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Title: Six new variants of the *Terminalia* cloud forest in the Dhofar Mountains of Oman

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Running head: Six new variants of the *Terminalia* forest in Dhofar, Oman

Abstract

Background and Aims: The *Terminalia* cloud forest is endemic to a 200-km stretch of coastal mountains in southern Arabia. This research aims to describe patterns of variation in the species composition of the *Terminalia* forest in Dhofar, Oman and examine causal environmental factors. Study area: The Jabal Qamar mountain range, Dhofar, Oman. Methods: Hierarchical cluster analysis and indicator species analysis were used to identify and describe variants of the *Terminalia* forest. Topoclimatic factors, vegetation characteristics and disturbance factors were compared between the variants using ordination and ANOVA or Kruskal-Wallis tests. Results: Six new variants of the *Terminalia* forest are described. These are the *Dodonaea viscosa* subsp. *angustifolia* shrubland variant, *Cadia purpurea-Olea europaea* forest variant, *Euclea racemosa-Jasminum grandiflorum* shrubland variant, *Gymnosporia dhofarensis-Ficus sycomorus* woodland variant, *Jatropha dhofarica-Zygocarpum dhofarense* sparse woodland variant and the *Premna resinosa-Hybanthus durus* forest variant. A seventh variant was identified, which was previously described by Kürschner *et al.* (2004); the broad-leaved *Blepharispermum hirtum* shrubland. The species composition and environmental conditions indicate that two variants are the result of anthropogenic disturbance, whilst the other variants are well separated along fog density and topographic position gradients. Conclusions: Distinct variants of the *Terminalia* forest in Jabal Qamar result from spatial variability in environmental conditions associated with the complex topography, monsoon fog distributions, and anthropogenic disturbance. The results of this study could assist practitioners to rapidly identify and prioritise these variants for conservation.

Keywords: Terminalia dhofarica, Anogeissus, Arabia, arid rangelands, camels, cloud forest, Dhofar Oman, livestock browsing, Mahra Yemen, ordination, overgrazing,

Taxonomic reference: Nomenclature follows the Royal Botanic Gardens Kew Plants of the World Online database (POWO 2019).

Syntaxonomic reference: Nomenclature follows Kürschner *et al.* (2004).

Abbreviations: CCA = constrained correspondence analysis; PCQ = point-centered quarter; r.ind.g = group-equalized individual-based correlation indices;

Introduction

The *Hybantho durae-Anogeissetum dhofaricae* is a drought deciduous cloud forest community (Kürschner et al. 2004), previously referred to as the *Anogeissus* forest, but herein referred to as the *Terminalia* forest following recent taxonomic changes. It is endemic to the southern escarpments of a 200 km stretch of the central south Arabian mountains in Mahra, Yemen and Dhofar, Oman. It is part of the Horn of Africa biodiversity hotspot (Mittermeier et al. 2004). It is the remnants of a once continuous tropical flora which spanned Africa and Arabia, the remainder of which disappeared with Arabia's increasing aridity in the late Tertiary (Meister et al. 2005). Major studies of the *Terminalia* forest include a detailed ethnobotanical account of the woody species in Dhofar (Miller et al. 1988) and a phytosociological description using data from 38 relevés in Mahra (Kürschner et al. 2004). Here, we add to our ecological understanding of the *Terminalia* forest via a phytosociological study in a topoclimatically complex part of its range in Dhofar, Oman.

Water is the primary limiting factor for plant growth in southern Arabia, and the *Terminalia* forest occupies mountain escarpments that receive fog moisture from the southern monsoon, popularly known as the khareef. From mid-June to mid-September south-western winds cause an upwelling of cold sea water off the coast. The warmer moist winds blowing over it are subsequently cooled to dew point and dense fog forms against the southern mountain escarpments (Stanley Price et al. 1988). Cloud shading reduces evapotranspiration rates, allowing for deep infiltration of soil water (Hildebrandt et al. 2007). Furthermore, fog interception by the forest contributes as much water as rainfall (mean annual precipitation ~ 200 mm) to net precipitation which reaches the ground. An altitudinal gradient of vegetation communities has long been recognised in Dhofar (Radcliffe-Smith 1980; Raffaelli & Tardelli 2006), but recently, localized and longitudinal patterns in satellite-derived vegetation greenness have been linked to the interplay between the complex topography and the incoming fog (Ball & Tzanopoulos, 2020a).

Anthropogenic activities have also affected vegetation communities in Dhofar, both historically via deforestation for pasturage and timber (Kürschner et al. 2004; Janzen 1990), and more recently via high livestock grazing and browsing pressure (Hildebrandt & Eltahir 2008; Patzelt 2011). How livestock disturbances interact with vegetation dynamics and tree-grass coexistence in Dhofar is poorly understood. However, research has found that livestock browsing, predominantly by camels, has impacted the composition, structure and phytomorphology of the *Terminalia* forest (Ball & Tzanopoulos 2020b). In addition, research has revealed the potential for irreversible forest-grassland regime shifts, due to reduced fog interception following removal of woody vegetation by browsing livestock (Hildebrandt & Eltahir 2006; Hildebrandt & Eltahir 2008).

The vegetation communities in Dhofar have been the subject of botanical inventories for several decades (Radcliffe-Smith 1980; Miller et al. 1988; Miller & Cope 1996; Ghazanfar & Fisher 1998; Mosti et al. 2012). Some communities have been described qualitatively (Patzelt

2015; Al-Zidjali 1995; Knees et al. 2007; Kilian et al. 2002; Raffaelli & Tardelli 2006) whilst others, such as the coastal vegetation (Ghazanfar 1996; Ghazanfar 1999) and a mid-altitude plateau grassland (Patzelt 2011), have been subject to quantitative phytosociological sampling. Botanical inventories have recorded 262 vascular plant species (19% of the total flora of Oman) from the *Terminalia* forest in Dhofar (Patzelt 2015), but a quantitative phytosociological study has not been conducted.

The first aim of this study was to describe patterns of variation in the species composition of the *Terminalia* forest in the topoclimatically complex Jabal Qamar mountain range, in western Dhofar, Oman. The second aim was to examine how topoclimatic and anthropogenic factors differ between variants of the *Terminalia* forest. This study will assist practitioners to rapidly identify and prioritise these variants for conservation.

Study area

Jabal Qamar is situated in western Dhofar and to the east of the governorate of Mahra in Yemen (Figure 1). It boasts the most extensive tracts of *Terminalia* forest in the region and the highest botanical diversity (515 vascular species) of any area in Oman (Patzelt 2015). When travelling through Jabal Qamar one can clearly observe changes in the species composition and structure of the *Terminalia* forest, both with elevation and longitudinally. The *Terminalia* forest is the dominant habitat of the southern escarpments at elevations of 100–1000 m above sea level (asl). It is interspersed in flatter areas, with grasslands dominated by *Apluda mutica, Arthraxon junnarensis* and *Themeda quadrivalvis* (Patzelt 2011). 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).

#Fig. 1 approximately here#

Methods

Field sampling

The point-centered quarter (PCQ) method (Cottam & Curtis 1956) was used to sample the composition, density and structure of woody vegetation at 30 sites in Jabal Qamar. Sites were selected within the altitudinal range (100-1000 m asl) of the *Terminalia* forest, between 300 and 900 m asl. Sites were selected based on their stocking histories but spanned a range of topoclimatic conditions. Sites generally had slope gradients of <30° so they were safely accessible to the research team. Thirty PCQ point locations were randomly generated using a GIS over an area of ~1 km^2 at each site, with a minimum distance between points of 50 m. Large sites were preferred to avoid overemphasising vegetation responses to livestock activity which can be patchy (Briske et al. 2003). Sites were visited on four occasions, every two months during the growing season and early dry 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. Consecutively rotating site visits improved comparability between sites by controlling for seasonal vegetation change from senescence and livestock browsing. Furthermore, minor adjustments could be made to the methodology between each round of visits.

At each PCQ point, the distances to the closest adult and the closest juvenile woody plants were recorded in each of four quarters, resulting in a total of 120 adult and 120 juvenile records per site. In total, 7,200 woody plants were measured. Measurements included the diameter at root collar, height, browsing intensity, proportion of broken, bent and/or cut branches, and area of stripped bark. In addition, at each PCQ point a 1.2 m^2 quadrat was deployed to sample the ground vegetation which also served to guide the PCQ quarters. Grass and herb species richness and the percentage cover of grasses, herbs, rock and bare ground were recorded. Additionally, the percentage cover of the three most abundant species was estimated. Soil pH levels were tested using a pH meter electrode from four composite soil samples collected from each site from the top 20 cm of soil.

Environmental variables

One-way analysis of variance (ANOVA) with Tukey post-hoc tests for normally distributed data, or Kruskal-Wallis with Dunn post hoc tests for non-normally distributed data, were used to compare topoclimatic variables, vegetation characteristics and disturbance factors between variants. The ArcGIS Spatial Analyst toolbox and the Geomorphometry and Gradient Metrics toolbox (Evans et al., 2014) were used to calculate a range of topographic variables from ASTER 30 m Global Digital Elevation Model (GDEM). Fog density values were calculated on a per cell basis as the mean of the near-infrared fog reflectance values of 119 Landsat 5 scenes, 17 Landsat 7 scenes and 121 Landsat 8 scenes (Ball & Tzanopoulos 2020a). Long-term stocking rates were estimated by ranking the sites based on measures of plant damage and path distances to concentrators like waterpoints and settlements, akin to the piosphere model (Andrew 1988). Ten of the topoclimatic variables were measured at the PCQ point locations and an additional 30 randomly located points within a minimum bounding polygon at each site, to increase site-level precision. Other variables were measured at the individual level (n/site = 120), point level (n/site = 30) or site level, or a different level based on the sampling procedure (e.g. soil pH where n/site = 4). The geospatial datasets used in this analysis are listed in Table 1 and hosted in the PANGAEA data repository (doi.org/10.1594/PANGAEA.902295).

Classification

Hierarchical cluster analysis (HCA) using Bray-Curtis dissimilarly indices and average linkage clustering was carried out on the woody species count data. Unlike in non-nested clustering algorithms such as K-means clustering, in HCA the number of clusters of interest is not pre-specified. Rather, a single nested hierarchy of clusters is produced and visualised in a dendrogram, and the selection of clusters representing biologically important subpopulations is left to the researcher. In this study, the hierarchy of clusters was partitioned at seven groups ($K = 7$) for two reasons. Firstly, the seventh group conformed to the pre-described broad-leaved *Blepharispermum hirtum* variant of the *Terminalia* forest (Kürschner et al. 2004). Secondly, the clustering corresponded to the qualitative descriptions of seven variants made by the lead author in the field.

The Bray-Curtis dissimilarity measure was used as it is appropriate for raw count data including zeros (Greenacre & Primicerio 2013; Legendre & Legendre 1998) and is well suited to uniform sample sizes which resulted from our PCQ sampling method (Chao et al. 2006). Average linkage clustering was used as it is a natural compromise between single and complete linkage clustering and provides a more accurate reflection of the distance between clusters as it incorporates information about variance (Yim & Ramdeen 2015). Data on the herbaceous species was not included in the cluster analysis as we recorded only the three most abundant species. Furthermore, due to the short growing season and rapid senescence of the herbaceous layer it does not characterise habitats per se.

The clusters were visualised in a constrained correspondence analysis (CCA) biplot of site scores, to observe the relationship between the proposed variants and the three most important environmental constraints (Ball & Tzanopoulos, 2020b). The CCA models were built in the R ‘vegan’ package (Oksanen et al. 2018; R Core team 2020) using 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).

Indicator species analysis

Diagnostic species of the proposed variants were determined by calculating group-equalized individual-based correlation indices (r.ind.g) for each species within each cluster (De Cáceres & Legendre 2009). This index is suited to our sampling design where an equal number of individuals were sampled at each site (De Cáceres & Legendre 2009). In addition, it equalizes the relative sizes of all clusters, allowing for comparisons between values corresponding to clusters of different sizes (De Cáceres & Legendre 2009; Tichý & Milan 2006). This method reduces the candidacy of rare species. The same method was used for herbaceous species, however due to unequal cover totals we transformed the data set by dividing each abundance value by the sum of the abundances at each site (De Cáceres & Legendre 2009).

The significance of species-variant memberships for diagnostic species was tested using permutation tests (999 permutations) under the null hypothesis that the abundance of a given species in sites belonging to the variant was not higher than its abundance in sites not in the variant (Bakker 2008). Species were assigned to the variant for which they had the lowest significant *p*-value after Sidak's correction for multiple testing. Diagnostic species were selected based on statistically significant species variant associations (p = < 0.05). The analysis used the R 'indicspecies' package (De Cáceres & Jansen 2016).

Results

We recorded 47 woody species (42 adult and 43 juvenile) and 110 herbaceous species (Supplement S1; Mendeley Data: doi.org/10.17632/dc97zn6gzc.1). In the following section we present the results of the hierarchical cluster analysis and the indicator species analysis. Then we describe the variants using the species and environmental data, and qualitative field notes. The HCA dendrogram (Figure 2) shows the hierarchical associations between sites and the seven clusters. The biplot (Figure 3) provides a rapid means to compare the most important environmental factors across variants. The cluster symbols are consistent through Figures 1 to 3. The ANOVA tests (Table 1) provide a more detailed comparison of the topoclimatic, vegetation and disturbance variables. The synoptic table (Table 2) shows the species-variant associations and diagnostic species from the indicator species analysis.

#Fig. 2 approximately here#

The CCA found fog density, topographic position and long-term stocking rate were the most powerful variables, and they explained 31% of the inertia in woody species composition. In the biplot there is no overlap between variant clusters showing that the clusters are associated with different environmental conditions (Figure 3). Clusters A and E are both found under high stocking rates, but whilst cluster A occupies high topographic positions (on hilltops rather than in wadis) with high fog densities, cluster E occupies low topographic positions with low fog densities. Clusters F and G both occur in low topographic positions with average fog densities and low stocking rates. Clusters B and C both occur in foggy areas with relatively low stocking rates, but cluster C occupies higher topographic positions. Cluster D is found in locations with above-average stocking rates and topographic positions and below-average fog densities.

#Fig. 3 approximately here#

#Table 1 approximately here#

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Cluster A: *Dodonaea viscosa* subsp. *angustifolia* shrubland variant

Dodonaea viscosa subsp. *angustifolia* can form a continuous shrub layer, or a shrubland-grassland mosaic, with few accompanying shrub and tree species. Woody species diversity (H = 2.15) and mean adult tree height (236 cm) are lower than the other variants. There are no diagnostic herbaceous species. The CCA and ANOVA results show that this shrubland occupies areas with gentle gradients (mean of 9°), low terrain roughness, and average fog moisture levels, within the monsoon-influenced zone (400-800 m asl). There was soil compaction and desiccation cracks at the sites in this variant, due to cattle stocking following the monsoon. Almost all *Terminalia dhofarica* trees had been subject to arboricultural practises due to the proximity of settlements.

Cluster B: *Cadia purpurea*-*Olea europaea* forest variant

This tall mixed forest community attains an average height of 4.6 m and particularly tall individuals of *Euphorbia smithii, Croton confertus* and *Olea europaea* subsp. *cuspidata* are present. The latter grew to heights of 15 m, but saplings were rarely seen or recorded. *Cadia purpurea* is highly abundant. The proportion of standing dead adult woody plants is significantly higher than the other variants, and mosses and lichens are abundant. This forest occupies rugged, rocky terrain with a naturally terraced topography, on medium-gradient slopes (mean of 13°), between 600 and 900 m asl. This variant received the highest fog densities. The forest grows on and around huge fallen boulders, some of which are over 20 m in height. This is the dominant habitat across an area of approximately 1,000 hectares beneath the plateau cliffs in western Jabal Qamar. Here, the cliffs obstruct the inland movement of fog, resulting in high rates of fog interception and deep soil infiltration at the base of the cliffs. Elsewhere in Jabal Qamar similar species assemblages occur in isolated fragments along gullies and drainage channels at equivalent altitudes. Stocking rates were high across much of this habitat due to the proximity of two relatively large settlements. Browsing damage was visible on many plants and branch management practises had been carried out extensively on *Terminalia dhofarica* and *Olea europaea* subsp. *cuspidata*.

Cluster C: *Euclea racemosa-Jasminum grandiflorum* shrubland variant

Woody species richness (31 of 42 recorded adult species) and diversity (*H* = 3.10) were higher than other variants. Large individuals of uncommon species such as *Pavetta longiflora* and *Searsia somalensis*, and large individuals of usually stunted species such as *Hybanthus durus* and *Zygocarpum dhofarense* were exclusive to this variant. The density of adult plants was high (mean of 1485 plants/hectare). Mature shrubs and trees were clustered amongst boulders, which neighboured small grassland patches, which together repeated over terraced slopes, forming a rugged, terraced grassland-shrubland mosaic. This shrubland occupied steep slopes (mean of 21°) between 600 and 900 m asl in areas where dense monsoon fogs accumulate, such as at the heads of wadis and tributaries and at the base of cliffs.

Cluster D: *Gymnosporia dhofarensis-Ficus sycomorus* sparse woodland variant

Adult woody plant density is significantly lower than all other variants (mean of 322 adult plants/hectare). However, isolated mature individuals of *Terminalia dhofarica*, *Ficus vasta, Ficus sycomorus* and *Gymnosporia dhofarensis* result in the highest mean adult basal area of all variants. This variant occurs in accessible, gently-sloping areas (mean of 10°), with intermediate fog moisture levels, across a wide elevation range (200-800 m asl). It had the highest stocking rates and levels of browsing damage out of all the variants. The unpalatable species *Calotropis procera* and *Blumea lacera* are diagnostic. Most saplings were growing under the protection of rocks, soils were heavily compacted with desiccation cracks, and there were numerous, corrugated livestock trails. Ground cover of palatable plant species was mostly absent at six months after the monsoon.

Cluster E: *Jatropha dhofarica-Zygocarpum dhofarense* sparse woodland variant

Jatropha dhofarica and *Zygocarpum dhofarense* are widespread species in Jabal Qamar but were abundant and diagnostic in this variant. *Adenium obesum* was almost exclusive to this variant and *Terminalia dhofarica* was the dominant large tree species. This sparse woodland with high rock cover (mean of 20%) occupies the gentle-gradient (mean of 8°) plateau hills (700-900 m asl) throughout central and eastern Jabal Qamar, covering an area of approximately 17,000 hectares. It is absent from western Jabal Qamar where the plateau is

200 m higher. Areas with high rock cover, have higher tree densities and a more diverse herbaceous layer. Fog density is the lowest of all variants as the intensity of the monsoon diminishes on the plateau. Stocking rates were high because the plateau is easily accessed by livestock from the numerous nearby villages (mean distance to house = 1.1 km). Most woody individuals were heavily browsed.

Cluster F: Broad-leaved *Blepharispermum hirtum* variant (Kürschner et al., 2004)

In gently-sloping lowland areas (300–500 m asl) with average fog moisture levels, *Blepharispermum hirtum* can form an almost continuous shrub layer. Soils are markedly alkaline (pH of 8.4) and rock cover is low (6%). The proportion of standing dead adults (5.42%) is the lowest of all variants. Of the two sites we surveyed, the westernmost is severely degraded due to high stocking rates during the winter months, whilst the easternmost is far from human settlements and subject to low stocking rates. This variant has been previously identified and described by Kürschner *et al.* (2004).

Cluster G: *Premna resinosa-Hybanthus durus* forest variant

This forest variant had the second highest species diversity (H = 2.87) of all variants and is characterised by its high woody plant density (1706 adult plants/hectare) and diversity of diagnostic herbaceous and subshrub species. It is associated with relatively steep slopes (mean of 19°) in drier areas with lower fog densities, and is widespread in Jabal Qamar (300-800 m asl). Large tracts of this forest occupy the mid-altitude escarpments of central and eastern Jabal Qamar. It is likely that soil moisture levels are low, as this variant occupies slopes in lee positions, which receive less fog moisture than windward slopes. Herbs tend to outnumber grasses and steeper areas are characterised by scattered herbs, bare red soils and a shallow leaf litter. Rock cover is low (6%), soils are markedly alkaline (pH of 8.25), and terrain roughness can be high, although the terrain is not rocky and rugged as in other variants, but rather undulating with numerous small wadis. Stocking rates are low as there are few nearby settlements (mean distance to house = 6.04 km). Six species are transgressive (based on a simple average abundance threshold of > 5% within variants) with the broad-leaved *Blepharispermum hirtum* variant, reflecting the close syntaxonomical relation between both communities, which share similar environmental conditions.

Discussion

In this research we used hierarchical cluster analysis and indicator species analysis to describe patterns of variation in the species composition of the *Terminalia* cloud forest in Jabal Qamar, Dhofar, Oman. Seven variants were identified with varying environmental conditions. In the following section we discuss how topoclimatic factors give rise to the observed variants. Then, we discuss the variants and their diagnostic species in relation to previous research and provide some conservation recommendations.

The spatial distribution of fog influences plant distributions in Dhofar (Ball & Tzanopoulos 2020a), as is common in arid environments where fog provides for a large part of the water balance (Scholte & De Geest 2010; Martorell & Ezcurra 2002; Cavelier & Guillermo 1989). Accordingly, in this phytosociological study of the *Terminalia* forest in Dhofar, we identified seven forest variants which are well separated along fog density and topographic position gradients (Figure 3 and Table 1). In Jabal Qamar, these gradients may be especially pronounced due to higher topoclimatic complexity compared to neighbouring mountain ranges. Subsequently, heterogenous fog moisture levels affect vegetation species composition. For instance, the *Cadia purpurea-Olea europaea* forest variant and *Euclea racemosa-Jasminum grandiflorum* shrubland variant occupy hotspots of fog accumulation beneath cliffs and at the tops of wadi tributaries. Conversely, the *Premna resinosa-Hybanthus durus* forest is found on drier slopes in lee positions. These results highlight the importance of considering fog distributions and terrain variables, in addition to elevation, when examining species and habitat distributions in Dhofar.

Shrublands dominated by *Dodonaea viscosa* subsp. *angustifolia* have been described qualitatively in Yemen (Kürschner et al. 2004; Al Khulaidi 2006; Kilian et al. 2002) and in Jabal Akhdar in northern Oman (Brinkmann et al. 2009). *Dodonaea viscosa* subsp. *angustifolia* was traditionally cut and burnt as a fertiliser for seasonal rain-fed agricultural plots (Miller et al. 1988). This variant in Jabal Qamar, which grows close to settlements in areas with high fog moisture levels, were confirmed by pastoralists to be the remnants of agricultural plots. *Dodonaea viscosa* subsp. *angustifolia* is fast-growing, unpalatable to livestock and may encroach degraded areas (Schlecht et al. 2014). Control and/or removal of extensive areas of this shrubland could help to restore community composition and improve the quality and quantity of forage close to settlements.

Cadia purpurea is a light-demanding shrub and is unpalatable for livestock. It is an indicator of disturbance in Afromontane *Olea-Juniper* forests in Ethiopia (Aynekulu et al. 2009; Aynekulu et al. 2016; Giday et al. 2018) and may indicate disturbance in the *Cadia purpurea-Olea europaea* forest variant. It may have become more abundant in recent decades and its population should be monitored. Interestingly, it was not included in the Plants of Dhofar book (Miller et al. 1988). *Cadia purpurea* and *Croton confertus* are diagnostic for the *Cadia purpurea-Olea europaea* forest variant and restricted to rugged slopes in the wettest areas of Jabal Qamar. They are not highly constant species of the *Terminalia* forest as described by Kürschner *et al.* (2004). Miller, Morris and Stuart-Smith

(1988) attributed sharp declines in populations of *Olea europaea* subsp. *cuspidata* in Dhofar to harvesting of its hardwood. However, substantial numbers of adults were recorded in the *Cadia purpurea-Olea europaea* forest variant, although *Olea europaea* subsp. *cuspidata* was rarely recorded as a juvenile. Traditionally, *Olea europaea* subsp. *cuspidata* was an unfavoured browse species (Miller et al. 1988) but we observed high browsing pressure on the accessible sucker foliage. Stocking rates should be reduced in this variant to support forest regeneration.

Kürschner *et al.* (2004) identified a sparse altitudinal variant of the *Terminalia* forest in Yemen with evergreen Afromontane species. The *Euclea racemosa-Jasminum grandiflorum* shrubland and the *Cadia purpurea-Olea europaea* forest variants are equivalent in Jabal Qamar. They both occur at higher elevations (600-900 m asl) and common character species include *Dodonaea viscosa* subsp. *angustifolia*, *Jasminum grandiflorum* subsp. *floribundum*, *Pavetta longifolia*, *Olea europaea* subsp. *cuspidata* and *Searsia somalensis*. Similar semi-evergreen species assemblages have been described in Dhofar at elevations above 500 m asl by Miller *et al.* (1988), which together with our results provide further evidence for the former existence of a belt of palaeo-tropical vegetation across the southern Arabian region (Kürschner et al. 2004; Borrell et al. 2019). Our results show that topographic factors (position, slope and aspect) are the decisive environmental factors which separate the *Euclea racemosa-Jasminum grandiflorum* shrubland variant from the *Cadia purpurea-Olea europaea* forest variant, which both persist at similar altitudes under similarly high fog densities. Topography can affect soil conditions, which can affect community composition (Mullins Christopher et al. 2002; Querejeta et al. 2009). The *Euclea racemosa-Jasminum grandiflorum* shrubland variant had the second lowest stocking rates, and effort should be made to ensure that they do not increase.

Several indicators suggest that the *Gymnosporia dhofarensis-Ficus sycomorus* sparse woodland variant is the result of anthropogenic disturbance on forests in the monsoon influenced zone of Jabal Qamar. Long term signs of degradation include isolated trees and forest fragments, and diagnostic unpalatable species. Short term signs of degradation, including arboricultural practises, soil compaction, desiccation cracks, stunted phytomorphology and dead stumps. Similar habitats described in Yemen and Dhofar have been attributed to forest clearance for pasturage (Kürschner et al. 2004; Patzelt 2011) and timber (Janzen 1990). The very large adults of *Terminalia dhofarica*, *Ficus vasta* and *Ficus sycomorus* are resilient to browsing and could have been protected by pastoralists to provide shade (Buffington & McCorriston 2018). Similarly, the sharp spines of *Gymnosporia dhofarensis* may enable it to persist under high stocking rates (Scholes & Archer 1997).

Conservation efforts through managed grazing regimes and tree planting could facilitate forest recovery in this degraded habitat that receives high fog densities.

The *Jatropha dhofarica-Zygocarpum dhofarense* sparse woodland variant occupies the upper altitudinal range of the *Terminalia* forest. At higher altitudes, fog densities are low and the forest transitions to a community dominated by stunted *Jatropha dhofarica, Commiphora* spp. *and Adenium obesum*, and then to the *Euphorbia balsamifera* cushion shrub community (Kürschner et al. 2004; Patzelt 2015; Al-Zidjali 1995; Knees et al. 2007; Kilian et al. 2002). *Zygocarpum dhofarense* has been reported as a rare species, favouring steeper slopes (Miller et al. 1988), but it was abundant in this variant, albeit heavily damaged and stunted, unless inaccessible to livestock. Stocking rates are highest in this variant due to the proximity to villages, and livestock browsing has impacted woody species composition and structure (Ball & Tzanopoulos 2020b). Efforts should be made to substantially reduce stocking rates throughout this variant.

Blepharispermum hirtum is regionally endemic and was speculated to have formerly dominated the entire length of the foothills of the monsoon-influenced escarpments (Miller et al. 1988). However, it has a disjunct distribution in Jabal Qamar and transitions to the *Premna resinosa-Hybanthus durus* forest variant on steep slopes. Kürschner *et al.* (2004) stated that *Jatropha dhofarica* was absent from this variant but this is not the case in Jabal Qamar. Kürschner *et al.* (2004) also described the typical *Terminalia* forest variant as having a high cover-abundance of *Euphorbia smithii* and *Jatropha dhofarica*, however our results show that these two species do not co-dominate in Jabal Qamar. Rather, *Jatropha dhofarica* dominates in flat plateau woodlands, whilst *Euphorbia smithii* is associated with steeper slopes at lower altitudes with higher fog densities. Due to its disjunct distribution in fragmented patches in Jabal Qamar, the broad-leaved *Blepharispermum hirtum* variant should be prioritized for conservation, and stocking rates should be drastically reduced in this variant in western Jabal Qamar.

In the central South Arabian mountains, the *Terminalia* forest occupies the monsoon-influenced escarpments, whilst *Acacia-Commiphora* woodlands are typical of the arid escarpments (Kürschner et al. 2004; Ghazanfar & Fisher 1998; Miller & Cope 1996). The *Premna resinosa-Hybanthus durus* forest variant is syntaxonomically similar to the *Acacia-Commiphora* woodland sharing several diagnostic drought-tolerant woody species (*Premna resinosa, Hybanthus durus* and *Senegalia senegal*). This variant is widespread in the more remote areas of Jabal Qamar and has lower stocking rates than the other variants. Efforts should be made to maintain or reduce current stocking rates.

Conclusion

In this research we conducted the first phytosociological study of the *Terminalia* forest in the Dhofar Mountains of Oman. From a sample of 7,200 woody plants and 900 quadrats across thirty sites, we identified seven variants of the *Hybantho durae-Anogeissetum dhofaricae* in Jabal Qamar. Six are new and one was previously described by Kürschner *et al.* (2004). Several vegetation and disturbance indicators suggest two of the variants are the result of anthropogenic activities. The other variants are well separated along fog density and topographic position gradients. This study could assist practitioners to rapidly identify and prioritise variants of the *Terminalia* forest for conservation.

Author contributions: LB and JT designed, conducted and reported the research.

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References

Al-Zidjali, T. 1995. *Oman: Country Report to the FAO International Technical Conference on Plant Genetic Resources*, Muscat.

Andrew, M.H. 1988. Grazing impact in relation to livestock watering points. *Trends in Ecology and Evolution* 3: 336–339. DOI: 10.1016/0169-5347(88)90090-0

Aynekulu, E., Aerts, R., Denich, M., Negussie, A., Friis, I., Demissew, S. & Boehmer, H.J. 2016. Plant diversity and regeneration in a disturbed isolated dry Afromontane forest in northern Ethiopia. *Folia Geobotanica* 51: 115–127. DOI: 10.1007/s12224-016-9247-y

Aynekulu, E., Denich, M. & Tsegaye, D. 2009. Regeneration Response of Juniperus procera and Olea europaea subsp cuspidata to Exclosure in a Dry Afromontane Forest in Northern Ethiopia. *Mountain Research and Development* 29: 143–152. DOI: 10.1659/mrd.1076

Ball, L. 2019. Geospatial datasets for the central South Arabian mountains (CSAM) in Al Mahrah (Yemen) and Dhofar (Oman) including spatial variability in monsoon fog density. *PANGAEA*. DOI: 10.1594/PANGAEA.902295

Ball, L. 2019. Data from a botanical survey of the Anogeissus cloud forest in Jabal Qamar, Dhofar, Oman. *Mendeley Data*. DOI: 10.17632/dc97zn6gzc.1

Ball, L. & Tzanopoulos, J. 2020a. Interplay between topography, fog and vegetation in the central South Arabian mountains revealed using a novel Landsat fog detection technique. *Remote Sensing in Ecology and Conservation*. DOI: 10.1002/rse2.151

Ball, L. & Tzanopoulos, J. 2020b. Livestock browsing affects the species composition and structure of cloud forest in the Dhofar Mountains of Oman. *Applied Vegetation Science*. 23: 363-376. DOI: 10.1111/avsc.12493

Borrell, J.S., Issaey, G. Al, Lupton, D.A., Starnes, T., Hinai, A. Al, Hatmi, S. Al, Senior, R.A., Wilkinson, T., Milborrow, J.L.H., Stokes-rees, A. & Patzelt, A. 2019. Islands in the desert: environmental distribution modelling of endemic flora reveals the extent of Pleistocene tropical relict vegetation in southern Arabia. *Annals Of Botany* mcz085: 1–12. DOI: 10.1093/aob/mcz134

Brinkmann, K., Patzelt, A., Dickhoefer, U., Schlecht, E. & Buerkert, A. 2009. Vegetation patterns and diversity along an altitudinal and a grazing gradient in the Jabal al Akhdar mountain range of northern Oman. *Journal of Arid Environments* 73: 1035–1045. DOI: 10.1016/j.jaridenv.2009.05.002

Briske, D.D., Fuhlendorf, S.D., & Smeins, F. E. 2003. Vegetation dynamics on rangelands: A critique of the current paradigms. *Journal of Applied Ecology* 40: 601–614. DOI: 10.1046/j.1365-2664.2003.00837.x

Buffington, A. & McCorriston, J. 2018. Wood exploitation patterns and pastoralist–environment relationships: charcoal remains from Iron Age Ṡhakal, Dhufar, Sultanate of Oman. *Vegetation History and Archaeobotany* 1–12. DOI: 10.1007/s00334-018-0682-y

De Cáceres, M. & Jansen, F. 2016. Package ‘indicspecies’ (Version 1.7.6). *R Package Vignettes* 1–31.

De Cáceres, M. & Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90: 3566–3574. DOI: 10.1890/08-1823.1

Cavelier, J. & Guillermo, G. 1989. Mist and fog interception in elfin cloud forests in Colombia and Venezuela. *Journal of Tropical Ecology* 5: 309–322.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62: 361–371. DOI: 10.1111/j.1541-0420.2005.00489.x

Cottam, G. & Curtis, J.T. 1956. The Use of Distance Measures in Phytosociological Sampling. *Ecology* 37: 451–460. DOI: 10.2307/1930167

Friesen, J., Zink, M., Bawain, A. & Müller, T. 2018. Hydrometeorology of the Dhofar cloud forest and its implications for groundwater recharge. *Journal of Hydrology: Regional Studies* 16: 54–66. DOI: 10.1016/j.ejrh.2018.03.002

GBIF.org 2020. GBIF Home Page.

Ghazanfar, S.A. 1996. Analysis of the vegetation of saline, brackish and freshwater pools in Dhofar, Sultanate of Oman. *Plant Life in Southwest and Central Asia* 501–508.

Ghazanfar, S.A. 1999. Coastal vegetation of Oman. *Estuarine, Coastal and Shelf Science* 49: 21–27. DOI: 10.1006/ecss.1999.0482

Ghazanfar, S.A. & Fisher, M. 1998. *Vegetation of the Arabian Peninsula*, Dordrecht: Kluwer Academic Publishers.

Giday, K., Humnessa, B., Muys, B., Taheri, F. & Azadi, H. 2018. Effects of livestock grazing on key vegetation attributes of a remnant forest reserve: The case of Desa'a Forest in northern Ethiopia. *Global Ecology and Conservation* 14: 1–14.

Greenacre, M. & Primicerio, R. 2013. *Multivariate Analysis of Ecological Data*, Bilbao: Fundación BBVA.

Hildebrandt, A., Al Aufi, M., Amerjeed, M., Shammas, M. & Eltahir, E.A.B. 2007. Ecohydrology of a seasonal cloud forest in Dhofar: 1. Field experiment. *Water Resources Research* 43: 1–13. DOI: 10.1029/2006WR005261

Hildebrandt, A. & Eltahir, E.A.B. 2006. Forest on the edge: Seasonal cloud forest in Oman creates its own ecological niche. *Geophysical Research Letters* 33: 2–5. DOI: 10.1029/2006GL026022

Hildebrandt, A. & Eltahir, E.A.B. 2008. Using a horizontal precipitation model to investigate the role of turbulent cloud deposition in survival of a seasonal cloud forest in Dhofar. *Journal of Geophysical Research* 113: 1–11. DOI: 10.1029/2008JG000727

IPNI.org 2020. IPNI.

Janzen, J. 1990. *Land Tenure and Land Use in the Pastoral Living Areas of Dhofar, Sultanate of Oman*, Rome: FAO.

Al Khulaidi, A. 2006. *Environmental and human determinates of vegetation distribution in the Hadhramaut region, Republic of Yemen*. University of Edinburgh, UK.

Kilian, N., Hein, P. & Hubaishan, M.A. 2002. New and noteworthy records for the flora of

Yemen, chiefly of Hadhramaout and Al-Mahra. *Willdenowia* 32: 239–269.

Knees, S., Laser, S., Miller, A. & Patzelt, A. 2007. A New Species of Barleria (Acanthaceae) from Oman. *Edinburgh Journal of Botany* 64: 107–112. DOI: 10.1017/S0960428607000789

Kürschner, H., Hein, P., Kilian, N. & Hubaishan, M.A. 2004. The Hybantho durae-Anogeissetum dhofaricae ass. nova - Phytosociology, structure and ecology of an endemic South Arabian forest community. *Phytocoenologia* 34: 569–612. DOI: 10.1127/0340-269X/2004/0034-0569

Legendre, P. & Legendre, L. 1998. *Numerical Ecology* 2nd ed., Amsterdam: Elsevier. DOI: 10.1017/CBO9781107415324.004

Martorell, C. & Ezcurra, E. 2002. Rosette scrub occurrence and fog availability in arid mountains of Mexico. *Journal of Vegetation Science* 13: 651–662. DOI: 10.1111/j.1654-1103.2002.tb02093.x

Meister, J., Hubaishan, M.A., Kilian, N. & Oberprieler, C. 2005. Chloroplast DNA variation in the shrub Justicia areysiana (Acanthaceae) endemic to the monsoon affected coastal mountains of the southern Arabian Peninsula. *Botanical Journal of the Linnean Society* 148: 437–444.

Miller, A., Morris, M. & Stuart-Smith, S. 1988. *Plants of Dhofar, The Southern Region of Oman: Traditional, Economic, and Medicinal Uses*, Muscat: Office of the Adviser for Conservation of the Environment, Diwan of Royal Court.

Miller, A.G. & Cope, T.A. 1996. *Flora of the Arabian Peninsula and Socotra, Vol. 1* 1st ed., Edinburgh: Edinburgh University Press.

Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Fonseca, G.A.B. da & Lamoreux, J. 2004. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions* R. A. Mittermeier, ed., Rugby: CEMEX. DOI: 10.2744/ccab-14-01-2-10.1

Mosti, S., Raffaelli, M. & Tardelli, M. 2012. Contribution to the Flora of Central-Southern Dhofar (Sultanate of Oman). *Webbia* 67: 65–91. DOI: 10.1080/00837792.2012.10670909

Mullins Christopher, E., Burslem David, F.R.P., Daws Matthew, I., Paton Steven, R. & Dalling James, W. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil* 238: 79–90.

NCSI 2017. National Centre for Statistics and Information Data Portal.

Oksanen, A.J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. 2018. Package ‘vegan’ (Version 2.6). *R Package Vignettes* 1–292. DOI: ISBN 0-387-95457-0

Patzelt, A. 2015. Synopsis of the Flora and Vegetation of Oman, with Special Emphasis on Patterns of Plant Endemism. *Abhandlungen der Braunschweigischen Wissenschaftlichen Gesellschaft* 282–317.

Patzelt, A. 2011. The Themeda Quadrivalvis Tall-Grass Savannah of Oman at the Crossroad Between Africa and Asia. *Edinburgh Journal of Botany* 68: 301–319. DOI: 10.1017/S0960428611000217

POWO. 2019. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Retrieved August 27, 2020, from http://www.plantsoftheworldonline.org/

Querejeta, J.I., Egerton-warburton, L.M. & Allen, M.F. 2009. Topographic Position Modulates the Mycorrhizal Response of Oak Trees to Interannual Rainfall Variability. *Ecology* 90: 649–662.

R Core team 2020. *R: A language and environment for statistical computing*, Vienna, Austria: R Foundation for Statistical Computing.

Radcliffe-Smith, A. 1980. The Vegetation of Dhofar. In *The scientific results of the Oman flora and fauna survey 1977 (Dhofar), Journal of Oman Studies Special Report No. 2*. Oman Office of the Government Adviser for Conservation of the Environment, ed. Muscat: Ministry of Information and Culture, pp. 59–86.

Raffaelli, M. & Tardelli, M. 2006. Phytogeographic zones of Dhofar (Southern Oman). *Bocconea* 19: 103–108.

Schlecht, E., Zaballos, L.G.H., Quiroz, D., Scholte, P. & Buerkert, A. 2014. Traditional land use and reconsideration of environmental zoning in the Hawf Protected Area, south-eastern Yemen. *Journal of Arid Environments* 109: 92–102. DOI: 10.1016/j.jaridenv.2014.05.016

Scholes, R.J. & Archer, S.R. 1997. Tree-Grass Interactions in Savannas. *Annual Review of Ecology and Systematics* 28: 517–544. DOI: 10.7567/JJAP.55.06GF04

Scholte, P. & De Geest, P. 2010. The climate of Socotra Island (Yemen): A first-time assessment of the timing of the monsoon wind reversal and its influence on precipitation and vegetation patterns. *Journal of Arid Environments* 74: 1507–1515. DOI: 10.1016/j.jaridenv.2010.05.017

Stanley Price, M.R., Al-Harthy, A.H. & Whitcombe, R.P. 1988. Fog moisture and its ecological effects in Oman. In *Arid Lands: Today and Tomorrow*. E. E. Whitehead, C. F. Hutchinson, B. N. Timmermann, & R. G. Varady, eds. Boulder, Colorado: Westview Press, pp. 69–88.

Tichý, L. & Milan, C. 2006. Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science* 17: 809–818. DOI: 10.1111/j.1654-1103.2006.tb02504.x

Yim, O. & Ramdeen, K.T. 2015. Hierarchical Cluster Analysis: Comparison of Three Linkage Measures and Application to Psychological Data. *The Quantitative Methods for Psychology* 11: 8–21. DOI: 10.20982/tqmp.11.1.p008

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Appendices

Electronic supplements

Supplement S1. The woody (count data) and herbaceous (cover data) species recorded at the thirty sites.

Tables and figures

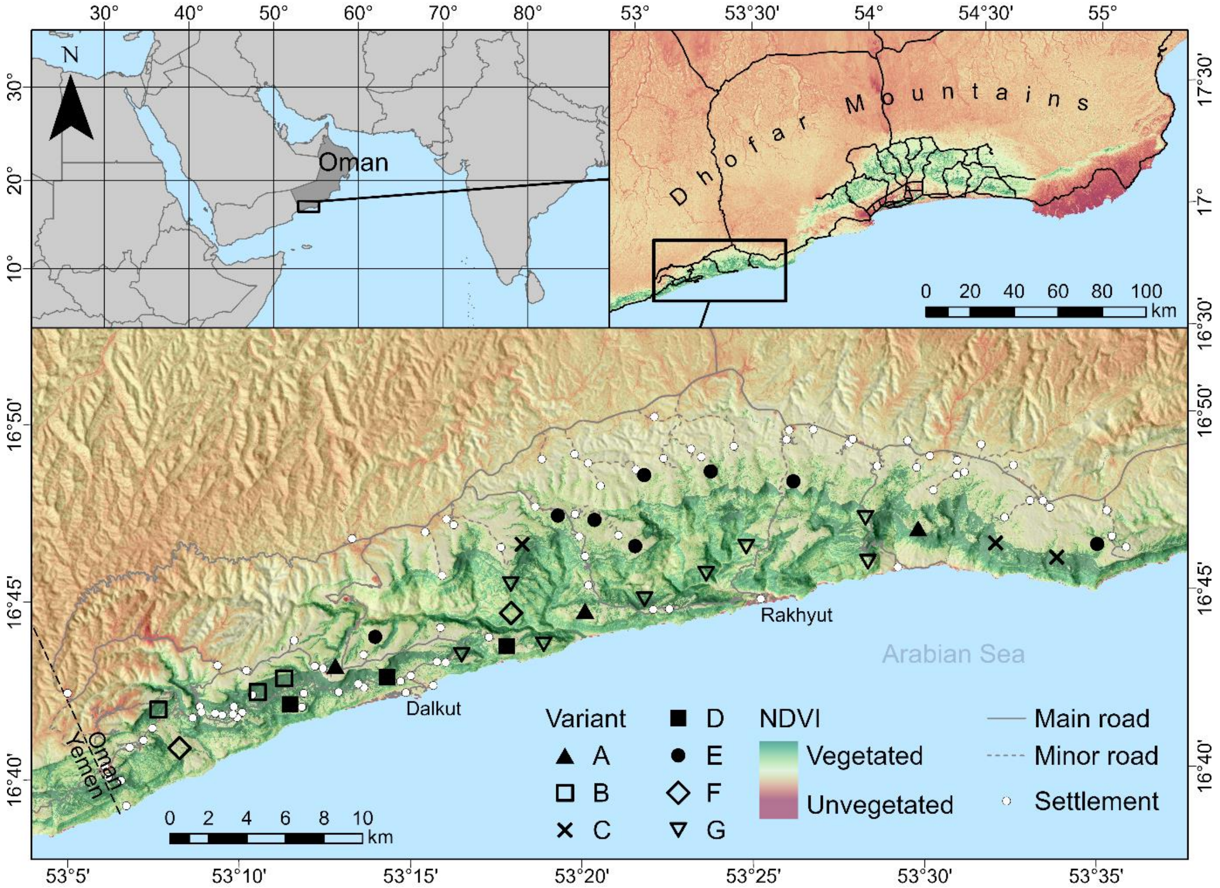

Figure 1. The locations of the thirty sampling sites in Jabal Qamar. The site symbols indicate the seven habitat variants (A-G) described in this study.

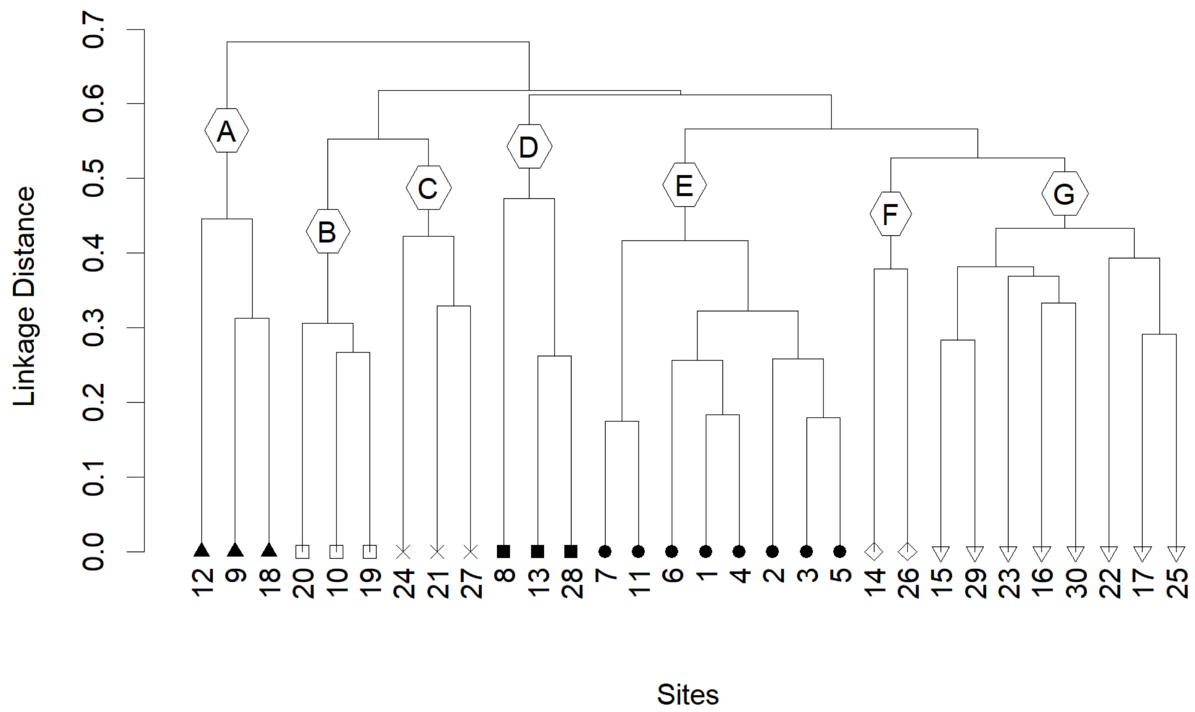

Figure 2. Dendrogram of seven clusters of thirty sites using Bray-Curtis dissimilarity indices and average linkage clustering.

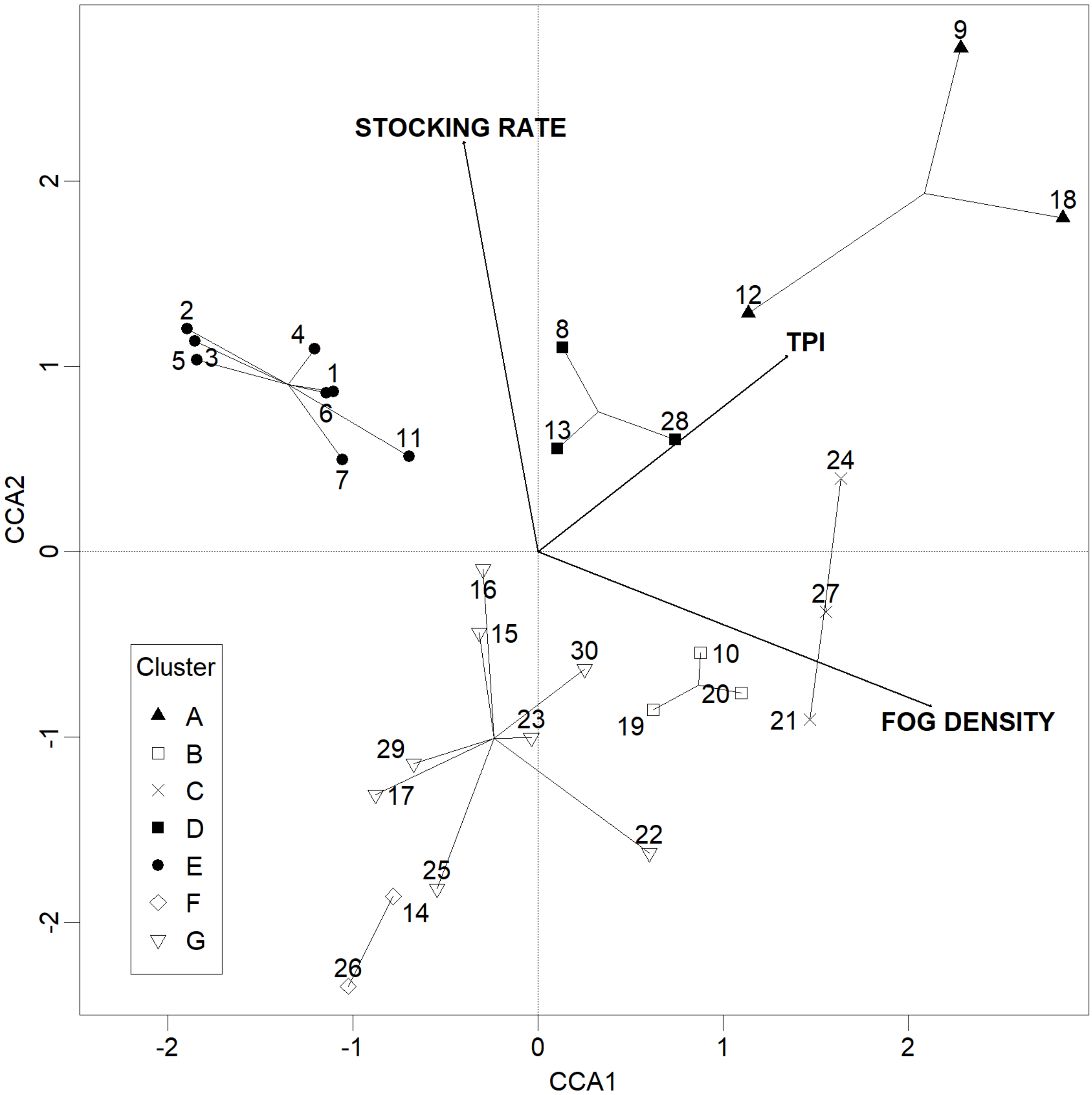

Figure 3. Constrained correspondence analysis biplot of site scores with clusters shown as spider plots. The symbols match those in the dendrogram (Figure 2) and the map (Figure 1). The environmental variables are shown as arrows, the mean value is at the origin (0,0), and the length of the arrow indicates the strength of the variable.

Table 1. Mean and standard deviation (SD) values for measured topoclimatic, vegetation and disturbance variables for each variant. Differences between variants were tested with ANOVA or Kruskal-Wallis tests. Letters signify the results of Tukey or Dunn post-hoc tests and indicate pairwise non-significant results. The last column shows overall significance: < 0.001 '***'; < 0.01 '**'; < 0.05 '*'.

Variables	***A: Dodonaea viscosa subsp. angustifolia* shrubland variant**				**B: *Cadia purpurea-Olea europaea* forest variant**				**C: *Euclea racemosa-Jasminum grandiflorum* shrubland variant**				**D: *Gymnosporia dhofarensis-Ficus sycomorus* woodland variant**				**E: *Jatropha dhofarica-Zygocarpum dhofarense* sparse woodland variant**				**F: Broad-leaved *Blepharispermum hirtum* variant (Kürschner et al., 2004)**				**G: *Premna resinosa-Hybanthus durus* forest variant**				**P**
Topoclimatic factors	N	Mean	SD	No signf.	N	Mean	SD	No signf.	N	Mean	SD	No signf.	N	Mean	SD	No signf.	N	Mean	SD	No signf.	N	Mean	SD	No signf.	N	Mean	SD	No signf.	
Elevation (m) (n/site = 60) KW-D	180	672.00	132.00		180	781.00	55.00	C	180	793.00	46.00	B	180	400.00	52.00	FG	480	823.00	53.00		120	387.00	37.00	D	600	469.00	153.00	D	***
Northness (-1-1) (n/site = 60) KW-D	180	-0.17	0.82	E	180	-0.64	0.39	CF	180	-0.55	0.40	BDF	180	-0.39	0.61	C	480	-0.25	0.64	A	120	-0.57	0.42	BC	600	-0.02	0.74		***
Eastness (-1-1) (n/site = 60) KW-D	180	-0.12	0.54	CG	180	0.58	0.32	ADF	180	-0.05	0.74	E	180	0.44	0.54	BF	480	0.06	0.72	C	120	0.51	0.49	BD	600	-0.23	0.64	A	***
Slope (°) (n/site = 60)	180	8.84	3.14	E	180	13.44	6.51		180	20.80	5.77		180	9.96	3.94	F	480	8.40	3.32	A	120	10.50	3.68	D	600	18.53	5.90		***
Fog density (arb. 0-1) (n/site = 60)	180	0.55	0.03	F	180	0.61	0.02		180	0.57	0.02		180	0.54	0.06		480	0.49	0.04		120	0.55	0.05	A	600	0.51	0.04		***
Fog variability (arb. 0-1) (n/site = 60)	180	0.27	0.02	DG	180	0.24	0.02		180	0.25	0.01		180	0.26	0.02	AG	480	0.29	0.02		120	0.25	0.02		600	0.27	0.02	AD	***
Topographic Position Index r = 5000 (-567.20-656.38) (n/site = 60) KW-D	180	188.29	32.26		180	6.04	39.51		180	150.39	61.81		180	62.96	83.52		480	87.71	73.76		120	-39.59	26.77		600	110.15	70.19		***
Terrain Ruggedness Index (0-14800.22) (n/site = 60) (log)	180	18.08	12.84	E	180	48.23	38.84		180	103.88	59.34		180	23.25	19.66	F	480	16.78	12.49	A	120	25.62	18.62	D	600	83.25	52.16		***
Compound Topographic Index (3.18-26.37) (n/site = 60) (log)	180	7.92	1.21	BDEF	180	8.12	1.40	AEF	180	7.34	1.31	G	180	7.79	1.68	AEF	480	7.93	1.28	ABDF	120	7.92	1.60	ABDE	600	7.20	1.29	C	***
Solar radiation (kWH/m2) (n/site = 30)	90	1775.87	40.35	BC	90	1790.02	34.64	AE	90	1749.71	77.35	ADF	90	1716.93	53.00	CF	240	1794.76	54.05	B	60	1732.43	35.23	CD	240	1632.58	135.38		***
Soil pH (n/site = 4)	12	8.06	0.10	BCDE	12	7.99	0.08	ACDE	12	7.90	0.20	ABE	12	8.12	0.09	ABEFG	32	8.00	0.17	ABCD	8	8.35	0.09	DG	32	8.25	0.09	DF	***
Rock cover (%) (n/site = 30)	90	7.50	15.00	BDFG	90	13.57	17.80	ACF	90	17.13	20.15	BE	90	4.96	12.75	AFG	240	20.19	19.45	C	58	6.41	15.72	ABDG	240	6.36	11.63	ADF	***
Vegetation characteristics																													
Proportion of dead adults (%) (n/site = 1)	3	12.50	3.82		3	16.94	1.27		3	9.16	5.77		3	10.28	3.36		8	10.21	3.69		2	5.42	4.12		8	8.33	5.23		.
Adult density (plants/hectare) (n/site = 30)	90	1213.79	995.49	BCEF	90	1106.62	616.86	ACEF	90	1485.46	1031.94	ABG	90	321.77	440.22		240	956.31	940.71	ABF	60	1001.60	882.67	ABE	240	1705.57	1212.84	C	***
Juvenile density (plants/hectare) (n/site = 30)	90	2058.50	2281.68	BCDEF	90	5526.79	6975.08	ACDEF	90	5609.90	6172.52	ABDEF	90	1270.96	1897.35	ABCEF	240	4968.08	6980.62	ABCDF	60	2509.89	2345.26	ABCDE	240	11231.09	19982.74		***
Adult basal area (cm2) (n/site = 120)	360	105.86	380.61	CEG	360	370.39	838.15	CDFG	360	197.93	444.93	ABEFG	360	560.08	1724.22	BF	960	178.39	338.02	ACG	240	224.91	427.12	BCDG	960	169.53	317.05	ABCEF	***
Adult height (cm) (n/site = 120)	360	235.74	126.85		360	464.87	294.89		360	374.28	214.28	DFG	360	354.80	300.13	CF	960	304.70	228.21		240	359.28	215.43	CD	960	414.06	220.00	C	***
Juvenile basal area (cm2) (n/site = 120)	360	5.62	9.61	E	360	3.56	6.83	DF	360	2.13	4.13	G	360	3.25	5.09	BF	960	4.73	9.09	A	240	4.92	8.43	BD	960	2.38	5.17	C	***
Juvenile height (cm) (n/site = 120)	360	85.39	60.43	BCF	360	77.38	75.85	ACFG	360	73.45	82.40	ABFG	360	46.11	42.78	E	960	56.96	43.01	D	240	80.31	74.63	ABCG	960	70.40	76.06	BCF	***

Disturbance/livestock factors																													
Long-term stocking rate (arb. scale 1-30) (n/site = 1)	3	19.33	7.09	BCDEF	3	19.33	5.03	ACDEF	3	8.00	2.65	ABFG	3	25.00	7.81	ABEF	8	21.63	4.53	ABDF	2	12.00	15.56	ABCDEG	8	6.63	3.62	CF	***
Distance to road (km) (n/site = 30)	90	1.86	1.33		90	2.03	0.42	CG	90	2.88	1.04	B	90	1.07	0.61		240	0.73	0.46		60	4.47	1.80		240	2.40	1.41	B	***
Distance to vehicular access (km) (n/site = 30)	90	0.32	0.30	D	90	1.55	0.88	CFG	90	1.13	0.65	BFG	90	0.53	0.55	A	240	0.68	0.47		60	3.03	2.53	BCG	240	1.67	0.98	BCF	***
Distance to house (km) (n/site = 30)	90	2.30	1.28	D	90	2.13	1.09	D	90	3.38	1.25		90	1.51	0.72	AB	240	1.09	0.63		60	5.14	1.24		240	6.04	3.77		***
Distance to camp (km) (n/site = 30)	90	1.34	1.12	CDE	90	1.82	0.88	CFG	90	1.54	0.66	ABFG	90	1.20	0.73	AE	240	0.86	0.45	AD	60	3.40	2.96	BCG	240	2.15	1.58	BCF	***
Distance to waterpoint (km) (n/site = 30)	90	1.04	0.75		90	4.51	0.82	G	90	3.15	0.83	D	90	3.16	1.07	C	240	2.78	1.64		60	1.89	1.07		240	5.50	2.79	B	***
Adult broken (avg. 1-5 classes) (n/site = 120)	360	2.43	1.21		360	2.83	1.21		360	2.13	1.06		360	2.89	1.33		960	2.97	1.36		240	2.83	1.20		960	2.36	1.05		-
Adult bent (avg. 1-5 classes) (n/site = 120)	360	1.06	0.39		360	1.33	0.90		360	1.10	0.47		360	1.53	1.10		960	1.25	0.72		240	1.19	0.66		960	1.12	0.48		-
Bark stripping (cm2) (n/site = no. of bark-stripped individuals)	22	228.86	448.68	CDFG	21	985.33	1336.44	CDEFG	3	147.33	121.99	ABDEFG	22	867.09	1211.50	ABCEFG	121	1216.39	2209.76	BCDFG	17	1415.59	4795.85	ABCDEG	16	478.00	967.71	ABCDEF	*
Adult browsing intensity (avg. 1-5 classes) (n/site = no. of palatable individuals)	144	3.83	1.54		257	3.49	1.69		300	3.43	1.69		279	4.19	1.43		610	3.78	1.60		202	3.78	1.55		890	3.76	1.69		-
Juvenile browsing intensity (avg. 1-5 classes) (n/site = no. of palatable individuals)	138	4.73	0.55		237	4.50	0.97		288	3.45	1.35		273	4.81	0.54		562	4.76	0.59		196	3.71	1.49		831	3.80	1.34		-

Table 2. Synoptic table of the proposed habitat variants. Numbers represent percentage frequencies and modified correlation indices multiplied by 100 (superscript). The correlation indices refer to the strength of the association between species and variants. Diagnostic species were selected based on the significance of the association ($p = < 0.05$) and the level of significance is indicated with asterisks in the last column: < 0.001 '***'; < 0.01 '**'; < 0.05 '*'. Only marginally significant ($p = < 0.1$) herbaceous species-variant associations are shown under companion herbs. Marginally significant ($p = < 0.1$) species-variant associations are indicated with '·'. The most significant species-variant association is highlighted in grey.

Variant (cluster)	A	A r	B	B r	C	C r	D	D r	E	E r	F	F r	G	G r		
Number of sites	3		3		3		3		8		2		8			
Mean woody species richness	15		18		25		19		16		17		20			
Mean herbaceous species richness	14		16		20		18		17		14		18			
Shannon Diversity Index	2.15		2.56		3.10		2.47		2.26		2.37		2.87			
Number of diagnostic species	1		4		3		5		7		1		10		p-value	
Cluster A: *Dodonaea viscosa* subsp. *angustifolia* shrubland variant																
Woody plants																
Dodonaea viscosa subsp. *angustifolia*	43.2	51.8	-	-12.3	6.5	-2.6	7.5	-1.1	0.1	-12.2	-	-12.3	0.6	-11.3	0.007	**
Cluster B: *Cadia purpurea-Olea europaea* forest variant																
Woody plants																
Cadia purpurea	0.6	-8.4	28.6	43.7	1.7	-6.4	0.3	-8.9	0.1	-9.4	3.3	-3.3	1.1	-7.4	0.007	**
Olea europaea subsp. *cuspidata*	0.7	-3.0	7.8	20.1	1.4	-0.7	0.4	-3.9	0.8	-2.7	-	-5.2	0.2	-4.7	0.007	**
Croton confertus	-	-6.3	9.6	19.8	0.8	-4.0	1.7	-1.7	0.4	-5.3	2.5	0.5	1.1	-3.1	0.007	**
Herbs																
Oplismenus burmanni	0.4	-10.1	19.5	28.8	6.8	4.3	3.2	0.4	-	-10.9	-	-10.9	2.7	-1.7	0.028	*
Cluster C: *Euclea racemosa-Jasminum grandiflorum* shrubland variant																
Woody plants																
Euclea racemosa subsp. *schimperi*	2.4	0.9	1.3	-2.3	10.1	23.3	0.3	-5.1	-	-5.9	-	-5.9	0.3	-5.0	0.007	**
Jasminum grandiflorum subsp. *floribundum*	3.5	5.2	2.6	2.7	5.4	11.2	0.6	-3.8	0.2	-4.8	-	-5.5	0.2	-5.0	0.048	*
Pavetta longiflora	-	-2.5	0.7	2.0	1.9	10.3	-	-2.5	0.1	-2.2	-	-2.5	-	-2.5	0.007	**
Cluster D: *Gymnosporia dhofarensis-Ficus sycomorus* woodland variant																
Woody plants																
Gymnosporia dhofarensis	3.1	-5.2	6.4	0.5	5.1	-1.6	21.8	26.9	3.2	-5.0	1.3	-8.3	1.8	-7.4	0.014	*
Ficus sycomorus	-	-1.3	-	-1.3	-	-1.3	0.7	7.7	-	-1.3	-	-1.3	-	-1.3	0.048	*
Calotropis procera	-	-1.0	-	-1.0	-	-1.0	0.4	6.0	-	-1.0	-	-1.0	-	-1.0	0.021	*
Herbs																
Moorochloa eruciformis	-	-2.2	-	-2.2	-	-2.2	0.9	10.1	0.3	-0.1	-	-2.2	0.1	-1.2	0.041	*
Blumea lacera	-	-0.8	-	-0.8	-	-0.8	0.2	4.7	-	-0.8	-	-0.8	-	-0.8	0.048	*
Cluster E: *Jatropha dhofarica-Zygocarpum dhofarense* sparse woodland variant																
Woody plants																
Jatropha dhofarica	3.8	-5.6	1.7	-8.8	1.0	-9.9	3.2	-6.4	27.9	32.3	9.2	2.9	4.5	-4.4	0.007	**
Zygocarpum dhofarense	2.5	-6.3	6.8	1.0	7.4	1.9	1.4	-8.2	15.2	15.1	1.0	-8.8	9.3	5.2	0.007	**
Adenium obesum	-	-2.7	-	-2.7	0.4	-0.1	-	-2.7	2.6	13.5	-	-2.7	-	-2.7	0.007	**
Herbs																
Arthraxon junnarensis	52.2	13.5	26.6	-2.0	17.8	-11.1	38.4	15.0	51.1	14.6	7.2	-16.8	16.3	-13.1	0.007	**
Setaria spp.	2.6	4.3	-	-5.0	-	-5.0	1.8	1.6	5.2	12.2	0.0	-4.6	0.4	-3.6	0.048	*
Dactyloctenium aegyptium	-	-1.2	-	-1.2	-	-1.2	-	-1.2	0.6	7.2	-	-1.2	-	-1.2	0.041	*
Orobanche dhofarensis	0.0	-0.4	-	-0.6	-	-0.6	-	-0.6	0.1	3.2	-	-0.6	-	-0.6	0.021	*
Cluster F: Broad-leaved *Blepharispermum hirtum* variant (Kürschner et al., 2004)																
Woody plants																
Blepharispermum hirtum	0.4	-9.9	-	-10.6	0.1	-10.3	0.6	-9.6	0.2	-10.3	34.6	47.7	8.0	3.0	0.014	*
Cluster G: *Premna resinosa-Hybanthus durus* forest variant																
Woody plants																
Premna resinosa	0.1	-2.9	-	-3.5	0.6	-0.9	0.3	-2.2	0.3	-2.0	0.4	-1.5	3.5	13.1	0.007	**

Hybanthus durus	-	-7.8	5.6	4.4	3.6	0.1	-	-7.8	3.6	0.1	3.1	-0.9	9.0	11.9	0.021	*
Euphorbia smithii	5.8	3.4	4.7	1.2	5.4	2.6	1.3	-5.9	1.6	-5.2	2.3	-3.8	7.9	7.7	0.021	*
Senegalia senegal	0.6	-7.0	3.8	-0.3	4.3	0.9	3.1	-1.7	0.5	-7.1	8.1	9.0	6.8	6.2	0.048	*
Herbs																
Launaea crassifolia	0.1	-3.5	0.2	-2.7	0.1	-3.5	-	-3.9	-	-3.9	0.4	-0.9	4.4	18.3	0.007	**
Rungia pectinata	4.3	-3.8	11.9	13.6	5.6	1.4	1.0	-8.0	0.6	-9.8	0.9	-5.7	11.3	12.3	0.021	*
Lepidagathis calycina	-	-2.3	-	-2.3	-	-2.3	-	-2.3	-	-2.3	0.1	-0.7	1.4	12.0	0.028	*
Megalochlamys violacea	-	-2.2	0.2	-0.6	-	-2.2	-	-2.2	-	-2.2	-	-2.2	1.2	11.6	0.007	**
Barleria hochstetteri	-	-1.1	-	-1.1	-	-1.1	-	-1.1	-	-1.1	-	-1.1	0.4	6.9	0.007	**
Ruttya fruticosa	-	-1.6	0.2	1.3	0.1	-0.3	-	-1.6	0.0	-1.3	-	-1.6	0.4	5.2	0.048	*
Companion woody plants																
Acridocarpus sp. nov.	-	-0.4	-	-0.4	-	-0.4	-	-0.4	-	-0.4	-	-0.4	0.1	2.1	0.903	
Allophylus rubifolius	1.1	-6.3	3.6	-1.1	2.5	-3.4	8.6	9.1	2.2	-3.9	4.4	0.4	6.8	5.3	0.126	
Azima tetracantha	-	-0.8	-	-0.8	0.3	4.9	-	-0.8	-	-0.8	-	-0.8	-	-0.8	0.055	·
Blepharis dhofarensis	-	-4.7	0.8	-1.6	5.4	15.0	-	-4.7	-	-4.7	-	-4.7	2.8	5.3	0.463	
Boscia arabica	-	-2.1	-	-2.1	-	-2.1	-	-2.1	-	-2.1	1.3	8.1	0.5	2.2	0.463	
Delonix elata	-	-1.6	-	-1.6	-	-1.6	-	-1.6	-	-1.6	0.4	2.7	0.7	5.4	0.081	·
Denisophytum eriantherum	-	-0.6	-	-0.6	-	-0.6	-	-0.6	-	-0.6	-	-0.6	0.2	3.7	0.871	
Carissa spinarum	0.6	1.7	-	-2.3	0.8	3.7	0.1	-1.3	0.6	1.8	-	-2.3	0.2	-1.2	0.690	
Commiphora gileadensis	3.5	-1.6	1.4	-5.8	6.5	4.6	5.7	2.9	3.9	-0.7	1.9	-4.8	6.9	5.4	0.276	
Commiphora kua	13.9	3.8	3.5	-9.8	11.0	0.0	10.0	-1.3	16.0	6.6	9.8	-1.6	12.8	2.4	0.446	
Cordia monoica	-	-1.3	-	-1.3	0.1	0.4	0.3	2.2	0.1	0.0	-	-1.3	0.2	1.3	0.823	
Cordia perrottetii	-	-0.5	-	-0.5	-	-0.5	-	-0.5	0.1	1.2	-	-0.5	0.1	1.2	0.987	
Ehretia obtusifolia	-	-0.8	-	-0.8	-	-0.8	-	-0.8	-	-0.8	-	-0.8	0.3	4.7	0.897	
Ficus vasta	-	-2.5	0.6	1.1	1.5	7.5	0.4	0.2	0.2	-1.5	-	-2.5	0.1	-2.2	0.055	·
Flueggea virosa	0.1	-2.6	0.4	-1.2	0.1	-2.6	2.8	10.9	0.1	-3.0	-	-3.3	1.0	1.8	0.132	
Grewia bicolor	0.3	1.0	-	-1.7	0.4	2.4	-	-1.7	0.3	0.9	-	-1.7	0.3	0.9	0.826	
Grewia villosa	-	-0.6	-	-0.6	0.1	3.5	-	-0.6	-	-0.6	-	-0.6	-	-0.6	0.536	
Gomphocarpus fruticosus subsp. *setosus*	0.4	1.5	-	-2.0	1.3	8.5	-	-2.0	-	-2.0	-	-2.0	-	-2.0	0.061	·
Hildebrandtia africana subsp. *arabica*	-	-0.5	-	-0.5	-	-0.5	-	-0.5	0.1	1.2	-	-0.5	0.1	1.2	0.983	
Lawsonia inermis	-	-0.9	0.1	1.7	0.1	1.7	-	-0.9	0.1	0.1	-	-0.9	-	-0.9	0.908	
Rhamnus staddo	-	-0.6	-	-0.6	0.1	3.5	-	-0.6	-	-0.6	-	-0.6	-	-0.6	0.568	
Searsia flexicaulis	-	-0.8	-	-0.8	0.1	1.9	-	-0.8	0.1	0.2	-	-0.8	0.1	1.2	0.925	
Searsia somalensis	2.1	9.3	-	-2.9	1.3	4.4	-	-2.9	0.1	-2.6	-	-2.9	0.1	-2.6	0.088	·
Solanum incanum	8.5	3.3	5.7	-1.3	5.8	-1.1	11.8	8.8	6.0	-0.8	4.8	-2.8	2.8	-6.1	0.132	
Tamarindus indica	-	-2.1	-	-2.1	1.0	5.5	0.1	-1.0	-	-2.1	0.6	2.8	0.2	-0.9	0.571	
Terminalia dhofarica	2.5	-8.6	4.4	-5.8	4.0	-6.4	16.5	12.1	12.9	6.7	9.2	1.2	8.9	0.8	0.204	
Vachellia gerrardii	-	-2.9	-	-2.9	-	-2.9	-	-2.9	1.0	3.1	1.5	5.6	1.0	2.8	0.738	
Woodfordia uniflora	0.6	1.0	-	-2.6	1.5	7.3	0.3	-0.8	-	-2.6	0.4	0.1	-	-2.6	0.061	·
Companion herbs																
Apluda mutica	29.9	2.5	6.6	-13.4	15.1	-2.2	6.6	-10.3	26.7	3.3	35.8	20.3	18.9	-0.3	0.075	·
Arundinella pumila	1.1	-7.2	5.1	3.4	8.8	13.0	1.1	-4.6	1.5	-5.6	0.7	-4.7	5.4	5.7	0.061	·
Blumea axillaris	1.1	3.2	0.2	-2.0	0.1	-2.8	2.1	11.7	-	-3.4	-	-3.4	-	-3.4	0.081	·
Dichanthium annulatum	2.4	4.6	-	-4.3	3.7	14.4	0.3	-2.6	0.1	-3.6	-	-4.3	-	-4.3	0.055	·
Dyschoriste dalyi	-	-1.0	-	-1.0	-	-1.0	-	-1.0	0.3	5.9	-	-1.0	-	-1.0	0.088	·
Enteropogon dolichostachyus	-	-2.3	0.7	4.5	1.0	6.9	-	-2.3	-	-2.3	-	-2.3	-	-2.3	0.094	·
Ruellia discifolia	-	-3.0	0.2	-1.8	-	-3.0	-	-3.0	-	-3.0	0.1	-2.6	2.2	16.2	0.061	·

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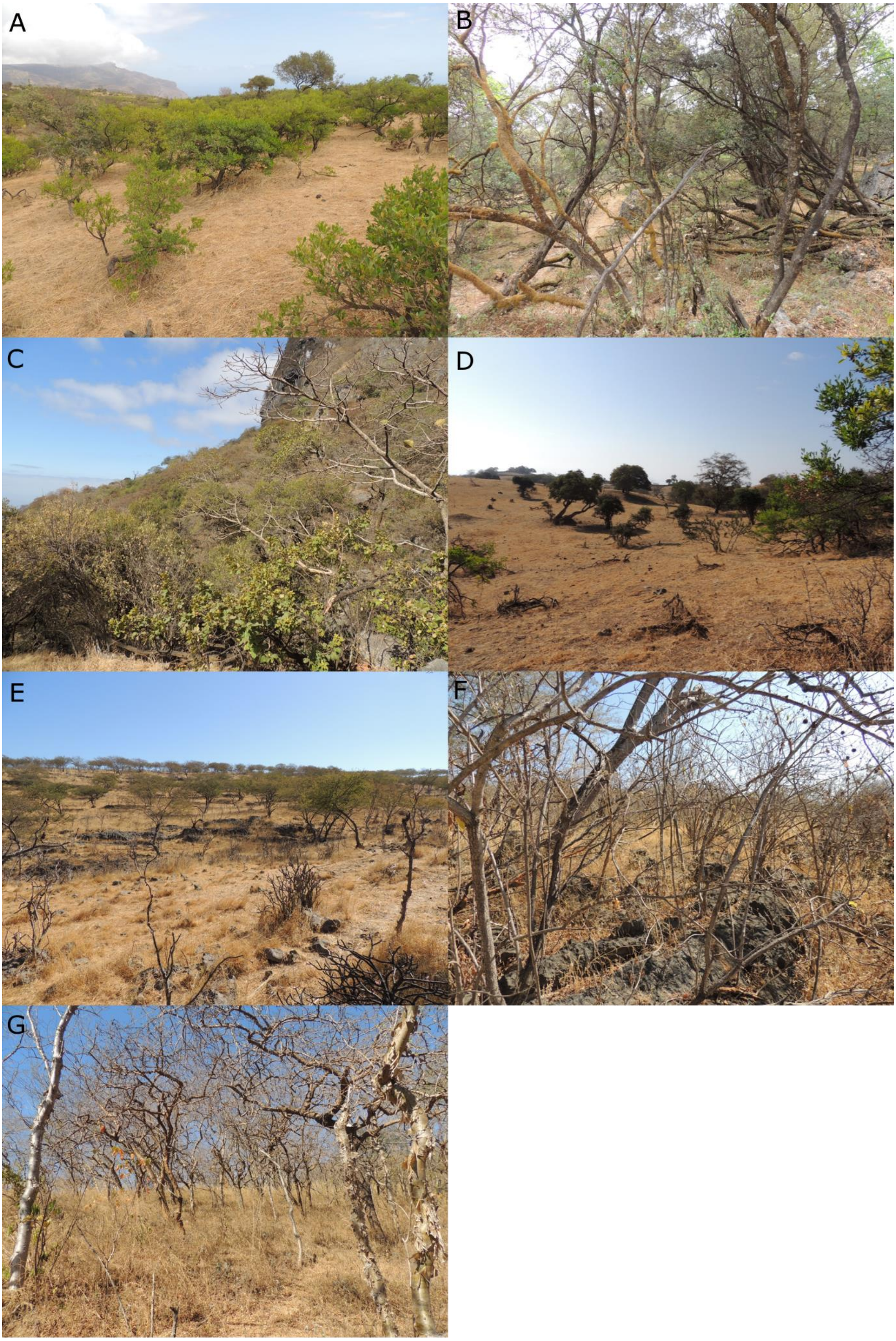

Figure 4. Photographs of the seven variants described in this study. A: *Dodonaea viscosa*

subsp. *angustifolia* shrubland variant, B: *Cadia purpurea-Olea europaea* forest variant, C: *Euclea racemosa-Jasminum grandiflorum* shrubland variant, D: *Gymnosporia dhofarensis-Ficus sycomorus* sparse woodland variant, E: *Jatropha dhofarica-Zygocarpum dhofarense* sparse woodland variant, F: Broad-leaved *Blepharispermum hirtum* variant, G: *Premna resinosa-Hybanthus durus* forest variant