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Divergent ecological effects of oceanographic anomalies on terrestrial ecosystems of the Mexican Pacific coast

Margarita Caso*, Charlotte González-Abraham[†‡], and Exequiel Ezcurra[†§]

*Instituto Nacional de Ecología, Periférico Sur 5000, Coyoacán, 04530 Mexico Distrito Federal, Mexico; and [†]San Diego Natural History Museum, 1788 El Prado, San Diego, CA 92101

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Precipitation pulses are essential for the regeneration of drylands and have been shown to be related to oceanographic anomalies. However, whereas some studies report increased precipitation in drylands in northern Mexico during El Niño years, others report increased drought in the southern drylands. To elucidate the effect of oceanographic/atmospheric anomalies on moisture pulses along the whole Pacific coast of Mexico, we correlated the average Southern Oscillation Index values with total annual precipitation for 117 weather stations. We also analyzed this relationship for three separate rainfall signals: winter-spring, summer monsoon, and fall precipitation. The results showed a distinct but divergent seasonal pattern: El Niño events tend to bring increased rainfall in the Mexican northwest but tend to increase aridity in the ecosystems of the southern tropical Pacific slope. The analysis for the separated rainfall seasons showed that El Niño conditions produce a marked increase in winter rainfall above 22° latitude, whereas La Niña conditions tend to produce an increase in the summer monsoon-type rainfall that predominates in the tropical south. Because these dryland ecosystems are dependent on rainfall pulses for their renewal, understanding the complex effect of ocean conditions may be critical for their management in the future. Restoration ecology, grazing regimes, carrying capacities, fire risks, and continental runoff into the oceans could be predicted from oceanographic conditions. Monitoring the coupled atmosphere–ocean system may prove to be important in managing and mitigating the effects of large-scale climatic change on coastal drylands in the future.

coastal drylands | deserts | El Niño | rainfall pulses | tropical dry forests

The large coastal deserts of the world, the Namib in Southern Africa, Atacama in Chile, the Saharan Atlantic Coastal Desert, and Baja California in Mexico, are found on the west side of the African and American continents, which are associated with cold coastal currents (the Benguela, Humboldt, Canary, and California streams) that move toward the equator along the eastern fringe of the Atlantic and Pacific oceans. These deserts are normally flanked by semiarid regions in their tropical margin, mediterranean sclerophyllous scrubs in their high-latitude boundary and tropical dry scrubs toward the equator. In North America, this chain of dry ecosystems runs almost uninterruptedly from California in the United States to Chiapas in southern Mexico (Fig. 1*A*). In its northern limit, the Pacific coast is occupied by the mediterranean scrubs of the California Floristic Province. Southward, these ecosystems are followed by the arid communities of the Baja Californian and Sonoran deserts. Farther south, the desert is replaced by the subtropical thorn scrubs and dry forests of Sinaloa, in the mainland, and the Cape Region in Baja California. And even farther into the tropics, a long corridor of tropical dry deciduous forests and scrubs runs along the coast and into some inland valleys all of the way from the coast of Jalisco into the central plains of Chiapas (and continue southward into Central America).

The seasonality of precipitation in these drylands changes dramatically from north to south: Whereas the Californian scrubs survive mostly with winter rains brought in from the Pacific northwest, moisture in the southern tropics is almost entirely provided by summer rains delivered by the Mexican monsoon and, secondarily, by late summer Pacific hurricanes and tropical storms, locally called *chubascos* (1–3). Even within a single ecological region, the transition from winter to summer rains can be marked. The Sonoran Desert receives mostly winter rains in its northwestern reaches near the Mojave but is fed predominantly by summer monsoon rains in its tropical southern boundary with the Sinaloan thorn scrubs (1, 4). Winter- or summer-dominated seasonality generates different types of drylands. Winter-rain drylands are dominated by evergreen shrubs with small and/or tough leaves (California chaparral and other sclerophyllous scrubs) (5), whereas the tropical summer-rain drylands in western and southern Mexico are dominated by drought-deciduous trees and shrubs, often with succulent stems or fleshy trunks and tropical evolutionary origins, such as elephant trees (Burseraceae), kapoc trees (Bombacaceae), euphorbs (Euphorbiaceae), boojum trees (Fouquieriaceae), and giant columnar cacti (6–8).

Climatic Variability and Rainfall Pulses in Mexican Pacific Drylands. In most arid and semiarid ecosystems, rainfall events trigger short periods of high moisture abundance, which can saturate the resource demand of many biological processes for a short time (9). Thus, although deserts and drylands are often characterized by their mean climatologic conditions, they are really driven by a succession of short pulses of abundant water availability against a background of relatively long periods of drought. Plants and animals have developed very specific adaptations to take advantage of ephemeral abundance, especially with regard to establishment, growth, population dynamics, and the cycling of organic matter and nutrients (10). Thus, high-rainfall anomalies play a critical role in the renewal of arid and semiarid ecosystems.

Pulse-type variations in desert environments have been linked to global atmospheric and oceanic phenomena (11). Large-scale drivers of regional precipitation patterns include the position of the jet streams, the movement of polar-front boundaries, the intensity of the summer monsoon, the surface temperature of

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Abbreviations: ENSO, El Niño Southern Oscillation; SOI, Southern Oscillation Index.

[‡]Present address: Center for Conservation Biology, University of California, Riverside, CA 92521.

[§]To whom correspondence should be addressed. E-mail: eezcurra@sdnhm.org.

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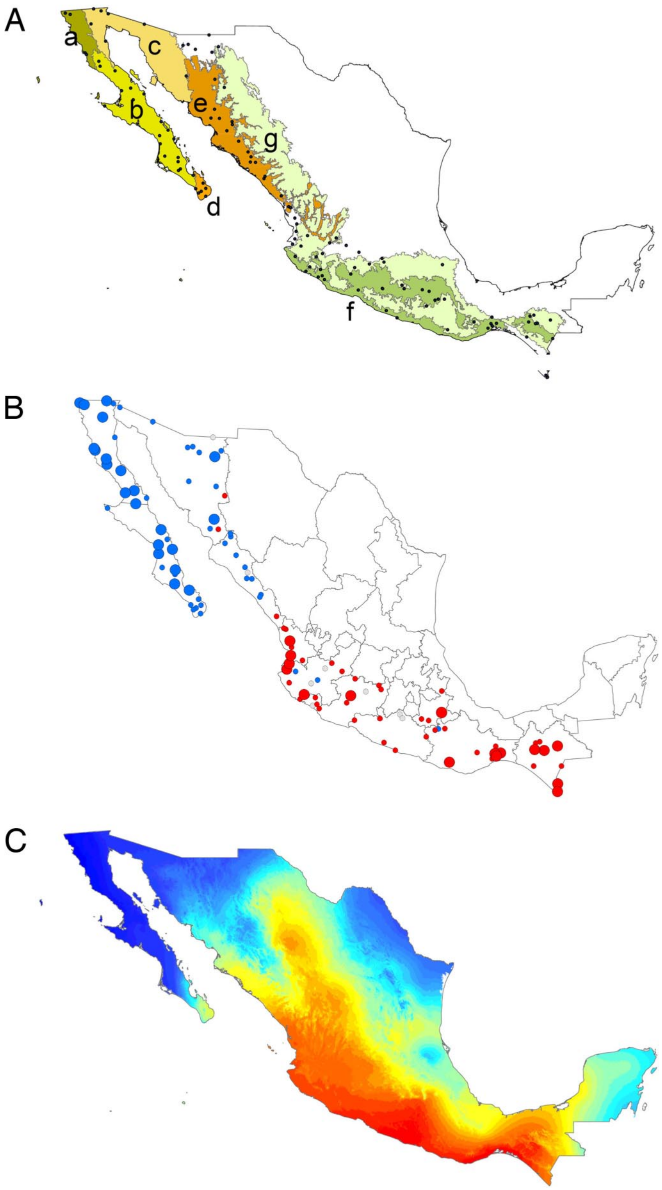

Fig. 1. The climatic and ecoregional dryland gradient along the Pacific coast of Mexico. (*A*) The dry ecoregions of the Pacific coast: mediterranean California (*a*), Baja Californian Desert (*b*), Sonoran Desert (*c*), Cape Region Thorn-scrubs and Dry Forests (*d*), Sinaloan Thorn-scrubs and Dry Forests (*e*), and Tropical Dry Forests (*f*); the high-elevation oak and conifer forests of the Sierra Madre and the Transversal Volcanic Range are shown for reference (*g*). The dots in the figure mark the location of the weather stations used in the analysis. (*B*) Correlation between mean annual SOI values and mean total annual precipitation: Blue dots indicate negative correlation, and red dots indicate positive values. Large dots indicate statistically significant correlations ($P < 0.05$) according to the *F* test. (*C*) Concentration of winter-spring rainfall in Mexico calculated from 1-km resolution interpolated climate surfaces. Blue colors indicate areas with a high proportion of annual precipitation falling between December and April (winter-spring precipitation), and red colors indicate areas where winter-spring rainfall is very low or nonexistent, and hence where summer and fall rains dominate.

neighboring oceans, often regulated by oceanographic events such as the El Niño Southern Oscillation (ENSO) phenomenon, and even by longer-term ocean cycles, such as the Pacific Decadal Oscillation (12–14). As a result, the intensity and frequency of moisture pulses at a local scale may vary substantially with time and often in a seemingly unpredictable fashion.

Of these factors, the El Niño phenomenon, has gained considerable attention during the last two decades. During El Niño years, the trade winds and the west-bound equatorial currents slow down, and the upwelling of nutrient-rich waters in the coasts of the American Continent decreases. As a result, sea surface temperatures increase near the coast of the Americas, the thermocline descends, and the eastern Pacific becomes less productive, while the coastal deserts of North and South America experience a marked increase in rainfall originating from the warmer sea waters (15, 16). Many of the studies on the influence of the El Niño phenomenon on terrestrial ecosystems, however, have been based in only one or a few recorded events. Thus, it is often difficult in the published literature to isolate the systematic component brought into the observed rainfall pattern by the oceanographic/atmospheric anomaly and distinguish it from other possible unrelated effects. Having observed an anomalously rainy period in an arid/semiarid area during an El Niño year, researchers often attribute the observed pattern to the effect of El Niño (17–20). The lack of a long time series to test the consistency of the phenomenon, however, subtracts generality from the conclusions.

The reports of a recent international symposium on the effects of ENSO in drylands of North America, South America, and Australia underscored "the strong increase in rainfall associated with ENSO events in dry ecosystems, during the El Niño phase of the oscillation in the Americas and the La Niña phase in Australia" (20). Most of the studies supporting these conclusions for the Americas, however, have been done on winter-rain drylands in Chile, northwest Mexico, and the southwest of the United States (19). In contrast, few studies have yielded comparable information on monsoon-type arid regions fed almost entirely by summer rains, such as the tropical dry deciduous forests of the Mexican and Central American Pacific coasts. Based on the general assumption that warmer Pacific waters (i.e., El Niño conditions) bring more rainfall to arid lands, recent research has suggested that the ENSO anomaly can open a window of opportunity for the successful restoration of degraded drylands (18). Although this conclusion is undoubtedly true (and reflects good research) for some drylands of the Americas, other studies suggest that other dry regions may actually become substantially drier during ENSO events (11, 21, 22).

This divergent trend is particularly noticeable in published research work done along the western slopes of the Sierra Madre in North America (United States and Mexico). Whereas some papers argue that El Niño conditions tend to increase rainfall (especially winter precipitation) in the Pacific slopes of the Western Sierra Madre in northern Mexico and the southwestern United States (e.g., refs. 23–28, among many others), other studies report that El Niño conditions induce "severe drought" in the southern reaches of the same Sierra Madre (e.g., refs. 29 and 30). Although some of the ecosystems of the Sierra Madre show certain ecological similarities from north to south (pine-oak forests dominate the higher elevations all of the way from Arizona to Chiapas, whereas giant columnar cacti with deciduous dryland trees dominate the lowlands from the Arizona uplands to the dry coasts of Oaxaca), these observations imply that the same oceanographic anomaly may trigger diverging climatic pulses north and south of the Tropic of Cancer. This knowledge gap is not only of theoretical interest but potentially also of great applied importance, because many ecosystem processes such as the germination and establishment of dryland plants, annual seed rains, biomass productivity, forest fires, riparian runoff, and nutrient pulses in coastal lagoons and estuaries, among many others, depend critically on high rainfall pulses.

Because of its long latitudinal expanse, the Pacific coast of Mexico is an exceptional area to study the effect of the El Niño phenomenon along its long fringe of arid and semiarid ecosystems. Because the long rain shadow of the Sierra Madre prevents the arrival of much of the Atlantic moisture transported by the trade winds, most of the Mexican Pacific coast is formed by a narrow corridor of arid and semiarid ecosystems that receive moisture from the Pacific Ocean and the Gulf of California (Fig. 1*A*). Despite their differences in seasonality, all of the ecological regions along the coastal corridor, the mediterranean scrubs, the deserts, the subtropical thorn scrubs, and the tropical dry deciduous communities, are seriously limited by water during a significant part of the year and all show ecological nurse–plants relationships, which are indicative of severely limited establishment and recruitment (e.g., refs. 31 and 32). As a result, positive rainfall anomalies are critically important in all these regions for ecosystem renewal (e.g., refs. 33–36, among many others). Indeed, many studies have shown that drylands such as the ones found along this corridor need moisture pulses for new plants to become established and for the community to renew its populations (see, for example, refs. 37–41). Similarly, precipitation pulses in large continental areas may have a strong influence on drought periods (13) and forest fires (25–28, 42), and the ensuing runoff may flush large amounts of nutrients from the desert into the sea (16, 43). Thus, understanding more clearly the oceanographic factors that drive precipitation pulses along the Pacific coastal drylands of Mexico, from the tropical dry forests of the south to the mediterranean scrubs of the Californian Floristic Province, may be of great importance to understand the drivers of large-scale ecosystem dynamics.

Research Questions. Based on the previous analysis, the main question we address in this paper is how oceanographic anomalies affect environmental pulses of moisture availability on dryland ecosystems along the dry Pacific coast of Mexico. To answer this, we investigated two related questions.

The first question is, given a sufficiently long time series of local precipitation for a large number of weather stations along the Pacific drylands, what proportion of the total variation in precipitation can be attributed to variations in atmospheric and oceanographic conditions, such as those imposed by variations in sea surface temperatures and the El Niño phenomenon? That is, we evaluate the statistical predictability of high-rainfall anomalies on arid and semiarid ecosystems based on the Southern Oscillation Index (SOI) (44, 45), a measure of monthly fluctuations in the air pressure above the equatorial Pacific Ocean that is strongly correlated with sea-surface temperature in the Mexican Pacific (46).

A second problem we investigate is, given the wide range of summer/winter seasonality observed along the long corridor of Pacific drylands in North America (from California to southern Mexico), which of these arid/semiarid regions actually tend to increase their precipitation during the warm phase of the oscillation (i.e., when El Niño conditions develop), and which ones, if any, tend to become drier when these conditions occur? That is, based on a long-term meteorological time series, we test whether the SOI has an effect on monsoon-type rainfall, as suggested by some researchers (29, 30).

Results

Annual Precipitation and SOI Values. For each one of the 117 weather stations along the Pacific slope of Mexico, we classified the slopes of the regression lines between annual rainfall and the mean SOI into three categories: negative slopes ($b < -10$), positive slopes ($b > 10$), and neutral slopes ($|b| < 10$). This no-effect threshold was selected based on the fact that a slope >10 (in absolute terms) predicts a difference in precipitation of >40 mm between El Niño (SOI < -2) and La Niña (SOI > 2) periods, an amount of precipitation equal to the mean annual rainfall of the driest deserts in the corridor and sufficient to produce noticeable response in plant growth (47). These values were plotted on a geographic information system, highlighting the stations where the relationship was statistically significant according to an F test (Fig. 1*B*). The results were very clear cut:

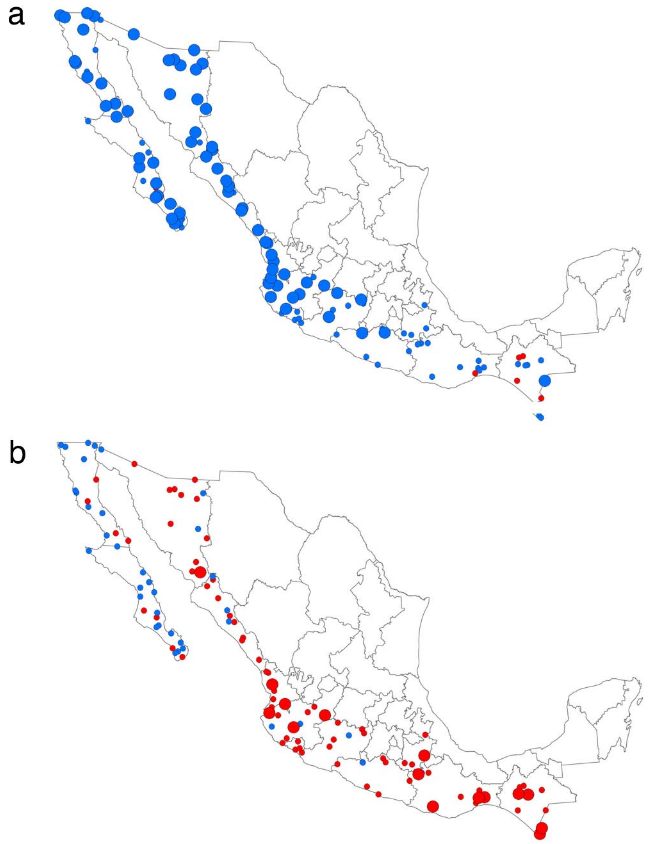

Fig. 2. Mediterranean and monsoon climate patterns and their relationship with oceanographic conditions. (*a*) Correlation between mean SOI values for winter-spring and mean precipitation for the same season. (*b*) Correlation between mean SOI values for summer and mean precipitation for the same season. In both graphs, blue dots indicate negative correlation, and red dots indicate positive values; the large dots indicate statistically significant correlations ($P < 0.05$).

North of the 22°30′N parallel, most of the regression lines showed a negative slope, whereas in southern Mexico, the slope was mostly positive. A simple sign test showed this pattern to be highly significant: 87% of all 60 stations north of 22°30′N had negative slopes, whereas 83% of all 57 stations south of this latitudinal boundary had positive values ($\chi^2 = 79.2$; df $= 2$; $P < 0.0001$). El Niño events tend to bring increased rainfall in the Mexican Pacific northwest but tend to increase aridity in the ecosystems of the southern tropical Pacific slope.

Seasonal Precipitation and SOI Values. When annual precipitation values were split into the three main different rainfall signals in the Mexican Pacific (winter-spring, summer monsoon, and fall precipitation), a very clear pattern appeared for winter-spring and summer (Fig. 2 *a* and *b*). In general, negative SOI values (El Niño conditions, Fig. 2*a*) produce a marked increase in winter rainfall throughout the Mexican Pacific coast (although the significant points tend to concentrate toward the northwest), whereas La Niña conditions (Fig. 2*b*) tend to produce an increase in monsoon-type rainfall all along the continental coast of Mexico, including the southern reaches of the Sonoran Desert. The results for the fall (hurricane) season were mostly nonsignificant. In short, El Niño events increase winter-spring precipitation but tend to decrease the intensity of the monsoon, whereas La Niña conditions produce the opposite effect.

Concentration of Winter Precipitation. From north to south, along the Mexican Pacific coast, there is a clear trend toward increased

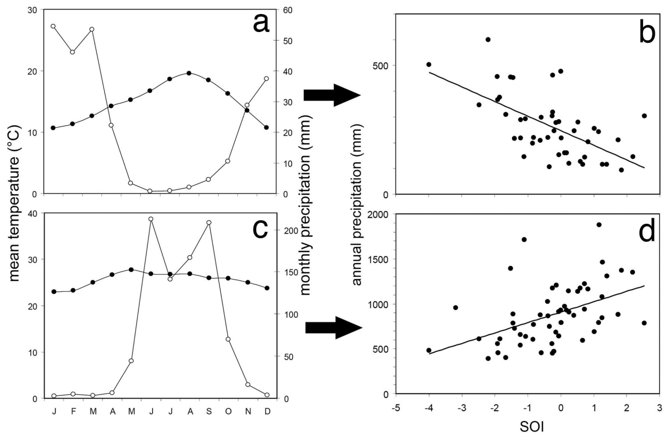

Fig. 3. Influence of ocean conditions on winter and summer rains. Climatic diagram for Ensenada, Baja California (lat 31°53′N, long 115°35′W), a typical winter-rain area in northern Mexico (*a*), and negative correlation between mean annual SOI values and annual precipitation for the same station (*b*). Climatic diagram for Ixtepec, Oaxaca (lat 16°33′N, long 95°05′W), a typical monsoon-rain area in southern Mexico (*c*), and positive correlation between mean annual SOI values and annual precipitation observed for that station (*d*). The two stations were selected for the completeness of their long-term data series and their respective central locations within areas of mediterranean and monsoon-type weather regimes.

precipitation in summer and fall (Figs. 3 and 4). Although >95% of all precipitation falls between November and April in Baja California near the U.S. border, the opposite is true in Oaxaca and Chiapas, where >90% of all precipitation falls in summer, between June and September (Fig. 3). In continental Mexico, there is a clear trend along the coast toward increased winter precipitation above the latitude of 23° (Fig. 1*C*), and especially between 26° and 32°N, where the proportion of winter precipitation rises rapidly from ≈10% to >50%, with a corresponding decrease in the importance of the monsoon (Fig. 4*a*). In the Baja California peninsula, in contrast, the influence of maritime weather is more pronounced, and at all latitudes, winter precipitation is much higher than in the mainland, rising from ≈15% in the Cape Region at 23° latitude to almost 90% in mediterranean California at 33°N. Finally, whereas the importance of fall precipitation decreases very gradually in the mainland from ≈35% in the south to 25% in the north, in Baja California, in contrast, the decrease is rapid. The southern Cape Region (lat 23°N) receives ≈60% of its annual precipitation from autumnal *chubascos*, but the proportion falls to ≈10% in the northern mediterranean California (lat 33°N).

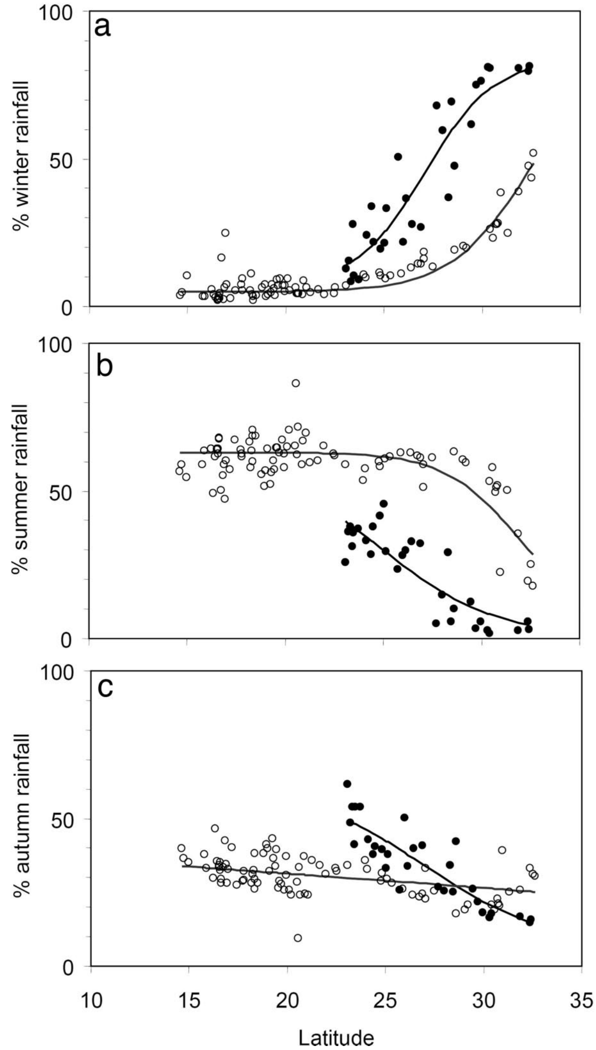

Fig. 4. Proportion of mean precipitation that falls in winter-spring (*a*), summer (*b*), and autumn (*c*), graphed for all weather stations as a function of latitude. The stations in the peninsula of Baja California are plotted in black circles, and mainland stations are plotted in open circles. The latitudinal trends have been highlighted by fitting a logistic model ($P < 0.01$ in all cases). Note that, for a given latitude, the influence of winter rains is much higher in the peninsula than in the mainland, where a larger land mass promotes the development of the summer monsoon. Also, note the impact of tropical storms (*chubascos*) during fall in the Cape Region in the tip of the peninsula.

Discussion

As a general rule, El Niño conditions (basically characterized along the Mexican Pacific coast by elevated sea surface temperatures) tend to bring increased rainfall north of the Tropic of Cancer and drought conditions southward. Upon closer inspection, however, it becomes clear that El Niño increases the amount of advective winter rainfall in general, whereas it decreases the intensity of the Mexican summer monsoon. Because summer rainfall dominates in the south while winter rainfall dominates in the north, the general north–south pattern develops. The results for the fall precipitation were mostly nonsignificant, implying that oceanographic conditions do not have a significant influence on the amount and location of rainfall reaching these coastal drylands in autumn. This finding does not rule out a possible influence of oceanographic conditions on the force and trajectory of Pacific hurricanes and tropical storms reaching land, but that question is not being analyzed in this paper.

In general, increased winter-spring moisture is expected during El Niño events, but this increase will have an impact mostly in the subtropical and higher-latitude drylands, such as mediterranean California, Baja California, and the Sonoran Desert. In the tropical dry forests of the southern Mexican Pacific coast, which are fed almost entirely by monsoon rains, El Niño conditions will increase the probability of summer drought. This trend, however, is not entirely deterministic, but strongly influenced by other factors. Indeed, the mean r^2 value between SOI and precipitation for winter rainfall in the Mexican northwest was 0.24, whereas the mean r^2 in the south with summer precipitation was 0.13. The highest r^2 value observed in the whole data set was 0.45 for Rosarito, in Baja California, where precipitation is associated with negative SOI values. These significant, but numerically low, values mean that even in the areas where the effect is most predictable, only 30–40% of variation in precipitation can be predicted from the atmospheric/oceanographic conditions described by the SOI. In our data set, it is also likely that the correlations between the SOI and precipitation may be better in reality than what we found because many of the weather stations that we analyzed have often operated under difficult financial conditions and with untrained personnel, a fact that almost surely is contributing to statistical noise in our data. In the Chihuahuan Desert, which does not form part of the Pacific dryland corridor but also receives both winter and monsoon rains, other authors (48) have also found that the connection between El Niño and winter precipitation appears to be significant but quite variable.

The predictive capacity of our simple SOI model, however, may be improved considerably by taking into account other, longer-term oceanographic signals. Recent studies have shown that the Pacific Decadal Oscillation may be also playing an important role in longer-term regional cycles of drought and moisture (13, 42), and some recent analyses suggest that synergistic effects may exist between the ENSO signal and the longer-term Pacific Decadal Oscillation (14). These results open the possibility of better predictions based on the effect of coupled ocean–atmosphere systems on moisture availability in terrestrial biomes.

We conclude that, despite probabilistic uncertainties, oceanographic conditions play a significant role in precipitation anomalies and moisture availability in the Pacific coast of Mexico. This effect, however, is not linear; the same anomaly that brings increased rainfall to mediterranean California and the northern Sonoran and Baja Californian deserts may also bring drought conditions to the tropical dry forests of Oaxaca. Could this pattern of El Niño- and La Niña-induced rainfall pulses be common to other monsoon-type drylands of the American continent? It may be the case. For example, using satellite data, Los *et al.* (11) found a marked decrease in precipitation and surface greenness (an index of foliage biomass) in some tropical, monsoon-type drylands of South America like the dry Chaco, the upper Monte Desert, and very especially the Brazilian Caatinga during the two El Niño events of the 1980s.

Because dryland ecosystems are critically dependent on rainfall pulses for their renewal and regeneration, understanding the complex effect of ocean conditions on all of these drylands may be critical for their management in the future. In the same manner as El Niño conditions can predict quite well the volume of some pelagic fisheries (46), it is also conceivable that restoration ecology, grazing regimes, carrying capacities, and fire risks may be predicted and managed better by analyzing the ENSO predictors and related oceanographic conditions. Furthermore, identifying the factors triggering moisture pulses may also be very important for the management of runoff-dependent systems, such as rivers, inland lakes, reservoirs, and coastal lagoons. And lastly, if El Niño anomalies are likely to increase in frequency or intensity with global climatic change (e.g., 49–54), then it is also likely that the Pacific tropical deciduous forests may be under increased pressure in the future for their survival and conservation. Careful monitoring of the coupled atmosphere–ocean system, supported by a good knowledge of its effects on the tropical monsoon and on higher-latitude winter precipitation, may prove to be important in managing and mitigating the effects of large-scale climatic change on coastal drylands.

Materials and Methods

We worked with the raw daily precipitation data from all weather stations along the Pacific slope of Mexico recorded by the country's Meteorological Service (*Servicio Meteorológico Nacional*), totaling 117 stations. The northernmost station was Mexicali, in Baja California (32°39′N), and the southernmost station was Ignacio López Rayón, in Chiapas (14°37′N), separated by a distance of ≈3,100 km. Years that had missing data (periods where readings were not taken) were eliminated from the analysis. The resultant data series for each station had between 29 and 83 years of recorded rainfall [supporting information (SI) Table 1].

We downloaded the SOI values from the National Climate Centre of the Australian Bureau of Meteorology (www.bom.gov.au/climate/current/soihtm1.shtml) from 1876 to present, and calculated linear regressions between the average yearly SOI values and total annual precipitation for each weather station. The SOI is the standardized anomaly of the mean sea level pressure difference between Tahiti and Darwin, Australia (44, 45). Sustained negative SOI values indicate a slackening of the Pacific trade winds, a decrease in coastal upwelling, and an accumulation of anomalously warm waters in the coast of the Americas, i.e., El Niño conditions. Positive values of the SOI are associated with stronger-than-average Pacific trade winds and intense, cool coastal upwellings in the eastern Pacific, i.e., La Niña episodes.

We then split annual precipitation values into three seasons that correspond to markedly different rainfall signals in the Mexican Pacific: (*i*) winter-spring precipitation from December to April, (*ii*) summer monsoon-type precipitation from May to August, and (*iii*) fall precipitation (mostly derived from hurricanes and tropical storms originating over the Pacific Ocean) from September to November. The three resulting data series (winter-spring, summer, and fall) were correlated against the average SOI values for the same months in all 117 weather stations. The results of each correlation were tested for statistical significance and plotted on a geographic information system. To test for potential time lag in the effect of oceanographic conditions on precipitation, we repeated the regression analysis, offsetting the SOI series by 1 and 2 months. The regression significances of the lagged data did not improve those of the direct correlations, and we only present in this paper the results of the latter.

Finally, we also downloaded the monthly precipitation raster files from the Climate Atlas of North America-Western Region, developed by S. Arundel (Department of Geography, Northern Arizona University, Flagstaff, AZ; data available at http://www.geog.nau.edu/global_change/climate_surfaces.html) by interpolating rainfall data at a 1-km pixel resolution using thin-plate smoothing splines [ANUSPLIN software by M. F. Hutchinson (Australian National University, Canberra, Australia); available at http://cres.anu.edu.au/outputs/anusplin.php)] (55, 56). With these raster maps, we calculated the percentage of annual precipitation in Mexico that falls in the winter-spring months for each 1-km pixel. For this purpose, we calculated for each pixel the winter-spring precipitation by adding the precipitation that falls between December and April and divided this by the total annual precipitation (i.e., falling between January and December). The resulting proportions were plotted on the geographic information system as percentage values.

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