RESEARCH ARTICLE

Elevation patterns of plant diversity and recent altitudinal range shifts in Sinai's high-mountain flora

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Abstract

Questions: Is there evidence of recent altitudinal range shifts in a hyper-arid Middle Eastern desert mountain flora? How do the directions of shift for upper and lower altitudinal range limits of plants vary?

Location: Hyper-arid mountain desert, St Katherine Protectorate, South Sinai, Egypt.

Method: We tested for shifts in both upper and lower altitudinal range limits by comparing a 1970s data set of recorded species' limits with recent surveys using altitudinal transects across 36 sites. Altitudinal limits between 63 paired upper-limit and 22 paired lower-limit values from the 1970s and 2014 were compared using paired *t*-tests; binomial tests were used to indicate the dominant direction of change. The upper and lower limits of 22 species were considered together to allow assessment of overall altitudinal range size changes. In order to avoid the potential effect of yearly environmental fluctuations on the distributions of annual species, subsets of upper and lower limit shifts were taken for perennials, and for trees and shrubs.

Results: Our results show significant overall up-slope shifts in mean upper altitudinal limits and significant overall down-slope shifts in mean lower altitudinal limits. A majority of assessed species expanded their altitudinal ranges, but the responses of individual species varied.

Conclusions: Since perennial herbs/graminoids, as well as trees and shrubs, show strong patterns of change, we suggest there has been a long-term shift in altitudinal range in South Sinai's mountain flora. More research effort needs to be focussed on the drivers of range shift responses in arid regions.

KEYWORDS
altitude, climate change, desert, endemic plants, mountains, plant diversity, range margins, relict plants

1 | INTRODUCTION

Recent range shifts in both latitudinal and altitudinal distributions have been recorded across animal and plant taxa in response to changes in climate, with ranges expanding at high latitudes and altitudes, and contracting at lower latitudes and altitudes (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Wilson et al., 2005). Lower latitudinal and altitudinal range limits, the rear or trailing edges of distributions, have received little attention (Hampe & Petit, 2005),

despite these margins often contributing to higher levels of regional genetic diversity (Hewitt, 2004) and being important in the maintenance of biodiversity (Hampe & Petit, 2005). Given the potential conservation implications of the lower margin shifts of plants, it is therefore surprising that empirical studies are so poorly represented in the literature (Lenoir & Svenning, 2015). It is true that lower limits are harder to assess, with a less clear-cut position influenced by a multitude of factors rather than mainly climatic (e.g., biotic interactions, and propagules moving downhill under gravity). Nevertheless,

in arid regions, water availability is a crucial factor, which is expected to ameliorate towards higher elevations through convective cloud formation, and hence lower limits may be more easily recognized.

Under conditions of global warming it seems logical that up-slope range shifts of plants attributed to changing climatic factors would be the norm (Gottfried et al., 2012; Jump, Huang, & Chou, 2012; Klanderud & Birks, 2003; Matteodo, Wipf, Stöckli, Rixen, & Vittoz, 2013; Pauli, Gottfried, Reiter, Klettner, & Grabherr, 2007; Stöckl, Wipf, Nilsson, & Rixen, 2011; Walther, Beißner, & Burga, 2005; Wipf, Stöckli, Herz, & Rixen, 2013). It is important to note that changes such as these are not necessarily always consistent with temperature being the sole dominant factor inducing change (Grytnes et al., 2014). However it seems probable that changes in both the thermal regime and water availability will be the main drivers of altitudinal changes, with adverse changes in both (e.g., warmer and drier) causing the greatest pressure (McCain & Colwell, 2011).

Globally, mountainous regions represent important hotspots of endemism (Körner, 2003; Nagy & Grabherr, 2009), but mountain species are especially vulnerable to extinction due to habitat loss induced by climate change, because shifting climatic zones will reduce suitable habitat area, leading to 'mountain-top extinctions' (Dirnböck, Essl, & Rabitsch, 2011). Plant species in arid regions may also be very susceptible to climate change, and the loss of arid-land endemics may occur in both lowland (Foden et al., 2007) and mountain (Van de Ven, Weiss, & Ernst, 2007) environments under increased levels of global warming.

There are very few studies of recent altitudinal changes in plant distributions from subtropical or arid regions (Jump et al., 2012; Lenoir & Svenning, 2015). We study here the flora of the hyper-arid desert mountains of South Sinai, Egypt. Egypt and the wider Middle East region has seen recent temperature increases (Domroes & El-Tantawi, 2005; Zhang et al., 2005), with average warmest daily maximum temperatures increasing by >1°C since the 1970s (Donat et al., 2014). Sinai's southern montane regions contain relatively high levels of biodiversity (Zalat et al., 2009), and are home to 19 of Egypt's 33 endemic plant species (Rashad, Basset, Hemeed, Alqamy, & Wacher, 2002). The area is recognized as one of the most important centres of plant diversity in the Middle East (IUCN 1994). Greater botanical diversity has been suggested to occur at higher altitudes in Sinai due to a diversity of habitat types and favourable environmental factors, especially the increased water availability, precipitation and soil moisture retention in high-altitude areas (Moustafa & Klopatek 1995; Moustafa & Zaghloul, 1996).

Many species of plants in the high mountains of southern Sinai exhibit disjunct distributions of Holarctic species found more commonly further north, suggesting that these species are relics of a more humid, colder past (Shmida, 1977). The isolation of plants that thrive in cooler damper climates in refugia on the highest of Sinai's mountains suggests their vulnerability to rising temperatures. Recent shifts in plant altitudinal distributions in the Middle East are expected, but remain completely unstudied until now, and especially not with the multifaceted approach of looking at leading and trailing edge changes simultaneously.
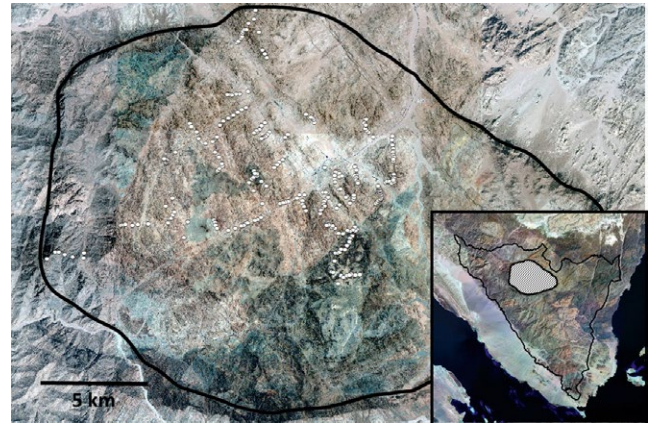

FIGURE 1 Outline of igneous ring-dyke delimiting the high mountain region within the St Katherine Protectorate. Positions of 2014 survey sites shown as white dots with 5-km scale bar. Inset: St Katherine Protectorate outline in South Sinai; shaded area St Katherine ring-dyke and region of 1970s transect surveys [Colour figure can be viewed at wileyonlinelibrary.com]

Therefore, we focus here on the following hypotheses. First we ask whether there is evidence of recent range shifts in the high-mountain flora in South Sinai, predicting that these should be evident as largely up-slope movements. The null hypothesis is of course no change, but alternatively the mean response may be zero because of idiosyncratic responses of the different species, which may not respond to temperature but to other factors, especially water balance (cf. Rapacciuolo et al., 2014). Second, we study the directions of shift for upper and lower altitudinal range limits, and split the species into growth forms to help interpret the results. The prediction is that upper and lower limits should move in concert, and that all plants should show the same patterns.

2 | METHODS

We use the approach of comparing modern with historical data (Stöckl et al., 2011). Ideally the methodologies and locations should be identical, but in this case the earlier surveys were not quantitative and did not locate the transects with geographic coordinates. With this caveat, the unique existence of the earlier data for the Middle East makes the comparison worthwhile.

2.1 | Study region

The St Katherine Protectorate covers much (4,350 km^2, almost half the area) of the southern peninsula of Sinai, encompassing the majority of a high-altitude massif and reaching down to sea level to form one of Egypt's largest protected areas (Grainger & Gilbert, 2008). An igneous pre-Cambrian ring-dyke encircles 640 km^2 of the centre of the Protectorate. The ring-dyke contains Egypt's highest mountain, Mt St Katherine, at 2,643 m. The mountainous terrain is inter-cut with dry steep-sided wadis (valleys). South Sinai receives higher than

average rainfall (62 mm; Zahran & Willis, 2008) and generally cooler temperatures (summer mean: 30°C) than the rest of Egypt (Grainger & Gilbert, 2008).

2.2 | Historical data

To assess temporal changes in upper altitudinal range limits, we compared our field data with a 1970s data set compiled by Arbel and Shmida (1979) in a semi-quantitative format. Data were collected during the years 1974–1976 and focused on the mountainous area within the St Katherine ring-dyke (see Figure 1 map inset: shaded area).

Vegetation was sampled by recording species richness in quadrats of area 100 m^2. Quadrats were placed along transects divided into altitudinal units of 200 m running up wadis and mountain slopes. In addition, quadrats were placed wherever habitat type or plant dominance changed noticeably. Each altitudinal unit was sampled several times in different locations but the coordinates for each quadrat were not recorded. Additional incidental vegetation observations were included from lower altitudes in the St Katherine Protectorate falling outside the ring-dyke and its high mountains; these observations were incorporated into the main data set. Unfortunately the only remaining details of the original data set available to this study were records of minimum and maximum altitudes for plant species recorded at a resolution of 100 m altitude, together with a subjective assessment of relative abundance (common, very frequent, frequent, rare, very rare, found once) and statements of their common habitats (gorges, weathered slopes, gravel wadis, rock cracks, wet places, etc.; see Appendix S1: Table S1).

2.3 | New data

Quantitative data were collected during field surveys running from late Oct to mid-Dec 2014. Surveys were carried out in the high mountains within the igneous ring-dyke area over an altitude range of 1,324 m to 2,629 m (see Figure 1 for survey locations, Appendix S1: Table S3 for quadrat GPS locations, Appendix S1: Table S4 for site photos and descriptions, Appendix S1: Table S5 for species lists and abundances by quadrat). We were not able to revisit exact sites surveyed in the 1970s as quadrat location had not been recorded; instead we surveyed extensively within the same mountainous region (Figure 1) including the same mountains and habitats as the older surveys. It is probable that new and old quadrats were close or very close to one another.

Vegetation was sampled along sloped transects running through wadis, mountain slopes and gullies. The lengths of each transect were determined by the scale of the landscape, running from the lower to the upper altitudinal limits to encompass as large an altitudinal range as possible. As landform/habitat type is a major determinant of the diversity and community composition of the vegetation in Sinai (Moustafa & Klopatek 1995), the location of transects was chosen to cover all major habitat types.

Quadrats of area 100 m^2 were demarcated along transects approximately every 50-m change in elevation where terrain permitted. In total 283 quadrats were placed in 36 sites covering 28,300 m^2. Location and altitude above sea level were measured at the centre of the quadrats using a Garmin etrex 30 hand-held GPS with the GPS + GLONASS (±3 m) and barometric altimeter (±3 m) functions, respectively. At each quadrat, we recorded: aspect of slope to the nearest cardinal point; gradient to the nearest 5° (360° scale); a brief site description; and a photograph. All vascular plant species in the quadrats were identified (using Boulos, 1999–2005) and individually counted (with individuals of multiple stemmed/clumping plants defined as those with stems returning to a common root stock): plant names follow Boulos (1999–2005).

A total of 241 species were recorded from the 1970s: of these, notable absences compared with the plants of 2014 were *Lavandula pubescens* and *Gomphocarpus sinaicus*. The identity of *Chiliadenus montanus* was uncertain from records and was therefore not included in analyses to avoid inaccuracy due to ambiguity. *Fagonia arabica* and *F. bruguieri* were not differentiated in the earlier data set, and therefore for the purposes of comparison the records collected in 2014 were amalgamated for these species. In total, 81 species were available with upper altitudinal limits from both the 1970s and 2014. The significantly larger sampling effort required to accurately establish the lower altitudinal limits for the more widespread species was beyond the scope of this study, which deals specifically with the high-altitude flora of South Sinai. However, the lower altitudinal limits of 25 species fell within the altitudinal range surveyed, thereby permitting their analysis.

Numerical abundance data were not available for species from the 1970s data set. In the 2014 data set, to allow reasonably accurate estimation of altitudinal limits, only species for which more than ten individuals had been recorded during the entirety of the 2014 field surveys were selected (see Appendix S1: Table S2). This selection allowed the upper limits of 63 and lower limits of 22 species to be identified. Subsets of upper- and lower-limit shifts were taken for perennials, and trees and shrubs to allow comparisons to be made that avoided the potential effect of yearly environmental (specifically rainfall) fluctuation on the distributions of annual species.

2.4 | Statistical methods

All statistical and graphical analyses were carried out using R (v 3.1.2, R Foundation for Statistical Computing, Vienna, AT).

2.4.1 | Patterns of diversity in the new data

To describe the 2014 data set, weighted mean (±*SE*) elevations were calculated for all species recorded (see Figure S1 & S2). For each quadrat, the three Hill's numbers (Chao, Chiu, & Hsieh, 2012) were calculated as measures of components of diversity representing effective species richness. The general equation is:

$$^qD = \left(\sum p_i^q \right)^{(1/(1-q))}$$

TABLE 1 Description of pattern of movement of upper and lower altitudinal limits for 22 individual plant species where both upper and lower limits could be measured

Species	Upper limit 1970s	Upper limit 2014	Lower limit 1970s	Lower limit 2014	Limit movement patterns		Range size change
					Lower limit	Upper limit	
Alkanna orientalis	2,500	2,575	1,500	1,375	Down	Stationary	expanded
Astragalus echinus	2,600	2,425	2,000	1,825	Down	Down	no change
Calipeltis cucullaris	2,100	2,425	1,500	1,425	Stationary	Up	expanded
Colchicum guessfeldtianum	2,500	2,325	1,500	1,925	Up	down	contracted
Cotoneaster orbicularis	2,200	2,425	1,800	1,725	Stationary	up	expanded
Crataegus x sinaica	2,300	2,375	1,600	1,625	Stationary	stationary	no change
Globularia arabica	2,100	2,275	1,700	1,425	Down	Up	expanded
Nepeta septemcrenata	2,640	2,325	1,700	1,725	Stationary	Down	contracted
Origanum syriacum	2,000	1,975	1,600	1,425	Down	Stationary	expanded
Phlomis aurea	2,200	2,425	1,550	1,375	Down	Up	expanded
Polygala sinaica	2,640	2,625	1,900	1,675	Down	Stationary	expanded
Pterocephalus sanctus	2,640	2,575	1,600	1,625	Stationary	Stationary	no change
Pulicaria undulata	1,900	2,175	1,400	1,375	Stationary	Up	expanded
Rubus sanctus	1,800	1,725	1,800	1,625	Down	Stationary	expanded
Salvia multicaulis	2,100	1,975	1,900	1,725	Down	Down	expanded
Scariola orientalis	2,500	2,325	1,800	1,525	Down	Down	expanded
Silene leucophylla	2,300	2,625	1,750	1,425	Down	Up	expanded
Silene schimperiana	2,300	2,175	1,500	1,521	Stationary	Down	contracted
Stipa parviflora	2,500	2,325	1,600	1,525	Stationary	Down	contracted
Thymus decussatus	2,400	2,275	1,900	1,725	Down	Down	expanded
Verbascum decaisneanum	2,300	2,525	1,600	1,525	Stationary	Up	expanded
Verbascum sinaiticum	2,400	2,575	1,500	1,375	Down	Up	expanded

Limits are in m a.s.l.

where q = 0, 1 or 2. Ascending Hill's numbers (q values) give reducing weight to the less-abundant species, reflecting the relative ecological importance of more abundant species (Hill, 1973). Thus ^0D measures species richness, ^1D represents the number of 'typical' common species, while ^2D represents the number of 'very abundant' species present in the community (Chao et al., 2012). Therefore, considered together, Hill's numbers present a picture of community evenness.

To describe altitudinal patterns of diversity in the 2014 data, abundances were assigned to altitudinal bands of 50 m. Smoothing splines were fitted to the three Hill's numbers with altitude as the predictor, using the GAM (Generalized Additive Model) function of R-package *ggplot2* (Wickham, 2009).

2.4.2 | Range shift comparison

To estimate shifts in altitudinal ranges, the altitudinal limits between 63 paired upper-limit and 22 paired lower-limit values from the 1970s and 2014 were compared using paired *t*-tests to test the null hypothesis that the mean difference was zero. Sign tests (i.e., binomial tests on the numbers of negative and positive changes) were used to indicate the dominant direction of change. 22 species had estimates of both upper and lower limits, and so were considered together to allow assessment of overall altitudinal range size changes. Species were categorized as showing no change, expanded range or contracted range (Table 1). Movement of <100 m

for either limit was regarded as stationary in view of the measurement resolution of the 1970s data. A binomial test was used to identify whether expansion or contraction of ranges was the dominant pattern.

As an aid to interpretation, reasons for the changes were explored in a GLM using the differences in altitudinal limits between 2014 and the 1970s as the response variable, and a variety of predictors: flowering season(s), basic growth form (herb, shrub or tree), Raunkiær life form, and basic life form (annual or perennial). The best fitting models and predictors were selected through use of AICs.

3 | RESULTS

3.1 | Patterns of diversity in the new data

The overall patterns of diversity were indicated from the three Hill numbers, but each followed a distinct altitudinal pattern (see Figure 2). The highest levels of species richness (^0D) were found at higher altitudes, decreasing down a shallow concave curve with the lowest values at lower altitude (~1,400–1,600 m). The number of 'typical' (common) species, ^1D, was highest at lower-middle elevations (~1,700–1,800 m), and declined with increasing altitude. In contrast, the number of abundant species, ^2D, was lowest at lower-middle elevations, with highest values at the top of the altitude range. The summary data are in Appendix S1: Tables S2 and S3.
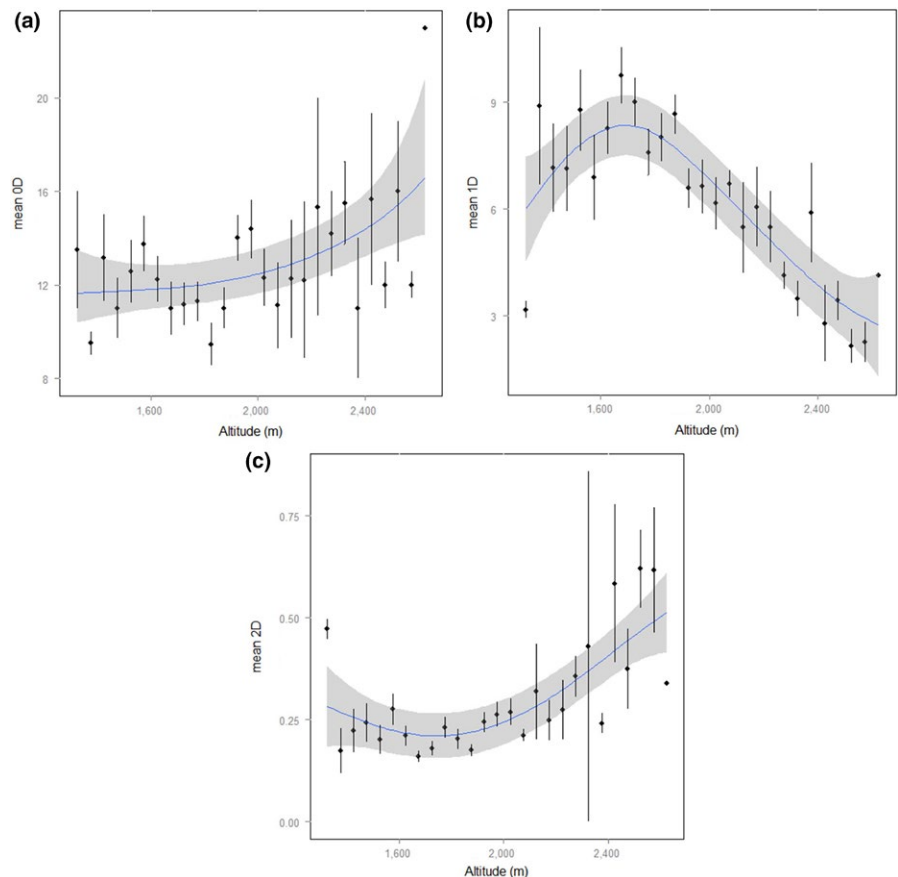

FIGURE 2 Hill's numbers (see Chao et al., 2012) for diversity by altitude with fitted GAM model with Normal errors and 95% confidence region. Ascending Hill numbers give reducing weight to less-abundant species: (a) mean ^0D species richness; (b) mean ^1D (number of 'typical' common species); (c) mean ^2D (number of 'abundant' species) [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Range shift comparisons

Comparison of the upper altitudinal limits from the 1970s and 2014 for 63 plant species indicated a significant difference between mean past and present upper altitudinal limits, with the current limit (mean: 2,228.6 ± 294.5 m) larger than in the past (mean: 2,125.2 ± 350.2 m; paired t = 3.37, df = 61, p = 0.0013). Although the mean upper altitude limit for all species was found to be significantly higher, there was no evidence of a preponderance of species increasing rather than decreasing their upper altitudinal limit (38 of 63 spp.; binomial test p = 0.065; see Figure 3 for details). However, for species differing by >100 m, a significantly larger number of species moved up-slope (26/40; binomial test p = 0.04). This was also the case for species differing by >250 m (16/18; binomial test p < 0.001).

The 22 species whose lower altitudinal limits were assessed showed a significantly downward shifted mean lower altitudinal limit (current mean: 1,568.0 ± 162.1 m, past mean: 1,668.2 ± 166.6 m; paired t = 3.02, df = 20, p = 0.0064). In addition to this downward shift overall, a significantly larger number of species shifted their individual lower altitudinal limits downwards than did not (17/22; binomial test p = 0.008; see Figure 4 for details). This finding also held true when only considering species for which movement was >100 m (12/13; binomial test p = 0.002).

In species with measurements for both upper and lower altitudinal limits, a significant majority expanded their altitudinal ranges between the 1970s and 2014 (15/22′ binomial test p < 0.001). Three species showed divergence of altitudinal limits (lower limit moved down-slope, upper limit moved up-slope) and one convergence (lower limit up-slope, upper limit down-slope; see Table 1), whilst four showed parallel down-slope movement of upper and lower limits. The upper and lower limits of each species thus appeared to move independently. Lower limits moved down in 12 species, up in one and remained stationary for nine. Upper limits moved down in eight species, up in eight and remained stationary for six species. Of the species that shifted their lower limits down-slope, there was no preponderance of species that also showed parallel down-slope movement of their upper limits (4/12; binomial test p = 0.927).

Basic life form (annual or perennial) was the best predictor of the change in upper altitudinal limit ($F_{1,61}$ = 6.9, p = 0.01), with annuals on average moving up four times further than perennials (292 m vs 72 m). There was only one annual and 21 perennials with measured changes in lower altitudinal limit, and the value for the former (down-slope 75 m) was not different from the distribution of values for the perennials (which on average moved down-slope 101.4 ± 34.7 m; one-sample t = 0.76, df = 19, n.s.). Basic life form was the best additional predictor in a GLM predicting the 2014 upper limits from
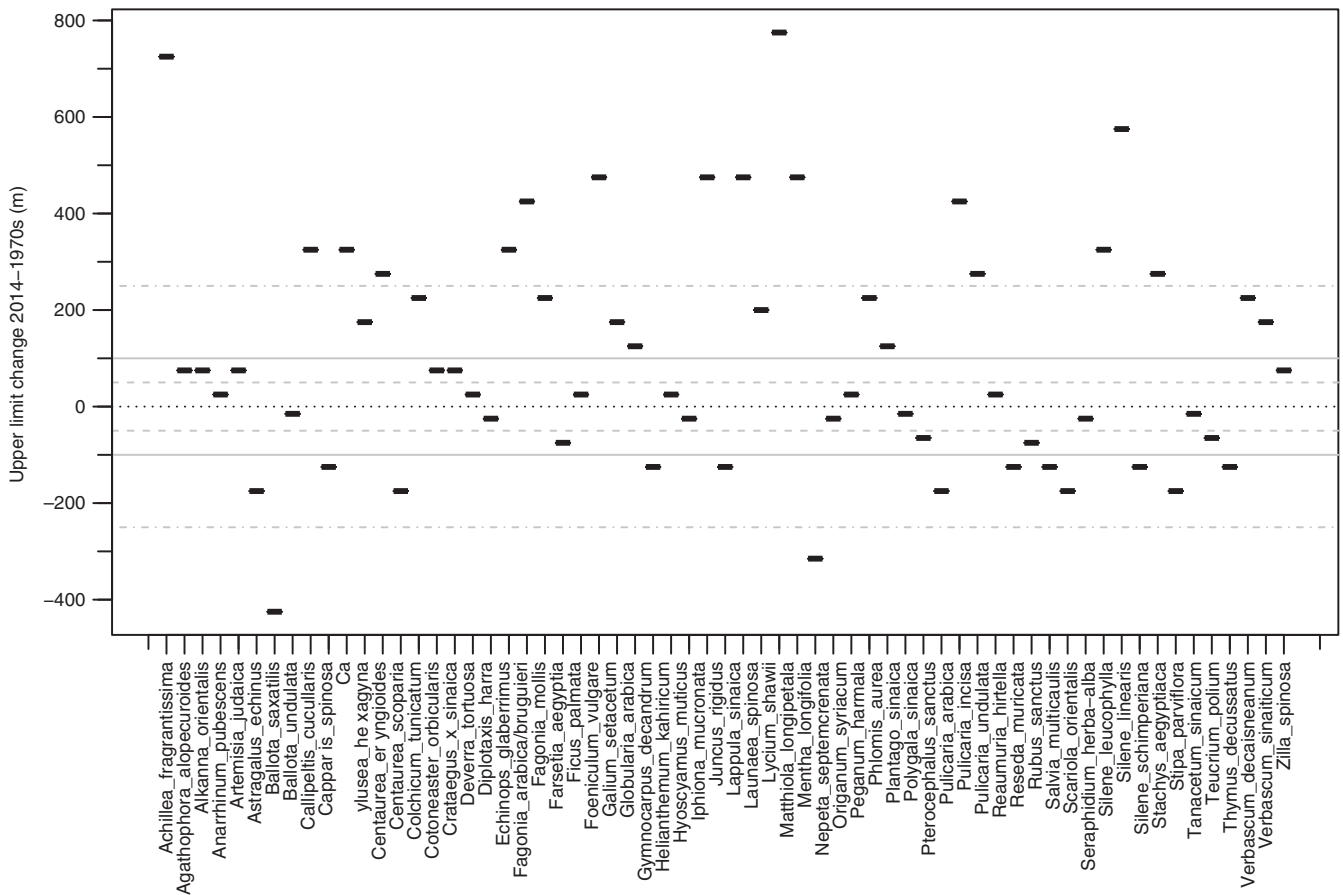

FIGURE 3 Difference in upper altitude limit for each plant species between the 1970s and 2014
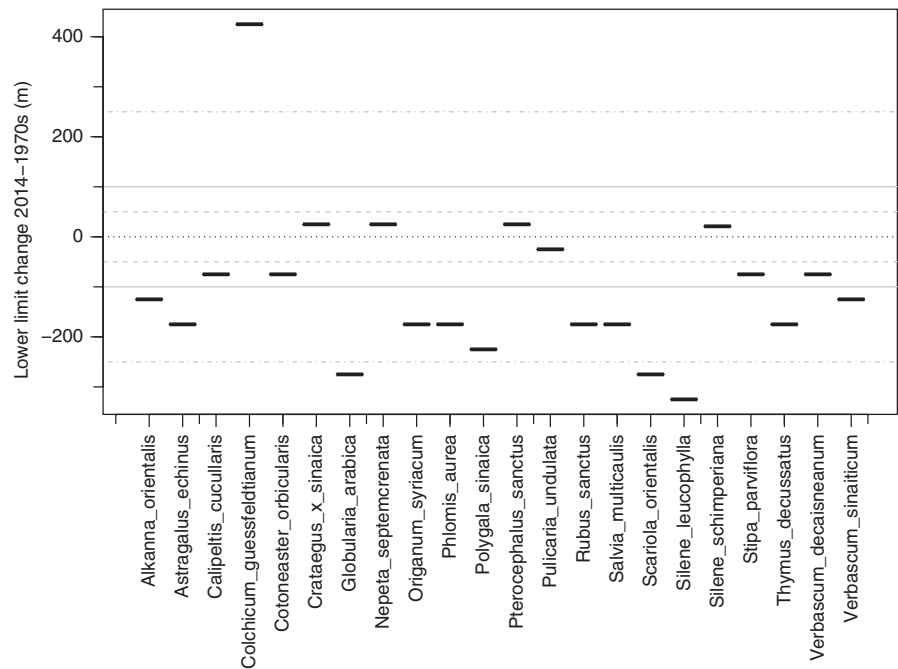
FIGURE 4 Difference in lower altitude limit for each plant species between the 1970s and 2014

those of the 1970s, with a much steeper slope for perennials (0.70) than annuals (0.29; $F_{1,59}$ = 4.49, p = 0.038).

Analysis of only the perennial species showed significantly higher mean upper altitudinal limits in 2014 (mean: 2,220.8 ± 307.3 m) than in the 1970s (mean: 2,148.9 ± 342.6 m; paired t = 2.45, df = 52, p = 0.018). There was no evidence of a majority of perennial species increasing their upper limits (31/54; binomial test p = 0.17), even among those that differed by >100 m (20/32; binomial test p = 0.12). However, for species that differed by >250 m, a significantly larger number moved up-slope (10/12; binomial test p = 0.02).

The subset of only shrubs and trees also showed significantly higher mean upper limits (present mean: 2,219.1 ± 311.2 m, past mean: 2,139.5 ± 353.3 m; paired t = 2.30, df = 36, p = 0.027). Again there was no preponderance of increased upper limits among all species (21/38; binomial test p = 0.31) or those that differed by > 100 m (15/22; binomial test p = 0.07). Again, however, among species that differed by > 250 m, there was a preponderance of up-slope movement (7/8; binomial test p = 0.04).

The mean lower altitudinal limits of perennials moved significantly downwards in 2014 compared to the 1970s (present mean: 1,574.8 ± 162.9 m, past mean: 1,676.2 ± 166.3 m; paired t = 2.92, df = 19, p = 0.009). As with all plant species, a significantly larger number of species moved their lower limit downwards (16/21; binomial test p = 0.01), even among those that differed by >100 m (12/13; binomial test p = 0.002). The mean lower limits of shrubs and trees also shifted significantly downwards in the 2014 data (1,585.7 ± 145.7 m) than in the 1970s (1,725.0 ± 171.8 m; paired t = 5.27, df = 12, p = 0.0002). Again a significantly larger number of species moved down-slope (14/16; binomial test p = 0.006) and this was particularly the case for species that differed by >100 m (9/9; binomial test p = 0.002).

4 | DISCUSSION

4.1 | Patterns of diversity in the new data

The three Hill's number diversity indices provide greater insight than a single measure (Chao et al., 2012), with higher-order measures emphasizing more dominant species. Each index exhibited a different pattern of diversity with altitude. Species richness (^{0}D) was largest at high altitudes, with low richness found at low to mid-altitudes. This pattern contrasts with more humid mountain systems, where plant species richness typically peaks at low to mid-altitudes (Poulos, Taylor, & Beaty, 2007; Vetaas & Grytnes, 2002). The refugial nature of South Sinai's high mountains may explain the discrepancy in the pattern of species richness. Favourable climatic conditions, primarily increased availability and retention of moisture (Moustafa & Klopatek 1995; Moustafa & Zaghloul, 1996), at higher altitudes support increased richness than the comparative extremes of temperature and water stress encountered at mid- to low altitudes. While the temperate flora has largely been lost from much of low-altitude Sinai, in the mountain region of St Katherine remnant species remain only at higher altitudes, leading to a pattern of increasing species richness with increasing altitude (Moustafa, Zaghloul, El_Wahab, & Shaker, 2001). The Hill's number ^{1}D (number of typical common species) was highest at the lower altitudes sampled, decreasing at higher areas, whilst ^{2}D (number of very abundant species) increases with altitude. These patterns suggest that higher-altitude communities are dominated to a greater extent by a few abundant species. The joint interpretation of the patterns of all three diversity indices is that species richness increases with altitude, most likely due to more favourable climatic conditions of lower temperatures and greater moisture on mountain peaks and, although richer, communities become more

uneven at higher altitudes, with a few species showing increasing levels of dominance. The endemic species recorded in this study peaked in density at generally high altitudes and around mountain peaks, as in other studies in arid landscapes (Noroozi, Pauli, Grabherr, & Breckle, 2011) and more widely (Essl et al., 2009; Vetaas & Grytnes, 2002), although glaciation history is often also important in more northern studies.

4.2 | Range shifts since the 1970s

We have found clear evidence of temporal altitudinal range shifts in South Sinai's high-mountain flora, although species showing shifts of <100 m may be artefacts of the differing methodologies of the 1970s and 2014 studies, using different resolutions and elevation intervals for vegetation recording. Species with larger range shifts, however, showed an obvious pattern of up-slope movement of the upper limit, but also down-slope movement of the lower limit.

There have certainly been globally reported trends towards upwards shifts in range limits and changing community assemblages on mountain peaks, often attributed to climate change (Gottfried et al., 2012; Matteodo et al., 2013; McCain & Colwell, 2011). Indeed climate change is expected to be the main cause of range shifts, especially when considering both core components: temperature and precipitation. Nevertheless, wider consequences of climate change, including changes in water balance (Crimmins, Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011), the area of bare soil surface (Walther et al., 2002) and elevated atmospheric carbon dioxide levels (Wayne, Reekie, & Bazzaz, 1998) can all influence range shifts in plants, albeit probably of lesser importance. In the case of South Sinai, unfortunately we do not have reliable local long-term site-specific climatic and environmental information. Coupled with high levels of small-scale variability in microhabitat conditions (Moustafa & Klopatek, 1995; Moustafa & Zaghloul, 1996) means that accurately determining causes for the observed range shifts is beyond the scope of this study. No good data on long-term precipitation in the South Sinai mountains exist. It is therefore difficult conclusively to attribute downward shifts of lower limits to increased precipitation. Donat et al. (2014) suggest "a slight wetting trend" across the Arab region since the 1970s. However this must be viewed in light of high site-specificity in precipitation and moisture availability in the South Sinai mountains, as noted by Moustafa and Zaghloul (1996).

During the period 1971–2000 Egypt as a whole showed overall mean annual temperature increases of 0.62°C per decade (Domroes & El-Tantawi, 2005), which greatly exceeds the global trend of 0.17°C per decade (IPCC 2001). Measures of precipitation across the wider Middle East and North Africa show increasing spatial and temporal variability (Zhang et al., 2005) but little evidence of significant changes in average values in Egypt (Donat et al., 2014).

Overgrazing by livestock has been suggested to be a determinant of vegetation diversity and range, including in the South Sinai mountains (Moustafa, 2001), but as with grazing by indigenous peoples worldwide (Davis, 2016), these are interpretations with little if any

empirical evidence (see Gilbert, 2013 for full discussion). Numbers of grazing livestock and flock sizes have decreased substantially since the 1960s (Gilbert, 2013; Perevolotsky, Perevolotsky, & Noy-Meir, 1989), and hence it is possible that relaxed grazing pressure has permitted down-slope movement of plant range limits. However, the bulk of livestock flock size decreases occurred before the date of the 1974–1976 surveys (Perevolotsky et al., 1989), with average flock sizes changing from 78 pre-1968 to ~13 in the 1970s, ten in 1982, and seven to eight now (Gilbert, 2013). Rashad et al. (2002) found the majority of grazing occurred in an altitudinal band between 1,500 and 1,800 m. Only one species (*Rubus sanctus*) in our data set has its upper limit within this grazing zone, and this was stationary between the 1970s and 2014. Thus we do not believe that grazing has affected the upper altitudinal limits. Of the lower limits recorded in our data set from the 1970s, 17 of the 22 species fell within this altitudinal grazing zone, but only eight of these showed down-slope movement between the 1970s and 2014 (see Table 1 for detail). Therefore, whilst changes in grazing intensity *may* have affected down-slope range shifts, we suggest that climatic change explains the observed upward range shifts better.

Here, in this arid mountain system, we have documented what we think is the first record of significant down-slope shifts of plant lower-altitudinal limits outside Europe. Despite the less-than-ideal quality of the historical data, mean upper limits have increased while lower limits have decreased since the 1970s, leading to a divergent pattern of mean altitude limits. When considering the upper and lower altitudinal limits of individual species, we found heterogeneity in the joint responses, with no clear dominant pattern. One must bear in mind that these species are a subset of the selected group of high-mountain species that may not be representative of all the species present in that environment.

We now know that there have been significant upward shifts in the upper altitudinal limits of South Sinai plant species since the 1970s. Our data are limited to those species with lower limits within the sampled range, but a significantly large proportion show expansions of the altitudinal ranges, suggesting that, at least for now, range contractions are not affecting the majority of high-mountain species. However, the Sinai endemic *Silene schimperiana* has contracted in altitudinal range. The risk imposed by contracting ranges and habitat loss would therefore be best considered on a case-by-case basis with regard to Sinai's endemic and rare species. No plant extinctions have been recorded for South Sinai, at least within the last 30 yrs, although some are very close to extinction (e.g., *Primula boveana*: Omar, 2014; Jimenez, Mansour, Keller, & Conti, 2014). However this does not mean that shifts in altitudinal limits are not a cause for concern. Modelling of plant ranges under climate change has indicated lags in population dynamics leading to extinction debts (Dullinger et al., 2012). The isolated, refugial nature of South Sinai's plant communities leaves them vulnerable to extinction from a number of ecological factors, not limited to climate warming. Whilst we cannot conclusively state that observed shifts in altitudinal limits constitute 'fingerprints' of climate warming, they do point to ecological change posing potential ecological and conservation issues for the future.

In this study we have presented the first recorded instance of contemporary altitudinal limit shifts in Middle Eastern mountain flora. The fine-scale variability of environmental and ecological factors within the South Sinai mountain ecosystem highlights the necessity of ecological monitoring, and makes a case for increasing the comprehensiveness and quality of the region's environmental monitoring programmes. Our GPS-marked survey quadrats (Appendix S1: Table S2) will provide a baseline for future fine-scale monitoring. We also stress how important it is to consider both upper and lower altitudinal limits to obtain an accurate indication of overall altitudinal range changes. We need to focus on lower limits to understand better the ecological drivers and dynamics underlying heterogeneous responses at the range limits.

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REFERENCES

Arbel, O., & Shmida, A. (1979). *The vegetation of the high mountains of South Sinai*. Tel Aviv, IL: Society for the Protection of Nature, 67 pp. [in Hebrew].

Boulos, L. (1999-2005). *The Flora of Egypt*. Cairo, Egypt: Al Hadara Publishing.

Chao, A., Chiu, C. H., & Hsieh, T. C. (2012). Proposing a resolution to debates on diversity partitioning. *Ecology*, 93, 2037–2051. https://doi.org/10.1890/11-1817.1

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026. https://doi.org/10.1126/science.1206432

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., & Mynsberge, A. R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, 331, 324–327. https://doi.org/10.1126/science.1199040

Davis, D. K. (2016). *The arid lands: History, power, knowledge*. Cambridge, MA: MIT Press.

Dirnböck, T., Essl, F., & Rabitsch, W. (2011). Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, 17, 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

Domroes, M., & El-Tantawi, A. (2005). Recent temporal and spatial temperature changes in Egypt. *International Journal of Climatology*, 25, 51–63. https://doi.org/10.1002/(ISSN)1097-0088

Donat, M. G., Peterson, T. C., Brunet, M., King, A. D., Almazroui, M., Kolli, R. K., … Al Shekali, M. N. (2014). Changes in extreme temperature and precipitation in the Arab region: Long-term trends and variability related to ENSO and NAO. *International Journal of Climatology*, 34, 581–592. https://doi.org/10.1002/joc.3707

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., … Hülber, K. (2012). Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, 2, 619–622. https://doi.org/10.1038/nclimate1514

Essl, F., Staudinger, M., Stöhr, O., Schratt-Ehrendorfer, L., Rabitsch, W., & Niklfeld, H. (2009). Distribution patterns, range size and niche breadth of Austrian endemic plants. *Biological Conservation*, 142, 2547–2558. https://doi.org/10.1016/j.biocon.2009.05.027

Foden, W., Midgley, G. F., Hughes, G., Bond, W. J., Thuller, W., Hoffman, M. T., & Hannah, I. (2007). A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity & Distributions*, 13, 645–653. https://doi.org/10.1111/j.1472-4642.2007.00391.x

Gilbert, H. (2013). 'Bedouin overgrazing' and conservation politics: Challenging ideas of pastoral destruction in South Sinai. *Biological Conservation*, 160, 59–69. https://doi.org/10.1016/j.biocon.2012.12.022

Gottfried, M., Pauli, H., Futschik, A., Akhalkasti, M., Barancok, P., Alonso, J. L. B., … Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2, 111–115. https://doi.org/10.1038/nclimate1329

Grainger, J., & Gilbert, F. (2008). Around the sacred mountain: The St Katherine Protectorate in South Sinai, Egypt. In J. M. Mallarach (Ed.), *Values of protected landscapes and seascapes: Protected landscapes and cultural and spiritual values* (pp. 21–37). Gland, Switzerland: IUCN.

Grytnes, J.-A., Kapfer, J., Jurasinski, G., Birks, H. H., Henriksen, H., Klanderud, K., … Birks, J. B. (2014). Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecology & Biogeography*, 23, 876–884. https://doi.org/10.1111/geb.12170

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, 8, 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 359, 183–195. https://doi.org/10.1098/rstb.2003.1388

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, 54, 427–432. https://doi.org/10.2307/1934352

IPCC (2001). *Climate change 2001*. Geneva, Switzerland: The Intergovernmental Panel on Climate Change 3rd assessment report.

IUCN (1994). *Centres for plant diversity: A guide and strategy for their conservation*. Cambridge, UK: IUCN.

Jimenez, A., Mansour, H., Keller, B., & Conti, E. (2014). Low genetic diversity and high levels of inbreeding in the Sinai primrose (*Primula boveana*), a species on the brink of extinction. *Plant Systematics & Evolution*, 300, 1199–1208. https://doi.org/10.1007/s00606-013-0955-y

Jump, A. S., Huang, T. J., & Chou, C. H. (2012). Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. *Ecography*, 35, 204–210. https://doi.org/10.1111/j.1600-0587.2011.06984.x

Klanderud, K., & Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene*, 13, 1–6. https://doi.org/10.1191/0959683603hl589ft

Körner, C. (2003). *Alpine plant life: Functional plant ecology of high mountain ecosystems; with 47 tables*. Berlin, Germany: Springer. https://doi.org/10.1007/978-3-642-18970-8

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, 38, 15–28. https://doi.org/10.1111/ecog.00967

Matteodo, M., Wipf, S., Stöckli, V., Rixen, C., & Vittoz, P. (2013). Elevation gradient of successful plant traits for colonizing alpine summits under climate change. *Environmental Research Letters*, 8, 1–10.

McCain, C. M., & Colwell, R. K. (2011). Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, 14, 1236–1245. https://doi.org/10.1111/j.1461-0248.2011.01695.x

Moustafa, A. R. A. (2001). Impact of grazing intensity and human disturbance on the population dynamics of *Alkanna orientalis* growing in Saint Catherine, South Sinai, Egypt. *Pakistan Journal of Biological Science*, 4, 1020–1025.

Moustafa, A. R. A., & Klopatek, J. M. (1995). Vegetation and landforms of the Saint Catherine area, southern Sinai, Egypt. *Journal of Arid Environments*, 30, 385–395. https://doi.org/10.1006/jare.1995.0033

Moustafa, A. R. A., & Zaghloul, M. S. (1996). Environment and vegetation in the montane Saint Catherine area, south Sinai, Egypt. *Journal of Arid Environments*, 34, 331–349. https://doi.org/10.1006/jare.1996.0114

Moustafa, A. R. A., Zaghloul, M. S., El_Wahab, R.H.A., & Shaker, M. (2001). Evaluation of plant diversity and endemism in Saint Catherine Protectorate, South Sinai, Egypt. *Egyptian Journal of Botany*, 41, 121–139.

Nagy, L., & Grabherr, G. (2009). *The biology of alpine habitats*. Oxford, UK: Oxford University Press. online

Noroozi, J., Pauli, H., Grabherr, G., & Breckle, S. W. (2011). The subnival–nival vascular plant species of Iran: A unique high-mountain flora and its threat from climate warming. *Biodiversity & Conservation*, 20, 1319–1338. https://doi.org/10.1007/s10531-011-0029-9

Omar, K. (2014). Assessing the conservation status of the Sinai Primrose (*Primula boveana*). *Middle-East Journal of Scientific Research*, 21, 1027–1036.

Pauli, H., Gottfried, M., Reiter, K., Klettner, C., & Grabherr, G. (2007). Signals of range expansions and contractions of vascular plants in the high Alps: Observations (1994-2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology*, 13, 147–156. https://doi.org/10.1111/j.1365-2486.2006.01282.x

Perevolotsky, A., Perevolotsky, A., & Noy-Meir, I. (1989). Environmental adaptation and economic change in a pastoral mountain society: The case of the Jabaliyah Bedouin of the Mt. Sinai region. *Mountain Research & Development*, 9, 153–164. https://doi.org/10.2307/3673478

Poulos, H. M., Taylor, A. H., & Beaty, R. M. (2007). Environmental controls on dominance and diversity of woody plant species in a Madrean, Sky Island ecosystem, Arizona, USA. *Plant Ecology*, 193, 15–30. https://doi.org/10.1007/s11258-006-9245-x

Rapacciuolo, G., Maher, S. P., Schneider, A. C., Hammond, T. T., Jabis, M. D., Walsh, R. E., … Beissinger, S. R. (2014). Beyond a warming fingerprint: Individualistic biogeographic responses to heterogeneous climate change in California. *Global Change Biology*, 20, 2841–2855. https://doi.org/10.1111/gcb.12638

Rashad, S., Basset, Y., Hemeed, M., Alqamy, H., & Wacher, T. (2002). *Grazing patterns in the high-altitude mountains around St Katherine town*. Cairo, Egypt: EEAA/St Katherine Protectorate.

Shmida, A. (1977). Remarks on the palaeo-climates of Sinai based on the distribution patterns of relict plants: Prehistoric investigation in Gebel Maghara, Northern Sinai. *Kedem*, 6, 36–54.

Stöckl, V., Wipf, S., Nilsson, C., & Rixen, C. (2011). Using historical plant surveys to track biodiversity on mountain summits. *Plant Ecology & Diversity*, 4, 415–425. https://doi.org/10.1080/17550874.2011.651504

Van de Ven, C. M., Weiss, S. B., & Ernst, W. G. (2007). Plant species distributions under present conditions and forecasted for warmer climates in an arid mountain range. *Earth Interactions*, 11, 1–33.

Vetaas, O. R., & Grytnes, J. A. (2002). Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology & Biogeography*, 11, 291–301. https://doi.org/10.1046/j.1466-822X.2002.00297.x

Walther, G. R., Beißner, S., & Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, 16, 541–548. https://doi.org/10.1111/j.1654-1103.2005.tb02394.x

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., … Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. https://doi.org/10.1038/416389a

Wayne, P. M., Reekie, E. G., & Bazzaz, F. A. (1998). Elevated CO_2 ameliorates birch response to high temperature and frost stress: Implications for modeling climate-induced geographic range shifts. *Oecologia*, 114, 335–342. https://doi.org/10.1007/s004420050455

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer. https://doi.org/10.1007/978-0-387-98141-3

Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., & Monserrat, V. J. (2005). Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, 8, 1138–1146. https://doi.org/10.1111/j.1461-0248.2005.00824.x

Wipf, S., Stöckli, V., Herz, K., & Rixen, C. (2013). The oldest monitoring site of the Alps revisited: Accelerated increase in plant species richness on Piz Linard summit since 1835. *Plant Ecology & Diversity*, 6, 447–455. https://doi.org/10.1080/17550874.2013.764943

Zahran, M. A., & Willis, A. J. (2008). *The vegetation of Egypt (vol. 2)*. London, UK: Springer.

Zalat, S., Gilbert, F., Fadel, H., El-Hawagry, M. S., Saleh, M., Kamel, S., & Gilbert, J. (2009). Biological explorations of Sinai: Flora and fauna of Wadi Isla and Hebran, St Katherine Protectorate, Egypt. *Egyptian Journal of Natural History*, 5, 6–15.

Zhang, X., Aguilar, E., Sensoy, S., Melkonyan, H., Tagiyeva, U., Ahmed, N., … Albert, P. (2005). Trends in Middle East climate extreme indices from 1950 to 2003. *Journal of Geophysical Research: Atmospheres*, 110, 1–12.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Table S1 Altitudinal distributions of each species from 2014 data

Table S2 Summary data on the occupancy and abundance of each species from the 2014 surveys. There were a total of 283 quadrats in 36 sites in the study

Table S3 Gps locations (decimal degrees) of 100 m^2 quadrats (centre point ± 3 m) along with site information and hill's number diversity indices for each quadrat sampled in 2014

Table S4 Site descriptions and photos for 100 m^2 quadrats sampled in 2014

Table S5 Species abundance for quadrats surveyed in 2014

Figure S1 Abundance-weighted altitudinal distributions of each species from 2014 data

Figure S2 Altitudinal distributions of each species from 2014 data