1 **Islands in the desert: Environmental distribution modelling**

2 **of endemic flora reveals the extent of Pleistocene tropical**

3 **relict vegetation in southern Arabia**

4

5 James S. Borrell[1*], Ghudaina Al Issaey[2], Darach A. Lupton[2], Thomas Starnes[3], Abdulrahman

6 Al Hinai[2], Saif Al Hatmi[2], Rebecca A. Senior[4], Tim Wilkinson[1], Jo L.H. Milborrow[5], Andrew

7 Stokes-Rees[6], Annette Patzelt[2].

8

9 [1]Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS, UK. [2]Oman

10 Botanic Garden, Muscat, Oman. [3]RSPB Centre for Conservation Science, Royal Society for

11 the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK. [4]Department of

12 Animal and Plant Sciences, Alfred Denny Building, University of Sheffield, Western Bank,

13 Sheffield, S10 2TN. [5]Biodiversity Information Service, Unit 4, Royal Buildings, 6 Bulwark,

14 Brecon, Powys, LD3 7LB. [6]Outward Bound Canada, 550 Bayview ave., Building 1 suite 201,

15 Toronto, ON, M4W 3X8

16 **Running title**: A pleistocene refugium in southern Arabia

17 ***Author for correspondence:** Dr. James Borrell (j.borrell@kew.org)

18

19

20

21

ABSTRACT

Background and Aims: Southern Arabia is a global biodiversity hotspot with a high proportion of endemic desert-adapted plants. Here we examine evidence for a Pleistocene climate refugium in the southern Central Desert of Oman, and its role in driving biogeographical patterns of endemism.

Methods: Distribution data for seven narrow-range endemic plants were collected systematically across 195 quadrats, together with incidental and historic records. Important environmental variables relevant to arid coastal areas, including night time fog and cloud cover were developed for the study area. Environmental niche models were built and tuned for each species and spatial overlap examined.

Key Results: A region of the Jiddat Al Arkad reported independent high model suitability for all species. Examination of environmental data across southern Oman indicates that the Jiddat Al Arkad displays a regionally unique climate with higher intra-annual stability, due in part to the influence of the southern monsoon. Despite this, relative importance of environmental variables was highly differentiated among species, suggesting characteristic variables such as coastal fog are not major cross-species predictors at this scale.

Conclusions: The co-occurrence of a high number of endemic study species within a narrow monsoon-influenced region is indicative of a refugium with low climate change velocity. Combined with climate analysis, our findings provide strong evidence for a southern Arabian Pleistocene refugium in the Oman's Central Desert. We suggest this refugium has acted as an isolated temperate and mesic island in the desert, resulting in the evolution of these narrow-range endemic flora. Based on the composition of species, this system may represent the northernmost remnant of a continuous belt of mesic vegetation formerly ranging from Africa

2

45   to Asia, with close links to the flora of East Africa. This has significant implications for future

46   conservation of endemic plants in an arid biodiversity hotspot.

47

48   **KEYWORDS**

49   Arabian Peninsula, Central Desert, Coastal fog desert, Desert endemic, Ecological niche

50   modelling, Important Plant Areas, Oman, Pleistocene, Refugia.

51

52   **INTRODUCTION**

53   Southern Arabia is part of the Horn of Africa global biodiversity hotspot, and is one of only

54   two hotspots that are entirely arid (Mittermeier *et al.* 2005; Mallon 2013). The flora of southern

55   Arabia arises from the relatively late separation of Arabia from Africa and Asia around 25

56   million years before present (Raven and Axelrod 1974; Delany 1989). During the Miocene

57   Arabia supported palaeo-tropical vegetation with swamps and open savannah grassland

58   (Whybrow and Mcclure 1981). This was progressively replaced by more drought-adapted

59   vegetation through the Pliocene, with mesic elements of the flora persisting only in climatically

60   favourable refugia (Kürschner 1998; Jolly *et al.* 2009). The environment of southern Arabia

61   subsequently oscillated between climatic extremes throughout the Quaternary period

62   (Fleitmann and Matter 2009; Parker 2010; Jennings *et al.* 2015). These oscillations, combined

63   with the relative stability of localized climatic refugia may have contributed to the high degree

64   of species endemism (Patzelt, 2015; Sandel et al., 2011).

65   The biogeographic consequences of contraction and expansion from glacial refugia have been

66   well described in the temperate zones of Europe and North America (Bennett *et al.* 1991;

67   Comes and Kadereit 1998; Birks and Willis 2008; Keppel *et al.* 2012; Wang *et al.* 2014). By

68   comparison, these processes are poorly known in the arid environments of the Arabian

69   Peninsula (Ghazanfar, 1998; Meister, Hubaishan, Kilian, & Oberprieler, 2006; Patzelt, 2015).

70   Therefore establishing the spatiotemporal distribution of past climate refugia in southern

71   Arabia is likely to have important implications for future conservation planning (Al-Abbasi *et*

72   *al.* 2010), building evolutionary resilience under climate change (Sgrò *et al.* 2011; Keppel *et*

73   *al.* 2012) and even interpreting the history of hominid dispersal out of Africa (Jennings *et al.*

74   2015; Gandini *et al.* 2016).

75   A key center for plant endemism in southern Arabia is Oman's Central Desert (Ghazanfar,

76   2004; Miller & Nyberg, 1990; Patzelt, 2014; White & Léonard, 1990). The Central Desert is a

77   hyper-arid region, characterized by scarce precipitation often less than 100 mm/pa with high

78   inter-annual variability and temperatures ranging from 6°C to more than 50°C (Stanley Price

79   *et al.* 1988; Fisher and Membery 1998; Almazroui *et al.* 2013). Provisionally divided into

80   'northern' and 'southern' systems, the Central Desert has relatively low species diversity, but

81   the highest proportion of range restricted endemic and regionally endemic plants in Oman

82   (Patzelt, 2015). This represents an ideal study system in which to test for evidence of climatic

83   refugia and their influence on the floral biogeography of southern Arabia.

84   Despite significant progress in documenting the flora of Oman (Brinkmann et al., 2011;

85   Ghazanfar, 1998, 2004; Ghazanfar & Fisher, 2013; Miller & Cope, 1996; Patzelt, 2009, 2014)

86   high resolution plant diversity and distribution data are limited or lacking for many areas,

87   hindering our ability to test these biogeographic hypotheses and identify putative refugia. To

88   address this knowledge gap, here we report results of a systematic botanic survey of the

89   southern Central Desert. We focus on seven high priority narrow range endemic desert plants

90   (Table 1; Figure 1), restricted to the coastal belt and the adjacent escarpment and identified

91   through development of the Oman Red Data Book (Patzelt, 2014).

92   To enable a transition from survey data to predictive distribution maps we use an environmental

93   niche modelling (ENM) approach. ENMs are a suite of methods used to establish the

4

94   relationship between a species and a set of environmental variables (Elith and Leathwick, 2009;

95   Peterson, Papeş and Soberón, 2015). In principle, ENMs evaluate the environmental conditions

96   in grid cells known to be occupied by a species and identify additional cells that represent

97   similar environmental conditions (Merow, Smith and Silander, 2013). The species' niche can

98   then be projected across the study area to predict its spatial distribution and identify

99   environmental variables that contribute significantly to model performance (Searcy and Shaffer

100   2016). In this study we benefit from both presence and absence survey data and a stratified

101   survey design, which negates many of the biases common in environmental niche models

102   (Jiménez-Valverde *et al.* 2008; Warren and Seifert 2011).

103   To distinguish amongst alternative environmental drivers for local endemism, selection of

104   appropriate environmental modelling variables in arid environments is important (Dilts *et al.*

105   2015; Title and Bemmels 2018). In other coastal desert systems, endemic plant distributions

106   are strongly influenced by the presence of cloud shade and fog, which causes condensation on

107   leaves and stems that trickles down to root systems (Cereceda *et al.* 2008; Fischer *et al.* 2009).

108   Given the extreme temperatures and low precipitation, the presence of coastal fog and the

109   cooling effect of the prevailing wind have been hypothesised to be a key driver of Central

110   Desert flora distributions (Miller, 1994; Patzelt, 2015; Price et al., 1988). The presence of

111   coastal fog is supported by data from the northern Central Desert in 1984, where water collected

112   from fog collectors at Jiddat al Harasisi ranged from 0.08 L/m^2 in January to 3.6 L/m^2. A total

113   of 93 nights with fog moisture were recorded across the year, with fog moisture at ground level

114   coinciding with reduced night-time temperatures, increased humidity and a wind speed less

115   than 15 Km/h (Price et al., 1988). In a subsequent study (Fisher and Membery 1998) a monthly

116   maximum of 4.0 L/m^2 during March and a minimum 2.5 L/m^2 during January, May, June and

117   December was recorded. To our knowledge, no empirical data is available on coastal fog from

118   the southern central desert.

119   Validation of environmental variables across a large, arid and sparsely populated study area

120   such as the Central Desert is also exacerbated by the paucity of weather stations (meaning that

121   global climate models are highly interpolated) and the fact that where weather stations do exist,

122   cloud cover and coastal fog are rarely recorded. To address these shortfalls, we make use of

123   the newly available WorldClim2 dataset that incorporates high accuracy remotely sensed

124   maximum and minimum land surface temperature (Fick and Hijmans 2017), together with

125   remotely sensed cloud cover data (Wilson and Jetz 2016). We also incorporate remotely sensed

126   fog and putative fog covariates, to explore whether these variables contribute significantly to

127   Central Desert species distributions. Specifically, we derive night time fog intensity from

128   MODIS data (MODIS Characterization Support Team (MCST) 2018) using the approach of

129   Chaurasia et al. (2011), as well as topography (including elevation, slope, aspect and terrain

130   roughness, as locally higher areas may catch more moisture (Schemenauer *et al.* 1987)), wind

131   speed and night time land surface temperature (LST) (Wan, Hook, & Hulley, 2018). As an

132   additional line of evidence in assessing the importance of coastal fog, we also survey

133   physiological fog capture adaptations across our study species using the approach of Larraín-

134   Barrios *et al.* (2018).

135   Here, building on novel systematic survey data from the Central Desert, we aim to address

136   three main questions. First, we use newly available climate data to examine the influence of

137   the southern monsoon and coastal fog influx on the Central Desert climate. Second, we model

138   the distributions of seven high priority narrow-range endemics, and test the hypothesis that the

139   same environmental variables are consistently important across taxa. Third, we consider

140   evidence for past climatic refugia and their influence on the current floral biogeography of the

141   Central Desert. We consider these data in the context of conserving rare desert endemics across

142   southern Arabia, a global biodiversity hotspot.

143   **MATERIALS AND METHODS**

144 **Study area**

145 The southern Central Desert is dominated by the Jiddat Al Arkad, a meandering escarpment of

146 50 to 100 m dissected by extensive wadi systems, depressions and runnels which discharge

147 into the Sahil Al Jazir coastal plain. Surface flows are only present following heavy rains.

148 Geologically, the study area is dominated by Oligocene – Miocene white bioclastic limestone

149 with coral debris flow deposits and laminated dolomitic limestone (Patel 1992). Soil is

150 predominantly Calciorthids – gravelly sandy loam on alluvial fans and stream terraces and

151 torriorthents (rock outcrops) weakly or undeveloped, low in organic matter and moderately

152 calcareous (Dregne 1976).

153 The vegetation is classified into three units as per Patzelt, (2015): i) *Acacia tortilis – Prosopis*

154 *cineraria* open woodland. Common grass and shrub species include the endemic shrubs,

155 *Convolvulus oppositifolius* and *Ochradenus harsusiticus* and endemic grass *Stipagrostis*

156 *sokotrana.* ii) Xeromorphic dwarf shrubland intermixed with grasses and annual species. The

157 dwarf palm *Nannorrhops ritchieana* and *A. ehrenbergiana* are common in sandy depressions

158 close to the coastal escarpments. iii) Xeromorphic dwarf shrubland with *Searsia gallagheri* and

159 *O. harsusiticus*. In addition to flowering plants, several species of corticolous and saxicolous

160 lichens and epilithic cyanobacteria occur here, of which most are restricted to the putatively

161 fog-affected zones (Ghazanfar & Gallagher, 1998). The seven study species (Figure 1) are

162 considered a part of, though not restricted to, the xeromorphic dwarf shrubland community. A

163 description of their known habitat and conservation status is provided in Table 1.

164 **Field surveys and plant morphology**

165 Fieldwork was conducted during the period 13th – 24rd January 2017, from Ras Madrakah,

166 across the Sahil Al Jazer (coastal plain) to the southern extent of the Jiddat Al Arkad, as part

167 of the Central Desert Botanic Expedition 2017. A stratified survey strategy was designed

168 orientating ten 20 km transects at 315 degrees (NW) along a 270 km portion of coastline, at 30

169 km intervals. This approach was designed to cross multiple environmental gradients that

170 frequently run perpendicular to the coastline. Stratified quadrat locations at 1 km intervals were

171 plotted prior to field work and their coordinates uploaded to handheld GPS units (Garmin,

172 Oregon). Due to the remote nature of the study area, with several deep wadis bisecting these

173 transects and inhibiting access, some portions of these transects were not surveyed. When

174 moving between transects we opportunistically sampled additional quadrats at 5 km intervals

175 and recorded incidental observations of target species to maximise data collection. These

176 additional quadrats were positioned via random number generation to determine distance and

177 bearing from the vehicle. A significant portion of travel was away from roads, but where roads

178 (mostly gravel tracks) were present, quadrat positioning began > 100 m from the road to

179 mitigate disturbance bias in the vegetation recorded.

180 The following data were recorded for each quadrat: location, soil texture, soil pH, soil electrical

181 conductivity (EC) (following the method of Zhang *et al.* 2005), total vegetation cover,

182 maximum vegetation height, elevation, topography description and the presence, absence and

183 count of the seven study species. Voucher specimens were collected for subsequent analysis,

184 and are deposited in the Oman Botanic Garden herbarium (OBG) (Table 1). Summary statistics

185 of quadrats were calculated in in R software V3.1.2, implemented in RStudio (R Development

186 Core Team, 2014; RStudio Team, 2015). A checklist of fog moisture capture and water use

187 efficiency functional traits commonly observed in xerophytic plants was also collated,

188 following the approach of (Larraín-Barrios *et al.* 2018). Each study species was examined and

189 scored for their presence/absence and degree of development (see Tables S1 and S2,

190 Supporting Information). In addition to observations recorded during this field study, historical

191 records were included from relevant national and international collections, specifically; Oman

192 Botanic Garden Herbarium (OBG), Sultan Qaboos University (SQUH), the Oman Natural

8

193   History Museum National Herbarium (ON) and the Royal Botanic Garden Edinburgh (E)

194   (Summarised in Table 2; Figure S1, Supporting Information).

Preparation of environmental variables

196   To ensure we captured important environmental variation, we collated 54 bioclimatic variables

197   covering the study area at 1 km resolution (Table S3, Supporting Information). In addition to

198   WorldClim2 and Bioclim variables (Fick and Hijmans 2017), we generated a complementary

199   set of bioclimatic layers that may better characterise arid environments using the 'ENVIREM'

200   package (Title and Bemmels 2018). We also sought to include night time fog, an important

201   candidate variable in determining plant distributions in this region (Price et al. 1988).

202   Specifically we followed the approach of Chaurasia *et al.* (2011) and classified fog based on

203   the brightness temperature difference (ΔBT) of the 3.9 and 10.75 µm bands (channels 22 and

204   31) of the MODIS satellite. The emissive properties of these two bands differ for fog water

205   droplets which are typically small, and do not excite the 3.9 µm band, whereas emissivity for

206   both cloud and fog droplets is approximately the same for the 10.75 µm band (Hunt 1973).

207   Twice nightly images at 1 km resolution were collated for the period 2001-17 (MODIS product:

208   MOD021KM) from the LAADS database (MCST, 2018). Raw radiance values were converted

209   to brightness temperature using Planck's function implemented in ENVI software (Harris

210   Geospatial) and the difference calculated. In contrast to Chaurasia *et al.* (2011), high quality

211   real-time ground truth data is not available for our region, therefore we did not apply a fog

212   classification threshold, instead we retained the data as a continuous variable with higher (less

213   negative) values considered more likely to represent smaller fog water droplets.

214   At a fine spatial scale, other variables may also interact with fog moisture and influence the

215   local ecology (Rastogi *et al.* 2016; Chung *et al.* 2017), thus we also incorporated several

216   relevant fog proxies or co-variates. Cloud cover data (period 2001-15) was extracted from the

217   global high-resolution cloud cover dataset generated by Wilson & Jetz (2016). Roughness,

9

218   Terrain Ruggedness Index (TRI), slope and aspect were generated from a digital elevation

219   model (GTOPO30) using the R package 'Raster' (Hijmans, 2017). Night time Land Surface

220   Temperature (LST) was obtained from the MODIS satellite mission at 1 km resolution (Wan

221   et al., 2018). Important climate variables are plotted, together with the study, area using the

222   package 'RasterVis' (Lamigueiro, 2018).

223   To compare and characterize the range of environmental conditions across the Central Desert

224   and other regional centres of endemism we randomly sampled all environmental variables for

225   *n* cells in each region (with *n* being proportional to the area of the sampled polygon) and

226   performed principal components analysis (PCA). We report variable loadings of the first and

227   second principal components in Figure S2 (Supporting Information). To provide an additional

228   line of evidence for local climatic stability, we compared interpolated Worldclim data (mean

229   for 1970-2000) to more recent independent meteorological records from four contemporary

230   weather stations (data period 1999-2017) in the central desert. Additional mapping and data

231   visualization was performed using 'ggplot2' (Wickham 2009) and 'rgeos' (Bivand *et al.* 2018).

232   **Environmental niche modelling**

233   The suite of environmental layers retained for modelling was refined in three stages. First,

234   layers that had low variability at the spatial scale of our study area were removed (e.g. soil).

235   Second, correlated environmental variables across the study area (r > |0.7|) were grouped, with

236   a single variable from each group considered to be most relevant to arid environment plant

237   ecology retained. Third, we performed an iterative selection procedure by removing variables

238   with the highest Variance Inflation Factor (VIF) using the package 'usdm' (Naimi *et al.* 2014),

239   with an upper threshold of VIF ≤ 2.5. Retained environmental variables are reported in Table

240   S3 (Supporting Information).

241 Environmental niche modelling was performed with MAXENT v3.3.3 (Phillips et al., 2006),

242 implemented in the packages 'Dismo' (Hijmans et al., 2011) and 'ENMeval' (Muscarella *et al.*

243 2014). To minimise model over-fitting, species data (including historic and incidental

244 observations) were geographically rarefied to a 3 km bin size and examined across

245 environmental space. Models were individually run and tuned for each study species over a

246 study area encompassing the southern system, with quadrat surveys providing both presence

247 and true absence data. Due to low sample sizes, data were partitioned using a jackknife

248 approach where the number of model runs is equal to the number of occurrence localities, with

249 a single data point excluded from each run for testing. Runs were performed iteratively across

250 the full range of feature classes, with regularization multiplier values increasing from 1 to 4 in

251 0.5 increments.

252 Models were evaluated based on Akaike's Information Criterion corrected for small sample

253 sizes (i.e. (ΔAICc = 0), which penalises models that employ a greater number of parameters to

254 describe the data (Warren and Seifert 2011; Muscarella *et al.* 2014). We report AUC_{TEST}

255 averaged over all iterations, with higher values reflecting better model discrimination of

256 presence locations from background absences. To quantify model overfitting we use two

257 metrics. First, we report the mean difference in AUC between training and test data (AUC_{DIFF});

258 this is expected to be higher where models are overfit to training data (Muscarella *et al.* 2014).

259 Second, we report the proportion of testing localities with predicted habitat suitability values

260 lower than the training locality with the lowest reported value (OR_{MTP}). For each species, the

261 best performing model was projected across the study area and a Maximum Training

262 Sensitivity Plus Specificity (MaSS) logistic threshold, which balances the trade-off between

263 omission and commission errors (Lobo *et al.* 2008; Liu *et al.* 2016), was employed to estimate

264 habitat area. For two species (OH, SG) where model evaluation indicated evidence of weak

265 overfitting, we used a Minimum Training Presence (MTP) threshold to ensure that all training

266 observations are included within the predicted suitable habitat area.

267 In an effort to understand the abiotic drivers of the resulting distributions, several studies have

268 shown that ranking variable contributions successfully captures biologically important factors

269 (Kearney and Porter 2009; Searcy and Shaffer 2016). To assess relative variable importance

270 across species we compare ranked permutation importance using Kendall's W, corrected for

271 ties, implemented in the package 'irr' (Gamer *et al.* 2012). Secondly, we use linear regression

272 to assess the relationship between the contribution of mean annual fog to model performance,

273 and the species' trait score (see Tables S1-2, Supporting Information). Finally we calculated

274 niche overlap across study species using the method of Warren, Glor and Turelli, (2008) and

275 then combined thresholded species distribution classifications to identify areas of spatial

276 overlap and co-occurrence of multiple species. RBG images were obtained from Sentinel 2

277 (Copernicus Sentinel data 2015, processed by ESA, accessed from https://remotepixel.ca/ on

278 20/12/2018) and plotted with increased contrast. Surface wind direction data, averaged for the

279 months June to August (2015-17), was obtained from the Global Forecasting System, via the

280 package 'rWind' (Fernández-López 2018).

281

282 **RESULTS**

283 Evaluation of regional climate identifies a weak influence of the southern monsoon system on

284 the Jiddat Al Arkad of the southern system (Figure 2). Concurrently, increased summer fog

285 incidence in the southern Central Desert coincides with the warmest temperatures of the

286 summer months, which appears to result in cooler coastal night time temperatures. Principal

287 component analysis of abiotic variables clearly differentiated the major regions of endemism

288 (Figure 3). Overall temperature related variables were the major contributors to PC1, with

289   precipitation differentiating PC2 (Figure S2, Supporting Information). The two Central Desert

290   systems are found to be differentiated, but partially overlapping with 88.5% and 62% of points

291   representing a unique climate variables for the northern and southern systems respectively.

292   Fieldwork surveys assessed 195 quadrats throughout the Southern System and successfully

293   located all seven regional endemics. Study species were recorded in 41% of quadrats. In

294   addition, 288 incidental and 68 historical observations were collated. After spatial filtering,

295   177 records were retained (Table 2; Figure S1, Supporting Information). Mean pH and EC

296   across all quadrats was 7.73 (SD = 0.44) and 14.99 (SD = 27.13) respectively. No significant

297   difference in pH or EC values was identified across species (ANOVA p > 0.05). In our

298   assessment of fog and drought functional trait adaptation, *P. pulvinata* scored highest, and *S.*

299   *gallagheri* scored lowest, with low stature, low leaf area and hairs the most frequent

300   adaptations.

Environmental niche modelling and variable importance

302   After filtering, we retained nine environmental variables for modelling (Table S3, Supporting

303   Information). Ecological niche model evaluation statistics are reported in Table 2. Modelling

304   was not performed for *P. jazirensis* due to insufficient data. AUC_{TEST} ranged from 0.76 (PP)

305   to 0.93 (SG). AUC values are often lower for more widespread species, which may be the case

306   for *P. pulvinata* and *O. Harsusiticus* (Jiménez-Valverde *et al.* 2008). Model logistic habitat

307   suitability projections are plotted in Figure 4, with the percentage contribution of variables

308   reported in Table 3. Binary threshold maps are provided in Figure S3 (Supporting Information).

309   The most important variables varied substantially, with no evidence of consistent rank

310   importance across species (*Wt* = 0.079, p = 0.87). Annual mean fog did not appear to rank

311   highly for any species, and was not significantly associated with fog adaptation trait scores ($F_{1,4}$

312   = 0.76, p = 0.4). Niche overlap was high in all pairwise comparisons (median = 0.87; Table S4,

313   Supplementary Information).

13

314 **Identification of climate refugia**

315 Combined binary species distributions identified a key area where all study species are

316 predicted to co-occur (Figure 5A). High predicted habitat suitability across all models was

317 localized to the southern Jiddat al Arkad. Satellite imagery shows the region, seasonal cloud

318 cover and the prevailing summer wind direction in Figure 5B. Independent contemporary

319 weather station records provide an additional line of evidence. Whilst the three northern

320 stations show elevated maximum daily temperatures (period 2002-17) compared to the

321 Worldclim 2 reference (1970-2000), Shalim station – close to our putative coastal fog and cloud

322 affected area – shows summer maximum temperatures below the Worldclim 2 reference

323 (Figure 6).

324

325 **DISCUSSION**

326 In this study we present evidence for a Southern Arabian Pleistocene refugium in Oman's

327 Central Desert (Figures 2, 5). As shown by Sandel et al. (2011), the negative relationship

328 between endemism and the increasing velocity of changing climate is strongest in poorly

329 dispersing species such as plants. Therefore co-occurrence of a high number of endemic study

330 species within a narrow monsoon-influenced region is indicative of a refugium with low

331 climate change velocity (Sandel *et al.* 2011; Abellán and Svenning 2014; Harrison and Noss

332 2017). Climate analysis identified cooler mean annual temperatures in the study area and the

333 influence of coastal cloud and fog (Figure 2), which combined with novel survey data and

334 environmental distribution modelling suggests that the vegetation of the southern Central

335 Desert is a relict of an earlier, more mesic period. This is further supported by the biogeography

336 of genera such as *Aerva*, *Searsia* and *Ochradenus* which have global distributions from Africa

337 to South-East Asia, yet with endemic species restricted to Arabia (POWO 2018), indicating

338 support for a refugium further back into the Neogene. Thus, this system may represent the

14

339   northernmost remnant of a continuous belt of mesic vegetation formerly ranging from Africa

340   to Asia, with close links to the flora of East Africa (Kürschner, 1998; Patzelt, 2011).

341   The relictual distributions that we observe appear to be driven by the interaction of climate and

342   topographic factors, in particular the influence of the southern monsoon. It had been speculated

343   that parts of the Central Desert may be at the fringe of the monsoon-affected area (Patzelt,

344   2015), thus benefiting from occasional low clouds, cool winds and coastal fog during the

345   southern monsoon, but previously this could not be tested because of the lack of climate

346   stations. Here, using evidence from remote sensing, we demonstrate that the southern monsoon

347   does indeed influence the southern system of the Central Desert, with patterns of night time

348   fog detected via the MODIS satellite also consistent with the limited reports available. This

349   putatively places the southern Arabian coastal fog-influenced Central Desert together with

350   other coastal fog deserts such as the Namib and Peruvian lomas (Cereceda *et al.* 2008; Henschel

351   and Seely 2008), though based on limited fog adaptation traits in the flora, fog intensity may

352   be lower.

353   By applying these climate data to systematic field records of endemic plants, we develop a

354   suite of models characterizing each species' environmental niche. We show that despite small

355   sample sizes it is possible to generate robust niche models, incorporating true absence data,

356   which identify important areas of plant diversity. Surprisingly, the relative importance of

357   retained climatic and topographic variables differed substantially across study species.

358   Therefore, we conclude that it is not a single set of environmental variables contributing to the

359   distribution of this unique flora. For example, whilst overall, aridity and mean annual

360   temperature are unsurprisingly important predictors in an arid environment, almost all retained

361   variables are important across specific taxa. Therefore our analysis does not support the

362   hypothesis that it is predominantly fog that influences the distribution of this endemic flora,

363   rather a range of factors appear to be important, consistent with the diverse traits and

15

364   phylogenetic provenance of the species. We note however that on a finer spatial scale, factors

365   such as microrefugia and fog hydrology may have greater importance (Mclaughlin *et al.* 2017).

366   Despite being recognised for its global importance, the arid Horn of Africa biodiversity hotspot

367   is one of the most severely degraded, with less than 5% of habitat considered to be in pristine

368   condition (Mittermeier *et al.* 2005; Mallon 2013). Key threats to the Central Desert include

369   overgrazing (Ghazanfar, 2004), and climate change (Almazroui *et al.* 2013), with mean annual

370   temperature for the Arabian Peninsula increasing at 0.6°C per decade and a significant

371   decreasing trend in annual rainfall (Almazroui *et al.* 2013). It is also concerning that climate

372   change has been associated with a historic shifts in intensity and northward extent of the

373   monsoon (Fleitmann and Matter 2009) and elsewhere a contemporary decline in coastal fog

374   frequency (Johnstone and Dawson 2010), with strong implications for persistence of endemic

375   flora. In our study area, a relatively minor shift in the northward extent of the monsoon could

376   have significant implications for regional climate.

377   Refugia have been suggested as priority sites to conserve global biodiversity under climate

378   change precisely because of their demonstrated ability to facilitate species survival under

379   adverse conditions (Keppel *et al.* 2012). Based on previous studies, it is also likely that refugial

380   populations harbour the highest genetic diversity across the species' distribution (Meister,

381   Hubaishan, Kilian, & Oberprieler, 2005), helping building future evolutionary resilience (Sgrò

382   *et al.* 2011). This may be particularly important in the Central Desert, where many endemic

383   species have been restricted to only a single refugial location, reducing potential for subsequent

384   population admixture (Petit *et al.* 2003). The southern coast of the Arabian peninsula has also

385   been predicted to contain a significant proportion of unassessed at-risk vascular plant species

386   (Pelletier *et al.* 2018). In recent years, an Important Plant Area (IPA) programme has been

387   initiated for the Middle East, which highlights the value of an ecological and evolutionary

388   process-based view in identifying candidate conservation sites (Al-Abbasi *et al.* 2010).

16

389   Therefore, the site outlined here (Figure 5), covering approximately 880 km^2, may be candidate

390   for further evaluation and consideration as an IPA.

391   In conclusion, this study makes an important contribution to our understanding of southern

392   Arabian climate refugia, and the biogeographical origins of the endemic flora of Oman's

393   Central Desert. In the future we highlight the value of a network of detectors to characterise

394   coastal fog across the landscape, particularly in the southern Central Desert. These would better

395   enable an assessment of how coastal fog co-varies with other readily available datasets such as

396   topography, cloud cover and land surface temperature to enable higher resolution predictions

397   of the influence of coastal fog on species distributions. More generally, we emphasise the value

398   of predictive modelling in the region to advance beyond initial presence-absence grids, both to

399   identify the drivers of biogeographic patterns and to prioritise sites for the conservation. In the

400   future, further identification and characterisation of southern Arabian climate refugia may be a

401   useful strategy to support conservation in a global biodiversity hotspot.

402

403

404

405

406

407

408

409

410

411 **ACKNOWLEDGEMENTS**

414 **FUNDING INFORMATION**

417

418

419

420

421

422

423

424

425

426

427

428

429

430

431 **LITERATURE CITED**

432 **Abellán P, Svenning JC**. **2014**. Refugia within refugia - patterns in endemism and genetic

433 divergence are linked to Late Quaternary climate stability in the Iberian Peninsula. *Biological*

434 *Journal of the Linnean Society* **113**: 13–28.

435 **Al-Abbasi TM, Al-Farhan A, Al-Khulaidi AW, *et al.* 2010**. Important plant areas in the

436 arabian peninsula. *Edinburgh Journal of Botany* **67**: 25–35.

437 **Almazroui M, Abid MA, Athar H, Islam MN, Ehsan MA**. **2013**. Interannual variability of

438 rainfall over the Arabian Peninsula using the IPCC AR4 global climate models. *International*

439 *Journal of Climatology* **33**: 2328–2340.

440 **Bennett KD, Tzedakis PD, Willis KJ**. **1991**. Quaternary refugia of north European trees. :

441 103–115.

442 **Birks HJB, Willis KJ**. **2008**. Alpines, trees, and refugia in Europe. *Plant Ecology and*

443 *Diversity* **1**: 147–160.

444 **Bivand R, Stuetz R, Ove K, Giraudoux P, Davis M, Santilli S**. **2018**. Package ' rgeos .'

445 **Brinkmann K, Dickhoefer U, Schlecht E, Buerkert A**. **2011**. Quantification of

446 aboveground rangeland productivity and anthropogenic degradation on the Arabian Peninsula

447 using Landsat imagery and field inventory data. *Remote Sensing of Environment* **115**: 465–

448 474.

449 **Cereceda P, Larrain H, Osses P, Farías M, Egaña I**. **2008**. The spatial and temporal

450 variability of fog and its relation to fog oases in the Atacama Desert, Chile. *Atmospheric*

451 *Research* **87**: 312–323.

452 **Chaurasia S, Sathiyamoorthy V, Paul Shukla B, Simon B, Joshi PC, Pal PK**. **2011**. Night

453 time fog detection using MODIS data over Northern India. *Meteorological Applications* **18**:

19

454   483–494.

455   **Chung M, Dufour A, Pluche R, Thompson S**. **2017**. How much does dry-season fog

456   matter? Quantifying fog contributions to water balance in a coastal California watershed.

457   *Hydrological Processes* **31**: 3948–3961.

458   **Comes HP, Kadereit JW**. **1998**. The effect of quaternary climatic changes on plant

459   distribution and evolution. *Trends in Plant Science* **3**: 432–438.

460   **Delany MJ**. **1989**. The zoogeography of the mammal fauna of southern Arabia. *Mammal*

461   *Review* **19**: 133–152.

462   **Dilts TE, Weisberg PJ, Dencker CM, Chambers JC**. **2015**. Functionally relevant climate

463   variables for arid lands: A climatic water deficit approach for modelling desert shrub

464   distributions. *Journal of Biogeography* **42**: 1986–1997.

465   **Dregne HE**. **1976**. *Soils of Arid Regions*. Amsterdam: Elsevier Scientific Publishing

466   Company.

467   **Elith J, Leathwick J**. **2009**. Species distribution models: ecological explanation and

468   prediction across space and time. *Annual Review of Ecology, Evolution, ...* **40**: 677–697.

469   **Fernández-López J**. **2018**. rWind: Download, edit and include wind data in ecological and

470   evolutionary analysis. *Ecography* **42**.

471   **Fick SE, Hijmans RJ**. **2017**. *Fick, Hijmans - 2017 - WorldClim 2 new 1-km spatial*

472   *resolution climate surfaces for global land areas.pdf*.

473   **Fischer DT, Still CJ, Williams AP**. **2009**. Significance of summer fog and overcast for

474   drought stress and ecological functioning of coastal California endemic plant species. *Journal*

475   *of Biogeography* **36**: 783–799.

476 **Fisher M, Membery DA**. **1998**. Climate In: Ghazanfar SA, Fisher M, eds. *Vegetation of the*

477 *Arabian Peninsula*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 5–38.

478 **Fleitmann D, Matter A**. **2009**. The speleothem record of climate variability in Southern

479 Arabia. *Comptes Rendus - Geoscience* **341**: 633–642.

480 **Gamer M, Lemon J, Fellows I, Singh P**. **2012**. Irr package for R, version 0.84.

481 **Gandini F, Achilli A, Pala M,** *et al.* **2016**. Mapping human dispersals into the Horn of

482 Africa from Arabian Ice Age refugia using mitogenomes. *Scientific Reports* **6**: 1–13.

483 **Ghazanfar SA**. **1998**. Status of the flora and plant conservation in the sultanate of Oman.

484 *Biological Conservation* **85**: 287–295.

485 **Ghazanfar SA**. **2004**. Biology of the central desert of Oman. *Turkish Journal of Botany* **28**:

486 65–71.

487 **Ghazanfar SA, Fisher M**. **2013**. *Vegetation of the Arabian peninsula*. Springer Science &

488 Business Media.

489 **Ghazanfar S, Gallagher M**. **1998**. *Remarkable lichens from the Sultanate of Oman*.

490 **Harrison S, Noss R**. **2017**. Endemism hotspots are linked to stable climatic refugia. *Annals*

491 *of Botany* **119**: 207–214.

492 **Henschel JR, Seely MK**. **2008**. Ecophysiology of atmospheric moisture in the Namib Desert.

493 *Atmospheric Research* **87**: 362–368.

494 **Hijmans RJ**. **2017**. raster: Geographic Data Analysis and Modeling. R package version 2.6-

495 7.

496 **Hijmans RJ, Philips S, Leathwick J, Elith J**. **2017**. dismo: Species Distribution Modeling.

497 R package version 1.1-4.

498 **Hunt GE**. **1973**. Radiative properties of terrestrial clouds at visible and infra-red thermal

499 window wavelengths. *Quarterly Journal of the Royal Meteorological Society* **99**: 346–369.

500 **Jennings RP, Singarayer J, Stone EJ,** *et al.* **2015**. The greening of Arabia: Multiple

501 opportunities for human occupation of the Arabian Peninsula during the Late Pleistocene

502 inferred from an ensemble of climate model simulations. *Quaternary International* **382**: 181–

503 199.

504 **Jiménez-Valverde A, Lobo JM, Hortal J**. **2008**. Not as good as they seem: The importance

505 of concepts in species distribution modelling. *Diversity and Distributions* **14**: 885–890.

506 **Johnstone JA, Dawson TE**. **2010**. Climatic context and ecological implications of summer

507 fog decline in the coast redwood region James. *Proceedings of the National Academy of*

508 *Sciences* **107**: 4533–4538.

509 **Jolly D, Prentice IC, Bonnefille R,** *et al.* **2009**. Biome Reconstruction from Pollen and Plant

510 Macrofossil Data for Africa and the Arabian Peninsula at 0 and 6000 Years Published by :

511 Blackwell Publishing Stable URL : http://www.jstor.org/stable/2846197.

512 **Kearney M, Porter W**. **2009**. Mechanistic niche modelling: Combining physiological and

513 spatial data to predict species' ranges. *Ecology Letters* **12**: 334–350.

514 **Keppel G, Van Niel KP, Wardell-Johnson GW,** *et al.* **2012**. Refugia: Identifying and

515 understanding safe havens for biodiversity under climate change. *Global Ecology and*

516 *Biogeography* **21**: 393–404.

517 **Kürschner H**. **1998**. Biogeography and Introduction to Vegetation. In: Ghazanfar, S.A.,

518 Fisher M, ed. *Vegetation of the Arabian Peninsula.* Dordrecht: Springer, .

519 **Larraín-Barrios B, Faúndez-Yancas L, Búrquez A**. **2018**. Plant functional trait structure in

520 two fog deserts of America. *Flora: Morphology, Distribution, Functional Ecology of Plants*

22

521   **243**: 1–10.

522   **Liu C, Newell G, White M**. **2016**. On the selection of thresholds for predicting species

523   occurrence with presence-only data. *Ecology and Evolution* **6**: 337–348.

524   **Lobo JM, Jiménez-Valverde A, Real R**. **2008**. AUC: a misleading measure of the

525   performance of predictive distribution models. *Global Ecology and Biogeography* **17**: 145–

526   151.

527   **Mallon DP**. **2013**. Global hotspots in the Arabian Peninsula. *Zoology in the Middle East*

528   **7140**.

529   **Mclaughlin BC, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson S**. **2017**.

530   Hydrologic refugia, plants, and climate change. *Global Change Biology* **23**: 2941–2961.

531   **Meister J, Hubaishan MA, Kilian N, Oberprieler C**. **2005**. Chloroplast DNA variation in

532   the shrub Justicia areysiana (Acanthaceae) endemic to the monsoon affected coastal

533   mountains of the southern Arabian Peninsula. *Botanical Journal of the Linnean Society* **148**:

534   437–444.

535   **Meister J, Hubaishan MA, Kilian N, Oberprieler C**. **2006**. Temporal and spatial

536   diversification of the shrub Justicia areysiana Deflers (Acanthaceae) endemic to the monsoon

537   affected coastal mountains of the southern Arabian Peninsula. *Plant Systematics and*

538   *Evolution* **262**: 153–171.

539   **Merow C, Smith MJ, Silander JA**. **2013**. A practical guide to MaxEnt for modeling

540   species' distributions: What it does, and why inputs and settings matter. *Ecography* **36**:

541   1058–1069.

542   **Miller AG**. **1994**. Dhofar Fog Oasis, Oman and Yemen. In: Davis SD, Heywood VH,

543   Hamilton A., eds. *Centres of Plant Diversity, Vol. 1*. Gland: WWF, IUCN., 143–155.

23

544   **Miller AG, Cope TA**. **1996**. *Flora of the Arabian Peninsula and Socotra, 1*. Edinburgh:

545   Edinburgh University Press.

546   **Miller AG, Nyberg JA**. **1990**. Patterns of endemism in Arabia In: *Contributiones selectae ad*

547   *floram et vegetationem orientis: proceedings of the Third Plant Life of southwest Asia*

548   *Symposium, held*.3–8.

549   **Mittermeier RA, Gil PR, Hoffman M, *et al.* 2005**. *Hotspots Revisited: Earth's Biologically*

550   *Richest and Most Endangered Terrestrial Ecoregions*. Monterrey, Mexico: Cemex,

551   Conservation International and Agrupación Sierra Madre.

552   **MODIS Characterization Support Team (MCST)**. **2018**. *MODIS 1km Calibrated*

553   *Radiances Product*.

554   **Muscarella R, Galante PJ, Soley-Guardia M, *et al.* 2014**. ENMeval: An R package for

555   conducting spatially independent evaluations and estimating optimal model complexity for

556   Maxent ecological niche models. *Methods in Ecology and Evolution* **5**: 1198–1205.

557   **Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG**. **2014**. Where is

558   positional uncertainty a problem for species distribution modelling? *Ecography* **37**: 191–203.

559   **Parker AG**. **2010**. Pleistocene Climate Change in Arabia: Developing a Framework for

560   Hominin Dispersal over the Last 350 ka.

561   **Patel**. **1992**. Geological Map of Juzor Al Halaaniyaat, Sheet NE 40 - 10 and Duqm and

562   Madraca Sheet NE 40 - 03/07.

563   **Patzelt A**. **2009**. *The mountain vegetation of northern Oman: Ecology, phytosociology and*

564   *biogeography of Olea europaea and Juniperus excelsa woodlands and of weed vegetation on*

565   *cultivated terraces. In: Victor, R., Robinson, M. (eds.) Al Jabal Al Akhdar Monograph.*

566   **Patzelt A**. **2011**. The themeda quadrivalvis tall-grass savannah of Oman at the crossroad

567   between Africa and Asia. *Edinburgh Journal of Botany* **68**: 301–319.

568   **Patzelt A**. **2014**. *Oman Plant Red Data Book*. Diwan of Royal Court, Oman Botanic Garden.

569   **Patzelt A**. **2015**. Synopsis of the Flora and Vegetation of Oman, with Special Emphasis on

570   Patterns of Plant Endemism. *Abhandlungen der Braunschweigischen Wissenschaftlichen*

571   *Gesellschaft*: 282–317.

572   **Pelletier TA, Carstens BC, Tank DC, Sullivan J, Espíndola A**. **2018**. Predicting plant

573   conservation priorities on a global scale. *Proceedings of the National Academy of Sciences*

574   **115**: 201804098.

575   **Perpinan Lamigueiro O**. **2018**. Package "rasterVis" - Visualization Methods for Raster

576   Data.

577   **Peterson AT, Papeş M, Soberón J**. **2015**. Mechanistic and Correlative Models of Ecological

578   Niches. *European Journal of Ecology* **1**: 28–38.

579   **Petit RJ, Petit J, Aguinagalde I,** *et al.* **2003**. Genetic Diversity Glacial Refugia : Hotspots

580   But Not. *Science* **1563**: 1563–5.

581   **Phillips SJ, Anderson RP, Schapire RE**. **2006**. Maximum entropy modeling of species

582   geographic distributions. *Ecological Modelling* **190**: 231–259.

583   **POWO**. **2018**. *Plants of the World Online*. http://www.plantsoftheworldonline.org/. 29 Dec.

584   2018.

585   **R Development Core Team**. **2014**. R: A language and environment for statistical

586   computing. *Foundation for Statistical Computing, Vienna, Austria.*

587   **Rastogi B, Williams AP, Fischer DT,** *et al.* **2016**. Spatial and temporal patterns of cloud

588   cover and fog inundation in coastal California: Ecological implications. *Earth Interactions*

25

589   **20**.

590   **Raven PH, Axelrod DI**. **1974**. Angiosperm Biogeography and Past Continental Movements.

591   *Annals of the Missouri Botanical Garden* **61**: 539–673.

592   **RStudio Team**. **2016**. RStudio: Integrated Development for R. *RStudio, Inc., Boston, MA*.

593   **Sandel B, Arge L, Dalsgaard B,** *et al.* **2011**. The Influence of Late Quaternary. *Science* **334**:

594   660–664.

595   **Schemenauer RS, Cereceda P, Carvajal N**. **1987**. Measurements of Fog Water Deposition

596   and Their Relationships to Terrain Features. *Journal of Applied Meteorology* **26**: 1285–1292.

597   **Searcy CA, Shaffer HB**. **2016**. Do Ecological Niche Models Accurately Identify Climatic

598   Determinants of Species Ranges? *The American Naturalist* **187:4**: 423–435.

599   **Sgrò CM, Lowe AJ, Hoffmann AA**. **2011**. Building evolutionary resilience for conserving

600   biodiversity under climate change. *Evolutionary Applications* **4**: 326–337.

601   **Stanley Price MR, Al-Harthy AH, Whitcombe RP**. **1988**. Fog moisture and its ecological

602   effects in Oman In: *Arid Lands: Today and Tomorrow*.69–88.

603   **Title PO, Bemmels JB**. **2018**. ENVIREM: an expanded set of bioclimatic and topographic

604   variables increases flexibility and improves performance of ecological niche modeling.

605   *Ecography* **41**: 291–307.

606   **Wan Z, Hook S, Hulley G**. **2018**. *MOD11A1 MODIS/Terra Land Surface Temperature and*

607   *the Emissivity Daily L3 Global 1km SIN Grid.*

608   **Wang N, Borrell JS, Bodles WJ a, Kuttapitiya A, Nichols R a., Buggs RJ a**. **2014**.

609   Molecular footprints of the Holocene retreat of dwarf birch in Britain. *Molecular Ecology* **23**:

610   2771–2782.

611 **Warren DL, Glor RE, Turelli M**. **2008**. Environmental niche equivalency versus

612 conservatism: Quantitative approaches to niche evolution. *Evolution* **62**: 2868–2883.

613 **Warren DL, Seifert SN**. **2011**. Ecological niche modeling in Maxent : the importance of

614 model complexity and the performance of model selection criteria. *Ecological Applications*

615 **21**: 335–342.

616 **White F, Léonard J**. **1990**. Phytogeographical links between Africa and southwest Asia In:

617 *Contributiones selectae ad floram et vegetationem orientis: proceedings of the Third Plant*

618 *Life of southwest Asia Symposium, held*.3–8.

619 **Whybrow PJ, Mcclure HA**. **1981**. Fossil Mangrove Roots and Palaeoenvironments of the.

620 **32**: 213–225.

621 **Wickham H**. **2009**. ggplot2. Elegant graphics for data analysis. *Springer*: 210.

622 **Wilson AM, Jetz W**. **2016**. Remotely Sensed High-Resolution Global Cloud Dynamics for

623 Predicting Ecosystem and Biodiversity Distributions. *PLoS Biology* **14**: 1–20.

624 **Zhang H, Schroder JL, Pittman JJ, Wang JJ, Payton ME**. **2005**. Soil Salinity Using

625 Saturated Paste and 1:1 Soil to Water Extracts. *Soil Science Society of America Journal* **69**:

626 1146.

627

628

629

630

631

632

27

633 **TABLES**

634

635 **Table 1.** Summary of the seven study taxa, including Red List status from Patzelt (2014).

ID	Species[1]	Family	Habitat description	Status[2]
AA	*Aerva artemisoides* Vierh. & O. Schwartz subsp. *Batharitica* A.G. Mill	Amaranthaceae	Coastal areas including dry cliffs, rocky slopes and wadi banks on limestone, 20-300 m.	VU
HG	*Hyoscyamus gallagheri* A.G. Mill. & Biagi.	Solanaceae	Low sand dunes and gravel desert, 0-250 m.	VU
OH	*Ochradenus harsusiticus* A.G. Mill.	Resedaceae	Open *Acacia tortilis - Prosopis cineraria* woodland, in sandy and gravelly depressions of the central desert, 100-210 m.	VU
PJ	*Polycarpaea jazirensis* R. A. Clement.	Caryophyllaceae	Coastal areas of Sahil al Jazir in sandy depressions and on limestone cliffs, 100-210 m.	CR
PP	*Pulicaria pulvinate* E. Gamal-Eldin	Asteraceae	Limestone cliffs and central limestone plateau on sand and gravel, 0-300 m.	NT
SG	*Searsia gallagheri* Ghaz.	Anacardiaceae	Stony wadis and depressions, 130-205 m.	VU
SH	*Salvia* aff. *Hillcoatiae* R.A. Clement	Lamiaceae	Dry limestone plateau of the central desert, 0-300 m.	VU

636 [1]Voucher specimens are deposited at the Oman Botanic Gardens, accession numbers (OH: CDBE-1; PP: CDBE-
637 3; PJ:CDBE-4; SG: CDBE-5, 6). [2]All assessments are global assessments which have been submitted to IUCN to be included
638 to the Global Red List of Threatened Species, with the exception of a national assessment for *S. gallagheri*. The relationship
639 between *S. gallagheri* (formerly *Rhus*) and *S. vulgaris* awaits more detailed taxonomic investigation, thus a national
640 assessment is reported.

641

642

643

644

645

646

647

648

649

650

651

652

653

654

Table 2. Environmental niche model input and evaluation statistics.

Species	Pre-filtering observations			Post-filtering	Model evaluation					
	Incidental	Quadrats	Historical		Features	RM	AUC_{TEST}	AUC_{DIFF}	OR_{MTP}	Parameters
AA	161	20	12	41	L	2.5	0.84	0.11	0.05	6
HG	34	4	19	23	L	1.5	0.82	0.08	0.04	5
OH	16	3	13	13	L	0.5	0.79	0.15	0.23	6
PJ	8	0	1	4	-	-	-	-	-	-
PP	19	45	18	54	LQHP	2.5	0.76	0.11	0.04	10
SG	35	7	0	17	L	2	0.93	0.03	0.12	4
SH	15	15	0	25	LQ	1.5	0.89	0.05	0.04	8

Feature classes: Linear L, Quadratic Q, Hinge H, Product P and Threshold T. RM = regularization multiplier.

680   **Table 3.** Percentage contribution of environmental variables to environmental niche models
681   across study species.

Environmental variable	AA	HG	OH	PP	RG	SH	Mean (SD)
Night LST	22.7	0.0	0.0	1.3	4.1	2.6	5.1 (8.8)
Mean annual cloud cover	0.0	2.2	0.0	2.4	0.0	1.6	1.0 (1.2)
Cloud cover seasonality	0.5	31.2	0.0	2.9	0.4	9.4	7.4 (12.2)
Thornthwaite aridity index	44.5	0.0	4.2	0.0	82.3	0.8	22.0 (34.3)
Aspect	0.0	0.0	10.2	1.6	0.0	33.7	7.6 (13.4)
Elevation	0.0	40.6	33.1	37.7	0.0	26.7	23.0 18.4)
Mean annual fog	8.0	3.4	13.7	2.5	0.9	9.0	6.2 (4.8)
Terrain roughness index	24.0	0.0	7.6	21.1	12.4	5.0	11.7 (9.4)
Annual mean temperature	0.5	22.6	31.3	30.4	0.0	11.1	16.0 (14.2)

682

683

684

685

686

687

688

689

690

691

692

693

694

695

696

697

698

699

700

701

702

703

704

705 **FIGURE LEGENDS**

706 **Figure 1.** Images of the endemic Central Desert plant species included in this study. a) *Aerva*

707 *artemisoides subsp. batharitica*; b) *Hyoscyamus gallagheri*; c) *Ochradenus harsusiticus*; d)

708 *Polycarpaea jazirensis*; e) *Pulicaria pulvinata*; f) *Salvia aff. hillcoatiae*; g) *Searsia gallagheri*;

709 h) A typical Central Desert landscape.

710 **Figure 2.** a) Elevation map of Oman, with annual offshore cloud cover percentage identifying

711 the major southern and Indian monsoon climate patterns. Cloud cover over land is not shown,

712 but is negligible for the Central Desert. Northern and southern study systems are denoted by

713 shaded polygons. b) Quarterly mean temperature across the Central Desert. c) Quarterly night

714 time fog intensity (change in brightness temperature) across the Central Desert. Higher values

715 (less negative) are indicative of greater fog intensity.

716 **Figure 3**. Principal component analysis of abiotic variables across principal ecoregions of

717 Oman. Grey points denote a random background sample from across Oman. The five major

718 centres of plant endemism comprise i) the Hajar Mountains; ii-iii) the Dhofar Mountains

719 comprising the Jabal Samhan and Jabal Al Qamar/Qara centres of endemism, combined for the

720 purposes of this figure; iv) the Northern Central Desert consisting of the Jiddat Al Harasis/Huqf

721 and v) the Southern Central Desert comprising the Sahil Al Jazir/Jiddat Al Arkad. The Empty

722 Quarter is plotted (yellow) for reference as it comprises a significant proportion of Oman's

723 land area, but is not considered a centre of endemism. The candidate refugium (red) is a subset

724 of the southern system of the Central Desert.

725 **Figure 4**. Environmental niche models for each of six study species across the southern Central

726 Desert. Higher values indicative of greater modelled habitat suitability. Dashed line denotes

727 the southern Central Desert system.

728 **Figure 5.** Identification of endemic species co-occurrence in the southern Central Desert. a)

729 Composite map of the binary distributions of six study species. Dashed line identifies a region

730 of high diversity with potential as a candidate Important Plant Area. b) False colour Sentinel 2

731 image of the high diversity area. Red line shows a primary road crossing the study area. Inset

732 rose diagram shows the prevailing wind direction during the Khareef (Southern Monsoon).

733 Cloud cover mean is shown in blue.

734 **Figure 6.** Locations of Omani weather stations contributing to interpolated climate variables

735 used in this study (1970-2000), as well as four independent validation weather stations from

736 the Central Desert (1999-2017). Maximum daily temperature recorded at these stations is

737 reported (coloured by year), with the black line denoting the historic Worldclim 2 average for

738 this period. Northern and southern systems are depicted in blue and orange, respectively.

739
740
741
742
743
744
745

746 **FIGURES**
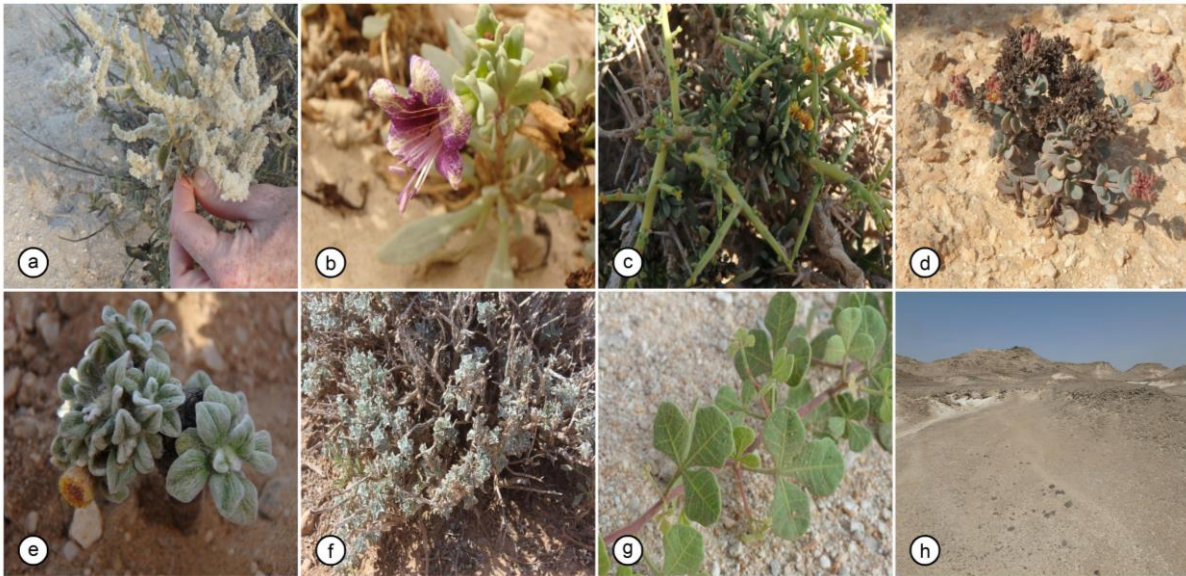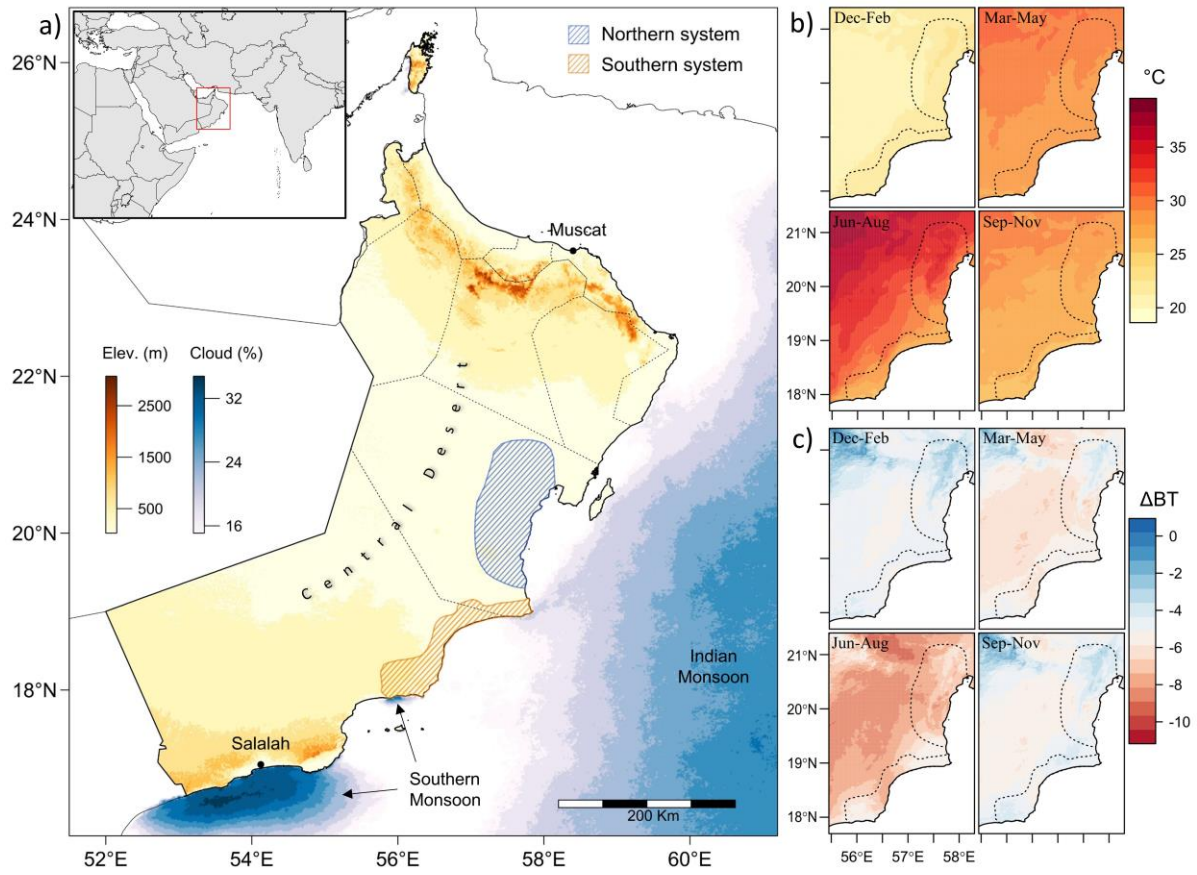

747

748 **Figure 1.**

749
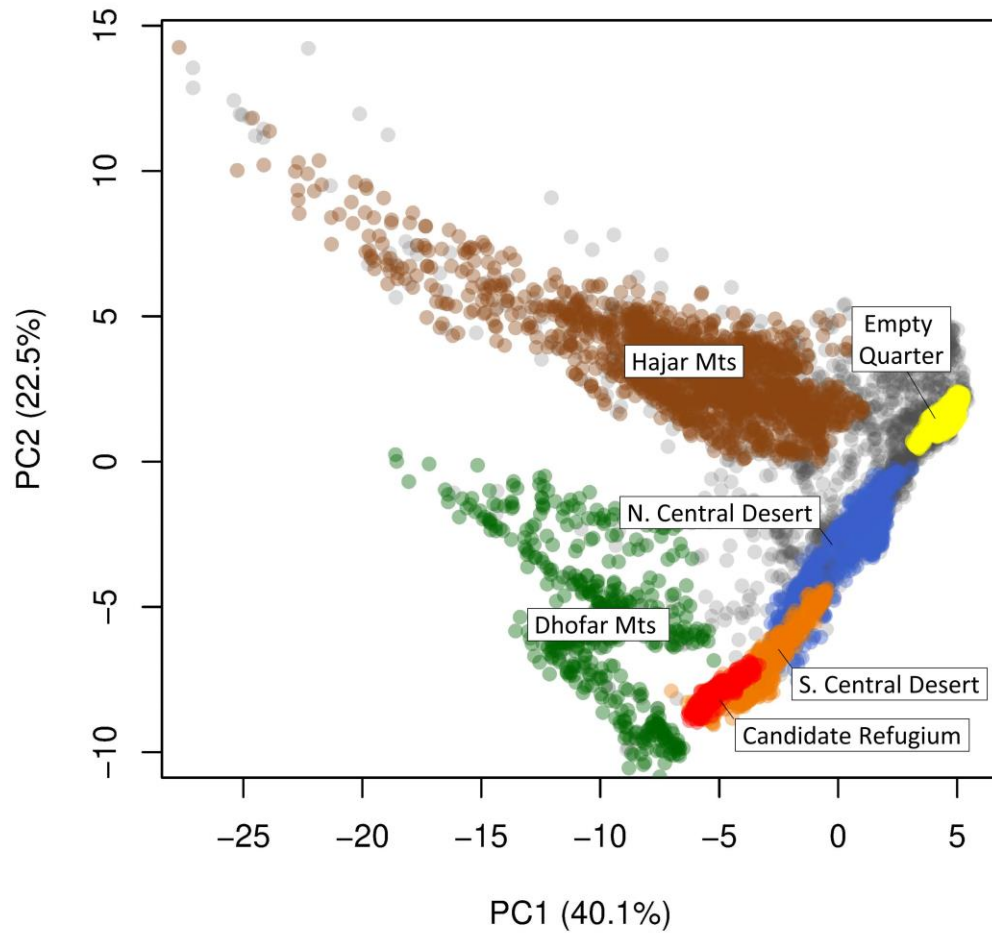
750

751
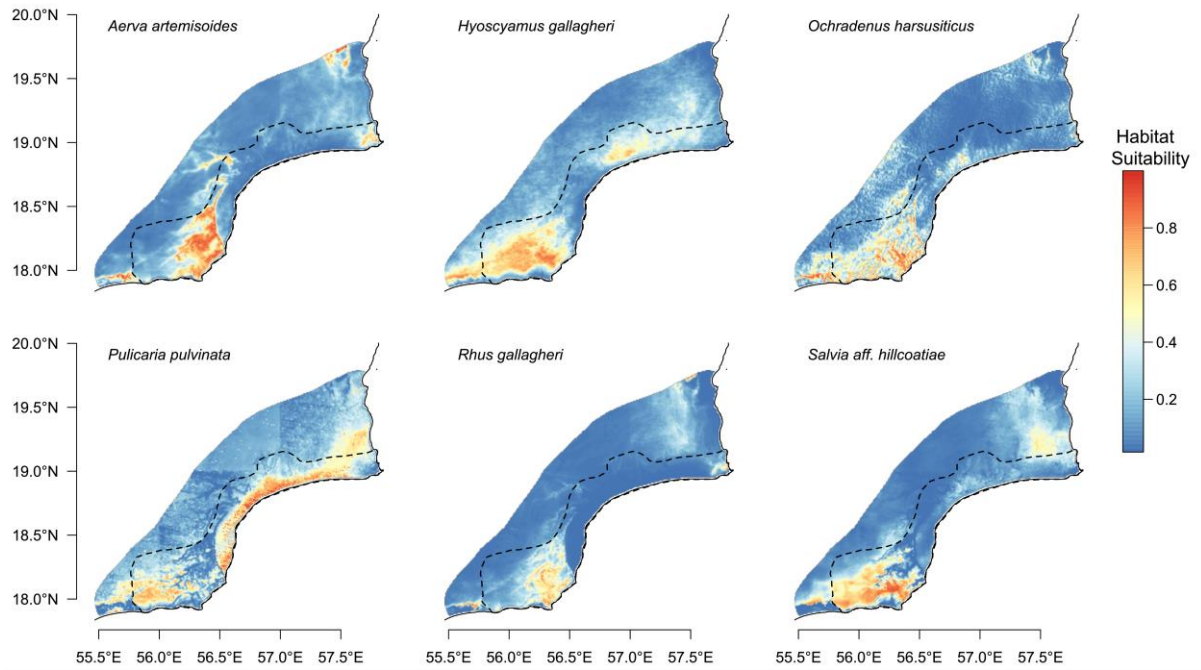
752

753

754

755

Figure 2.

761

Figure 3.

763

764

765

766

767

768

Figure 4.

770

771

772

773

774

775

776

777

778

779

780
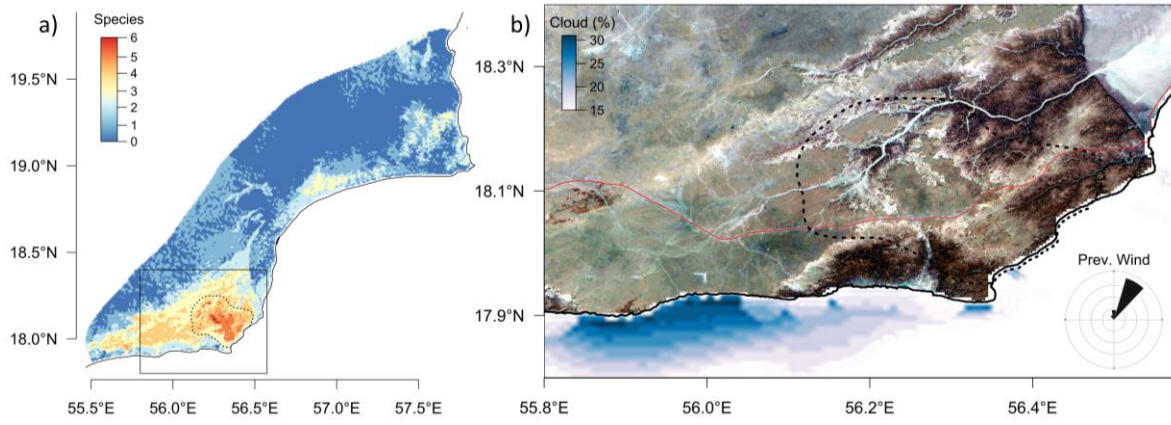
781

782

783

784

785

786

Figure 5.
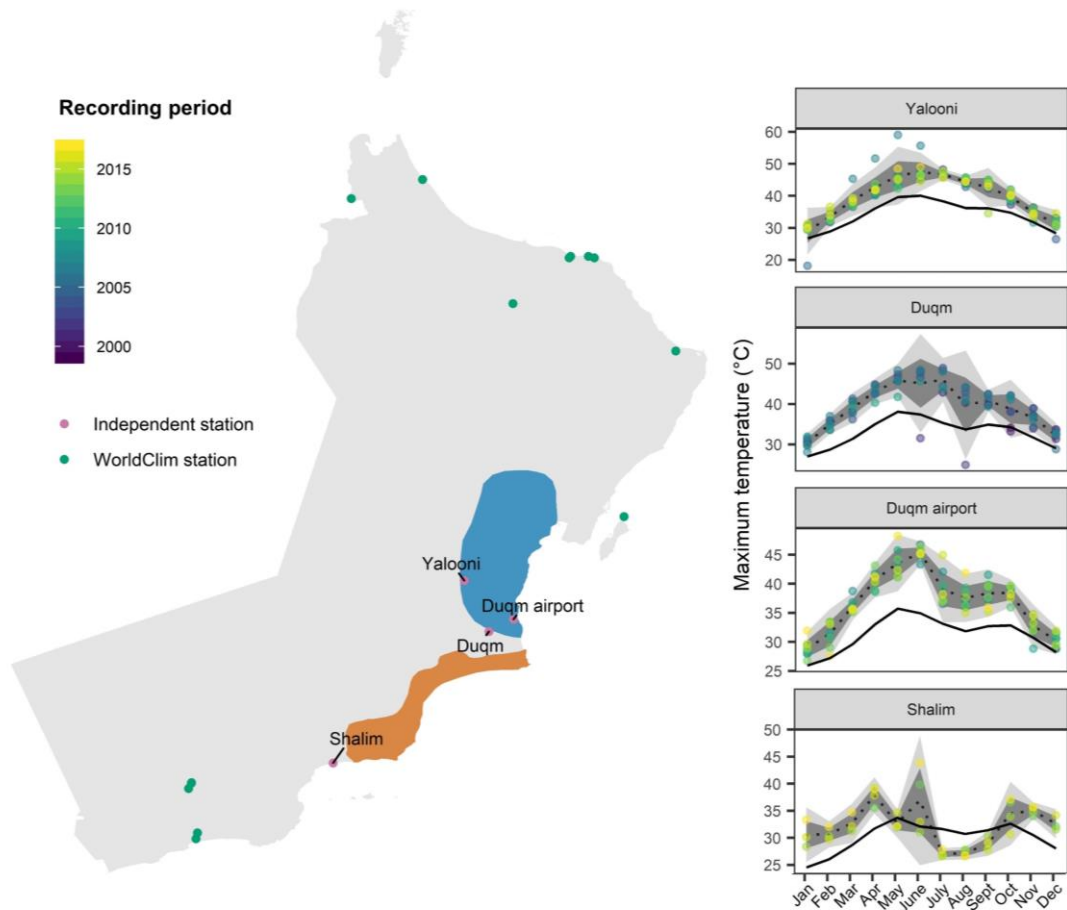
803

804 **Figure 6.**

805

806

807

808

809

810

811

812

813

814

815

DATA ACCESSIBILITY

All topographic and environmental GIS layers used in this study are freely available from the sources outlined in Table S3, Supporting Information. Raw meteorological data for Central Desert climate stations are available on request from the Meteorological Society of Oman. Novel species observation records from the Central Desert will be provided on the Global Biodiversity Information Facility.

BIOSKETCH

The research reported here emerged from the Central Desert Botanic Expedition 2017 and is the result of an ongoing collaboration between British scientists, volunteer participants and the Oman Botanic Garden. Initiated in collaboration with the British Exploring Society in 2012, collaborative teams have conducted research across several locations in Dhofar with further research planned in the Musandam peninsula. Fieldwork has been generously supported by the Anglo-Omani Society which seeks to promote understanding and friendship between Britain and Oman, particularly through scientific and cultural exchange. J.B., G.I., D.L., A.S.R. and A.P. conceived the idea, all authors (bar T.W. and A.P.) participated in fieldwork. J.B., T.S., R.S. and T.W. performed analysis and J.B., D.L. and A.P. led the writing. All authors approved the final version of this manuscript.