

Copyright Notice

This electronic reprint is provided by the author(s) to be consulted by fellow scientists. It is not to be used for any purpose other than private study, scholarship, or research.

Further reproduction or distribution of this reprint is restricted by copyright laws. If in doubt about fair use of reprints for research purposes, the user should review the copyright notice contained in the original journal from which this electronic reprint was made.

Marine influence controls plant phenological dynamics in Mediterranean Mexico

Sula E. Vanderplank^{1,2,*} and *Exequiel Ezcurra*²

¹ Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, TX 76107, USA

² Department of Botany and Plant Sciences, University of California, 900 University Ave, Riverside CA 92521, USA

*Correspondence address. Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, TX 76107, USA. Tel: +1 817 332 4441 Ext. 251; Fax: +1 817 332 4112; E-mail: sula.vanderplank@gmail.com

Abstract

Aims

To assess the role of moisture in phenological timing in the mediterranean coastal flora of Baja California, and specifically to assess the role of coastal fog and ocean-derived moisture in plant phenology. Moisture seems to be the primary driver of flowering times and durations at the arid end of the mediterranean-climate region, where rainfall is often sporadic (temperature and day length can be expected to play a much lesser role as they are not growth limiting). We aimed to understand: What factors drive climatic variation between sites? Are there general flowering patterns allowing us to identify phenological categories? Do flowering patterns vary in relation to site-specific weather? and most importantly, does maritime influence on weather affect flowering dynamics in coastal mediterranean ecosystems?

Methods

The southernmost extent of the California Floristic Province (in Baja California, Mexico) is a biological diversity hotspot of high endemism and conservation value, with two steep moisture gradients: rainfall (N–S) and coastal fogs (W–E), providing an ideal study system. We installed five weather stations across the moisture gradients, recording data hourly. We monitored flowering phenology in the square kilometer surrounding each weather station from 2010 to 2013. About 86 plant taxa were monitored across the five sites,

every 6–8 weeks. Averaged climatic data is presented with general trends in flowering, and specific flowering syndromes were observed. Data for flowering intensity across the sites was analyzed using a principal components analysis.

Important Findings

Data analysis demonstrates a general seasonal pattern in flowering times, but distinct differences in local weather and phenology between the five study sites. Three flowering syndromes are revealed in the flora: (i) water responders or spring bloomers, (ii) day-length responders or fall-blooming taxa and (iii) aseasonal bloomers with no seasonal affinity. The two moisture gradients are the strongest drivers of flowering times. Inland sites showed higher phenological variation than coastal sites where seasonality is dampened by ocean-derived moisture, which extends and buffers perennial plant phenology and is a probable driver of local endemism. Phenological controls vary globally with climate and geography; moisture is the primary driver of phenology in mediterranean climates and fog is an important climatic variable in coastal Mexico.

Keywords: flowering times, Baja California, maritime succulent scrub, moisture gradient

Received: 7 June 2015, Revised: 17 September 2015, Accepted: 26 September 2015

INTRODUCTION

Each of the five mediterranean regions of the world has an adjacent equatorward hot desert and an adjacent poleward temperate region. Mediterranean regions generally fall between 30° and 45° latitude, where daylight is not limiting, temperatures are amenable to plant growth and moisture availability is seasonal. The primary environmental cues acting on plant phenology are photoperiod, temperature and

moisture (Rathcke and Lacey 1985). However, given their climatic conditions, phenology in mediterranean regions is expected to be more dependent on available moisture than on temperature and day length, neither of which are severely limiting in these environments.

Mediterranean ecosystems around the world are particularly diverse, and seem to display a springtime flowering peak during the transition from the cool wet winters into the hot dry summers, at a time when mild spring temperatures and

winter-accumulated soil moisture generate optimal conditions for plant growth (Cowling *et al.* 1996). Sclerophyllous, or mediterranean type, vegetation may also occur outside winter-rain areas, shifting their flowering peak to the summer monsoon when water availability is maximum (Barbour and Minnich 1990; Peñuelas *et al.* 2002; Sniderman *et al.* 2013; Verdú *et al.* 2002). Thus, it appears that spring flowering in mediterranean vegetation is a phenomenon that is triggered by available moisture. Recorded climatic anomalies seem to support this hypothesis: For example, Minnich (1985) looked at the impacts of an unusual summer rainfall event in southern California that occurred with Hurricane Doreen, and found that species that normally flower only in spring were able to put on new leaves and flower profusely after the summer rain. Other studies show that, even in more mesic mediterranean-climate regions, rainfall has a stronger influence than temperature or day length on reproductive phenology (Peñuelas *et al.* 2002, 2004).

Phenological response to abiotic environmental factors is individual to each species (Bowers and Dimmit 1994; Rathcke and Lacey 1985). Synchronicity of flowering presents an interesting case of ecological tradeoffs: While some synchronicity is essential for pollen transfer and seed set, high synchronicity can increase predation of flowers and fruits (Rathcke and Lacey 1985). Flowering of short duration is commonly synchronous, while extended flowering is more common in aseasonal environments and is often seen in tropical forest understorey species (Gentry 1974; Rathcke and Lacey 1985).

The southernmost extreme of the California Floristic Province (CFP) along the Pacific coast of North America (located in Baja California, Mexico), harbors coastal sage scrub and maritime succulent scrub, two Californian mediterranean vegetation types dominated by facultatively deciduous low shrubs, in areas of low precipitation. Coastal sage scrub reaches its highest floristic diversity in northwestern Baja California, due to long-term climatic stability (Axelrod 1978; Raven and Axelrod 1978; Westman 1981). Further north, the increased rains during the last glacial maximum made vegetation shifts disruptive and *chaparral* (the name given in California and Mexico to mediterranean sclerophyllous vegetation) was found right down to the coast (Lyle *et al.* 2010; Minnich *et al.* 2014; Minnich 2007; Rhode 2002).

The composition and diversity of coastal sage scrub species along the coasts of the Californias has been shown to be most strongly related to summer temperatures (Westman 1981). The marine layer of northwestern Baja California reduces temperature and evapotranspiration and as a result has the richest coastal sage scrub assemblages in North America. The climatic buffering that coastal fogs provide has long been seen to affect plant phenology and historical accounts from the 1800s note the extended (earlier and later) flowering of annual plants along the coast (Minnich 2010). Yet there have been no previous studies on the perennial phenology of the coastal sage scrub and its variation as a function of proximity to the ocean. We hypothesize that maritime climate has a

decisive influence on the flowering phenology of the perennial coastal flora, and that oceanic influence plays a central role in the long ecotonal transition of the CFP into the deserts along the Pacific coast of Baja California.

The driving question in our study was: How does phenological timing in the mediterranean coastal flora of Baja California vary with available moisture, and what role does coastal influence play in plant phenology? Within this general problem, we asked four relevant questions: (a) What are the main factors driving climatic variation between sites located at different distances from the coast? (b) Are there general flowering patterns that respond to the seasonality of available moisture, allowing us to classify perennial species into simple phenological categories? (c) How do site-specific flowering patterns vary along the rainfall gradient? And, lastly, (d) what is the importance of maritime influence on flowering dynamics in coastal mediterranean ecosystems?

The study area

This study focuses on the southernmost extreme of the CFP (see Fig. 1), in the mediterranean-to-desert ecotone in Baja California, Mexico, where CFP species still prevail, but environmental conditions begin to transition into those typical of the coastal desert of the Vizcaíno peninsula to the south.

Endemism

One of the intriguing properties of this ecotone is the presence of a band of coastal endemism. Forrest Shreve (1936) first noted the precipitation gradient and the transition in the vegetation, with an increased number of succulent species as one moves south combined with decreasing numbers of mediterranean species and an increase in locally endemic taxa. The flat coastal plains of northwestern Baja California, between parallels 30°N' and 31.5°N', are one of the areas of highest endemism in the peninsula (Garcillán *et al.* 2010; O'Brien *et al.* 2016; Riemann and Ezcurra 2005, 2007). Microclimatic conditions appear to have a strong influence on the distribution of endemics, and putatively ancient vegetation associations are fragmented in northwestern Baja California (Delgadillo 1998; Peinado *et al.* 1994; Raven and Axelrod 1978). In coastal NW Baja California mean annual rainfall drops sharply from 280 mm in Ensenada (lat 31° 52' N) to 140 in San Quintín (lat 30° 25' N).

Oceanic influence

In the coastal plain, ocean-derived moisture appears to buffer the low winter rainfall regime, reducing evapotranspiration and promoting the growth of 'nebulophytes' (rosette-forming plants that are able to capture fog; Rundel *et al.* 1972; Martorell and Ezcurra 2002). The vegetation is dominated by plants that respond rapidly to pulses in moisture availability (Franco-Vizcaíno 1994; Minnich 1985; Shreve 1951).

This coastal region offers an ideal system to study the effect of oceanic influence on ecosystem dynamics. As stated above, the N–S precipitation gradient and the E–W fog gradient vary

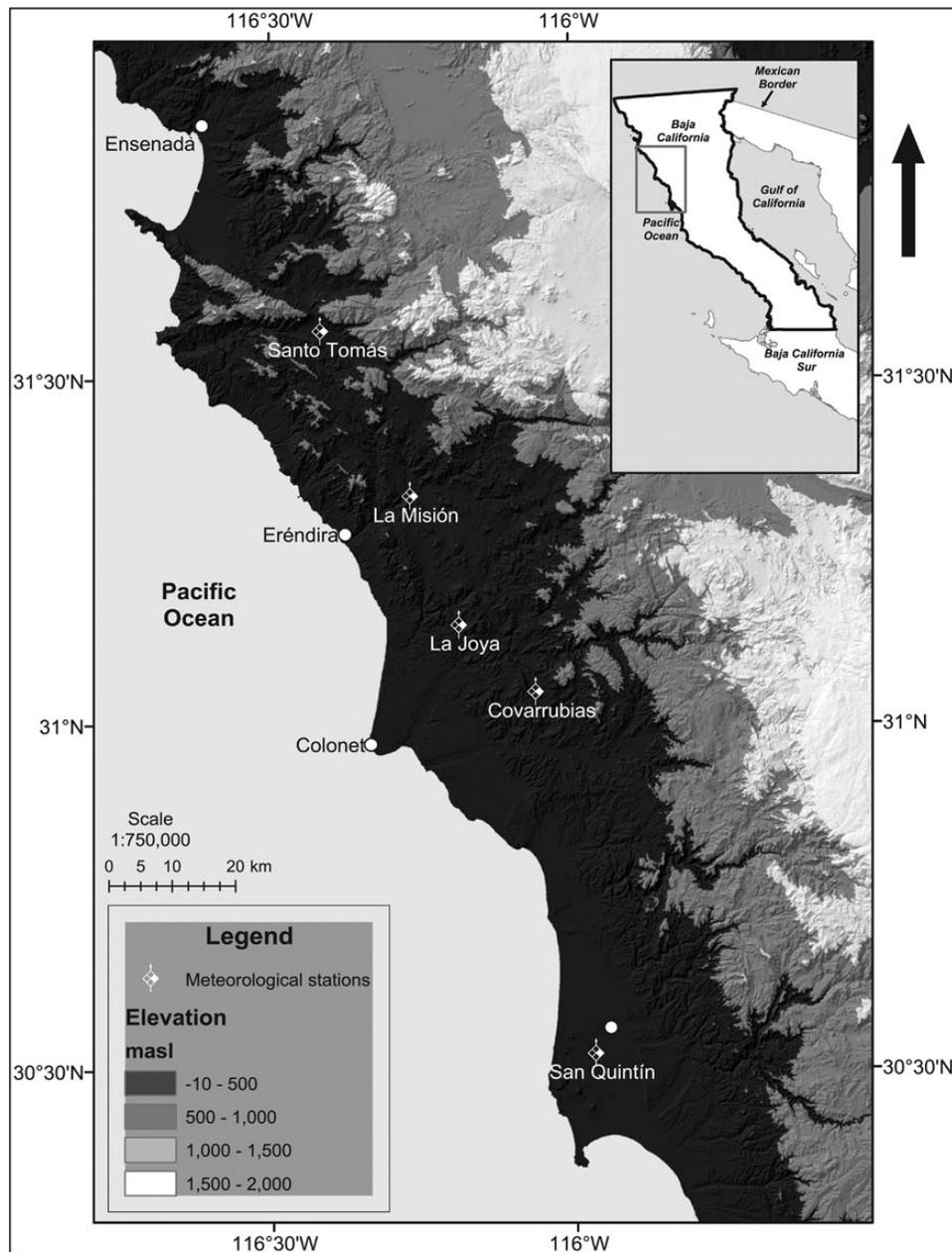


Figure 1: locations of weather stations and study sites on the Baja California Peninsula.

in a nearly orthogonal manner: While precipitation decreases towards the tropics, fog decreases inland. The relatively undisturbed habitats of the region (compared to California) allow a fine scale analysis that can avoid confused data signals from large numbers of invasive species or from human-induced disturbance.

MATERIALS AND METHODS

Weather data

Five weather stations were installed, spanning a 140-km-long north–south winter rainfall gradient (high to low) from 32.0°N to 30.5°N. The weather stations (HOBO Microstations, Onset

Computer Corporation, Bourne, MA) record hourly data on temperature, relative humidity and total rainfall each hour. In the third year of the project, a HOBO leaf-wetness sensor was added to each station to better understand the wet–dry dynamics of plant leaves under varying maritime conditions.

Hourly data were transformed to daily means of temperature and humidity, and daily cumulative totals of rainfall. Daily values were averaged in turn into monthly means for temperature and humidity, and monthly cumulative totals for rainfall. The monthly values were averaged across the 3 years of our study period. Additionally, a time-series analysis was conducted on the daily temperature and humidity averages, by fitting the first harmonic of a Fourier series to

detect the existence and magnitude of periodic oscillations (Bloomfield 2000). Leaf wetness data were analyzed calculating the frequency of wet leaves on the untransformed hourly data, i.e. the proportion of time in which leaf wetness is greater than 90% and leaves are almost entirely covered by water.

Phenological data

Each weather station became the center of a study site having an area of 1 km² (0.56 km radius around the station marker; see Fig. 1). This scale was chosen to eliminate microclimatic effects and assess the broader climatic influence. Within each study site, all perennial shrubs were identified (herbarium specimens at Rancho Santa Ana Botanic Garden—RSA). Phenological data was collected for all 86 taxa. Native spring ephemerals were combined into a single data set (see Supplementary Table 1 for a list of all species). Data were collected every 6–8 weeks from March 2010 to January 2013, for a total of 17 sampling events. The frequency of observations was limited by the access and logistical difficulties imposed by the remoteness of the sites. Data were initially recorded intensively, estimating for each species phenological abundances (% of the population in the different phenophases). After the first year, a simplified ordinal scale for data collection was developed based on observed flowering intensities, from a value of one for low flowering intensity to three for peak bloom (>75% of the population in full flowering), and a zero score for species not flowering (see Supplementary Table 2). For each site, we developed a time-series data matrix with sampling dates (columns) and species (rows), showing the flowering score of each species at each date.

Isotope analysis

Mulroy and Rundel (1977), in their studies of annual plants in California deserts asserted that summer flowering annuals are almost always C4 plants, as compared to winter annuals that are C3 plants. In order to test whether perennial fall-blooming species, which flower at the driest time of the year, might have a C4 photosynthetic metabolism, leaf samples of these species were sent to the University of California, Riverside, Facility for Isotope Ratio Mass Spectrometry to quantify $\delta^{13}\text{C}$, a measurement that can distinguish between C4 and C3 photosystems. Stable carbon isotopic compositions were expressed as delta values relative to the VPDB standard (Vienna Peedee Belemnite), following the USGS guidelines (USGS40, <http://isotopes.usgs.gov/lab/referencematerials/USGS40.pdf>).

Data analysis

In order to analyze the time trajectory of phenological samples across dates, we used principal component analysis (PCA) of the raw (i.e. non-standardized) dates \times species matrices. We used the broken-stick distribution to test for significant axes (i.e. axes that possess more variation than can be expected by chance, see Jackson 1993). We then used the resulting axes (a linear combination of species flowering times) to test their

scores against external climatic and environmental variables using linear models. Additionally, following Noy-Meir (1973), who proposed partitioning PCA axes as a means to classify multivariate objects, we classified the species along each axis according to their scores: Species with scores (>0.5) were classified as positively associated to the axis, those with low scores (<-0.5) as negatively associated, and the rest as not distinctly associated. The critical threshold value (0.5) is the mean species score necessary for an axis to reach the critical variation demanded by the broken-stick model in order to accept the axis as significantly departing from randomness.

We performed three distinct analyses. In the first analysis, aimed at finding the general phenological dynamics for the region as a whole, all sites were combined together to obtain a regional 17 dates \times 86 species matrix, and an average score of flowering intensity was taken across all five sites in order to get a general measure of flowering phenology across the gradient. Two additional analyses were conducted to understand how the dynamics of dates and species may differ within the region. We first eliminated all the species that were present in less than four sites, retaining only 16 regionally common species. To understand the differential dynamics of dates within sites, the 17 dates were replicated within each of the 5 sites (i.e. the analysis was performed on a matrix of 16 species \times 85 dates-nested-within-sites). Conversely, to understand the divergent dynamics of species within different sites, the 16 species were replicated within each of the 5 sites (i.e., we used a matrix of 17 dates \times 80 species-nested-within-sites). In both matrices, we performed a PCA as described above.

Using standard astronomical equations (Meeus 1988), we calculated the day length at the median latitude of all sites (30.5° N) for all days of our study period. Day length measures the winter-solstice-to-summer-solstice signal: for the winter solstice day length is minimum (8.9 h), while for the summer solstice it is maximum (15.1 h). We also calculated the daily change in day length, i.e. the difference between the day length of any given day and that of the preceding day. Day length change measures the spring-equinox-to-autumn-equinox signal: for the spring-equinox, when day are getting longer, day-length change is maximum and positive (3.0 min), while for the autumn-equinox it is negative (-3.0 min).

RESULTS

Climatic gradients

All sites showed a similar seasonal pattern in both monthly precipitation and mean temperatures (Fig. 2). There was a marked effect of the ocean as a temperature buffer, as mean summer temperatures were higher at the inland sites than at coastal ones (4.5°C higher in August, on average). Additionally, there was a strong interaction between seasonal variability in air humidity and proximity to the ocean: Inland sites showed maximum humidity values in winter and a generally dry air in summer, while coastal sites maintained high levels of air humidity in summer. Data from the two most

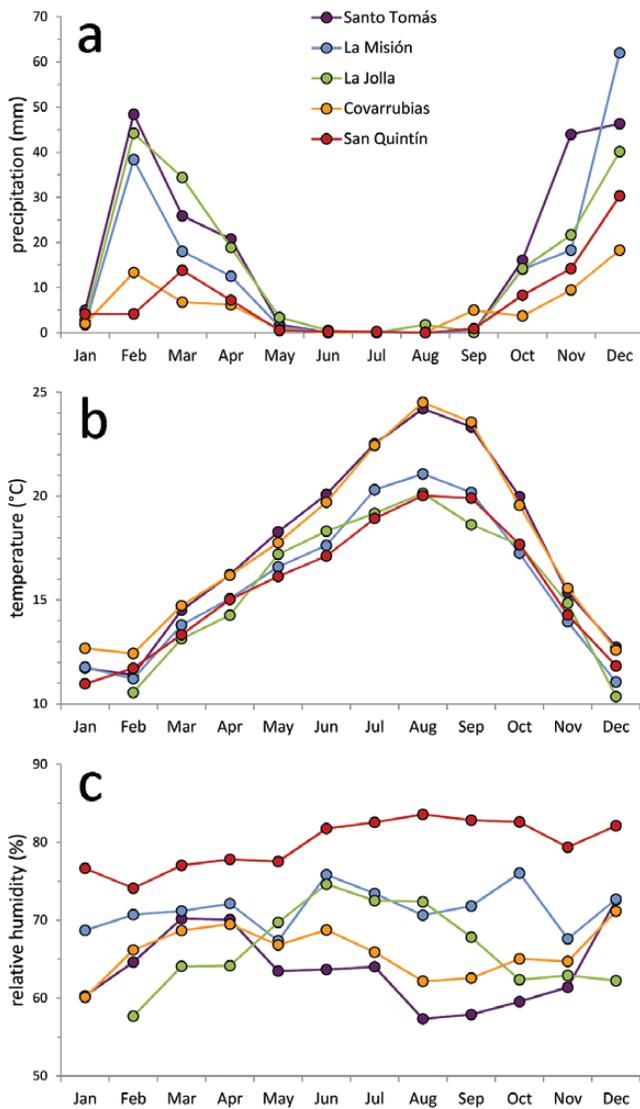


Figure 2: (a) mean monthly precipitation (mm), (b) mean monthly temperature ($^{\circ}\text{C}$) and (c) monthly averaged daily relative humidity (%), for the five sites studied, averaged between March 5, 2010 to January 5, 2013.

extreme sites (Santo Tomás, an inland and our northernmost site, with high rainfall and low fog, and San Quintín, our southernmost and most coastal site, with low rainfall and high fog) clearly show the buffering effect that the marine layer has on summer temperatures and air humidity (Fig. 3).

Apart from the clear differences in seasonal dynamics between sites, annual mean values also showed distinct patterns: Total precipitation was positively correlated with latitude, although the significance was weak ($r = 0.78$, $n = 5$, $P = 0.1$). The inland-to-coast gradient was strongly and negatively correlated with both annual mean relative air humidity ($r = -0.88$, $n = 5$, $P = 0.04$) and the frequency of wet leaves ($r = -0.95$, $n = 5$, $P = 0.007$). Additionally, the frequency of wet leaves in each site was also highly correlated with annual mean relative air humidity ($r = 0.92$, $n = 5$, $P = 0.01$).

General flowering pattern at a regional scale (PCA analysis 1)

According to the broken-stick test, two significant PCA axes were found for the combined sites matrix. Axis 1 explained 32% and axis 2 explained 20% of the total variation (both proportions were higher than the random expectation derived from the broken-stick model, which is 21 and 15%, respectively). The analysis showed strong cyclical dynamics of the pooled regional data from March 2010 to January 2013. Time-specific data points showed a circular trajectory in flowering times, or ‘phenological space,’ that is visible in the first two multivariate axes (Fig. 4). Axis 1 separated spring sampling dates to the right from late summer and fall dates to the left. Axis 2, in contrast, separated late-spring and early-summer dates above, from winter dates below. In agreement with this interpretation, axis 1 was significantly correlated with change in day length (the spring-to-autumn signal), while axis 2 was significantly correlated with day length itself (the summer-to-winter signal, $r = 0.86$ and $r = 0.83$, respectively; see Fig. 4b and c).

An analysis of the scores of all species in these two PCA axes allowed a first characterization of phenological strategies in the flora, which was classified into (i) spring bloomers (positive loadings on axis 1, >0.5); (ii) fall bloomers (negative loadings on axis 1, <-0.5) and (iii) species that showed good flowering during the study but did not show a consistent flowering time, classified as aseasonal or opportunistic bloomers. While axis 2 also represents aseasonal summer-to-winter gradient, none of the species responsible for this axis can be classified strictly as summer bloomers. Most (44%) of the between-dates variation in axis 2 is due to one single species: *Eriogonum fasciculatum*, a strong seasonal responder and spring bloomer that, if provided with enough moisture, will continue flowering throughout the summer. Prolonged flowering in *Eriogonum* is statistically very important: if the species is removed from the analysis, axis 2 would not pass the broken-stick significance test. With less statistical weight than *E. fasciculatum*, a few other species also showed high levels of flowering during summer in some sites and contribute to axis 2, such as *Malosma laurina* and *Aesculus parryi*, two aseasonal responders that in some sites continued flowering in July and August. Although, statistically, the flowering of these species while most other spring bloomers have ceased to bloom will accurately characterize the summer months, they really form part of other flowering strategies different from strict summer bloomers. The multivariate summer-to-winter axis (axis 2) is hence more related to flowering duration in some species than to a distinct summer-flowering strategy (Supplementary Fig. 1). The list of species derived from this regional analysis is presented in Table 1.

All fall-blooming species showed $\delta^{13}\text{C}$ values in their leaves consistent with a C3 photosynthetic metabolism (Supplementary Table 3). The values ranged between -24 and -32 and fall within the range of C3 plants, which is ~ -28 , and removed from the expected value for C4 plants, which is ca.

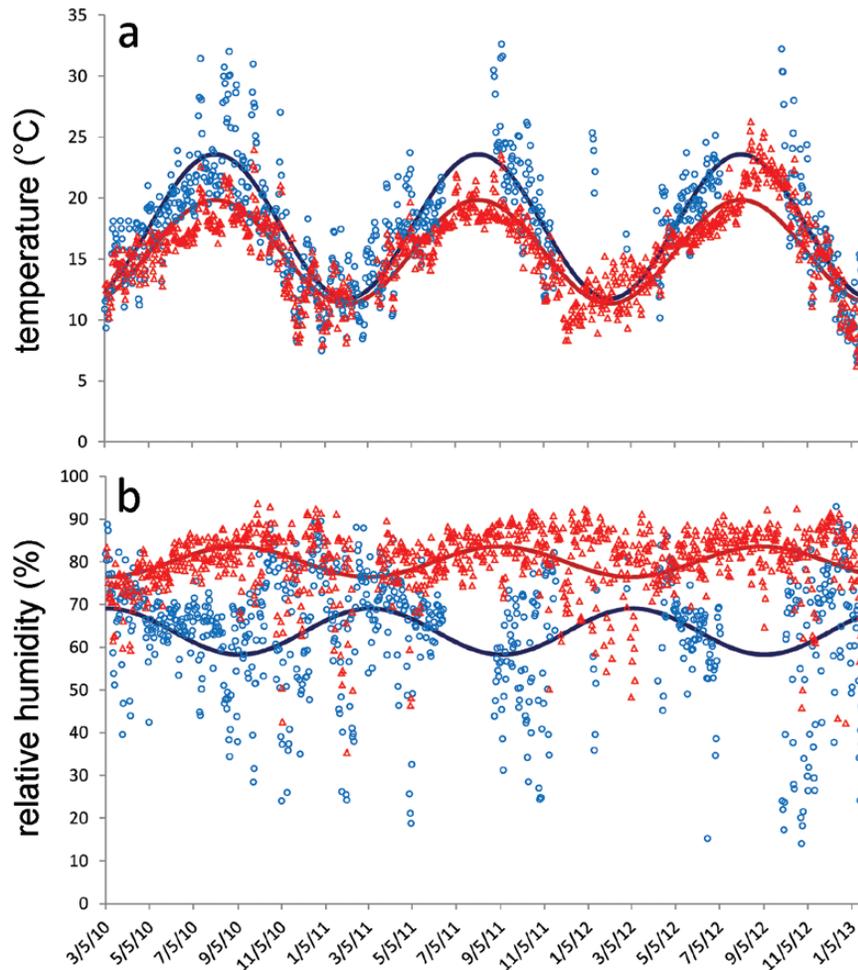


Figure 3: (a) mean daily temperature ($^{\circ}\text{C}$), and (b) mean daily relative humidity (%), for two study sites in the extremes of our study gradient: Santo Tomás (blue dots), a relatively rainy inland site and San Quintín (red dots), a more arid but coastal site subject to frequent fogs. The sinusoidal lines show the periodic trend captured by the first harmonic of a Fourier series (in all cases, the variance explained by the periodic trends was highly significant; $P < 0.0001$).

–13. Thus no evidence of C4 photosynthesis was detected in these taxa.

Environment-phenology correlations (PCA analysis 2)

The PCA for all dates nested within sites showed a similar pattern as that of the pooled dataset analysis, with axis 1 separating spring samples from fall samples and axis 2 separating summer surveys from the rest of the cluster. Not all sites, however, varied with similar amplitude. Coastal sites (San Quintín and La Misión) showed lower variation relative to the other, more inland, sites (Santo Tomás, Covarrubias, and La Joya). We found a significant and negative correlation ($r = -0.80$, $P = 0.05$) between the standard deviation of each site along axis 1 (a measure of fall-to-spring phenological variation) and frequency of wet leaves for each site, suggesting that phenological variation and seasonality are dampened by the proximity to the coast and the ocean-derived moisture (Fig. 5a). This last hypothesis was corroborated by the fact that mean flowering

intensity (the percentage of spring-blooming plants in flower) for the three sites nearer to the coast was lower in spring compared to the two inland sites, but also showed higher flowering in summer when inland sites were largely dormant (Fig. 5b).

The phenological dynamics of species nested within sites (PCA analysis 3)

The species-nested-within-sites PCA also yielded a similar result to the pooled data PCA: spring-flowering species and fall-flowering plants separating along axis 1. Notably, fall taxa had a significantly lower variance along axis 1 than the spring bloomers, indicating that flowering in fall-bloomers is in general more synchronous across sites than in spring flowerers ($F_{(46,14)} = 3.09$, $P = 0.01$), which may differ considerably in their flowering times from one site to another. Like in the first PCA, axis 2 positioned on one side of the axis a species with long duration of flowering, *E. fasciculatum*, which starts flowering in spring but keeps on producing flowers late into the summer (see Supplementary Fig. 1).

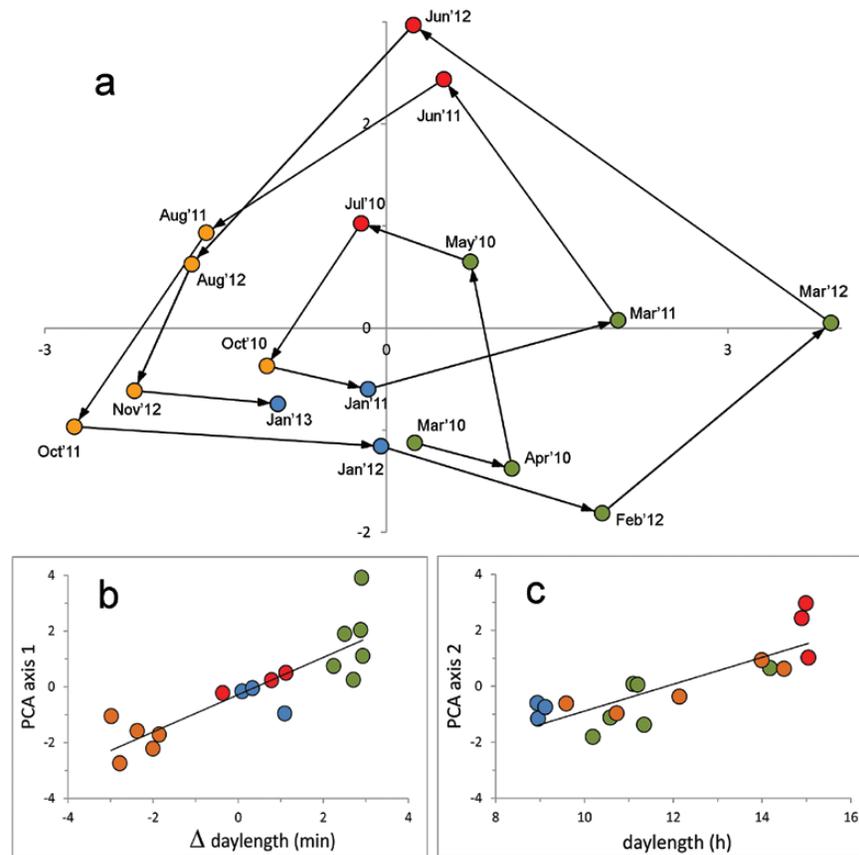


Figure 4: (a) principal component plot showing the trajectory of all sites together in phenological space. Each dot corresponds to a different sampling date, and arrows join succeeding dates. Species arranged according to their PCA loadings along axis 1 are presented in Table 1. (b) Correlation between axis 1 and day-length change (i.e. Δ day length, or the spring-to-fall time vector; $r = 0.86$, $df = 15$, $P < 0.0001$). (c) Correlation between axis 2 and day length (i.e. the summer-to-winter time vector; $r = 0.83$, $df = 15$, $P < 0.0001$). Colors indicate the season: green = spring, red = summer, orange = fall; blue = winter.

DISCUSSION

General phenological dynamics

Most of the statistically significant phenological variation of species between dates (axis 1 of the PCA) is driven by the spring-to-fall seasonal flowering gradient. Based on their seasonal behavior, species can be divided into three groups according to their dominant phenological trends and their position along axis 1 of the PCA:

Spring bloomers (water responders)

A group of species flowered in spring, when winter-accumulated moisture is abundant and temperatures begin to rise (Table 1). This group includes many deciduous species, such as deerweed (*Acmispon glaber*), California sunflower (*Encelia californica*), San Diego sunflower (*Bahiopsis laciniata*) and goosefoot (*Ambrosia chenopodiifolia*), but also includes other non-deciduous life forms, such as the sclerophyllous jojoba (*Simmondsia chinensis*), the bushrue *Cneoridium dumosum*, the globose cactus *Mammillaria dioica* and *Ephedra californica*, a leafless perennial. Although most of these water responders are insect-pollinated, some, such as *Ambrosia chenopodiifolia*,

Simmondsia chinensis and *Ephedra californica* are pollinated by wind. Despite a shared response to available moisture cues, there was a high degree of variability in onset, duration and synchrony across species. Accordingly, the phenological patterns in the rainfall-responder species show variation in lag-times synchrony and duration of flowering.

Fall bloomers (off-season flowering)

This syndrome was observed almost entirely in the family Asteraceae, within the tribe Astereae (e.g. *Isocoma menzeisii*, *Ericameria palmeri*, *Baccharis sarothroides* etc.), a fact that suggests the possible existence of a phylogenetic constraint. Interestingly, evidence of C4 photosynthesis was not found in any of the autumnal bloomers assessed in this study, nor did we find any other evident physiological adaptation to the summer heat and drought, which could promote or drive the off-season floral display. In contrast with spring bloomers, which show important variation in their flowering times associated to moisture availability, fall bloomers have a much greater synchronicity in their flowering onset (possibly triggered by photoperiod), coupled with a rather generalist pollination syndrome.

Table 1: species belonging to the three dominant phenological syndromes

Family	Scientific name ^a	Life form ^b	Pollination syndrome	Fruit type
Spring bloomers (water responders) high on axis 1				
Fabaceae	<i>Acmispon glaber</i>	H	Vector	Dry
	<i>Native annual species</i>	A	Vector	Dry
Asteraceae	<i>Encelia californica</i>	H	Vector	Wind dispersed
Malvaceae	<i>Sphaeralcea ambigua</i>	H	Vector	Dry
Asteraceae	<i>Bahiopsis laciniata</i>	H	Vector	Dry
Asteraceae	<i>Trixis californica</i>	H	Vector	Wind dispersed
Polygonaceae	<i>Eriogonum fasciculatum</i>	E	Vector	Dry
Asteraceae	<i>Ambrosia chenopodiifolia</i>	H	Wind	Dry
Rutaceae	<i>Cneoridium dumosum</i>	Dd	Vector	Dry
Fabaceae	<i>Astragalus trichopodus</i>	H	Vector	Dry
Simmondsiaceae	<i>Simmondsia chinensis</i>	E	Wind	Dry (large)
Convolvulaceae	<i>Calystegia macrostegia</i>	V	Vector	Dry
Cactaceae	<i>Mammillaria dioica</i>	Ss	Vector	Fleshy
Adoxaceae	<i>Sambucus mexicana</i>	Dd	Vector	Fleshy
Nyctaginaceae	<i>Mirabilis laevis</i>	H	Vector	Dry
Rubiaceae	<i>Gallium nuttallii</i>	H	Vector	Dry
Ephedraceae	<i>Ephedra californica</i>	E	Wind	Dry
Fall bloomers (off-season flowering) Low on axis 1				
Grossulariaceae	<i>Ribes tortuosum</i>	Dd	Vector	Fleshy
Asteraceae	<i>Ambrosia monogyra</i>	E	Wind	Wind dispersed
Asteraceae	<i>Hazardia berberidis</i>	E	Vector	Wind dispersed
Asteraceae	<i>Baccharis salicifolia</i>	E	Wind	Wind dispersed
Apocynaceae	<i>Asclepias subulata</i>	H	Vector	Wind dispersed
Asteraceae	<i>Baccharis sarothroides</i>	E	Wind	Wind dispersed
Asteraceae	<i>Ericameria palmeri</i>	E	Vector	Wind dispersed
Asteraceae	<i>Isocoma menziesii</i>	E	Vector	Wind dispersed
Aseasonal flowerers (abundant but close to 0 on axis 1)				
Solanaceae	<i>Nicotiana glauca</i>	E	Vector	Dry
Cactaceae	<i>Myrtillocactus cochal</i>	Ss	Vector	Fleshy
Plantaginaceae	<i>Gambelia juncea</i>	E	Vector	Dry
Brassicaceae	<i>Brassica tournefortii</i>	A	Vector	Dry
Asteraceae	<i>Stephanomeria diegensis</i>	A	Vector	Wind dispersed
Agavaceae	<i>Agave shawii</i>	Rs	Vector	Dry (large)
Anacardiaceae	<i>Rhus integrifolia</i>	E	Vector	Fleshy
Asteraceae	<i>Helianthus niveus</i>	E	Vector	Dry
Asteraceae	<i>Gutierrezia californica</i>	H	Vector	Wind dispersed
Cleomaceae	<i>Peritoma arborea</i>	Dd	Vector	Dry (large)
Euphorbiaceae	<i>Euphorbia misera</i>	Dd	Vector	Fleshy
Anacardiaceae	<i>Malosma laurina</i>	E	Vector	Fleshy

Life form, pollination syndrome and fruit type are included for each taxon.

^aBold scientific name indicates that the species was also included in the second PCA of dominant species only.

^bLife-form categories: Stem succulents (Ss); Rosette succulents (Rs); Vines (V); Drought-deciduous perennials (Dd); Evergreen perennials (E); Perennial herbs/herbaceous perennials (H); Annuals (A).

If a plant is able to cope with the summer and fall drought, off-season flowering can have important advantages. By flowering at a time when few other species are in bloom, the plant can more effectively attract pollinators while reducing inter-specific pollen transfer, but seed dispersal pressures may also

play a selective role on flowering times. In wind-dispersed Asteraceae, producing seeds in fall—a normally windy time of the year—may enhance dispersal and reduce the risk of seed-bank predation, as seeds are released shortly before the onset of winter rains.

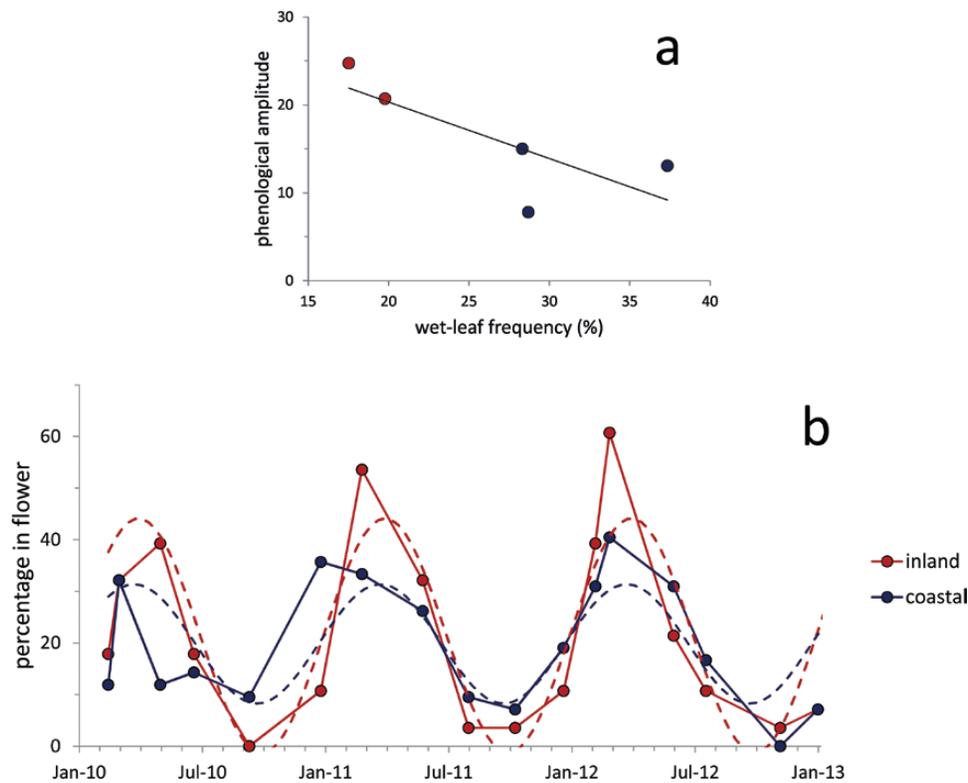


Figure 5: Environment-phenology correlations. (a) Correlation between the amplitude in the proportion of spring-blooming plants in flower (the phenological wave signal) at each site against the frequency of wet leaves (a measure of the influence of coastal moisture on the plants' water supply; $r = -0.80$, $P = 0.05$). (b) Mean flowering intensity (percentage of spring-blooming plants in flower) for two inland sites (Santo Tomás and Covarrubias) and three coastal sites (La Misión, La Joya and San Quintín), during the 3 years of our study. The sinusoidal dotted lines show the first harmonic of a Fourier series, which in both datasets showed a significant fit to the data points ($r^2 = 0.69$, $P = 0.0002$ for inland sites and $r^2 = 0.42$, $P = 0.016$ for coastal sites).

Aseasonal flowerers

A last group of species failed to display a strong seasonal pattern, despite their frequent flowering. Within this group, a distinction can be made between truly aseasonal species whose individuals flower more or less continually throughout the year, and species whose individuals flower for short periods of time, but in which different individuals may flower at different times. In the second group, the individuals themselves may display a canalized flowering period, but their asynchronous pattern makes the species aseasonal at a population level. Thus, this general syndrome may in fact be a grab-bag of different strategies, expressed either at the population or at the individual level.

An example of these aseasonal flowerers is *Gutierrezia californica*, a drought-deciduous herbaceous perennial that has canalized development and therefore must leaf-out following a rainfall event before flowering. Since rainfall is strongly seasonal in the CFP, this plant normally initiates flowering in spring, yet in our coastal sites it was found flowering almost every month of the year, presumably as a result of localized rainfall or available maritime moisture. Notably two short-lived taxa, the non-native invasive *Brassica tournefortii* and native annual/biennial *Stephanomeria diegensis* were strongly aseasonal in their

flowering, behaving as opportunistic species. Succulent species such as *Myrtillocactus* and *Agave*, and the large woody shrubs *Rhus* and *Malosma*, all have canalized-flowering individuals but aseasonal populations. They are also found in a variety of environments without fog mitigation of drought, and the individuals seem to be responding to water availability on a very fine scale. These species may be the most robust in the face of climatic change, but asynchronous flowering may significantly reduce out-crossing, and could potentially result in adaptive radiations.

Species without distinct flowering patterns have been shown to be associated with aseasonal climates (Rathcke and Lacey 1985, Gentry 1974) and, interestingly, many of these taxa are present (often uniquely present*) at the San Quintín site, which is the foggiest year-round (e.g., *Helianthus**, *Ribes**, *Nicotiana**, *Peritoma*, *Rhus*, *Malosma*, *Stephanomeria* and *Euphorbia*). It is interesting to note that the majority of the species in this category have fleshy and/or vector-dispersed fruits. It is possible that seed dispersal in these taxa is placing a selective pressure on year-round reproduction, or conversely that plasticity of phenology favors vector dispersal of fruits. Low synchrony (low levels of flowering throughout a long flowering season) may help some individuals to avoid

temporal bouts of predation from specific insects (Elzinga *et al.* 2007).

Weather patterns across the gradient

Our weather monitoring system revealed the large effect that the proximity to the ocean has on climatic traits in this region. Average air humidity and the frequency of water-soaked leaves decrease rapidly as a function of distance to the coast, while peak summer temperatures increase along the same gradient. Coastal environments, in short, have milder summer temperatures and receive larger amounts of ocean-derived moisture than inland sites. On top of this east–west gradient, there is also a latitudinal rainfall gradient in which mean annual precipitation decreases from north to south at a rate of ca. 1 mm per km. Interestingly, the environmentally buffering effect of the California Current is highest in summer, when climate in the inland sites is hot and dry but when the summer fogs bring moisture and cooler temperatures to the coastal ecosystems.

Between-site differences in phenological variation

The multivariate analyses for all sites taken as separate samples confirmed the importance of the spring-to-fall seasonal flowering gradient as the major driver of plant phenology. This general trend, however, varied significantly from site to site: Sites near the coast and under a stronger influence of coastal fogs showed lower variances along the multivariate phenological axes than sites further inland (Fig. 5a). A simple analysis of local flowering intensity, completely independent from the more complex multivariate analyses, confirmed these results: The percentage of spring-blooming plants in flower near the coast was lower than in the inland sites, but coastal sites kept on producing flowers in summer and fall, when the plants in the inland sites were barren (Fig. 5b). This underscores the more buffered and stable nature of coastal ecosystems, confirming that ocean-derived moisture plays an extremely important role in the phenological variation observed between sites.

Land–ocean interactions and plant flowering dynamics

Land–ocean linkages are clear drivers of plant phenology: the presence of fog from the cold California current creates a local weather pattern that to a large extent modulates flowering. Physical data suggest that ocean currents have been stable for millions of years, so one can assume heavy fogs in the presence of high radiant loadings through deep time. The presence of these fogs thus may well have had a strong role in the creation of species refugia and the survival of many endemic species found here. In that sense, it is important to note that many of the local endemic or near-endemic taxa correspond to obvious fog-adapted life forms, such as succulent rosettes (*Dudleya* spp., *Agave shawii*) or densely spined cacti (*Berberocactus emoryi*). As in other coastal drylands where

it has been shown that plants can absorb water directly from the leaves (e.g. Mooney *et al.* 1980), fog and dew are playing a critically important role in the extension of the southern range limit of many CFP species. Similarly, the inland fog limit is likely to define the inland (eastern) range limit of many taxa.

Finally, the lower variance along PCA axis 1 of fall bloomers in the species-nested-within-sites analysis, indicates more synchronous flowering from site to site in autumnal bloomers. Since fall tends to be the driest time of the year, this general pattern suggests that, while spring flowering is generally triggered by local moisture availability, fall flowering of Asteraceae such as *Baccharis sarothroides* and *Ericameria palmeri* seems to be more dependent on photoperiod.

CONCLUSIONS

The southern edge of the CFP is an area of high local endemism and outstanding conservation value. With strong gradients both N–S and E–W, this large geographic ecotone harbors a fragile endemic flora. Within a generalized spring-driven cyclic phenological pattern, important differences occur between species and between sites. At a community level, sites near the coast have significantly milder environmental conditions than inland sites. The thermally buffering effect of the coastal California Current induces cooler summers, while the marine layer brings frequent fogs to coastal plains.

The effect of fog and maritime climate as a buffer of plant phenology merits further research in other coastal ecosystems worldwide. In the southern edge of the mediterranean region in Baja California, the climatic stability provided by coastal fogs has probably been a critical driver of the region's high endemism by providing a refugium of predictable growth and flowering, and thus buffering reproductive success against long-term climatic changes. This ecological haven effect should be given serious consideration in conservation planning. Although our global climate is changing and will continue to do so, fog and ocean-derived moisture will continue to buffer the coasts in warmer weather and ameliorate local weather extremes.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology*

ACKNOWLEDGMENTS

Our deep appreciation is expressed to O'Malley Miller and the Miller Family Charitable Trust, and Wade Killifer and Club La Misión of San Vicente, for the generous resources that made this study feasible. Numerous people assisted with fieldwork over the years, Vanderplank is particularly grateful to Heriberto Arauz. We thank the following landowners for their generosity in permitting the installation and visitation of the weather stations: Pedro Verduzco, Izaias Rudamedkin, Guadalupe Panyagua and Jose Gabino Covarrubias. James Sickman at UCR graciously facilitated the Carbon analyses; Jon Rebman at

SDNHM assisted with plant identification and taxonomy. Francisco Jose del Toro Guerrero and Terra Peninsular. A.C. assisted with Fig. 1. We thank Will McClatchey and Harold Keller for their helpful edits to this manuscript, and Patricia Balvanera and two anonymous reviewers for their excellent comments and constructive criticisms, which substantially improved the article. We also thank the following collaborating institutions: Rancho Santa Ana Botanic Garden; San Diego Natural History Museum; Huntington Botanical Gardens; the Next Generation of Sonoran Desert Researchers, and UCMEXUS. This work was done under SEMARNAT permit # SGPA/DGVS/05088/11. *Conflict of interest statement.* None declared.

REFERENCES

- Axelrod DI (1978) The origin of coastal sage vegetation, Alta and Baja California. *Am J Bot* **65**:1117–31.
- Barbour MG, Minnich RA (1990) The myth of chaparral convergence. *Israel J Bot* **39**:453–63.
- Bloomfield P (2000) *Fourier Analysis of Time Series: An Introduction*. Wiley Series in Probability and Statistics. New York, NY: Wiley-Interscience.
- Bowers JE, Dimmitt MA (1994) Flowering phenology of six woody plants in the northern Sonoran Desert. *Bull Torrey Bot Soc* **121**:215–29.
- Cowling RM, Rundel PW, Lamont BB, et al. (1996) Plant diversity in mediterranean-climate regions. *Trends Ecol Evol* **11**:362–6.
- Delgadillo J (1998) *Florística y ecología de norte de Baja California*. Universidad Autónoma de Baja California, Mexicali, Mexico.
- Elzinga JA, Atlán A, Biere A, et al. (2007) Time after time: flowering phenology and biotic interactions. *Trends Ecol Evol* **22**:432–39.
- Franco-Vizcaíno E (1994) Water regimes in soils and plants along an aridity gradient in central Baja California, Mexico. *J. Arid Envir.* **27**:309–23.
- Garcillán PP, Gonzalez-Abraham CE, Ezcurra E (2010) The cartographers of life: two centuries of mapping the natural history of Baja California. *J Southwest* **52**:1–40.
- Gentry AH (1974) Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* **6**:64–8.
- Jackson DA (1993) Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology* **74**:2204–14.
- Lyle M, Heusser L, Ravelo C, et al. (2010) Pleistocene water cycle and eastern boundary current processes along the California continental margin. *Paleoceanography* **25**:PA4211.
- Martorell C, Ezcurra E (2002) Rosette scrub occurrence and fog availability in arid mountains of Mexico. *J. Veg. Sci.* **13**:651–62.
- Meeus J (1988) *Astronomical Formulae for Calculators*, 4th edn. Richmond, VA: Willmann-Bell.
- Minnich RA, Franco-Vizcaíno EF, Goforth BR (2014) Distribution of chaparral and pine-oak “skyislands” in central and southern Baja California and implications of packrat midden records on climate change since the Last Glacial Maximum. In: Whencke E, Álvarez-Borrego S, Lara-Lara R, et al. (eds). *The Gulf of California Region: An Ecological Synthesis*. Instituto Nacional de Ecología, CICESE, UC MEXUS.
- Minnich RA (2010) *California's Fading Wildflower; Lost Legacy and Biological Invasions*. Berkeley, CA: University of California Press, p 143.
- Minnich RA (2007) California climate, paleoclimate and paleovegetation. In Barbour MG, Keeler-Wolf T, Schoenherr AS (eds). *Terrestrial Vegetation of California*, 3rd edn. University of California Press.
- Minnich RA (1985) Evolutionary convergence or phenotypic plasticity? Responses to summer rain by California chaparral. *Phys Geogr* **6**:272–87.
- Mooney HA, Gulmon SL, Rundel PW, Ehleringer J (1980) Further observations on the water relations of *Prosopis tamarugo* of the northern Atacama desert. *Oecologia* **44**:177–80.
- Mulroy TW, Rundel PW (1977) Annual plants: adaptations to desert environments. *Bioscience* **27**:109–14.
- Noy-Meir I (1973) Divisive polythetic classification of vegetation data by optimized division on ordination components. *J Ecol* **61**:753–60.
- O'Brien B, Delgadillo J, Junak SA, et al. (2016) Rare, endangered, and endemic vascular plants of the California Floristic Province portion of Northwestern Baja California, Mexico. *Aliso* (in press).
- Peinado M, Alcaraz F, Delgadillo J, et al. (1994) Fitogeografía de la península de Baja California, México. *Anales Jard Bot Madrid* **51**:255–77.
- Peñuelas J, Filella I, Comas P (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Glob Chang Biol* **8**:531–44.
- Peñuelas J, Filella I, Zhang X, et al. (2004) Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytol* **161**:837–46.
- Rathcke B, Lacey EP (1985) Patterns of terrestrial plants. *Ecology* **16**:179–214.
- Raven PH, Axelrod DI (1978) Origin and relationships of the California flora. *Univ Calif Publ Bot* **72**:1–134.
- Rhode D (2002) Early Holocene juniper woodland and chaparral taxa in the central Baja California peninsula, Mexico. *Quatern. Res.* **57**:102–8.
- Riemann H, Ezcurra E (2005) Plant endemism and natural protected areas in the peninsula of Baja California, Mexico. *Biol. Cons.* **122**:141–50.
- Riemann H, Ezcurra E (2007) Endemic regions of the vascular flora of the peninsula of Baja California, Mexico. *J Veg Sci* **18**:327–36.
- Rundel PW, Bowler PA, Mulroy TW (1972) A fog-induced lichen community in Northwestern Baja California, with two new species of *Desmazieria*. *The Byrologist* **75**:501–8.
- Shreve F (1936) The transition from desert to chaparral in Baja California. *Madroño* **3**:257–64.
- Shreve F (1951) Vegetation of the Sonoran Desert. Publ. Carnegie Inst. Washington No. 591. Reprinted as vol. 1. In Shreve F, Wiggins IL (eds). *Vegetation and Flora of the Sonoran Desert*. Stanford, CA: Stanford University Press.
- Sniderman JMK, Jordan JG, Cowling RM (2013) Fossil evidence for a hyperdiverse sclerophyll flora under a non-Mediterranean-type climate. *Proc Natl Acad Sci USA* **110**:3423–8.
- Verdú M, Barron-Sevilla JA, Valiente-Banuet A, et al. (2002) Mexican plant phenology: is it similar to Mediterranean communities? *Bot J Linn Soc* **138**:297–303.
- Westman WE (1981) Factors influencing the distribution of species of Californian Coastal sage scrub. *Ecology* **62**:439–55.