Livestock browsing affects the species composition and structure of cloud forest in the Dhofar Mountains of Oman

Livestock browsing affects forests in Dhofar, Oman

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Abstract

Questions: It is frequently reported that overstocking of camels, cattle and goats is degrading the *Anogeissus* cloud forest, which is endemic to a 200 km stretch of coastal mountains in southern Arabia. However, livestock impacts on the vegetation have not been assessed. Furthermore, we have a limited understanding of the impacts of large-bodied browsing livestock, such as camels, in woodland and forest rangelands. Therefore, in this study, we examine the effects of livestock browsing on the species composition, density, and phytomorphology of woody vegetation in the *Anogeissus* cloud forests in the Dhofar Mountains of Oman.

Location: Data was collected at 30 sites in the Jabal Qamar mountain range in western Dhofar, Oman.

Methods: The point-centered quarter method was used to sample the composition, density and structure of woody vegetation. Constrained correspondence analysis was used to quantify the effects of livestock browsing on woody plant species composition, whilst effects on plant density were analysed using mixed effects models. Standardised major axis regression was used to examine differences in height-diameter allometry (stunting) under different stocking rates.

Results: Fog density, topographic position and long-term stocking rates were found to be important factors affecting woody species composition. We found lower species diversity and plant density, and higher frequencies of unpalatable species, under higher stocking rates. Juveniles showed a stronger response to stocking rates than adults, and several common species exhibited stunted morphology under high stocking rates.

Conclusions: Browsing by large-bodied livestock, such as camels and cattle, can substantially alter the species composition, structure, and phytomorphology of woody vegetation in semi-arid woodlands and forests. Juveniles are particularly susceptible to browsing which alters woody vegetation demography and inhibits regeneration potential. Our results support previous suggestions of overstocking in Dhofar and highlight the importance of swift measures to reduce livestock browsing pressure in the *Anogeissus* cloud forests.

Keywords

livestock browsing, rangelands, cloud forest, overgrazing, camels, woody vegetation, pastoralism, tree allometry, Dhofar Mountains, Oman, ordination, constrained correspondence analysis (CCA)

Introduction

One billion people practise pastoralism in rangelands which compose c. 35% of the world's terrestrial surface. Many of the world's rangelands are in a degraded state (Sayre, McAllister, Bestelmeyer, Moritz, & Turner, 2013), and livestock production in rangelands is expected to intensify to meet the food demand and preferences of the growing human population. Balancing the needs of humans and biodiversity in rangelands will require sustainable grazing practises that maximise livestock production, vegetation health, and ecosystem functioning and services (Holechek, 2013). However, despite over a century of scientific attention, we still lack a comprehensive understanding of the effects of livestock on vegetation. One key reason for this, is that the effects can be influenced by a wide range of social and ecological factors which often differ within and between rangelands (e.g. livestock management practises, soil properties and climate). Thus, there is no unified set of ecological principles that apply to livestock-vegetation processes (Sayre, Debuys, Bestelmeyer, & Havstad, 2012), making independent studies of different livestock types, in different rangeland ecosystems, important for understanding rangeland dynamics. Here we contribute a rather unique study of the effects of camel, cattle and goat browsing on a drought-deciduous cloud forest.

The most commonly reported effects of livestock on vegetation include reductions in vegetation biomass, and changes in community structure and/or species composition (Tzanopoulos, Mitchley, & Pantis, 2005). Livestock can also impact ecosystem hydrology, the physical and chemical properties of soils (Briske, 2017), biological soil crusts (Belnap & Lange, 2003), and wider biodiversity (Alkemade, Reid, van den Berg, de Leeuw, & Jeuken, 2013). A common effect of grazing on vegetation species composition is woody plant encroachment, which is a threat to the maintenance of savannah and grassland ecosystems (Briske, 2017). It occurs when herbaceous biomass (and subsequently fire frequency) is reduced, giving woody plants a competitive advantage (Tzanopoulos, Mitchley, & Pantis, 2007). Three other effects of grazing on vegetation species composition are recognised. These are shifts from palatable to unpalatable vegetation, shifts in dominant grass species, and shifts between grass and forb dominance (Vetter, 2005). Under certain conditions grazing lawns may form, which have reduced vegetation biomass but higher quality forage (Hempson et al., 2015).

Browsing herbivores affect vegetation differently to grazing herbivores. Whilst grazing often leads to woody plant encroachment, browsing usually reduces woody cover. Browsing can change woody vegetation demography and reduce woody vegetation regeneration potential through several processes. First, it can reduce seedling and sapling abundance through direct consumption (Khishigjargal, Dulamsuren, Lkhagvadorj, Leuschner, & Hauck, 2013). Second, it can suppress the maturation of juveniles into reproductive adults through sustained browsing pressure (Staver, Bond, Stock, Rensburg, & Waldram, 2009). Third, it can inhibit reproduction via the removal of reproductive components from adult plants (Augustine & Decalesta, 2003).

Browsing can also cause shifts in woody species composition, often to higher frequencies of unpalatable species (Yamada & Takatsuki, 2015). The impact of livestock production in woodland and forest rangelands is greatest when woody vegetation is cleared for pasturage. Wild browsers such as deer, moose and elk have received greater research attention than browsing livestock such as goats and camels. Moreover, few studies have addressed large browsing livestock such as camels, despite 80% of their diet comprising woody plants (Dereje & Uden, 2005).

Climate is the other major factor that interacts with livestock and other disturbances to affect rangeland vegetation. For example, in African savannahs, a mean annual precipitation of 650 mm is the threshold above which disturbances are required to maintain gaps in woody vegetation cover, and below which woody vegetation cover is constrained by precipitation (Sankaran et al., 2005). In arid rangelands, woody vegetation is important for controlling soil erosion, improving soil nutrient availability (Noumi, Touzard, Michalet, & Chaieb, 2010), and for climate regulation (Schlesinger et al., 1990). Furthermore, low primary productivity and slow vegetation regeneration, mean forage resources can be more vulnerable to overuse, than in wetter rangelands. However, in such 'non-equilibrium' rangelands, pastoral practises are often adapted to cope with unpredictable forage distributions (Moritz, Scholte, Hamilton, & Kari, 2013), and livestock often respond in a density-dependent manor to available forage resources (Ellis & Swift, 1988).

In the Dhofar Mountains of Oman high numbers of camels, cattle and goats do not respond in a density-dependent manor to available forage resources, due to twice-daily supplementary feeding for 10-12 months of the year. Subsequently, stakeholders, including scientists, government officials and pastoralists, are concerned about the impacts of livestock on the natural environment. A substantial growth in livestock populations since the 1970s is linked to numerous drivers including population growth, increased wealth, improved rural infrastructure, poor market access, strong pastoral values and subsidisation of feedstuffs (El-Mahi, 2011; Janzen, 1990). Whilst numerous reports have included objectives to tackle overstocking in Dhofar (e.g. GRM International, 1982; HTSL, 1978; UNEP, 2005; WS Atkins International, 1989), no studies have measured its impacts on the vegetation.

Quantifying the impacts of livestock browsing on woody vegetation in Dhofar is important because previous research has shown that reductions in woody vegetation cover, due to livestock browsing, could negatively affect the ecosystem hydrology. Fog interception by the *Anogeissus* cloud forest has been estimated to contribute as much water as rainfall to net precipitation which reaches the ground (Hildebrandt, Al Aufi, Amerjeed, Shammas, & Eltahir, 2007). Furthermore, woody vegetation intercepts more water than herbaceous vegetation, because the fog density is higher a few meters above than close to the ground (Stanley Price et al., 1988: 34-35 litres/m2 per day at 4.2 m, 13 litres/m2 per day at 0.9 m). Therefore, less woody vegetation cover, intercepts less fog, resulting in reduced soil infiltration, which could have adverse effects on ecosystem functioning (Hildebrandt & Eltahir, 2006) and groundwater recharge (Friesen, Zink, Bawain, & Müller, 2018).

In this study we aim to quantify the combined effects of camel, cattle and goat browsing on woody vegetation in the Jabal Qamar mountain range in western Dhofar. We examine the effects of livestock browsing on three woody vegetation attributes: (1) species composition, (2) density, and (3) phytomorphology. This will help to evaluate the ecological sustainability of current livestock management practises and strengthen our understanding of the effects of large-bodied browsing livestock, such as camels, on woody vegetation in woodland and forest rangelands.

Methodology

Study area

The Dhofar Mountains in Oman are the eastern part of the central South Arabian mountains, which span the Dhofar Governorate of Oman and the Mahra Governorate of Yemen. The mean annual precipitation exceeds 200 mm whilst the surrounding deserts and semi-deserts receive < 100 mm (Ghazanfar, 1992). Most of this is received during the summer monsoon, popularly known as the khareef, which occurs between mid-June and mid-September. South-westerly winds cause an upwelling of cold sea water off the coast, lowering the sea temperature to c. 18 degrees. The warmer moist winds blowing over it are subsequently cooled to dew point and a bank of dense fog forms against the southern escarpments (Stanley Price et al., 1988). For the rest of the year the climate is hot and dry (with temperatures in excess of 30 °C) apart from irregular (3-6 year) cyclonic events.

The local rainfall maximum, fog interception, and reduced evapotranspiration from cloud shading during the monsoon (Hildebrandt et al., 2007), enable the existence of the *Hybantho durae-Anogeissetum dhofaricae* (Kürschner, Hein, Kilian, & Hubaishan, 2004). This drought deciduous cloud forest community, comprising at least 262 floral species, is endemic to the southern escarpments of the central South Arabian mountains in Yemen and Oman (Patzelt, 2015). It is thought deforestation for pasturage (Kürschner et al., 2004), firewood, and construction materials (Janzen, 1990) has occurred in many areas.

Our study was conducted in Jabal Qamar, the westernmost of the three mountain ranges in Dhofar (Figure 1). It boasts the highest botanical diversity (515 vascular species) of any area in Oman (Patzelt, 2015). On the southern escarpments, the *Anogeissus* cloud forest is interspersed in flatter areas with grasslands dominated by *Arthraxon junnarensis*, *Apluda mutica* and *Themeda quadrivalvis*. At high altitudes on the fringes of the monsoon-influenced zone, the *Euphorbia balsamifera* cushion shrub community dominates (Patzelt, 2015). The main geologic formation in Jabal Qamar is limestone of tertiary origin. Layers of the Hadramout group are present. These are, from bottom to top, the Umm Er Radhuma (UER), the Rus (RUS) and the Dammam (DAM) formations (Friesen et al., 2018).

There are eighty-five villages in Jabal Qamar with a total human population of 7,799. The 2015 national livestock census recorded 15,164 dromedary camels, 27,522 head of cattle, and 14,217 goats (NCSI, 2017). Livestock-owning households are present in all villages. Pastoralists practise a transhumance regime to avoid the adverse conditions on the escarpments, caused by the monsoon; hematophagous flies are abundant, and camels can slip in the soft mud. Therefore, camels and goats are moved to the plateau or coastal plains and sustained on feedstuffs. Following the monsoon (September-January), livestock are moved down the escarpments to feed on natural vegetation in addition to feedstuffs. During the dry season (January-June) livestock are kept close to villages or camps and sustained primarily on feedstuffs.

Vegetation data

Study sites were selected in a low altitudinal band (300–500 m a.s.l.) and a high altitudinal band (700–900 m a.s.l.), within the altitudinal range (100–1000 m a.s.l.) of the *Anogeissus* cloud forest, on the southern escarpments (Kürschner et al., 2004). Within these ranges, land with a slope gradient > 30 degrees was omitted so sites were safely accessible to the research team and comparable in terms of vegetation communities, the composition of which can change substantially on steep slopes and cliffs (Patzelt, 2015). Thirty sites with varying stocking histories were then identified by livestock keepers during interviews and participatory mapping exercises (Figure 1). More precise estimates of long-term stocking rates were determined by a different method, which is described later in the methods section.

The point-centered quarter (PCQ) method (Cottam & Curtis, 1956) was used to sample the composition, density and structure of woody vegetation at each site. In this method, density estimates are derived from distance measures between points and the closest plants, which are subsequently studied to estimate composition and structure. It is a plotless method making it more efficient than plot-based techniques (Cottam & Curtis, 1956). Although the PCQ method was initially designed for forestry studies it has been widely applied to natural systems too (Dias, dos Santos, dos Santos, & Martins, 2017; Dickhoefer, Buerkert, Brinkmann, & Schlecht, 2010; Pereira et al., 2018). We followed the recommendations of Dahdouh-Guebas and Koedam (2006) to address multiple-stemmed trees.

Sites were visited on four occasions, every two months during the growing season from September 2016 to April 2017. Ten points were carried out during the first visit, ten during the second visit, five during the third visit and five during the fourth visit, resulting in a total of 30 points at each site. Consecutively rotating site visits controlled for intra-seasonal vegetation change from senescence and livestock browsing, to improve comparability between sites. It also allowed for minor adjustments to be made to the methodology between each round of visits. PCQ point locations were randomly generated in a GIS over an area of approximately 1 km^2 at each site. Camels are highly mobile, do not eat for long periods from a single plant and spread out during browsing, and cattle browsing can be patchy (Dereje & Uden, 2005). Therefore, large sites were preferred, to provide a representative average of the effects of browsing, and to avoid overemphasising vegetation responses (Briske, Fuhlendorf, & Smeins, 2003). At each sample point, the distances to the closest adult and the closest juvenile woody plant were recorded in each of the four PCQ quarters, resulting in a total of 120 adult and 120 juvenile records per site.

For each plant, the diameter at root collar (DRC), and where applicable diameter at breast height at 130 cm above the ground (DBH130), were measured using a diameter tape or callipers. For multi-stemmed plants all stems were measured, however thin suckers growing from large trees and shrubs were ignored. Stem status was recorded as alive, dead, broken or missing and stems that had been cut by a machete or chainsaw were noted. Very old or deteriorated cut or missing stems were ignored. If a plant only had dead stems at DBH130 but additional live stems were present, it was recorded as alive and stem statuses recorded accordingly. DBH130 was not recorded for juveniles. An adult individual was recorded as dead when more than 80 percent of the plant was dead and a DBH130 was present. Individuals with only dead stems below DBH130 were classed as stumps and were ignored. Preliminary work determined DRC thresholds to differentiate adult and juvenile plants for each species (Appendix S1), because existing methods that utilise diameter and height measurements could not be used as many plants have altered morphology due to browsing activity. Adult and juvenile height was measured from the ground to the top of the plant unless the plant had fallen horizontally then the trunk length was measured.

For all individuals, browsing intensity was estimated by five classes according to the percentage of browsed branches below the browse line (~3 m). For adults, the proportion of broken branches was estimated on a five-class scale according to the percentage of broken branches. To assess the prevalence of tree management practises, the proportion of bent or cut branches was estimated on a five-class scale. The classes were defined as, 1 = undamaged (~0%), 2 = low damage (1% – 33.3%), 3 = medium damage (33.3% – 66.6%), 4 = high damage (66.6% – 99%), and, 5 = entirely damaged (~100%). Areas of stripped bark and canopy cover were also recorded. At each PCQ point a 1.2 m quadrat was deployed to sample the relative cover of herbs, grasses, rock and bare ground. It also delineated the PCQ quarters.

Stocking rates and environmental data

To calculate precise estimates of long-term stocking rates we used both measures of plant damage and a GIS-based adaptation of the piosphere model (Andrew, 1988). Long term stocking rate (expressed using a discrete scale of 1-30) was calculated by ranking the sites for each of five measured variables and then summing the rankings and ordering these values (Appendix S2). While browsing intensity provided information about recent stocking rates, proportions of bent *A. dhofarica* branches and broken branches of all adults provided longer-term evidence (up to several decades) of stocking rates. There were no issues with circularity in our analysis as the response variables were unrelated to the damage indicators. Moreover, browsing intensity was limited to seven key forage species and the proportion of bent branches was limited to *A. dhofarica*, to minimise circularity associated with damage varying by species, and to ensure comparability between sites.

The piosphere model estimates the stocking rate of a given rangeland area based on the Euclidean distance to a concentrator and is frequently used in studies of arid grazing systems (Andrew, 1988; Heshmatti, Facelli, & Conran, 2002). It is applicable to Dhofar where there is low livestock dispersal around concentrators, such as houses, camps and vehicle routes, where livestock receive feedstuffs each morning and evening (Janzen, 1990). To account for the effects of the complex mountain topography on livestock mobility, we calculated path distances, rather than Euclidean distances, from each PCQ point to these concentrators. Path distances were calculated from a cost raster in ArcGIS (Esri, 2018). A cost raster identifies the cost of travelling through each cell. In our cost raster, we included information on slope (derived from DLR TanDEM-X 12 m global digital elevation model) and access routes (e.g. roads, vehicle tracks and livestock trails). The cost of travel increased exponentially with slope steepness and all slopes with > 50 degree inclines and no access routes were considered inaccessible to livestock. Access routes were assigned as less costly on steeper slopes (> 10 degree incline) and no less costly on flatter terrain (≤ 10 degree incline). The PCQ points with the longest and shortest path distances were confirmed to be accurate by the fieldwork team.

The stocking rates at the sites during the fieldwork period are not representative of long-term stocking histories. For instance, pastoralists might avoid sites which have been intensively grazed for several years. However, for comparability with other studies we estimated prevailing stocking rates at the sites in two standard units of measure (animals/km² and Tropical Livestock Units), using dung transects (1 m x 50 m) and the Faecal Accumulation Rate (FAR) method (Putman, 1984). Using the FAR method, stocking rate is calculated as:

$$Stocking\ rate\ (animals\ per\ km^2) = \frac{number\ of\ dung\ piles\ per\ km^2}{no. of\ days\ between\ visits\ \times defecation\ rate}$$

Two transects were deployed during the first visit, two during the second, and one during the third visit, resulting in a total of eleven transect accumulation periods per site. The average accumulation period was 54 days. A long accumulation period was preferred due to the slow decomposition rate of dung. Camel defecation rate was measured by following 22 animals for a total of 24 hours. The mean camel defecation rate (assuming animals could be present and defecating for 12 hours per day) was 26 defecations per day (min 8, max 68, median 21, SE 3.3). Stocking rate estimates for cattle and goats were based on defecation rates (defecations per day) of ten (Lantinga, Keuning, Groenwold, & Deenen, 1987; Oudshoorn, Kristensen, & Nadimi, 2008) and eight, respectively (Rollins, Bryant, & Montandon, 1984).

Topographic variables were calculated for each PCQ point from DLR TanDEM-X 12 m global digital elevation model. Fog density values were extracted at each point from a raster layer of mean fog density; calculated on a per cell basis as the mean of the nearinfrared fog reflectance values of 119 Landsat 5 TM scenes, 17 Landsat 7 ETM+ scenes and 121 Landsat 8 OLI TIRS scenes (Ball & Tzanopoulos, 2020). To measure topographic exposure to fog, we reclassified aspect with highest values on slopes facing offshore in the direction of maximum fog exposure (an aspect of 160°) and lowest values on slopes facing inland (an aspect of 340°) (Abdul-Wahab, 2003). In addition, we calculated a binary layer of exposure to fog (windward/leeward), from the viewsheds of three observer points situated c. 60 km offshore at an altitude of 500 m a.s.l. (Ball, 2019).

Geology is known to affect soil properties such as acidity and vegetation (Barnes, Zak, Denton, & Spurr, 1997). Therefore, the geology of the sites was determined from georeferenced 1:100 000 geological maps (Ministry of Petroleum and Minerals, 1986), and soil pH levels were tested from four composite soil samples at each site. A one-way ANOVA found soil pH did not differ significantly by bedrock type ($F(4,25) = 0.846$, $p = 0.509$). This may be because the bedrock throughout the research area is variations of limestone (Friesen et al., 2018; Ministry of Petroleum and Minerals, 1986). Given that geology did not significantly affect soil pH, and acted as a strong proxy for topography, geology was excluded from the analysis. This also preserved degrees of freedom in the CCA.

Statistical analysis

Bivariate statistical tests were performed on each combination of environmental variables and vegetation measures, to examine associations between single variables (Appendix S3). To quantify the effect of long-term stocking rates on the species composition of woody vegetation relative to other environmental factors, constrained correspondence analysis (CCA) was carried out in the R 'vegan' package (Oksanen et al., 2018; R Core team, 2019). Adults and juveniles respond differently to browsing and so separate analyses were performed. The CCA models were built following a stepwise forward selection procedure. Permutation tests for the joint and separate effects of the variables, as well as for marginal (Type III) effects, were performed to test the significance of the variables. The model was chosen which maximised the proportion of explained inertia with the fewest significant constraints. Variance Inflation Factor (VIF) values were calculated after each model as a diagnostic tool to identify collinear constraints (VIF > 3). Canopy cover was not considered as a constraining variable for adult woody species as it is a product of species composition.

In addition to the ordination, we analysed the effects of the environmental variables on palatable woody plant density using linear mixed-effects models in the R 'lme4' package (Bates, Maechler, Bolker, & Walker, 2015; R Core team, 2019). Sites and points were assigned as random effects to control for the spatial autocorrelation nested within our data. Site eight was excluded as it was very sparse woodland, with low woody plant density. The point-plant distances were log-transformed to improve the normality of the residuals.

To investigate stunting due to browsing pressure, we examined differences in the allometric relationship between height and DRC in five common woody plant species under five stocking rate classes. Height-diameter relationships approximately follow a power law. Therefore, the data were log-transformed prior to analysis to be approximately linearly related. Their relationship is described as height = $a\text{drc}^{b}$ where the scaling exponent b is the slope of the linear relationship and the proportionality coefficient a is the elevation of the line (Warton, Duursma, Falster, & Taskinen, 2012). We used standardised major axis in the R 'smatr' package (R Core team, 2019; Warton et al., 2012) to analyse differences in b and a across stocking rate classes.

Species nomenclature follows Miller, Morris, & Stuart-Smith (1988), with revised nomenclature sourced from the Global Biodiversity Information Facility (GBIF.org, 2020), and cross-checked with the International Plant Names Index (IPNI.org, 2020).

Results

Forty-two adult and 43 juvenile (total 47) woody plant species were recorded (Appendix S4). *Commiphora habessinica*, *Jatropha dhofarica*, and *Anogeissus dhofarica* were the most abundant species accounting for 12.2%, 10.2% and 9.2% of the 7,200 measured woody individuals, respectively. For adults alone the order changed to *A. dhofarica* (14.8%), *C. habessinica* (13.2%) and then *J. dhofarica* (10.3%). For juveniles the order was *Zygocarpum dhofarense* (11.8%), *C. habessinica* (11.2%) and then *J. dhofarica* (10.1%). Several species had low abundances. *Acridocarpus orientalis, Azima tetracantha, Grewia villosa, Rhamnus staddo, Hildebrandtia africana, Cordia perrottetii, Lawsonia inermis, Caesalpinia erianthera, Calotropis procera, Searsia pyroides, Ficus sycomorus* and *Ehretia obtusifolia* occurred at a frequency of less than 0.1 percent. Advanced growth, which is the ratio of juveniles to adults, was low for *Delonix elata* (15%), *Ficus vasta* (16%) and *Olea europaea* subsp. *cuspidata* (7%).

For comparability with other studies, we measured the stocking rates at the sites during the fieldwork period (Appendix S2). Stocking rates (animals/km^2) ranged from 1 to 244 (mean = 53) for camels, 0 to 130 (mean = 34) for cattle, and 0 to 54 (mean = 5) for goats. Stocking rates, in Tropical Livestock Units (TLU/km^2), ranged from 2 to 386 (mean = 98).

The CCA analysis identified fog density, topographic position and long-term stocking rate as the most powerful constraining variables for woody species composition (Table 1). They explained 28% and 29% of the inertia in adult and juvenile woody species composition, respectively. Long-term stocking rate was the third most important factor affecting adult woody species composition, and the most important factor affecting juvenile woody species composition. Long-term stocking rate also significantly correlated with thirteen vegetation responses (Appendix S3). Notably, species diversity and plant density decreased, and tree limb damage and bark stripping prevalence increased, with increasing stocking rate. Stocking rate decreased with increasing slope gradient but did not differ with elevation range.

The CCA biplots of species scores enable interpretation of the effects of the environmental variables on species composition (Figure 2). For adults, we see higher species diversity in areas with higher fog densities and lower stocking rates. For both adults and juveniles, we see higher frequencies of uncommon species under lower stocking rates. The dominant and most important browse species, *A. dhofarica,* is more frequent under higher stocking rates. Juveniles of *Z. dhofarensis, Maytenus dhofarensis, Allophylus rubifolius* and *Croton confertus* occur more frequently under higher stocking rates than adults. Conversely, both *Commiphora* species are more abundant under higher stocking rates as adults than as juveniles. The CCA biplots also show that several unpalatable or unfavoured species have their optimums in areas with above-average stocking rates. *Adenium obesum* (unpalatable) and *J. dhofarica* (unfavoured) are associated with high stocking rates in areas with lower fog densities. *Dodonaea viscosa subsp. angustifolia* (unpalatable) has its optimum in high topographic positions, with above-average fog densities and stocking rates. *Solanum incanum* (unfavoured) is strongly associated with high stocking rates.

The results of the linear mixed-effects regression analysis of palatable woody plant density (Figure 3), show that very high long-term stocking rates reduce adult palatable woody plant densities, whilst high or very high long-term stocking rates reduce juvenile palatable woody plant densities. Palatable woody plant densities are lower at lower elevations, higher on steeper slopes and increase with rock cover. Adult density increased with fog density and juvenile density decreased with southerliness.

Ten percent of adult woody plants (4% total adult basal area) were dead. Of the adult trees and large shrubs, 85% had broken limbs, 13% had been subject to branch-bending arboricultural practises (see Appendix S5 for photographs of browsing impacts), and ten percent had exposed cambium due to bark stripping by livestock (Table 2). *Dodonaea viscosa* subsp. *angustifolia*, *C. gileadensis* and *O. europaea* subsp. *cuspidata* were the most frequently dead species. Most adults of all species had broken limbs. Over half (57%) of *A. dhofarica* trees had been subject to branch-bending arboricultural practises, and other managed species included *F. vasta, Tamarindus indica*, *C. confertus*, *A. rubifolius* and *O. europaea* subsp. *cuspidata*. The most frequently bark-stripped species were *A. dhofarica*, *Blepharispermum hirtum*, *J. dhofarica*, *F. vasta* and *F. sycomorus*. On average, *O. europaea* subsp. *cuspidata* had the largest areas of stripped bark.

We performed standardised major axis to examine differences in height-diameter relationships of five woody species under five stocking rate classes. Scatterplots with fitted standardised major axes are shown in Figure 4 (see Appendix S6 for significant differences in slope *b* and elevation *a* of the height-diameter relationships under different stocking rates and Appendix S7 for plots fitted with a common slope). Apart from *A. dhofarica* adults, the species had on average shorter heights for equivalent DRC measurements as stocking rates increased. This shows that they tend towards stunted forms with increasing stocking rates. Differences were most significant between non-neighbouring and the lowest and highest stocking rate classes (Appendix

S6). The slopes *b* of the height-diameter relationships for adults of the *Commiphora* species were significantly steeper under higher stocking rates due to stunting of small (DRC = < 10 cm) adult individuals.

Discussion

Our CCA analysis identified fog density as the most powerful environmental factor influencing species composition of the *Anogeissus* forest. This is because water is the limiting factor for plant growth and fog moisture is critical to the persistence of forest in the region (Ball & Tzanopoulos, 2020; Hildebrandt et al., 2007). Vegetation responses to fog have also been documented in other arid environments, such as xerophytic plants in Oman's central desert (Borrell et al., 2019), dragon trees on the island of Socotra (Scholte & De Geest, 2010) and succulent rosettes in the arid mountains of Mexico (Martorell & Ezcurra, 2002).

Topographic position was also an important environmental factor in our CCA models. The topographic position index with a 5 km neighbourhood, describes at a coarse scale whether land is within valleys or on hilltops. Climate, soils and hydrology vary with topographic position. Notably, vegetation in depressions responds to the contribution of additional moisture from upslope areas (Mullins Christopher, Burslem David, Daws Matthew, Paton Steven, & Dalling James, 2002). In Dhofar, these upslope areas are large steep cliffs or deep wadis which intercept substantial fog moisture. Livestock abundance may also differ with topographic position because wadis are less accessible. Topographic position was found to be more important, in terms of its influence on vegetation, than elevation. This is because TPI values incorporate more topographic information, for example slope and curvature, in addition to altitude (Ball & Tzanopoulos, 2020). Altitudinal effects were also limited because our study was restricted to the altitudinal range of the *Anogeissus* forest, outside of which different communities persist.

Our CCA results found that stocking rate affects woody plant species composition, with stronger effects on juveniles. This is because seedlings and saplings are more susceptible to browsing than adults due to their smaller size (Scholes & Archer, 1997; Staver et al., 2009). Browsing can reduce seedling and sapling abundance through direct consumption (Khishigjargal et al., 2013) or suppress the maturation of juveniles into reproductive adults (Staver et al., 2009). Therefore, under current browsing conditions, we could expect to see further change in species composition, and woody vegetation demography, as the forest regenerates.

The CCA shows that as stocking rates increase, species diversity decreases, and frequencies of the unpalatable or unfavoured species *A. obesum*, *J. dhofarica*, *S. incanum* and *D. viscosa* subsp. *angustifolia* increase. It should be noted however, that *A. obesum* naturally occurs in the more xeric conditions of the plateau, where coincidently stocking rates are amongst the highest due to the proximity to settlements. Camel browsing reduced plant species richness in two independent studies in the United Arab Emirates (El-Keblawy, Ksiksi, & El Alqamy, 2009;

Gallacher & Hill, 2008). Decreases in species diversity and increases in populations of unpalatable species are well-known symptoms of overstocked rangelands (Briske, 2017; Tzanopoulos et al., 2005), which have been previously described from Dhofar (Ghazanfar, 1998; Miller et al., 1988).

Our results show species-specific responses to browsing pressure. The characteristic species, *A. dhofarica*, is more frequent under higher stocking rates. This could be because other species populations have decreased or because over half of the adult trees are subject to arboricultural practises which may serve to protect the trees (Lawton, 1978). Alternatively, their large size, the hardness of their wood, or other physiological traits could make them resilient to browsing. Adults of the less common tree, *F. sycomorus*, show a similar but more extreme trend. Under higher stocking rates both *Commiphora* species are more abundant as adults but less abundant as juveniles. This suggests adults are somewhat resilient to browsing, whilst juveniles are more vulnerable; possibly because their soft wood means they can be consumed in their entirety.

Juveniles of *M. dhofarensis*, *A. rubifolius* and *Z. dhofarense* were more abundant under higher stocking rates than adults. Their survivability is surprising as all three are important browse species (although *M. dhofarensis* is unfavoured by cattle) (Miller et al., 1988). They may be encroaching due to low herbaceous biomass and the absence of fires (Scholes & Archer, 1997), exhibiting higher seed production under stress (Huntley & Walker, 1982) or hold a competitive phenological advantage due to early bud burst (Scholes & Archer, 1997). It is also plausible that the strength and hardness of the wood of these species, which was traditionally favoured for construction and to make weapons such as fishing spears (Miller et al., 1988), makes them somewhat resilient to browsing pressure. These species could be important for restoration of degraded areas in Dhofar.

The effect of livestock on woody plant cover can vary based on several factors such as livestock type, stocking regimes and vegetation species, as well as abiotic and climatic factors (Plachter & Hampicke, 2010). While woody plant encroachment is common in grazing systems, in heavily browsed wooded environments, decreased woody plant density, especially of the understory layer, is widely reported (Shackelford, Kelsey, Robertson, Williams, & Dicks, 2017). We found palatable woody plant density decreased with increasing stocking rates. In fact, we see plant density decreases significantly, and quite substantially, under very high and high stocking rates, for adults and juveniles respectively. This may indicate an ecological threshold, whereby woody plant density decreases abruptly under high stocking rates.

If high stocking rates persist, then seedling recruitment is affected, which is generally considered the main process by which browsers maintain open ecosystems (Khishigjargal et al., 2013; Staver et al., 2009). Akin to our results for species composition, our results for density, suggest juveniles are more susceptible to browsing than adults. Camels, which select the freshest, most nutritious plant parts (Iqbal & Khan, 2001), can reduce seedling recruitment, as reported from the United

Arab Emirates (Gallacher & Hill, 2008). In arid environments, grazing livestock are often more dependent on browse forage and cattle can reduce seedling recruitment (Plachter & Hampicke, 2010; Pour, Mohadjer, Etemad, & Zobeiri, 2012). In Dhofar, it is likely cattle target seedlings once the grass and herb layer has senesced or been grazed short, especially as the foliage of adult woody plants may be out of reach due to camel browsing.

Palatable woody plant density was found to be higher at higher elevations, despite no significant altitudinal variation in long-term stocking rates. However, ground cover of rocks was greater at high elevations and plant density increased with rock cover (Appendix S5). For example, high densities of *Commiphora* shrubs occurred at rocky sites at high elevations, whilst several flat lowland sites had sparse understories. High rock cover may reduce accessibility to livestock and protect saplings in a similar way that Carson *et al.* (2005) found boulders protected woody species from deer browsing. In addition, low herbaceous cover in rocky areas may allow woody plants to quickly achieve vertical dominance (Scholes & Archer, 1997). Higher plant densities on steeper slopes may also be linked to accessibility, where slopes act as refuges for forest (Nüchel, Bøcher, & Svenning, 2019). Steep areas may also intercept more fog, bolstering local soil moisture levels for forest vegetation (Ball & Tzanopoulos, 2020).

Anogeissus dhofarica is the most abundant tree, and from an ecological and ethno-botanical perspective, the most important woody species in Dhofar. It was traditionally used as a building material and has a long history of use as a fuel wood and fodder plant (Miller et al., 1988). This long history of use was apparent in our data. Fifty-seven percent of the adult *A. dhofarica* trees measured in this study (n = 534) had been subject to branch-bending arboricultural practises. Branches are bent to bring the tree foliage in reach of livestock (Appendix S5). We found high frequencies of *A. dhofarica* trees at sites with high stocking rates, which suggests that branch-bending arboricultural practises may have a limited impact on tree survivability, but this should be a priority for future research.

Adult *A. dhofarica* trees were over four times as abundant as juveniles indicating low advanced growth and subsequently poor forest regeneration. Several other species also had low advanced growth and several others had small populations which should be monitored. Only nine percent of *A. dhofarica* trees were dead indicating a resilience to heavy browsing pressure and the amount of standing dead adults of all species was low compared to other studies (Angelstam, 1997: 30% - 40% of individuals compared to 10% in our study; Tritton and Siccama, 2014: 3% - 43% of basal area compared to 4% in our study). This may be due to harvesting of dead wood for firewood and livestock bomas.

Pastoralists in Dhofar perceive bark stripping (Appendix S5) as a serious threat to the woody vegetation, and the teeth of camels are often removed. Yet we found only 10 percent of trees and large shrubs had stripped bark (with an average bark-stripped area of 800 cm^2). The cause of this behaviour in camels and cattle in Dhofar is unknown. Based on a review by Nicodemo and Porfírio-da-Silva (2018), it is most likely associated with diet and pasture quality, although behaviour and parasite control factors could be relevant. Camels may also selectively browse plant parts to balance the chemical composition of their diet (Amin, Abdoun, & Abdelatif, 2007), and so bark, which contains beneficial substances such as polysaccharides and phenolic polymers (Nicodemo & Porfírio-da-Silva, 2018), could contribute beneficial nutrients and medicines to their diet. An assessment of the chemical composition of the most bark-stripped tree species (Table 2) and of livestock feedstuffs should be a priority for future research in Dhofar.

We performed standardised major axis to examine differences in height-diameter relationships of five woody species under five stocking rate classes. We found significantly shorter heights for equivalent DRC measurements with increasing stocking rates, indicating stunting (Appendix S5). Stunting was not evident amongst adult *A. dhofarica*, but the *Commiphora* species appeared susceptible. This is likely because the latter have very soft wood and branches up to 1 cm in diameter can be consumed by camels (Appendix S5). Stunting has been reported before in Dhofar (Miller et al., 1988), and as a result of camel and cattle browsing in other arid environments (Box et al., 2016; Pour et al., 2012).

Conclusion

We measured the impacts of camel, cattle and goat browsing on the woody vegetation in the *Anogeissus* cloud forest in the Dhofar Mountains of Oman. As one would expect given the arid climate, topoclimatic conditions linked to fog moisture availability, best describe adult woody plant species composition. However, livestock browsing has affected the compositional and structural characteristics of the woody vegetation. In agreement with several other browsing studies, we recorded lower woody plant densities, lower species diversity, higher frequencies of unpalatable species, and stunted phytomorphology, under higher stocking rates. We found that browsing has changed the species composition and reduced the density of juveniles, more so than adults, and several characteristic forest species have low advanced growth. This indicates that browsing has reduced seedling recruitment, which will inhibit the regeneration potential of the *Anogeissus* forest. Overall, our results show that browsing by large-bodied livestock, such as camels and cattle, can substantially alter the species composition, structure, and phytomorphology of woody vegetation in semi-arid woodlands and forests. Thus, the impacts of camel browsing should be monitored where domesticated camel populations are increasing.

Our results show that current livestock management practises threaten the natural environment of the Dhofar Mountains. At 28 of the 30 sites, stocking rates (TLU) prevailing at the time of data collection exceeded the sustainable limit of $20/km^2$ for arid rangelands (Jahnke, 1982). Furthermore, at all sites, camel densities far exceeded the limit imposed in arid Australia ($0.25/km^2$) to avoid undesirable levels of vegetation damage (Box et al. 2016). The ecological impacts of pastoralism in Dhofar must be reduced to limit further degradation of the *Anogeissus* cloud forests, which are globally unique, have a high conservation value, and provide important ecosystem services.

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Author contributions

LB and JT designed, conducted, analysed and reported this research.

Data accessibility

The environmental variables used in this analyses are available in GeoTIFF raster format in the Pangaea data repository (https://doi.org/10.1594/PANGAEA.902295). The botanical survey data is hosted in the Mendeley data repository (doi.org/10.17632/dc97zn6gzc.1).

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Table 1. Results of the CCA analysis of adult and woody species composition. We report the absolute explained inertia from the CCA, and the chi-squared, F and P values from the permutation tests of the marginal (Type III) effects of each constraining variable.

Vegetation abundance measure	Absolute explained inertia (%)	Constraining variable	χ^2	F	P
Adult woody species composition	28.19	Fog Density	0.260	3.790	0.001
		Topographic Position Index	0.241	3.510	0.001
		Long-term stocking rate	0.209	3.056	0.001
Juvenile woody species composition	28.75	Long-term stocking rate	0.218	3.708	0.001
		Fog Density	0.206	3.512	0.001
		Topographic Position Index	0.200	3.395	0.001

Table 2. Proportions of individuals of adult trees and large shrubs (n = 2949) that were dead, had broken or bent limbs, or were bark stripped.

n =	Species	Dead (%)	Broken limbs (%)	Bent limbs (%)	Bark stripped (%)	Average area of stripped bark (cm^2)
534	*Anogeissus dhofarica*	9	97	57	19	1490
474	*Commiphora habessinica*	5	81	0	5	245
371	*Jatropha dhofarica*	12	76	1	11	322
274	*Dodonaea viscosa* subsp. *angustifolia*	25	79	1	5	188
223	*Euphorbia smithii*	4	87	2	1	61
214	*Blepharispermum hirtum*	11	89	5	38	336
194	*Commiphora gileadensis*	13	74	2	9	997
155	*Allophylus rubifolius*	12	89	18	8	266
153	*Maytenus dhofarensis*	5	80	5	0	0
89	*Croton confertus*	3	86	19	5	69
86	*Olea europaea* subsp. *cuspidata*	13	98	16	7	2930
60	*Euclea racemosa* subsp. *schimperi*	7	76	0	0	0
44	*Acacia senegal*	11	80	2	2	20
19	*Ficus vasta*	0	80	24	16	1897
18	*Acacia gerrardii*	0	80	0	0	0
13	*Delonix elata*	8	100	0	0	0
11	*Tamarindus indica*	0	88	20	0	0
10	*Rhus somalensis*	10	86	11	0	0
5	*Ficus sycomorus*	0	100	0	40	1378
2	*Boscia arabica*	0	100	0	0	0
2949	Grand total	10	85	13	10	802.43

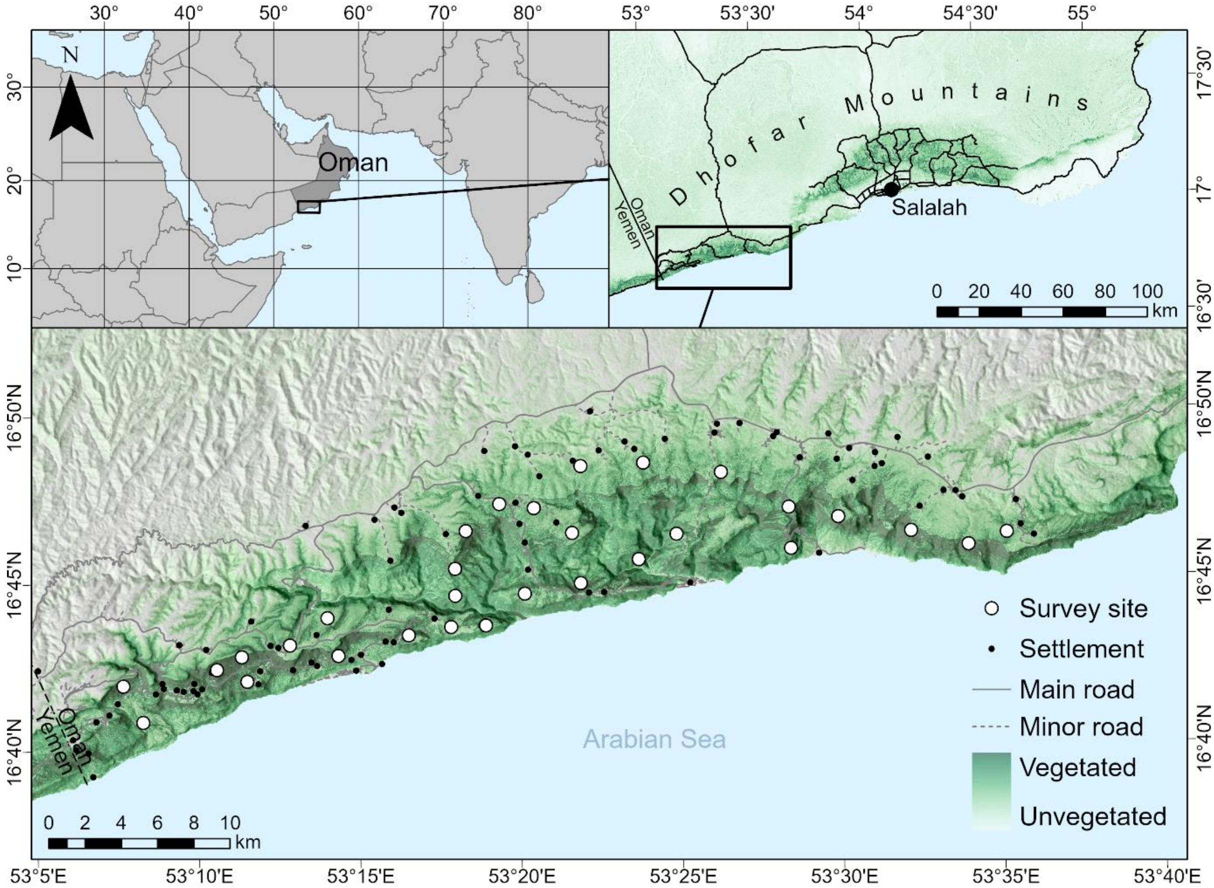
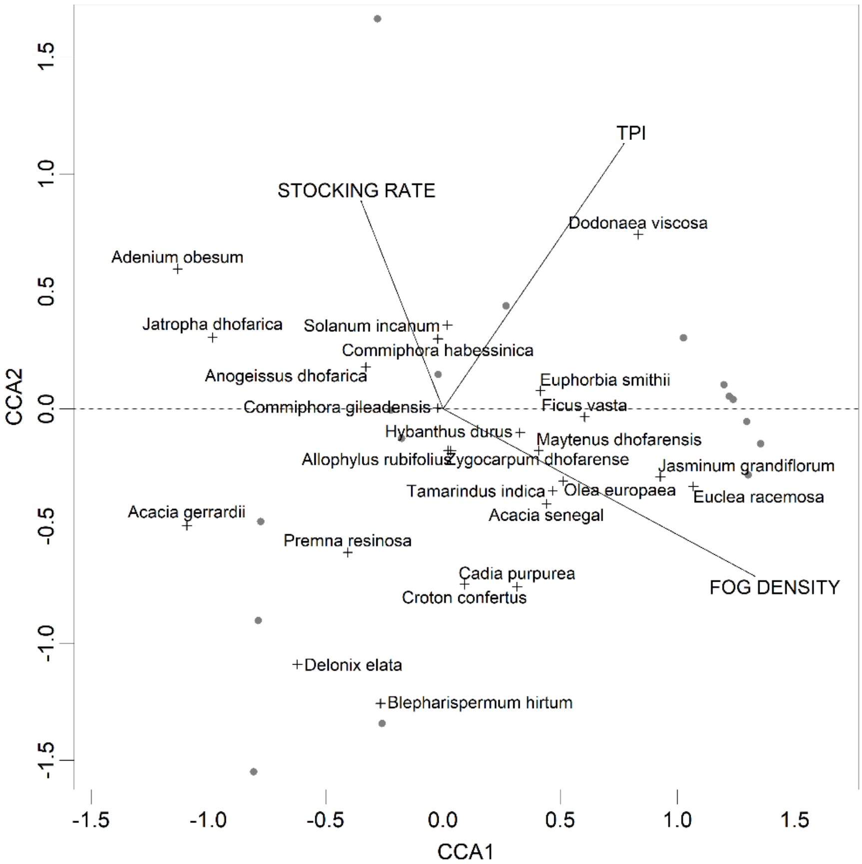


Figure 1. Map of Jabal Qamar showing locations of the survey sites, settlements and roads, overlaid on a vegetation greenness (NDVI) base map. Two inset maps show the whole Dhofar Mountains and their location in Oman.

a) Adults



b) Juveniles

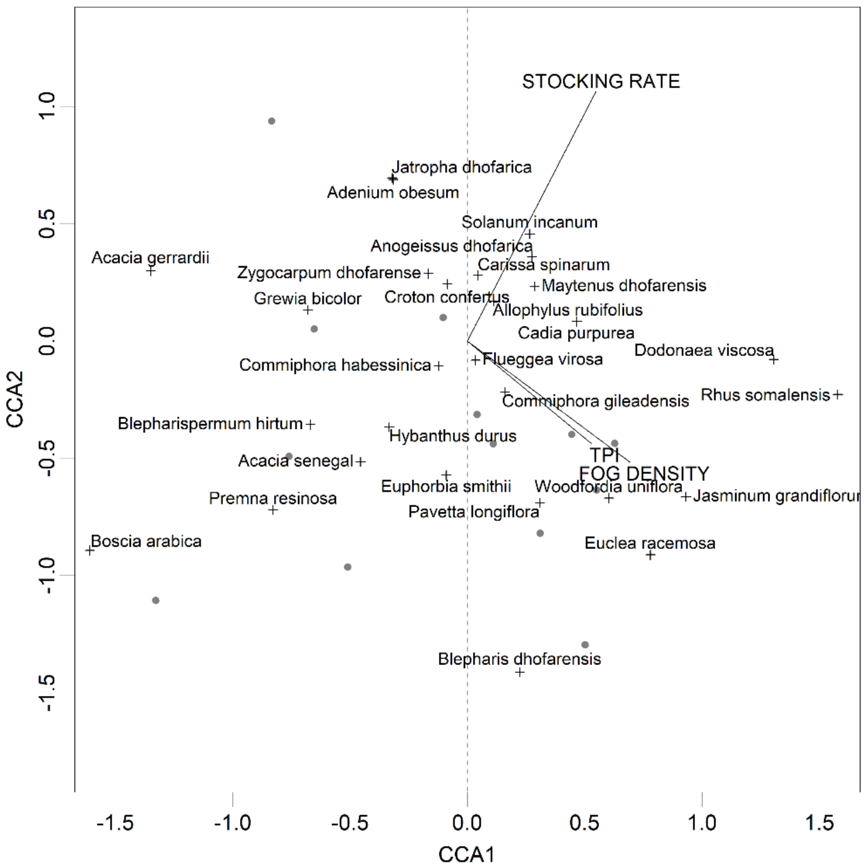


Figure 2. Constrained correspondence analysis (CCA) biplots of (a) adult and (b) juvenile woody species composition. Common species (overall frequency > 10) are labelled and represented by a + symbol, and the other species are represented by a point. The environmental variables are shown as arrows and the length of the arrow indicates the strength of the variable. The Topographic Position Index (TPI) describes at a coarse resolution whether land is within valleys or on hilltops.

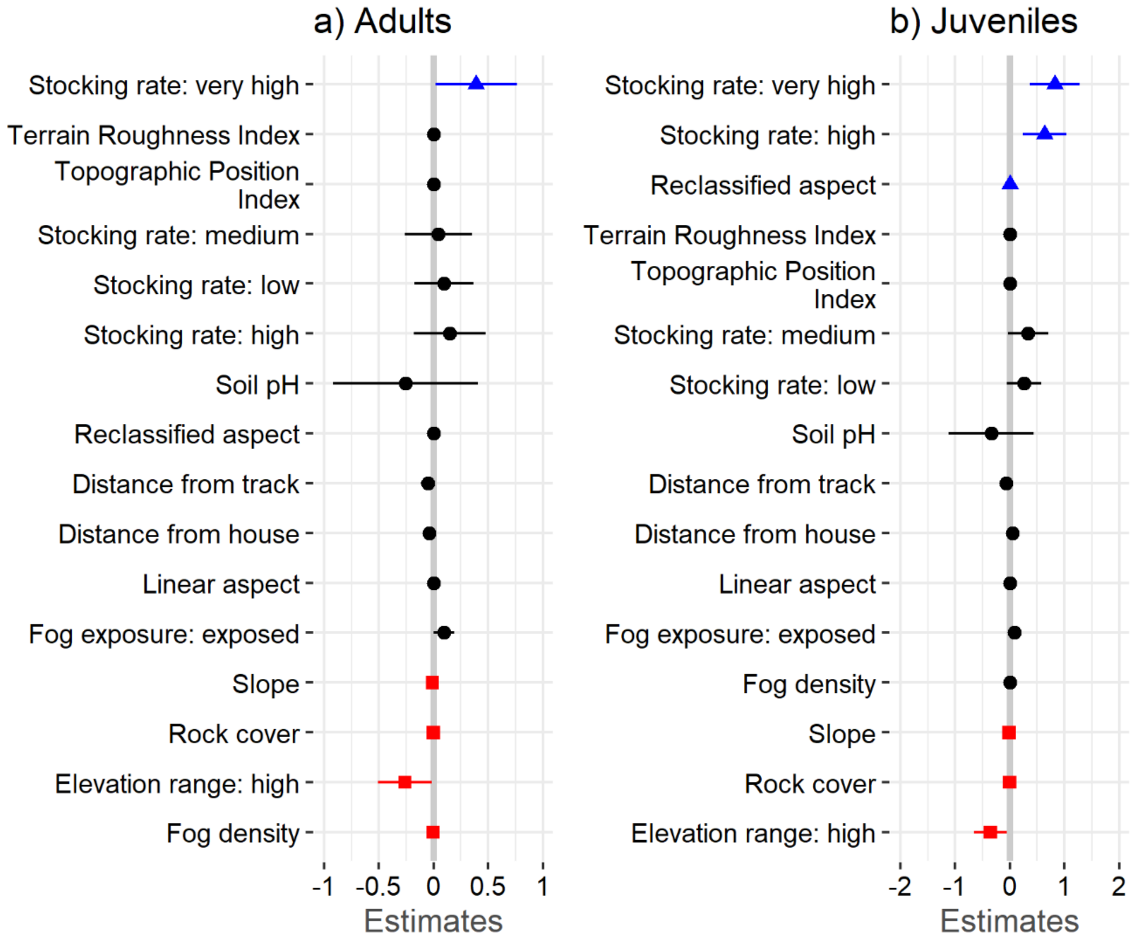


Figure 3. Coefficient estimates (points) and confidence intervals (lines) of log (a) adult (n = 2591) and (b) juvenile (n = 2531) point-plant distances (palatable species only) for each environmental variable in a linear mixed-effects regression model with sites, points and species as random group effects. A positive coefficient (blue triangle) indicates lower plant densities and a negative coefficient (red square) indicates higher plant densities. Very low stocking rate, low elevation range and leeward exposure are the reference classes for categorical variables. A very sparse woodland site was excluded from the analysis.

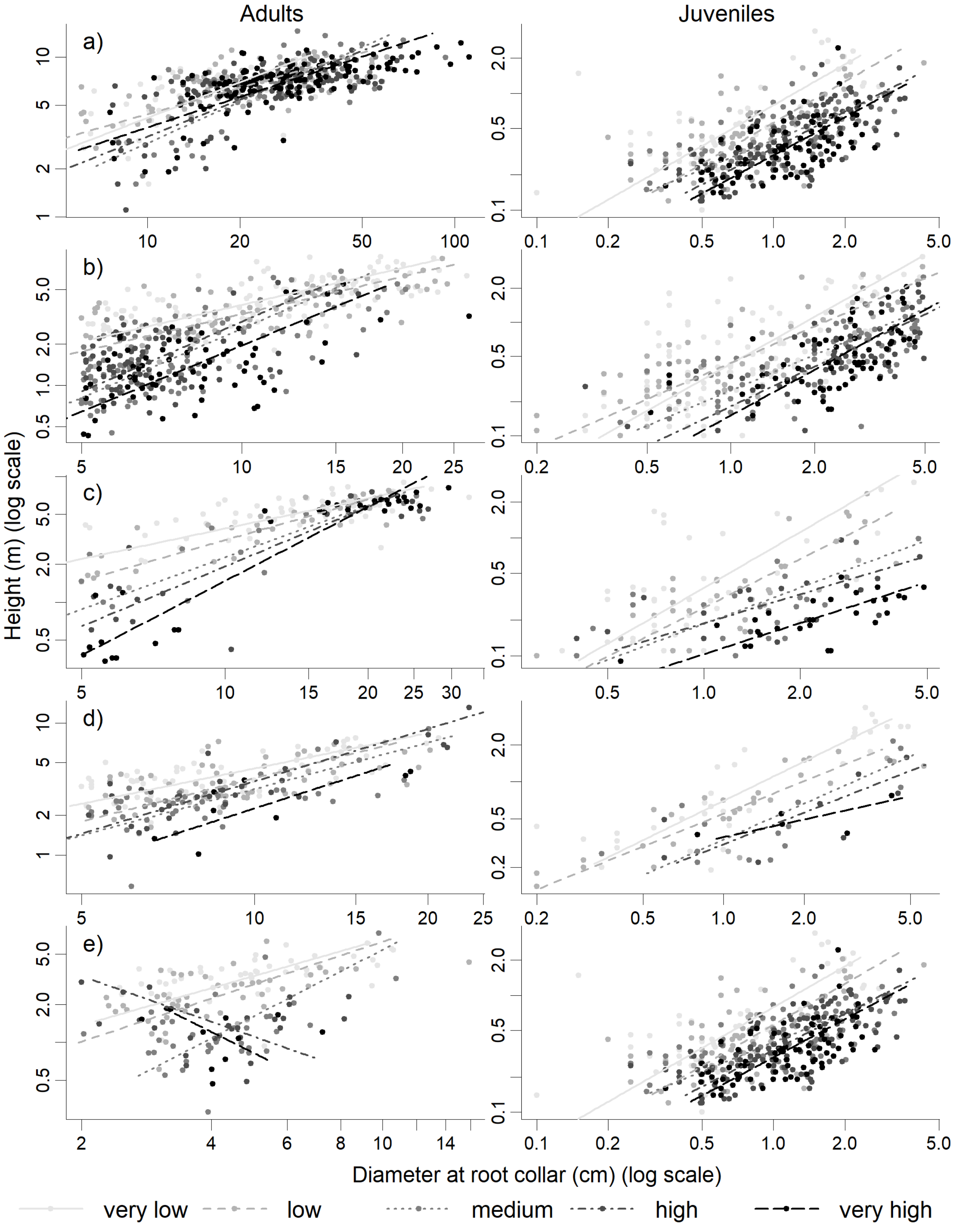


Figure 4. Scatterplot of height against diameter at root collar with fitted standardised major axes under five stocking rate classes, for A) *Anogeissus dhofarica*, B) *Commiphora habessinica*, C) *Commiphora gileadensis*, D) *Euphorbia smithii* and E) *Zygocarpum dhofarense*. All data are log-transformed.

Appendix S1. DRC thresholds to distinguish adults and juveniles.

Appendix S2. Site ranks to quantify long term stocking rates.

Appendix S3. Bivariate test results matrix.

Appendix S4. List of recorded species.

Appendix S5. Photographs of browsing impacts.

Appendix S6. Statistical significance of differences in height-diameter relationships between stocking rates.

Appendix S7. SMA plots with common slopes fitted.