Flowering range changes across an elevation gradient in response to warming summer temperatures

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Abstract

Many studies have demonstrated plant response to warming temperatures, both as advancement in the timing of phenological events and in range shifts. Mountain gradients are ideal laboratories for studying species range changes. In this study of 363 plant species in bloom collected in five segments across a 1200 m (4158 ft) elevation gradient, we look for changes in species flowering ranges over a 20-year period. Ninety-three species (25.6%) exhibited a significant change in the elevation at which they flowered from the first half to the second half of the record, with many of these changes occurring at higher elevations. Most of the species exhibiting the changes were perennial plants. Interestingly, though many changes in flowering range were specific to higher elevations, range changes occurred all across the gradient. The changes reported in this study are concurrent with significant increases in summer temperatures across the region and are consistent with observed changes around the globe.

Keywords: Arizona, climate, climate change, elevation gradient, flowering range, phenology, range shift, species distribution, species response to climate, warming temperatures

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Introduction

Plant distribution is strongly influenced by climatic conditions (Holdridge, 1947, 1967; Box, 1981). Many models have predicted that the margins of species ranges or boundaries of biomes will move higher in latitude or elevation in response to warming temperatures (e.g., Sykes et al., 1996; Iverson & Prasad, 1998; Geiffert et al., 1999; Bakkenes et al., 2002; Hannah et al., 2003). Field studies have already documented shifts in species ranges (Walther et al., 2002; Tape et al., 2006) as well as shifts upward in elevation occurring in response to recent warming (Wardle & Coleman, 1992; Grabherr et al., 1994; Kullman, 2002; Penuelas & Boda, 2003; Kelly & Goulden, 2008). These range changes may be generalized as shifts in elevation or latitude, characterized by the upper and lower bounds of the species’ range moving upslope, as an expansion to higher elevation or latitude; or as a contraction to higher elevation or latitude, characterized by the lower bound moving upslope (Fig. 1). Ranges could shift, expand, or contract to lower elevations or latitudes as well.

Temperatures have steadily increased in recent decades across much of the western United States, resulting in less frequent freezing events and lengthening of the frost-free season (Cayan et al., 2001; Easterling, 2002; Weiss & Overpeck, 2005). It has been proposed that plant species of this region, once less limited by freezing events, may also expand their ranges and move upslope in response to this warming (Lyford et al., 2003). In this study, we present an analysis of changes to flowering ranges in plants across a 1200 m (4158 ft) elevation gradient in southwestern Arizona using a 20-year phenological record. The data analyzed in this study were collected across an elevation gradient ranging from 945 to 2213 m (3100–7258 ft) near Tucson, AZ, USA, encompassing biotic communities from desert scrub to montane conifer forest. Plants observed in flower at higher elevations in the latter half of the record suggest increasing reproductive success at higher elevations, which could lead to changes in distribution and abundance over time. Southwestern ‘sky islands’, mountain islands of forests isolated by intervening valleys of grassland or
desert, are ideal laboratories for studying species range changes. Such mountain ranges, including our study site, encompass biotic variability equivalent to a latitudinal transect ranging from southern Arizona to southern Canada. Our objectives in this study are (1) to document changes in the elevation range of flowering for 363 plant species over 20 years and (2) to interpret these range changes within the context of a 1200 m (>4000 ft) elevation gradient. Finally, we discuss the possible relative impact of warming temperatures on these plant communities.

Materials and methods

A record of species in flower for 363 plant species was documented along the Finger Rock and Pima Canyon trails, an 8 km (5 mile) hiking route located on the south slope of the Santa Catalina Mountains north of Tucson, AZ, USA for 20 years by one of us (C. D. B.). The Finger Rock trail climbs 4.5 miles from an elevation of 945 m (3100 ft) at the trailhead through Finger Rock Canyon to the junction with the Pima Canyon Trail at 2088 m (6850 ft); the Pima Canyon trail continues 0.5 miles to the peak of Mt. Kimball at 2213 m (7258 ft). The data analyzed in this study are 111,012 observations of plant species in flower and are the result of 124 round-trip (10 mile) hikes of the route to Mt. Kimball and 30 partial trips of 2–8 miles made over a period (January 1984 to December 2003) [4.1 hikes yr⁻¹ (mean ± SE)]. The observer recorded species observed in bloom, with the primary focus being a series of cliffs and steep rocky slopes. The last third of mile 1 and the beginning of mile 2 are in an ephemeral riparian area (Fig. 2).

The observed species were recorded along five trail segments approximately 1 mile in length (Table I) both on ascent and descent; on the descent, attention was given to verifying records and adding any taxa not recorded. Blooming was defined as the presence of pollen on anthers in angiosperms; gymnosperms were considered 'in bloom' by the presence of pollen. Any species not recognized was collected for expert identification.

Weather data from six National Weather Service Cooperative Observer sites within 100 km of the study area were obtained from the National Climatic Data Center (NCDC, 2008; Fig. 2). No long-term climate records are available at or near the study site; trends were plotted against the range of elevation of the study site.

Fig. 1 Conceptual model of possible plant flowering range changes across an elevation gradient. Diagrams depict flowering range shift upslope (a), flowering range expansion upslope (b), flowering range contraction upslope (c), flowering range expansion downslope (d), flowering range contraction downslope (e), flowering range expansion upslope and downslope (f), flowering range shift downslope and flowering range contraction in both up and downslope directions (h).
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Fig. 2. Finger Rock study area and weather stations used in analysis. Finger Rock trail shown in white. Shaded areas approximate vegetation communities: DS, desert scrub; SG, scrub grassland; OW, oak woodland; OPW, oak-pine woodland; FT, pine forest; RS, resistant scrub.

Nino-Southern Oscillation and the North American Monsoon System (Sheppard et al., 2002). Seasons were defined as winter (DJFM), spring (AMJJ), summer (JAS), and fall (ON) to capture the seasonality of temperature and precipitation unique to the Sonoran Desert region (Crimmins & Comrie, 2004).

Statistical analyses

For each species, the highest mile and the lowest mile in which it was observed in flower for a particular year was extracted from the record. Species for which the count of observations in the first half of the study period (1984-1993) or the count of observations in the second half of the study period (1994-2003) was less than five were removed from further analyses. Independent one-tailed t-tests assuming unequal variance were applied to each species record to test whether the highest mile...
Table 1  Elevation range and dominant biotic communities represented within each mile segment along the Mt. Kimball route, Santa Catalina Mountains, Tucson, AZ, USA

<table>
<thead>
<tr>
<th>Trail segment</th>
<th>GPS coordinates</th>
<th>Elevation (m)</th>
<th>Elevation range (m)</th>
<th>Dominant biotic community [based on Brown (1982)]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mile 1</td>
<td>32°20'14.70, -110°54'35.78&quot; to 32°20'13.30&quot;</td>
<td>945-1079</td>
<td>134</td>
<td>Desert scrub, riparian</td>
</tr>
<tr>
<td>Mile 2</td>
<td>32°20'54.30, -110°54'13.30&quot; to 32°21'11.80&quot;, -110°53'45.60&quot;</td>
<td>1079-1372</td>
<td>29</td>
<td>Desert scrub, scrub grassland</td>
</tr>
<tr>
<td>Mile 3</td>
<td>32°21'11.80&quot;, -110°53'45.60&quot; to 32°21'33.10&quot;, -110°53'14.10&quot;</td>
<td>1372-1671</td>
<td>299</td>
<td>Scrub grassland, oak woodland</td>
</tr>
<tr>
<td>Mile 4</td>
<td>32°21'33.10&quot;, -110°53'14.10&quot; to 32°21'57.70&quot;, -110°52'45.90&quot;</td>
<td>1671-1939</td>
<td>268</td>
<td>Oak-pine woodland</td>
</tr>
<tr>
<td>Mile 5</td>
<td>32°21'57.70&quot;, -110°52'45.90&quot; to 32°22'37.70&quot;, -110°52'44.70&quot;</td>
<td>1939-2213</td>
<td>274</td>
<td>Oak-pine woodland, pine forest</td>
</tr>
</tbody>
</table>

Fig. 3  Species that exhibited a shift upslope in flowering range over the 5 mile gradient along the route to Mt. Kimball, Santa Catalina Mountains, Tucson, AZ, USA. Endcaps denote the mean highest and lowest miles species were observed in flower in the first (first bar in each pair) and second half (second bar in each pair) of the record.

observed for a particular species was higher or lower in the second half of the study period than in the first half of the study period (two t-tests per species). These analyses were repeated for each species using the lowest miles recorded in each year (two additional t-tests per species). We use the highest and lowest miles for which a species appeared over the 5 year period as a proxy for the species assuming unequal sample sizes with the sample sizes used in analyses which were performed using Stata v9.2 (StataCorp, College Station, TX, USA).

We used these analyses to determine if there was a shift in the distribution of flowering times between the first and second half of the study period for each species. We used the highest and lowest miles observed for each species in the first half of the study period and the highest and lowest miles observed for each species in the second half of the study period.

Results

Of the 363 species observed, 93 species (25.6%) exhibited a shift upslope in flowering range from the first half of the study period to the second half of the study period. Species that exhibited a shift are characterized by the highest and lowest miles where species were observed in flower in the first half of the study period and the second half of the study period.

Twelve species exhibited a shift upslope, characterizing the highest (P < 0.05) and lowest (P > 0.05) miles in the second half of the study period. These species are listed in Table 1. The upper limit of the flowering range of these species was significantly higher in the second half of the study period than in the first half of the study period.
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... which species was observed in flower in a particular year was a proxy for the upper and lower elevation limits of the species' flowering range for that year. The t-test assuming unequal variance was used because of small sample sizes (Ruxton, 2006). Statistical tests were performed using MATLAB v.R2007b.

We used the Fisher's combined test to compare the distribution of species-specific responses for each of the tests (highest mile higher or lower in the second half of the record; lowest mile higher or lower in the second half of the record) to that which would be expected by chance. These tests were performed using R2007b (StatCorp, 2006).

Sexual climate data were analyzed in a similar way with split study period (1984–1993 vs. 1994–2003). Independent two-tailed t-tests assuming unequal variance were conducted to determine if significant differences in mean climate existed between the first and second half of the study period. T-tests were performed on mean seasonal temperature and total seasonal precipitation for each station and each season. Statistical tests with weather variables were performed using R2007b. (Mathworks, Inc, 2008)

Results

Of the 33 species tested for flowering range changes, 32 species (97%) show some sort of significant change between the first and second halves of the record. The distribution of species-specific responses to the test of the highest mile appearing higher in the second half of the record is significantly different from that which would be expected by chance ($\chi^2 = 886.80$, $P < 0.001$; Fisher's combination procedure). Similarly, the distribution of species-specific responses to the test of the lowest mile appearing higher in the second half of the record is also significantly different from that which would be expected by chance ($\chi^2 = 533.79$, $P = 0.99$; lowest mile: $\chi^2 = 346.29$, $P = 0.99$; Fisher's combination procedure).

Flowering range shift upslope

Twelve species exhibited shifts in their flowering ranges upslope, characterized by both significantly higher (P < 0.05) 'highest' miles and 'lowest' miles in the second half of the record than in the first half (Fig. 3). Nine of these species are perennial plants and three are annuals. The upper boundaries of many of these species' flowering ranges advanced into the next highest mile, the lower boundaries of these species' flowering ranges advanced nearly as much. Several species (Aris- tolochia watsonii, Baccharis serothroides, Fleischmannia sonorensis, and Toreldmania occidentalis var. scapulorum) demonstrated remarkable upslope advancement in ranges. Species exhibited flowering range shifts within all 5 miles of the gradient, however, six of the twelve species in this category shifted into the highest mile of the study gradient.

Flowering range expansion upslope

Thirty-four species (21 perennials, 13 annuals) demonstrated a significant upslope expansion of their flowering ranges, defined as a significantly higher (P < 0.05) 'highest' mile in the second half of the record than in the first half (Fig. 4). Over half of the species in this category expanded their flowering ranges into the highest mile of the study gradient.

Flowering range contraction upslope

Twenty-three species (18 perennials, 5 annuals) demonstrated a significant upslope contraction of their flowering ranges, characterized as a significantly higher (P < 0.05) 'lowest' mile in the second half of the record (Fig. 5). Of these, 17 species (74%) exhibited flowering range contraction within the lowest 2 miles of the study gradient.

Changes in flowering range downslope

Eleven species (10 perennials, 1 annual) demonstrated a significant downslope expansion of their flowering ranges, defined as a significantly lower (P < 0.05) 'lowest' mile in the second half of the record than in the first half. Approximately half of these species expanded their flowering ranges downslope into the lower miles of the study gradient and the other half expanded their flowering ranges downslope within the upper miles of the study gradient.

Seven species (three annuals, four perennials) demonstrated a significant downslope contraction of their flowering ranges, defined as a significantly lower (P < 0.05) 'highest' mile in the second half of the record than in the first half. These species were confined to lower study miles (miles 1–3). Two species (both perennial) exhibited flowering range contraction in both directions, defined as a significantly lower (P < 0.05) 'highest' mile and a significantly higher 'lowest' mile in the second half of the record than in the first half. Additionally, two species (one annual, one perennial) exhibited flowering range expansion in both the uphill and downhill directions.

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Temperatures have generally warmed at all stations in Chang es in climatic variables significantly warmer in the second half of the record significantly higher in the first half.

Fig. 4 Species that exhibited a flowering range expansion upslope over the 5 mile gradient along the route to Mt. Catalina Mountains, Tucson, AZ, USA. Endcaps denote the mean highest and lowest miles species were observed in flower in the first half (first bar in each pair) and second half (second bar in each pair) of the record.

and downhill directions, characterized by a significantly higher (P<0.05) 'highest' mile and a significantly lower 'lowest' mile in the second half of the record than in the first half.

Changes in climatic variables
Temperatures have generally warmed at all stations in most seasons across the region around the study area when comparing the first to the second half of the study period (Table 2). Summer (JAS) temperatures were significantly warmer in the second half of the record than in the first half at all six stations. All six stations observed significant temperature differences ranging from 0.8 to 1.2°C warmer in the second half of the study period. The magnitude of the summer temperature differences do not appear to be related to elevation, so it can be assumed that temperature trends are generally constant along the study gradient. No significant temperature differences were observed in any of the other seasons. Similarly, there was no difference in seasonal precipitation between the first and second halves of the record in any season at any of the stations tested.

Discussion
Flowering is an energetic investment for plants and therefore a measure of individual plant fitness (Ba mack, 1980; O'Neill, 1997). A change in a species flowering range is biologically significant, suggesting increasing plant fitness in new areas, in this case, different elevations. Flowering, a part of the reproductive cycle, is directly linked to plant establishment, persistence, spread, and abundance. Indeed, the changes in flowering range reported in this study do not represent changes in species distributions, as the plants could have been present but not flowering at higher elevations in the past. However, plants observed in the latter half of the study period are reproductive individuals.
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Species that exhibited a flowering range contraction upslope over the 5 mile gradient along the route to Mt. Kimball, Santa Catalina Mountains, Tucson, AZ, USA. Endcaps denote the mean highest and lowest miles species were observed in flower in the first half (first bar in each pair) and second half (second bar in each pair) of the record.

Table 2: Changes in seasonal average temperatures between 1984-1993 (first period) and 1994-2003 (second period) at six weather stations in southeastern Arizona.

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>Winter (DJFM)</th>
<th>Spring (AMJ)</th>
<th>Summer (JAS)</th>
<th>Fall (ON)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Second period-first period (°C)</td>
<td>P</td>
<td>Second period-first period (°C)</td>
<td>P</td>
</tr>
<tr>
<td>Mt. Peak</td>
<td>2069</td>
<td>0.8</td>
<td>0.109</td>
<td>-0.1</td>
</tr>
<tr>
<td>C-rule</td>
<td>1374</td>
<td>0.1</td>
<td>0.898</td>
<td>-0.3</td>
</tr>
<tr>
<td>Santa Rita</td>
<td>1310</td>
<td>0.8</td>
<td>0.009</td>
<td>0.1</td>
</tr>
<tr>
<td>Tucson</td>
<td>999</td>
<td>0.3</td>
<td>0.37</td>
<td>-0.2</td>
</tr>
<tr>
<td>Tucson UNW</td>
<td>781</td>
<td>0.0</td>
<td>0.946</td>
<td>-0.2</td>
</tr>
<tr>
<td>Tucson Airport</td>
<td>777</td>
<td>0.1</td>
<td>0.729</td>
<td>-0.4</td>
</tr>
</tbody>
</table>

Significant values in bold.

Higher elevations in the earlier part of the record favored plants observed in flower at higher elevations in the latter half of the record suggest increasing reproductive success at higher elevations, which could lead to changes in distribution and abundance over time. Strong relationships exist between the distribution of plant communities and temperature and available radiation.
moisture conditions (Holderidge, 1947, 1967; Box, 1981). In the northern hemisphere, the northern and upper-elevation range limits for plants in a variety of vegetation communities are widely attributed to low temperatures, either freezing temperatures or the absolute value and duration of low temperatures (Bowers, 1981; Sakai & Innes, 1998; Inouye, 2000; Pither, 2003; Scheiflinger et al., 2003). Similarly, many phenological events in plants are cued by temperature and moisture conditions (Rathcke & Lacey, 1985). Accordingly, changes in temperature or moisture characteristics have been predicted to impact the spatial distribution of plant species as well as the timing of phenological events. In the southwestern United States, as in much of the globe, changes in temperature conditions are being documented, as are plant and animal responses.

**Uplike changes in flowering range**

Given the observed increase in average temperatures over the study period, the upside flowering range shifts and expansions documented in this study are consistent with expectations. They are also consistent with several other studies of species range limits. Range boundaries have been documented to shift higher in elevation or poleward in a variety of biomes ranging from low to high elevations and encompassing tropical rainforest (Read & Hill, 1985), deciduous broad-leaved (Penuelas & Boada, 2003), woody evergreen broad-leaved (Waller, 2002; Berger & Waller, 2003), treeline (Lescop-Sinclair & Fayette, 1995; Kullman, 2002; Luckman & Kavanagh, 2002), and montaintop vegetation communities (Grabherr et al., 1994). In nearly all these studies, the range changes have been attributed to fundamental changes in limiting environmental factors, namely, to increasing seasonal or annual temperatures. Increasing temperatures have resulted in a lengthening of the growing season and an expansion of the area in which seedlings can survive, thereby increasing the range in which plants can successfully complete their life cycles and persist. In the Finger Rock dataset, flowering range shifts and expansions are occurring all across the gradient, in all vegetation community types, though many of the species exhibiting flowering range changes occurred in the montane community of the highest miles. High summer temperatures have been shown experimentally to stimulate the establishment, survival, and growth in high elevation plant communities (Swimbyrsson et al., 1996; Kullman, 2002). Indeed, the warmer summer temperatures recorded in this study may account for the range changes observed in the highest miles of the Finger Rock study.

The upslope flowering range contractions documented in some species in the present study are similarly consistent with patterns documented elsewhere. Walther (1997), Carraro et al. (1999) as cited in Walther (2003), and Walther & Grundmann (2001) all report a retreat tendency of montane species at the lower ends of their distributions and conditions may be such that low temperatures necessary to complete life cycle events such as breaking dormancy are not being reached (Vegis, 1964). In this present dataset, upslope flowering range contractions has been observed primarily at lower elevations. Community organization and distribution of semiarid plant communities such as those at the lower elevations along this gradient are strongly limited by precipitation as well as temperature (Noy-Meir, 1973; Woodward, 1989). Changes in both the timing and the amount of seasonal rainfall have been suggested as drivers behind community reorganization, especially in desert communities (Turner et al., 1995; Brown et al., 1997; Allred & Bresehears, 1998). Though we found no difference in seasonal precipitation between the first half and the second half of the record, the range contractions observed in the lowest miles may be the result of changes in the duration, frequency, or timing of individual precipitation events, precipitation characteristics not explored in this study. Alternatively, constant seasonal precipitation and average temperatures yield increased evapotranspiration rates, resulting in effectively drier conditions from 2002. This may also account for the continuing flowering range observed in some species.

In several long-term studies undertaken in European mountain ranges, the upward shift or expansion of species ranges has been expressed as an increase in species richness at high elevations, rather than displacement of plants off mountain tops (Grabherr et al., 1994; Keller et al., 2000; Pauli et al., 2001; Kondrat & Birks, 2003). Indeed, this pattern has been documented for Finger Rock as well (Crimmins et al., 2003). As in European studies, the pattern of increasing altitude in species of bloom on Finger Rock appears to be closely tied to increasing summer temperatures (Crimmins et al., 2008). Recent observations on the Finger Rock trail by the observer show that this upward trend is continuing (C. D. Bertelsen, unpublished data).

**Changes in flowering range downslope**

Of the 11 species demonstrating significant downhill expansions in their flowering ranges, three were served in a lower mile but still in the same vegetation association and biologically (Asantia laxculum, and Eriogonum viride) in the second half of the study. Accordingly, changes in temperature or moisture availability of a boulder, persisting as found in these populations a restricted flora and fauna of a biotic community organization, especially in desert communities (Turner et al., 1995; Brown et al., 1997; Allred & Bresehear, 1998). Though we found no difference in seasonal precipitation between the first half and the second half of the record, conditions observed in the lowest miles may be the result of changes in the duration, frequency, or timing of individual precipitation events, precipitation characteristics not explored in this study. Alternatively, constant seasonal precipitation and average temperatures yield increased evapotranspiration rates, resulting in effectively drier conditions from 2002. This may also account for the continuing flowering range observed in some species. In several long-term studies undertaken in European mountain ranges, the upward shift or expansion of species ranges has been expressed as an increase in species richness at high elevations, rather than the displacement of plants off mountain tops (Grabherr et al., 1994; Keller et al., 2000; Pauli et al., 2001; Kindrat & Birks, 2003). Indeed, this pattern has been documented for Finger Rock as well (Crimmins et al., 2003). As in European studies, the pattern of increasing altitude in species of bloom on Finger Rock appears to be closely tied to increasing summer temperatures (Crimmins et al., 2008). Recent observations on the Finger Rock trail by the observer show that this upward trend is continuing (C. D. Bertelsen, unpublished data).
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Several studies documenting species range changes have also recorded the concurrent spread and proliferation of non-native plants (Klotzi et al., 1996; Walther, 1997, 2000, 2003). The spatial shift in native species’ distributions combined with warming temperatures may open niches into which aggressive plants can invade. This phenomenon has been observed on Finger Rock; Engelritis lomelhannana, a nonnative perennial grass, has spread from miles 1, 2, and 3 in the early years of the study up to mile 5 in 2001. Pennisetum ciliare, a nonnative perennial grass species not tested in this study due to lack of observations in the early half of the record, first appeared in mile 1 in 1990. In 1999, it was observed in mile 2; it is now well established up to 4500 ft and has been collected at 5200 ft. Rapidly changing environmental conditions may indeed favor highly mobile, opportunistic species such as these, resulting in very different species assemblages into the future (Malcolm et al., 2002).

Implications of observed changes

In many studies of plant distribution, species have been demonstrated to respond independently to climate change (e.g., Huntley, 1991; Harrington et al., 1999; Kullman, 2002; Voigt et al., 2003). For example, Kullman (2002) found that in response to warming temperatures, some montane tree species are expanding their ranges upslope very rapidly, whereas shrub species in the same region are responding at a much slower rate. The changes in flowering range documented in the Finger Rock dataset similarly show individualistic responses. It is especially interesting to note that the majority of species exhibiting changes in flowering range, especially in the upslope direction, are perennial plants.

Biology. We believe these small populations are persisting as a result of the more suitable conditions found in these small microhabitats; they are not showing any indications of spreading beyond these microhabitats. The final four species that were observed in bloom at a lower elevation were observed in the ephemeral drain area in miles 1 or 2, where moisture and shade are more abundant. Seeds from plants are possibly being moved downslope by wind, water, and gravity; these plants are thought to have persisted at these lower elevations due to the more suitable conditions encountered in the riparian area. We feel that none of the species in this category are actually depicting biologically significant downhill flowering range expansion.

A number of non-native perennial grass species not tested in this study due to lack of observations in the early half of the record, first appeared in mile 1 in 1990. In 1999, it was observed in mile 2; it is now well established up to 4500 ft and has been collected at 5200 ft. Rapidly changing environmental conditions may indeed favor highly mobile, opportunistic species such as these, resulting in very different species assemblages into the future (Malcolm et al., 2002).

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This seems to support the suggestion that plants are indeed expanding their distributions into higher elevations. We may expect to see continued changes in community composition across this mountain gradient into the future, as climatic conditions continue to change and species migrate in response.

Pollen records have demonstrated that the fundamental response of taxa to rapid and continuous climate change has been migration, that is, species follow suitable environmental conditions (Huntley & Webb, 1989). The flowering range changes documented in the present study may indeed be evidence of plant species migrating, primarily upslope, to follow suitable temperature conditions. Global temperatures are expected to continue to increase (i.e., more frost-free days (IPCC, 2007)). With continued warming, species of this region are expected to expand their distributions northward (Lyford et al., 2003) as well as upward in elevation (Weiss & Overpeck, 2005). We may also expect increasing invasion by exotic species, an increase in wildfires in desert areas not adapted to fires, and perhaps the loss of species off the tops of mountains.

The changes in flowering range documented in this study may be the result of factors other than climate, exerting influence independently or in concert with a changing climate. However, many obvious candidates seem unlikely. No fires have burned in the canyon for over 100 years. Additionally, there have been no changes in the land use of the Finger Rock canyon or proximate landscape over the period of the study, though the nearby city of Tucson increased in size and density during the period of record. The consequent increase in air pollution in the valley could perhaps account for plant species’ flowering range changes; however, studies linking altitudinal vegetation redistribution are lacking (Kelly & Goulden, 2008). The spread of invasive plants in the canyon, which may also be related to climate change, is indeed affecting community composition and flowering ranges (Archer & Pre- dick, 2008); the magnitude of influence that invasive species exert on the plant communities of this watershed merits further study. The findings of this study are consistent with many other studies documenting the influence of climate change on plants’ distribution, phenology, and community organization; it seems very plausible that the changes recorded in this study are mainly attributable to the concurrent warming temperatures.

The rate of temperature change predicted for the future is 10–100 times faster than that experienced during the last glacial retreat (Huntley, 1991). This may require species to migrate at rates much faster than those observed during past glacial times to follow their climatic envelopes (Malcolm et al., 2002). It has been suggested that such rapidly changing conditions may favor highly mobile and opportunistic species, affecting community composition and structure, ecosystem properties and processes, and reducing biodiversity [Malcolm et al. (2002) and cites within; Walter (2003) and cites within]. The results presented in the study suggest that many plants along an elevational gradient are responding to changing climate conditions similar to plants in other parts of the globe; blooming progressively higher elevations all along the gradient than in previous years. Given these observations, we expect plant flowering distributions to continue to be affected under continued warming conditions.

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