

**A peer-reviewed version of this preprint was published in PeerJ on 13 August 2019.**

[View the peer-reviewed version](https://doi.org/10.7717/peerj.7296) (peerj.com/articles/7296), which is the preferred citable publication unless you specifically need to cite this preprint.

Kirk DA, Hébert K, Goldsmith FB. 2019. Grazing effects on woody and herbaceous plant biodiversity on a limestone mountain in northern Tunisia. PeerJ 7:e7296 <https://doi.org/10.7717/peerj.7296>

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

David Anthony Kirk<sup>Corresp., 1</sup>, F. B. Goldsmith<sup>2</sup>

<sup>1</sup> Aquila Conservation & Environment Consulting, Ottawa, Ontario, Canada

<sup>2</sup> 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.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20

Running head: Effect of grazing on maquis vegetation

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

David Anthony Kirk<sup>1,2</sup> and F. B. Goldsmith<sup>1</sup>

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

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

### 43 **Introduction**

44 Mediterranean shrublands are highly disturbed landscapes that have been subjected to  
45 anthropogenic influence for millennia (Mazzoleni et al. 2004; Papanastasis, 1998; Rundel, 1998;  
46 Vogiatzakis et al. 2006). Thus, balancing human use and disturbance with conservation of  
47 biodiversity in the Mediterranean region is an ongoing challenge (Falcucci, Maiorano, & Boitani,  
48 2007; Rundel et al., 2016), but at the outset needs to recognize the historical and integrale role  
49 played by humans and their livestock (Blondel et al. 2010). Humans have coevolved with the  
50 Mediterranean landscape for millennia (Naveh 1990).

51       Historically, low intensity grazing by domestic livestock and fires set by shepherds may  
52 have provided a substitute for previously more abundant native herbivores in maintaining the  
53 floristically rich, spatially heterogeneous landscapes of Mediterranean maquis (Le Houérou, 1981;  
54 Papanastasis, 1998; Papanastasis, Kyriakakis, & Kazakis, 2002). The shrubland communities that  
55 result from this disturbance or those in various successional stages have been highly valued  
56 ecologically because of their rich diversity of annuals, and geophytes from the Orchidaceae,  
57 Iridaceae and Liliaceae (Pons 1981; Quézel 1981). However, these values have often been based  
58 on the belief that diversity begets stability or resilience, which is controversial (see de la Riva et al.  
59 2016). Without such disturbance, many shrublands develop into forests, with concomitant loss of  
60 plant diversity, and a build up of organic matter over time, later rendering them susceptible to hot  
61 wildfires (Rackham & Moody 1996; Perevolotsky and Seligman 1998; Henkin 2011). Indeed it has  
62 been suggested that without management, many endemic species might become extinct (Gomez-  
63 Campo 1985). On the other hand, overgrazing and uncontrolled wood-cutting can also lead to loss  
64 of plant diversity, erosion and in some areas desertification (Hill et al. 1998; Papanastasis 1998;  
65 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 (Olf 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 composition; 3) loss of biodiversity in forest species; and 4)  
110 increases in invasive plants (Quézel et al. 1999).

111           Jebel Ichkeul, a limestone mountain within Le Parc National de L'Ichkeul in the north of the  
112 Republic of Tunisia, represents a microcosm of many of the conservation issues and human threats  
113 facing Mediterranean vegetation including overgrazing, wood-cutting and invasive plant species. In  
114 a recent assessment of the threats to Important Plant Areas (IPAs) in the south and eastern  
115 Mediterranean, (Radford et al. 2011) identified overgrazing as the main threat to IPAs in Tunisia  
116 (see also Underwood et al. 2009). In the early 1980s when we conducted our study, the forests  
117 and maquis of Jebel Ichkeul provided nutritious grazing (graminoids and legumes) for livestock  
118 (goats, sheep and cattle), particularly during the autumn and winter months (Hollis 1977). The  
119 marshlands and wetlands of the National Park were a source of nutritious forage at other times of  
120 year and over 2,500 livestock grazed in the national park (Anon 1988). Combined with  
121 uncontrolled wood-cutting for firewood on the southern slopes of the mountain this grazing caused  
122 loss of vegetation cover, reduced species diversity, soil erosion and spread of invasive plants (Fay  
123 1980). These impacts were most apparent in close proximity to gourbi village settlements and the  
124 Hammams (hot springs) located at the foot of the mountain. Illegal quarries, since closed, also  
125 mined limestone on the southern slopes of the Jebel, and contributed to the xeric conditions at these  
126 sites, and potentially dust pollution (Kirk 1983). One potentially ecologically sustainable use was  
127 ethnobotany; the mountain provided medicinal herb species for local people (Fay 1980), but the  
128 impact on plants was not monitored. Collection of plants for medicinal use has to be carried out  
129 sustainably otherwise it can lead to endangerment as in Syria (Radford et al. 2011).

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



134 environmental drivers and 3) what is the effect of *Olea europaea* size and density on herbaceous or  
135 other woody plant species compared to abiotic natural features(Osem et al. 2007; Shachak et al.  
136 2008; Agra and Ne'eman 2009). Our results can provide a framework for the conservation and  
137 sustainable use of the Jebel's forests and maquis and contribute to the broader question of the impact  
138 of grazing and the structure of woody vegetation on maquis vegetation elsewhere in the  
139 Mediterranean, both inside and outside protected areas. They also provide a baseline of plant  
140 species composition prior to the onset of climate change.

141

## 142 **Methods**

### 143 *Study area*

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

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

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

164       Jebel Ichkeul was listed in the European Red list of Habitats as one of the most typical  
165 examples of *Olea europaea* var *sylvestris* with *Ceratonia siliqua* and *Pistacia lentiscus* along with  
166 southern Andalusia, Menorca, Sardinia, Sicily, Calabria and Crete (European Environment Agency  
167 2017). It has extremely high vegetation heterogeneity because of its varied geology (dolomite,  
168 calc-schist and marble), dissected relief, high altitude (maximum 512 m.a.s.l.), adjacent Lac Ichkeul  
169 and spatially varying anthropogenic factors (Daoud-Bouattour et al. 2007). The northern slopes  
170 facing Lac Ichkeul are generally mesic with high spatial heterogeneity and often continuous  
171 vegetation cover. By contrast, the southern aspects of the mountain had illegal limestone quarries  
172 (now abandoned), contained most of the gourbi village settlements and as a consequence had xeric  
173 plant communities. A road running along the southern flanks of the mountain links the villages and  
174 quarries and is served by some secondary roads from the Mateur Plain (Figure 1). On the southern  
175 slopes of the mountain sites with high soil pH occur due to their calc-schist parent material, while  
176 the northern slopes are mostly dolomitic. Jebel Ichkeul occurs in the Mediterranean bioclimatic  
177 zone with a summer drought (Daget 1977). Mean monthly temperatures range from 11.3°C in  
178 January (winter minimum 0°C) to a mean of 25.2°C in July (summer maximum 40°C). The  
179 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*;

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

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

212

213

#### 214 *Measuring grazing intensity*

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

223

#### 224 *Controlling for biophysical features*

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

235 We recorded altitude with a field altimeter. Because slope aspect plays an important role in  
236 the distribution of woody vegetation in the Mediterranean (Sternberg and Shoshany 2001) we also  
237 measured slope using an inclinometer (Abney Level - Eugene Dietzgen, Chicago, USA) and  
238 recorded compass aspect as a proxy for solar insolation. Soil depth and characteristics play a strong  
239 role in shaping Mediterranean shrub communities (Molina-Venegas et al. 2016), so we recorded the  
240 percentage of rock outcropping or rock cover at quadrats. Because soils on the Jebel were highly  
241 variable (ranging from deep loams to sandy substrates - Fay 1980), we collected soil samples at 50  
242 sites for analysis. Soils were often very shallow and compacted, so we removed samples with a  
243 hand trowel from the A horizon. We placed soils in sealed plastic bags and refrigerated them for  
244 about six weeks before analysis. We measured pH by wetting soil to a paste-like consistency, and  
245 took the average of duplicate readings from different parts of the sample with a glass electrode. We  
246 also compared calcium-magnesium ratios for six contrasting sites, three on the degraded southern  
247 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 
$$A = \sum A_i$$

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

271 10.5.1, ESRI 2017) to extract and download satellite imagery and calculate the distance from  
272 survey sites to the nearest road and the nearest settlement. For roads, the ArcGIS shapefile was  
273 extracted from CloudMade data (OpenStreetMap contributors 2015) collected in 1982. For  
274 settlements we manually dropped pins on buildings from the ArcGIS Google Earth Imagery  
275 basemap (imagery 2016, data from the 1980s were not available at sufficiently accurate  
276 resolution). Because distance to road and distance to settlement were highly correlated (Pearson  
277  $R = 0.89$ ), we included only one of these variables in separate models. To account for nonlinear  
278 plant responses to spatial location, we normalized latitude and longitude and derived trend surface  
279 variables (latitude<sup>2</sup>, latitude<sup>3</sup> etc.) which we then included in models.

280

#### 281 *Treatment of species data and environmental covariates*

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

292 For the environmental covariates we inspected draftsman plots to determine whether  
293 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°  
302 (NNE); 2: 46-90° (ESE); 3: 91-135° (SSE); 4: 136-180° (SSW); 5: 181-225° (WSW); 6: 226-270°  
303 (WNW); 7: 271-315° (NNW); 8: 316-360° (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 (*dbRDA* -  
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 *dbRDA* 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 *dbRDA* 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

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

347

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

349 First, to provide a visualization of the variability in the averages within each grazing group we  
350 calculated 95% bootstrapped averages (Anderson et al. 2008). Comparison of the relative sizes  
351 of these ellipses provided information on differences in the underlying variation in average  
352 values (beta diversity) within grazing classes. Second, we performed two tests to evaluate  
353 whether differences between grazing classes were due to variation in multivariate dispersion (test  
354 for the homogeneity of multivariate dispersions) or location in multivariate ordination space  
355 (permutational multivariate ANOVA), or both. The first test was performed using the routine  
356 PERMDISP, which provides a direct measure of beta diversity (Anderson et al. 2008). The  
357 second test was done using a one-way permutational multivariate ANOVA to ascertain whether  
358 there were differences in multivariate locations between grazing classes. This model was set up  
359 with grazing class as a fixed effect; we also conducted *post hoc* pairwise t-tests between grazing  
360 classes. We performed a second, two-way permutational multivariate ANOVA model including  
361 grazing as a fixed effect, and aspect (eight classes) as a random effect. We inspected P values  
362 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).

408 We compiled the best 10 *dbRDA* models for all 78 sites for woody and herbaceous species  
409 (Tables 2 and 3, respectively). For woody species, spatial location was most important and  
410 occurred in all models. Grazing was clearly confounded with spatial location and other variables  
411 (Figure 4a) and occurred in two of the top 10 models (Table 2). This was demonstrated by the fact  
412 that the grazing index did not occur in models until five variables were included (altitude, slope,  
413 distance to road and spatial location). Biophysical variables such as slope, altitude and rock  
414 outcrop occurred in 4, 2 models each, respectively. In model 10, which included the grazing  
415 index, axis 1 explained 23.9% and axis 2 explained 6.2% of the total variation respectively (Figure  
416 4a). In model 6, which included distance to roads, axis 1 explained 24.6% of the variation and axis  
417 2, 6.2% of the variation. We also ran a second set of *dbRDA* models to test the effect of using  
418 distance to settlement - detailed models are not reported as results were similar to distance from  
419 roads.

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

428

429 *Effects of grazing*

430 We classified 71% of sites as grazing class 1 (unbrowsed,  $n = 55$ ), 12.8% as grazing class 2 (10),  
431 11.5% as grazing class 3 (9) and 5% as grazing class 4 (4). Heavily grazed sites were generally of  
432 low altitude with more rock outcropping and smaller-diameter olive trees (Supplementary Figure 2).  
433 According to the test for the homogeneity of multivariate dispersions based on 78 sites, we found a  
434 marginally significant difference in woody species beta diversity among the four grazing regimes  
435 ( $F_{3,74} = 3.16$ ,  $P = 0.0872$ ; Figure 5a). Highest beta diversity for woody species was in grazing  
436 classes 2 and 1 followed by grazing classes 3 and 4 (Figure 5a). Pairwise comparisons for woody  
437 species demonstrated significant differences between grazing classes 1 and 4 and 2 and 4. The  
438 difference among grazing classes for herbaceous plant species beta diversity was highly significant  
439 ( $F_{3,74} = 19.85$ ,  $P < 0.0001$ ). No difference was found among grazing classes for woody legumes  
440 (Figure 5b). For all forb species, beta diversity was highest in grazing class 1, and was similar in  
441 grazing classes 2 and 3 (though slightly higher in 3) and lowest in grazing class 4 (Figure 5c).  
442 Pairwise comparisons demonstrated significant differences between all grazing classes except  
443 between grazing class 2 and 3 (Figure 5c). These results relate to differences in dispersion in  
444 multivariate ordination space and suggested that effects of grazing were greater in this respect for  
445 herbaceous than for woody species (the opposite to what was found for the *dbRDA* models).  
446 Separate models for Gramineae revealed similar results to those for forbs overall, except that  
447 grazing class 3 had lower beta diversity than class 2 (Figure 5d). However, results for Geophytes  
448 and Leguminosae differed, with beta diversity being higher at intermediate levels of grazing  
449 (Figures 5e and 5f respectively; tests of main effects overall were non-significant).

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

453 permutations; see also Supplementary Figure 3 for species richness and Shannon index). The two-  
454 way permutational multivariate ANOVA demonstrated that grazing still had a significant effect for  
455 both woody (pseudo- $F_{3,57} = 2.08$ ,  $P = 0.0555$ ) and herbaceous species (pseudo  $F_{3,57} = 1.73$ ,  $P =$   
456  $0.0218$ ) even after controlling for aspect. However, aspect (8 classes) was not significant for either  
457 group (woody pseudo- $F_{3,57} = 1.01$ ,  $P > 0.1$ ; herbaceous pseudo- $F_{3,57} = 0.80$ ,  $P > 0.1$ ) and the  
458 interaction was also non-significant (Table 4a). Results differed when aspect was categorized as  
459 'north' and 'south' and was significant for Graminoids, all herbs, all other shrubs and all  
460 shrubs/trees (Table 4b). When all biophysical parameters were controlled for as covariates in the  
461 one way permutational multivariate ANOVA, the effect of grazing was not significant for either  
462 woody or herbaceous species (pseudo- $F_{3,74} = 0.936$  and  $0.817$ , respectively, both  $P_s > 0.1$ ). This was  
463 not surprising because of the strong relationships between grazing, and biophysical factors (e.g.,  
464 altitude, slope and some slope aspects - positively with SSW, negatively with NNW). We also  
465 conducted similar models for other functional groups and detailed results for Gramineae,  
466 Geophytes, forbs and shrubs are in Table 4a. However, no significant effect of grazing was found  
467 for either herbaceous or woody legume functional groups in the multivariate permutational  
468 ANOVA (Table 4a).

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

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

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

479

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

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

490

#### 491 **Discussion**

492 Our results demonstrated that grazing had a significant effect on plant beta diversity at Jebel  
493 Ichkeul, even after controlling for aspect. Some differences were found among functional groups  
494 with significant effects of grazing for woody shrubs, forbs, graminoids, and geophytes but not for  
495 herbaceous or woody legumes in terms of multivariate location. In relation to beta diversity  
496 (distance from centroids), the most striking difference among groups was a clear negative  
497 relationship between grazing intensity and woody shrubs, herbaceous forbs overall and especially  
498 graminoids. Our results support those from the Canary Islands, 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 *dbRDA* 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 *dbRDA*) 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<sup>3</sup> 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° and 3° 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

636 (2017) all of the gourbi villages have been abandoned, together with reductions in livestock (?).  
637 Similar removals of livestock took place over large areas of the Mediterranean in the 1980s and  
638 1990s (Papanastasis 1998). It is not known the extent to which livestock still graze on the Jebel (?)  
639 but we recommend that surveys of livestock and their ongoing effects on vegetation be monitored.  
640 This is partly because cessation of long-term grazing can have unintended consequences - including  
641 continued degradation of vegetation, increased abundance of invasive species or succession into  
642 dense thickets or closed canopy forest (Mata et al. 2014; Fernández-lugo 2016). However, it has  
643 been argued that sustaining ecosystem goods and services by managing goat grazing is preferential  
644 to complete eradication of livestock (Fernández-lugo 2016; Lázaro et al. 2016). As well as  
645 maintaining biodiversity values this provides ecologically sustainable resource use for often  
646 impoverished rural communities.

647

## 648 **Conclusions**

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



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

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

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



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

700

701

702 **Acknowledgements**

703 This research was conducted as part of a M.Sc. Thesis in Conservation at University College  
704 London by the first author and was funded by the Natural Environment Research Council (NERC)  
705 and Ivan and Thelma Kirk. We thank the Direction Générale des Forêt (Republic of Tunisia) for  
706 allowing us to conduct this research. Special thanks to J. M. Fay for pioneering this project (a plant  
707 inventory of Jebel Ichkeul completed in 1980), and his devotion to protected area conservation in  
708 Africa. A.C. Stevenson and R. Vickery of the British Museum (Natural History) helped with plant  
709 species identifications. We would also like to thank J. M. Fay, B. Green, the late G.E. Hollis, J.D.  
710 Skinner, A. Warren and J.B. Wood for logistical support or advice. B.T. Collins helped with the  
711 equations for olive diameter measurements. We are especially indebted to M. J. Anderson for  
712 statistical advice, L. Olson for help with variance partitioning, G. Perkins for preparing Figure 1,  
713 C. Fauvelle for help with GIS, and M. Ouali and A. Daoud-Bouattour for checking plant  
714 nomenclature. We thank A. Daoud-Bouattour, R. G. Gavilan, P. W. Rundel and A. C. Stevenson  
715 for general comments on earlier drafts of this manuscript.

716  
717 **References**

- 718 Agra H, Ne'eman G (2009) Woody species as landscape modulators: Their effect on the  
719 herbaceous plants in a Mediterranean maquis. *Plant Ecol* 205:165–177. doi:  
720 10.1007/s11258-009-9606-3
- 721 Anderson M, Gorley RN, Clarke KR (2008) PERMANOVA + for PRIMER : by.
- 722 Anon (1988) Two Problematical National Parks in the Mediterranean Region.
- 723 Arevalo JR, De Nascimento L, Fernandez-Lugo S, et al (2011) Effects of abandoning long-term  
724 goat grazing on species composition and species richness of pastures at La Gomera, Canary  
725 Islands. *Spanish J Agric Res* 9:113–123. doi: 10.5424/sjar/20110901-076-10
- 726 Arévalo JR, de Nascimento L, Fernández-Lugo S, et al (2011) Grazing effects on species

- 727 composition in different vegetation types (La Palma, Canary Islands). *Acta Oecologica*  
728 37:230–238. doi: 10.1016/j.actao.2011.02.006
- 729 Blondel, J., Aronson, J., Bodiou, J-Y and Boeuf G (2010) *The Mediterranean Region: Biological*  
730 *Diversity in Space and Time, Second*. Oxford University Press, Oxford
- 731 Brinkmann K, Patzelt A, Dickhoefer U, et al (2009) Vegetation patterns and diversity along an  
732 altitudinal and a grazing gradient in the Jabal al Akhdar mountain range of northern Oman.  
733 *J Arid Environ* 73:1035–1045. doi: 10.1016/j.jaridenv.2009.05.002
- 734 Bunce RGH (1982) A field key for classifying British woodland vegetation. Part 1. 103.
- 735 Campbell K, Donlan CJ (2005) Feral goat eradications on islands. *Conserv Biol* 19:1362–1374.  
736 doi: 10.1111/j.1523-1739.2005.00228.x
- 737 Clarke K.R., Gorley RN (2014) *Primer v7: User manual/tutorial*. Plymouth, United Kingdom
- 738 Core Development Team R (2014) *R: A language and environment for statistical computing*.
- 739 Cowling RM, Rundel PW, Lamont BB, et al (1996) Plant diversity in mediterranean-climate  
740 regions. *Trends Ecol Evol* 11:362–366. doi: 10.1016/0169-5347(96)10044-6
- 741 Daget P (1977) LE BIOCLIMAT MEDITERRANEEN: ANALYSE DES FORMES  
742 CLIMATIQUES PAR LE SYSTEME D'EMBERGER. *Vegetatio* 34:87–103.
- 743 Dakhlaoui H, Ruelland D, Trambly Y, Bargaoui Z (2017) Evaluating the robustness of  
744 conceptual rainfall-runoff models under climate variability in northern Tunisia. *J Hydrol*  
745 550:201–217. doi: 10.1016/j.jhydrol.2017.04.032
- 746 Daly-Hassen H (2017) *Valeur économique des services écosystémiques du Parc National de*  
747 *l'Ichkeul, Tunisie*. IUCN, Gland, Switzerland. Malaga, Spain.
- 748 Daoud-Bouattour, A., Gammar Ghrabi, Z., and Limam Ben Saad S (2007) *Guide illustré des*  
749 *Plantes du Parc National de L'Ichkeul*. Eco-Ressources International, Ariana Tunisie

- 750 de la Riva EG, Lloret F, Pérez-Ramos IM, et al (2016) The importance of functional diversity in  
751 the stability of Mediterranean shrubland communities after the impact of extreme climatic  
752 events. *J Plant Ecol* 10:rtw027. doi: 10.1093/jpe/rtw027
- 753 Di Castri F (1981) Mediterranean-type shrublands of the world. In: Di Castri F, Goodall DW SR  
754 (ed) *MediterraneanType Shrublands*. Amsterdam, pp 1–52
- 755 Dovrat G, Perevolotsky A, Ne’eman G (2014) The response of Mediterranean herbaceous  
756 community to soil disturbance by native wild boars. *Plant Ecol* 215:531–541. doi:  
757 10.1007/s11258-014-0321-3
- 758 ESRI (2017) *ArcGIS Desktop: Release 10*.
- 759 European Environment Agency (2017) G2.4 *Olea europaea-Ceratonia siliqua* woodland.
- 760 Falcucci A, Maiorano L, Boitani L (2007) Changes in land-use/land-cover patterns in Italy and  
761 their implications for biodiversity conservation. *Landsc Ecol* 22:617–631. doi:  
762 10.1007/s10980-006-9056-4
- 763 Fay M (1980) *Flora of the National Park of Ichkeul, Tunisia*.
- 764 Fernández-lugo S (2016) *Grazing management and impact in the Canary islands : Rethinking*  
765 *sustainable use*.
- 766 Fernández-Lugo S, Arévalo JR, de Nascimento L, et al (2013) Long-term vegetation responses to  
767 different goat grazing regimes in semi-natural ecosystems: A case study in Tenerife (Canary  
768 Islands). *Appl Veg Sci* 16:74–83. doi: 10.1111/j.1654-109X.2012.01211.x
- 769 Gabay O, Perevolotsky a, Shachak M (2006) *Landscape mosaic for enhancing biodiversity : On*  
770 *what scale and how to maintain it ?* *Options* 49:45–49.
- 771 Gauquelin T, Michon G, Joffre R, et al (2016) *Mediterranean forests, land use and climate*  
772 *change: a social-ecological perspective*. *Reg Environ Chang* 1–14. doi: 10.1007/s10113-

- 773 016-0994-3
- 774 Geri F, Amici V, Rocchini D (2010) Human activity impact on the heterogeneity of a  
775 Mediterranean landscape. *Appl Geogr* 30:370–379. doi: 10.1016/j.apgeog.2009.10.006
- 776 Ghrabi-Gammar Ghrabi Z LCZ and ZM (2006) ÉVOLUTION DE LA COUVERTURE  
777 VÉGÉTALE DU PARC NATIONAL DE L' ICHKEUL ( TUNISIE ). *Rev Écol (Terre*  
778 *Vie)* 61:317–326.
- 779 Glasser, T., Hadar, L., Navon, Y., Perevolotsky A (2013) Innovative monitoring of goat grazing  
780 effects on landscape structural properties. doi: 10.13140/2.1.2680.8003
- 781 Gomez-Campo C (1985) *Plant Conservation in the Mediterranean*. W. Junk, Dordrecht, The  
782 Netherlands
- 783 Harrison S, Noss R (2017) Endemism hotspots are linked to stable climatic refugia. *Ann Bot*  
784 119:207–214. doi: 10.1093/aob/mcw248
- 785 Henkin Z (2011) Cattle grazing and vegetation management for multiple use of Mediterranean  
786 shrubland in Israel. *Isr J Ecol Evol* 57:43–51. doi: 10.1560/IJEE.57.1-2.43
- 787 Hill, J., Hostert, P., Tsiourlis, G., Kasapidis, P. & Udelhoven T (1998) Monitoring 20 years of  
788 intense grazing impact on the Greek island of Crete with earth observation satellites. *J Arid*  
789 *Environ* 39:165–178.
- 790 Hollis GE (1977) *A Proposed Management Plan for the Internationally Important Parc National*  
791 *de L'Ichkeul, Tunisia*. London
- 792 Hollis GE (1986) *The Modelling and Management of the Internationally Important Wetland at*  
793 *Garaet El Ichkeul, Tunisia*. I.
- 794 Kirk DA (1983) *The plant associations of Djebel Ichkeul, northern Tunisia, in relation to site*  
795 *factors and conservation implications*. University College London

- 796 Lázaro A, Tscheulin T, Devalez J, et al (2016) Moderation is best: Effects of grazing intensity on  
797 plant-flower visitor networks in Mediterranean communities. *Ecol Appl* 26:796–807. doi:  
798 10.5061/dryad.p3c75
- 799 Le Floc'h E, Boulos L, Vela E (2010) Flore tunisie.
- 800 Le Houerou HN (1981) Impact of man and his animals on Mediterranean vegetation. In: Di  
801 Castri, F., Goodall, D.W. & Specht RL (ed) *Ecosystems of the World Vol II: Mediterranean*  
802 *type shrublands*. Elsevier, London,
- 803 Legendre, P., Anderson MJ (1999) Distance-Based Redundancy Analysis : Testing Multispecies  
804 Responses in Multifactorial Ecological Experiments. *Ecol Monogr* 69:1–24. doi:  
805 doi:10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2
- 806 Legendre, P., Legendre L (2012) *Numerical Ecology*, Third Edit. Elsevier
- 807 Levin N, Watson JEM, Joseph LN, et al (2013) A framework for systematic conservation  
808 planning and management of Mediterranean landscapes. *Biol Conserv* 158:371–383. doi:  
809 10.1016/j.biocon.2012.08.032
- 810 Loidi J, del Arco M, Pérez de Paz PL, et al (2010) Understanding properly the 'potential  
811 natural vegetation' concept. *J Biogeogr* 37:2209–2211. doi: 10.1111/j.1365-  
812 2699.2010.02302.x
- 813 Mata J, de Nascimento L, Fernández-Lugo S, et al (2014) The inefficient planning of goat  
814 grazing: Causes and consequences. The Palmera breed case (Canary Islands). *Small Rumin*  
815 *Res* 121:125–130. doi: 10.1016/j.smallrumres.2014.03.010
- 816 Mazzoleni, S., G. di Pasquale, M. Mulligan, M. di Martino and FR (2004) *Recent dynamics of*  
817 *the Mediterranean vegetation and landscape*. Wiley, West Sussex, England UK
- 818 McLaughlin BC, Ackerly DD, Klos PZ, et al (2017) Hydrologic refugia, plants, and climate

- 819 change. *Glob Chang Biol* 23:2941–2961. doi: 10.1111/gcb.13629
- 820 Médail, F. and Quézel P (1997) Hot-spots analysis for conservation of plant biodiversity in the  
821 Mediterranean Basin. *Ann Missouri Bot Gard* 84:112–127.
- 822 Miguel-Ayanz AS, García-Calvo RP, Fernández-Olalla M (2010) Wild ungulates vs. Extensive  
823 livestock. Looking back to face the future. *Options Méditerranéennes* 92:27–34.
- 824 Molina-Venegas R, Aparicio A, Lavergne S, Arroyo J (2016) How soil and elevation shape local  
825 plant biodiversity in a Mediterranean hotspot. *Biodivers Conserv* 25:1133–1149. doi:  
826 10.1007/s10531-016-1113-y
- 827 Morandini E (1977) Problems of conservation, management and regeneration of Mediterranean  
828 forests: research priorities. In: MAB Technical Notes 2. UNESCO, Paris,
- 829 Naveh Z (1990) Fire in the Mediterranean – A Landscape Ecological Perspective. In:  
830 Goldammer, J.F. JMJ (ed) *Fire in Ecosystems Dynamics.*, Proceeding. SPB Academic  
831 Publishing, The Hague, Netherlands,
- 832 Nogués-Bravo D, Araújo MB, Lasanta T, López-Moreno JI (2008) Climate Change in  
833 Mediterranean Mountains during the 21st Century. *AMBIO A J Hum Environ* 37:280–285.  
834 doi: 10.1579/0044-7447(2008)37[280:CCIMMD]2.0.CO;2
- 835 Nogués-Bravo D, López-Moreno JI, Vicente-Serrano SM (2012) Climate Change and its Impact.  
836 *Mediterr Mt Environ* 185–200. doi: 10.1002/9781119941156.ch9
- 837 Noy-Meir I, Oron T (2001) Effects of grazing on geophytes in Mediterranean vegetation. *J Veg*  
838 *Sci* 12:749–760.
- 839 Olff H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. *Trends Ecol Evol*  
840 13:261–265. doi: 10.1016/S0169-5347(98)01364-0
- 841 Olsvig-Whittaker L, Frankenberg E, Perevolotsky A, Ungar ED (2006) Grazing, overgrazing and

- 842 conservation: Changing concepts and practices in the Negev rangelands. *Sci Chang*  
843 *planétaires / Sécheresse* 17:195–199.
- 844 OpenStreetMap contributors (2015) Roads of Tunisia.
- 845 Osem Y, Perevolotsky A, Kigel J (2007) Interactive effects of grazing and shrubs on the annual  
846 plant community in semi-arid Mediterranean shrublands. *J Veg Sci* 18:869–+. doi:  
847 10.1111/j.1654-1103.2007.tb02603.x
- 848 Ouali, M., Daoud-Bouattour, A., Etteieb, S., Mokhtar Gammar, A., Ben Saad-Limam, S., Grabi-  
849 Gammar Z (2014) Le marais de Joumine, Parc national de L'ichkeuL, tunisie : diversité  
850 floristique, cartograPhie et dynamique de La végétation (1925-2011). *La terre la vie* 63:3–  
851 23.
- 852 Paeth H, Born K, Girmes R, et al (2009) Regional climate change in tropical and Northern Africa  
853 due to greenhouse forcing and land use changes. *J Clim* 22:114–132. doi:  
854 10.1175/2008JCLI2390.1
- 855 Papanastasis VP (1998) Livestock grazing in Mediterranean ecosystems: an historical and policy  
856 perspective. In: Papanastasis, V P and Peters D (ed) *ECOLOGICAL BASIS OF*  
857 *LIVESTOCK GRAZING IN MEDITERRANEAN ECOSYSTEMS*. Proceedings of the  
858 International Workshop held in Thessaloniki (Greece) on October 23-25, 1997, Belgium, pp  
859 5–9
- 860 Papanastasis VP, Kyriakakis S, Kazakis G (2002) Plant diversity in relation to overgrazing and  
861 burning in mountain mediterranean ecosystems. *J Mediterr Ecol* 3:53–63.
- 862 Perevolotsky A (2005) Livestock grazing and biodiversity conservation in Mediterranean  
863 environments: the Israeli experience. *Sustain grazing, Nutr Util Qual sheep goat Prod* 51–  
864 56.



- 865 Perevolotsky A, Seligman NG (1998) Role of Grazing in Mediterranean Rangeland Ecosystems.  
866 *Bioscience* 48:1007–1017. doi: 10.2307/1313457
- 867 Peterken, G. L. and Radford GF (1971) Report on field-trials in Tunisia. In: IBP/CT Progress  
868 Report. pp 36–94
- 869 PlantBase E (2017) The Euro+Med PlantBase - the information resource for Euro-Mediterranean  
870 plant diversity. <http://www.emplantbase.org/home.html>. Accessed 1 Jan 2017
- 871 Pons A (1981) The history of Mediterranean shrublands. In: Di Castri F., Goodall, D. W. &  
872 Specht RL (Else (ed) *Mediterranean-Type Shrublands*. Elsevier, Amsterdam, pp 131–138
- 873 Quézel P (1981) Floristic composition and phytosociological structure of sclerophyllous matorral  
874 around the Mediterranean. In: Di Castri, F., Goodall, D.W. & Specht RL (ed) *Ecosystems of*  
875 *the World Vol II: Mediterranean type shrublands*,. Elsevier, London, p 107–121.
- 876 Quézel P, Médail F, Loisel R, et al (1999) Biodiversity and conservation of forest species in the  
877 Mediterranean basin Biodiversity and conservation of forest species in the Mediterranean  
878 basin THE RICHNESS OF MEDITERRANEAN FOREST SPECIES: CALIFORNIA AND  
879 THE MEDITERRANEAN BASIN. *Unasyuva* 50:21–28.
- 880 Rackham, O., Moody J (1996) *The Making of the Cretan Landscape*. Manchester University  
881 Press, Manchester
- 882 Radford E., Catullo G, de Montmollin B (2011) *Important Plant Areas of the South and East*  
883 *Mediterranean Region: Priority Sites for Conservation*.
- 884 Roberts DW (1986) Ordination on the Basis of Fuzzy Set Theory. *Vegetatio* 66:123–131.
- 885 Rundel PW (1998) *Landscape disturbance and biodiversity in Mediterranean-type ecosystems*.  
886 Springer, New York, pp 3–22
- 887 Rundel PW, Arroyo MTK, Cowling RM, et al (2016) *Mediterranean Biomes: Evolution of their*

- 888 Vegetation, Floras and Climate. *Annu Rev Ecol Evol Syst* 47:383–407. doi:  
889 10.1146/annurev-ecolsys-121415-032330
- 890 Sardans J, Peñuelas J (2013) Plant-soil interactions in Mediterranean forest and shrublands:  
891 Impacts of climatic change. *Plant Soil* 365:1–33. doi: 10.1007/s11104-013-1591-6
- 892 Segoli M, Ungar ED, Giladi I, et al (2012) Untangling the positive and negative effects of shrubs  
893 on herbaceous vegetation in drylands. *Landsc Ecol* 27:899–910. doi: 10.1007/s10980-012-  
894 9736-1
- 895 Shachak M, Boeken B, Groner E, et al (2008) Woody Species as Landscape Modulators and  
896 Their Effect on Biodiversity Patterns. *Bioscience* 58:209. doi: 10.1641/B580307
- 897 Sternberg M, Shoshany M (2001) Influence of slope aspect on Mediterranean woody formations:  
898 Comparison of a semiarid and an arid site in Israel. *Ecol Res* 16:335–345. doi:  
899 10.1046/j.1440-1703.2001.00393.x
- 900 Tomaselli R (1977) The degradation of the Mediterranean maquis. *Ambio* 6:356–362.
- 901 Tomaselli R (1981) Main physiognomic types and geographic distribution of shrub systems  
902 related to Mediterranean climates. In: Di Castri, F., Goodall, D.W. and Specht RL (ed)  
903 *Ecosystems of the World Vol II: Mediterranean type shrublands*. Elsevier, London, pp 95–  
904 106
- 905 Trambly Y, El Adlouni S, Servat E (2013) Trends and variability in extreme precipitation  
906 indices over maghreb countries. *Nat Hazards Earth Syst Sci* 13:3235–3248. doi:  
907 10.5194/nhess-13-3235-2013
- 908 Underwood EC, Viers JH, Klausmeyer KR, et al (2009) Threats and biodiversity in the  
909 mediterranean biome. *Divers Distrib* 15:188–197. doi: 10.1111/j.1472-4642.2008.00518.x
- 910 UNEP/WCMC (2003) Ichkeul National Park. *Management* 1–10.

- 911 Verdú JR, Crespo MB, Galante E (2000) Conservation strategy of a nature reserve in  
912 Mediterranean ecosystems: the effect of protection from grazing on biodiversity. *Biodivers*  
913 *Conserv* 9:1707–1721.
- 914 Vogiatzakis IN, Mannion AM, Griffiths GH (2006) Mediterranean ecosystems: problems and  
915 tools for conservation. *Prog Phys Geogr* 30:175–200. doi: 10.1191/0309133306pp472ra
- 916 Warton DI, Wright ST, Wang Y (2012) Distance-based multivariate analyses confound location  
917 and dispersion effects. *Methods Ecol Evol* 3:89–101. doi: 10.1111/j.2041-  
918 210X.2011.00127.x
- 919 Wilson KA, Underwood EC, Morrison SA, et al (2007) Conserving biodiversity efficiently:  
920 What to do, where, and when. *PLoS Biol* 5:1850–1861. doi: 10.1371/journal.pbio.0050223  
921

**Table 1** (on next page)

Biophysical variables measured at Jebel Ichkeul

1

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

2

3

4

5

6

7

8

9

10

11

**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 <sup>2</sup>	RSS	N	Variables
1	552.03	0.33553	73283	1	Spatial*** (latitude, latitude <sup>2</sup> , latitude <sup>3</sup> , longitude, longitude <sup>2</sup> , longitude <sup>3</sup> , 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 <sup>n</sup>
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

---

2

3

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

1  
2

**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,  $P < .05$ )

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.

1

	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
<i>P (Perm)</i>	<b>0.016</b>	0.655	<b>0.002</b>	<b>0.000</b>	0.586	<b>0.000</b>	<b>0.000</b>
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)
<i>P (perm)</i>	<b>0.014</b>	0.111	0.311	0.118	--	0.243	0.283
Grazing x aspect	---	--	--	--	--	--	--

2

3

- 4
- 5 Mean abundance (% cover) and standard error (in parentheses) are given for main factors. Different letters indicate significant
- 6 differences for grazing effect (pair-wise t-test,  $P < 0.05$ ). Column headings: Graminoids (22 spp.), Herbaceous legumes (22 spp.),
- 7 Geophytes (16 spp.), Forbs (88 spp.), All herbaceous (144 spp.), Shrub legumes (5 spp.), All other shrubs (30 spp.), All shrubs/trees (35
- 8 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)

1  
2

	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
<i>P</i> (perm)	<b>0.029</b>	0.661	<b>0.003</b>	<b>0.001</b>	--	<b>0.000</b>	<b>0.000</b>
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)
<i>P</i> (perm)	<b>0.002</b>	0.084	--	<b>0.005</b>	--	<b>0.012</b>	<b>0.016</b>
Grazing x aspect	--	--	--	--	--	--	--

3

**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

1

Model	AICc	R <sup>2</sup>	RSS	N	Variables
1	509.22	0.40153	78377	3	Spatial*** (latitude, latitude <sup>2</sup> , latitude <sup>3</sup> , longitude, longitude <sup>2</sup> , longitude <sup>3</sup> , latitude x longitude), rock outcrop**, log (# <i>Olea</i> 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 <i>Olea</i> diameter 30 cm**
4	509.84	0.37164	82292	2	Spatial***, log (# <i>Olea</i> 16-21 cm 30 cm)**
5	510.09	0.39395	79370	3	Spatial***, rock outcrop**, frequency <i>Olea</i> diameter 30 cm <sup>n</sup>
6	510.19	0.36842	82714	2	Spatial***, mean <i>Olea</i> diameter 30 cm**
7	510.20	0.39299	79496	3	Spatial***, rock outcrop**, log (# <i>Olea</i> 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 (# <i>Olea</i> > 20 cm at 30 cm ht)
10	510.34	0.36712	82884	6	Spatial***, log (# <i>Olea</i> 11-15 cm 30 cm)**

2

3



**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

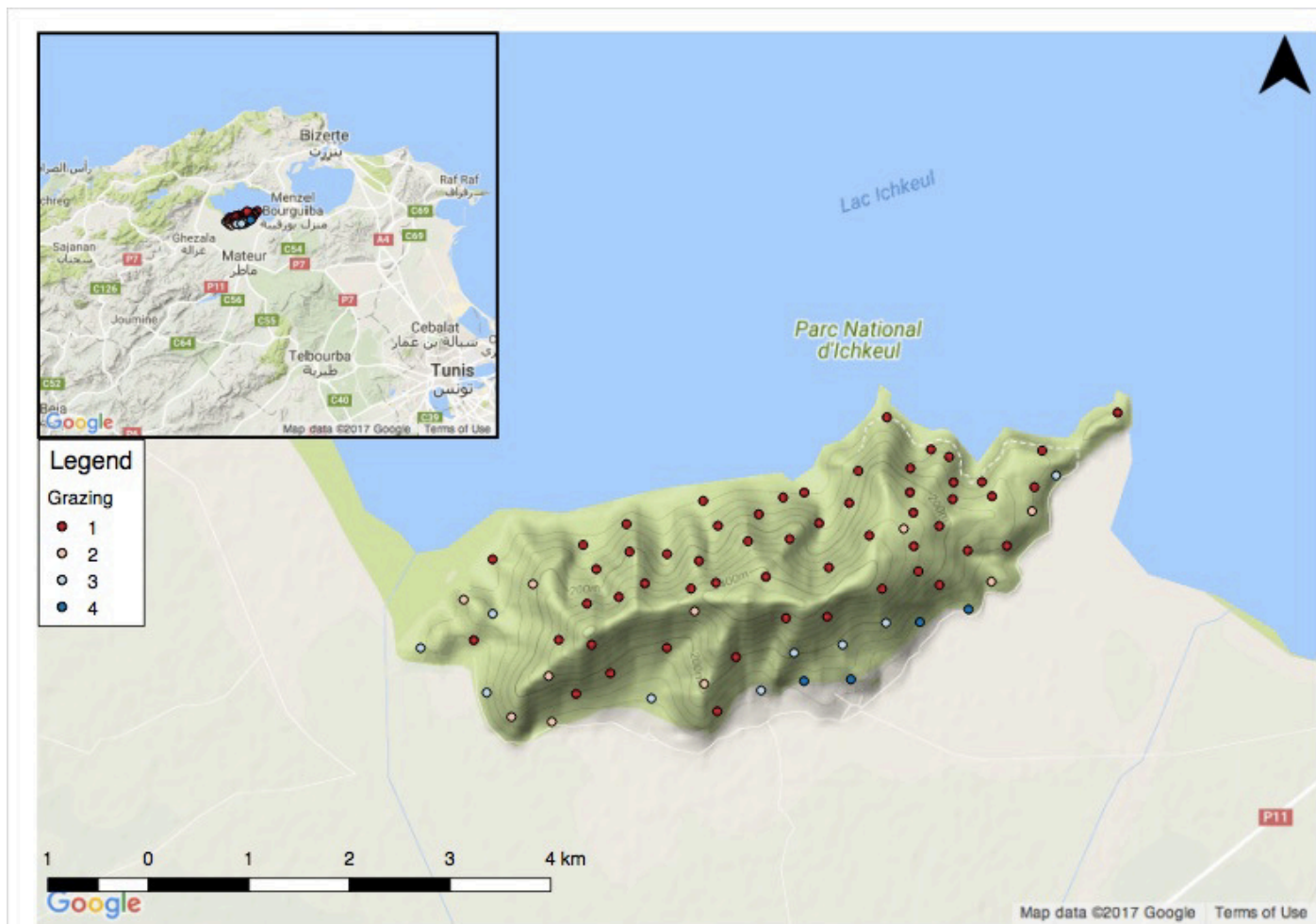
Model	AICc	R <sup>2</sup>	RSS	N	Variables
1	552.35	0.14593	1.7638E+05	4	Log (distance to road) <sup>***</sup> , log (altitude) <sup>**</sup> , rock outcrop <sup>**</sup> , log (# <i>Olea</i> 16-21 cm 30 cm height) <sup>**</sup>
2	552.47	0.11509	1.8275E+05	3	Log (distance to road) <sup>***</sup> , log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

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.

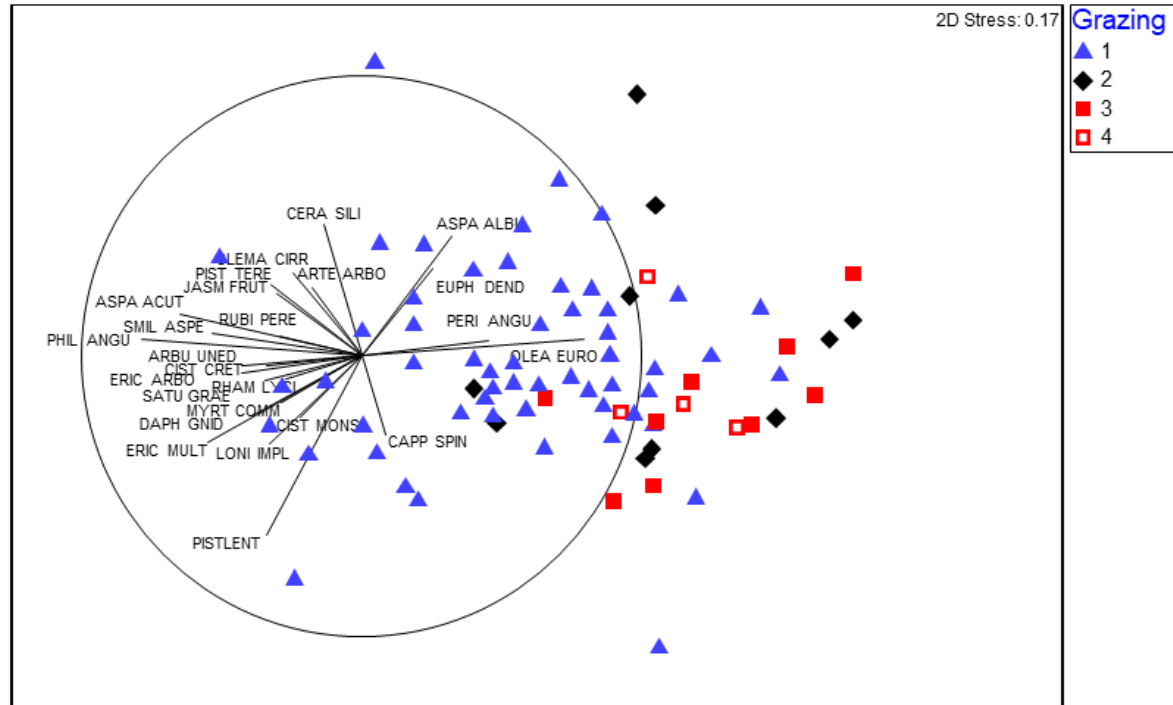


1035

**Figure 2**(on next page)

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

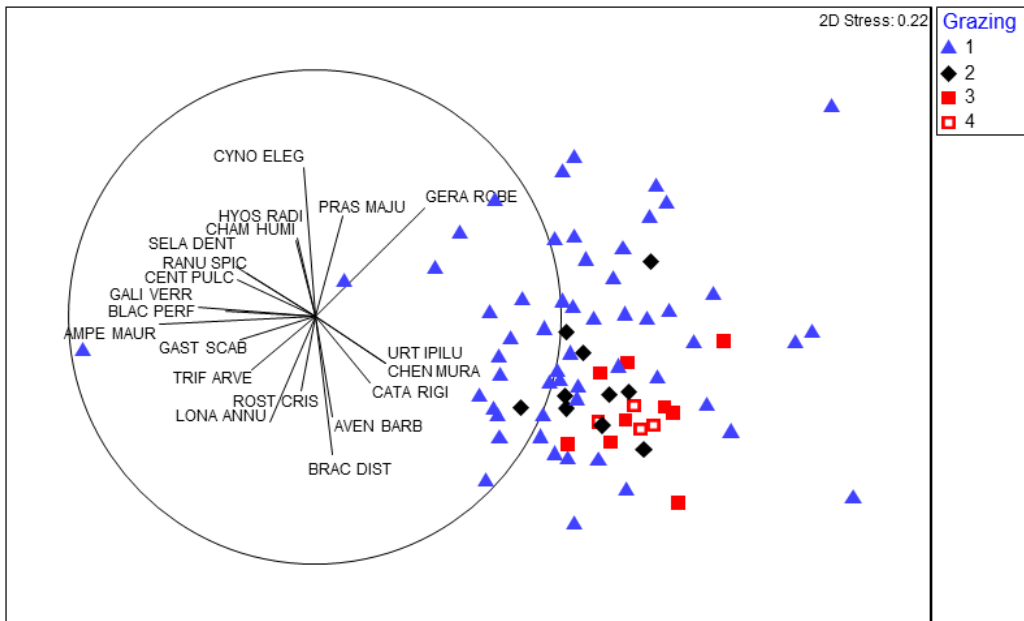
Species acronyms: CAPP SPIN - *Capparis spinosa*; PERI ANGU - *Periploca angustifolia*; OLEA EURO - *Olea europaea*; EUPH DEND - *Euphorbia dendroides*; ASPA ALBU - *Asparagus albus*; CERA SILI - *Ceratonia siliqua*; CLEM CIRR - *Clematis cirrhosa*; JASM FRUT - *Jasminum fruticans*; SMIL ASP - *Smilax 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  $\geq 0.3$  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 RADII - *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

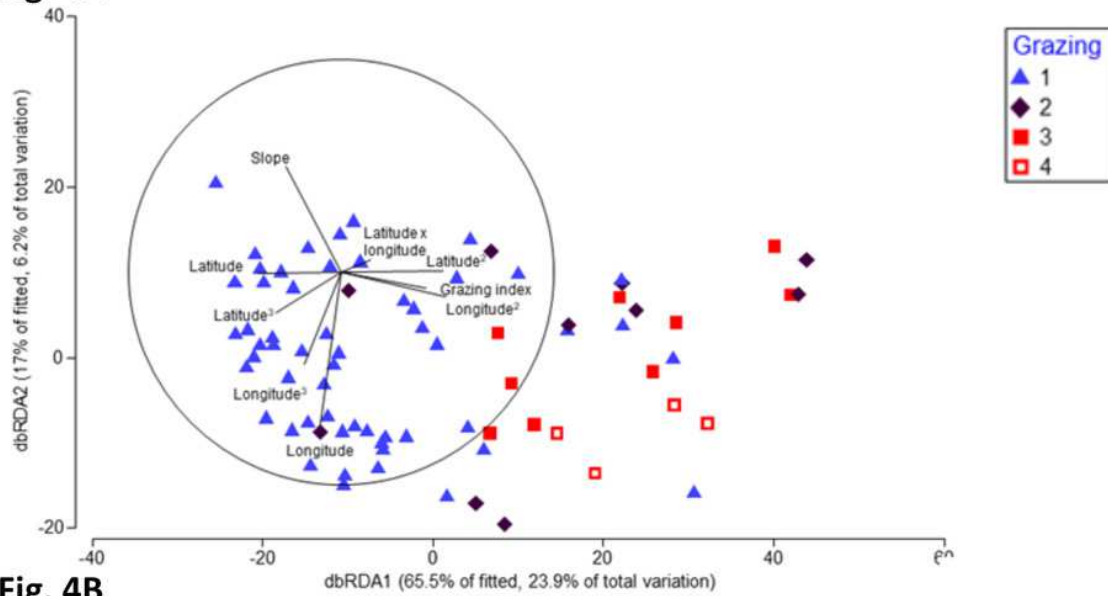


Fig. 4B

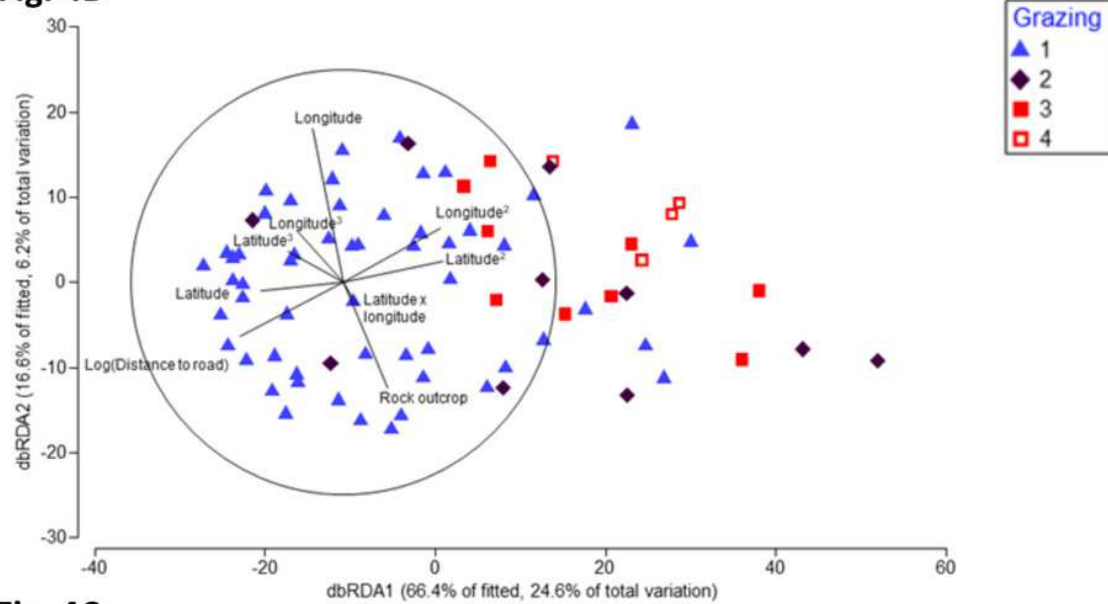
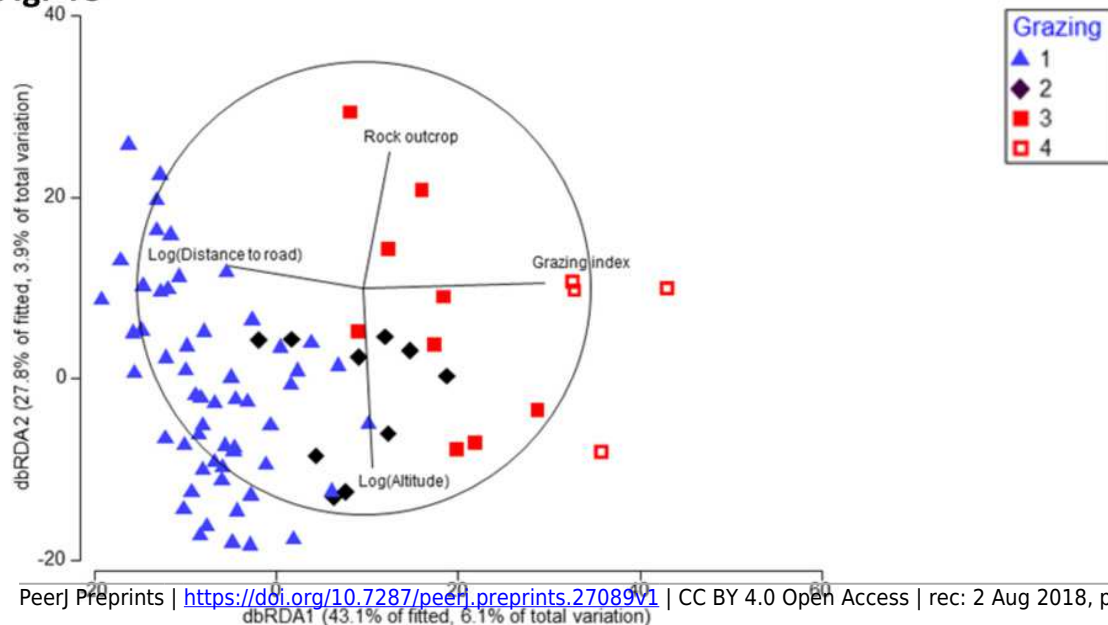
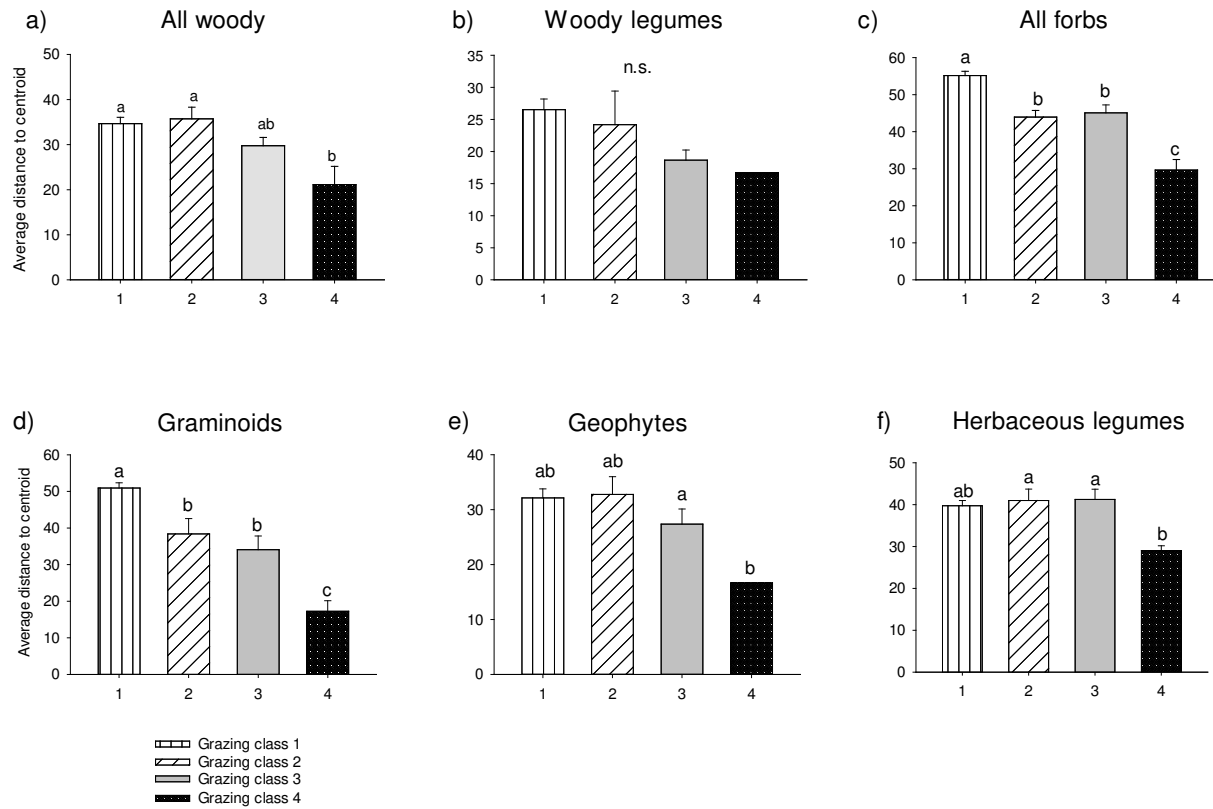


Fig. 4C



**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) herbaceous

Fig. 6A

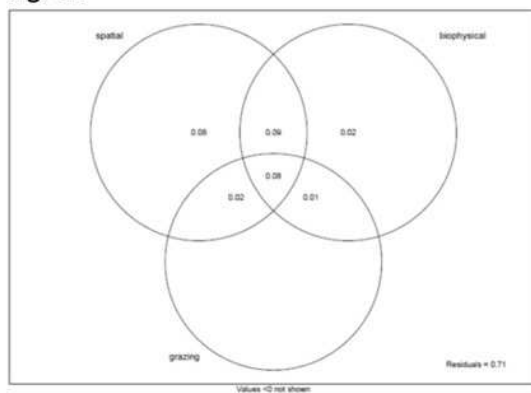


Fig. 6B

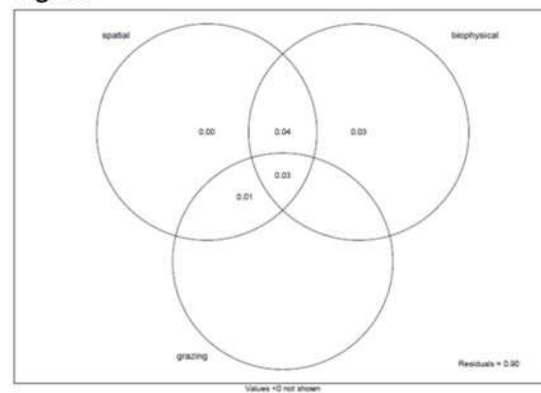


Fig. 6C

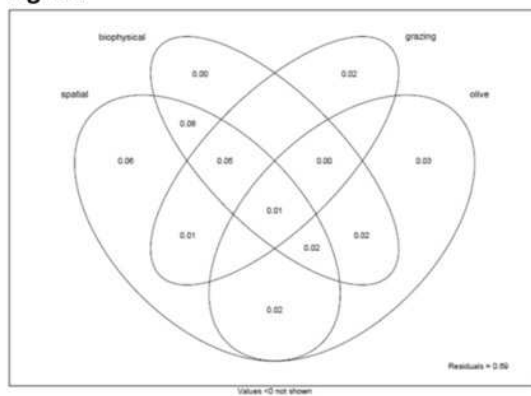
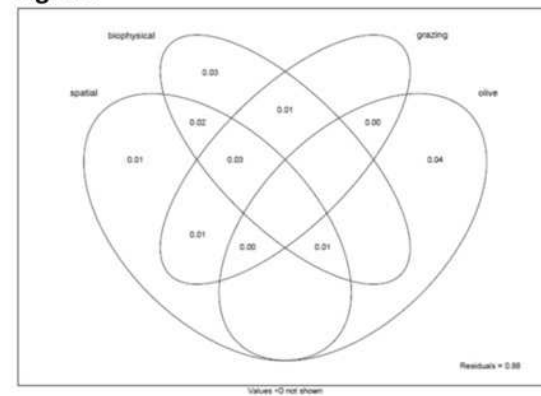


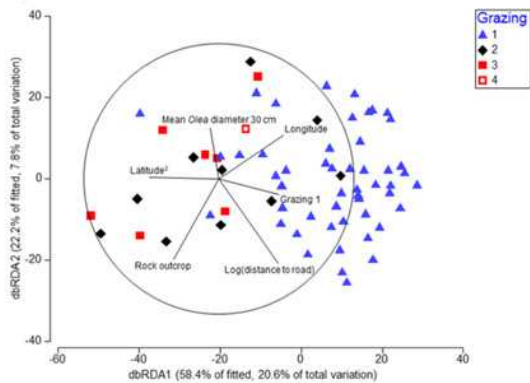
Fig. 6D



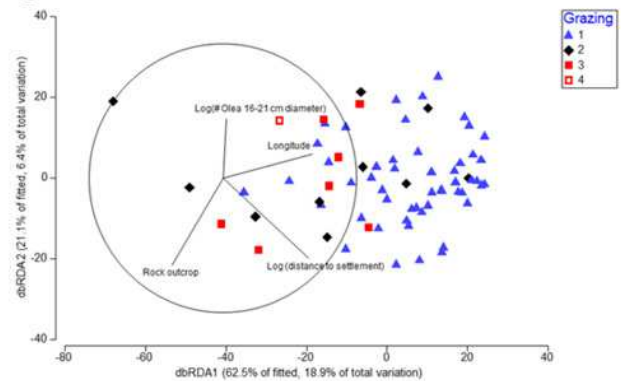
# Figure 7

Distance-based redundancy analysis plot of plant species based on best model solutions (AIC<sub>c</sub>) 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

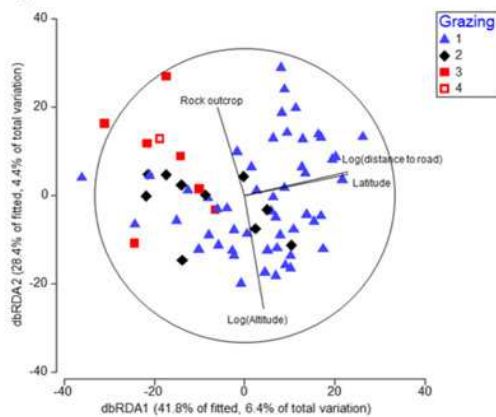
**Fig. 7A**



**Fig. 7B**



**Fig. 7C**



**Fig. 7D**

