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

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

[1] Aquila Conservation & Environment Consulting, Ottawa, Ontario, Canada
[2] Department of Biology, University College London, University of London, London, United Kingdom

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

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

Running head: Effect of grazing on maquis vegetation

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

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

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

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

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

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

Introduction

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

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

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

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

Only 4.7% of the Mediterranean basin has primary ‘natural’ vegetation (Geri et al. 2010) and many of the remaining 'wildlands' of the Mediterranean are restricted to mountainous or coastal regions with slopes too steep for cultivation. Given their long history of human use the question of how to protect and manage these hotspots of biodiversity is a conservation dilemma (Blondel et al. 2010). Prioritizing and setting aside protected areas such as National Parks or nature reserves is one approach to conserving Mediterranean shrublands, but these constitute a relatively small area, and even in these protected landscapes vegetation quality has declined (Wilson et al. 2007). With predicted high impacts of climate change, areas of high plant endemism in the Mediterranean are a cause for concern and it has been forecasted that the frequency and intensity of drought and desertification will lead increasingly to loss of plant biodiversity (Gauquelin et al. 2016) and this could influence functional heterogeneity (de la Riva et al. 2016). Thus, fundamental to the conservation of Mediterranean flora is the question of intervention or protection to maintain the diversity of plant communities and the challenge of integrating multiple uses of Mediterranean landscapes in the face of climate change.

Although concern has been expressed about conservation of the Mediterranean wooded landscape significant knowledge gaps in plant ecology still exist, particularly in North Africa (Radford et al. 2011). About 11% of the 48.2 million ha of forests occurring in the Mediterranean Basin occur within this region and in some areas deforestation and overgrazing has created serious ecological disfunction, especially in high altitude forests (Quézel et al. 1999). This has resulted in four consequences: 1) disruption of natural disturbance cycles; 2) homogenization of plant assemblages in terms of structure and compostion; 3) loss of biodiversity in forest species; and 4) increases in invasive plants (Quézel et al. 1999).

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

In this paper we ask: 1) what is the impact of grazing on plant biodiversity of functional groups (woody and herbaceous as well as grasses, legumes and Geophytes) at Jebel Ichkeul and how much unique variation in species composition and abundance is explained by this factor; 2) is the impact of grazing on plant beta diversity still significant after controlling for the main environmental drivers and 3) what is the effect of *Olea europaea* size and density on herbaceous or other woody plant species compared to abiotic natural features(Osem et al. 2007; Shachak et al. 2008; Agra and Ne'eman 2009). Our results can provide a framework for the conservation and sustainable use of the Jebel's forests and maquis and contribute to the broader question of the impact of grazing and the structure of woody vegetation on maquis vegetation elsewhere in the Mediterranean, both inside and outside protected areas. They also provide a baseline of plant species composition prior to the onset of climate change.

Methods

Study area

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

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

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

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

Plant surveys and sampling design

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

Identifying plant species

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

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

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

Measuring grazing intensity

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

Controlling for biophysical features

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

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

Tree diameter measurements and relative abundance estimates

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

$$r_i = c_i/2\pi$$

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

$$A = \Sigma A_i$$

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

where r_i = radius of stem i, c_i = circumference of stem i, π = 3.146; A_i = surface area of stem i, A = total surface area of all stems and r = equivalent radius.

Spatial variation and other human footprint variables

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

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

Treatment of species data and environmental covariates

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

For the environmental covariates we inspected draftsman plots to determine whether variable distributions were approximately linear. For example, untransformed altitude data showed a quadratic (bell-shaped) relationship with latitude, which was improved by transformation. We log-transformed altitude, distance to roads and settlements and olive diameters using natural logarithms (+0.1 was added as a constant to the latter because of zero values) to reduce skewness after examining draftsman plots (Anderson et al. 2008). Distributions of other variables were not improved by transformation. Because it is a circular variable we also transformed aspect using a trigonometric function (Roberts 1986) into two variables ‘northness’ (the cosine of aspect) and ‘eastness’ (the sine of aspect). Since these were not significant and not easily interpretable in ordination models, we also created eight classes of aspect based on compass bearings: (1: 0-45^{o} (NNE); 2: 46-90^{o} (ESE); 3: 91-135^{o} (SSE); 4: 136-180^{o} (SSW); 5: 181-225^{o} (WSW); 6: 226-270^{o} (WNW); 7: 271-315^{o} (NNW); 8: 316-360^{o} (ENE). For alternate models we pooled the aspect classes into ‘north’ and ‘south’ to simplify model structure. For the eight aspect classes we grouped variables into an indicator group as this was a binary categorical variable; trend surface variables were treated similarly as these were all derived from spatial coordinates. We explored models treating grazing as a grouped categorical variable and as a semi-quantitative variable.

What are the main patterns in plant species distribution and abundance and how do these relate to environmental factors?

Because the effects of grazing and other human activities could differentially affect plant species, we subdivided plant species into woody and herbaceous categories and other functional groups (see above; Appendix 1). We visualized woody and herbaceous species groups using non-metric multi-dimensional scaling (*n*MDS) to investigate general patterns in plant species composition and abundance for all 78 sites (Clarke and Gorley, 2014). Superimposing species and environmental covariate vectors (Pearson correlations) on *n*MDS ordinations enabled us to identify indicator species for grazing pressure and of different plant assemblages. Doing so allowed us to use all 78 sites and all variables in the ordination as these correlations were *post-hoc* (thus missing values, and sites for which we did not have environmental data, such as soil pH, could be included in exploratory analyses).

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

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

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

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

Effects of grazing on woody and herbaceous plant distribution and abundance

First, to provide a visualization of the variability in the averages within each grazing group we calculated 95% bootstrapped averages (Anderson et al. 2008). Comparison of the relative sizes of these ellipses provided information on differences in the underlying variation in average values (beta diversity) within grazing classes. Second, we performed two tests to evaluate whether differences between grazing classes were due to variation in multivariate dispersion (test for the homogeneity of multivariate dispersions) or location in multivariate ordination space (permutational multivariate ANOVA), or both. The first test was performed using the routine PERMDISP, which provides a direct measure of beta diversity (Anderson et al. 2008). The second test was done using a one-way permutational multivariate ANOVA to ascertain whether there were differences in multivariate locations between grazing classes. This model was set up with grazing class as a fixed effect; we also conducted *post hoc* pairwise t-tests between grazing classes. We performed a second, two-way permutational multivariate ANOVA model including grazing as a fixed effect, and aspect (eight classes) as a random effect. We inspected P values for the two-way permutational multivariate ANOVA and removed the interaction term (grazing x aspect) when P >0.8. We also pooled the aspect variable when P values were > 0.25 to avoid Type II errors (Anderson et al. 2008). We ran a third one-way permutational multivariate ANOVA to test if the effect of grazing was still significant after controlling for all biophysical covariates. Because our design was unbalanced we used Type I sums of squares for our models to partition the variation explained by different factors and when covariates were used in the models. We performed these models for all functional groups. It is important to note that the multivariate models that we used differentiated between location and dispersion in multivariate space, which has been a criticism of these types of modeling platforms (Warton et al. 2012). We also used Bray-Curtis and not Euclidean distances for resemblance matrices based on compositional species data. Statistical modelling was performed using the software, Primer (Clarke and Gorley 2006), PERMANOVA + (Anderson et al. 2008) and variance partitioning was done in R (R. Core Development Team 2014).

Results

Plant species

We identified 219 of the 348 plant species recorded for Jebel Ichkeul (Fay 1980). Species richness and diversity were highly variable; high altitude, northerly, ridge crest assemblages were most species-rich, while species-poor sites were prevalent on the heavily grazed and cleared lower southerly slopes, where invading ruderals were abundant. Overall, 21% of sites had more than 50 species, 32% had 40-50 species, 32% had 30-40 species, and the remainder had less than 30 species. The richest site contained 65 species (site 35) and was located near the summit at an altitude of 352 m.a.s.l. Only 16 species were found in the most species-poor quadrat (site 57) which comprised *Ceratonia siliqua* and *Olea europaea* forest. The influence of soil limitations, exposure and grazing in high matorral created clearings rich in herbaceous species, while in deep valleys subject to ephemeral winter flooding closed canopy climax forest had lower species richness.

Patterns in plant species distribution and abundance and relationship to environmental factors

According to Tomaselli's criteria (Tomaselli 1977), 75% of the sites we examined comprised forest or matorral with trees, while only 25% of sites had no arborescent individuals. The latter included degraded matorral or 'potential natural vegetation' on ridge crests and valley sides. Grazing had a large impact as shown by the woody species *n*MDS ordination which demonstrated a gradient from low altitude sites with moderate to heavy grazing to high altitude sites with low grazing pressure (Figure 2). Spatial location (latitude) represented a surrogate for a moisture gradient from xeric sites on the southern slopes of the mountain to mesic sites on the northern slopes adjacent to Lac Ichkeul (Figure 2). Similar patterns were evident in the herbaceous species *n*MDS (Figure 3).

Woody species indicators associated with unbrowsed sites included *Ceratonia siliqua, Erica multiflora, Erica arborea, Pistachia terebinthus* and *Phillyrea angustifolia* (Figure 2; Supplementary Figure 1a, b). These species were associated with mesic sites on the northern slopes of the mountain. By contrast, *Olea europaea* was indicative of heavily grazed sites (Figure 2; Supplementary Figure 1c). A similar pattern was evident for herbaceous species with widespread (often invasive) species - *Chenopodium murale* and *Urtica pilulifera* being indicative of heavily grazed sites, whereas *Geranium robertianum* was typical of shaded locations under closed canopy *Olea* on alluvial fans (Figure 3).

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

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

Effects of grazing

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

Significant differences among grazing classes were also found according to one-way permutational multivariate ANOVA for both woody (pseudo-$F_{3,74}$ = 3.80, P = 0.0001, 9981 unique permutations) and herbaceous plant species (pseudo-$F_{3,74}$ = 1.88, P = 0.0006, 9824 unique permutations; see also Supplementary Figure 3 for species richness and Shannon index). The two-way permutational multivariate ANOVA demonstrated that grazing still had a significant effect for both woody (pseudo-$F_{3,57}$ = 2.08, P = 0.0555) and herbaceous species (pseudo $F_{3,57}$ = 1.73, P = 0.0218) even after controlling for aspect. However, aspect (8 classes) was not significant for either group (woody pseudo-$F_{3,57}$ = 1.01, P > 0.1; herbaceous pseudo-$F_{3,57}$ = 0.80, P > 0.1) and the interaction was also non-significant (Table 4a). Results differed when aspect was categorized as 'north' and 'south' and was significant for Graminoids, all herbs, all other shrubs and all shrubs/trees (Table 4b). When all biophysical parameters were controlled for as covariates in the one way permutational multivariate ANOVA, the effect of grazing was not significant for either woody or herbaceous species (pseudo-$F_{3,74}$ = 0.936 and 0.817, respectively, both Ps >0.1). This was not surprising because of the strong relationships between grazing, and biophysical factors (e.g., altitude, slope and some slope aspects - positively with SSW, negatively with NNW). We also conducted similar models for other functional groups and detailed results for Gramineae, Geophytes, forbs and shrubs are in Table 4a. However, no significant effect of grazing was found for either herbaceous or woody legume functional groups in the multivariate permutational ANOVA (Table 4a).

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

According to variance partitioning, grazing accounted for a very small amount of variation in models for the 78 sites, and shared 8% and 3% of the variation with spatial and biophysical factors for woody and herbaceous species separately (Figure 6). However, in the models for 69 sites including *Olea* densities, grazing explained 2% of the unique variation for woody species (see Figure 6).

Olea size and density and herbaceous and woody species assemblages

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

Discussion

Our results demonstrated that grazing had a significant effect on plant beta diversity at Jebel Ichkeul, even after controlling for aspect. Some differences were found among functional groups with significant effects of grazing for woody shrubs, forbs, graminoids, and geophytes but not for herbaceous or woody legumes in terms of multivariate location. In relation to beta diversity (distance from centroids), the most striking difference among groups was a clear negative relationship between grazing intensity and woody shrubs, herbaceous forbs overall and especially graminoids. Our results support those from the Canary lslands, where woody shrubs also declined strongly from abandoned to heavily grazed areas (Fernández-Lugo et al. 2013). However, we found that beta diversity of graminoids was negatively impacted by grazing pressure, whereas they found that annual grasses were more frequent in heavily grazed areas. We also found that low intensity or intermediate grazing appeared to result in higher beta diversity for geophytes and legumes, which supports the 'intermediate grazing' hypothesis (Gabay et al. 2006; Miguel-Ayanz et al. 2010).

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

Our second main finding was that spatial location was much more highly confounded with grazing in woody than herbaceous species. The grazing index occurred in all models for herbaceous species but in only two models for woody species. However, in terms of a shift in means (i.e. variation explained in *db*RDA) far more variation was explained by the models for woody species than herbaceous species. In terms of multivariate dispersion the effect of grazing was greater for herbaceous species than woody species. Third, *Olea* size and density was strongly related to the grazing gradient and *Olea* was also the woody species most affected by wood-cutting. However, we could only record incidence of wood-cutting qualitatively; in most instances this was strongly associated with heavily grazed sites.

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

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

Medium intensity grazing on some areas of Jebel Ichkeul may increase plant species richness by maintaining openings between woody vegetation patches, removing competing plant biomass and providing nutrients from livestock manure. Those species maintained by such intermediate levels of grazing include most of the orchid species found growing in the *Ampelodesma* stand at Saida Lalia Hadan, which also contains the largest *Olea europea* in the Park (Fay 1980). For example, the resident herd of 45-60 cattle and numerous Wild Boar which forage in this area (Fay 1980) created the open conditions needed by Orchidaceae and Liliaceae, as well as various pasture grass species which have socio-economic importance (Noy-Meir and Oron 2001). However, a high density of paths resulted in soil compaction and erosion.

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

In the vicinity of the gourbi villages, at the south-eastern perimeter, on the southern face and the western end of the mountain, denuded xeric slopes are common and form scattered low matorral. Herbaceous indicators of overgrazing in these areas included weedy species (Asteraceae) like *Atractylis cancellata, Carthamus lanatus* and *Scolymus hispanicus*. In addition, there is a lack of woody browse species in these areas (e.g., *Ceratonia siliqua, Coronilla valentina, Erica arborea* and *Rhamnus lycioides*) and even species like *Pistacia lentiscus*, normally resistant to grazing (Le Houerou 1981), had low cover values. These woody species do occur on the southern slopes of the mountain but at higher elevations beneath the ridge crest, outside the normal range of goat herds and their keepers. Overgrazing on the southern slopes of the mountain creates inhospitable conditions for establishment of other protective vegetation and high insolation and aridity (previously including limestone dust) may exacerbate this problem.

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

One question is how has the vegetation of Jebel Ichkeul changed over the the 35 year period since the fieldwork for this study was done and what predictions can be made regarding vegetation changes in relation to conservation and management? Four major changes have occurred since 1983. First, in the 1990s, dams were installed at all of the major rivers flowing into Lac Ichkeul, resulting in a decline in lake water levels, and associated increasing salinity (UNEP/WCMC 2003). However, this trend was reversed by substantial rainfall in 2003-2005/2006. Second, the gourbi villages that occurred along the southern flanks of the Jebel within the national park boundaries have been evacuated and their inhabitants evicted, together with their livestock. However, the village that was present close to the limestone quarries is still inhabited (?) and agricultural land, including pasture, still occurs along the southern flanks so livestock presumably continue to graze in the national park. Third, the limestone quarries which were having a substantial local impact on vegetation through dust deposition have been closed down (UNEP/WCMC 2003). Finally, ongoing climate change has already occurred in Tunisia between the 1970s and 1999 (Paeth et al. 2009) and compared with this earlier period it is predicted that precipitation will decrease by 20% and temperatures increase by between 1^{o} and 3^{o} C by 2050 (Tramblay et al. 2013; Dakhlaoui et al. 2017).

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

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

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

Conclusions

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

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

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

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

Acknowledgements

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

References

Agra H, Ne'eman G (2009) Woody species as landscape modulators: Their effect on the herbaceous plants in a Mediterranean maquis. Plant Ecol 205:165–177. doi: 10.1007/s11258-009-9606-3

Anderson M, Gorley RN, Clarke KR (2008) PERMANOVA + for PRIMER : by.

Anon (1988) Two Problematical National Parks in the Mediterranean Region.

Arevalo JR, De Nascimento L, Fernandez-Lugo S, et al (2011) Effects of abandoning long-term goat grazing on species composition and species richness of pastures at La Gomera, Canary Islands. Spanish J Agric Res 9:113–123. doi: 10.5424/sjar/20110901-076-10

Arévalo JR, de Nascimento L, Fernández-Lugo S, et al (2011) Grazing effects on species composition in different vegetation types (La Palma, Canary Islands). Acta Oecologica 37:230–238. doi: 10.1016/j.actao.2011.02.006

Blondel, J., Aronson, J., Bodiou, J-Y and Boeuf G (2010) The Mediterranean Region: Biological Diversity in Space and Time, Second. Oxford University Press, Oxford

Brinkmann K, Patzelt A, Dickhoefer U, et al (2009) Vegetation patterns and diversity along an altitudinal and a grazing gradient in the Jabal al Akhdar mountain range of northern Oman. J Arid Environ 73:1035–1045. doi: 10.1016/j.jaridenv.2009.05.002

Bunce RGH (1982) A field key for classifying British woodland vegetation. Part 1. 103.

Campbell K, Donlan CJ (2005) Feral goat eradications on islands. Conserv Biol 19:1362–1374. doi: 10.1111/j.1523-1739.2005.00228.x

Clarke K.R., Gorley RN (2014) Primer v7: User manual/tutorial. Plymouth, United Kingdom

Core Development Team R (2014) R: A language and environment for statistical computing.

Cowling RM, Rundel PW, Lamont BB, et al (1996) Plant diversity in mediterranean-climate regions. Trends Ecol Evol 11:362–366. doi: 10.1016/0169-5347(96)10044-6

Daget P (1977) LE BIOCLIMAT MEDITERRANEEN: ANALYSE DES FORMES CLIMATIQUES PAR LE SYSTEME D’EMBERGER. Vegetatio 34:87–103.

Dakhlaoui H, Ruelland D, Tramblay Y, Bargaoui Z (2017) Evaluating the robustness of conceptual rainfall-runoff models under climate variability in northern Tunisia. J Hydrol 550:201–217. doi: 10.1016/j.jhydrol.2017.04.032

Daly-Hassen H (2017) Valeur économique des services écosystémiques du Parc National de l’Ichkeul, Tunisie. IUCN, Gland, Switzerland. Malaga, Spain.

Daoud-Bouattour, A., Gammar Ghrabi, Z., and Limam Ben Saad S (2007) Guide illustré des Plantes du Parc National de L’Ichkeul. Eco-Ressources International, Ariana Tunisie de la Riva EG, Lloret F, Pérez-Ramos IM, et al (2016) The importance of functional diversity in the stability of Mediterranean shrubland communities after the impact of extreme climatic events. J Plant Ecol 10:rtw027. doi: 10.1093/jpe/rtw027

Di Castri F (1981) Mediterranean-type shrublands of the world. In: Di Castri F, Goodall DW SR (ed) MediterraneanType Shrublands. Amsterdam, pp 1–52

Dovrat G, Perevolotsky A, Ne'eman G (2014) The response of Mediterranean herbaceous community to soil disturbance by native wild boars. Plant Ecol 215:531–541. doi: 10.1007/s11258-014-0321-3

ESRI (2017) ArcGIS Desktop: Release 10.

European Environment Agency (2017) G2.4 Olea europaea-Ceratonia siliqua woodland.

Falcucci A, Maiorano L, Boitani L (2007) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. Landsc Ecol 22:617–631. doi: 10.1007/s10980-006-9056-4

Fay M (1980) Flora of the National Park of Ichkeul, Tunisia.

Fernández-lugo S (2016) Grazing management and impact in the Canary islands : Rethinking sustainable use.

Fernández-Lugo S, Arévalo JR, de Nascimento L, et al (2013) Long-term vegetation responses to different goat grazing regimes in semi-natural ecosystems: A case study in Tenerife (Canary Islands). Appl Veg Sci 16:74–83. doi: 10.1111/j.1654-109X.2012.01211.x

Gabay O, Perevolotsky a, Shachak M (2006) Landscape mosaic for enhancing biodiversity : On what scale and how to maintain it ? Options 49:45–49.

Gauquelin T, Michon G, Joffre R, et al (2016) Mediterranean forests, land use and climate change: a social-ecological perspective. Reg Environ Chang 1–14. doi: 10.1007/s10113-

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

Lázaro A, Tscheulin T, Devalez J, et al (2016) Moderation is best: Effects of grazing intensity on plant-flower visitor networks in Mediterranean communities. Ecol Appl 26:796–807. doi: 10.5061/dryad.p3c75

Le Floc'h E, Boulos L, Vela E (2010) Flore tunisie.

Le Houerou HN (1981) Impact of man and his animals on Mediterranean vegetation. In: Di Castri, F., Goodall, D.W. & Specht RL (ed) Ecosystems of the World Vol II: Mediterranean type shrublands. Elsevier, London,

Legendre, P., Anderson MJ (1999) Distance-Based Redundancy Analysis : Testing Multispecies Responses in Multifactorial Ecological Experiments. Ecol Monogr 69:1–24. doi: doi:10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Legendre, P., Legendre L (2012) Numerical Ecology, Third Edit. Elsevier

Levin N, Watson JEM, Joseph LN, et al (2013) A framework for systematic conservation planning and management of Mediterranean landscapes. Biol Conserv 158:371–383. doi: 10.1016/j.biocon.2012.08.032

Loidi J, del Arco M, P??rez de Paz PL, et al (2010) Understanding properly the ??potential natural vegetation' concept. J Biogeogr 37:2209–2211. doi: 10.1111/j.1365-2699.2010.02302.x

Mata J, de Nascimento L, Fernández-Lugo S, et al (2014) The inefficient planning of goat grazing: Causes and consequences. The Palmera breed case (Canary Islands). Small Rumin Res 121:125–130. doi: 10.1016/j.smallrumres.2014.03.010

Mazzoleni, S., G. di Pasquale, M. Mulligan, M. di Martino and FR (2004) Recent dynamics of the Mediterranean vegetation and landscape. Wiley, West Sussex, England UK

McLaughlin BC, Ackerly DD, Klos PZ, et al (2017) Hydrologic refugia, plants, and climate change. Glob Chang Biol 23:2941–2961. doi: 10.1111/gcb.13629

Médail, F. and Quézel P (1997) Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. Ann Missouri Bot Gard 84:112–127.

Miguel-Ayanz AS, García-Calvo RP, Fernández-Olalla M (2010) Wild ungulates vs. Extensive livestock. Looking back to face the future. Options Meditérraneennes 92:27–34.

Molina-Venegas R, Aparicio A, Lavergne S, Arroyo J (2016) How soil and elevation shape local plant biodiversity in a Mediterranean hotspot. Biodivers Conserv 25:1133–1149. doi: 10.1007/s10531-016-1113-y

Morandini E (1977) Problems of conservation, management and regeneration of Mediterranean forests: research priorities. In: MAB Technical Notes 2. UNESCO, Paris,

Naveh Z (1990) Fire in the Mediterranean – A Landscape Ecological Perspective. In: Goldammer, J.F. JMJ (ed) Fire in Ecosystems Dynamics., Proceeding. SPB Academic Publishing, The Hague, Netherlands,

Nogués-Bravo D, Araújo MB, Lasanta T, López-Moreno JI (2008) Climate Change in Mediterranean Mountains during the 21st Century. AMBIO A J Hum Environ 37:280–285. doi: 10.1579/0044-7447(2008)37[280:CCIMMD]2.0.CO;2

Nogués-Bravo D, López-Moreno JI, Vicente-Serrano SM (2012) Climate Change and its Impact. Mediterr Mt Environ 185–200. doi: 10.1002/9781119941156.ch9

Noy-Meir I, Oron T (2001) Effects of grazing on geophytes in Mediterranean vegetation. J Veg Sci 12:749–760.

Olff H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. Trends Ecol Evol 13:261–265. doi: 10.1016/S0169-5347(98)01364-0

Olsvig-Whittaker L, Frankenberg E, Perevolotsky A, Ungar ED (2006) Grazing, overgrazing and conservation: Changing concepts and practices in the Negev rangelands. Sci Chang planétaires / Sécheresse 17:195–199.

OpenStreetMap contributors (2015) Roads of Tunisia.

Osem Y, Perevolotsky A, Kigel J (2007) Interactive effects of grazing and shrubs on the annual plant community in semi-arid Mediterranean shrublands. J Veg Sci 18:869–+. doi: 10.1111/j.1654-1103.2007.tb02603.x

Ouali, M., Daoud-Bouattour, A., Etteieb, S., Mokhtar Gammar, A., Ben Saad-Limam, S., Grabi-Gammar Z (2014) Le marais de Joumine, Parc nationaL de L'ichkeuL, tunisie : diversité fLoristique, cartograPhie et dynamique de La végétation (1925-2011). La terre la vie 63:3–23.

Paeth H, Born K, Girmes R, et al (2009) Regional climate change in tropical and Northern Africa due to greenhouse forcing and land use changes. J Clim 22:114–132. doi: 10.1175/2008JCLI2390.1

Papanastasis VP (1998) Livestock grazing in Mediterranean ecosystems: an historical and policy perspective. In: Papanastasis, V P and Peters D (ed) ECOLOGICAL BASIS OF LIVESTOCK GRAZING IN MEDITERRANEAN ECOSYSTEMS. Proceedings of the International Workshop held in Thessaloniki (Greece) on October 23-25, 1997, Belgium, pp 5–9

Papanastasis VP, Kyriakakis S, Kazakis G (2002) Plant diversity in relation to overgrazing and burning in mountain mediterranean ecosystems. J Mediterr Ecol 3:53–63.

Perevolotsky A (2005) Livestock grazing and biodiversity conservation in Mediterranean environments: the Israeli experience. Sustain grazing, Nutr Util Qual sheep goat Prod 51–56.

Perevolotsky A, Seligman NG (1998) Role of Grazing in Mediterranean Rangeland Ecosystems. Bioscience 48:1007–1017. doi: 10.2307/1313457

Peterken, G. L. and Radford GF (1971) Report on field-trials in Tunisia. In: IBP/CT Progress Report. pp 36–94

PlantBase E (2017) The Euro+Med PlantBase - the information resource for Euro-Mediterranean plant diversity. http://www.emplantbase.org/home.html. Accessed 1 Jan 2017

Pons A (1981) The history of Mediterranean shrublands. In: Di Castri F., Goodall, D. W. & Specht RL (Else (ed) Mediterranean-Type Shrublands. Elsevier, Amsterdam, pp 131–138

Quézel P (1981) Floristic composition and phytosociological structure of sclerophyllous matorral around the Mediterranean. In: Di Castri, F., Goodall, D.W. & Specht RL (ed) Ecosystems of the World Vol II: Mediterranean type shrublands,. Elsevier, London, p 107–121.

Quézel P, Médail F, Loisel R, et al (1999) Biodiversity and conservation of forest species in the Mediterranean basin Biodiversity and conservation of forest species in the Mediterranean basin THE RICHNESS OF MEDITERRANEAN FOREST SPECIES: CALIFORNIA AND THE MEDITERRANEAN BASIN. Unasylva 50:21–28.

Rackham, O., Moody J (1996) The Making of the Cretan Landscape. Manchester University Press, Manchester

Radford E., Catullo G, de Montmollin B (2011) Important Plant Areas of the South and East Mediterranean Region: Priority Sites for Conservation.

Roberts DW (1986) Ordination on the Basis of Fuzzy Set Theory. Vegetatio 66:123–131.

Rundel PW (1998) Landscape disturbance and biodiversity in Mediterranean-type ecosystems. Springer, New York, pp 3–22

Rundel PW, Arroyo MTK, Cowling RM, et al (2016) Mediterranean Biomes: Evolution of their

Vegetation, Floras and Climate. Annu Rev Ecol Evol Syst 47:383–407. doi: 10.1146/annurev-ecolsys-121415-032330

Sardans J, Peñuelas J (2013) Plant-soil interactions in Mediterranean forest and shrublands: Impacts of climatic change. Plant Soil 365:1–33. doi: 10.1007/s11104-013-1591-6

Segoli M, Ungar ED, Giladi I, et al (2012) Untangling the positive and negative effects of shrubs on herbaceous vegetation in drylands. Landsc Ecol 27:899–910. doi: 10.1007/s10980-012-9736-1

Shachak M, Boeken B, Groner E, et al (2008) Woody Species as Landscape Modulators and Their Effect on Biodiversity Patterns. Bioscience 58:209. doi: 10.1641/B580307

Sternberg M, Shoshany M (2001) Influence of slope aspect on Mediterranean woody formations: Comparison of a semiarid and an arid site in Israel. Ecol Res 16:335–345. doi: 10.1046/j.1440-1703.2001.00393.x

Tomaselli R (1977) The degradation of the Mediterranean maquis. Ambio 6:356–362.

Tomaselli R (1981) Main physionomic types and geographic distribution of shrub systems related to Mediterranean climates. In: Di Castri, F., Goodall, D.W. and Specht RL (ed) Ecosystems of the World Vol II: Mediterranean type shrublands. Elsevier, London, pp 95–106

Tramblay Y, El Adlouni S, Servat E (2013) Trends and variability in extreme precipitation indices over maghreb countries. Nat Hazards Earth Syst Sci 13:3235–3248. doi: 10.5194/nhess-13-3235-2013

Underwood EC, Viers JH, Klausmeyer KR, et al (2009) Threats and biodiversity in the mediterranean biome. Divers Distrib 15:188–197. doi: 10.1111/j.1472-4642.2008.00518.x

UNEP/WCMC (2003) Ichkeul National Park. Management 1–10.

Verdú JR, Crespo MB, Galante E (2000) Conservation strategy of a nature reserve in Mediterranean ecossystems: the effect of protection from grazing on biodiversity. Biodivers Conserv 9:1707–1721.

Vogiatzakis IN, Mannion AM, Griffiths GH (2006) Mediterranean ecosystems: problems and tools for conservation. Prog Phys Geogr 30:175–200. doi: 10.1191/0309133306pp472ra

Warton DI, Wright ST, Wang Y (2012) Distance-based multivariate analyses confound location and dispersion effects. Methods Ecol Evol 3:89–101. doi: 10.1111/j.2041-210X.2011.00127.x

Wilson KA, Underwood EC, Morrison SA, et al (2007) Conserving biodiversity efficiently: What to do, where, and when. PLoS Biol 5:1850–1861. doi: 10.1371/journal.pbio.0050223

Table 1(on next page)

Biophysical variables measured at Jebel Ichkeul

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

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; **

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

Table 3 (on next page)

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

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

Table 4(on next page)

Results of permutational multivariate ANOVA tests for functional groups.

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

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

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

Table 5 (on next page)

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

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

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

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

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

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

PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

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.

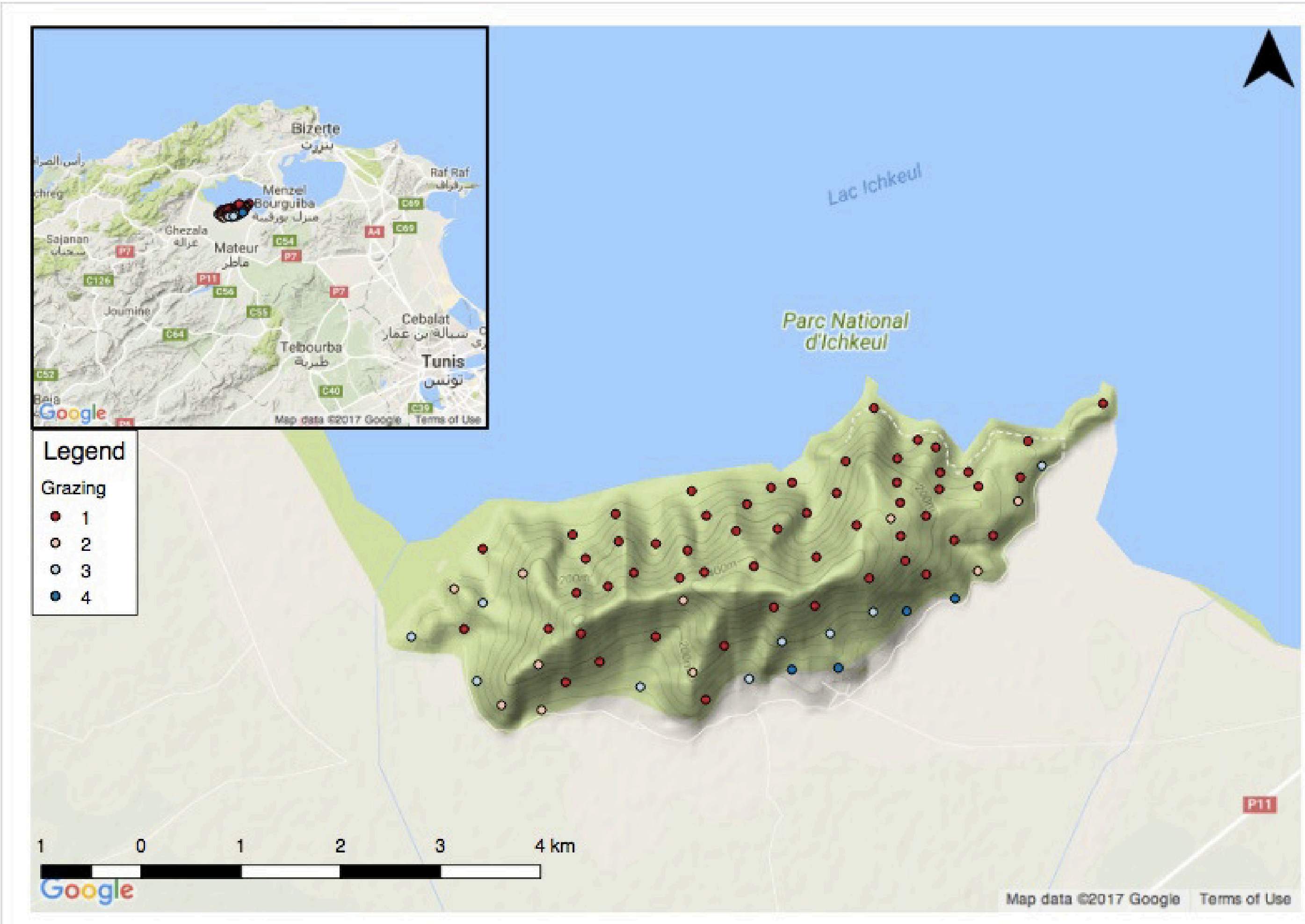

Bizerte
Menzel Bourguiba
Ghezala
Sajanan
Mateur
Joumine
Cebalat
Tebourba
Tunis
Raf Raf
Map data ©2017 Google Terms of Use
Legend
Grazing
1
2
3
4
Lac Ichkeul
Parc National d'Ichkeul
P11
1 0 1 2 3 4 km
Google
Map data ©2017 Google Terms of Use

Figure 2 (on next page)

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

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

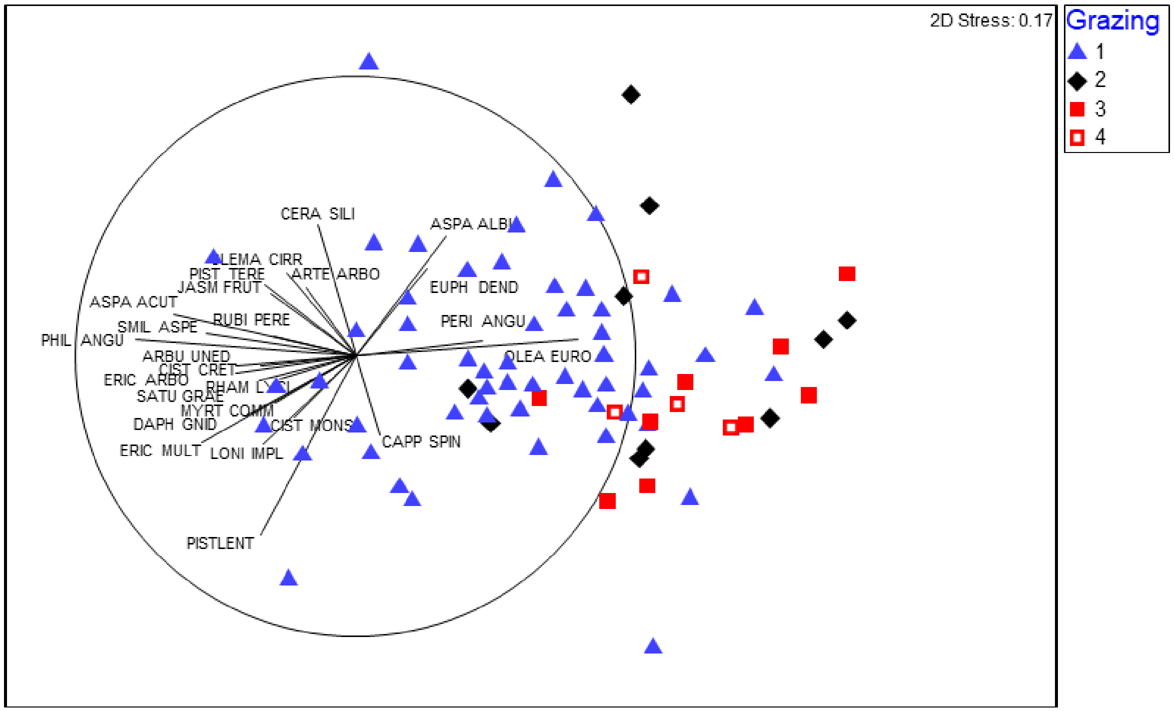

2D Stress: 0.17
Grazing
1
2
3
4
CERA SILI
ASPA ALBI
LEMA CIRR
PIST TERE
ARTE ARBO
JASM FRUT
EUPH DEND
ASPA ACUT
RUBI PERE
PERI ANGU
SMIL ASPE
PHIL ANGU
ARBU UNED
OLEA EURO
CIST CRET
ERIC ARBO
RHAM LYCI
SATU GRAE
MYRT COMM
DAPH GNID
CIST MONS
CAPP SPIN
ERIC MULT
LONI IMPL
PISTLENT

Figure 3(on next page)

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

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

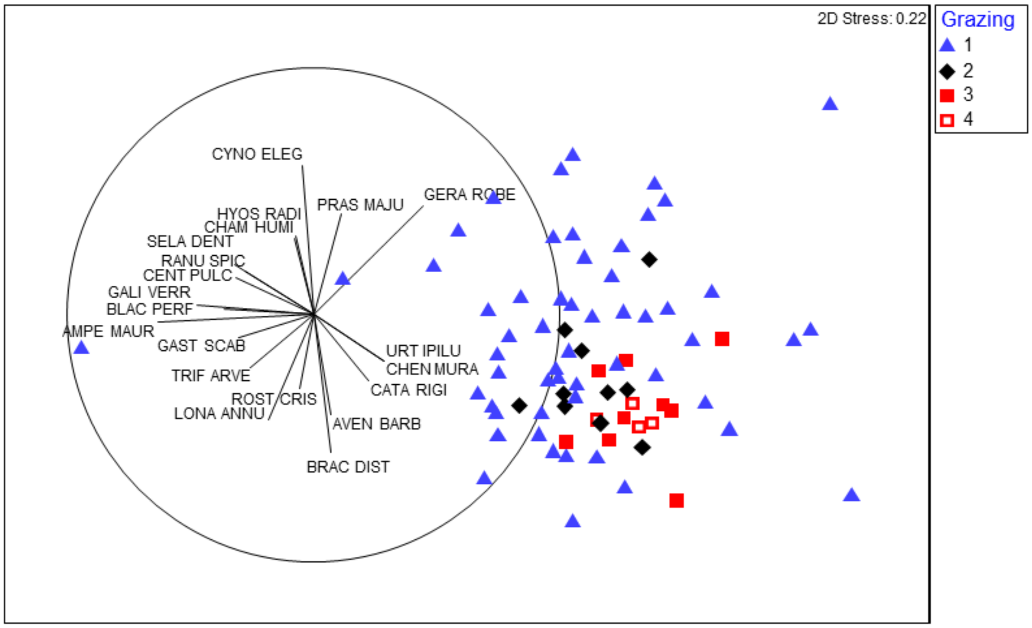

2D Stress: 0.22
Grazing
1
2
3
4
CYNO ELEG
PRAS MAJU
GERA ROBE
HYOS RADI
CHAM HUMI
SELA DENT
RANU SPIC
CENT PULC
GALI VERR
BLAC PERF
AMPE MAUR
GAST SCAB
TRIF ARVE
ROST CRIS
LONA ANNU
URT IPILU
CHEN MURA
CATA RIGI
AVEN BARB
BRAC DIST

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

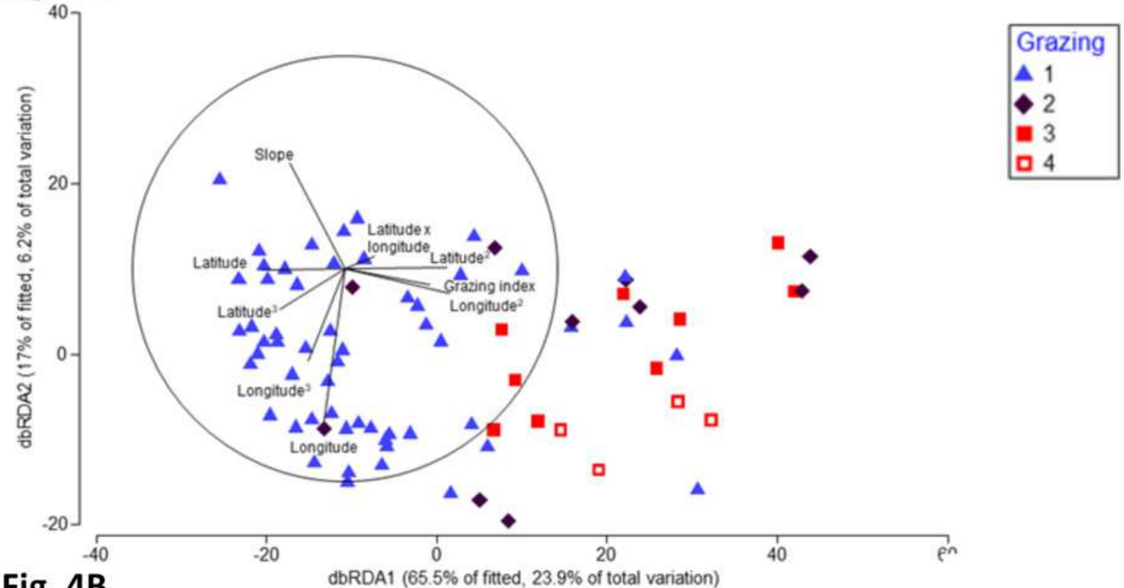


Fig. 4B

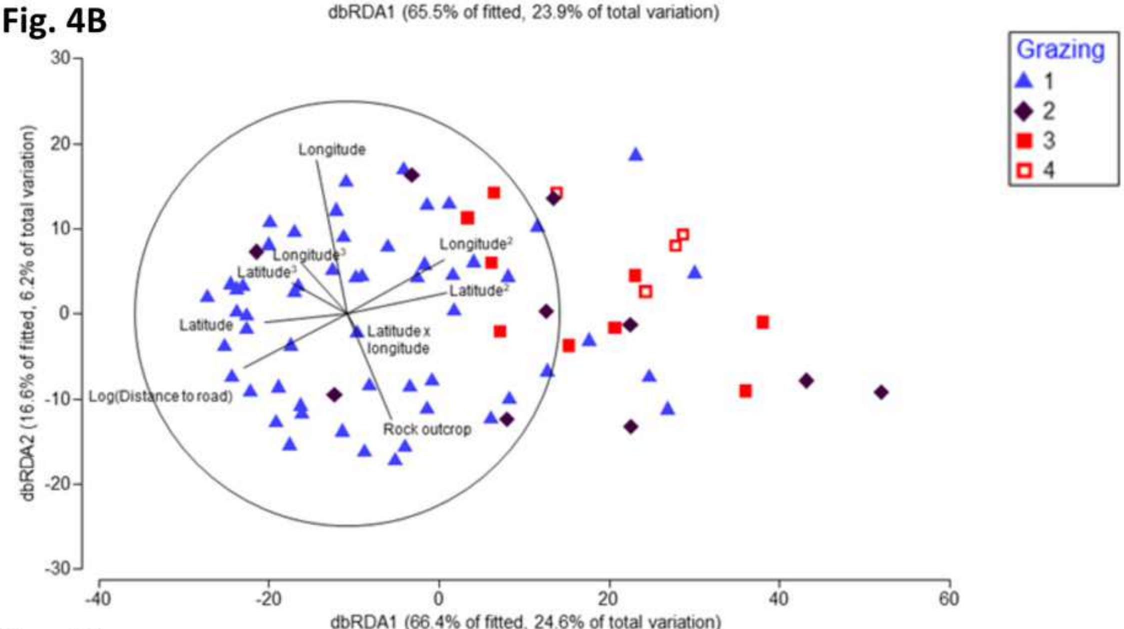


Fig. 4C

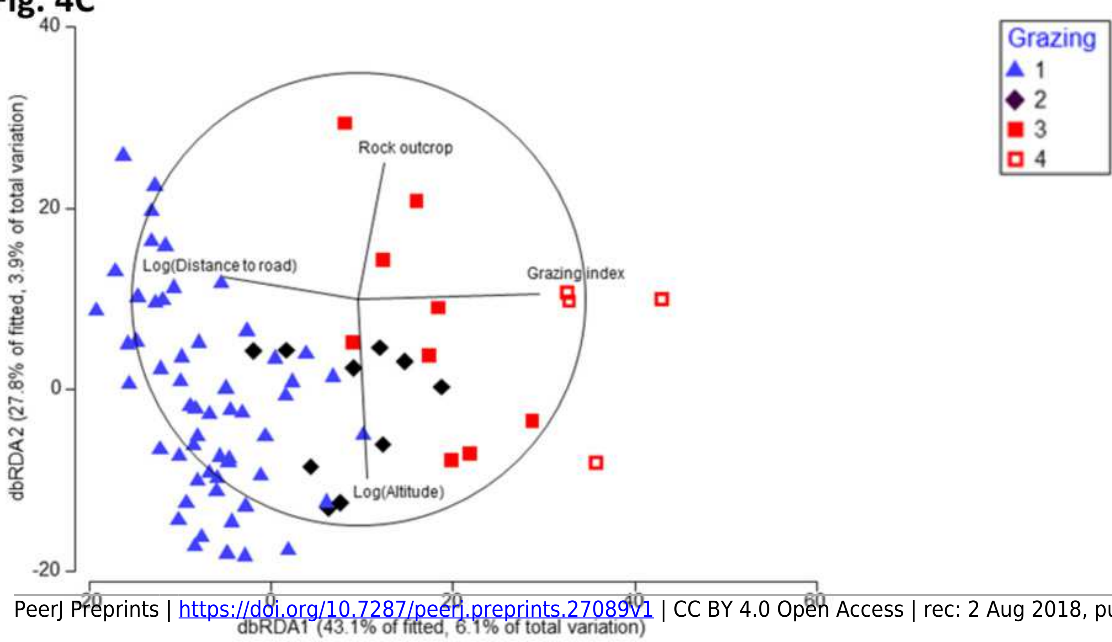
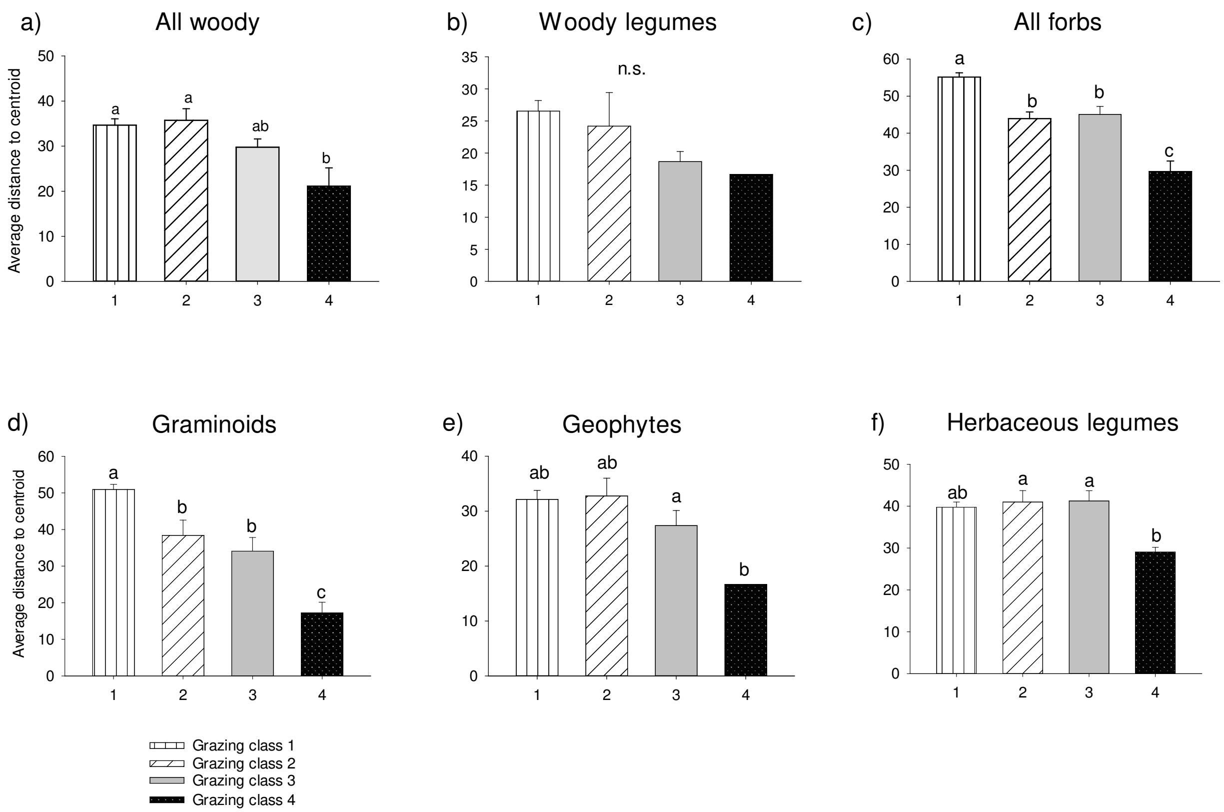


Figure 5

(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.



PeerJ Preprints | https://doi.org/10.7287/peerj.preprints.27089v1 | CC BY 4.0 Open Access | rec: 2 Aug 2018, publ: 2 Aug 2018

Figure 6

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

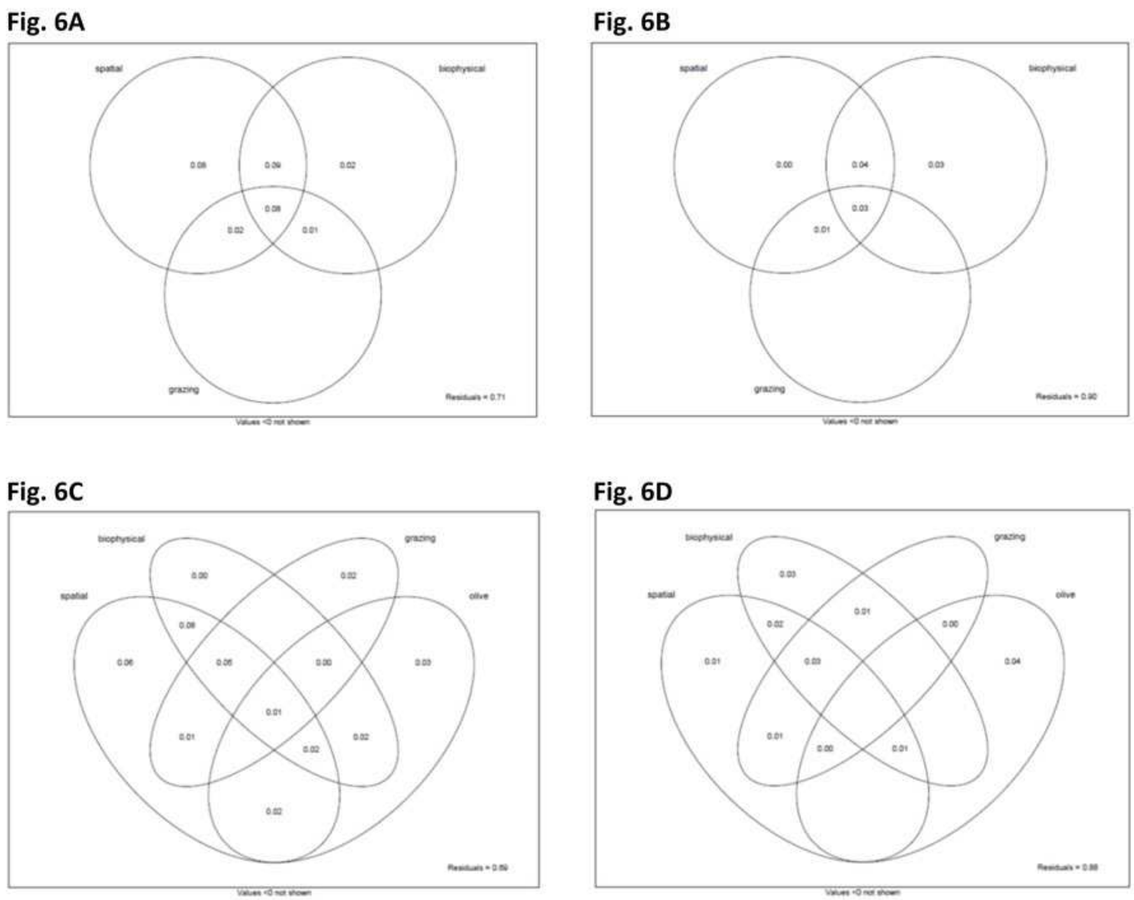


Figure 7

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