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**Spatio-temporal variation in the endangered *Thymus decussatus* in a hyper-arid environment**

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Manuscripts

Review

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3 **Spatio-temporal variation in the endangered *Thymus decussatus* in a hyper-arid**  
4 **environment**  
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10 Katy Thompson<sup>1</sup> and Francis Gilbert<sup>1</sup>

11  
12 1. School of Life Sciences, University of Nottingham, Nottingham NG7 2RD

13  
14  
15 Corresponding author: Katy Thompson

16  
17 kathy\_thompson\_@hotmail.co.uk  
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For Peer Review

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3 **1 Abstract**  
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8 3 *Aims:* Arid environments are resource-limited, with scarcity of water the key limiting factor, but  
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10 4 hyper-arid environments are rarely studied. *Methods:* The endangered Sinai Thyme (*Thymus*  
11  
12 5 *decussatus*) exists as a set of patches on mountaintops within the St Katherine Protectorate,  
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14 6 South Sinai, a hyper-arid environment with rare events of good rains (every 10-15 years).  
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16  
17 7 *Important findings:* From spatial and temporal patterns of plant mortality, size, condition and  
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19 8 flowering among ten patches on the Mt Sinai massif, we deduce that the incidence and amount of  
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21 9 flowering responds relatively quickly (1-2 years) to rainfall fluctuations, but plant growth  
22  
23 10 through increases in size or leaf number respond only very slowly. Small individuals are most at  
24  
25 11 risk of death during drought, and a high proportion of plants were dead at the end of eight years  
26  
27 12 of very low or no rainfall. No recruitment of seedlings was observed even in years of good  
28  
29 13 rainfall. Droughts are expected to become increasingly frequent due to climate change: this may  
30  
31 14 have important consequences for Sinai Thyme and also its associated herbivores, particularly the  
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33 15 Critically Endangered Sinai Baton Blue (*Pseudophilotes sinaicus*) whose larval stage feeds  
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35 16 exclusively upon the flowers of this plant.  
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43 **18 Keywords**  
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46 19 Spatial variation; temporal fluctuations; resource availability; Egypt; *Pseudophilotes sinaicus*  
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## 22 Introduction

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24 Resource availability in arid environments is primarily governed by water (Pueyo et al., 2008)  
25 with variation in plant performance predominantly explained by environmental and climatic  
26 variation, with water availability frequently cited as the limiting factor in arid landscapes (Boyer,  
27 1982). The 'pulse-reserve' model of arid plant communities focuses on the idea that sporadic  
28 rainfall leads to a pulse of plant growth (Reynolds et al., 2004). Water stress can reduce available  
29 soil resources by lowering the abundance and activity of micro-organisms, with knock-on effects  
30 on the levels of available nitrogen (Aguilera et al., 1999), impacting nutrient uptake from the soil  
31 and impairing acropetal translocation (Hu and Schmidhalter, 2005). Lower soil moisture reduces  
32 overall plant condition, i.e. leaf nitrogen content, photosynthetic ability, turgor pressure, etc., all  
33 with consequences for associated herbivores (Ostfeld and Keesing, 2000; Harrison, 2001).

34  
35 The key regulator of the pulsed response is thought to be the initial soil condition, itself  
36 influenced by numerous factors such as topography, soil texture, atmospheric conditions, plant  
37 cover and biomass (Reynolds et al., 2004). Ecosystems can store water and nutrients from  
38 previous pulses, and the size of these reserves may then influence sensitivity to further pulses -  
39 sometimes called the 'memory effect' (Schwinning et al., 2004). If there are consecutive dry  
40 years, the influence of prior levels of soil moisture, if low, can exaggerate the effects of  
41 diminished water resources on plant condition and performance, or, if high, can act as a buffer  
42 (Reynolds et al., 2004). In such marginal conditions, the trade-off between reproduction and  
43 survival may be even more important than usual, with reproduction sacrificed until rain occurs  
44 (Allen et al., 2010).

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3 45  
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6 46 There are often complex interactions between abiotic and biotic components affecting the growth  
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8 47 and condition of plants, including many spatial effects (Bai et al., 2008), and hence no single  
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10 48 variable can predict plant growth (Robertson et al., 2009). Environmental variation can act  
11  
12 49 synergistically with geomorphological and edaphic features to cause variation in distribution  
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14 50 (Bestelmeyer et al., 2006; Ju et al., 2008), abundance (Reynolds et al., 2004), productivity (Popp  
15  
16 51 et al., 2009) and mortality (Hamerlynck and McAuliffe, 2008). Habitat heterogeneity can also  
17  
18 52 influence plant life history traits such as growth and phenology (Gaston et al., 2004; Montesinos-  
19  
20 53 Navarro et al., 2010). For example, populations of *Arabidopsis thaliana* (Brassicaceae) have  
21  
22 54 different biomass allocation, fecundity and phenology depending upon altitude; these traits have  
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24 55 a genetic basis indicating previous selection for local adaptation (Montesinos-Navarro et al.,  
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26 56 2010).

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34 58 Life history strategies change depending upon environmental conditions. One response to a  
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36 59 stressor such as drought could be for the plant to become dormant, reducing growth and  
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38 60 fecundity to enhance survival until conditions improve, a tactic often seen in long-living clonal  
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40 61 species existing in harsh conditions (Forbis, 2003; Thompson et al., 2007). Flowering entails a  
41  
42 62 high water cost, so flowering and leaf production is often reduced under such conditions until  
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44 63 there are more available resources (Harrison, 2001), inevitably affecting animal food webs based  
45  
46 64 on plant resources. The population dynamics of herbivores in arid regions seem particularly  
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48 65 sensitive to rain-driven bursts in primary productivity, with cascading effects in the ecosystem to  
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50 66 higher trophic levels (Schwinning et al., 2004; Letnic and Dickman, 2010). Herbivore population  
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52 67 explosions are frequently observed when the rains come after drought (Harrison, 2001).

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6 69 Here we study a rare plant growing in the arid mountains of the St Katherine Protectorate in  
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8 70 South Sinai in Egypt, the most arid country in the world (FAO, 2012). Its flowers are the sole  
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10 71 food for the Critically Endangered Sinai Baton Blue butterfly, the flagship conservation target of  
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12 72 the Protectorate. Thus understanding the key drivers of plant condition and flowering is an  
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15 73 important component of the long-term strategy to conserve both plant and butterfly.  
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## 22 76 **Materials and Methods**

### 23 24 25 77 26 27 78 *The study system* 28 29 30 79

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32 80 The Sinai Thyme (*Thymus decussatus* Bentham, 1834) is an endangered plant occurring only  
33  
34 81 above 1500 m altitude within the St Katherine Protectorate (and recorded once from an adjacent  
35  
36 82 area in Saudi Arabia) (James, 2006a). It grows best in well-defined soil at the base of cliffs and  
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38 83 wadis, resulting in a naturally patchy distribution (Nakamura, 1975). *Thymus* species are  
39  
40 84 regarded as indicators of degradation by grazing in arid environments because their characteristic  
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43 85 small leaves resist the impact of drought and grazing (Navarro et al., 2006). The fieldwork was  
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45 86 carried out upon the Mount Sinai massif above the town of St Katherine, where there are ten  
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48 87 patches of thyme: Farsh Shoeib, Farsh Loza, Farsh El Hammar (Lower and Upper), Farsh Elia,  
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50 88 Elia Garden, Elia Circle, Farsh Safsafa, Gulley Zahtuna and Gulley Sharr (Fig. 1). The first five  
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52 89 patches were discovered in 2001 (James et al., 2003), but the rest were only found in 2011. The  
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3 90 Farsh Shoeib patch was studied in detail in 2002 (James, 2006d), and our fieldwork studied it  
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6 91 again in spring 2010: all patches were studied in 2011 and 2012.  
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9 92

10 93 In 2001 Farsh Shoeib held one of the largest populations of the Critically Endangered Sinai  
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12 94 Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura 1975), whose larval stages are  
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14  
15 95 monophagous on the flower buds of Sinai Thyme (James et al., 2003). As a conservation effort to  
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17 96 protect both plant and butterfly, the majority of the patch was fenced off in 2003 to prevent  
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20 97 public access, grazing and any damage to the plants: only a few plants are found outside the  
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22 98 enclosure in this patch. Two large dams were built specifically for conservation purposes in 2003  
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25 99 to hold more water in the soil after flash floods.  
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28  
29 101 There have been severe fluctuations in the weather over the past decade. Since 2002, when the  
30  
31 102 first and only other study was carried out, there has been severe drought with very little (<50  
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33 103 mm) or no rain every year until March 2010. This drought was broken in May 2010 when there  
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36 104 was heavy rainfall which left parts of Farsh Shoeib submerged for over a week. 2011 was again  
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39 105 extraordinarily wet, with heavy rainfall and snow in the winter and spring, whilst 2012 had very  
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41 106 little rainfall and was colder than normal. The extent to which these variations are normal for the  
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44 107 area is uncertain because of incomplete meteorological records and we are dependent on local  
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46 108 Bedouin knowledge. Undoubtedly, however, the long period of little or no rain will have had  
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48 109 effects on the thyme.  
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53 111 *Mapping and measuring the plants*  
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3 113 The boundary of each patch was mapped by walking around the perimeter and recording the  
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5 114 track using a hand-held GPS unit (Garmin etrex Venture HC, found to be accurate to  $\pm 10$   
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8 115 metres): the waypoints from the tracks were then imported into ArcGIS 9.3. Each plant situated  
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10 116 outside a patch was individually labelled and its position recorded using the GPS unit. We  
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12 117 decided whether plants formed a discrete patch if there were more than 30 plants closely situated,  
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14 118 separated from another patch by either 100 m or a natural barrier (which was often the situation  
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16 119 on the Mt. Sinai massif). The plants located outside the patches were sparsely distributed with  
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18 120 considerable distances between them and took considerably longer to locate.  
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21 121  
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24 122 We mapped the plants of Farsh Shoeib in more detail. Each individual plant was recorded  
25  
26 123 relative to the nearest of 12 landmarks by measuring its distance and the bearing. The  
27  
28 124 coordinates of each landmark were repeatedly recorded during March and April at varying times  
29  
30 125 of day using a hand-held GPS unit; the repeat measurements were then averaged to gain greater  
31  
32 126 precision in the location of the landmarks. The distances and bearings were converted into  
33  
34 127 coordinates to get an accurate location for each plant in Farsh Shoeib relative to the landmark  
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36 128 features, plotted using ArcGIS. This map was compared to the one created for 2002 by James  
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38 129 (2006b).  
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46 131 In order to compare the number and quality of thyme plants in Farsh Shoeib to the data collected  
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48 132 in 2002, in 2010 and 2011 each plant was identified and labelled, and its height, two  
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50 133 perpendicular widths and condition (the proportion of the plant that was green) measured, the  
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52 134 same variables that James (2006b) recorded in 2002. We did not record the size in 2012 due to  
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54 135 the slow growth rate and the relatively large measurement error involved in determining the  
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3 136 widest part of the plant. The 'resource area' for each plant was then calculated from 'plant size'  
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6 137 (the surface area, assuming each plant was a hemi-ellipsoid described by the height and recorded  
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8 138 widths) multiplied by the condition (as a proportion). The numbers of flowers on 50 randomly  
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11 139 chosen plants from an area particularly dense with plants (the Gulley: see Fig. 4) were counted  
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13 140 during the first six weeks of flowering in 2010, 2011 and 2012. The proportion of flowering  
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15 141 plants were compared by weekly inspections of 637 individuals in 2010, and of 100 randomly  
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18 142 selected plants in 2011 and 2012.

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22 144 The average plant quality in the other patches was calculated in 2011 by measuring the height,  
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24 145 two perpendicular widths and the condition (% green) to get the resource area per plant for 100  
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27 146 or all plants in each patch, whichever was the smaller number. The condition of 50 randomly  
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29 147 selected or all plants in each patch was rerecorded in 2012. The density of inflorescences was  
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32 148 counted in both 2011 and 2012 towards the end of the flowering season in a randomly placed 10  
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34 149 x 10 cm quadrat for 50 randomly chosen plants per patch (i.e. regardless of whether they were  
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36 150 flowering or not), and from these data we calculated the proportion of plants that flowered.

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#### 40 41 152 *Analysis of data*

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46 154 All analyses used the statistical package R 2.14.1 (R Development Core Team, 2012) and models  
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48 155 were simplified in accordance to Zuur et al. (2009) based on the Akaike Information Criterion  
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50 156 (AIC) criterion and stepwise backwards deletion of model terms. To test for spatial differences  
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53 157 across the massif, a GLM compared plant size amongst patches in 2011. Size was  
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55 158 logarithmically transformed (normalising it) and analysed using the R routine *glm*, with

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3 159 significance assessed with an F-ratio. Plant condition, density of inflorescences and proportion of  
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6 160 plants that flowered were compared in turn using a GLM to test for differences between years  
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8 161 (2011 and 2012) and among patches. Condition and density of inflorescences were over-  
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11 162 dispersed and so the GLM had a quasi-poisson error structure with significance tested with an F-  
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13 163 ratio; the proportion of flowering plants had a binomial distribution, tested with a  $\chi^2$ .

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17 165 To test for temporal differences within Farsh Shoeib we used data for 2002 and 2010-2012. The  
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20 166 2010 mapping was much more detailed than in 2002, when James (2006b) did not map all of the  
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23 167 plants individually within Farsh Shoeib; instead he mapped particular individuals and attributed  
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25 168 the surrounding set of close neighbours to that location. This made it impossible to re-identify his  
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27 169 individuals to monitor the changes over time directly. He did, however, divide the site into five  
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29  
30 170 sections, and we could therefore compare all individuals within each of these sections. Using the  
31  
32 171 R routine *glm*, we therefore compared the number and quality of sets of plants (sections) in 2002,  
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34 172 2010 and 2011. We used plant condition and size as response variables, and year (2002, 2010  
35  
36 173 and 2011) and section as predictors. Condition and log(size) were normally distributed:  
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39 174 significance was assessed for both with an F-ratio. Similar GLMs with binomial distributions  
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41 175 compared the mortality and the proportion of flowering plants, tested with a  $\chi^2$ . To see if there  
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44 176 was a significant difference in the characteristics of the plants which have died since 2010, we  
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46 177 ran a t-test to compare the size and condition of surviving individuals against those which  
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49 178 subsequently died.

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## 52 53 180 **Results**

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3 182 *Spatial variation across the massif*  
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8 184 Across the ten patches upon the Mt Sinai massif there was a combined resource area of 174 m<sup>2</sup> in  
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10 185 2011. Farsh Shoeib held the largest amount of resource, with 54.8 m<sup>2</sup> of green thyme (32% of the  
11  
12 186 total on the massif). Plant size (only measured in 2011) showed significant spatial differences  
13  
14 187 (F=9.82, df=9,1460, p<0.001)(Fig. 2). There was also significant spatial variation in condition  
15  
16 188 (F=6.05, df=9,2426, p<0.001), but no differences between years (F=0.82, df=1,2426, p=0.36),  
17  
18 189 nor any evidence of an interaction (F=1.82, df=9,2426, p=0.06). In 2011 there was a 15.1%  
19  
20 190 difference between the healthiest (largest average condition) and unhealthiest patches and a  
21  
22 191 10.4% difference in 2012 (Fig. 3a). Overall the average condition decreased by 0.7% between  
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24 192 2011 and 2012, and if plant size remained constant this would have caused a loss of 5.6 m<sup>2</sup> of  
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26 193 green thyme across the massif.  
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34 195 The density of inflorescences varied significantly amongst patches (F=3.89, df=9,953, p<0.001)  
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36 196 and between years (F=193, df=1,953, p<0.001), with a significant interaction between these two  
37  
38 197 factors (F=3.8, df=9,953, p<0.01). The average density of inflorescences across the massif  
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40 198 decreased from 47.2 per 10 cm<sup>2</sup> in 2011 to 24.9 in 2012. The largest decline (of 33.2 per 10 cm<sup>2</sup>,  
41  
42 199 n=50) was seen in Elia Garden, the patch that had flowered most prolifically in 2011 (Fig. 3b).  
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45  
46 200 The proportion of flowering plants also varied significantly between years ( $\chi^2=41.8$ , df=2,  
47  
48 201 p<0.001), but there was no evidence of any spatial variation ( $\chi^2=9.64$ , df=9, p=0.38), nor of any  
49  
50 202 interaction ( $\chi^2=14.5$ , df=9, p=0.11). The overall proportion of flowering plants decreased from  
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52 203 98% to 89% in 2012, with inconsistent changes amongst patches (Fig. 3c).  
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205 *Temporal variation within Farsh Shoeib*

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207 Between 2002 and 2010 the number of thyme plants in Farsh Shoeib reduced from 1208 to 669  
208 i.e. 44.6% of the plants disappeared (assumed to have died). The majority (>60%) of plants in the  
209 southern part of the patch (Fig. 4) appear to have died: the mortality rate varied considerably  
210 among the five sections ( $\chi^2=136$ ,  $df=4$ ,  $p < 0.001$ ) (Table 1). The frequency distribution of plant  
211 size showed that the vast majority of plants lost were the smaller individuals. This has been  
212 accompanied with growth, shown by a higher frequency of larger individuals (Fig. 5). Because it  
213 was impossible to identify individual plants between 2002 and 2010, we cannot tell if any new  
214 plants were recruited into the population. The death rate between 2010 and 2011 was 1.6%,  
215 whilst between 2011 and 2012 it was 1.1%. No recruits to the population were observed in either  
216 year. The plants which died since 2010 were significantly smaller in size than survivors ( $t=2.04$ ,  
217  $df=1$ ,  $p < 0.05$ ). Their condition was not significantly different ( $t=0.87$ ,  $df=16$ ,  $p=0.40$ ), despite  
218 the plants which died having, on average, a lower preceding condition (Fig. 6).

219

220 Plant condition varied significantly with year ( $F=774$ ,  $df=3,3035$ ,  $p < 0.001$ ) and patch ( $F=22.4$ ,  
221  $df=4,3035$ ,  $p < 0.001$ ), and there was also an interaction ( $F=73.7$ ,  $df=12,3035$   $p < 0.001$ ). Between  
222 2002 and 2010 plant condition decreased from 53% to 25%, a huge difference; one third of the  
223 surviving plants were less than 10% green (Fig. 7). Average plant condition rose to 29.3% in  
224 2011, before dropping slightly to 28.6% in 2012. The plants in Farsh II (see Fig. 4) consistently  
225 had the poorest condition, and this was the location of more than half of the mortalities.

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3 227 Plant size (not measured in 2012) varied significantly with both year ( $F=783$ ,  $df=2,2470$ ,  
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6 228  $p<0.001$ ) and patch ( $F=135$ ,  $df=4,2470$ ,  $p<0.001$ ), and an interaction was also present ( $F=5.34$ ,  
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8 229  $df=8,2470$ ,  $p<0.001$ ). Between 2002 and 2010, average plant size increased in every section of  
9  
10 230 the study site, with the largest increase observed in the Gulley. In contrast, there was a slight  
11  
12 231 decrease in average size across the patch between 2010 and 2011 (Fig. 8a).

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14 232  
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16 233 Between 2002 and 2010 there was an overall increase in resource area of  $28\text{ cm}^2$  per plant, but  
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18 234 the change was inconsistent across the patch; plants in the Gulley gained  $189\text{ cm}^2$  resource area  
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20 235 per plant, whilst those of Farsh II lost  $254\text{ cm}^2$  (Fig. 8b). Although the average resource area per  
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22 236 plant remained similar, the loss of individuals meant that the total resource area reduced  
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25 237 dramatically from  $76\text{ m}^2$  in 2002 to  $45\text{ m}^2$  in 2010. Overall the plants were slightly smaller in  
26  
27 238 2011 than 2010 (Fig. 8a), but an increase in condition resulted in a rise in resource area per plant,  
28  
29 239 increasing the total patch resource area by  $9.7\text{ m}^2$  to  $55\text{ m}^2$ , despite the loss of ten individuals  
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31 240 (Fig. 8b). Plant size was not measured in 2012 because of the extremely low apparent growth  
32  
33 241 rates between 2010 and 2011: if plant size were the same between 2011 and 2012, then the total  
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35 242 resource area would have decreased by  $2.9\text{ m}^2$  to  $52\text{ m}^2$ , while remaining 15% greater than in  
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37 243 2010.  
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41  
42 245 The proportion of plants that flowered varied significantly amongst years ( $\chi^2=759$ ,  $df=4$ ,  $p<$   
43  
44 246  $0.001$ ). In 2002, 91% flowered ( $n=851$ ), but this dropped to 48% in the following year. In 2010  
45  
46 247 there were 96% of plants flowering ( $n=637$ ), remaining similar in 2011 at 98% ( $n=100$ ) before  
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48 248 dropping to 83% in 2012 ( $n=100$ ). The total number of flowers on 50 plants across 6 weeks of  
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3 249 flowering more than doubled between years, from 27,730 in 2010 to 63,704 in 2011, before  
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5 250 falling to 24,712 in 2012.  
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10 252 **Discussion**  
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15 254 Most of the theory of plant strategies in arid ecosystems actually concerns systems considerably  
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17 255 less arid than in Egypt. Although almost the wettest place in the country (second only to the  
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20 256 Mediterranean northwestern coast), according to the best (patchy) data we have the mountains of  
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22 257 South Sinai received only an average of 42.5 mm per year precipitation between 1970 and 1994,  
23  
24 258 and substantially less (15.5) between 2001 and 2009. These values are very much at the extreme  
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26  
27 259 end of considerations of the functioning of arid ecosystems: for example, Bai et al.'s (2012) study  
28  
29 260 of grazing and ecosystem function in the Eurasian steppe involved a precipitation gradient  
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31 261 running from 150 to 400 mm per year. This makes the Sinai situation interesting from a  
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33  
34 262 theoretical perspective. To unravel the drivers of plant reproduction and mortality will probably  
35  
36 263 require very long-term study because it is clear that many plants can survive for years of harsh  
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39 264 conditions, albeit with declining quality, only to resume flowering (and presumably growth)  
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41 265 when the occasional period (lasting 1-3 years) of good rain occurs. Although obscure because of  
42  
43  
44 266 lack of long-term meteorological data, the frequency of such periods appears to be every 10-15  
45  
46 267 years.  
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50 269 We found significant spatial variation in the size, condition and flowering amongst thyme  
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52 270 patches, indicating that the plant does respond to small-scale environmental variation. There  
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55 271 were large temporal fluctuations in flowering output, apparently in response to rainfall, with  
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3 272 important implications for populations of its associated herbivores. In one thyme patch there was  
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5 273 a 45% mortality rate over eight years of very little or no rainfall, whilst over the past 3 years,  
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8 274 despite heavy rainfall, there were further deaths and no recruitment. Droughts are predicted to  
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10 275 become increasingly frequent due to climate change (Giannakopoulos et al., 2009) and this may  
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12 276 have further detrimental consequences on this endangered plant, amplifying the extinction risk  
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15 277 (Verboom et al., 2010).  
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20 279 Arid environments often have high degrees of spatial and temporal variation in soil quality, with  
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22 280 nitrogen levels in the soil varying spatially across a few centimetres (Jackson and Caldwell,  
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24 281 1993). Nitrogen levels are often higher under shrub canopies than inter-shrub spaces, whilst  
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27 282 highly localised variation in rainfall also influences soil nutrient levels, leading to fitness  
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29 283 differences and differential survival. Varying amounts of shade will also influence plant fitness,  
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31 284 with light levels affecting photosynthesis and evaporation (Peek and Forseth, 2003). Despite this,  
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34 285 water is clearly the primary driver of productivity in arid environments and water levels are  
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36 286 influenced by many variables, such as soil permeability, incline or uneven rainfall distribution.  
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39 287 These variables interact to alter infiltration and surface run-off, which in turn affect the  
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41 288 vegetation (Davies et al., 2007; Pueyo et al., 2008). The patches on the massif vary in altitude,  
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43 289 gradient and shelter, and hence probably also climatically, with different temperatures, soil  
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46 290 moistures and nutrient levels. Patches on the Mt Sinai massif are fairly close and hence  
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48 291 presumably are not isolated from one another (currently under study), but there are a number of  
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50 292 more distant patches (James et al. 1983; Thompson, 2013) that may be completely isolated and  
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53 293 hence could potentially evolve different life history traits in flowering period or growth rate  
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55 294 (Montesinos-Navarro et al., 2010). Sinai Thyme has been marooned on these mountain-tops and  
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3 295 its population increasingly fragmented by long-term climate change over the last 5000 years.  
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6 296 Over the shorter term the threats come from habitat loss and damage from over-collection, and  
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8 297 possibly also over-grazing, resulting in smaller patch sizes and increased isolation (Hanski, 1991;  
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10 298 Hoyle and James, 2005), reducing or limiting dispersal and gene flow amongst patches.  
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15 300 Plant condition did not change significantly between years but there was great variation in the  
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17 301 density of inflorescences and proportion of flowering plants, with the magnitude but not the  
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19 302 direction of change differing among patches. This indicates that flowering responds much more  
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21 303 than leaf production to macro-variation in the climate. Flowering has a high water cost to the  
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23 304 plant (Galen et al., 1999): plants with fewer reserves probably conserve them by reducing  
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25 305 flowering during drought, or may simply be unable to bear the costs of flowering at all. Drought  
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27 306 stress thus negatively affects flowering but this typically increases again after renewed rainfall  
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29 307 (Galen et al., 1999; Carroll et al., 2001; Harrison, 2001).  
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32 308  
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36 309 Nearly half of the plants of Farsh Shoeib died between 2002 and 2010, a loss likely to be due to  
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38 310 drought-induced mortality because the patch was fenced off to prevent collection or grazing.  
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40 311 Plants in the Gulley fared best, probably because this drains the rest of the site and hence may  
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42 312 retain water the longest. The strong reduction in the condition of surviving plants occurred across  
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44 313 the whole patch, suggesting this is a stress response to reduced rainfall in an already arid  
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46 314 environment. Surviving thyme plants grew detectably larger over eight years, while smaller  
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48 315 individuals were clearly more at risk of dying. Smaller plants and juveniles are often more  
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50 316 susceptible to drought-based mortality in arid environments (Hamerlynck and McAuliffe, 2008;  
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52 317 Gilad et al., 2004), lacking the reserves of larger individuals that improve chances of survival  
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3 318 during adverse years (Reynolds et al., 1999). Drought can also reduce recruitment, an essential  
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5 319 process in maintaining populations; however recruitment is already an irregular event in arid  
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8 320 environments, dependent on sporadic rainfall (Wiegand et al., 2004; Andersen and Krzywinski,  
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10 321 2007). Although surviving plants were larger, they were also in a poorer condition despite two  
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12 322 periods of heavy rainfall in 2010. This shows that short but heavy rain is insufficient to produce  
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14 323 immediate recovery, and perhaps more than one year with good rain is needed to improve plant  
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16 324 condition and prevent further deaths. Soil moisture is critical in nutrient uptake and translocation  
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18 325 (Hu and Schmidhalter, 2005). One mechanism of drought tolerance is for plants to become  
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20 326 dormant: this is known to occur in other thyme species, and perhaps was responsible for the  
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22 327 decline in average condition measured here (Thompson et al., 2007).  
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29 329 The lack of new individuals or seedlings suggests that recruitment rate is very low despite the  
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31 330 apparent return of good conditions. *Thymus decussatus* can produce daughter plants via asexual  
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33 331 propagation by the rooting of branches (Zalat, 2013), and hence potentially does not rely much  
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35 332 on sexual reproduction via seed set. Other thyme species such as *Thymus loscosii*, a rare endemic  
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37 333 in arid Spain, reproduce sexually via seeds or asexually through above-ground vegetative stolons  
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39 334 which grow horizontally before rooting (Matesanz et al., 2009). Despite the possibility of  
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41 335 vegetative reproduction, the apparent absence of recruitment from seed in Sinai Thyme is  
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43 336 surprising given its high flowering output, particularly in 2011 when soil conditions were  
44  
45 337 presumably good. However, recruitment in arid environments is often a rare event. The harsh  
46  
47 338 conditions decrease the likelihood of successful seedling establishment, with water being the  
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49 339 main limiting factor. The high variability in the intensity and timing of precipitation can result in  
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51 340 sporadic recruitment events (Wiegand et al., 2004). For example, tree recruitment in the hyper-  
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3 341 arid Eastern desert of Egypt is very low; annual recruitment is, on average, between 0.31 and  
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5 342 0.60% with high seedling mortality rates being the foremost problem in establishment (Andersen  
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8 343 and Krzywinski, 2007). Recruitment in many arid environments can be too low for long-term  
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10 344 population survival. This is a concern for acacia trees in the Negev desert of Israel (Wiegand et  
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12 345 al., 2004), where substantial recruitment happens only episodically with rainfall events and the  
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14 346 corresponding resource pulse. However, acacias lack smaller more continuous recruitment  
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16 347 events, partially attributed to insufficient rainfall, and this threatens long-term population  
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18 348 persistence. Reliance on episodic recruitment is only viable for larger populations which can  
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20 349 survive long periods without new individuals; small yet continuous recruitment is required to  
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22 350 buffer against long periods between pulse events to ensure population survival (Wiegand et al.,  
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24 351 2004).

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31 353 A high proportion of plants flowered in 2010 and 2011, but this was followed by a large decline  
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33 354 in 2012, perhaps due to climate (rain followed by a year of no rainfall) or perhaps because of the  
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35 355 cost of flowering itself. Superimposed on the incidence of flowering, there were very large  
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37 356 fluctuations in the density of flowers per plant, more than doubling in 2011, followed by a big  
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39 357 decline. The productivity of vegetation in arid Africa responds to rainfall of the previous and  
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41 358 current years. If there are successive years of low rainfall, populations become caught in a  
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44 359 downward spiral of less flowering, reduced population size and longer recovery period. After  
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46 360 particularly wet years, often a one-year time lag is observed, with the vegetation flourishing the  
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48 361 subsequent year (Schwinning et al., 2004). This may be the case here; the 2010 rains may have  
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50 362 caused the flowering surge in 2011. This is perhaps an example of the memory effect, the soil  
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52 363 retaining the effects of excess rainfall and impacting plant productivity (Schwinning et al., 2004,  
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3 364 Martiny et al., 2005). However, the subsequent decline in flowering in 2012 suggests that rainfall  
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6 365 in the previous winter or the current year is very influential, since rainfall in late 2011 was absent  
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8 366 and hence perhaps insufficient to maintain the flowering.  
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12 368 Fluctuations in the number of flowers will ultimately affect the number and abundance of their  
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15 369 associated herbivores, and the Sinai Baton Blue butterfly in particular. The large decline in  
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17 370 flowering between years supports previous studies that climatic fluctuations could be responsible  
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20 371 for the large decline in butterfly numbers observed between 2002 and 2003 (James, 2006c).  
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22 372 Reduced resources increase competition, affecting the growth, performance and population  
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24 373 dynamics of insects (Boggs and Freeman, 2005; Kay et al., 2010), particularly in short-lived  
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26 374 herbivores with highly specific interactions (Ostfeld and Keesing, 2000).  
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### 31 377 **Acknowledgements**

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38  
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40  
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42  
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45 382 species conservation fund which made this work possible.  
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385 **Table 1** Distribution of plants in sections of Farsh Shoeib in 2002, 2010, 2011 and 2012.

	Number of individuals				disappearing 2002 to 2010		disappearing 2010 to 2011		disappearing 2011 to 2012	
	2002	2010	2011	2012	N <sup>o</sup> .	%	N <sup>o</sup> .	%	N <sup>o</sup> .	%
Gulley	242	148	148	148	94	39	0	0	0	0
Farsh I	244	136	134	133	108	44	2	1.5	1	0.7
Farsh II	366	136	132	127	230	63	4	2.9	5	3.8
Side arm	283	224	221	221	59	21	3	1.3	0	0
South	73	25	24	23	48	66	1	4	1	4.2
Overall	1208	669	659	652	539	45	10	1.5	7	1.1

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3 388 **Figure 1.** Map of the perimeter of the Sinai thyme (*Thymus decussatus*) patches upon the Mount  
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6 389 Sinai massif, with the dots indicating isolated individuals outside patches. 1) Farsh Safsafa 2)  
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8 390 Farsh Shoeib 3) Farsh Loza 4) Lower Hammar 5) Upper Hammar 6) Gulley Zahtuna 7) Gulley  
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10 391 Sharr 8) Elia Circle 9) Elia Garden 10) Farsh Elia. The Monastery of St Katherine is seen in the  
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12 392 top right of the map.  
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17 394 **Figure 2.** Comparisons of the size per plant in the patches of Sinai Thyme (*Thymus*  
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19 395 *decussatus*) on the Mt Sinai massif in 2011. Mean values  $\pm$  SE (n=100 per patch).  
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25 397 **Figure 3.** Comparison of measured aspects of plant quality in *Thymus decussatus* on the Mt.  
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27 398 Sinai massif in 2011 (white bars) and 2012 (striped bars): a) condition b) density of  
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29 399 inflorescences c) proportion of flowering plants. Mean values  $\pm$  SE, n=50 plants per patch.  
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35 401 **Figure 4.** A map of the thyme plants in Farsh Shoeib in 2002 (black dots) and 2010 (grey).  
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40 403 **Figure 5.** Frequency distribution of a) the height and b) width of the thyme plants in Farsh  
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42 404 Shoeib in 2002 (white bars) and 2010 (striped), n= 1208 in 2002 and 642 in 2010.  
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47 406 **Figure 6.** Comparison of the a) size and b) condition in 2010 and of those which subsequently  
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49 407 died. Mean values  $\pm$  SE.  
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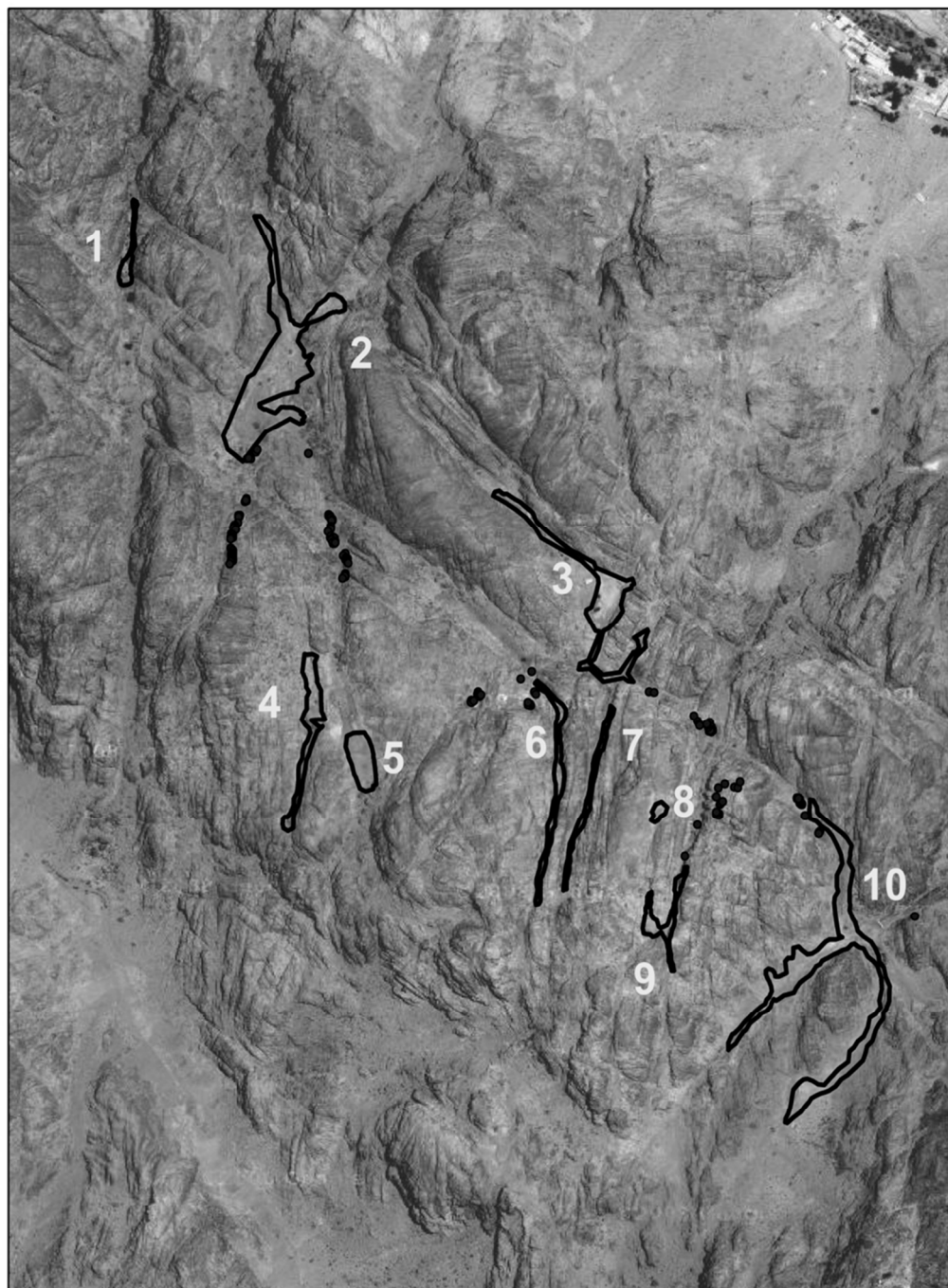
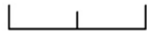
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3 409 **Figure 7.** Condition per plant amongst sections in Farsh Shoeib in 2002 (white bars), 2010  
4 (striped), 2011 (spotted) and 2012 (black). Mean values  $\pm$  SE, n= 1208, 642, 632 and 532  
5 410  
6 (striped), 2011 (spotted) and 2012 (black). Mean values  $\pm$  SE, n= 1208, 642, 632 and 532  
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8 411 respectively.  
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10 412  
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12 **Figure 8.** Comparisons of a) the average size and b) resource area per plant amongst sections in  
13 413  
14 Farsh Shoeib in 2002 (white bars), 2010 (striped) and 2011 (spotted). Mean values ( $\pm$  SE), n=  
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16 1208, 642, 632 respectively.  
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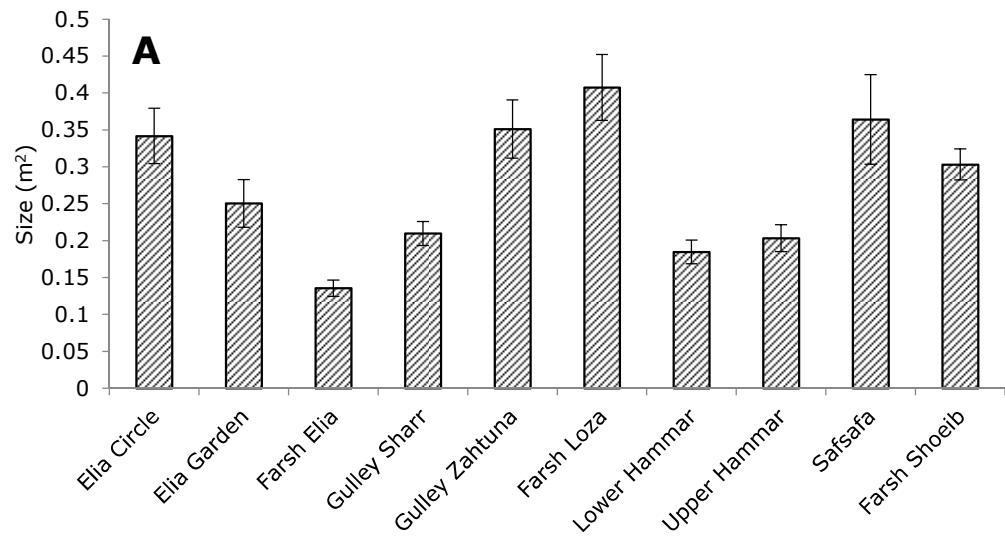
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418 Figure 1.





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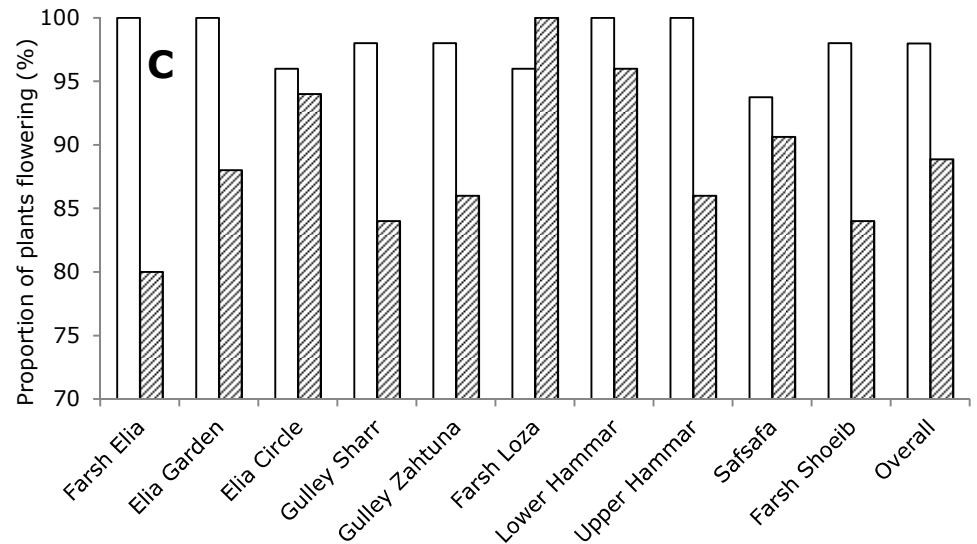
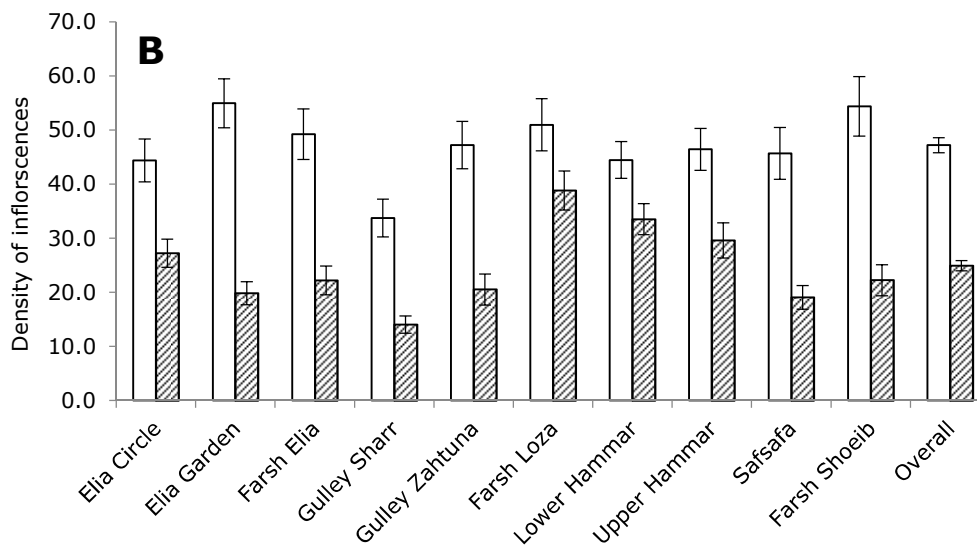
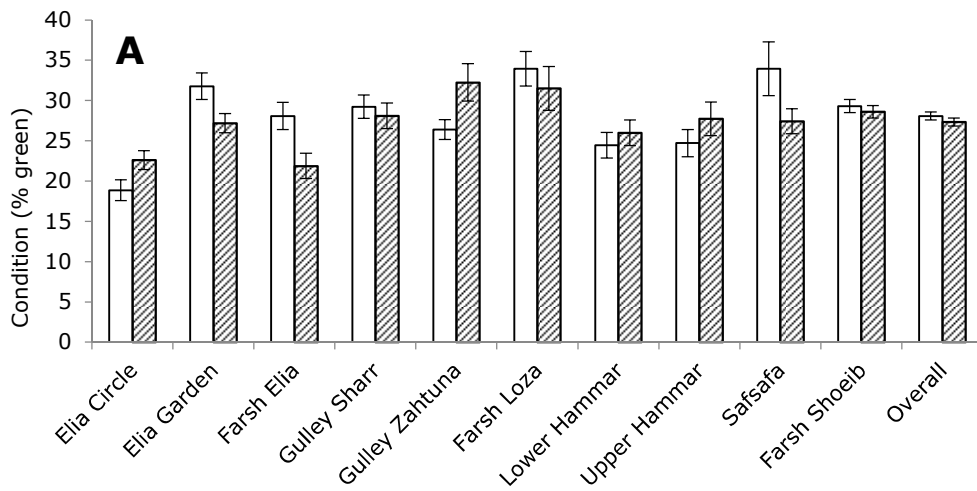
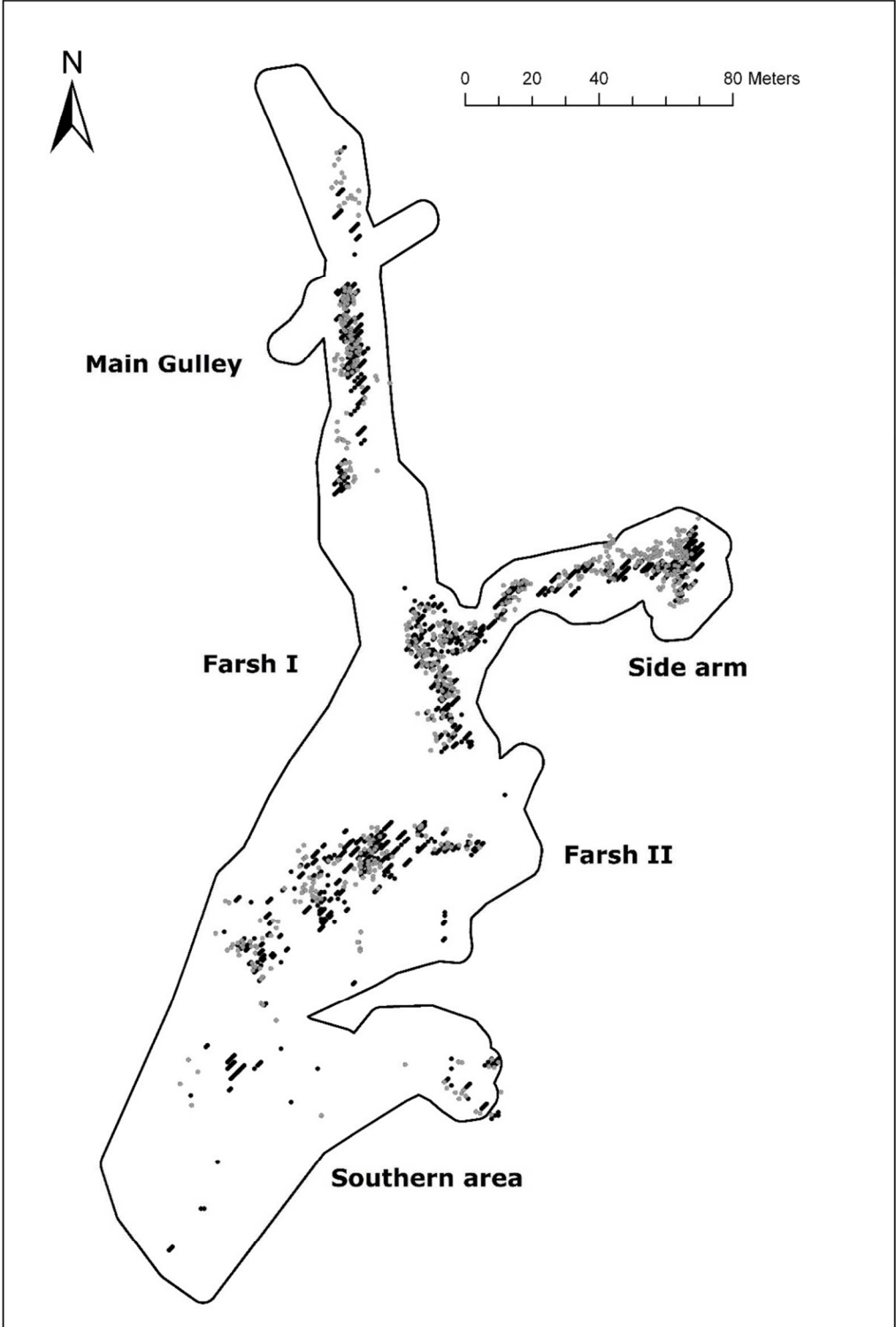


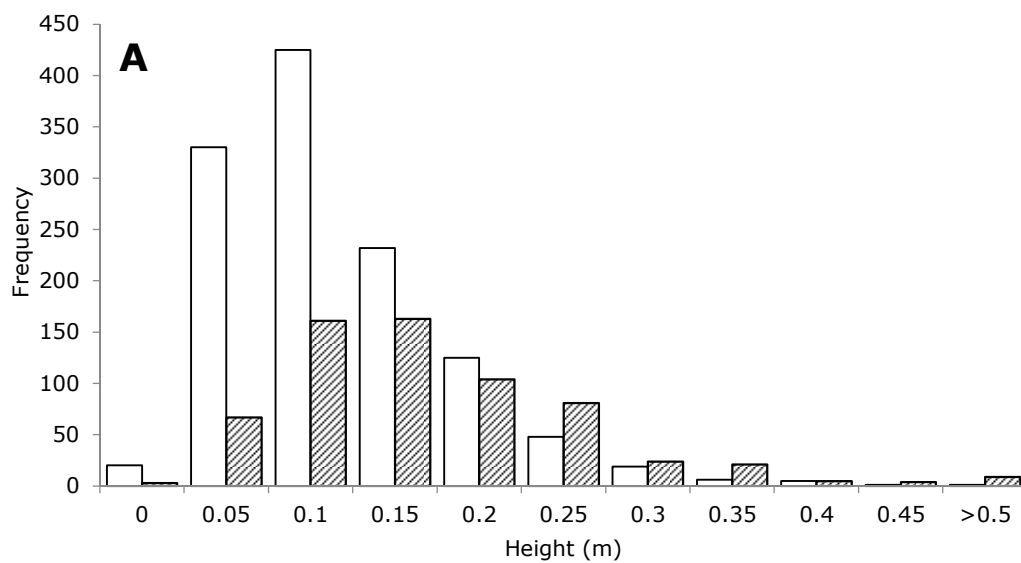
Figure 3.

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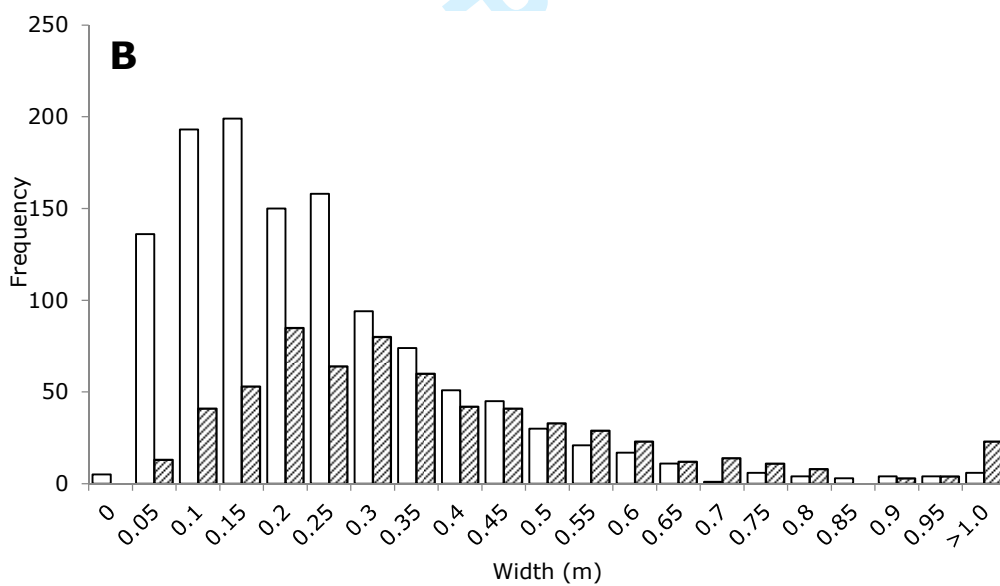


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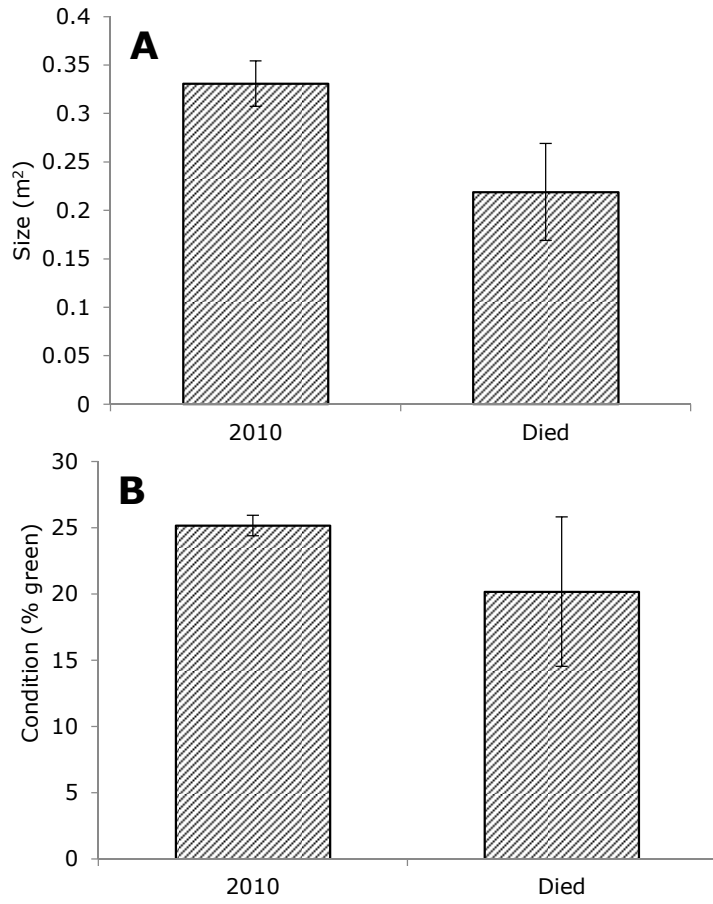
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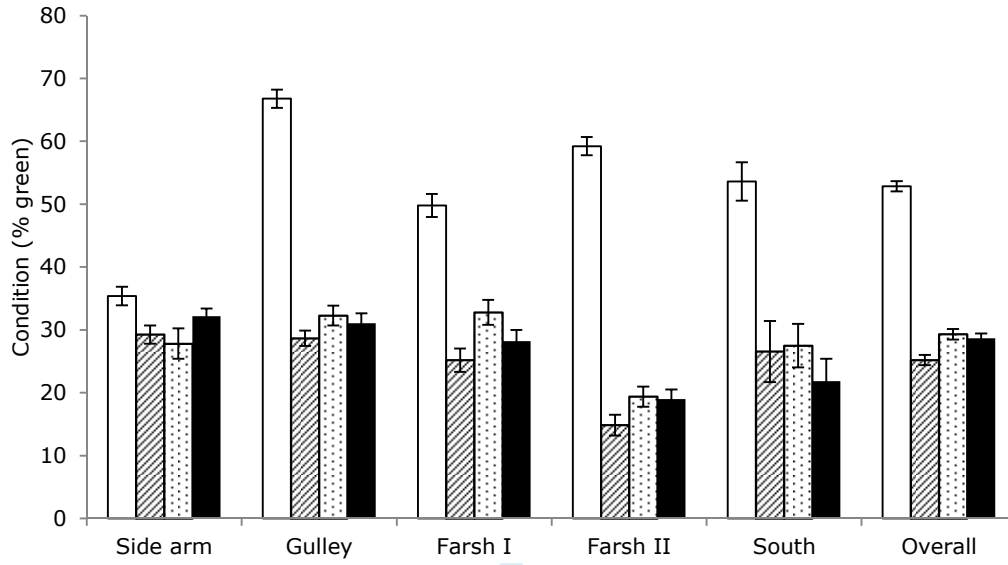
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434 Figure 6.

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437 Figure 7.

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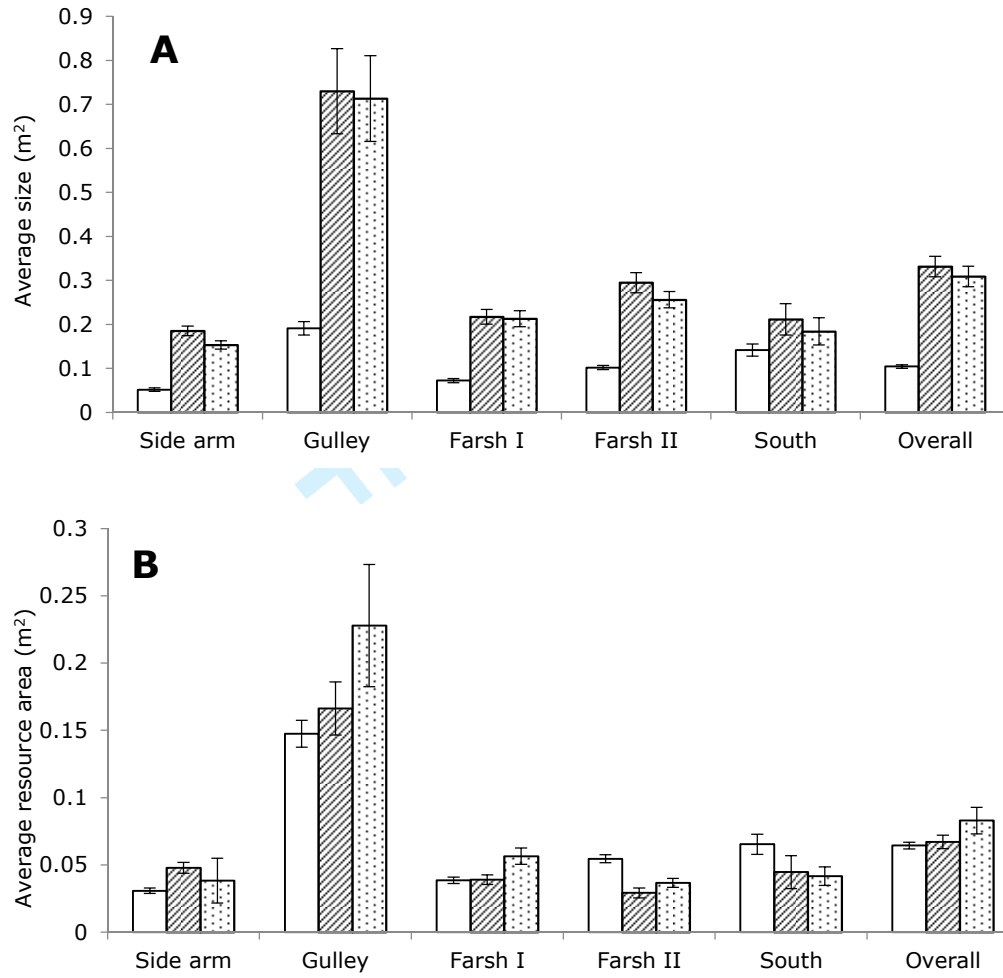


Figure 8.

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