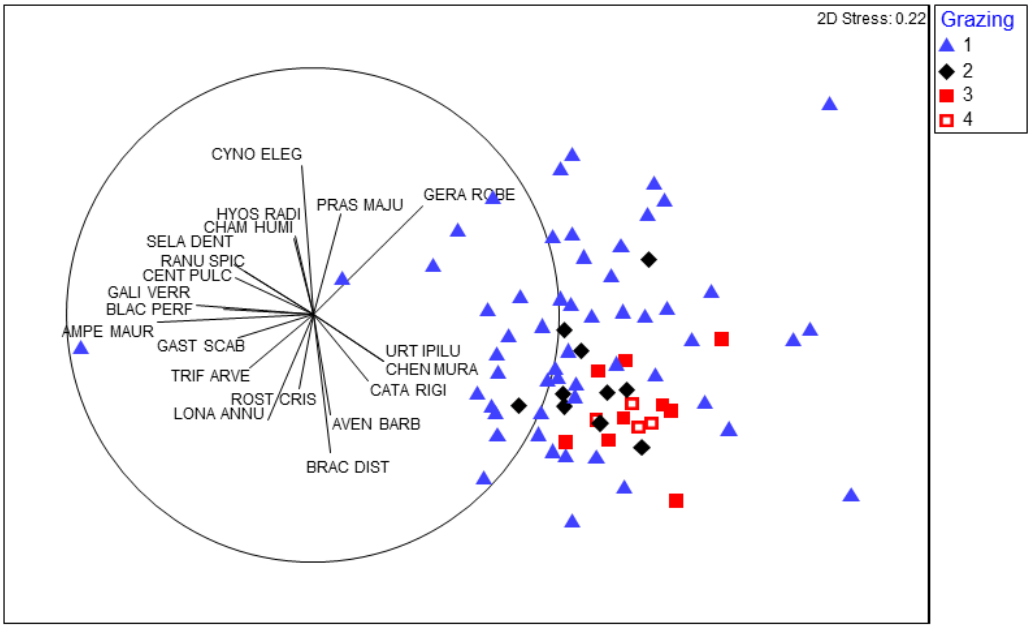
Species acronyms: CAPP SPIN - *Capparis spinosa*; PERI ANGU - *Periploca angustifolia*; OLEA EURO - *Olea europaea*; EUPH DEND - *Euphorbia dendroides*; ASPA ALBU - *Asparagus albus*; CERA SILI - *Ceratonia siliqua*; CLEM CIRR - *Clematis cirrhosa*; JASM FRUT - *Jasminum fruticans*; SMIL ASP - *Smilax aspera*; ASPA ACUTI - *Asparagus acutifolius*; ERIC ARBO - *Erica arborea*; PHIL ANGU - *Phillyrea angustifolia*; ARBU UNED - *Arbutus unedo*; CIST CRET - *Cistus creticus*; MYRT COMM - *Myrtus communis*; DAPH GNID - *Daphne gnidium*; ERIC MULT - *Erica multiflora*; LONI IMPL - *Lonicera implexus*; PIST LENT - *Pistachia lentiscus*. The circle is a unit circle and always has a radius of 1.0 (its scale is arbitrary, does not need to be centred on the ordination of the underlying plot to be interpretable, and is not necessarily at the same scale). Vector lengths and direction indicate the strength and sign, respectively, of the relationship between tree species and the ordination axes; they do not show other types of relationships (unimodal, multimodal) and so are used for exploration. The vectors begin at the origin of the circle and end at the x,y coordinates that consist of correlations between the tree species and each of axis 1 and axis 2 of the ordination, respectively.



## Figure 3(on next page)

*n*MDS ordination plot of herbaceous species for 78 sites at Jebel Ichkeul showing species with correlations of ≥ 0.3 with the axes (3D stress = 0.17).

Species acronyms (clockwise) CYNO ELEG - *Cynosurus elegans*; PRAS MAJU - *Prasium majus*; GERA ROBE - *Geranium robertianum*; URTI PILU - *Urtica pilulifera*; CHENMURA - *Chenopodium murale*; CATA RIGI - *Catapodium rigidum;* AVEN BARB - *Avena barbata*; BRACDIST - *Brachypodium distachyum*; ROST CRIS - *Rostraria cristata*; LONA ANNU - *Lonas annua*; TRIF ARVE - *Trifolium arvense*; GAST SCAR - *Gastridium scabrum*; AMPE MAUR - *Ampelodesmos mauritanicus;* BLAC PERF - *Blackstonia perfoliata*; GALI VERR - *Galium verrucosum*; CENT PULC - *Centaurium pulchellum*; RANU SPIC - *Ranunculus spicatus*; SELA DENT - *Selaginella denticulata*; CHAM HUMI - *Chamaerops humilis*; HYOS RADI - *Hyoseris radiata*.



# Figure 4

Distance-based redundancy analysis plot of plant species based on model solutions ($AIC_c$) at 78 sites on Jebel Ichkeul for A) woody species (model 10) including grazing index; B) woody species (model 6), including distance to road; C) herbaceous

**Fig. 4A**

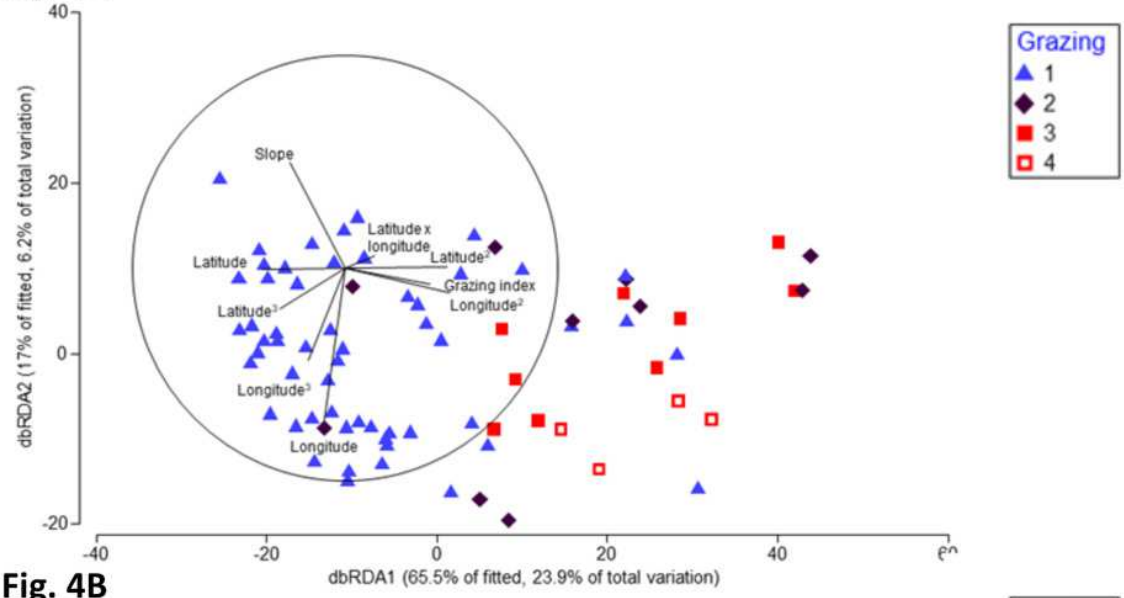



**Fig. 4B**

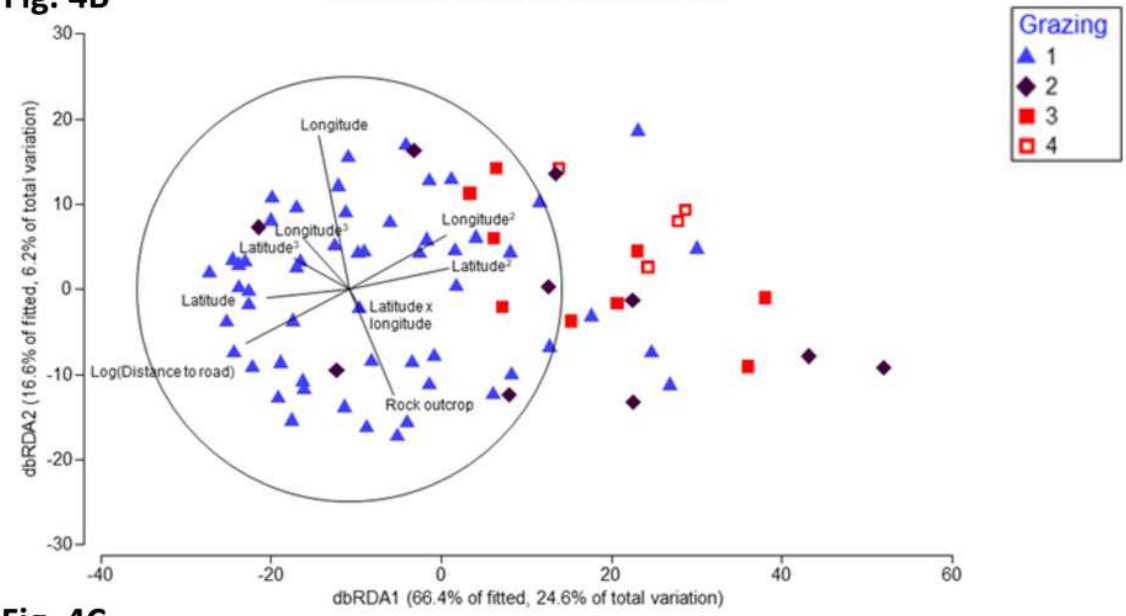
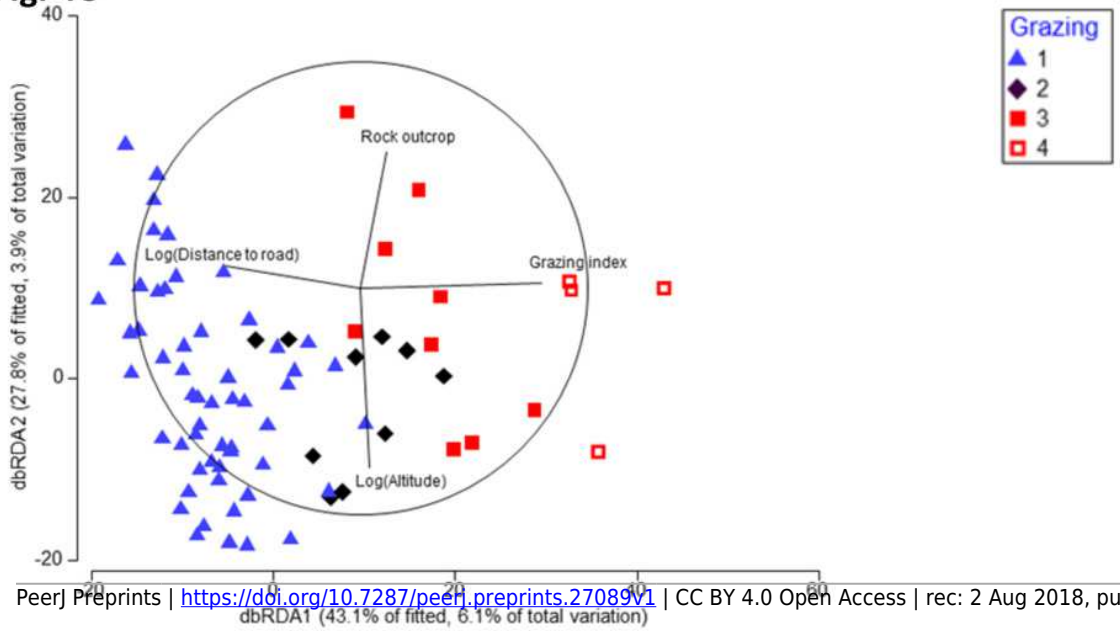
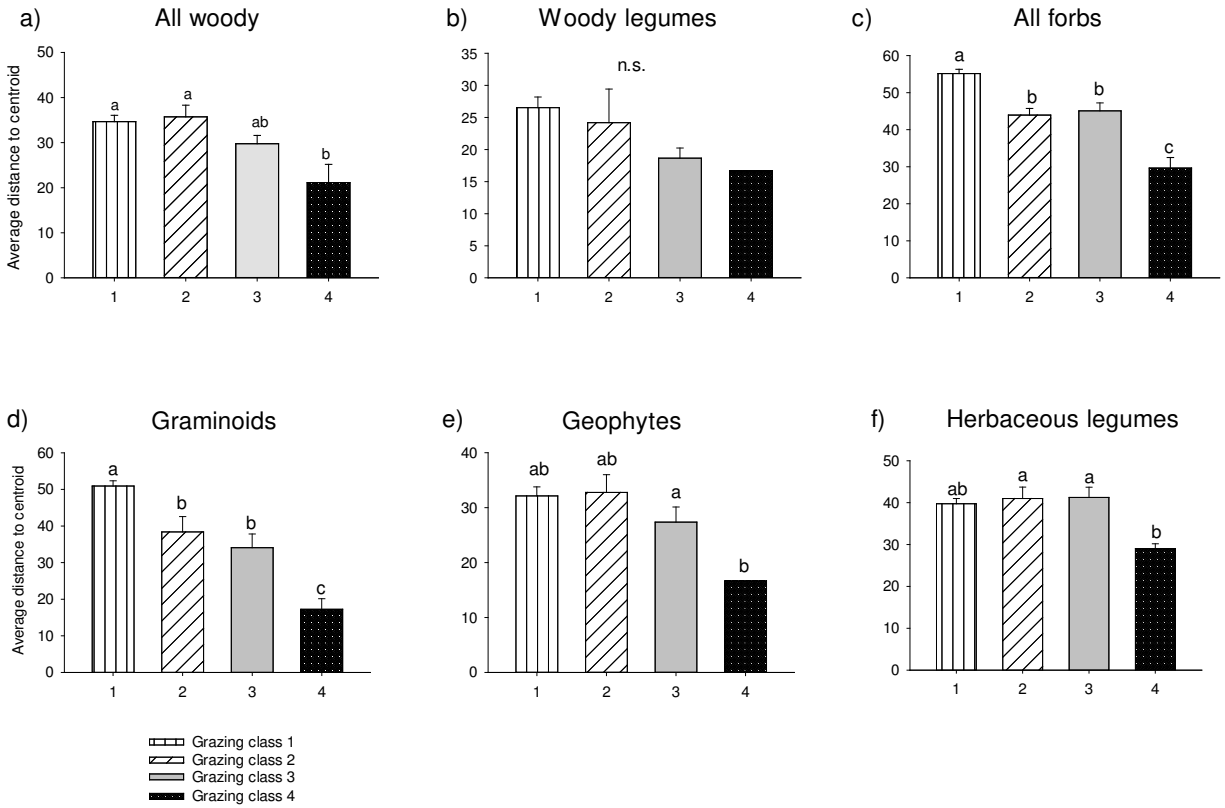



**Fig. 4C**



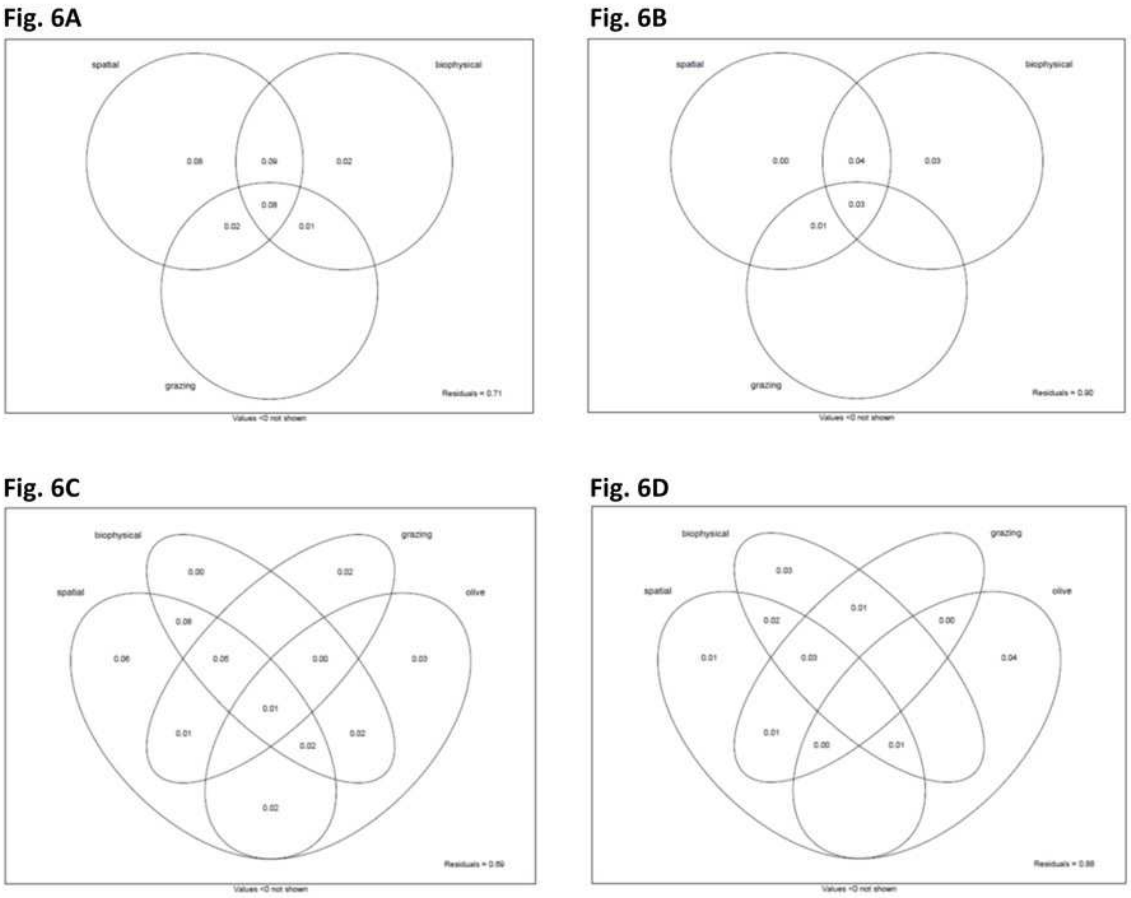
## Figure 5(on next page)

Average distance to centroids (beta diversity) for grazing classes derived from test for homogeneity of multivariate dispersions for: a) All woody (35 spp.); b) Woody legumes (5 spp.); c) All forbs (144 spp.); d) Geophytes (16 spp.); e) Gramineae (22 spp.



# Figure 6

Venn diagrams showing % of total variation explained by biophysical factors, spatial factors, *Olea* size and density, and grazing intensity for woody (left) and herbaceous (right) species. A) Woody species (spatial, biophysical, grazing), B) herbaceo



# Figure 7

Distance-based redundancy analysis plot of plant species based on best model solutions ($AIC_c$) for 69 sites with *Olea* size and densities on Jebel Ichkeul for A) woody species (model 4) with grazing and distance to road, B) woody species (mo