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Rapid shifts in plant distribution with recent climate change

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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).

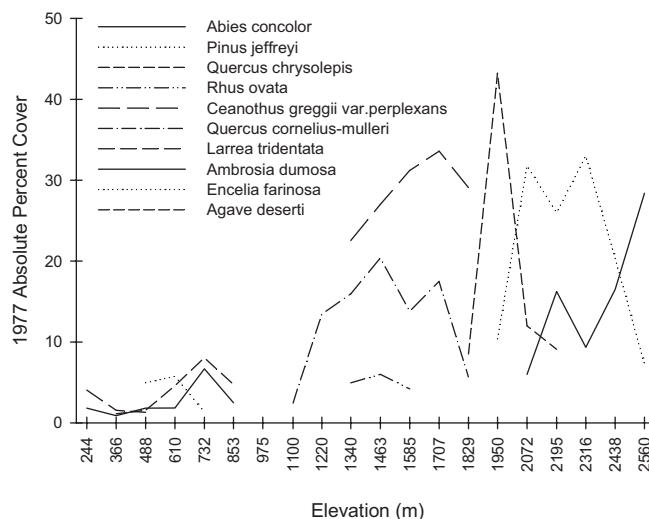


Fig. 1. Elevation distribution of absolute percent coverage of the ten dominant species across the Deep Canyon Transect in 1977.

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

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See Commentary on page 11591.

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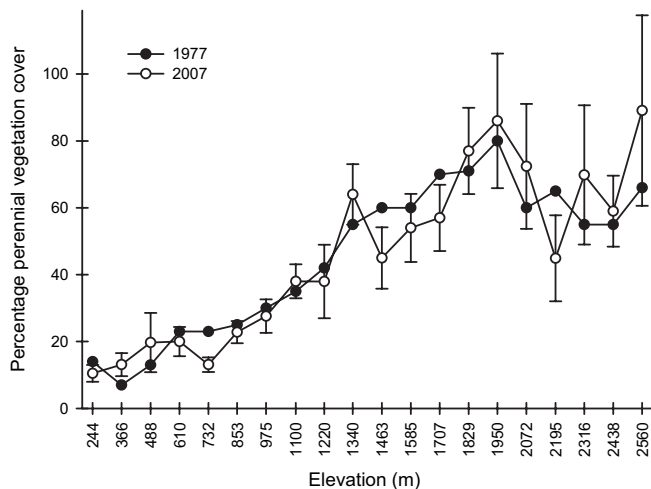


Fig. 2. Total percent coverage by perennial plants along the Deep Canyon Transect in 1977 and 2006–2007. Error bars, 95% confidence interval.

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.

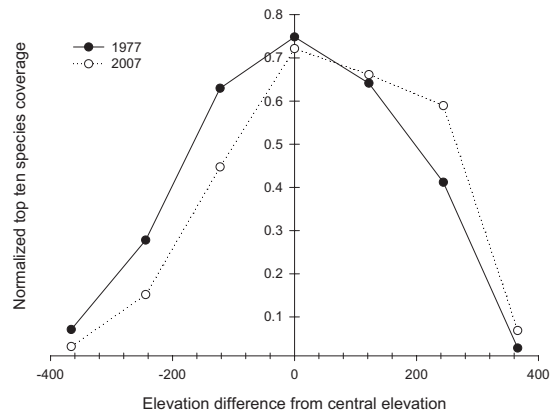


Fig. 3. Changing vegetation distribution from 1977 to 2006–2007. Elevation distribution of the mean normalized vegetation coverage of the ten most widely distributed species in 1977 and 2006–2007.

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.

Table 2. Climatic changes in inland Southern California from 1947–1976 to 1977–2006

Climate variable	Mean annual value		Change	95% CI	Elevation change, m
	1947–1976	1977–2006			
Precipitation, cm	40.0	47.3	7.3**	3.3	–138
Precipitation c_v (σ / μ)	0.48	0.61	0.13**	0.06	678
Snow / rain ratio	0.18	0.12	–0.06**	0.05	327
Maximum T, °C	24.8	25.0	0.19	0.50	24
Minimum T, °C	8.3	8.9	0.63**	0.53	83
Mean T, °C	16.5	16.9	0.41**	0.24	56

CI, confidence interval. **, $P < 0.05$.

vary strongly with elevation (17) (Table S2). Second, the vegetation shifts are consistent with the expected bioclimatic effects of most of the observed climatic shifts (Table 2). Increased temperature, frost-free period, snow line, and occurrence of severe drought, as indicated by precipitation variability, should increase plant stress in some years. This would be expected to decrease a species' ability to survive in the drier, warmer, lower parts of its range (18) and increase its competitive ability and tolerance in the wetter, cooler, upper parts of its range. Third, the change from a symmetrical vegetation distribution (14) to an upwardly skewed distribution (Fig. 3), when averaged across species and elevation, can be interpreted as both a spatial and a community representation sign-switching fingerprint of the impact of climate change on vegetation distribution (6). Fourth, the vegetation shifts resulted in part from mortality during the 1987–1990 and 1999–2002 droughts (15). The temporal correlation between mortality and drought implicates water balance and is consistent with a temporal sign-switching fingerprint of climate change (6).

Two alternative explanations for the vegetation redistribution, changes in fire frequency or air pollution, merit consideration. The wildfire regime in Southern California has changed over the last century, resulting in plant demographic shifts, especially in montane forest (15, 19). However, three considerations lead us to reject fire frequency as the main cause of plant redistribution. First, the degree of redistribution was independent of initial elevation (Table 1), whereas the degree of fire regime perturbation varied with elevation (20) (see *SI Text*). Second, most of the upper transect last burned in 1940 (20) (see *SI Text*), which is relatively recent for Southern California montane forest (15). The fire frequency in the upper transect has not diverged markedly from the historic regime, and forested sections of the transect are not thought to have experienced large demographic changes from fire suppression (21). Third, we are unaware of previous studies that have attributed a net altitudinal redistribution of vegetation (Fig. 3) to shifting fire frequency.

Some montane regions in Southern California are exposed to high levels of ozone and nitrogen deposition, resulting in increased vegetation mortality (22). However, five considerations lead us to reject air pollution as the main cause of plant redistribution. First, the Deep Canyon Transect is comparatively distant from Los Angeles' emission sources, and ozone-related conifer mortality has not been reported in the Santa Rosa Mountains (15). Second, air pollution typically varies with elevation in Southern California (22), whereas the changes in plant distribution were independent of initial elevation (Table 1). Third, overall plant cover remained constant (Fig. 2) and did not exhibit a general decline as might be expected with air pollution. Fourth, the species' elevation changes were unrelated to the known patterns of ozone sensitivity. *P. jeffreyi* is considered more sensitive to ozone than *Abies concolor* or *Q. chrysolepis* (22, 23), whereas *P. jeffreyi* exhibited less upslope movement (Table 1). Fifth, we are unaware of previous studies that have

attributed altitudinal vegetation redistribution (Fig. 3) to air pollution.

We therefore attribute the changes in vegetation distribution to climate. We hypothesize that species redistribution occurred episodically, with accelerated mortality in the lower parts of species' ranges during unusually dry periods (18, 24–26), as occurred in 1987–1990 and 1999–2002 (16) (see *SI Text*), and infilling across species' entire ranges (Figs. 2 and 3) during unusually wet periods, as occurred in 1978–1983, 1993–1995, and 2005. The establishment of species at locations well above their previous ranges appears to have been minimal, and the observed upslope movement is a result of shifting dominance within existing communities, rather than the expansion of ranges to new elevations. The changes were most apparent at the population and community levels (Fig. 3), and some ecosystem properties, such as total cover, were comparatively stable (Fig. 2). An accurate forecast of the shifts we observed would require a dynamic vegetation model that represented the effects of climate and weather on the local populations of individual species or plant functional types. We are unable to determine which aspect of the changing climate was most strongly related to species redistribution. In fact, the various observed climatic changes may interact and reinforce each other; climate warming coupled with increasing climate variability intensifies the effects of extreme yet unexceptional droughts (4, 7, 25).

Past studies have led to the conclusion that the distribution of plant species lags the climatic conditions during periods of rapid change (12). However, our results show that the distribution of the dominant species at Deep Canyon increased by ≈ 65 m in just 30 years (Table 1). We attribute this upward movement to recent changes in the local climate (Table 2). We cannot link the observed climate changes to greenhouse gas forcing; the local changes could be because of regional urban heat island effects (17) or long-term climate fluctuations, such as the Pacific Decadal Oscillation (27). Nonetheless, the climate changes observed are similar to climate changes that have been predicted with (4) or attributed to (28) greenhouse gas-forced global climate change. Our results imply that surprisingly rapid shifts in the distribution of plants can be expected with climate change, at least in areas where dispersal is not a major constraint, and that global climate change may already be impacting the distribution of vegetation.

Methods

We compared vegetation coverage by using the dataset, sites, and methods used by Zabriskie (13). Zabriskie surveyed twenty linear vegetation transects in 1977, which followed 400-m isocontours, equally spaced at 122-m elevation intervals from 244 m to 2,560 m. Individual perennial plant cover was measured along isocontours centered on north-facing slopes to minimize variation in hydrology and aspect. We resurveyed these sites in 2006 and 2007 to determine whether the cover and distribution of plants changed during the intervening 30 years (29) (see *SI Text*). Zabriskie toured the area with us at the beginning of our study to ensure consistency between surveys.

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).

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Supporting Information

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SI Text

Supporting Notes. Land use history. Zabriskie originally surveyed 22 locations from 0- to 2,560-m elevation. The two sites below 200 m were not protected and were developed through the expansion of the city of Palm Desert; we did not revisit these sites. The sites between 200 m and 1,000 m have been protected since the 1960s. These sites are within the Boyd Deep Canyon Reserve and access is strictly controlled. The sites above 1,000 m were publicly owned and had open access. Most of the area above 1,000 m was relatively inaccessible and received little use. The transects at 1,100, 1,220, 2,438, and 2,560 m were somewhat more accessible, although foot traffic and use was still light. The trends in plant cover at the more accessible sites were similar to those at the less accessible sites (Fig. 2).

Fire history. Two fires affected the Deep Canyon Transect in the past 100 years (1). Historical records indicate that all survey sites above 1,900 m burned in 1940. Charred pinyon pine trunks above 1,700 m indicate the sites at 1,707 m and 1,829 m likely also burned at that time. Records indicate the survey site at 2,560 m and half of the survey site at 2,438 m burned again in 1944. The forested vegetation above $\approx 2,000$ m is thought to have historically been exposed to moderate ground fires every 10–30 years (2). The shrubland from $\approx 1,400$ to 2,000 m is thought to have historically been exposed to severe crown fires approximately every 60 years. The open woodland, shrubland, and desert below $\approx 1,400$ m is thought to have historically been exposed to fire every 500 years or longer.

Methods. Survey methods followed Zabriskie (3). Plant coverage was measured at 20 elevations (Fig. 1) along the north slope of the Santa Rosa Mountains. Mixed conifer, chaparral, and pinyon juniper sites were surveyed July–October 2006. Desert scrub sites were surveyed in March 2007, although they had received no rainfall in the 2007 rainfall year. These dates approximate the times of year of Zabriskie's survey.

Each of the 20 surveys extended 400 m linearly along an isocontour at 122-m elevation intervals. Surveys straddled north-facing ridgelines to minimize local hydrological and aspect variations. Zabriskie toured the transect at the beginning of our study to identify the earlier survey sites and explain his methodology. Based on discussion with Zabriskie regarding site selection and reference to Zabriskie's original survey maps, we estimate the vertical elevation errors are within ± 5 m. The relocation errors are random and would not be expected to

influence the results. The vegetation within an elevation zone was broadly homogeneous, which diminished the effect of location error. The very long surveys would be expected to reduce errors associated with failure to resample the exact locations.

A 400-m tape was stretched along an isocontour at each site. Following Zabriskie, surveys deviated from the isocontours for only two reasons. To avoid areas of human disturbance, chiefly roadcuts, the survey lines circumvented these areas by a minimum of 10 m. Isocontours crossing impassible rocky barriers deviated by the minimum distance possible. Live perennial plants crossing the tape were recorded to the nearest centimeter, and each individual plant was recorded independently. Overlapping plants were counted separately; total vegetation coverage could theoretically be $>100\%$.

Dormant plants were counted as living, determined by examination of twigs, stems, and/or roots. Recent plant mortality was indicated by direct observations of intact dead plants standing with dead leaves and needles still attached. Older mortality was indicated by large amounts of woody debris with bleached surfaces, patchy intact bark, and complete loss of leaves. Time series of Thematic Mapper and Enhanced Thematic Mapper Plus remote-sensing observations showed that the Normalized Difference Vegetation Index and tasseled-cap wetness at the upper sites dropped markedly toward the end of the 1999–2002 drought, a pattern that is consistent with vegetation senescence and mortality.

The mean normalized vegetation coverage in Fig. 3 was calculated as $C_e = [\sum(c_{i,e}/c_{i,max77})]/10$, where C_e is the mean normalized vegetation coverage of the ten most widespread species at elevation e . Elevation e was measured in meters difference from the elevation of the central survey of species i . Total meters coverage of species i on the survey e meters away from the central survey is $c_{i,e}$, and this is normalized by $c_{i,max77}$, the maximum absolute coverage of species i in 1977.

Confidence intervals in coverage (Fig. 2) were calculated using the size distribution of individual plants along each survey. Individual plant coverages in 1977 were not available, so confidence intervals on 1977 data cannot be calculated.

Weather data were analyzed from seven weather stations that were selected for proximity to the center of the Deep Canyon Transect and the continuity and length of the data record (4) (Table S2). All of the stations were within 75 km of Deep Canyon and represent the range of elevations and climate zones within the transect.

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Table S1. Relationship between climate and elevation in inland Southern California

	Slope of relationship	Units	R^2 of relationship
Precip., cm	18.9	m/cm	0.80
Precip c_v (σ/μ)	-5106	m/ c_v	0.77
Snow/rain ratio	5146	m/ratio	0.97
Maximum T, °C	-126	m/°C	0.96
Minimum T, °C	-133	m/°C	0.71
Mean T, °C	-137	m/°C	0.89

