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DISTRIBUTION OF CHAPARRAL AND PINE-OAK “SKY ISLANDS” IN CENTRAL AND SOUTHERN BAJA CALIFORNIA AND IMPLICATIONS OF PACKRAT MIDDEN RECORDS ON CLIMATE CHANGE SINCE THE LAST GLACIAL MAXIMUM

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Chaparral, the evergreen sclerophyllous scrub characteristic of the mediterranean-climate region of North America, grows extensively in dense stands from northern California to lat. 30°N, but thins to a few isolated populations or “sky islands” on the highest mountains in the Central Desert of Baja California (~30°–27.5° N lat.), as well as on the highlands of Isla Cedros. Chaparral also occurs in small outlying populations at lower elevations in the Central Desert, and as understory in tropical thorn scrub and montane Mexican pine-oak woodland, extending nearly to Cabo San Lucas. We present the first detailed maps of chaparral populations in the north central and Mexican pine-oak woodlands in the southern Peninsula, interpreted from Google Earth™ imagery and herbarium databases. We also compare the present distribution of chaparral with available records from Pleistocene–Early Holocene packrat middens. We show that chaparral is unexpectedly widespread in the Central Desert and propose, on the basis of the cistern effect of bedrock surfaces of midden sites and the physical equatorward limit of jet stream precipitation, that climate change since the Last Glacial Maximum was not as pronounced as has been suggested in studies of packrat middens.

1. INTRODUCTION

The equatorward limit of mediterranean-type climate and evergreen sclerophyllous scrub lies near the 30th parallel on continental west coasts throughout the world, including Baja California (Mexico), central Chile, South Africa, southwest Australia, and the southern Mediterranean basin (Bahre 1979, Heusser 1994, Rundel *et al.* 1998, Minnich and Franco-Vizcaíno 1998, Dean and Milton 2000, Vaks *et al.* 2006).

This limit reflects the equatorward extent of reliable winter precipitation associated with frontal cyclones of the polar-front jet stream. In summer, the jet stream is poleward of mediterranean regions, and protracted drought is facilitated by suppressed convection over cold, upwelling ocean currents and their associated marine stratus layers. Equatorward of the 30th parallel, precipitation is unreliable year-round, and mediterranean scrub is replaced by desert vegetation.

On the Pacific coast of North America, mediterranean chaparral extends from northern California (USA) to the Sierra San Pedro Mártir at lat. 30°N in Baja California (Minnich and Franco-Vizcaíno 1998). To the south, small mountain chains in the Central Desert with summit elevations >1,500 m and Isla Cedros have “sky islands”, or isolated stands, of chaparral (Bullock *et al.* 2008) to as far south as 27.5°N. In the Central Desert, areas that host chaparral are characterized by locally cooler climate and orographic winter precipitation. Even farther south, chaparral species occur in thorn scrub and montane Mexican pine-oak woodlands that grow in summer rain climates of the North American monsoon nearly to Cabo San Lucas (lat. 23°N), similar to that in the mountains of mainland Mexico (see *e.g.* Minnich *et al.* 1994).

Knowledge of the history of Baja California vegetation since the Last Glacial Maximum (LGM, ~20,000 years before present) is critical to understanding the origins of chaparral “sky islands”, as well as the deep-time processes responsible for plant diversity and endemism in the Peninsula (Wiggins 1980, Case and Cody 1983). Packrat middens dating to the Late-Pleistocene show that chaparral grew at lower elevations and farther south than at present (Wells 2000, Rhode 2002, Metcalfe 2006, Minnich 2007, Holmgren *et al.* 2011). Using a “vegetation analogy” method, midden studies deduce major climate shifts in the Central Desert based on macrofossil evidence and lake stands.

The evaluation of chaparral biogeography since the LGM requires baseline data of its present distribution and species composition. While botanical collections have described the chaparral flora in the Central Desert, vegetation maps are another source of biotic data for the interpretation of fossil packrat middens and paleoclimate. Chaparral in Baja California has been mapped as far south as lat. 30°N (Minnich and Franco-Vizcaíno 1998), but the distribution of chaparral sky islands in the Central Desert and pine-oak woodlands in the southern Peninsula has not been inventoried in detail. In this study, we conducted a comprehensive inventory of the Baja California Peninsula south of lat. 30°N, and used Google EarthTM imagery to produce the first maps of chaparral sky islands and Mexican pine-oak woodlands that contain chaparral understory, and utilized previously published data and herbarium databases to determine species composition. We compare modern

chaparral with chaparral records in Pleistocene–Early Holocene packrat middens (Wells 2000, Rhode 2002, Holmgren *et al.* 2011), and evaluate the unusual lithology, hydrology and vegetation of midden sites. Finally, we argue from first principles in atmospheric science that moist climates in the past were largely due to cooler temperatures, not increased precipitation, as seen farther north in the USA. We show that local populations of chaparral are unexpectedly widespread in the Central Desert and suggest that climate change since the Last Glacial Maximum, in particular total precipitation was not as large as has been proposed in packrat midden studies.

2. METHODS

2.1. Study area

We define the Central Desert as the region from the southern Sierra San Pedro Mártir (lat. 30.5°N) to San Ignacio in Baja California Sur (lat. 27.3°N). South of lat. 30°N the peninsular range—the region's mountainous backbone—includes a series of discontinuous ranges that parallel the Gulf of California (see Figure 1; all figures on pp. 279–290). The mountains comprise broad plateaus, with steep fault escarpments toward the Gulf, and westward-dipping slopes that grade into alluvial plains toward the Pacific. Mountain crests range from 1500 to 1932 m and include the Sierras La Asamblea (lat. 29.4°), La Libertad (28.8°), San Francisco (27.6°), La Giganta (27–25°), Las Cruces (24.1°) and La Laguna (23.5°), as well as Volcán Las Tres Vírgenes (27.5°) and Isla Cedros (28.2°). Coordinates of place names are given in Table 1.

From the Sierra La Libertad northward, the mountains consist mostly of exposed plutonic bedrock of the Cretaceous peninsular range batholith, with local caprock of Tertiary volcanics and prebatholithic metasedimentary and metamorphic rocks (Gastil *et al.* 1975, INEGI 1988). Extensive post-batholithic volcanics, ranging from Miocene age to recent, are exposed from Cataviña to west of the Sierra La Asamblea, an area of numerous dry lake beds and playas, such as Laguna Chapala. In the southern peninsula, south of San Ignacio, the region from the Sierra San Francisco to the Sierra La Giganta comprises mostly Tertiary volcanics. Intrusive rocks of the peninsular batholith also dominate the mountains of the cape region.

The Baja California Peninsula presents one of the world's clearest Mediterranean-tropical transitions, with essentially uniform mean annual precipitation and temperature across the Central Desert, but an increasing proportion of summer precipitation towards the south (see Table 2). North of latitude 30°, the climate in the coastal plains and mountains of Baja California is Mediterranean with winter precipitation and summer drought. From the Sierra San Pedro Mártir northward, the orographic

TABLE 1. Location of place names (degrees, decimal minutes).

Location	Latitude N	Longitude W
Arroyo El Encinal near Cerro Loreto	26 6.0	111 36.0
Arroyo El Horno near Cerro Loreto	26 4.2	111 34.8
Arroyo Las Palmas	29 19.2	114 6.0
Arroyo Zamora	29 51.6	114 40.2
Bahía San Cristobal	27 25.0	114 30.0
Bahía Tortugas	27 43.2	114 54.0
Cataviña	29 45.6	114 43.8
Cerro "1590"	27 34.2	113 1.8
Cerro "1063"	28 16.8	115 12.6
Cerro El Alguatosa	29 49.8	114 36.3
Cerro La Borreguera	28 48.0	113 36.0
Cerro La Libertad	28 51.6	113 36.6
Cerro La Sandia	28 24.4	113 26.3
Cerro Loreto	26 6.0	111 34.8
Cerro Los Pocros	26 39.0	112 7.8
Cerro Matomí	30 22.3	115 7.1
Cerro Pedregoso	29 35.4	114 30.0
Cerro Redondo	28 7.8	115 13.2
Cerro San Juan (C. La Bandera)	27 59.0	112 59.0
Cerro San Luís	29 22.0	114 5.4
El Progreso	29 58.2	115 12.0
El Rosario	30 4.2	115 42.0
Laguna Chapala	29 22.2	114 21.0
Laguna San Felipe (L. del Diablo)	31 7.8	115 16.8
Mesa Catarina	28 30.0	113 46.2
Mesa Corral Blanco	28 26.4	113 46.2
Mesa El Gato	29 34.4	114 36.1
Mesa El Mármol	29 57.0	114 45.0
Mesa El Salado	29 16.0	114 18.6
Mesa San Carlos	29 42.0	115 27.0
Mesa Santa Catarina	29 39.6	115 19.2
Misión San Fernando	29 58.2	115 14.2
Misión Santa Gertrudis	28 3.6	113 4.8

Location	Latitude N	Longitude W
North Point Isla Cedros	28 22.2	115 13.2
Punta Baja	29 57.0	115 48.6
Punta Canoas	29 25.6	115 11.2
Punta Eugenia	27 51.6	115 5.0
Punta Prieta	28 48.6	114 23.4
Santa Catarina Sur, summit 14 km NE	29 48.4	115 0.87
San Juan Mine	28 45.0	113 35.4
Santa Inés	29 43.7	114 41.7
Sierra Agua Verde (S. Cantil Blanco)	26 54.0	112 21.0
Sierra Las Cruces (S. Las Canoas)	24 6.0	110 7.2
Sierra La Laguna	23 31.8	109 57.0
Sierra San Pedro (S. La Giganta N)	26 57.0	112 27.0
Sierra San Pedro Mártir	31 0.0	115 30.0
Vizcaíno Peninsula	27 42.0	114 42.0

lift of frontal storm air masses from the North Pacific Ocean over continuous high terrain assure a reliable winter rainy season. To the south, storm air masses yield little orographic precipitation, due to the low elevation of the mountains (average annual precipitation < 30 cm). The entire peninsular range experiences summer thunderstorms of the North American monsoon. The heaviest summer precipitation occurs in the Sierra La Laguna, then decreases northward along the Sierra La Giganta to a minimum in the Sierra La Asamblea, then increases again in the Sierra San Pedro Mártir (see Table 2). In late summer, tropical cyclones of the east Pacific enter the Cape Region almost annually, decreasing to only once per decade in the northern Central Desert (Smith 1986). Mean annual precipitation ranges from 40–70 cm in the Sierra San Pedro Mártir (Franco-Vizcaíno *et al.* 2002), and is likely 20–35 cm at higher elevations in the low sierras of the Central Desert, 30–40 cm in the Sierra La Giganta (see Table 2), and 40–70 cm in the Sierra Laguna.

With the advantage of year-round photosynthesis, evergreen chaparral grows in spring, when temperatures warm under moist soil, and survive summer drought with sclerophyllous foliar metabolism, and by rooting deep into bedrock fractures with secure water in regolith (Hubbert *et al.* 2001a, 2001b, Witty *et al.* 2003). During drought, stomatal closure reduces photosynthetic rates, but this is compensated by efficient canopy maintenance (Keeley and Davis 2007). High foliar lignin, shrub morphology, and the “carpet” structure of chaparral (contiguous horizontal and

TABLE 2. Selected climatological data for the central and southern Baja California Peninsula (calculated from Reyes Coca *et al.* 1990, and Miranda *et al.* 1991).

Name of weather station and elevation in meters	Lat. N° "	Long. W° "	Nearby Sierra	Mean Temperature (°C)			Mean Precipitation (cm)	
				Jan	Jul	Annual	Annual	% Jun-Sep
Rancho Santa Cruz 1000	30 54	115 36	San Pedro Mártir	10.4	24.9	16.7	30.5	17
El Progreso 517	30 0	115 12	San Pedro Mártir	13	26.1	18.7	13.7	16.8
San Luís (Sta. Inés) 510	29 42	114 42	La Asamblea	13	26.6	19	11.3	18.4
Laguna Chapala 640	29 24	114 24	La Asamblea	10.9	25.4	17.6	12.5	21.8
Punta Prieta 217	28 54	114 12	La Libertad	17.6	25	19.7	11.2	15.3
San Borja 412	28 42	113 42	La Libertad	15.1	25.3	19.9	13.7	24.6
San Regis 495	28 36	113 48	La Libertad	14.2	25.1	19.3	13.8	23.2
Rancho Alegre 120	28 18	115 54	La Libertad	14.6	24.8	19.4	14.9	21.9
Santa Gertrudis 400	28 6	113 6	San Francisco	15	27.5	20.4	13.7	52.1
El Arco 300	28 0	113 24	San Francisco	16.5	26	20.8	11.9	35
Díaz Ordaz 70	27 48	113 24	San Francisco	13.7	23.9	18.6	10.3	34.3
Bahía de Tortugas 16	27 42	115 0	Vizcaíno Peninsula	15.4	22.3	18.9	9.3	17.2
San Ignacio 110	27 30	112 48	Las Tres Vírgenes	13.6	24.7	19.2	9.75	45.9
San Zacarías 125	27 12	112 48	La Giganta (S. Pedro)	15.2	23.7	19.2	9.79	41.8
San José Comondú 270	26 6	111 48	La Giganta	16.6	27.2	21.7	17	53.9
Tepentú 160	25 6	111 12	La Giganta	15.8	27.4	21.4	11.6	67.9
La Soledad Norte 340	24 48	110 48	La Giganta	15.2	26.2	21.8	24.1	67.3

Name of weather station and elevation in meters	Lat. N° "	Long. W° "	Nearby Sierra	Mean Temperature (°C)			Mean Precipitation (cm)	
				Jan	Jul	Annual	Annual	% Jun-Sep
El Cajoncito 78	24 12	110 12	Las Cruces	16.7	26.8	21.8	21.6	64.9
Sierra La Laguna 1800	23 30	110 0	La Laguna	7.7	16	12.2	67.3	73.2
Cabo San Lucas 45	22 54	109 42	La Laguna	18.6	27	23	21.6	64.9

vertical fuel continuity) encourage recurrent stand-replacement burning (Minnich and Chou 1997). Cumulative build-up of live canopy and increased leaf area contributes to desiccation and canopy flammability. Chaparral responds to fire by resprouting and mass recruitment from seed banks (Keeley and Davis 2007). Fire intervals are in the order of two events per century in the Sierras Juárez and San Pedro Mártir, where there is little effective fire control (Minnich and Chou 1997, Minnich *et al.* 2000). Pine-oak forests are dominated by deciduous oaks with mesophytic foliage. Trees respond rapidly to summer rains that coincide with high temperature, but experience leaf drop in response to winter drought.

2.2. Interpretation of chaparral vegetation in Google Earth imagery

We inventoried chaparral "sky islands" and Mexican pine-oak forests by using high-resolution Digital Globe and other imagery of Google Earth. Imagery was examined by graduated scaling, the zoom function allowing for the observation of broad-scale patterns of vegetation and terrain (at small scales), and near-ground (large scale) identification of vegetation features. Species ranges were delimited in KMZ files using the digitizer function of Google Earth. Maps of chaparral sky islands and Mexican pine-oak forest were developed by digitizing directly onto Google Earth imagery (Minnich *et al.* 2011a). Chaparral and Mexican pine-oak woodland were identified on the basis of morphology, stature and color. Species composition was determined by consulting databases of botanical collections at the San Diego Natural History Museum (SDNHM), the University of California, Riverside herbarium, the Flora of North America (eFloras 2010), and Wiggins (1980).

Google Earth imagery was scanned comprehensively in an "X-Y" format, including extensive areas where chaparral and forests are not found, to ensure that outliers were not omitted. Imagery was examined at the smallest possible scale consistent

with resolution of trees and shrubs (*ca.* 1,500 m above-ground), to maximize the efficiency of scanning. When a population was suspected or encountered, Google Earth was scaled to 600 m above-ground to confirm identification. Closer inspection was not possible due to pixelation of imagery. Although Google Earth imagery is monoscopic, the tilt feature was used for three-dimensional viewing of terrain and rock-substrate properties. Imagery was examined by looking “north-to-south” (south to top), in order to observe tree morphology independently of shadows; that is, to avoid the repetition of images of crowns and shadows that result from viewing towards the north. By looking south, shadows extend toward the bottom of the image and can thus be ignored. In order to distinguish between evergreen chaparral and deciduous species, multiple images taken at different seasons were examined. Chaparral and Mexican pine-oak woodland were defined at ~10% cover.

Imagery was examined online between August 2007 and August 2009. The database digitized on Google Earth was saved in the compressed version (kmz) of the keyhole markup language (kml) and placed into a compressed format. The file was subsequently saved in uncompressed (kml) format and converted to a standard GIS vector format, using ESRI ArcGIS Desktop 9.1 operating under an ArcInfo license (Environmental Systems Research Institute, Inc. 2010). Data were converted from the kml format to a feature classes (“shape”) file for use in ArcGIS.

3. DISTRIBUTION AND SPECIES COMPOSITION OF CHAPARRAL “SKY ISLANDS”

Chaparral covers the four highest sierras of the Central Desert, and the highlands of Isla Cedros (see Figure 1). Small outlying populations grow at lower elevations on volcanic mesas, bedrock slopes, and along washes. Extensive open stands grow on the Vizcaíno Peninsula. Several species extend into Baja California Sur as understory to Mexican oak woodlands. Botanical collections show that species composition is conspecific with chaparral in California and northern Baja California, but additional congeners from the Mexican mainland occur in chaparral from the Sierra San Francisco to the cape. See tables 3 and 5 for ranges of chaparral and pine-oak woodland species.

3.1. Sierra La Asamblea

Chaparral grows mostly on north-facing slopes >1,200 m of Cerro San Luis and granitic bedrock slopes of a plateau 7 km to the south (see Figure 2a). Contiguous chaparral dominated by *Adenostoma fasciculatum* covers the north-facing slope of Cerro San Luis (see Figure 3a). Other species recorded in botanical collections and

in photographs by K. Geraghty (pers. comm.) are *Ceanothus greggii* var. *perplexans*, *Arctostaphylos glauca*, *A. peninsularis*, *Cercocarpus betuloides*, *Garrya grisea*, *Rhus ovata*, *Quercus turbinella*, *Q. cedroscensis*, *Q. ajoensis*, *Rhamnus insula*, *Heteromeles arbutifolia*, and *Juniperus californica*. *Pinus monophylla* woodlands cover steep north-facing exposures. The plateau (1,200 to 1,400 m) is covered with open chaparral in association with scattered *Brahea armata* (Minnich *et al.* 2011a). Collections in the upper Arroyo Las Palmas drainage on the west side of the plateau record *Arctostaphylos peninsularis*, *Rhus ovata*, *Rhamnus insula*, *Prunus ilicifolia*, *Heteromeles arbutifolia*, *Quercus turbinella*, *Q. cedroscensis*, *Q. peninsularis*, *Garrya veatchii*, and *Adenostoma fasciculatum*. *Xylococcus bicolor* was reported in the range by Wiggins (1980). Sparse woodlands of *Quercus peninsularis* grow across the range, but most remarkable are stands of *Q. chrysolepis* in association with *Pinus monophylla* and *Brahea armata* on several resistant granite bedrock slopes of the plateau (see Figure 3b). North-facing slopes in the southeastern plateau are covered with *Pinus monophylla* woodland in association with *Quercus turbinella*, *Q. peninsularis*, *Rhus ovata*, and *Arctostaphylos peninsularis*. The plateau is the southern limit of *P. monophylla* (Critchfield and Little 1966).

3.2. Sierra La Libertad

Chaparral occurs for 60 km along the crest of the Sierra La Libertad (see Figure 2b), and on summits detached from the main sierra in the northwest (28.84°N, 113.71°W) and on Cerro La Sandia (1,772 m). Extensive open chaparral on granitic substrate in the north forms locally closed stands on the north-facing slopes of Cerro La Libertad, Cerro La Borreguera, and a summit near the San Juan mine. Although reported in botanical collections, *Adenostoma fasciculatum* is not as conspicuous as in the Sierra La Asamblea. Chaparral species recorded in the range include *Ceanothus greggii* var. *perplexans*, *Arctostaphylos glauca*, *A. peninsularis*, *Rhus ovata*, *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Rhamnus insula*, *Quercus cedroscensis*, *Q. turbinella*, *Garrya veatchii*, *Garrya grisea*, *Prunus ilicifolia*, and *Juniperus californica*. Intervening granite plateaus on the crest are covered with open chaparral, *Juniperus californica*, and rare colonies of *Q. peninsularis*. *Rhus kearneyi*, *Xylococcus bicolor*, and *Malosma laurina* grow at lower elevations, often along arroyos.

South of the Cerro San Juan mine, granites are capped by extensive porous basalts with little chaparral, especially on caprock plateaus and south-facing slopes. Open stands grow on steep north-facing slopes and talus to the highest summit on the range (1,640 m), the shrubs frequently arranged in elongated, parallel linear strips at the base of basalt cliffs, at contacts between lava flows, and along bedrock fractures. The association of these southern stands with *Brahea armata* (Minnich *et al.* 2011a)

suggests that chaparral is colonizing bedrock seeps. Botanical collections have not been taken in the volcanic caprock part of the Sierra La Libertad. Chaparral on Cerro La Sandía is restricted to talus and consists of *Garrya grisea*, *Quercus turbinella*, and *Rhus kearneyi*. *Malosma laurina* and *Xylococcus bicolor* grow in nearby washes.

3.3. Sierra San Francisco

Open chaparral occurs on north-facing slopes of the highest summit (Cerro “1590”), just south of the village of San Francisco, and several nearby summits in association with woodlands dominated by *Quercus oblongifolia*, a mainland Mexican species that is closely related to *Q. engelmannii* of northwest Baja California and southern California (see Figure 2c; Felger *et al.* 2001, eFloras 2008). Local chaparral patches grow on north-facing slopes of nearby summits, and *Q. oblongifolia* woodlands descend major canyons and arroyos with near-surface water in association with *Brabea armata* (Minnich *et al.* 2011a). A botanical collection by Tucker (SDNHM 95184) discusses the mixture of “intermediate oaks in the Sierra San Francisco.” A *Quercus ajoensis-turbinella* intermediate was also reported (SDNHM 59827). Dominant chaparral species include *Xylococcus bicolor*, *Rhus kearneyi*, *Prunus ilicifolia*, *Rhamnus insula*, and *Heteromeles arbutifolia*. *Malosma laurina* grows along arroyos (Rhode 2002).

3.4. Volcán Las Tres Vírgenes

Dense chaparral grows > 1,500 m on the north-facing slope of the primary volcano, with open stands descending to 1,350 m (see Figure 2d). Botanical collections reveal that upper slopes have *Ceanothus greggii* var. *perplexans*, *Ceanothus oliganthus*, *Garrya grisea*, and *Rhus kearneyi*. Collections below 1,500 m include *Xylococcus bicolor*, *Rhamnus insula*, *Rhus ovata*, and *Quercus ajoensis*. Open chaparral covers the north-facing slope of the northern volcano.

3.5. Isla Cedros

The crest of Isla Cedros has two narrow belts of chaparral at elevations > 300–600 m, one extending from North Point to Cerro “1063”, and the other along the north facing slope of Cerro Redondo (see Figure 2e). In the fog zone < 600 m are dense *Pinus radiata* forests, with chaparral understory, forming narrow ribbons of solid forest ca. 300 m wide, mostly along the primary ridgeline. One stand extends 4.3 km southward from North Point and the other for 6.2 km along an isthmus between Cerro “1063” and Cerro Redondo. Pine stands are flagged by winds from the west and north at right angles to local topography, due to persistent strong winds and fog drip that sustains these closed-cone forests. Stands are mostly open, but gradually increase in cover with elevation above the pine belt. Contiguous stands grow on

steep north facing slopes of Cerro "1063", and on Cerro Redondo. Species in the northern pine forest include *Rhus integrifolia*, *R. lentii*, *Malosma laurina*, *Ceanothus verrucosus*, *Heteromeles arbutifolia*, *Xylococcus bicolor*, *Juniperus californica*, *Rhamnus crocea*, and *Quercus cedrosensis*. Shrubs recorded on north-facing slopes of the southern summit include *Quercus cedrosensis*, *Garrya veatchii*, and *Xylococcus bicolor*. *Rhus lentii* and *Juniperus californica* were collected on the south face Cerro Redondo.

3.6. Chaparral outliers

Small patches of open chaparral grow in many localities below the primary sierras, but few botanists have collected them (see Figure 1). The north-coastal chaparral belt at Ensenada extends southward to the foothills of the Sierra San Pedro Mártir (Minnich and Franco-Vizcaíno 1998) and Mesas San Carlos and Santa Catarina, south of El Rosario. In the nearby coast range, small colonies grow on summits 8 km W of El Progreso, and along a ridge (800–1,050 m) ca. 14 km NE of Santa Catarina Sur. Local populations continue south along arroyos within 5 km of the beach from Punta Baja to Punta Canoas to locally near Bahía Blanco and Punta Prieta, where collections document *Rhus integrifolia* and *Malosma laurina*. On the Vizcaíno Peninsula, extensive stands of *Rhus lentii*, a close relative of *R. integrifolia*, occur with *M. laurina* in the hills and alluvial plains near Punta Eugenia and Bahía San Cristobal. This area is subject to frequent fog and low clouds, similar to nearby Isla Cedros, but appears to lack the chaparral diversity of the island.

Farther inland, many small populations occur between the southern limit of chaparral in Sierra San Pedro Mártir near Cerro Matomí and the Sierra La Asamblea. In the far northern Central Desert are stands growing in talus of basalt caprock on the north flank of Mesa El Mármol (1,070 m) and on a mesa 5 km to the east (29.94°, 114.70°), as well as on a granite bedrock slope beneath a volcanic mesa at 29.89°, 114.73°. Chaparral occurs intermittently for 6 km along the northern exposures of an 1,100–1,200 m high ridge near Arroyo Zamora. Nearby Cerro La Aguatosa (1,345 m) contains open stands consisting of *Rhus ovata*, *Juniperus californica*, *Quercus turbinella* and *Prunus ilicifolia*. Granite bedrock slopes at Cataviña have scattered patches that include *Juniperus californica* (Wells 2000). The north-facing slopes of a nearby basalt mesa (1,000 m) have *Rhus ovata* and *Juniperus californica*, as well as the chaparral leaf succulent *Yucca whipplei* (29.72°, 114.59°). Several chaparral patches grow on granite bedrock >800 m at 29.67°, 114.52°. Cerro El Pedregoso, an eroded cinder cone with summit elevations of 1400 m, is covered with open stands of *Juniperus californica*, *Rhus ovata*, *Quercus turbinella*, and *Rhamnus insula*. Farther south, chaparral grows on granite bedrock (900 m) just west of a basalt mesa (1,100 m, 29.57°, 114.63°), at Mesa El Gato where *Rhamnus insula* was collected, and on a

granite bedrock surface within lava flow/cinder cone terrain in the upper headwaters of Arroyo El Gato.

South of Laguna Chapala, open chaparral occurs on granitic bedrock slopes > 600 m in a coastal range south of Mesa El Salado. To the east are sparse chaparral stands on granite bedrock slopes, and a volcanic mesa 5 km S of the Sierra La Asamblea. Chaparral grows on the coastal foothills of the Sierra La Libertad west of Mesas Catarina and Corral Blanco, again on granite bedrock slopes > 600 m. A few colonies were found at 1000 m on a resistant granite bedrock exposure southeast of the Sierra La Libertad. Collections of *Malosma laurina* and *Xylococcus bicolor* have been recorded from Cerro San Juan in the northern Sierra San Francisco near Misión Santa Gertrudis. The total area of outlying chaparral populations totals 27,956 ha, mostly *Rhus lentii* stands on the Vizcaíno Peninsula.

3.7. Sierra La Giganta and the Cape Region

Chaparral stands are not clearly evident on Google Earth imagery of the Sierra La Giganta. Botanical collections in the mountains south of San Ignacio document several shrub species growing in Mexican-oak woodlands on the crest of the Sierra La Giganta, and along streams below in the thorn-scrub belt (see Figure 4a). The northern Sierra La Giganta (also known as Sierra San Pedro or Sierra Guadalupe), has widespread *Quercus oblongifolia* and *Q. ajoensis* woodland > 1200 m with understory of *Prunus ilicifolia*, *Xylococcus bicolor*, *Heteromeles arbutifolia*, and *Malosma laurina* (cf. De la Cueva *et al.* 2010). The nearby Sierra Agua Verde has scattered *Q. oblongifolia* woodlands with *H. arbutifolia*, *M. laurina* and *Rhus kearneyi*. Isolated oak woodlands grow on north-facing bedrock cliffs, talus, and canyon floors above 1000 m at several summits near 26.66°, 112.14°. Botanical collections record *Prunus ilicifolia*, *Malosma laurina*, and *Garrya silicifolia* along Arroyo El Horno near Cerro Loreto which hosts an isolated woodland of *Q. tuberculata*, the northernmost outpost of this oak on the Baja California Peninsula (see Figure 4b). Rare *Q. tuberculata* woodland also occurs on an unnamed summit at the headwaters of Arroyo El Encinal, and on several summits 25 km south of Loreto (1,375 m, see Figure 4c).

Botanical collections record rare coastal populations of *Malosma laurina* on washes from the Vizcaíno Peninsula to the cape region and *Rhus kearneyi* in desert drainages from the Sierra La Libertad to the Sierra La Giganta (see Figure 1). In the Cape Region, Mexican oak woodland dominated by *Quercus tuberculata* grows > 1,000 m on a few summits of the Sierra Las Cruces (1,243 m), east of La Paz, but chaparral has not been collected there (see Figure 4d). A few colonies grow 15 km south on the crest of Sierra El Novillo. In the Sierra La Laguna (2,067 m, see Figure 4e), *Q. tuberculata* woodland is extensive > 1000 m before giving place to

Q. devia woodland > 1300 m. *Pinus cembroides* (Mexican pinyon pine) is abundant > 1,500 m (e.g., Arriaga *et al.* 1994, Díaz *et al.* 2000, Arriaga and Mercado 2004). *Arbutus peninsularis* and *Q. rugosa* grow near watercourses. Botanical collections record chaparral along watercourses and as understory in pine-oak forest, including *Malosma laurina*, *Prunus ilicifolia*, *Heteromeles arbutifolia*, as well as the congeneric shrubs *Prunus serotina* and *Garrya salicifolia* which occur on the Mexican mainland.

4. PACKRAT MIDDENS, CLIMATE CHANGE, AND CHAPARRAL "SKY ISLANDS"

The biogeography of chaparral sky islands of the desert Baja California Peninsula is a legacy of plant migrations associated with climate change since the Last Glacial Maximum (LGM). Vegetation maps and botanical records presented in this study provide new insight on fossil floras of packrat middens. Plant macrofossil records represent one of the few direct proxy evidences for terrestrial (non-marine) environments. Evidences of climate change have been bolstered by the emergence of studies that infer environmental change from new data sources including high-resolution stable-isotope records from marine sediment cores (Gibbard and Van Kolfsholten 2004) that resolve orbital- and millennial-scale climate oscillation cycles (Dansgaard *et al.* 1993, Broecker *et al.* 1985, Alley and Clark 1999, Zachos *et al.* 2002, Rahmstorf 2002, Alley *et al.* 2003), as well as from global climate models (e.g., COHMAP 1984; and for the Pacific coast, Bartlein *et al.* 1998).

4.1. Fossil floras in LGM–Early Holocene packrat middens

Four Late Pleistocene and Early Holocene packrat midden sites (17.5–10 ka) in the Central Desert and the Sierra San Pedro Mártir record chaparral in areas that now host full-desert vegetation. The dominant species in this region at present include *Larrea tridentata*, *Yucca valida*, *Fouquieria columnaris*, *F. diguetii*, *Pachycormus discolor*, *Machaerocereus gummosus*, *Agave deserti*, *Ambrosia chenopodiifolia*, *Atriplex magdalenae*, *Atriplex polycarpa*, *Ambrosia bryantii*, *Lycium* spp., *Encelia farinosa*, *Opuntia* spp., *Ferocactus* spp., and *Jatropha cuneata* (Wiggins 1980, Rhode 2002). This is comparable to Late Holocene midden plants and arthropod fauna recorded near Cataviña (1.8 ka; Clark and Sankey 1999, Sankey *et al.* 2001).

Packrat middens show two trends in Late Glacial chaparral biogeography: lower altitudinal zonation, and species extensions to lower latitudes. A full Glacial midden NW of Santa Inés dated at 17.5 ka was found at 550 m elevation in granite bedrock terrain that characterizes the Cataviña region (Wells 2000). This midden recorded *Pinus quadrifolia*, *Juniperus californica*, *Adenostoma fasciculatum*, *Quercus turbinella*,

Prunus lyonii, and *Eriodictyon angustifolium*. Based on midden abundances, the dominant species are *Pinus quadrifolia* and *Juniperus californica*, followed by *Adenostoma fasciculatum* and *Quercus turbinella*. Another midden found by Wells (2000) in a rock shelter at 594 m in volcanic rock NW of Misión San Fernando at lat. 30°, dates to the Pleistocene–Holocene transition at 10–10.2 ka. Species recorded in the midden are *Juniperus californica*, *Adenostoma fasciculatum*, *Quercus turbinella*, *Prunus lyonii*, and *Arctostaphylos glandulosa*. Based on abundances, the dominant species was *Juniperus californica*, followed by *Adenostoma fasciculatum* and *Quercus turbinella*. This area presently has sparse chaparral cover of *Xylococcus bicolor* and few *Juniperus californica*. A third midden, found at the base of a 3-m high basalt outcrop in the western Sierra San Francisco at 780 m (Rhode 2002), ca. 300 km south of Cataviña, was dated to Late-Pleistocene, possibly Younger Dryas, with a carbon date of 10.2 ka calibrating to 12.4–11.5 ka. This midden recorded *Juniperus californica*, *Arctostaphylos peninsularis*, and *Malosma laurina*. No desert shrubs were recorded in these middens. Thirty-eight middens at three localities at 650–900 m on the eastern escarpment of the Sierra San Pedro Mártir show vegetation change spanning the past 33 ka (Holmgren *et al.* 2011). They found pinyon woodland 300–500 m below modern stands mapped in Minnich and Franco-Vizcaíno (1998), and Minnich *et al.* (2000). Full Glacial midden species are all found at nearby higher elevations including *Pinus monophylla* (*californarium*), *Juniperus californica*, *Arctostaphylos* spp., *Cercocarpus betuloides*, *Quercus chrysolepis*, *Q. Cornelius-mulleri* (*turbinella-john-tuckeri*) and *Rhus* spp. Desert taxa replaced pinyon woodlands beginning 14 ka.

4.2. Evidence of Late Pleistocene moist climate in surface hydrology and Glaciation

Until recently, midden biota was used as a primary source of evidence in the reconstruction of past environments. The occurrence of chaparral at lower elevations and lower latitudes in the Late-Pleistocene is supported by geomorphic evidences of greater landscape surface water in northern Baja California and the southwestern USA that is broadly consistent with stable isotope records of GRIPP /Vostok ice cores and marine cores (Rahmstorf 2002). These records show that moist LGM climates persisted globally until ca. 14 ka, with another episode at 12.5–11.5 ka (Younger Dryas). Moist climates also persisted in central Baja California during the Milankovitch solar maximum of the Early Holocene to ca. 7 ka. Laguna San Felipe (“Laguna del Diablo”) was a pluvial lake beginning at 34.0 ka. Planktonic saline-water diatoms were present from 34 to 28 ka and lacustrine conditions persisted until 12.0 ka, but the lake bed may have been dry in the Younger Dryas (11.0 to 10.0 ka; Ortega-Guerrero *et al.* 1999). In the Mojave Desert of southern California, high stands supported by

runoff from the Owens, Amargosa and Mojave Rivers occurred between 31 and 18 ka, with high persistent lakes from 26 to 16 ka. Most lakes had another high stand at ca. 12 ka (Benson *et al.* 1990, Enzel *et al.* 2003, Wells *et al.* 2003, Anderson and Wells 2003). Lake Elsinore, in coastal southern California, was an overflowing lake during the LGM from 19.2 to 17.2 ka, followed by drying through the Late Glacial/Holocene transition to 9.4 ka (Kirby 2005).

In the Sierra Nevada, cosmogenic dating of moraines in the Tioga series at Bishop Creek indicate that glaciers extended to the base of the mountains from 28 to 17 ka, then retreated abruptly to the crest of the range at 15.0–14.5 ka, followed by the minor Recess Peak advance at 13.5 ka (Gillespie and Zehfuss 2004, Phillips *et al.* 2009). Moraines on Mt. San Gorgonio in the San Bernardino Mountains of southern California, the southernmost mountain glaciation in the USA, recorded advances at 20 and 16 ka, and recessional moraines at the base of cirque headwalls at 12.5 ka (Owen *et al.* 2003). Moist climates along the Pacific coast of California and Baja California are attributed to the southward displacement of the polar jet stream, but is this the case in Baja California below lat. 30°N? We looked at this question from the standpoint of midden studies that use climate analogies, the cistern effect of midden habitats, chaparral species, and global paleocirculation.

4.3. Midden paleo-vegetation and "climate analogues"

Paleo-vegetation and climate interpretations from early packrat midden studies are based on a "vegetation analogy" model that points to locations where vegetation strongly resembles the fossil-species composition of the midden. Differences in climate between the midden and the analogue target are assumed to represent climate change since the midden date. Wells (2000) proposes an analogy between midden vegetation at San Fernando and Santa Inés to the west face of the Sierra San Pedro Mártir where *Pinus quadrifolia* grows in chaparral dominated by *Adenostoma fasciculatum*, *Quercus turbinella* and *Juniperus californica* between 1100 and 2100 m. Wells (2000) recognizes that pinyon pine, junipers and chaparral occur at lower latitudes at Cerro San Luis (Sierra La Asamblea), Sierra La Libertad and Volcán Las Tres Vírgenes. It was deduced that chaparral islands in the Central Desert represent remnants of former continuous distributions due to contagious expansion of *P. monophylla* and associated chaparral from the Sierra San Pedro Mártir.

The analogue for the Sierra San Francisco midden proposed by Rhode (2002) is the "soft" chaparral from Ensenada to San Diego". He concludes that the contents of the Sierra San Francisco midden extend the record of juniper and other chaparral taxa ca. 400 km further south of their present distributions in southern California and northern Baja California. Based on where *Juniperus californica* grows today in

the mountains of southern California, it was inferred that the Late Glacial climate in the Sierra San Francisco was mediterranean, with an average annual precipitation of 25 cm, compared to present-day values of 10–15 cm, and with a larger component of winter precipitation. Based on a comparison with southern California, mean annual temperature was 15°C, and average temperatures were 5–6°C colder in winter and 1–2°C colder in summer.

The interpretation of climate change from paleobotanical evidence is confounded by circularity, because plants and climate are not treated independently. The vegetation analogy method also relies on the now discredited Clementsian notion that species assemblages move in consort (Clements 1916). The LGM-Holocene vegetation history in the western USA, as seen in high-resolution taxonomic records from packrat middens, clearly shows that individual species each have independent histories of migration and distribution, thus resulting in temporally loose, changeable vegetation assemblages (Van Devender 1990, Davis and Shaw 2001). In addition, the most geographically widespread species adapt to broad environmental diversity through genetic variability and physiological plasticity of populations, limiting the precision of inferences with regard to paleoclimate. Hence, without spatial baselines of paleo-vegetation, a site-specific choice of analogue vegetation amounts to space-for-time substitution. This incorporates no baseline except the specific species assembly of the midden, which is difficult to generalize spatially or temporally.

But in a larger sense, why choose analogous vegetation near San Diego, as opposed to a nearby place in Baja California much closer to the midden site? The analogue vegetation for the San Fernando and Santa Inés middens is in the Sierra San Pedro Mártir, where chaparral grows in areas with mean precipitation of 40–50 cm (Minnich *et al.* 2000). But similar chaparral vegetation exists today, with far less precipitation, above 1200 m in the nearby Sierras La Asamblea and La Libertad (see Table 2). *Pinus quadrifolia* presently grows only 30 km upstream from the San Fernando site, compared to 130 km away at the Sierra San Pedro Mártir. Moreover, the possibility of long-distance vicariant dispersal was not considered, even though pinyon nuts and some chaparral fruits are dispersed and cached over great distances by corvids and other birds (Vander-Wall and Balda 1977). Both contagious expansion and vicariant dispersal operate simultaneously, and long-distance dispersal was doubtless made more effective by reduced distance between chaparral islands associated with the downward displacement of *P. quadrifolia* and chaparral species in the past.

The existence of “sky islands” is not necessarily evidence of continuous distributions in the past. Using current evidence, it is not possible to test whether Central Desert chaparral is a consequence of vicariant dispersal or of contagious expansion and retreat. Moreover, the premise of former continuous distributions does not account

for the ecological differences among these pinyons. In northwest Baja California, *P. quadrifolia* grows in dense chaparral on the west slope of the peninsular ranges, while *P. monophylla* grows with desert chaparral on the arid eastern escarpments (Minnich and Franco-Vizcaíno 1998, Minnich *et al.* 2011b). And many chaparral species extend farther south than the San Fernando/Santa Inés midden sites, with *Adenostoma fasciculatum* extending to the Sierra La Libertad, and *Quercus turbinella* to Volcán Las Tres Vírgenes. *Malosma laurina* in the Sierra San Francisco midden, which Rhode (2002) calls a characteristic coastal sage scrub plant, grows throughout the Peninsula to the cape region.

Rather, we propose that the biogeography of chaparral sky islands fundamentally represents the balance between plant migration and selection (Sauer 1988); in this case the southward expansion of chaparral during the LGM, and the selective elimination of chaparral during the Holocene. The most impressive range extensions in the Pleistocene were *Pinus quadrifolia* and *Arctostaphylos glandulosa* from the Sierra San Pedro Mártir (Minnich and Franco-Vizcaíno 1998) to Cataviña and San Fernando, and *A. peninsularis* from the Sierra La Libertad to the Sierra San Francisco. These range extensions of 50 to 100 km also demonstrate the areas of post-Glacial extinctions of these species.

Perhaps the most important findings in midden records are that chaparral grew 500 m lower than the present limits, and the relative impoverishment of chaparral midden materials at the Sierra San Francisco compared to middens at San Fernando and Santa Inés. The latter trend suggests decreasing chaparral abundance and diversity then, as now.

4.4. Habitat bias of rock shelters

All four midden sites were discovered in resistant granite or volcanic bedrock surfaces that act as cisterns. These sites host abnormally moist vegetation that can root into bedrock fractures and thus rely on bedrock runoff from surrounding impermeable rock surfaces. Impervious surfaces also retard evaporation from the regolith. In volcanics, water percolating through porous rock layers can produce springs at the contact with underlying impermeable basement. The midden sites at San Fernando and Sierra San Francisco lie at the base of basalt cliffs. Basalt exposures of the Sierra La Libertad currently exhibit bands of chaparral along contacts, including the lowest stands at the base of basalt outcrops. The Santa Inés site occurs in granite bedrock slopes with local sediment-filled depressions likely kept moist by runoff from surrounding impermeable rock surfaces.

An example of a moist-cistern habitat is a *Quercus chrysolepis* population growing on the rubble of a resistant pluton in the Sierra La Asamblea (see Figure 3b), which

is 175 km from the nearest stand in the Sierra San Pedro Mártir. That habitats in the Cataviña-Santa Inés-Misión Santa Maria region are unusually moist is best evidenced by the occurrence of thousands of dwarf upland populations of blue fan palm (*Brabea armata*) (Minnich *et al.* 2011a). The distribution of the dwarf phenotype is limited to widespread granitic bedrock units in parts of the Sierras La Asamblea and La Libertad, and at three other granite exposures to the north, near the Sierras San Pedro Mártir and Juárez. Chaparral outlier populations frequently occur on granitic bedrock slopes.

The occurrence of fossil middens on bedrock slopes is a generic problem because rock-sheltered sites are necessary for the preservation of paleo-middens from weather. The assessment of vegetation and climate change at midden sites may be appropriate for the specific site if the approach accounts for the presence of abnormally mesic species that rely on bedrock runoff. The regional extrapolation of midden materials in the vegetation analogy method, across many geologic substrates, may lead to conclusions that favor anomalously large changes in vegetation and climate, because bedrock sites are likely abnormally moist (see *e.g.* Salama *et al.* 1994, Singhal and Gupta 1999, Murty and Raghavan 2002, Kosugi *et al.* 2006). Whether midden habitats in granitic or volcanic bedrock may have represented the model distribution of extensive paleo-chaparral, or alternatively, of isolated patches in a milieu of xeric vegetation, cannot be assessed from currently available evidence.

5. MODERN "SKY ISLAND" CHAPARRAL DIVERSITY AND CLIMATE CHANGE

Botanical and map distribution data of chaparral sky islands show large differences in species diversity and life trait properties from north to south despite small climate gradients (see Table 3). At present, mean winter temperatures differ by 5.0°C

TABLE 3. Species composition of chaparral "sky islands" in the Central Desert, and as understory of pine-oak woodland in Baja California Sur (north to south), determined by consulting databases of botanical collections at the San Diego Natural History Museum (SDNHM), the University of California Riverside (herbarium.ucr.edu), the Flora of North America (<http://www.efloras.org>), and Wiggins (1980). Obligate seeders: Ag, *Arctostaphylos glauca*; Cg, *Ceanothus greggii* var. *perplexans*; Cv, *Ceanothus verrucosus*; Non-obligate seeders: Af, *Adenostoma fasciculatum*; Ap, *Arctostaphylos peninsularis*; Co, *Ceanothus oliganthus*; *Arctostaphylos peninsularis*, Ap. Sprouters: Cb, *Cercocarpus betuloides*; Fc, *Fremontodendron californicum*; Gg, *Garrya grisea*; Gv, *Garrya veatchii*; Gs, *Garrya salicifolia*; Ha, *Heteromeles arbutifolia*; MI, *Malosma laurina*; Pi, *Prunus ilicifolia* (*lyonii*); Rc/i, *Rhamnus crocea* (*insula*); Ri, *Rhus integrifolia*; Rl, *Rhus lentii*; Rk, *Rhus kearneyi*; Ro, *Rhus ovata*; Qc, *Quercus cedrosensus*; Qt, *Quercus turbinella*; Xy, *Xylococcus bicolor*. Nonsprouting conifer: Jc, *Juniperus californica*.

TABLE 4. Diversity of chaparral species by life traits.

Location	Obligate Seeder	Sprouter/Seeder	Sprouter	Total
Sierra La Asamblea	2	4	9	16
Sierra La Libertad	2	3	11	16
Sierra San Francisco	0	0	7	7
Volcán Las Tres Vírgenes	1	1	7	9
Isla Cedros	0	1	8	9
Sierra La Giganta				
San Pedro	0	0	5	5
Cerro Loreto	0	0	4	4
Coast	0	0	1	1
Cape (Sierra La Laguna)	0	0	4	4

and mean summer temperatures by only 1.0°C across the Central Desert. Mean annual precipitation is uniformly 10–15 cm at stations on the desert floor, although the proportion of summer precipitation (July–September) increases from *ca.* 17% in the north to 46% at San Ignacio (see Table 2). Global climate models suggest that latitudinal precipitation gradients were stronger in the Central Desert (Bartlein *et al.* 1998) because the closer year-round proximity of the jet stream both increases winter precipitation in the north, and decreases monsoon precipitation in the south. Hence, species differences between sky islands may represent Late Glacial selection pressures contributing to chaparral migrations and modern distribution patterns.

The higher summits of the Sierras La Asamblea and La Libertad are covered with dense stands of floristically rich chaparral that rival those in mediterranean northern Baja California and California. These populations comprise both obligate “seeders” (non-sprouters if defoliated by fire) in the genera *Ceanothus* and *Arctostaphylos*, and nonobligate seeders in *Adenostoma*; as well as sprouting, fleshy-fruited shrubs in *Garrya*, *Quercus*, *Heteromeles*, *Rhamnus*, *Prunus*, *Rhus*, *Malosma*, *Cercocarpus*, and *Xylococcus* which are characterized by long-range seed dispersal through animal transport of fleshy fruits, as well as wind-dispersed seed (*Cercocarpus*) (see Table 4). In contrast, the Sierra San Francisco, Volcán Las Tres Vírgenes, and Isla Cedros all have floristically poor, open chaparral dominated by “sprouters” in *Garrya*, *Quercus*, *Heteromeles*, *Prunus*, *Malosma*, and *Rhus*. The seeding species *Ceanothus greggii* var. *perplexans* and *C. oliganthus* are restricted to the upper catchments of Volcán Las Tres Vírgenes, and *C. verrucosus* to the fog zone of Isla Cedros. Even fewer chaparral

species, entirely fleshy-fruited sprouters, grow sparingly at lower elevations of the Central Desert, especially on granite bedrock surfaces and talus slopes below basalt caprock mesas. The same resprouting species also occur farther south in Mexican pine-oak woodland and in arroyos in the Sierra La Giganta and the cape region. Some shrubs, such as *Malosma laurina* and *Rhus kearneyi*, transcend the entire Peninsula (see Table 3).

These patterns represent a continuation of the same trends in species composition that occur in southern California. Near Los Angeles, California Vegetation Type Maps (VTM) show that chaparral has an abundance of obligate seeders including *Ceanothus megacarpus* in coastal ranges, *C. crassifolius* in the Transverse Ranges and *C. greggii* var. *perplexans* in the peninsular ranges (Weislander 1938). At lower elevations near Los Angeles and farther south, the chaparral in San Diego County and northern Baja California southward to the Sierra San Pedro Mártir is dominated by non-obligate seeders (resprouters and seeders) such as *Adenostoma fasciculatum* and *A. sparsifolium*. Semiarid "petron" chaparral growing along the arid leeward slopes of the southern California mountains and the Sierras Juárez and San Pedro Mártir, with mean annual precipitation comparable to the Central Desert sky islands, is dominated by sprouting species *Quercus turbinella*, *Q. Cornelius-mulleri*, *Cercocarpus betuloides*, *Prunus ilicifolia*, *Rhamnus ilicifolia*, and *Rhus ovata*.

We propose that in the Central Desert, moist Glacial climates selected for seeding chaparral species, due to high productivity and fuel-accumulation rates, and consequent burning. The drier climate of the Holocene selectively eliminated seeders, with sprouters persisting in wet sites, even to the lowest elevations, through efficient dispersal and colonization. Chaparral "seeding" species are characterized by punctuated mass establishment of seedlings from refractory seed immediately after fires. Impermeable and indigestible refractory seed not only links germination to disturbance, but also discourages long-distance dispersal by birds and mammals. However, locally dispersed seed banks result in mass recruitment and species dominance that overwhelms fleshy-fruited sprouters. In the north, "seeders" may still benefit from high rates of burning due to higher winter rainfall and productivity. Seeders may also benefit from widespread water-retaining granitic substrate, as opposed to the porous volcanics that dominate the Sierra San Francisco and fresh lava flows of Volcán Las Tres Vírgenes. In the south, limited productivity lengthens fire intervals, which selects against seed banking, but fleshy-fruited sprouters reproduce continuously at low rates and are dispersed by birds and other animals. Sprouters adapt to large climate variability by efficient vicariant seed dispersal and recolonization of suitable habitat.

5.1. Climate of the Central Desert and Global Paleo-Circulation

It is useful to establish the equatorward limit of moist Pacific coast LGM climate from first principles of atmospheric physics, which may help to constrain conclusions of past chaparral elevational zonation and latitude limits in the central Peninsula. Here we examine atmospheric lapse rates, the role of the coastal marine layer, and limits of the jet stream precipitation based on the conservation of momentum and vorticity of global atmospheric circulation.

5.2. Atmospheric lapse rates

Past elevational limits of chaparral can be estimated from the atmospheric lapse rate; that is, the decrease in temperature with altitude. In the Central Desert, the current lower limit of chaparral is virtually isotropic, ranging from 1,200 m in the Sierra La Asamblea to 1,350 m at Volcán Las Tres Vírgenes. Packrat middens document a downward zonation of chaparral by 500 m. The atmospheric lapse rate is globally uniform at *ca.* 6.5°C 1,000 m⁻¹ (International Civil Aviation Organization 2010); this is clearly seen in climatological data for the mountains of southern California and northern Baja California (Minnich 2001, 2007). During peak evapotranspiration (ET) in summer, ambient temperatures at 850 mbar (*ca.* 1500 m) range from 23–25°C and are isotropic through northern Baja California and southern California (National Climatic Data Center 2010).

Because mean lapse rates represent the integration of marine and continental evapotranspiration, subcloud adiabatic mixing, and latent heat-flux warming aloft from condensation and precipitation (Barry and Carleton 2001), we assume that the lapse rate was the same in full Glacial climates as at present. Hence, temperature departures since the Last Glacial Maximum were broadly dependent on departures in sea-surface temperature in the tropical oceans of that time. Stable-isotope records of marine and ice-sheet environments give temperature decreases of 3°C in tropical seas during the LGM (Rahmstorf 2002). This departure is consistent with glacier mass-balance modeling and geomorphic evidences from tropical glaciers (Hostetler and Clark 2000, Kaser and Osmaston 2002). Since air-mass thermal structure is isothermal at constant pressure (\approx altitude) in the tropics, temperature departures in the Peninsula since the Glacial Maximum were likely also *ca.* 3°C cooler than at present. Using the standard lapse rate, we can infer that eustatic sea-level lowering from the build-up of ice sheets increased the elevation of local mountains \sim 100 m, producing an additional local cooling of *ca.* 0.6°C. Thus, based strictly on temperature and evapotranspiration, a 3–4°C cooling of the local troposphere would lower the 25°C isotherm *ca.* 500–700 m, consistent with the elevation departure of chaparral packrat middens.

5.3. The coastal marine layer and Isla Cedros

Chaparral on Isla Cedros, and also in the coastal regions of northern Baja California, grows to as low as 300 m, nearly 1000 m below the present limits of chaparral in the Central Desert. This disparity is a result of the cool, moist Pacific marine layer, a steady-state feature that forms from the cooling and moistening of the tropospheric boundary layer overlying the cold, upwelling California Current. Sea-surface temperatures at the latitude of the Central Desert average *ca.* 20°C. The marine layer, which is associated with extensive coastal low clouds (stratus), is capped by a strong thermal inversion that separates it from warm and dry subsiding air masses aloft.

In the present climate, the marine layer fluctuates from 300 to 800 m depth in summer, restricting its influence to the immediate coast. We suggest that a strong summer jet stream produced by the Laurentide ice sheet in the LGM, as modeled in global climate models (*e.g.*, Bartlein *et al.* 1998), would produce a climatological increase in the depth of the marine layer, and more extensive penetration of cool, moist air and reduced ET in the central desert interior than at present. Given fixed standard lapse rates, a deep full Glacial marine layer (*ca.* 20°C at sea level and with mean depth > 1,000 m) would have produced larger negative temperature departures, from the coast to the base of the mountains, than from global cooling alone.

We hypothesize that during Glacial Maximum, summer climates in the Central Desert were comparable to deep marine-layer conditions usually seen in April and May in the present climate. Strong negative-temperature departures would expand chaparral habitat nearly to sea level and inland to the sierras, as suggested by Pleistocene packrat midden records. A modern analogy occurs at the latitude of the Sierra San Pedro Mártir, where chaparral gives place to coastal sage scrub below 1000 m, but coastal sage scrub turns to chaparral near the coast at Colonet and Eréndira. Marine layer climate may help to explain the presence of the Catalina Cherry trees (*Prunus lyonii*) of the southern California Channel Islands in the San Fernando and Santa Inés middens (Wells 2000).

5.4. Southern limit of jet stream precipitation in full Glacial Baja California

Global lake-stand data indicate that mediterranean-climate regions along the southern margin of the Northern Hemisphere polar-front jet stream experienced heavier precipitation during the LGM than at present (Street and Grove 1979, Vaks *et al.* 2006). This is consistent with global climate models, which show a southward dislocation of the jet stream from present climate (COHMAP 1984, Bartlein *et al.* 1998). A critical question is whether the southward displacement of the jet stream by the Laurentide ice sheet would have brought greater precipitation to the Central Desert. Rainfall along the Pacific coast is almost exclusively linked to mechanical

atmospheric lift of stable air from positive vorticity advection in cold frontal disturbances ahead of troughs in the jet stream. In a classical study of extratropical cyclones in California, Elliot (1958) documented the deepening of the marine layer that merges with upper cloud layers before the passage of cold fronts, giving rise to extensive cloud shields and long periods of steady precipitation.

The climatological dislocation of the jet stream has an equatorward limit based on conservation of angular momentum and absolute vorticity. Frictional loss of atmospheric angular momentum in tropical easterly flow is transferred as frictional gain in westerly flow at high latitudes, thus resulting in a net global exchange of angular momentum ($mv = 0$). To conserve momentum, equatorward expansion of the westerlies would require the strengthening of tropical easterlies, in effect constraining the equatorward extent of the westerlies (Palmén and Newton 1969, Barry and Carleton 2001). The jet stream also has a theoretical limit near latitude 30°N due to the conservation of absolute vorticity, which is supported by data on the latitudinal atmospheric profiles of geostrophic zonal winds. To conserve absolute vorticity, atmospheric cyclonic curvature and shear in troughs increases equatorward, due to the decreasing vorticity contribution of the coriolis force (Barry and Carleton 2001). For the jet stream to reach the equator would require that the contribution of curvature and shear to vorticity approaches infinity. The limit varies with Rossby wave number, and ranges from 35°N (high Rossby wave number) in zonal (west-east) atmospheric flow, to 30°N (low Rossby number) in meridional (north-south) flow.

These conservation principles assert that *the equatorward limit of the jet stream at 30° must be retained regardless of climate state*, modern or Glacial. Hence, for storms passing through the Central Desert at the LGM, a potential increase in precipitation in Baja California would have been inhibited by the region's equatorward position to the jet stream. The resulting negative vorticity advection and atmospheric subsidence would detach the marine layer from upper cloud layers in the frontal zone, thus virtually precluding precipitation. The marine layer would then move anticyclonically in northeast flow, away from the Peninsula, as part of the trade wind layer of the subtropical North Pacific Ocean. Similarly, the equatorward limit of reliable jet stream precipitation in the Mediterranean climate of Chile is also at 30° latitude (Dirección Meteorológica de Chile 2010), even though the southern hemisphere jet stream is stronger under the current ice-sheet climate, than in the northern hemisphere.

We hypothesize that increases in precipitation in the Central Desert during Glacial times were small and latitude dependent, with cooler temperatures and reduced ET largely contributing to moister climates and interior lakes. Laguna San Felipe (~lat. 31°) was closer to the jet stream and likely received increased frontal

precipitation and runoff from orographic precipitation on the Sierra San Pedro Mártir, but not at levels of the Mojave Desert (Enzel *et al.* 2003), as evidenced by the lack of shorelines that would indicate deep lakes. Large precipitation changes are unlikely at Laguna Chapala (lat. 29.4°), which now forms shallow lakes, even with modest precipitation variability. The playa lies in a volcanic field of extensive basalt flows and hardpan soils that are conducive to flash flooding. The sensitivity of Laguna Chapala to variability in full Glacial climate is made uncertain by its low sill level. Although the western playa receiving runoff from Laguna Chapala has a sill level of 15 m above the lake bed, shorelines indicative of deep lakes are again not evident on Google Earth, nor at other playas in the volcanic field. As suggested by packrat midden records, Late Pleistocene chaparral extended south of present distributions, but this trend is phased with minimal increase in precipitation. Chaparral expansion was instead encouraged by reduced temperature and evapotranspiration, bolstered by more robust marine layer penetration onto the Peninsula. These trends are supported by a stronger summer jet stream in an ice sheet climate, as predicted by global climate models. An analogy of LGM summer climate would be present-day climate in May and June before the jet stream retreats to Canada.

5.5. Climate and vegetation in the Early Holocene solar maximum

The LGM was followed by the Milankovitch solar maximum, the warmest phase of the Holocene with more extensive global monsoons than present, including the North American monsoon (*e.g.*, Poore *et al.* 2005). Moist climate, sediment-accumulating lakes, and widespread chaparral persisted in the Central Desert into the Early Holocene (Metcalf 2006), at a time when pluvial lakes had desiccated or disappeared in the Great Basin (Street and Grove 1979). Laguna Chapala accumulated lacustrine sediments from 10.0 to until 7.45 ka (Davis 2003), while Laguna San Felipe was a small lake until 7.0 ka (Ortega Guerrero *et al.* 1999). Early Holocene lakes have been attributed to increasing winter precipitation, in part due to catastrophic drainage of Lake Agassiz into the North Atlantic, which would produce stronger westerlies and more upwelling (Van Devender 1990, Davis 2003). However, the relatively small water volume of ice-sheet lake discharges should have had only ephemeral influence on sea-surface temperatures in the Atlantic, as compared with ice-sheet purges (Heinrich events) (MacAyeal 1993, Alley and MacAyeal 1994). Van Devender (1990) proposed an increase in Early Holocene winter rainfall and cool-summer vegetation in Baja California, due to strengthening of the California current and upwelling. Colder seas during a period of warming atmosphere, however, would produce stronger temperature inversions and diminish precipitation (*cf.* Ingram 1998). This is supported by pollen data that indicate drier-than-present climate in

the Oregon Cascades (Long *et al.* 1998), and results from global climate models that show the jet stream moving northward with the retreating ice sheets from the LGM to the Early Holocene (COHMAP 1984, Bartlein *et al.* 1998). Only a poleward shift of the jet stream is consistent with both drier climate in Oregon (Long *et al.* 1998) and wet climate in Baja California. Studies of the Mid-Holocene in California provide evidences of dry climate. For example, submerged pine stumps dated from 6.3 to 4.8 ka (cal) reveal that Lake Tahoe was below sill heights (Lindstrom 1990), and glaciers may have been entirely absent in the Sierra Nevada during much of the Holocene (Clark and Gillespie 1997, Phillips *et al.* 2009).

Simulation of the North American monsoon by Bartlein *et al.* (1998) shows that Milankovitch forcing would result in increasing sensible and convective heating over the southwest USA deserts, and monsoon precipitation along the Baja California Peninsula. An enhanced summer monsoon is parsimonious with earlier lake disappearances northward from Baja California (7.0–7.45 ka) to Arizona and California (8–9.0 ka), and the Great Basin (10.0 ka) because monsoon moisture is progressively depleted northward from the Gulf. At the same time, high lake stands may arise from singular flood-producing events of a single season (Enzel *et al.* 1992). For example, lacustrine conditions in the region could be produced by a slight increase in the frequency of tropical cyclones.

We conclude that Late Pleistocene chaparral survived into the warmer Early Holocene by responding to increased summer rain of the North American monsoon linked to the Milankovitch solar maximum (Metcalf 2006). This view is consistent with the northward retreat of the jet stream as simulated in global climate models, and high monsoon lakes in Old-World deserts in association with the Milankovitch solar maximum (Street and Grove 1979, COHMAP 1984).

5.6. Vegetation lag time and phenological plasticity

Fossil midden records at San Fernando (Wells 2000) and Sierra San Francisco (Rhode 2002) at the warmer Late Pleistocene-Holocene transition may have a legacy of plant distributions lagging behind climatic fluctuations, even at scales of millennia. In long-lived communities such as chaparral, extirpation to desert vegetation may require centuries or even millennial-scale climate change (cf. Thompson 1988, 1990, Nowak *et al.* 1994). The vegetation-lag hypothesis is not trivial, considering recent discoveries of chronic, abrupt century-to-millennial scale climate change in association with Dansgaard-Oeschger cycles and Heinrich events in full Glacial climates (*e.g.*, reviews in Rahmstorf 2002, Alley *et al.* 2003, Seidov and Maslin 1999, 2001, Schmittner *et al.* 2002). The combination of migrational lags and

millennial-scale climate changes may produce only gradual, buffered plant migrations against climate fluctuations.

The Early Holocene persistence of California chaparral may be related to the capacity of evergreen shrubs to be phenologically plastic to precipitation at any season. Plasticity is adaptive because of the advantage conferred by flexibility in the initiation and duration of growth, in response to an unpredictable environment. For example, an August tropical cyclone in southern California (5 cm precipitation) was followed by chaparral growth, flowering and fruiting (Minnich 1985). Most chaparral congeners live in summer-rain climates in Arizona, central and southern Baja California, and mainland Mexico. Flowering data from herbarium collections show growth flushes in spring in California; but flushes occur in spring and early fall in Arizona and central Baja California, and fall in Mexico, the late-season flush being a consequence of summer rain. Moreover, the geographic range of chaparral from winter-rain climates in California to summer-rain climates in Mexico suggest that sclerophylly is a generalized adaptation to drought, regardless of season (Minnich 1985, Barbour and Minnich 1990, Valiente-Banuet *et al.* 1998). Midden records suggest that chaparral persisted into summer-rain climates during the Milankovitch solar maximum. Phenotypic plasticity with climate change may explain the disjunct distributions—west and east of the Gulf of California—of the closely related or possibly conspecific *Quercus peninsularis* versus *Q. emoryi*, and *Q. engelmannii* versus *Q. oblongifolia*.

5.7. "Missing" chaparral in Baja California Sur

Wells (2000) points to an "isolating barrier" to chaparral at San Ignacio in the mid-Peninsula, noting that only a few sprouting chaparral species occur in the nearby Sierra La Giganta, only 50 km south, despite summit elevations of 1,600 m. He speculates that "pinyon pines and chaparral" never migrated past Volcán Las Tres Vírgenes during the LGM. The composition of oak woodlands also shifts from California to mainland Mexico species with decreasing latitude (see Table 5). The Sierra La Asamblea hosts conspecifics to the Sierra San Pedro Mártir including *Quercus chrysolepis* and *Q. peninsularis*. Only *Q. peninsularis* grows in Sierra La Libertad, while *Q. oblongifolia* and *Q. ajoensis*—both widespread in NW Mexico, Arizona and New Mexico (Felger 2001)—occur in the Sierra San Francisco and northern Sierra La Giganta (Sierra San Pedro). *Q. tuberculata*, another widespread drought-deciduous oak in northern Mexico, dominates oak woodlands on Cerro Loreto in the central Sierra La Giganta and pine-oak forest in the cape region in association with *Q. devia*.

TABLE 5. Distribution and species composition of pine-oak woodlands. Species: Qcr, *Quercus chrysolepis*; Qpn, *Quercus peninsularis*; Qob, *Quercus oblongifolia*; Qaj, *Quercus ajanensis*; Qtb, *Quercus tuberculata*; Qb, *Quercus brandegei*; Qdv, *Quercus de-via*; Qru, *Quercus rugosa*; Apn, *Arbutus peninsularis*; Pm, *Pinus monophylla*; Pr, *Pinus radiata*; Pc, *Pinus cembroides (lagunae)*.

Region/ species	Woodland oaks and other species								Conifers			
	Qcr	Qpn	Qob	Qaj	Qtb	Qb	Qdv	Qru	Apn	Pm	Pr	Pc
S. La Asamblea	x	x		x						x		
S. La Libertad		x										
S. San Francisco			x	x								
V. Las Tres Virgenes				x								
Isla Cedros											x	
S. La Giganta N (S. Pedro/ Guadalupe)			x	x								
S. La Giganta S (C. Loreto)					x							
Cape (S. La Laguna)			x		x	x	x	x	x			x

Several factors appear to contribute to the disappearance of chaparral at 27.5°N. lat. The southward displacement of the summer jet stream to lower latitudes by the Laurentide ice sheet, predicted in global climate models of the LGM, is unlikely to increase winter precipitation at this latitude, and also diminishes warm-season monsoon precipitation (Bartlein *et al.* 1998). Hence, Late Glacial climate in the southern Peninsula may have been drier than present. We further suggest that the southern limit of chaparral, present and past, is also related to the position of the large Vizcaíno Peninsula, which turns the California current and the marine layer westward into the open Pacific, thus resulting in discontinuously warmer waters along the Pacific coast south of Punta Eugenia. While sea breezes bring cool northwest winds to the Peninsula as far south as the Sierra San Francisco, southwesterly winds bring warmer, more unstable Pacific air masses and higher orographic monsoon

precipitation to the Sierra La Giganta and the cape ranges. The importance of the Vizcaíno Peninsula on modern climate is supported by present-day distribution of thorn scrub, which occurs locally as far north as the Sierra San Francisco but is widespread south of San Ignacio. Higher summer rain, under high ET, selects for shallow-rooted, summer active/drought-deciduous mesophyllous thorn scrub. In drought, thorn scrub persists near dormancy, thus placing this life strategy at an advantage over evergreen chaparral. Drought-deciduous trees may also compete against sun-demanding evergreen shrubs. The presence of chaparral along arroyos may be related to fluvial disturbances that denude thorn scrub, facilitating access to regolith water in the dry season, and thus encouraging chaparral recruitment. Chaparral also survives above the thorn-scrub belt on the highest peaks in drought-deciduous Mexican oak parklands. The Early Holocene Milankovitch solar maximum may have increased summer precipitation compared to present climate, and encouraged the expansion of thorn scrub and Mexican oak woodlands northward along the sierras of the southern Peninsula, but fossil evidence is not available.

6. CONCLUSIONS

The evaluation of chaparral biogeography since the LGM requires modern baseline data of its present distribution and species composition. We present the first detailed maps, interpreted from Google Earth imagery, of mediterranean chaparral and Mexican pine-oak woodland growing in the deserts of the Baja California Peninsula south of lat. 30°N. These vegetation maps can be refined in subsequent research. We show that chaparral is unexpectedly widespread in the Central Desert, occurring on the four highest sierras and on Isla Cedros. But small outlying populations also grow at lower elevations, especially on the Vizcaíno Peninsula, and on volcanic mesas, bedrock slopes, and along washes. Several species extend into Baja California Sur as understory to Mexican oak woodlands.

The interpretation of climate change from paleobotanical evidence in middens is confounded by circularity because plants and climate are not treated independently. Moreover, packrat middens are selectively preserved from weathering in abnormally moist bedrock habitats, in effect rock cisterns; thus broadscale interpretations from local middens may yield overestimations of climate change. The most important findings in Pleistocene midden records are that chaparral grew 500 m lower in elevation, and that several chaparral species had ranges 50 to 100 km further south than at present.

We suggest that changes in climate since the Last Glacial, especially of total precipitation, have been modest in the Baja California Peninsula. It is likely that moister

climates resulted instead from cooler temperatures and reduced evapotranspiration. We propose that moist LGM climate selected for seeding—as opposed to sprouting—species of chaparral due to increasing productivity, fuel accumulation rates, and burning. Drier climate in the Holocene selectively eliminated seeders, with sprouters persisting in wet sites, even to the lowest elevations, through efficient dispersal and colonization. The “isolating barrier” to chaparral migration south of Volcán Las Tres Vírgenes may have been due to the seaward diversion of the upwelling California current by the Vizcaíno Peninsula, with corresponding increases in summer rain and thorn scrub vegetation. In the southern Peninsula, full Glacial climates may have been arid year-round.

Recent global warming is unlikely to have immediate effects on the chaparral sky islands of the Central Desert. The dynamics and migrations of long-lived chaparral species and oak woodlands lag behind climatic fluctuations, perhaps at scales of millennia. Moreover, evergreen shrubs are phenologically plastic to precipitation at any season, making them adaptive in an unpredictable environment, as evidenced by the distribution of many genera, both in the winter-rain mediterranean climate along the Pacific coast and in the summer-rain tropical climate of Mexico.

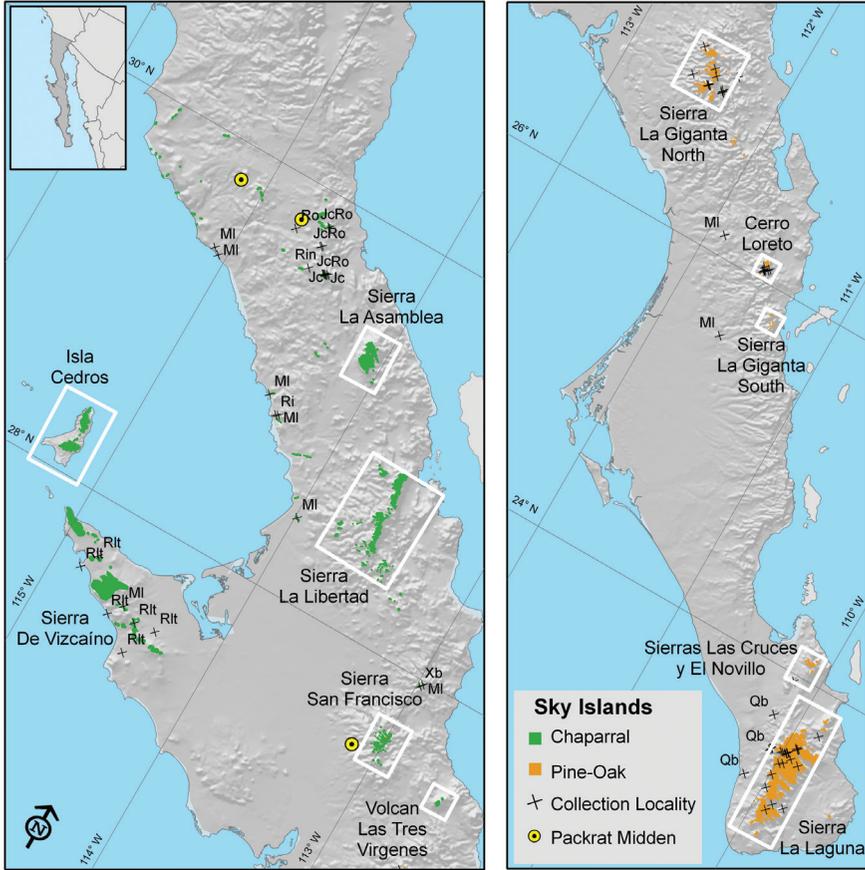


FIGURE 1. The distribution of chaparral and pine-oak "sky islands" in the central and southern Baja California Peninsula. For names of species see Tables 3 and 5.

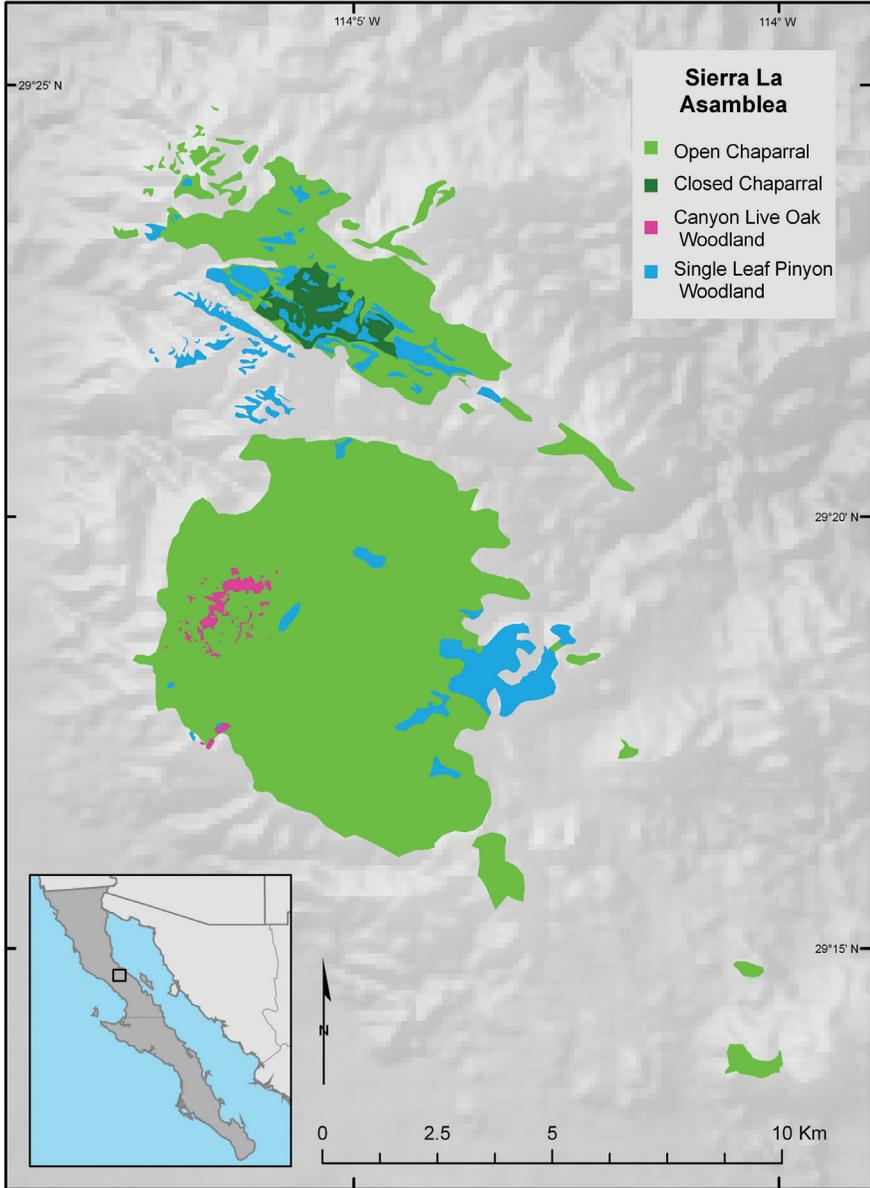


FIGURE 2. Detailed distribution of chaparral and oak woodlands in the Central Desert: (a) Sierra La Asamblea; (b) Sierra La Libertad; (c) Sierra San Francisco; (d) Volcán Las Tres Vírgenes; (e) Isla Cedros. FIGURE 2A (ABOVE)

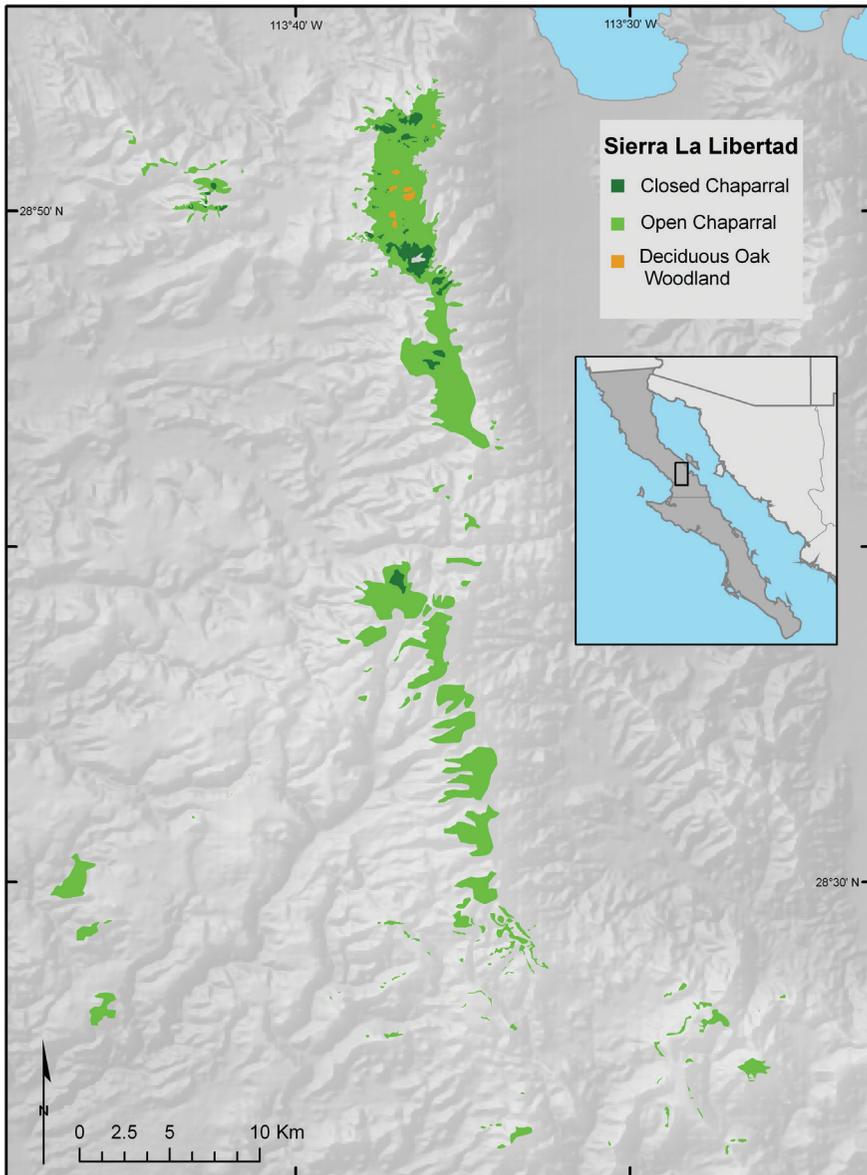


FIGURE 2B.

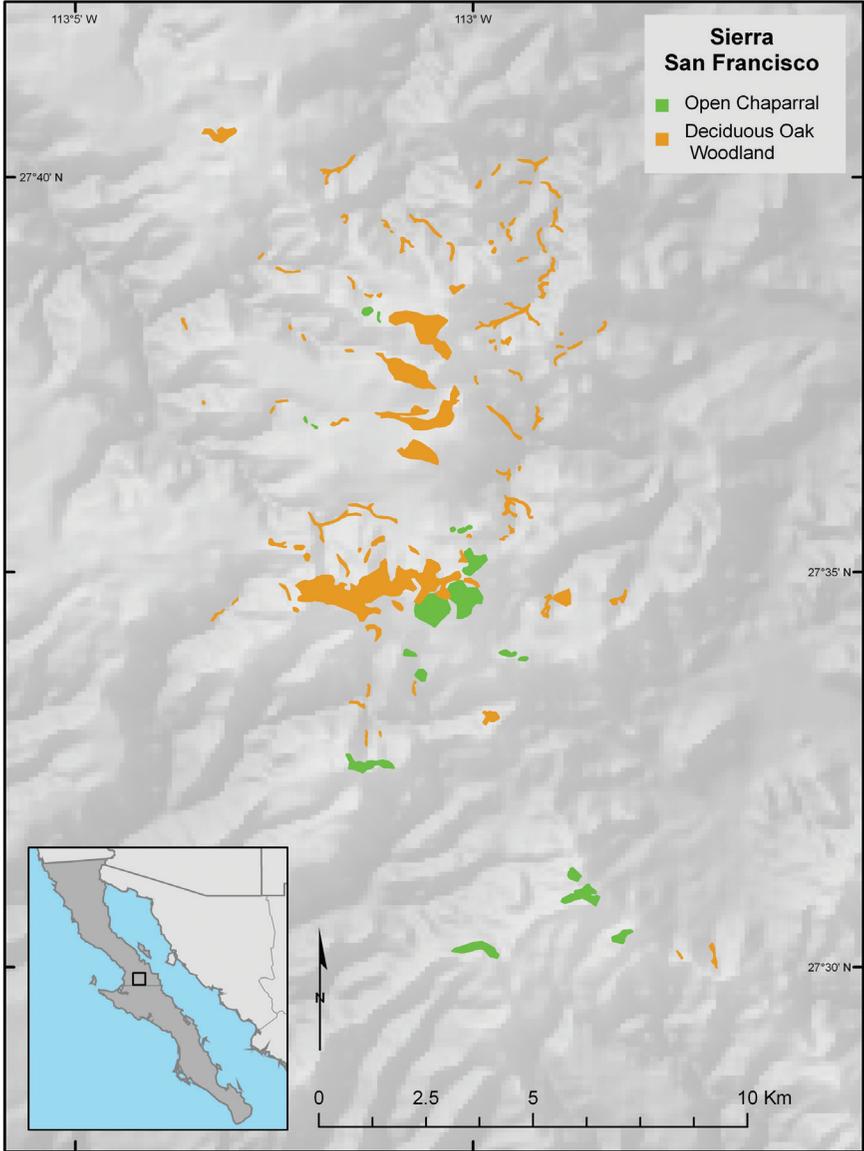


FIGURE 2C.

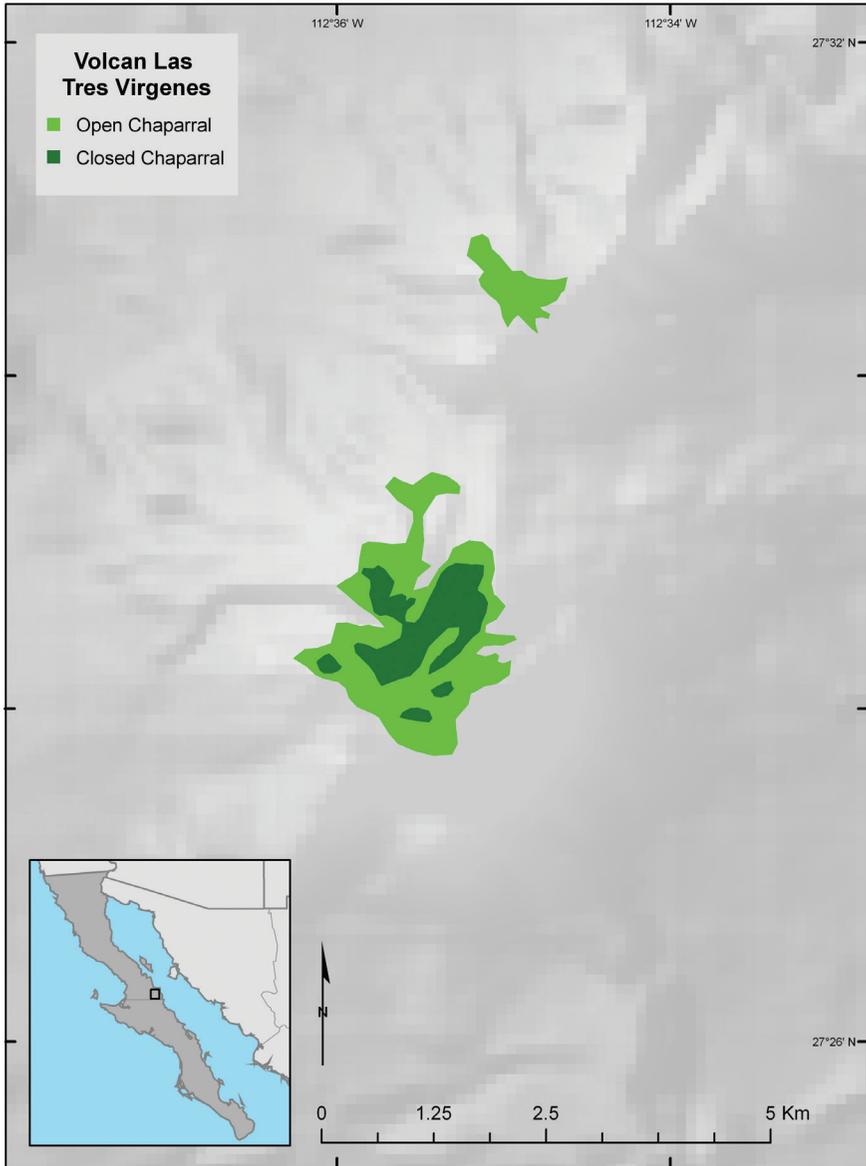


FIGURE 2D.

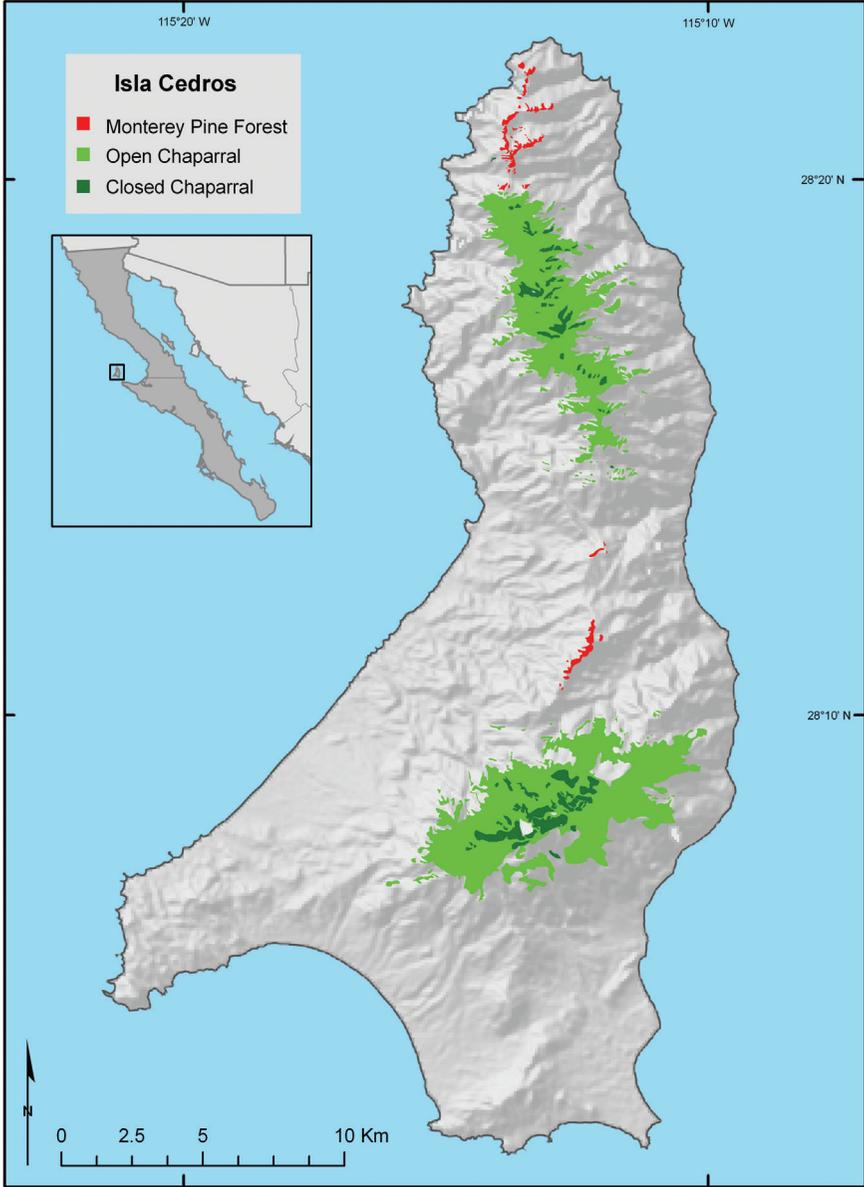


FIGURE 2E.



FIGURE 3A (ABOVE). Chaparral on Cerro San Luis in the Sierra La Asamble. *Adenostoma fasciculatum* (chamise) in the foreground growing with taller *Pinus monophylla*. The Gulf of California is in the distance (photo courtesy of K. Geraghty).

FIGURE 3B (BELOW). Resistant bedrock granite slope with *Quercus chrysolepis*, *Pinus monophylla*, and *Brabea armata* on the Sierra La Asamble plateau (photo courtesy of K. Geraghty).

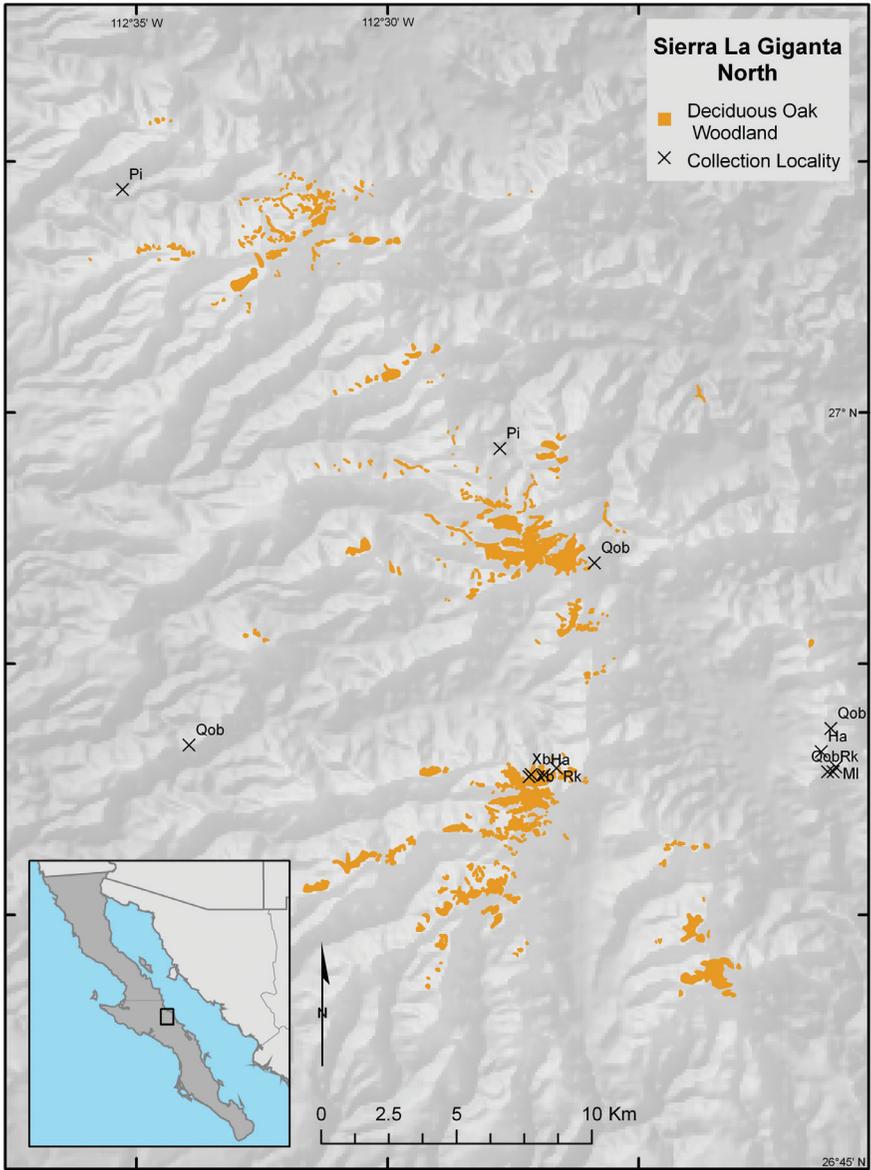


FIGURE 4. Detailed distribution of Mexican pine-oak woodlands in the Sierra La Giganta and the cape mountains: (a) Sierra La Giganta north (also known as Sierra San Pedro or Sierra Guadalupe); (b) Cerro Loreto; (c) Sierra La Giganta south; (d) Sierras Las Cruces and Novillo; (e) Sierra La Laguna. FIGURE 4A (ABOVE). For names of species see Tables 3 and 5.

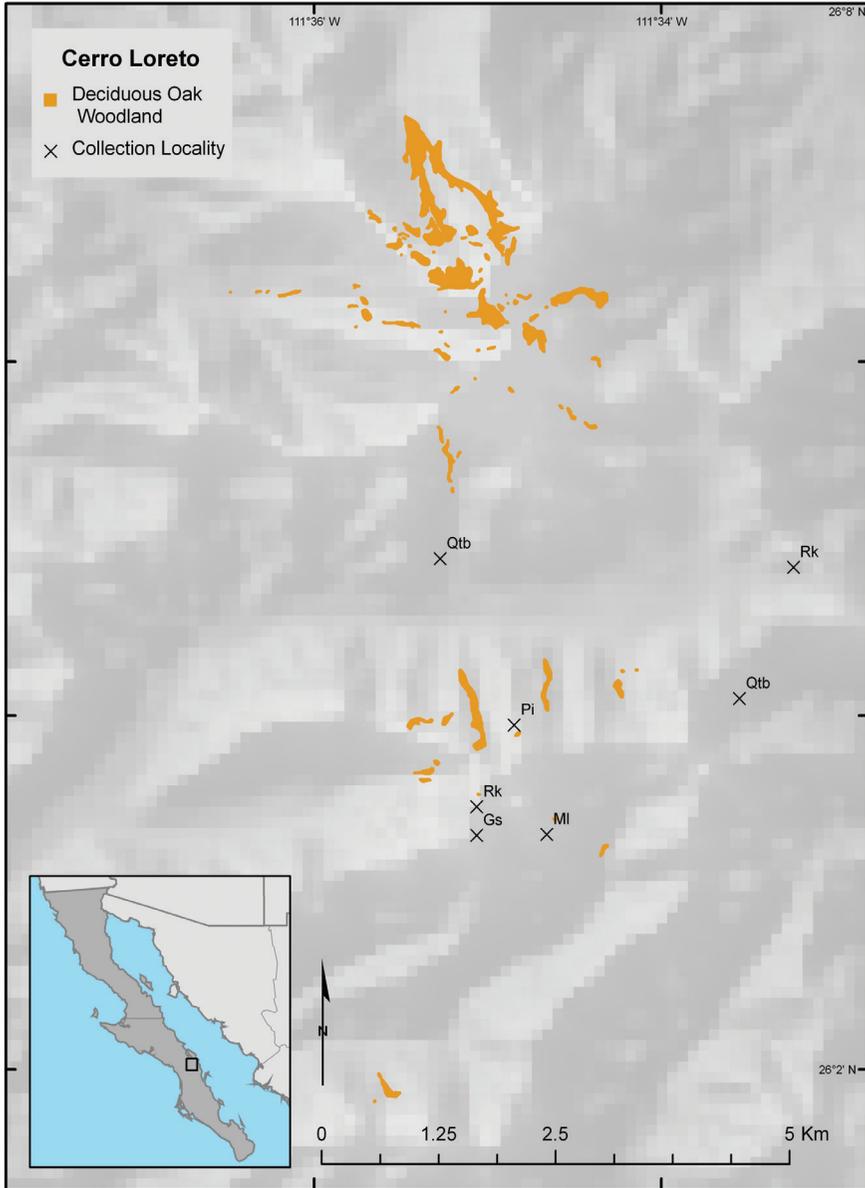


FIGURE 4B. For names of species see Tables 3 and 5.

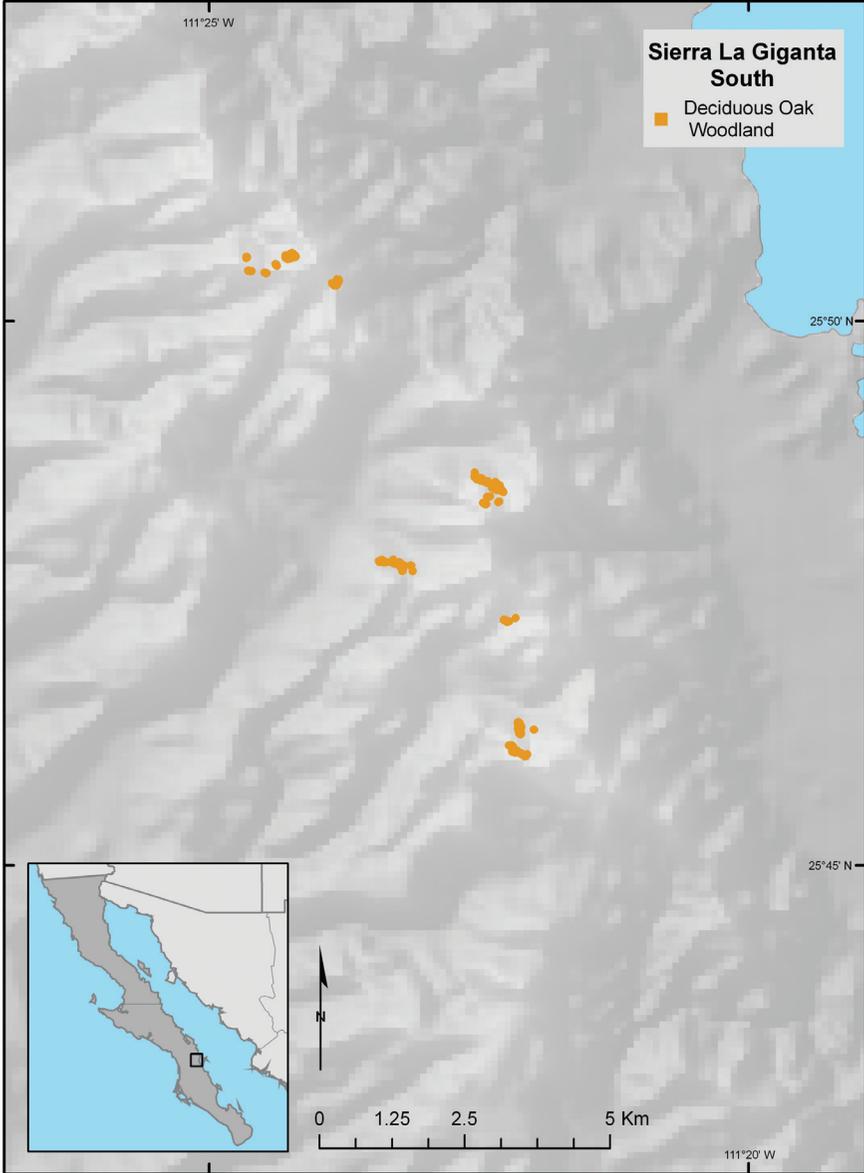


FIGURE 4C.

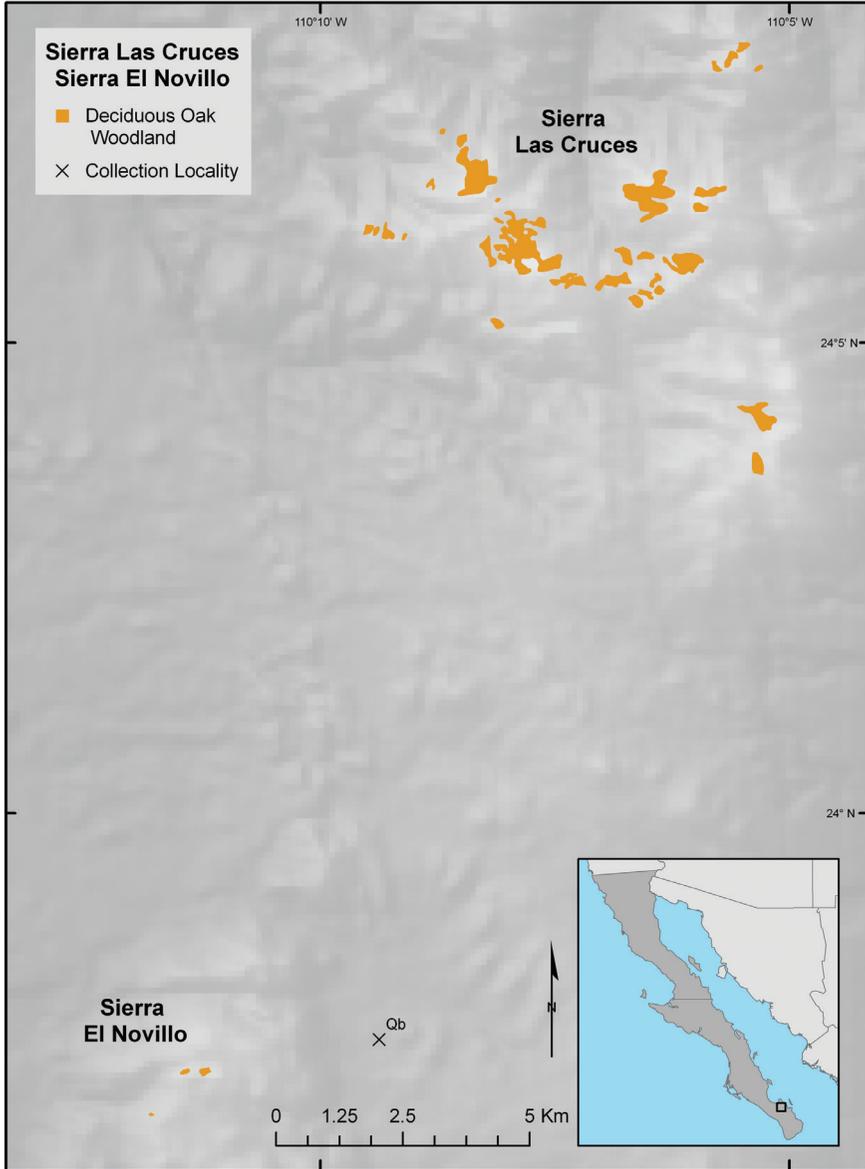


FIGURE 4D.

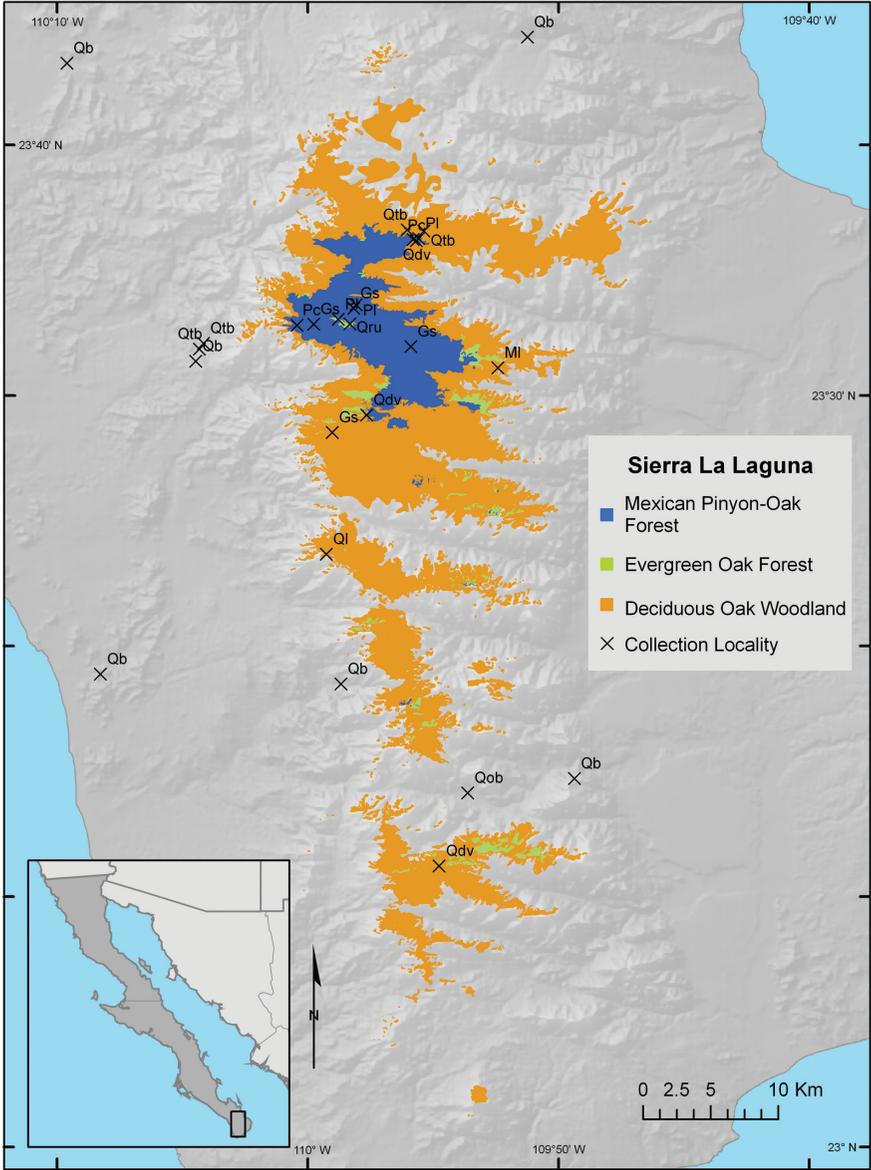


FIGURE 4E. For names of species see Tables 3 and 5.

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Exploring Mexico's northwest, the Baja California Peninsula, its surrounding oceans, its islands, its rugged mountains, and rich seamounds, one feels diminished by the vastness and the greatness of the landscape while consumed by a sense of curiosity and awe. In a great natural paradox, we see the region's harsh arid nature molded by water through deep time, and we feel that its unique lifeforms have been linked to this desert and sea for thousands of years, as they are now.

These landscapes of fantasy and adventure, this territory of surprising, often bizarre growth-forms and of immense natural beauty, has inspired a wide array of research for over two centuries and continues to inspire the search for a deeper knowledge on the functioning, trends, and conservation status of these ecosystems in both land and ocean.

This book offers a compilation of research efforts aimed at understanding this extraordinary region and preserving its complex richness. It is a synthesis of work done by some exceptional researchers, mostly from Mexico, who indefatigably explore, record, and analyze these deserts and these seas to understand their ecological processes and the role of humans in their ever-changing dynamics.

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