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

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Abstract

Aims

Arid environments are resource limited, with scarcity of water the key limiting factor, but hyper-arid environments are rarely studied. We test for spatial and temporal variation in ecologically important characteristics to deduce plant adaptations to the extreme climate.

Methods

The endangered Sinai Thyme (*Thymus decussatus*) exists as a set of patches on mountaintops within the St Katherine Protectorate, South Sinai, a hyper-arid environment with rare events of good rains (every 10–15 years).

Important Findings

From spatial and temporal patterns of plant mortality, size, condition and flowering among 10 patches on the Mt Sinai massif, we deduce that the incidence and amount of flowering responds relatively quickly (1–2 years) to rainfall fluctuations, but plant growth respond only very slowly. Small individuals are most at risk of death during drought, and a high proportion of plants were dead at the end of 8 years of very low or no rainfall. No recruitment of seedlings was observed even in years of good rainfall. Droughts are expected to become increasingly frequent due to climate change; this may have important consequences for Sinai Thyme and also its associated herbivores, such as the Critically Endangered Sinai Baton Blue (*Pseudophilotes sinaicus*) whose larval stage feeds exclusively upon the flowers of this plant.

Keywords: spatial variation, temporal fluctuations, resource availability, drought, Egypt

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INTRODUCTION

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

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

There are often complex interactions between abiotic and biotic components affecting the growth and condition of plants, including many spatial effects (Bai *et al*. 2008), and hence no single variable can predict plant growth (Robertson *et al*. 2009). Environmental variation can act synergistically with geomorphological and edaphic features to cause variation in distribution (Bestelmeyer *et al*. 2006; Ju *et al*. 2008), abundance (Reynolds *et al*. 2004), productivity (Popp *et al*. 2009) and mortality (Hamerlynck and McAuliffe 2008) of plants. Habitat heterogeneity can also influence plant life history traits such as growth and phenology (Gaston *et al*. 2004; Montesinos-Navarro *et al*. 2010). For example, populations of *Arabidopsis thaliana* (Brassicaceae) have different biomass allocation, fecundity and phenology depending upon altitude; these traits have a genetic basis indicating previous selection for local adaptation (Montesinos-Navarro *et al*. 2010).

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

Here we study a rare plant growing in the hyper-arid mountains of the St Katherine Protectorate in South Sinai in Egypt, the most arid country in the world (FAO 2012). The hyper-aridity of Egypt's ecosystems is well off the scale of most studies of gradients of precipitation (e.g. Bai *et al*. 2008, 2012; Rodriguez-Castañeda 2013), and there is very little research in arid ecosystems in general (Rodriguez-Castañeda 2013). The flowers are the sole food for the Critically Endangered Sinai Baton Blue butterfly, the flagship conservation target of the Protectorate. Thus understanding the key drivers of plant vitality and flowering output in the hyper-arid environment is an important component of the long-term strategy to conserve both plant and butterfly. We test for spatial and temporal differences in ecologically relevant plant characteristics to deduce the relative impact of large- or small-scale climate differences, and deduce adaptations to and consequences of the extreme conditions.

MATERIALS AND METHODS

The study system

The Sinai Thyme (*Thymus decussatus* Bentham 1834) is an endangered plant occurring only >1500 m altitude within the St Katherine Protectorate (and recorded once from an adjacent area in Saudi Arabia; James 2006a). It grows best in well-defined soil at the base of cliffs and wadis, resulting in a naturally patchy distribution (Nakamura 1975). Its population is becoming increasingly fragmented by long-term climate change over the last 5000 years. Over the shorter term, the threats come from habitat loss and damage from over-collection, and possibly also overgrazing, resulting in smaller patch sizes and increased isolation (Hanski 1991; Hoyle and James 2005). *Thymus* species are regarded as indicators of degradation by grazing in arid environments because their characteristic small leaves resist the impact of drought and grazing (Navarro *et al*. 2006). The fieldwork was carried out upon the Mt Sinai massif above the town of St Katherine, where there are 10 patches of thyme: Farsh Shoeib, Farsh Loza, Farsh El Hammar (Lower and Upper), Farsh Elia, Elia Garden, Elia Circle, Farsh Safsafa, Gulley Zahtuna and Gulley Sharr (Fig. 1). The first five patches were discovered in 2001 (James *et al*. 2003), but the rest were only found in 2011. We decided whether plants formed a discrete patch if there were more than 30 plants closely situated, separated from another patch by either 100 m or a natural barrier (which was often the situation on the Mt Sinai massif). The plants located outside the patches were sparsely distributed with considerable distances between them. The Farsh Shoeib patch (28.553° N, 33.965° E) was studied in detail in 2002 (James 2006d), which enabled us to look at temporal variation in the thyme: our fieldwork focused on Farsh Shoeib in spring 2010, whereas all patches were studied in 2011 and 2012.

In 2001, Farsh Shoeib held one of the largest populations of the Critically Endangered Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura 1975), whose larval stages are monophagous on the flower buds of Sinai Thyme (James *et al*. 2003). As a conservation effort to protect both plant and butterfly, the majority of the patch was fenced off in 2003 to prevent public access, grazing and any damage to the plants; only a few plants are found outside the enclosure in this patch. Two large dams were built specifically for conservation purposes in 2003 to hold more water in the soil after flash floods (Thompson and Gilbert 2013).

There have been severe fluctuations in the weather over the past decade. Since 2002, when the first and only other study was carried out, there has been severe drought with very little (<50 mm) or no rain every year until March 2010. This drought was broken in May 2010 when there was heavy rainfall, which left parts of Farsh Shoeib submerged for over a week. 2011 was again extraordinarily wet, with heavy rainfall and snow in the winter and spring, while 2012 had very little rainfall and was colder than normal. The extent to which these variations are normal for the area is uncertain because of incomplete meteorological records, and we are dependent on local Bedouin knowledge. Although almost the wettest place in the country (second only to the Mediterranean northwestern coast), according to the best (patchy) data we have, the mountains of South Sinai received only an average of 42.5 mm per year precipitation between 1970 and 1994, and substantially less (15.5) between 2001 and 2009 (data courtesy of the St Katherine Protectorate Management Unit).

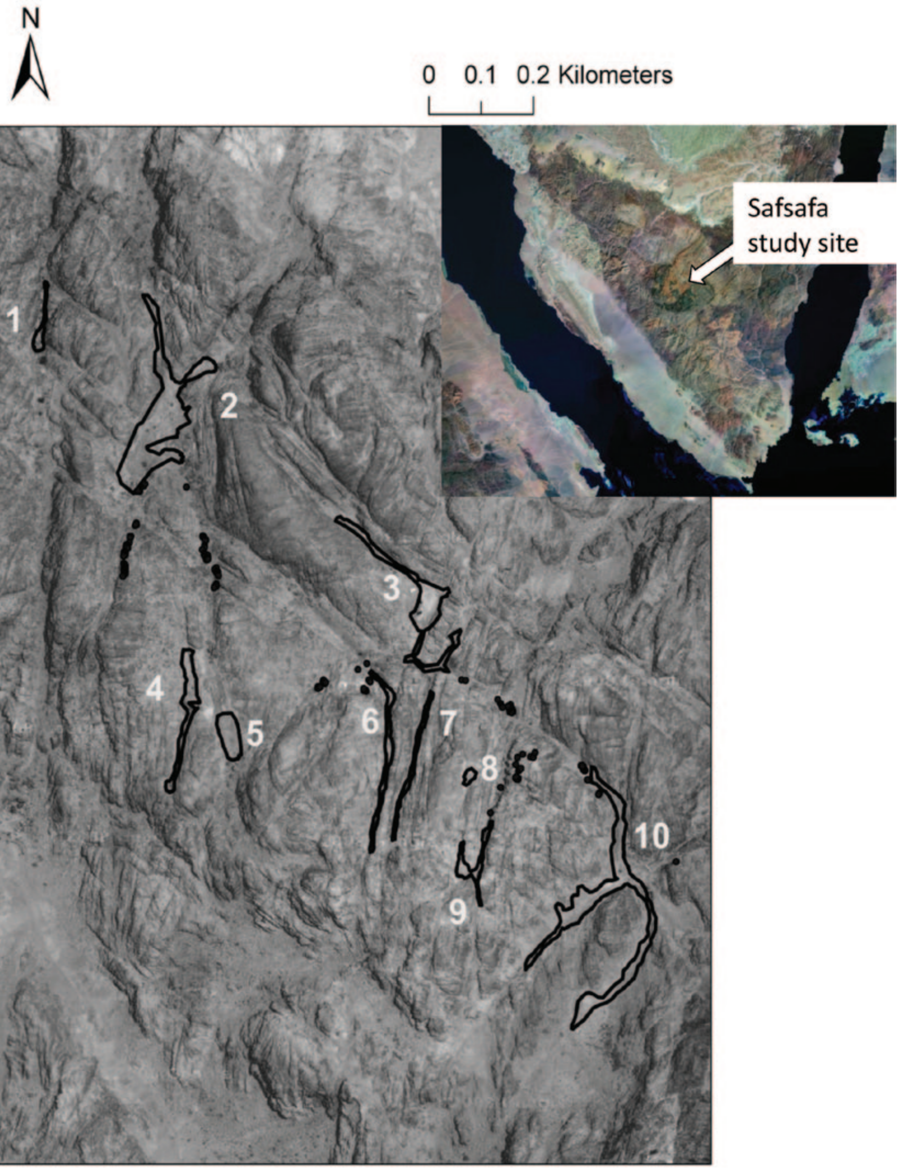

Figure 1: map of the perimeter of the Sinai thyme (*Thymus decussatus*) patches upon the Mt Sinai massif, with the dots indicating isolated individuals outside patches. (1) Farsh Safsafa, (2) Farsh Shoeib, 3) Farsh Loza, (4) Lower Hammar, (5) Upper Hammar, (6) Gulley Zahtuna, (7) Gulley Sharr, (8) Elia Circle, (9) Elia Garden and (10) Farsh Elia.

Mapping and measuring the plants

We carried out two different mapping techniques: a detailed map of the individual plants in Farsh Shoeib, and outline perimeters of the remaining nine patches. A fairly detailed map of the plants in Farsh Shoeib was created in 2002 by James (2006b), where he mapped particular individuals and attributed the surrounding set of close neighbours to that location. His data enabled us to study spatial and temporal variation in the thyme within Farsh Shoeib.

The boundary of the 10 patches on the massif were mapped by walking around the perimeter and recording the track using a hand-held Global Positioning System (GPS) unit (Garmin etrex Venture HC, found to be accurate to ±10 m); the waypoints from the tracks were then imported into ArcGIS 9.3. Each plant situated outside a patch was individually labelled and its position recorded using the GPS unit.

To map Farsh Shoeib, we recorded each individual plant relative to the nearest of 12 landmarks by measuring its distance and the bearing. The coordinates of each landmark were repeatedly recorded over several months using a hand-held GPS unit, providing accurate average positioning. The distances and bearings were converted into coordinates to get an accurate location for each plant in Farsh Shoeib relative to the landmark features, plotted using ArcGIS. The 2010 mapping was much more detailed than in 2002, when James (2006b) did not map all of the plants individually within Farsh Shoeib.

This made it impossible to re-identify his individuals to monitor the changes over time directly. He did, however, divide the site into five sections, and we could therefore compare all individuals within each of these sections.

In order to compare the quality, mortality and recruitment data of thyme plants in Farsh Shoeib with the data collected in 2002, in 2010 and 2011, each plant was identified and labelled, and its height, two perpendicular widths and condition (the proportion of the plant that was green) measured, the same variables that James (2006b) recorded in 2002. We did not record the size in 2012 due to the slow growth rate and the relatively large measurement error involved in determining the widest part of the plant. In these cushion plants, plant size was estimated by surface area, calculated by assuming each plant was a hemi-ellipsoid. The 'resource area' for each plant was then calculated from 'plant size' multiplied by the condition (as a proportion). The numbers of flowers on 50 randomly chosen plants from an area particularly dense with plants (the Gulley, see Fig. 4) were counted during the first 6 weeks of flowering in 2010, 2011 and 2012. The proportion of flowering plants were compared by weekly inspections of 637 individuals in 2010 and of 100 randomly selected plants in 2011 and 2012.

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

Analysis of data

All analyses used the statistical package R 2.14.1 (R Development Core Team 2012) and models were simplified in accordance to Zuur *et al.* (2009) based on the Akaike Information Criterion criterion and stepwise backwards deletion of model terms. To test for spatial differences across the massif, a generalized linear model (GLM) compared plant size among patches in 2011. Size was logarithmically transformed (normalising it) and analysed using the R routine *glm*, with significance assessed with an F ratio. Plant condition, density of inflorescences and proportion of plants that flowered were compared in turn using a GLM to test for differences between years (2011 and 2012) and among patches. Condition and density of inflorescences were over-dispersed and so the GLM had a *quasi*-poisson error structure with significance tested with an F ratio; the proportion of flowering plants had a binomial distribution, tested with χ^2.

Using the R routine *glm*, we compared the number and quality of sets of plants (sections) in 2002, 2010 and 2011. We used plant condition and size as response variables, and year (2002, 2010 and 2011) and section as predictors. Condition and log(size) were normally distributed; significance was assessed for both with an F ratio. Similar GLMs with binomial distributions compared the mortality and the proportion of flowering plants, tested with χ^2. To see if there was a significant difference in the characteristics of the plants that have died since 2010, we ran a t test to compare the size and condition of surviving individuals against those that subsequently died. For all analyses, we used all the collected data to increase the strength of our analysis regardless of the differences in sample sizes between patches.

RESULTS

Spatial variation across the massif

Across the 10 patches upon the Mt Sinai massif, there was a combined resource area of 174 m^2 in 2011. Farsh Shoeib held the largest amount of resource, with 54.8 m^2 of green thyme (32% of the total on the massif). Mean plant size showed significant spatial differences (F = 9.82, df = 9,1460, P < 0.001; Fig. 2). There was also significant spatial variation in condition (F = 6.05, df = 9,2426, P < 0.001), but no differences

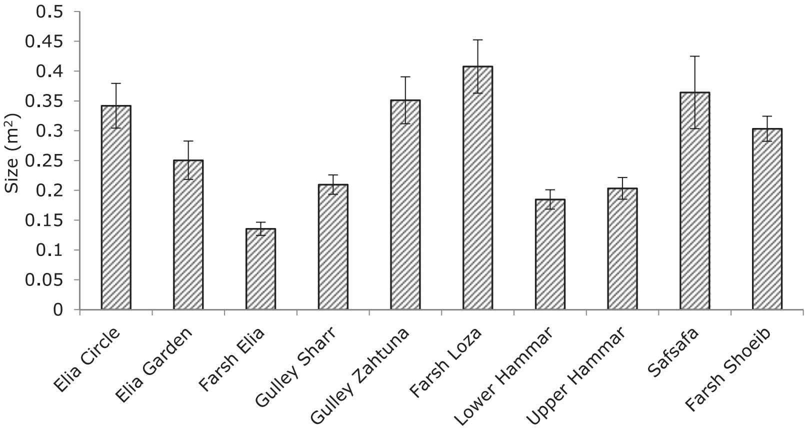

Figure 2: comparisons of the size per plant in the patches of Sinai Thyme (*Thymus decussatus*) on the Mt Sinai massif in 2011. Mean values ± SE.

between years ($F = 0.82$, df = 1,2426, $P = 0.36$) nor convincing evidence of an interaction ($F = 1.82$, df = 9,2426, $P = 0.06$). In 2011, there was a 15.1% difference between the healthiest (largest average condition) and unhealthiest patches and a 10.4% difference in 2012 (Fig. 3a). Overall, the average condition decreased by 0.7% between years, and if plant size remained constant, this would have caused a loss of 5.6 m^2 of green thyme across the massif.

The density of inflorescences varied significantly among patches ($F = 3.89$, df = 9,953, $P < 0.001$) and between years ($F = 193$, df = 1,953, $P < 0.001$), with a significant interaction between these two factors ($F = 3.8$, df = 9,953, $P < 0.01$). The average density of inflorescences across the massif decreased from 47.2 per 10 cm^2 in 2011 to 24.9 in 2012. The largest decline (of 33.2, $n = 50$) was seen in Elia Garden, the patch that had flowered most prolifically in 2011 (Fig. 3b). The proportion of flowering plants also varied significantly between years ($\chi^2 = 41.8$, df = 2, $P < 0.001$), but there was no evidence of any spatial variation ($\chi^2 = 9.64$, df = 9, $P = 0.38$) nor of any interaction ($\chi^2 = 14.5$, df = 9, $P = 0.11$). The overall proportion of flowering plants decreased from 98% to 89% in 2012, with inconsistent changes among patches (Fig. 3c).

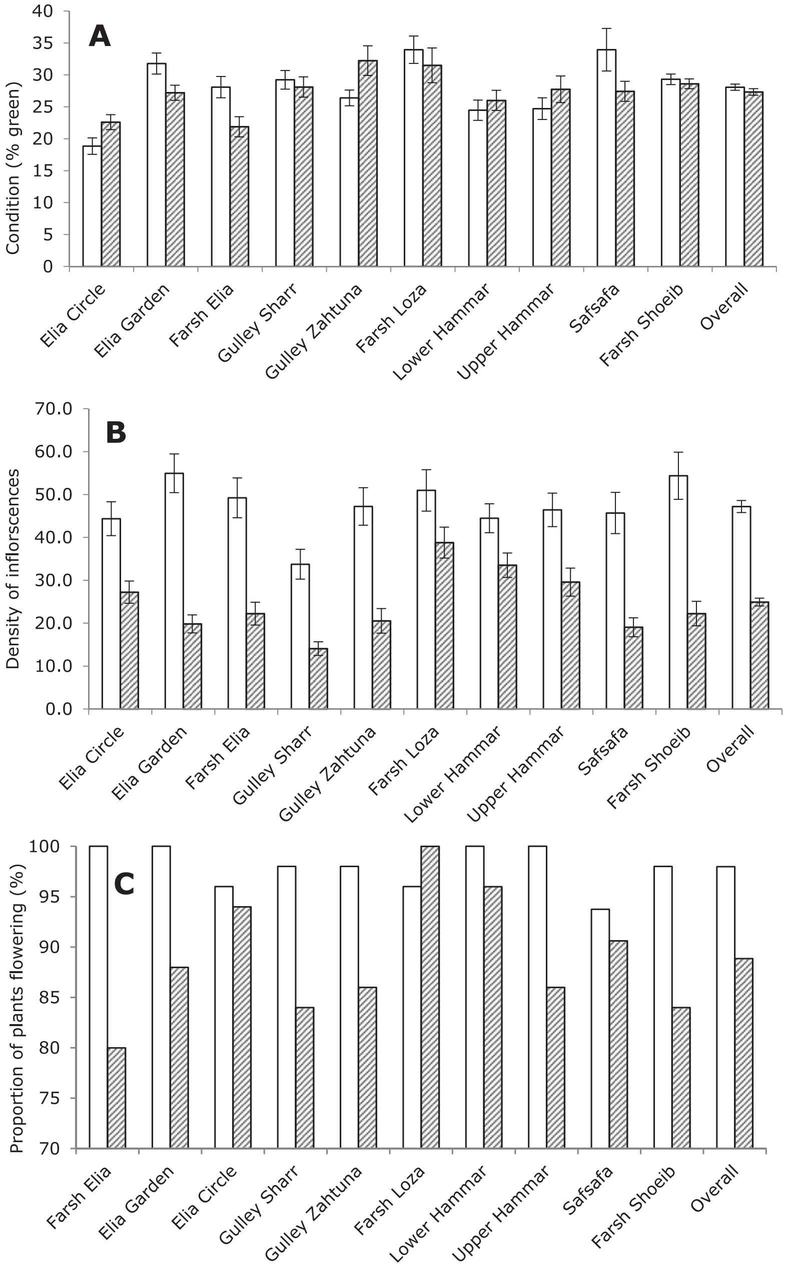

Figure 3: comparison of measured aspects of plant quality in *Thymus decussatus* on the Mt Sinai massif in 2011 (white bars) and 2012 (striped bars): (A) condition, (B) density of inflorescences in a 10 × 10 cm quadrat and (C) proportion of flowering plants. Mean values ± SE.

Temporal variation within Farsh Shoeib

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

Plant condition varied significantly with year ($F = 774$, df = 3,3035, $P < 0.001$) and patch ($F = 22.4$, df = 4,3035, $P < 0.001$), and there was also an interaction ($F = 73.7$, df = 12,3035 $P < 0.001$). Between 2002 and 2010, plant condition decreased from 53% to 25%; one-third of the surviving plants were <10% green (Fig. 7). Average plant condition rose to 29.3% in 2011, before declining slightly to 28.6% in 2012. The plants in Farsh II (see Fig. 4) consistently had the poorest

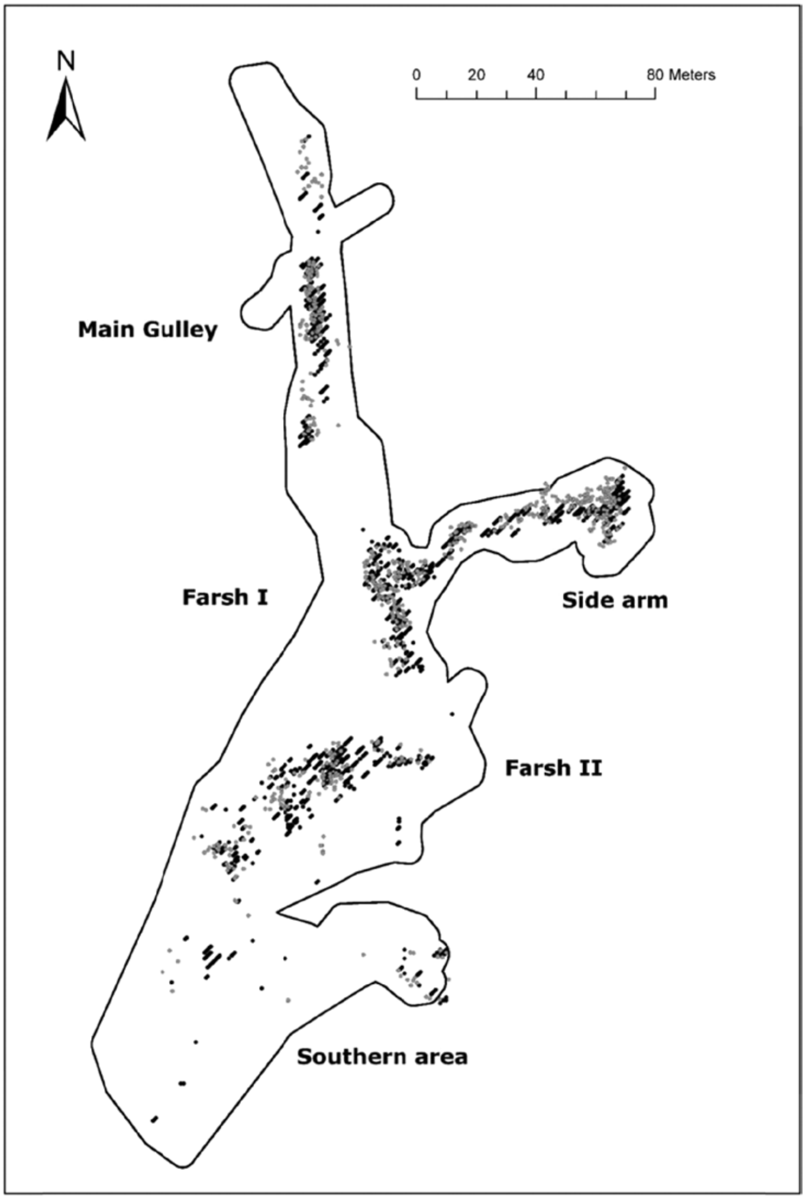

Figure 4: a map of the thyme plants in Farsh Shoeib in 2002 (black dots) and 2010 (grey).

Table 1: **distribution of plants in sections of Farsh Shoeib in 2002, 2010, 2011 and 2012**

	Number of individuals				Disappearing 2002–2010		Disappearing 2010–2011		Disappearing 2011–2012	
	2002	2010	2011	2012	*N*	(%)	*N*	(%)	*N*	(%)
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)

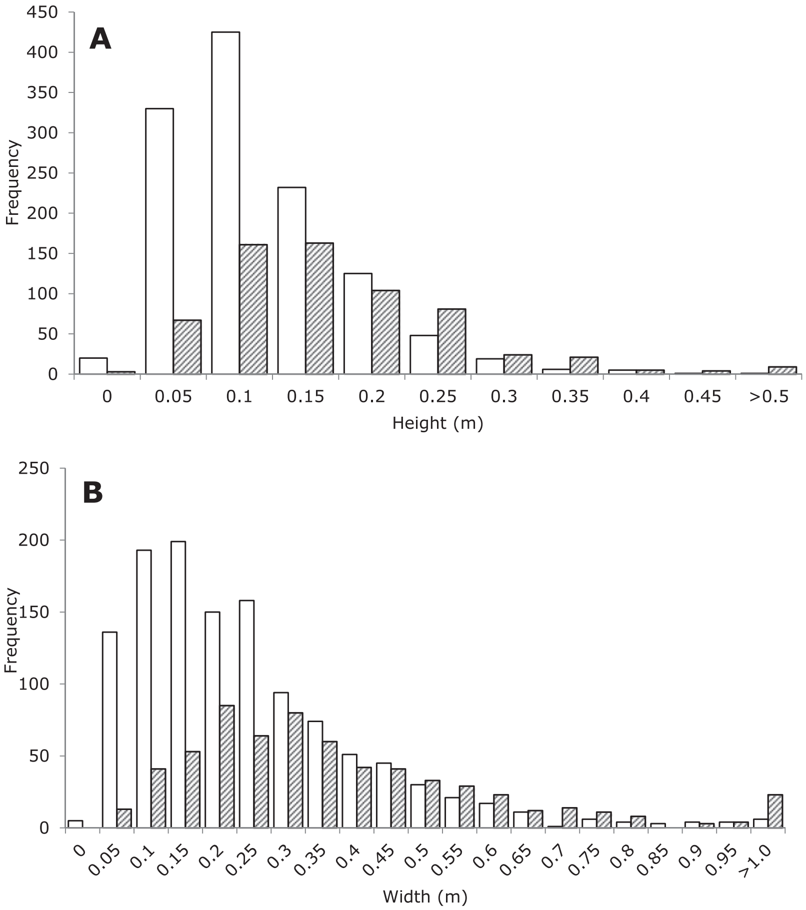

Figure 5: frequency distribution of (A) the height and (B) width of the thyme plants in Farsh Shoeib in 2002 (white bars) and 2010 (striped), *n* = 1208 in 2002 and 642 in 2010. Sample sizes are slightly different from Table 1 because extra individuals were discovered during the season.

condition, and this was the location of more than half of the mortalities.

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

Between 2002 and 2010, there was an overall increase in resource area of 28 cm^2 per plant, but the change was inconsistent across the patch; plants in the Gulley gained 189 cm^2 resource area per plant, while those of Farsh II lost 254 cm^2 (Fig. 8b). Although the average resource area per plant remained similar, the loss of individuals meant that the total

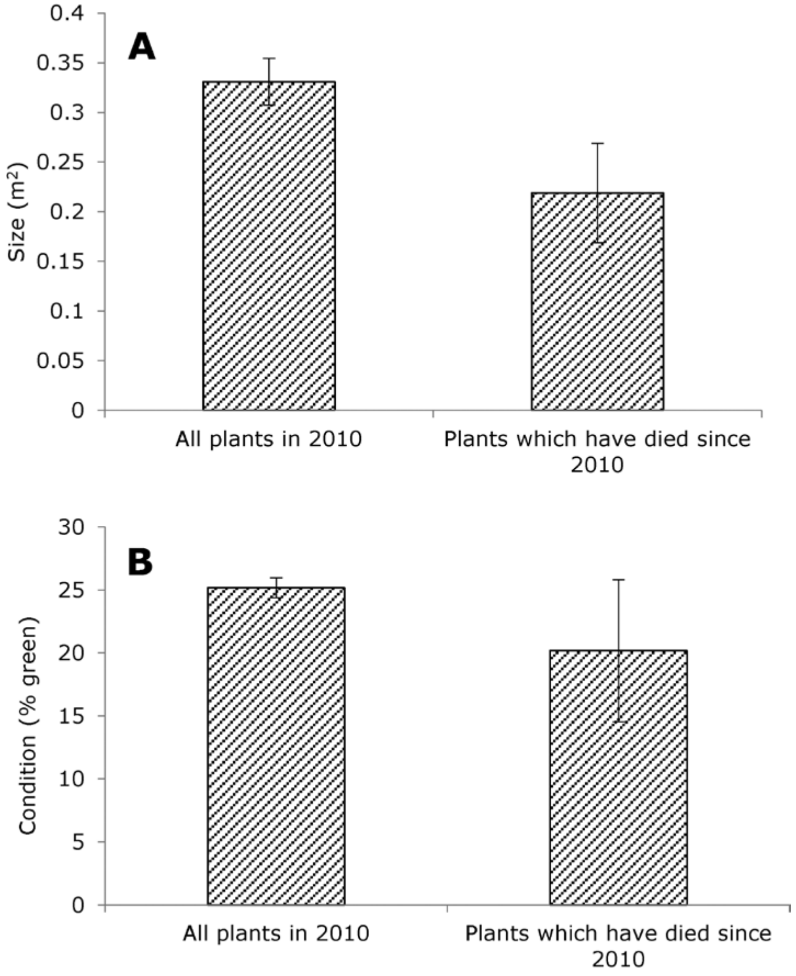

Figure 6: comparison of the (A) size and (B) condition in 2010 and of those which subsequently died. Mean values ± SE.

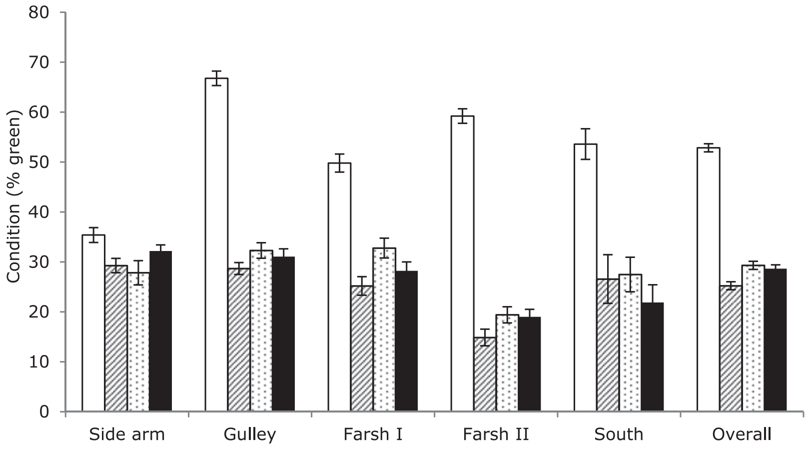

Figure 7: condition per plant among sections in Farsh Shoeib in 2002 (white bars), 2010 (striped), 2011 (spotted) and 2012 (black). Mean values ± SE, n = 1208, 642, 632 and 532, respectively. Sample sizes are slightly different from Table 1 because extra individuals were discovered during the season.

resource area reduced dramatically from 76 m^2 in 2002 to 45 m^2 in 2010. Overall, the plants were slightly smaller in 2011 than in 2010 (Fig. 8a), but an increase in condition resulted in a rise in resource area per plant, increasing the total patch resource area by 9.7–55 m^2, despite the loss of 10 individuals (Fig. 8b). Plant size was not measured in 2012 because of

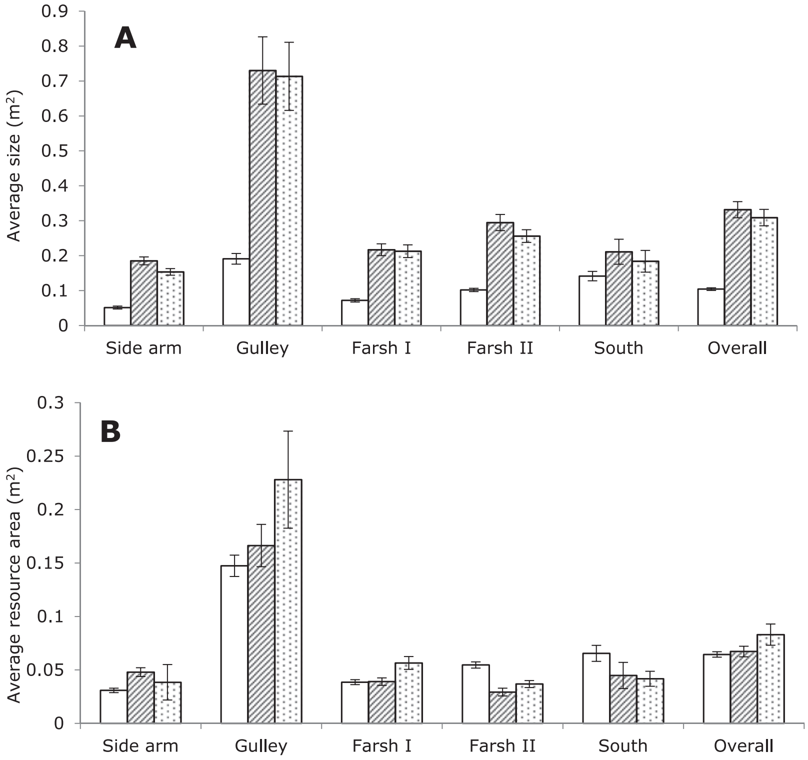

Figure 8: comparisons of (A) the average size and (B) resource area per plant among sections in Farsh Shoeib in 2002 (white bars), 2010 (striped) and 2011 (spotted). Mean values (± SE), *n* = 1208, 642, 632, respectively. Sample sizes are slightly different from Table 1 because extra individuals were discovered during the season.

the extremely low apparent growth rates between 2010 and 2011; if plant size were the same between 2011 and 2012, then the total resource area would have decreased by 2.9–52 m², while remaining 15% greater than in 2010.

The proportion of plants that flowered varied significantly among years (χ^2 = 759, df = 4, $P < 0.001$). In 2002, 91% flowered (*n* = 851), but this dropped to 48% in the following year. In 2010, there were 96% of plants flowering (*n* = 637), remaining similar in 2011 at 98% (*n* = 100) before declining to 83% in 2012 (*n* = 100). The total number of flowers on 50 plants across 6 weeks of flowering more than doubled between years, from 27 730 in 2010 to 63 704 in 2011, before falling to 24 712 in 2012.

DISCUSSION

Most of the theory of plant strategies in arid ecosystems actually concerns systems considerably less arid than the hyperaridity of Egypt. The levels of precipitation are very much at the extreme low end of considerations of the functioning of arid ecosystems: e.g. the study by Bai *et al.* (2012) on grazing and ecosystem function in the Eurasian steppe involved a precipitation gradient running from 150 to 400 mm per year, the minimum already almost 3 times higher than in Sinai. This makes the Sinai situation interesting from the theoretical perspective of adaptation to extreme environments, extending the range of responses to an aridity gradient. To unravel the drivers of plant reproduction and mortality will probably require very long-term study because it is clear that many plants can survive for years or even decades of harsh conditions, albeit with declining quality, only to resume flowering (and presumably growth) when the occasional period (lasting 1–3 years) of good rain occurs. Although obscure because of lack of long-term meteorological data, the frequency of such periods appears to be every 10–15 years. There were indications in our data that the thyme plants responded to rainfall by an increased flowering after a 1-year delay, and this effort was followed by reduced flowering in the subsequent year, perhaps because plants were devoting resources to growth. Only longer term data will tell. These changes in flowering output have important implications for populations of its associated herbivores, especially the Critically Endangered Sinai Baton Blue butterfly (James 2006a–d; James *et al.* 2003). Despite the recent rains, there has been high mortality of plants without any signs of recruitment. Droughts are predicted to become increasingly frequent due to climate change (Giannakopoulos *et al.* 2009) and this may have further detrimental consequences on this endangered plant, amplifying the extinction risk (Verboom *et al.* 2010).

The spatial variation in ecologically relevant characteristics among thyme patches indicates that the plant does respond to small-scale environmental variation. Arid environments often have high degrees of spatial and temporal variation in many aspects important for living organisms: e.g. nitrogen levels can vary spatially across a few centimetres (Jackson and Caldwell 1993; light variation is particularly strong between shade and sun, affecting photosynthesis and evaporation (Peek and Forseth 2003). Despite this, water is clearly the primary driver of productivity in arid environments, and in deserts, rainfall can be particularly highly localized in space (Sharon 1972) as well as in time. Water levels are influenced by many variables, such as soil permeability, incline or uneven rainfall distribution, interacting to alter infiltration and surface run-off, which in turn affect the vegetation (Davies *et al.* 2007; Pueyo *et al.* 2008). The patches on the Safsafa massif in Sinai vary in altitude, gradient and shelter and hence probably also climatically, with different temperatures, soil moistures and nutrient levels.

When comparing the plants within the patches on the massif, their condition did not change significantly between years, but there was great variation in the density of inflorescences and proportion of flowering plants, with the magnitude but not the direction of change differing among patches. This indicates that flowering responds much more to macro-variation in the climate than other aspects of the plant, such as leaf production or growth. Flowering has a high water cost to the plant (Galen *et al.* 1999): plants with fewer reserves probably conserve them by reducing flowering during drought, or may simply be unable to bear the costs of flowering at all. Drought stress thus negatively affects flowering, but this typically increases again after renewed rainfall (Carroll *et al.* 2001; Galen *et al.* 1999; Harrison 2001).

Nearly half of the plants in Farsh Shoeib died between 2002 and 2010, a loss likely to be due to drought-induced mortality because the patch was fenced off to prevent collection or grazing. Plants in the Gulley fared best, probably because this drains the rest of the site and hence may retain water the longest. The strong reduction in the condition of surviving plants occurred across the whole patch, suggesting this is a stress response to reduced rainfall in an already arid environment. Surviving thyme plants grew detectably larger over 8 years, while smaller individuals were clearly more at risk of dying. Smaller plants and juveniles are often more susceptible to drought-based mortality in arid environments (Gilad *et al.* 2004; Hamerlynck and McAuliffe 2008), lacking the reserves of larger individuals that improve chances of survival during adverse years (Reynolds *et al.* 1999). Drought can also reduce recruitment, an essential process in maintaining populations; however, recruitment is already an irregular event in arid environments, dependent on sporadic rainfall (Andersen and Krzywinski 2007; Wiegand *et al.* 2004). Although surviving plants were larger, they were also in a poorer condition than 2002, despite two periods of heavy rainfall in 2010. This shows that short but heavy rain is insufficient to produce immediate recovery, and perhaps more than 1 year with good rain is needed to improve plant condition and prevent further deaths. Soil moisture is critical in nutrient uptake and translocation (Hu and Schmidhalter 2005). One mechanism of drought tolerance is for plants to lose their leaves and become dormant; this is known to occur in other Mediterranean plants (Thompson *et al.* 2007), but Sinai thyme does not lose its leaves at any time during the year. If there were non-obvious summer dormancy, it might perhaps have been responsible for the decline in average condition measured here.

The lack of new individuals or seedlings suggests that recruitment rate is very low despite the apparent return of good conditions. *Thymus decussatus* can produce daughter plants *via* asexual propagation by the rooting of branches (Zalat 2013), and preliminary data show relatively low seed set per flower (Zalat 2013). Other thyme species such as *Thymus loscosii*, a rare endemic in arid Spain, also reproduce sexually *via* seeds or asexually through above-ground vegetative stolons that grow horizontally before rooting (Matesanz *et al.* 2009). Despite the possibility of vegetative reproduction, the apparent absence of recruitment from seed (either directly or from a seed bank in the extremely poorly developed and patchy soil) in Sinai Thyme is surprising given its high flowering output, particularly in 2011 when soil conditions were presumably good. However, recruitment in arid environments is often a rare event. The normally harsh conditions decrease the likelihood of successful seedling establishment, with water being the main limiting factor, so that the high variability in the intensity and timing of precipitation leads to sporadic recruitment events (Wiegand *et al.* 2004). For example, tree recruitment in the hyper-arid Eastern desert of Egypt is very low; annual recruitment is, on average, between 0.31% and 0.60% with high seedling mortality rates being the foremost problem in establishment (Andersen and Krzywinski 2007). Recruitment in many arid environments can be too low for long-term population survival. This is a concern for acacia trees in the Negev desert of Israel (Wiegand *et al.* 2004), where substantial recruitment happens only episodically with rainfall events and the corresponding resource pulse. The lack of small-scale, more continuous recruitment events threatens long-term population persistence. Reliance on episodic recruitment is only viable for larger populations that can survive long periods without new individuals; small yet continuous recruitment is required to buffer against long periods between pulse events to ensure population survival (Wiegand *et al.* 2004).

A high proportion of plants flowered in 2010 and 2011, but this was followed by a large decline in 2012, perhaps due to climate (rain followed by a year of no rainfall) or perhaps because of the cost of flowering itself. Superimposed on the incidence of flowering, there were very large fluctuations in the density of flowers per plant, more than doubling in 2011, followed by a big decline. The productivity of vegetation in arid Africa responds to rainfall of the previous and current years. If there are successive years of low rainfall, populations are caught in a downward spiral of less flowering, reduced population size and longer recovery period. After particularly wet years, often a 1-year time lag is observed, with the vegetation flourishing the subsequent year (Schwinning *et al*. 2004). This may be the case here; the 2010 rains may have caused the flowering surge in 2011. This is perhaps an example of the memory effect, the soil retaining the effects of excess rainfall and impacting plant productivity (Martiny *et al*. 2005; Schwinning *et al*. 2004). However, the subsequent decline in flowering in 2012 suggests that rainfall in the previous winter or the current year is very influential, since rainfall in late 2011 was absent and hence perhaps insufficient to maintain the flowering.

At the moment, we are far from understanding the population dynamics of Sinai thyme. We think the temporal scale of change is slow, with long-lived adult plants reproducing mainly vegetatively, with only relatively rare contributions from seed. The profuse flowering then is a conundrum that only further work can solve. Conserving this endangered plant will require knowledge upon which to base strategies to augment its numbers, which coincidentally is one major way of helping to boost numbers of the short-lived herbivores that depend on it utterly for their existence (cf. Ostfeld and Keesing 2000).

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