

Rapid shifts in plant distribution with recent climate change

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Edited by Christopher B. Field, Carnegie Institution of Washington, Stanford, CA, and approved June 6, 2008 (received for review March 24, 2008)

A change in climate would be expected to shift plant distribution as species expand in newly favorable areas and decline in increasingly hostile locations. We compared surveys of plant cover that were made in 1977 and 2006–2007 along a 2,314-m elevation gradient in Southern California's Santa Rosa Mountains. Southern California's climate warmed at the surface, the precipitation variability increased, and the amount of snow decreased during the 30-year period preceding the second survey. We found that the average elevation of the dominant plant species rose by ≈ 65 m between the surveys. This shift cannot be attributed to changes in air pollution or fire frequency and appears to be a consequence of changes in regional climate.

plant migration | range shift

Climate controls the distribution of many plants (1, 2). Future changes in climate are projected to cause changes in vegetation distribution (3). The global mean land surface has warmed 0.27 °C per decade since 1979 (4), but it is unclear whether this change has caused widespread shifts in plant distribution (5). Parmesan and Yohe (6) compiled studies on many species, including alpine herbs, birds, and butterflies, and found an average poleward shift of 6.1 km per decade. Several studies have attributed widespread changes in plant growth or mortality to climate change (7), but these efforts have focused on general trends within biomes rather than identifying spatially coherent redistribution patterns. Studies of plant phenology have attributed longer growing seasons, earlier onset of flowering, and earlier harvest to climate warming (5, 6). The few studies that have shown evidence of plant shifts have focused on the edges of plant ranges (8–10). The lack of evidence of widespread plant range shifts may reflect the limited dispersal of plants (11, 12), or it may simply reflect the paucity of long-term records of plant distribution.

The Deep Canyon Transect in Southern California's Santa Rosa Mountains spans several plant communities and climates (13) and provides an excellent opportunity to investigate the climatic controls on plant distribution (2, 14). The transect rises from 244 m to 2,560 m over 16 km, climbing through desert scrub, pinyon-juniper woodland, chaparral shrubland, and conifer forest. The overall climate is arid and semiarid, with predominantly cool-season precipitation. The annual precipitation, proportion of precipitation falling as snow, and probability of frost increase with increasing elevation, and the annual mean temperature and interannual precipitation variability decrease with increasing elevation [supporting information (SI) Table S1]. We compared two vegetation surveys of the Deep Canyon Transect, one made in 1977 and the other in 2006–2007, to determine whether the distribution of plants with elevation has shifted in response to recent climatic change.

Results

A total of 141 species were recorded along the transect in 2006–2007. Many of these species were found at only one or two elevations. Ten of the species were dominant at three or more elevations, and we focused our analysis on these plants (Fig. 1).

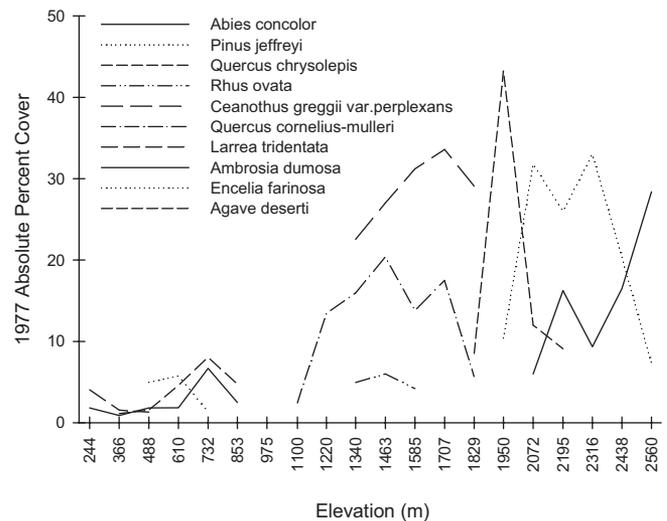


Fig. 1. Elevation distribution of absolute percent coverage of the ten dominant species across the Deep Canyon Transect in 1977.

The distributions of some of these species were similar; for example, *Ceanothus greggii* and *Quercus cornelius-mulleri* had broadly similar distributions throughout the mid-elevation shrubland. The distribution of other species was unique (14); for example, *Quercus chrysolepis* had a distinct distribution that bridged the midelevation shrubland and high-elevation forest.

The total plant cover across the transect was generally stable between 1977 and 2006–2007 (Fig. 2). The vegetation cover averaged over the entire transect increased insignificantly ($1.6\% \pm 3.2\%$; 95% confidence interval). Ten of the survey locations showed modest declines in cover; the other 10 showed modest increases. Nineteen of the twenty surveys experienced changes that were <3.5 standard errors. The qualitative and quantitative similarity of cover between surveys increased our confidence in the methodological consistency.

In contrast to the stability of overall plant cover, the distribution of individual species changed markedly from 1977 to 2006–2007. The cover-weighted mean elevation of nine of the 10 widely distributed species rose, together averaging an elevation gain of 64.7 m (± 33.8 m; 95% confidence interval) (Table 1) (see *SI Text*). The 10 dominant species together spanned a range

Author contributions: A.E.K. and M.L.G. designed research; A.E.K. performed research; A.E.K. and M.L.G. analyzed data; and A.E.K. and M.L.G. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/cgi/content/full/0802891105/DCSupplemental.

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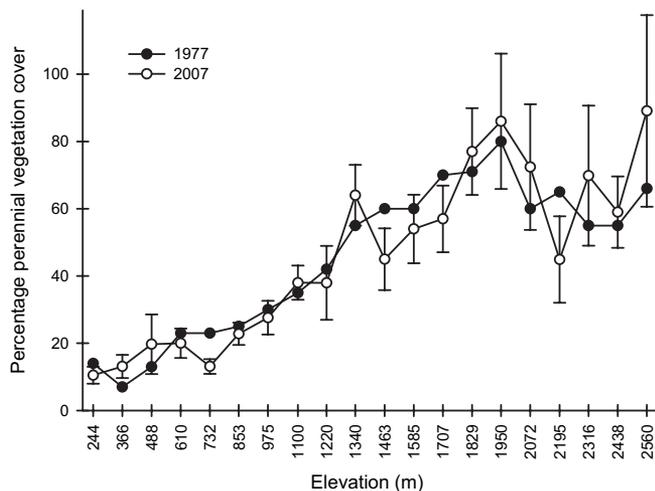


Fig. 2. Total percent coverage by perennial plants along the Deep Canyon Transect in 1977 and 2006–2007. Error bars, 95% confidence interval.

of elevations, climate zones, plant communities, and plant functional types (Fig. 1). The shifts in distribution did not vary with elevation ($R^2 = 0.024$). The mean elevation of desert, chaparral, and montane plants all increased at approximately the same rate.

The change in plant distribution may be attributed in part to a severe drought from 1999 to 2002. This drought caused marked vegetation mortality throughout Southern California, directly through water stress and indirectly through insect attack (15), and we observed many recently dead plants during the survey (see *SI Text*). However, recent mortality alone cannot explain the elevation shifts. We also observed many plants that had died before the 1999–2002 drought, and an increase in cover in the upper half of the species' ranges (Fig. 3). The 10 dominant species had a symmetric normalized elevation distribution in 1977 (14) and an upwardly skewed distribution in 2006–2007. Cover declined by a median of 46% from 1977 to 2006–2007 in the lower parts of the species' original ranges and increased by 12% in the upper parts of the original ranges ($p = 0.023$, two-tailed Student's t test, averaged across all elevations). These species shifts resulted in the upward movement of the boundaries between plant functional types. For example, the border between conifer forest and evergreen broadleaf woodland shifted upward as a result of *Pinus jeffreyi* mortality in the lower parts of its range and the proliferation of *Q. chrysolepis* in the upper parts of its range.

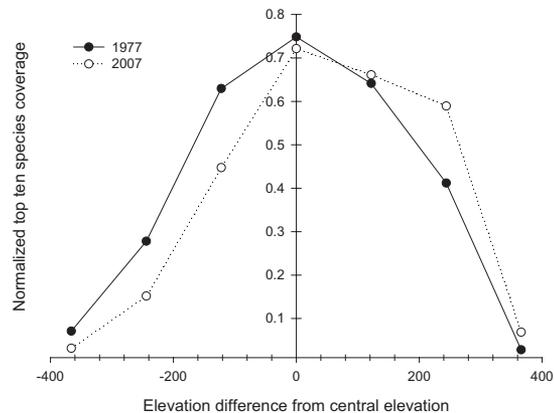


Fig. 3. Changing vegetation distribution from 1977 to 2006–2007. Elevation distribution of the mean normalized vegetation coverage of the ten most widely distributed species in 1977 and 2006–2007.

The climate at seven stations around Deep Canyon changed from the 1947-to-1976 30-year normal period to the 1977-to-2006 period. The mean and minimum air temperature and the mean precipitation and interannual precipitation variability, as indicated by the coefficient of variation, increased significantly (Table 2 and Table S2). The ratio of snowfall to total precipitation decreased at the three montane stations that historically received snow, although the seasonality of precipitation did not change. The rates of climate change at the two weather stations nearest Deep Canyon changed even more; the mean temperature at Indio and Idyllwild, CA increased by 0.77°C , the precipitation coefficient of variation increased by 0.19, and the ratio of snow to precipitation at Idyllwild decreased by 0.09 (Table S2). With the exception of the trend toward higher annual precipitation, each of these changes is consistent with an upward shift of climate. The average temperature lapse rate in the area is $-0.0073^{\circ}\text{C}/\text{m}$ (Table S1), implying an upward shift of mean temperature of 56 m (Table 2). These trends are typical of the broader region. The mean temperatures in the climate regions straddled by the transect increased by 0.63°C during the period (16, 17).

Discussion and Conclusions

Four considerations provide evidence that the observed vegetation redistribution is attributable to climate. First, the vegetation shifts were uniform across elevation (Table 1), implying that the ultimate causal factor was uniformly distributed. The recent climatic trends in Southern California do not appear to

Table 1. Change in cover-weighted mean elevation of ten most widely distributed species in the Deep Canyon Transect

Species	Mean elevation, m		Change, m
	1977	2006–2007	
<i>Abies concolor</i> (evergreen needleleaf tree)	2,421	2,518	96
<i>Pinus jeffreyi</i> (evergreen needleleaf tree)	2,240	2,267	28
<i>Quercus chrysolepis</i> (evergreen broadleaf tree or shrub)	1,987	2,033	47
<i>Rhus ovata</i> (evergreen shrub)	1,457	1,518	61
<i>Ceanothus greggii</i> var. <i>perplexans</i> (evergreen shrub)	1,602	1,671	70
<i>Quercus cornelius-mulleri</i> (evergreen shrub)	1,485	1,522	37
<i>Larrea tridentata</i> (evergreen shrub)	317	459	142
<i>Ambrosia dumosa</i> (drought deciduous shrub)	630	748	118
<i>Encelia farinosa</i> (drought deciduous shrub)	574	674	100
<i>Agave deserti</i> (evergreen succulent)	693	643	−50

Mean change in elevation, 65 m; 95% confidence interval, 34 m.

The mean normalized vegetation coverage in Fig. 3 was calculated by using the 10 most widespread species in the survey (Fig. 1). The vegetation cover observed at each elevation for each species (Fig. 1) was normalized by the maximum cover observed at any elevation for that species in 1977. The normalized cover as a function of relative elevation was then determined by averaging across all 10 species for the locations above and below the centers of the species' 1977 distributions. The mean cover-weighted elevations in Table 1 were calculated by dividing the product of the observed absolute cover and elevation (Fig. 1) summed across all elevations by the absolute cover summed across all elevations for each species.

Climate data came from seven weather stations that were near the Deep Canyon Transect and that had nearly continuous records from 1947 to 2007.

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These stations were within 75 km of the study site and spanned most of the elevation range found within the transect (Table S2).

ACKNOWLEDGMENTS. This work was performed in part at the University of California Natural Reserve System Boyd Deep Canyon Reserve. We thank J. Zabriskie, T. Chester, and I. Carbone for discussions and help in the field. This work was supported by grants from the National Aeronautics and Space Administration and the Department of Energy Program for Ecosystem Research. A.E.K. was supported by a National Science Foundation Center for Environmental Analysis-Centers of Research Excellence in Science and Technology Fellowship.