# *The Cartographers of Life: Two Centuries of Mapping the Natural History of Baja California*

Pedro P. Garcillán, Charlotte E. González Abraham, and Exequiel Ezcurra

In 1964, the outstanding biogeographer Leon Croizat published a book entitled *Space, Time, Form: The Biological Synthesis.* He never visited Baja California, but few places in the world can condense more deeply the powerful metaphor of Croizat's title. Indeed, biogeography has been for centuries a powerful way of looking at the world from a holistic perspective in which the large-scale processes that mold and maintain life on Earth can be seen, identified, and understood.

## The Biogeographical Singularity of Baja California

The peninsula of Baja California, in northwestern Mexico (fig. 1a), is the Mexican part of "Peninsular California" (Gastil, Phillips, and Rodríguez-Torres 1972), a biogeographic region stretching from the southern base of the Transverse Ranges in California to the Cape Region in the tip of Baja California Sur. The peninsula rides on the Pacific tectonic plate, separated from the rest of North America by the San Andreas Fault and the deep spreading centers of the Gulf of California. A series of factors have contributed to make it one of the most uniquely diverse regions in the world.

Geological formation. Six million of years ago, a sliver of continental crust started to drift away from the Mexican mainland (Riddle et al.

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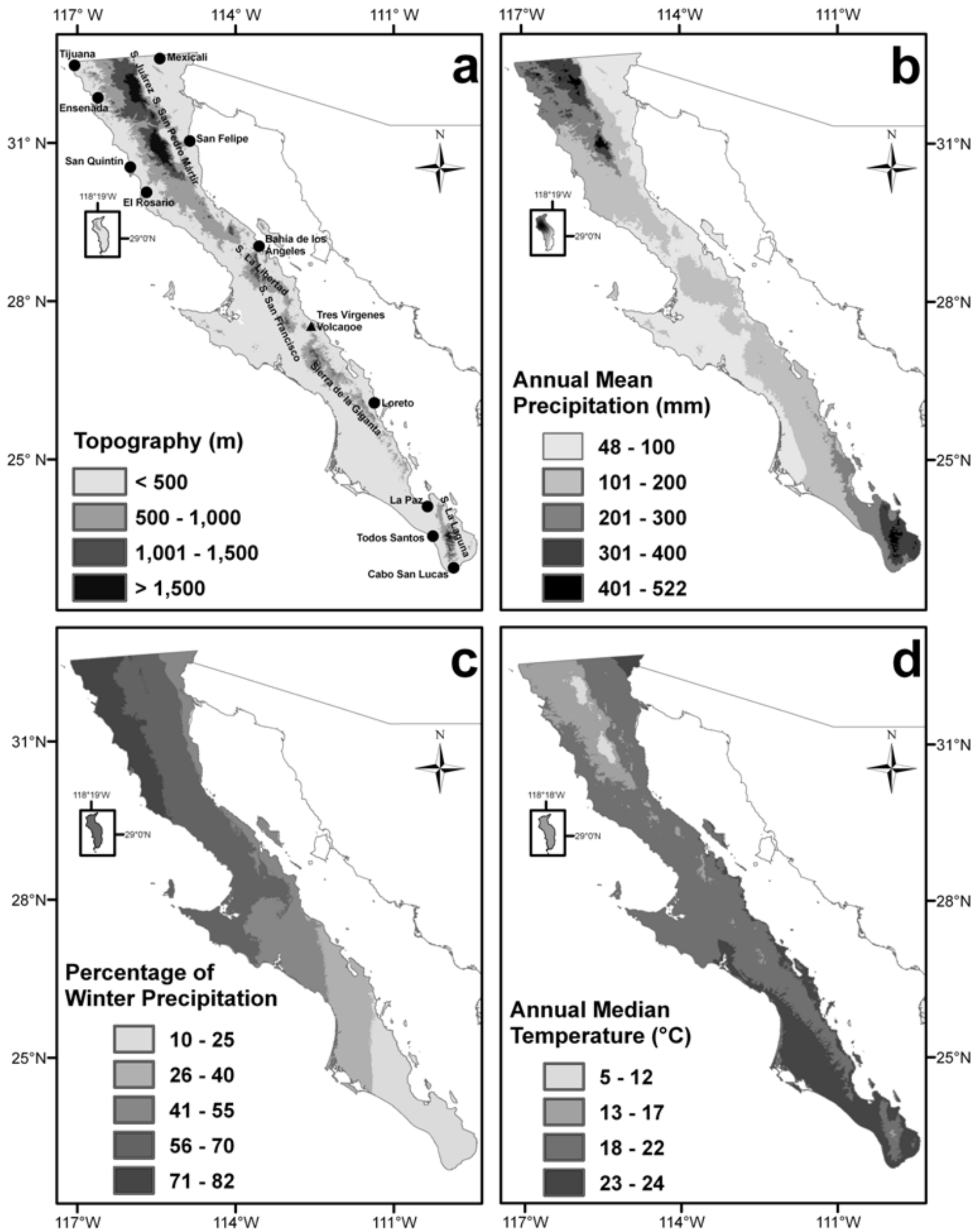


*Figure 1. Physical geography of Baja California: (a) Topography and places cited in the text; (b) annual mean precipitation, (c) percentage of winter precipitation, and (d) annual median temperature.*

2000). The Sea of Cortés, a result of the tectonic spreading centers in the Earth's deep mantle that push and drive the peninsula's drift, has kept Baja California biologically separated from the mainland, and the peninsula, in turn, has kept the Sea of Cortés engulfed, sequestering it from the Pacific Ocean. In this region, where land and sea mutually embrace each other, superimposed patches of insularity exist at even smaller scales, resulting in an amazingly diverse array of ecosystems, species, and unique life-forms.

Holocene climatic cycles. The successive expansion and contraction of ecosystems and biomes induced by glacial climatic cycles during the Quaternary created a series of "sky islands" in the highest ranges of Baja California, where remnants of the ancestral Madro-Tertiary temperate flora that covered the region during the Pliocene still survive in isolation (Axelrod 1958, 1979; Van Devender 1990; Riddle and Honeycutt 1990). Similarly, the deep, moist canyons that dissect the mountain slopes harbor palm oases with relicts of moister tropical vegetation (Grismer and McGuire 1993; Arriaga and Rodríguez-Estrella 1997). Isolated and distinct within the general matrix of sparse desert vegetation, these sky islands and oases create a complex mosaic of contrasting ecosystems.

Latitudinal span. The long latitudinal span of the peninsula, ranging from south of the Tropic of Cancer, at 22°50'N, to 32°45'N, determines the first great axis of ecological variation by creating along this elongated splinter of land a long ecological transition between the northern temperate region showered by winter rains and the southern dry tropical forest soaked by tropical storms, with an extensive desert area bridging both realms (figs. 1b, c).

Oceanic influence. The narrow peninsula also harbors a dramatic east-west transition: While the Pacific coast is strongly influenced by the cold California Current and has a cool, foggy, oceanic climate, the eastern coast is washed by the warm, enclosed waters of the Gulf of California, and the climate is continental—extremely hot in summer and cold in winter (figs. 1b, c, d).

Topography. Finally, a mountainous backbone runs along the length of the peninsula, introducing a third environmental gradient (fig. 1a): On the one hand, the rain shadow of the mountains makes the climate on the gulf slope distinctly different from that on the Pacific slope. On the other hand, temperatures decrease with altitude—approximately 1°C every 100 meters—making the high mountains much cooler than the lowland deserts. By cooling the ascending air and condensing its humidity, the sierras intercept atmospheric moisture and receive more precipitation than the lowlands. Thus, the highest sierras in the peninsula harbor cool and relatively lush forests and green scrublands that are absent from the harsh, hot, and dry environments of the lowland deserts.

As a result of its complex topography, climate, and evolutionary history, Baja California is one of the most spatially diverse regions of the world. In expanses of less than 100 km contrasting combinations of different climates and environments can be found, which normally occur thousands of kilometers apart in larger continental areas (Ezcurra 2001). The complex geological and biological history of the peninsula, combined with its geographical location in the tropical-temperate transition, produce a striking and unique replication of the larger-scale temperate-desert-tropical transition in the North American mainland.

## Quest for Patterns

This sort of "small-scale continent," that is, the unique microcosm of the peninsula, which can be used to understand the large-scale processes that determine the distribution and abundance of species around the globe, has fascinated scholars for almost two centuries. As a result, researchers have proposed several biological regionalizations for Baja California since the early 1900s, under different methodologies and with different perspectives. In this work we present a historical review of the scientific efforts to define and map the biological regions of the Baja California peninsula, and the lessons obtained by scientists throughout this long historic process. We also analyze commonalities in the findings of different researchers, and discuss the main discrepancies between different approaches.

To achieve this we have done an exhaustive review of the published literature on the natural geography of Baja California and, based on this review, we have attempted to understand and summarize the slow accumulation of a body of knowledge on the ecological processes that determine the distribution and abundance of species in the peninsula, and that have led to different biological regionalizations. We have also tried to synthesize the main driving ideas behind the views of these explorers, naturalists, and scientists, and to identify the main points of controversy or disagreement in their views of peninsular biogeography. The historical period we reviewed extends from the last half of the seventeenth century, when the first missionary accounts were written, to present times.

## Historical Review

### *Climatic Geography (Eighteenth Century)*

Biological exploration in Baja California with a clear scientific purpose and a systematic approach began in 1683 when the Jesuits visited the peninsula for the first time. Francisco Eusebio Kino, the father of missionary expansion into the Sonoran Desert, traveled the peninsula four times and, being a superb cartographer, he made a series of maps depicting his findings. In 1683 he visited the Bay of La Paz, and a few months later returned to explore the Sierra de la Giganta along the gorge where Mission San Javier stands today (Rudkin 1952; IHSJ 1954). In 1684–1685 he organized a third expedition to the peninsula, in which he crossed the peninsular ranges north of the Cerro de la Giganta from the estuary of San Bruno to the oasis of La Purísima and to the Pacific coast. In his notes of this trip (Kino 1685) he described in good detail the landscape and vegetation of the peninsula. Later in his life, between 1698 and 1700, having realized that California was not an island but a peninsula, he attempted several times to find a land crossing between the Pimería Alta and California. He finally succeeded in 1701, when he crossed the Colorado River and reached the delta (Kino 1710). Apart from his reports and notes, he made several pioneering maps (Burrus 1965): In 1693 he finished a map of the southern part of the peninsula, describing all of the Sierra de la Giganta south to the Bay of La Paz and including all the gulf islands. In 1696 he finished a map of the Pimería and California, the latter appearing as a large island ending in the north at Cape Mendocino (*Cabo Mendozino*). In 1701 he drew a map of the same region, this one showing for the first time the land bridge to California and confirming that Baja California was indeed a peninsula. Finally, in 1710, a year before passing away, he drew a last map of the region, depicting the meanders and islands of the Colorado River delta in much better detail (fig. 2). Although Kino cannot be described as a biogeographer, his cartographic contributions opened the way for future studies on the geography of life. Other Jesuit missionaries followed his example, after their first permanent mission was established near Loreto in 1697. Although the accounts of biological and geographic characteristics in the peninsula found in the Jesuits' letters and books were general in nature, it is already possible to find some systematic descriptions of the natural geography of the region and an acute interest in its flora and fauna (e.g., del Barco ca. 1780; Baegert 1772; fig. 3).

In 1791–1792, almost three decades after the expulsion of the Jesuits in 1768, José Longinos Martínez, a scientist belonging to the Royal Botanical Expedition of New Spain led by Martín de Sessé and Mariano Mociño, traveled the whole of Baja California and southern California (known at that time as Alta California; Longinos 1792). He was the first trained natural scientist known to have done work in Baja California (McVaugh 1977) and left some interesting comments about local geography in his diary. He noted the remarkable north-south difference in rain seasonality along the peninsula, but the climatic contrast in fog and temperature between opposing coasts was what attracted his attention most powerfully. The ocean was clearly identified as a main driver of regional environmental conditions, and the natural geography of the peninsula was perceived during this first period as fundamentally the result of ocean-driven climatic dynamics.

### *The Beginnings of Biological Geography (Nineteenth Century)*

Because first of the war of independence from Spain, and later of civil wars, the first half of the nineteenth century was a turbulent period in Mexico, and by extension in Baja California. Internal turmoil discouraged scientific exploration in the isolated peninsula. After the presidency of Benito Juárez restored the Mexican Republic and consolidated its rule over the national territory, the federal government started to offer business opportunities in Baja California to foreign companies and investors through a system of *concesiones,* or land grants, often luring them with exaggerated reports of immense riches to be obtained in this largely unpopulated but supposedly opportunity-rich land. American investors and some governmental agencies funded a few exploratory trips aimed at assessing the true economic potential of the region, principally for mining purposes, and these studies yielded some interesting geographical information. The most notable example is that of William M. Gabb, an experienced geologist associated with the California Academy of Sciences, who traveled the entire peninsula in 1867 as part of an expedition led by J. Ross Browne for the Lower California Company to explore the mineral resources and colonization possibilities along the territory included in the company's land grant, which spanned almost the entire peninsula. Gabb wrote a report for Browne that was included as a chapter ("Exploration of Lower California") in Browne's book about the states and territories west of the Rocky Mountains (Browne 1869). Based on


*Figure 2. English edition of Kino's map of the passage to the Californias: "A Passage by Land to California Discover'd by ye. Rev. Fathr. Eusebius Francis Kino, Jesuite, between ye years 1698 & 1701"; in Henry Jones, The Philosophical Transactions, pt. II, p. 192 Printed for J. and J. Knapton et al., London (1731).*

the range of plant species he had observed on his trip, Gabb gave in this report the first detailed description of the mediterranean-to-desert transition. He described how "the belt from El Rosario to San Quintín (30°00'—30°30' N) may be laid down as the dividing line between the semitropical floras of the lower peninsula and the more northern vegeta-

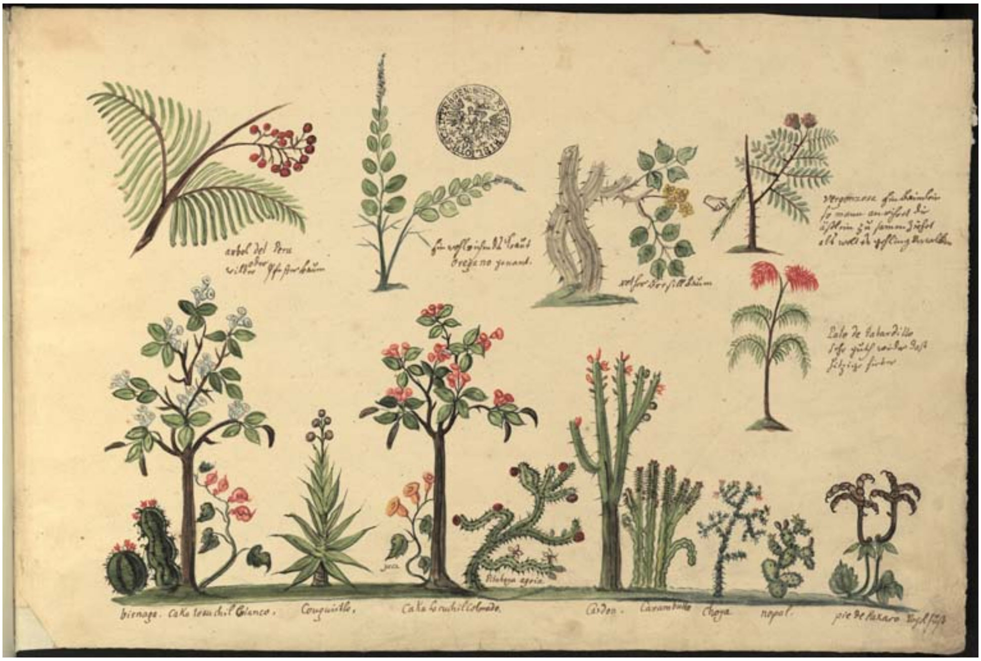

*Figure 3. Botanical illustrations from the Codex Pictoricus Mexicanus, a set of drawings of Baja California's plants and animals sketched around 1762 by the Jesuit Ignác Tirsch (1733–1781) during his missionary work in the Cape Region. (Courtesy of the National Library of the Czech Republic)*

tion of Upper California." He described clearly how the "southern" plant species decrease in number above El Rosario, and "cling tenaciously to the mountains or highlands, and are there scattered and thinning out." Indeed, he added that "the overlapping of forms takes place much more markedly in the high land than in the plains," where "the vegetation is much more sectional, that is, it resembles much more closely the district to which it belongs" (Browne 1869: 110).

A few years before Gabb's expedition, scientific biological collecting had started in the peninsula, mostly by American scientists attracted by the rarity of the peninsular biota (for a review, see Lindsay 1955; and Wiggins 1963, 1980). Biogeography, developed as a rigorous science half a century before by Alexander von Humboldt and other European explorers, made its full entry into Baja California with János Xántus (John Xantus), a naturalized American citizen born in Hungary in 1825 who was sent to Cabo San Lucas from 1859 to 1861 by the United States Coast Survey as a tidal observer (Zwinger 1987). Xantus was an interesting character with a volatile temperament, but also a formidable naturalist. He collected lizards, insects, crabs, starfish, mollusks, and fish, and pressed plants for the Smithsonian's Natural History Museum. The famous botanist Asa Gray described 121 new plant species from Xantus's specimens, and almost half of the mollusks, crustaceans, insects, and birds he collected were new to science. Many species of animals bear his name, including the Xantus hummingbird, Xantus murrelet, and a whole family of nocturnal lizards—the Xantusiidae; and so do several plants, such as the Xantus clarkia, Xantus pincushion, Xantus spineflower, and Xantus mimosa, among many others. By the beginning of the twentieth century Xantus's formidable effort had attracted to the southern tip of the peninsula naturalists eager to corroborate or expand his rich findings (Wiggins 1963). Although there was some biological collection in the northern and central part of the peninsula, the arrival of collectors to the southern tip in the wake of Xantus's explorations, according to Nelson (1921: 119), "contributed more material and had more published concerning it than any other section of the peninsula."

Among these exploration trips, a series of expeditions developed under the auspices of the California Academy of Sciences between 1888 and 1906 became a true landmark in the scientific knowledge of Baja California, and especially of the Cape Region. In 1890 Walter E. Bryant, an ornithologist at with the California Academy of Sciences, visited the Cape Region, and two years later he made a second visit, this time accompanied by Gustav Eisen, of the American Geographical Society and the California Academy of Sciences. The exploration of the peninsula was continued by Eisen in 1893 and 1894, often with T. S. Brandegee, who took part in some of these scientific expeditions.

T. S. Brandegee spent more time in Baja California between 1889 and 1902 that any other botanist had done before (Wiggins 1963). He made the most thorough nineteenth-century botanical exploration of the Cape Region, and published three papers (Brandegee 1889, 1891, 1892) that became the foundational botanical work for southern Baja California. In these papers he showed the distinctive character of the flora of the Cape Region and suggested that the greatest change in the flora takes place at about latitude 28° N.

In the same years, and studying fauna instead of plants, Bryant (1891) confirmed the unique character and geographical distinctiveness of the

Cape Region. Shortly thereafter, Allen (1893) defended in his regionalization of North American birds that the southern extreme of Baja California belonged to the tropical realm. A few years later, Gustav Eisen published two pioneer articles on the geography and geology of southern Baja California (Eisen 1897, 1900) where he described two general regions based on climate (summer tropical rains vs. winter rains), geology, and distribution of flora and fauna. In his first paper (Eisen 1897), he established this climatic transition around the isthmus of La Paz. Some time later, he refined this idea, still proposing the Cape Region as the core of Baja's tropical region but with a northward extension along the gulf coast, while he positioned the winter rain area in northwestern Baja California from the international border south along the Pacific coast all the way to San Quintín (30°30' N).

Thus, by the turn of the century the Cape was well recognized as a markedly distinct geographical region, and the three large-scale biological regions—or biomes—of the peninsula (mediterranean scrubs, desert, and tropical dry forests) had been described as distinct and well-identifiable entities. The early explorers had also described how the latitudinal transition (temperate to tropical) extends asymmetrically along the two coasts: the cool, winter-moist, mediterranean influence extends southward along the Pacific side of the divide, while the tropical influence spreads northward along the gulf coast.

Arthur W. North, an amateur but very well-read naturalist considered by some chroniclers as the first tourist to travel the length of the peninsula (Nieman 2002), made an outstanding summary of the state of the art at that moment. He divided Baja California from "a topographical standpoint" into four natural subdivisions (North 1907, 1908): (a) the *Cape Region,* extending northward to approx. 24°20' N; (b) *Central Lower California,* extending northward from the Cape Region to 28° N; (c) the *"Waist,"* a narrow, rugged region extending from 28° N to 30° N; and (d) *La Frontera,* including all the territory from latitude 30° N to the international boundary. Climatically, and also judging from their flora and fauna, he described Central Lower California and the Waist as intermediary between the Cape Region, which is semitropical, and La Frontera, which is not unlike Sonora and southern California. With respect to the biological asymmetry between the two coasts, he wrote that the Cape Region and the country bordering the Sea of Cortés receive their rainfall from the tropical summer rains, the heaviest and surest rainfall falling along the mountains of the peninsular backbone.

On the other hand, he reported that the west coast of La Frontera, or that portion of it above San Quintín, is subject to the most uncertain winter rains, receiving only the tail end of storms that originate in the far north (North 1907, 1908). Although North was not a trained scientist, his ability to read carefully the contemporary scientific descriptions and to contrast them with his own observations allowed him to compile the first biogeographic map of Baja California that put together the existing knowledge on plant and animal distributions with that on climate, ocean currents, and rainfall patterns.

*The First Synthesis: Edward W. Nelson (1921)*

At the beginning of the twentieth century, between May 1905 and March 1906, Edward W. Nelson and Edward A. Goldman of the U.S. Bureau of Biological Survey carried out one of the more fruitful expeditions ever done on the peninsula (fig. 4). In the words of Forrest Shreve (1926: 129) "they covered the region more thoroughly than earlier workers had been able to do, and resulted in the most important publications that have appeared on the distributional and ecological aspects of the vegetation."

Goldman published in 1916 a list of the plant records of the expedition and proposed two main vegetation types for the peninsula: mediterranean vegetation, similar to that of southern California, extending along the northwest coast and the San Pedro Mártir ranges; and a more southern flora, related to that of the adjacent mainland coast of Mexico, occupying the rest of the peninsula except for the higher mountains, and extending all the way to the U.S. border along a narrow northeastern strip (Goldman 1916).

A few years before, in 1911, Nelson had published a general description of his and Goldman's peninsular travel in *National Geographic* magazine, but it was not until 1921 that he published the groundbreaking book *Lower California and Its Natural Resources,* in which he synthesized the physical, climatic, and biological characteristics of Baja California. The book became a milestone in the knowledge of the natural history of the peninsula.

In his text, Nelson presented a very detailed physiographic description of Baja California and demonstrated the fundamental role of the peninsular ranges as a principal driver of environmental change and as the ecological backbone of the entire peninsula. He coined the names of

*Figure 4. Edward W. Nelson working in the central desert of Baja California during his expedition with Edward A. Goldman along the peninsula between May 1905 and March 1906. (Courtesy of Smithsonian Archives and San Diego Natural History Museum)*

the Vizcaíno Desert and Magdalena Plains, delimited these regions, and presented the first general discussion on the climate of Baja California, which despite the lack at that time of hard climatic data on which to base his arguments has been proven correct and accurate by subsequent quantitative studies (Humphrey 1974). Finally, he made the first detailed and scientifically rigorous proposal of biological regions for the flora, fauna, and life zones of the entire peninsula, delineating clear and well-defined boundaries for the biological transitions between (a) the mediterranean region and the true desert; and (b) the Colorado Desert, an extension of mainland deserts into the peninsula, versus the true Baja Californian deserts (which he called the Vizcaíno Desert District) that are rich in peninsular endemism (fig. 5a, b). He also clearly identified the extensive desert transition between the northern mediterranean region and the southern tropical zone; the Cape Region as a well-defined biological singularity within the southern tropical region, and the Sierra de la Giganta as a well-differentiated life zone within the faunal Cape District.

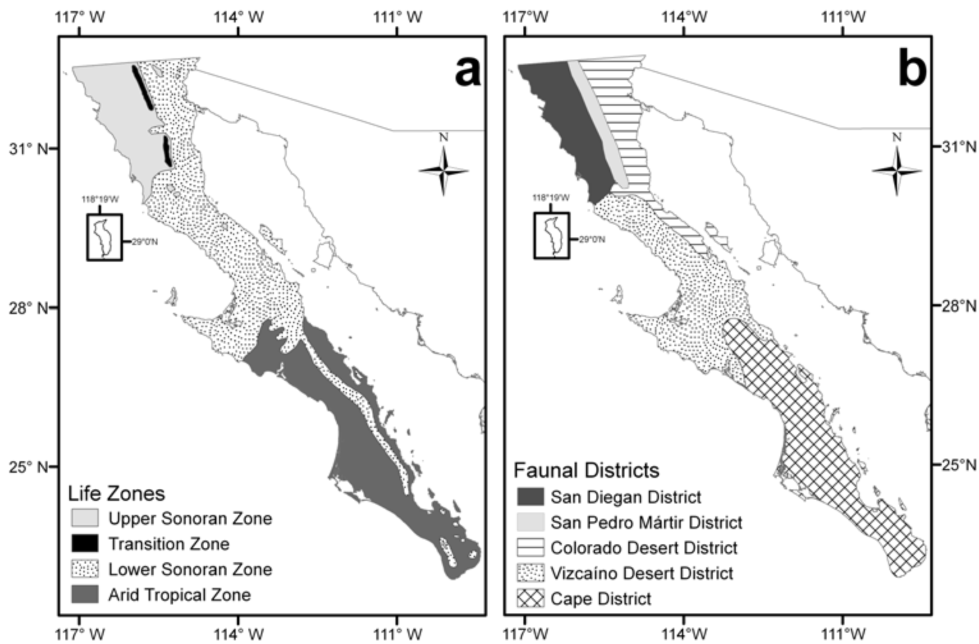


*Figure 5. The first biogeographical synthesis by Nelson (1921): (a) life zones, and (b) faunal districts of Baja California.*

In a manner quite similar to Brandegee's, Nelson proposed in his book three main sources for the flora of Baja California: (a) *southwestern California,* extending from the Juárez and San Pedro Mártir mountains westward to the Pacific coast; (b) *the deserts of Sonora-Arizona-California,* which spread southward along the upper gulf coast to occupy approximately two-thirds of the peninsula; and (c) *the arid tropical lowlands and foothills of Sinaloa,* limited to the southern third of Baja California and especially conspicuous in the Cape District.

Following the concept of life zones developed by Merriam in 1894, and based on the principle that precipitation, and especially temperature, vary with altitude as they do with latitude, Nelson (1921) proposed four life zones for Baja California (fig. 5a): (a) the *Arid Tropical zone* occupying all the lowlands south of the Tres Vírgenes volcano; (b) the *Lower Sonoran zone,* which included the Colorado and Vizcaíno districts and the high parts of La Giganta and La Laguna ranges; (c) the *Upper Sonoran zone,* which included all of the mediterranean scrub and some high-altitude spots in the central desert and in the highest peaks of the

Cape mountains; and (d) the *Transition zone,* defined by an isolated belt 20–25 km wide along the upper slopes of the Juárez and San Pedro Mártir mountains.

Although Merriam's law that altitudinal changes mimic latitudinal changes is in many aspects quite compelling, it also forced Nelson's observations into a conceptual straightjacket that ignored the powerful effects of historic and evolutionary biogeography, driving him, for example, to lump together the Cape mountains with the mediterranean chaparral, two ecosystems that are historically and climatically completely different. Nelson's faunal districts were less constrained by Merriam's theory; in his book Nelson suggested five natural faunal areas for Baja California (fig. 5b): (a) the *San Pedro Mártir District,* a narrow belt about 280 km long extending from the border to Matomí and containing the Juárez and San Pedro Mártir mountains; (b) the *San Diegan District,* occupying the westerly slopes of the mountain divide from southern California to El Rosario and from sea level up to an altitude of about 1,200 m; (c) the *Colorado Desert District* covering the northeastern quadrant of the peninsula; (d) the *Vizcaíno Desert District* in mid-peninsula; and (e) the *Cape District,* comprising all of the southern peninsula from the Tres Vírgenes volcano to the Cape. In this model, the evolutionary effects of geographic isolation were clearly taken into account, and Nelson's map became an obligate referenece for other researchers working in the region.

*Refining Nelson's Conceptual Model (1921–1950)*

Edward Nelson's seminal contributions established the first general biogeographic outline of the peninsula of Baja California. Over the following years many studies would focus on transitional areas between Nelson's main biotic regions or on the delimitation of subregions inside them, an effort that has continued to the present.

I. M. Johnston (1924), a botanist who explored the peninsula in 1921 for the California Academy of Sciences, largely mirrored Nelson's faunal districts, establishing near the 30° N parallel the northern boundary of the Baja California deserts (his "Comondú district," which included most of the peninsula south of this latitude except the mountains of the southern extreme—his "Cape Sierran" district). Johnston also subdivided his great Comondú district into three subdivisions: the Vizcaíno Desert, the Sierra de la Giganta, and the lowland Cape. Johnston's Vizcaíno

Desert subdivision was similar to Nelson's Vizcaíno District, while the other two coincided quite well with Nelson's Cape District (fig. 5b).

Shortly after the publication of Johnston's work, G. Bancroft (1926) published a proposal to define the faunal areas of northern Baja California based primarily on bird distributions. In his study Bancroft placed the southern limit of the Mediterranean area (Nelson's San Diegan District) to around latitude 31° N, almost 100 miles north of Nelson's original boundary, and reduced the extension of Nelson's San Pedro Mártir District to follow more closely the contour of the high mountains. He also reduced Nelson's Colorado Desert District, renaming it "Colorado Delta District" and restricting it to the region directly irrigated by the river, either subterraneously or by overflow. Finally, he redefined the southern border of Nelson's Vizcaíno Desert District based on the distribution of the boojum tree *Fouquieria columnaris,* which he observed "is always present in the interior and does not break until the mountains end" (Bancroft 1926: 213). Inferring that the mid-peninsular lowlands were an emerged ocean bed, he established the transition line between the Vizcaíno Desert District and the region immediately south of it, which he called the "San Ignacio District," following the 300 meter contour at the base of the San Francisco Mountains.

In a detailed synthesis of the distribution of bird species in the peninsula, J. Grinnell reaffirmed Nelson's temperate-desert boundary at around 30° N, but also suggested dividing the mediterranean part of Baja California into two main areas: the San Diegan District to the north, and the drier San Pedro Mártir District to the south, with a transition zone between 31° and 32° N (Grinnell 1928). The long-recognized singularity of the Cape Region was also reaffirmed by Grinnell, who characterized it as the most distinctive of the peninsular biotic areas, with a remarkable total of forty-six species and subspecies of endemic birds.

Based on vegetation observations, Forrest Shreve (1936) proposed the northern limit of the Baja California Desert—the transition from desert to chaparral—about twenty miles north of Rosario, at latitude 30°15' N, based on the observed increase in vegetation density, uniformity in the height of the dominant plants, and uniformity in the vegetative character of the dominants.

A year later, in 1937, Shreve defined a region of tropical dry forests that he named "Forest of the Cape Region," which included the Cape Region *sensu stricto* and the western and upper eastern slopes of the Sierra de la Giganta. His observations of the ecology and biogeography of the

Cape Region were foundational in their detail and their integration of different scientific dimensions, from geology, to climate, and to plant biology. He placed the transition between the Magdalena Plains and the Cape Region a short distance north of Todos Santos, and defined the Magdalena Plains and the eastern coastal band south of latitude 26° N as a true desert. He attributed the change in vegetation between the desert and the Cape Region to higher rainfall and more favorable rain seasonality. He also noted however that south of La Paz the character of the underlying rock and the derived soils was closely correlated with the distribution of forest and desert, being the first to recognize the biological transition associated with the La Paz fault that separates the Cape granite formations from the basalt mountains of La Giganta. He also described an altitudinal transition, with xeric vegetation below approx. 1,000 meters and a more mesic flora above. The xeric lowlands, he noted, bear some resemblance to the thorn forests of Sinaloa in height, density, and growth forms, but are not dominated by the thorny acacia type of tree that prevails in Sinaloa. With this simple observation, Shreve incorporated the effects of evolutionary history into his geographic studies of plant distribution.

In an analysis of the distribution and boundaries of the Sonoran Desert, L. R. Dice (1939) described three biotic provinces in Baja California: the Californian, Sonoran, and San Lucan provinces. The first one corresponded to the mediterranean ecosystems of the peninsula (Nelson's San Diegan and San Pedro Mártir districts), the second one to the northeastern part of the peninsula occupied by the lower Colorado basin (Nelson's Colorado Desert District), and the last one to the deserts and drylands of Baja California (Nelson's Vizcaíno and Cape districts). Dice defended a Californian–San Lucan transition around latitude 29° N, and a Californian-Sonoran transition along eastern escarpments of the Sierra Juárez with latitude 31° Nas southern limit for the Sonoran Desert in Baja California.

In 1942, C. Epling and H. Lewis revised Shreve's (1936) ideas on the transition from desert to chaparral in Baja California, highlighting the marked differences between chaparral and coastal sage scrub, which had previously been treated simply as a transitional form of chaparral. Their distinction was based on the marked differences in water regime and drought, the clear spatial and altitudinal differences, and the sharp variation in floristic composition between both communities, suggesting two well-defined vegetation types.

Near the middle of the twentieth century, in 1946, E. A. Goldman and R. T. Moore published an important paper on the biotic provinces of Mexico, based largely on the biogeography of mammalian communities. Edward A. Goldman had been a research associate and field assistant for Edward W. Nelson during their joint trip on horseback through Baja California, and had already published, in 1916, a preliminary, simplified summary of the main vegetation types for the peninsula. Although Goldman's paper with Moore addressed a much larger scale, the whole of Mexico, the influence of Nelson's synthesis and of Shreve's first attempts at refining Nelson's districts was clear in their description of Baja California, which agreed, if not exactly at least conceptually, with the geographic models of their two predecessors. A friend of Nelson's who was intimately acquainted with Nelson's perspectives and methods, and was also well aware of Shreve's growing intellectual presence as the leading naturalist and biogeographer of the Sonoran Desert, Goldman prepared the way for a new synthesis that was in the making.

A special mention is due to Howard Scott Gentry (1949) who, having read Nelson's account in detail, understood the importance of the oceanographic difference between the Pacific Ocean, dominated by the cool California Current and the Pacific westerlies, and the warmer, more tropical waters of the gulf, a contrast that makes the fog desert along the west coast of the peninsula entirely different from that in the gulf region. More importantly, however, Gentry inferred the existence of ancient seaways in the peninsula and understood that its landmass had been discontinuous in the geologic past. Two decades before the advent of the science of plate tectonics, and three decades before the plate tectonic evolution of Baja California was finally elucidated, he correctly inferred, based on the distribution of endemism, that the Cape District had been isolated from the peninsula until the Quaternary. The high ratio of endemism of the Cape Region, he asserted, correlated well with a tempo-spatial yardstick.

### *Forrest Shreve and the Physiognomic Geography of the Sonoran Desert (1951–1960)*

In 1932, Forrest Shreve (fig. 6) and Thomas D. Mallery from the Desert Laboratory of the Carnegie Institution of Washington at Tucson, together with Ira L. Wiggins from the Dudley Herbarium at Stanford, outlined an ambitious project to survey the vegetation and flora of the Sonoran

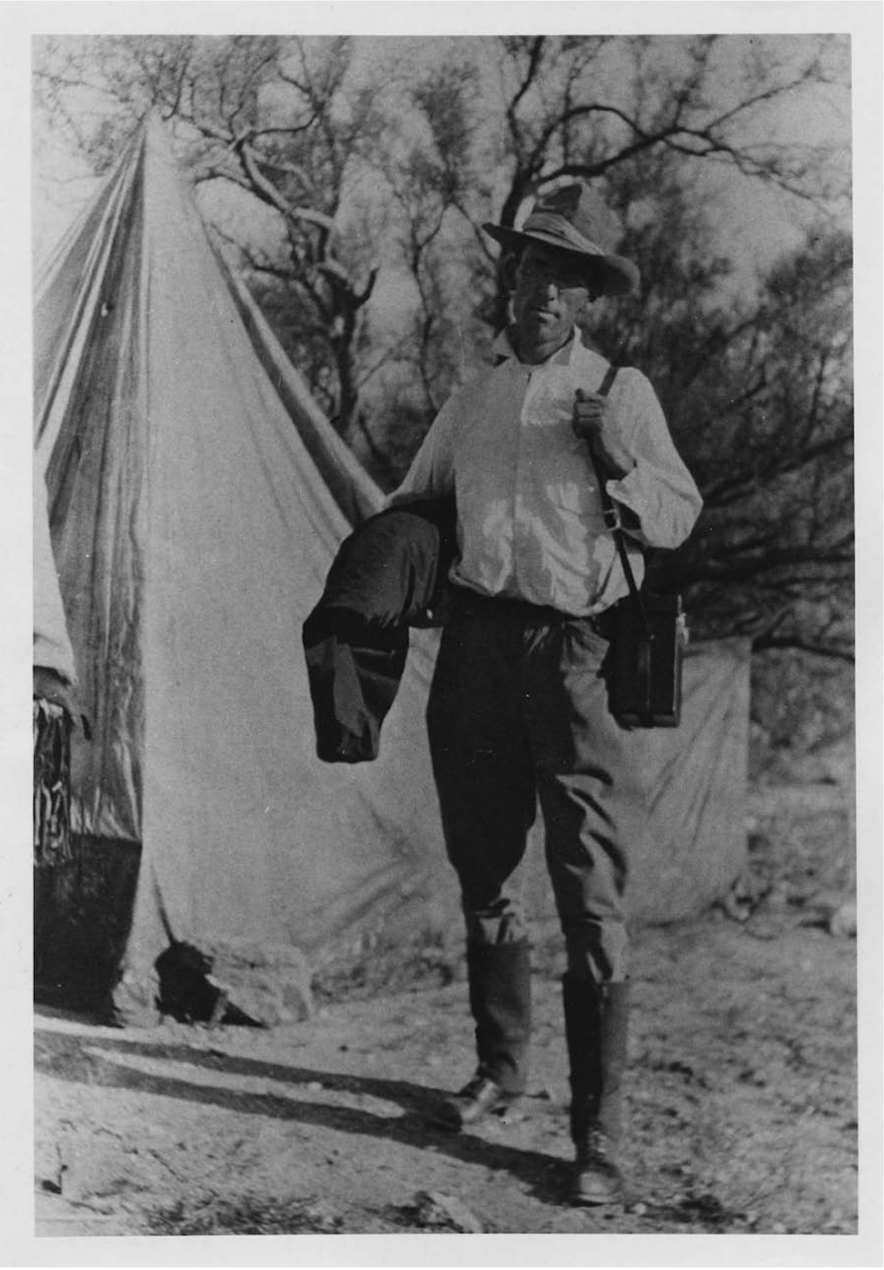

*Figure 6. Forrest Shreve. (Courtesy University of Arizona Library Special Collections)*

Desert (McGinnies 1981). The final product would appear more than thirty years later, in 1964, with the publication of the two volumes of *Vegetation and Flora of the Sonoran Desert,* by Shreve and Wiggins. The first part of the book had already been published in 1951, a year after Shreve's death, under the title *Vegetation of the Sonoran Desert* and under the single authorship of Forrest Shreve.

Shreve's work produced the first rigorous delimitation of the Sonoran Desert as a biotic region, and a detailed definition of its subdivisions. His work contains a detailed physiographic characterization of each subdivision and succeeded in describing with high accuracy the climate of the peninsula, as he had done previously for northern Mexico (Shreve 1944). Shreve's most original contribution, however, was the use of morphological characteristics of the dominant plants—not merely the floristic and taxonomic characteristics commonly used by biogeographers—in order to identify and map the subdivisions of the Sonoran Desert (McGinnies 1981). Like most biologists during the first half of the twentieth century, Shreve was familiar with the concept of life-forms developed by the Danish botanist Christen C. Raunkiaer, who classified plants according to the position of the renewal buds during winter (i.e., high aboveground on tree branches, near ground level in creeping stems, at ground level in basal rosettes and stolons, or below ground level in tubers and rhizomes; see Raunkiær 1934). Shreve was quick to comprehend that, although the idea of classifying plants according to their growth habits was extremely compelling, Raunkiær's method would not work in the Sonoran Desert where plant growth was limited not by freezing temperatures but by water availability. This was particularly noticeable in Baja California, where giant cacti often coexist with bizarre trees having giant fleshy stems and deciduous leaves, such as the boojum tree (*Fouquieria columnaris*), the copalquín (*Pachycormus discolor*), or the elephant tree (*Bursera microphylla*); and where the Pacific coastal landscape is dominated by stemless plants with succulent leaves arranged in whorls, or "rosettes"—like some species of *Agave,* having swordlike leaves with spiny edges, or *Dudleyas,* having rounded leaves with waxy cuticles of striking white-reddish colors. None of these remarkable growth forms could be easily classified using Raunkiær's model.

Shreve clearly understood that these growth forms are indicative of different strategies for storing moisture and coping with drought in different subregions within the larger desert: succulent rosettes can collect water from coastal fog, funneling the condensed moisture to the base of their juicy leaves; giant cacti can store hundreds of gallons of water in their immense barrel stems; small-leaved plants can minimize transpiration and survive drought by using very little water, and trees with both deciduous leaves and giant fleshy stems can store water in their trunks but can also grow quickly when the rains set in by producing new leaves and maximizing photosynthesis. Thus, based on his approach to desert life-forms, Shreve recognized "mycrophyllous" deserts, where small-leaved shrubs predominate; "crassicaulescent" deserts, where succulent-stemmed plants, such as giant cacti, dominate; "suffrutescent," or shrub-dominated, deserts; "arborescent," or tree-dominated, deserts; "sarcocaulescent," or fleshy-stemmed, deserts dominated by deciduous trees with gigantic trunks and smooth bark; and "sarcophyllous," or fleshy-leaved, deserts, where plants such as agaves, with succulent leaves arranged in basal rosettes, prevail (Shreve and Wiggins 1964; Ezcurra 2001).

Armed with this simple but powerful conceptual tool, Shreve could rapidly identify the subdivisions of the Sonoran Desert simply by mapping areas where similar dominant strategies prevailed. He mapped almost the entire peninsula of Baja California as part of the Sonoran Desert, with the exception of the northwestern mediterranean region and the tropical region, in which he included most of the Cape Region and the Sierra de la Giganta, which he identified as too wet to be classified as true deserts (fig. 7a).

Four of the seven subdivisions proposed by Shreve for the Sonoran Desert are present in Baja California. Two of them, the Vizcaíno Desert and the Magdalena Plains, are confined to the peninsula, while the other two subdivisions also extend into the Mexican mainland: the Lower Colorado Valley is a narrow coastal fringe in the northeast of the peninsula where the deserts of the Sonora-California-Arizona borderlands extend along the coast of the upper gulf; and the Central Gulf Coast subdivision consists of a coastal band along the southern peninsula that has a disjunct sister area on the coast of Sonora near Punta Cirio.

A few years later, in his book about North American deserts, E. C. Jaeger (1957) incorporated Shreve's regionalization for the Sonoran Desert. Notably, it would not be until 1959, when the Society of Systematic Zoology organized the Biogeography of Baja California and Adjacent Seas symposium (*Systematic Zoology* 9, no. 2 [1960]), that an excellent synthesis was made by bringing together biotic regionalizations of Baja California for different groups of organisms: mammals (Orr 1960), reptiles and amphibians (Savage 1960), birds (Stager 1960), insects

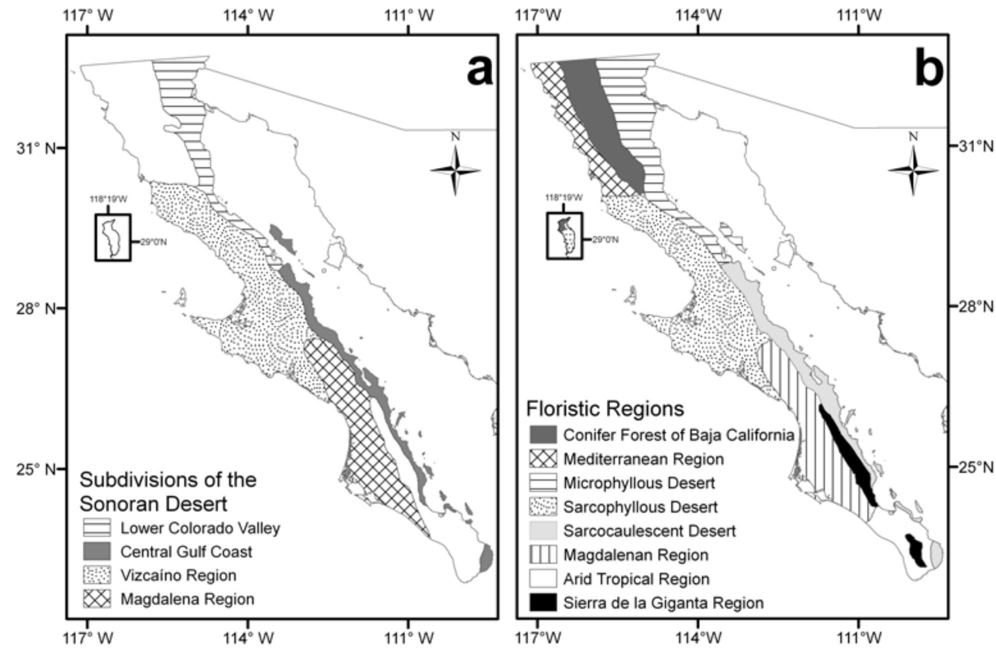


*Figure 7. The second biogeographical synthesis: (a) Shreve's (1951) subdivisions of the Sonoran Desert in Baja California, and (b) Wiggins' (1980) regionalization, including the non-desert regions of the peninsula.*

(Truxal 1960), and plants (Wiggins 1960). All these studies, with a few variations, reaffirmed the Nelson-Shreve framework by recognizing (a) a mediterranean area in the northwestern part of Baja California; (b) a tropical area in the southern third of the peninsula (Sierra de la Giganta and the Cape Region), and (c) a large desert area lying between the two extremes and connected through a northeastern fringe (the Colorado Desert) to the rest of the Sonoran Desert.

*New Scientific Tools, New Evolutionary Paradigms (1960 to present)*

During the decades that followed, great improvements in our natural knowledge of Baja California evolved as a consequence of three complementary—and groundbreaking—scientific developments. The first was the advent of plate tectonics and the ensuing radical change in paradigms on continental drift that took place in the 1960s. The second was the development of new tools of analysis in molecular biology, allowing first the measurement of genetic variation and later the sequencing of specific genes, and hence revealing previously hidden biological information. The last was the development of informatics and data-basing tools, and the growing ability of different institutions to accumulate and process biological, geological, and climatic data that can be used to test research hypotheses.

This rapid and intense scientific transformation, with its increasing ability to analyze large data sets on biological patterns at a geographical level and to process and interpret their complex connections with geological and climatic history, resulted in numerous new biological regionalizations for the entire peninsula or for parts of it.

Plate tectonics, molecular biology, and historic biogeography. The rapid acceptance of plate tectonics theory as a new geologic paradigm in the 1960s and the development of new techniques for phylogenetic analysis in the 1990s constituted two critical scientific developments that have brought a wealth of information to peninsular biogeography and new evolutionary interpretations of observed patterns. Before the advent of plate tectonics, explanatory models of biological patterns in Baja California were based on the assumption of a static and permanent peninsula whose biological traits were explained only by dispersal events and Pleistocene climatic changes. A profound change in our understanding of the biogeography of North American deserts took place with the understanding that widespread taxa might have been isolated by tectonically driven landscape transformations. The foundational 1983 work of Robert Murphy—who developed a vicariance model of species distributions based on plate tectonics—established a new framework and a novel approach for historic analyses. Despite the crudeness of his first analyses, where he merely fitted species distributions to the stratigraphic models known at that time without a rigorous phylogenetic methodology (which did not exist for the allozyme data available at that time), Murphy's foundational research was followed by numerous subsequent studies that used more a rigorous phylogenetic methodology and verified using molecular data several previously perceived biological discontinuities along the peninsula (e.g., Murphy and Aguirre-León 2002; Aguirre-León, Morafka, and Murphy 1999; Riddle et al. 2000; Crews and Hedin 2006; Lindell, Ngo, and Murphy 2006). These works document the complex insularity and fragmentation that have occurred intermittently along the peninsula, creating a true "Peninsular Archipelago" as described by

Aguirre-León, Morafka, and Murphy (1999). This intermittent insularity has deeply influenced the biological patterns of distribution of many species along Baja California. As scientists accumulate more data from these analyses, researchers are increasingly able to understand and interpret the complex biogeographic evolution of the peninsula.

Informatics and biogeography. Informatics has made in recent decades similar strides to genetic analyses. Research using large floristic databases and complex multivariate analysis in the Sonoran Desert region was pioneered by McLaughlin (1989, 1992, 1995). Following Shreve's idea that the mainland Sonoran Desert and the Baja Californian drylands were part of the same biogeographic province, McLaughlin found through his computerized analyses that the floristic affinities between the Mojave and Sonoran deserts were sufficiently high to consider the former a subdivision of the latter.

In Mexico, the National Institute of Geography and Statistics (INEGI) and the National Commission for Biodiversity (CONABIO), both Mexican federal agencies, have carried out in recent decades a great effort to build climatic, geographic, and biological databases for the entire country, including Baja California. An excellent example of the potential value of these databases was the proposed ecological and biogeographical regionalization of Mexico done by CONABIO (Arriaga et al. 1997).

Simultaneously, the growing availability of better climate data as a result of the efforts of Mexico's Water Commission (CNA) and Meteorological Institute (INM), also federal agencies, have allowed more sophisticated studies of the climatic geography of Baja California (e.g., Hastings 1964; García 1964; Hastings and Turner 1965; García and Mosiño 1968; Markham 1972; Lebrija 1973; Salinas-Zavala et al. 1990; Álvarez 1983; Díaz, Salinas-Zavala, and Arriaga 1994; Peinado et al. 1994; Bullock 2003; Caso, González-Abraham, and Ezcurra 2007).

An explosion of studies. The gradual accumulation of information as a result of these studies led to various efforts to make more recent scientific syntheses of the biological information about the peninsula than Shreve's seminal work; examples are *Flora of Baja California* by I. Wiggins (1980), the first complete flora of the peninsula; *Sonoran Desert Plants: An Ecological Atlas* by Turner, Bowers and Burgess (1995), a more complete work covering plant species distributions of the larger Sonoran Desert; *Amphibians and Reptiles of Baja California, Including Its Pacific Islands and the Islands in the Sea of Cortés,* by Grismer (2002), an extensive study of peninsular herpetofauna; and *A New Island Biogeography of the Sea of*

*Cortés,* edited by Case, Cody and Ezcurra (2002), a collective effort to synthesize ecological knowledge of the gulf islands.

Modern regionalizations. This intense scientific advance, with its increasingly deeper knowledge of the geography of the biological patterns and of their complex connections with geological and climatic history, has yielded numerous and varied analyses of biological patterns in the entire peninsula or in parts of it. Describing each study in detail would be far beyond the scope of our paper, but mentioning them may be of some importance. For the entire peninsula, the following papers have attempted different approaches to biogeographical regionalization during the last three decades: Taylor and Regal 1978; Gentry 1978; Seib 1980; Williams 1980; Wiggins 1980; Faulkner 1982; Lawlor 1983; Murphy 1983; Due and Polis 1986; Brown 1987; Smith et al. 1990; Brown et al. 1992; Peinado et al. 1994; Peinado, Alcaraz, Aguirre, and Delgadillo 1995; Turner, Bowers, and Burgess 1995; Daniel 1997; McPeak 2000; Johnson and Ward 2002; Garcillán, Ezcurra, and Riemann 2003; Garcillán and Ezcurra 2003; and Riemann and Ezcurra 2005, 2007. For the Mediterranean Region the following studies are noteworthy: Mooney and Harrison 1972; Axelrod 1978; Westman 1983; Minnich 1987; Kratter 1992; Delgadillo 1992; Peinado, Alcaraz, Aguirre, Delgadillo, and Aguado 1995; Minnich and Franco-Vizcaíno 1998, 1999; Welsh 1988; Mellink 2002; and Delgadillo 2004. For the Desert Region see Aschmann 1959; Humphrey 1974; Delgadillo and Macías-Rodríguez 2002; Peinado, Delgadillo, and J. L. Aguirre 2005; and Peinado et al. 2006. Finally, for the Tropical Region see Woloszyn and Woloszyn 1982; Arriaga and León de la Luz 1989; León de la Luz and Domínguez-Cadena 1989; Arriaga and Ortega 1988; Lenz 1992; León de la Luz 2000; and León de la Luz, Domínguez-Cadena, and Coria-Benet 2000.

Some of these studies contain explicit proposals for mapping the biological regions in the peninsula as a whole (e.g., Gentry 1978; Williams 1980; Wiggins 1980; Faulkner 1982; Case and Cody 1983; Case, Cody, and Ezcurra 2002; Murphy 1983; Smith et al. 1990; Brown 1994; Peinado et al. 1994; Zippin and Vanderwier 1994; Garcillán and Ezcurra 2003; Rojas-Soto, Alcántara-Ayala, and Navarro 2003), or in part (Mediterranean Region: Minnich and Franco-Vizcaíno 1998, 1999; Cape Region: León de la Luz, Domínguez-Cadena, and Coria-Benet 1988; León de la Luz, Pérez Navarro, and Breceda 2000; León de la Luz and Domínguez-Cadena 1989).

Although these studies have addressed varied objectives, with dissimilar geographical scopes, and using different methodological tools, they share the same general biogeographic framework; yet, they inevitably show differences and highlight controversial points. With the aim of showing this diversity of approaches, we have chosen from these explicit proposals of biological regions seven relevant examples for the entire peninsula: Wiggins (1980) produced a floristic regionalization of the peninsula, partially based on Shreve's work (fig. 7b); Murphy (1983) identified herpetological areas based on species vicariance and plate tectonics (fig. 8a); Peinado et al. (1994) mapped the peninsula based on bioclimatic data and a phytosociological analysis of plant communities (fig. 8b); Zippin and Vanderwier (1994) identified vegetation types for Baja California based on the characteristics of the dominant scrubs (fig. 8c); Arriaga et al. (1997) mapped the ecoregions of Mexico based on multiple, large-scale criteria such as geology, climate, elevation, physiography, mastofauna, and dominant plant communities (fig. 8d); Garcillán and Ezcurra (2003) attempted a regionalization of the peninsula based on herbarium collection records of woody legumes and a numerical classification algorithm (fig. 9a); and Rojas-Soto, Alcántara-Ayala, and Navarro (2003) produced a map of ecoregions based on the potential distribution of bird species built from collections data (fig. 9b). Two additional noteworthy studies were done for the two non-desert parts of the peninsula: Minnich and Franco-Vizcaíno (1999) mapped the plant communities of the Mediterranean Region based on aerial photos and field descriptions of the dominant vegetation (fig. 9c), while León de la Luz, Pérez Navarro, and Breceda (2000) mapped the vegetation types of the Cape Region based on a quantitative multivariate analysis of plant distributions (fig. 9d).

## Final Comments: The Legacy of the Cartographers of Life

Not surprisingly, most biogeographical maps of the peninsula (e.g., Nelson 1921; Shreve 1951; Wiggins 1980; Murphy 1983; Peinado et al. 1994; Arriaga et al. 1997) agree on a general framework defined by the three main peninsular biomes: two non-desert areas in the peninsular extremes (the mediterranean scrubs of the California Floristic Region in the northwest, fed by winter rains; and the tropical deciduous forests of

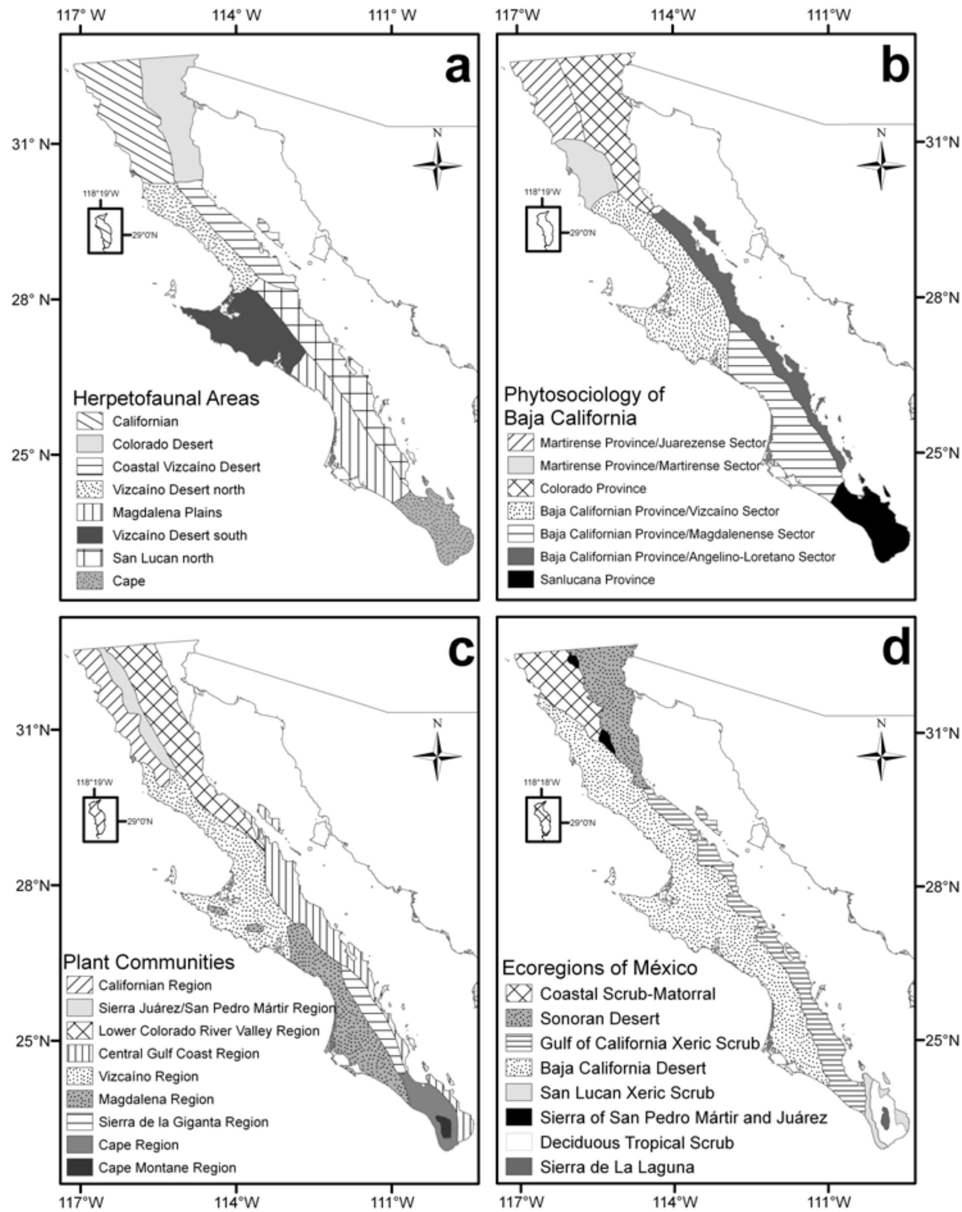


*Figure 8. Biological regionalizations: (a) herpetofaunal areas (Murphy 1983), (b) phytosociology of Baja California (Peinado et al. 1994), (c) floristic provinces (Zippin and Vandervier 1994), and (d) ecoregions of Mexico (Arriaga et al. 1997).*

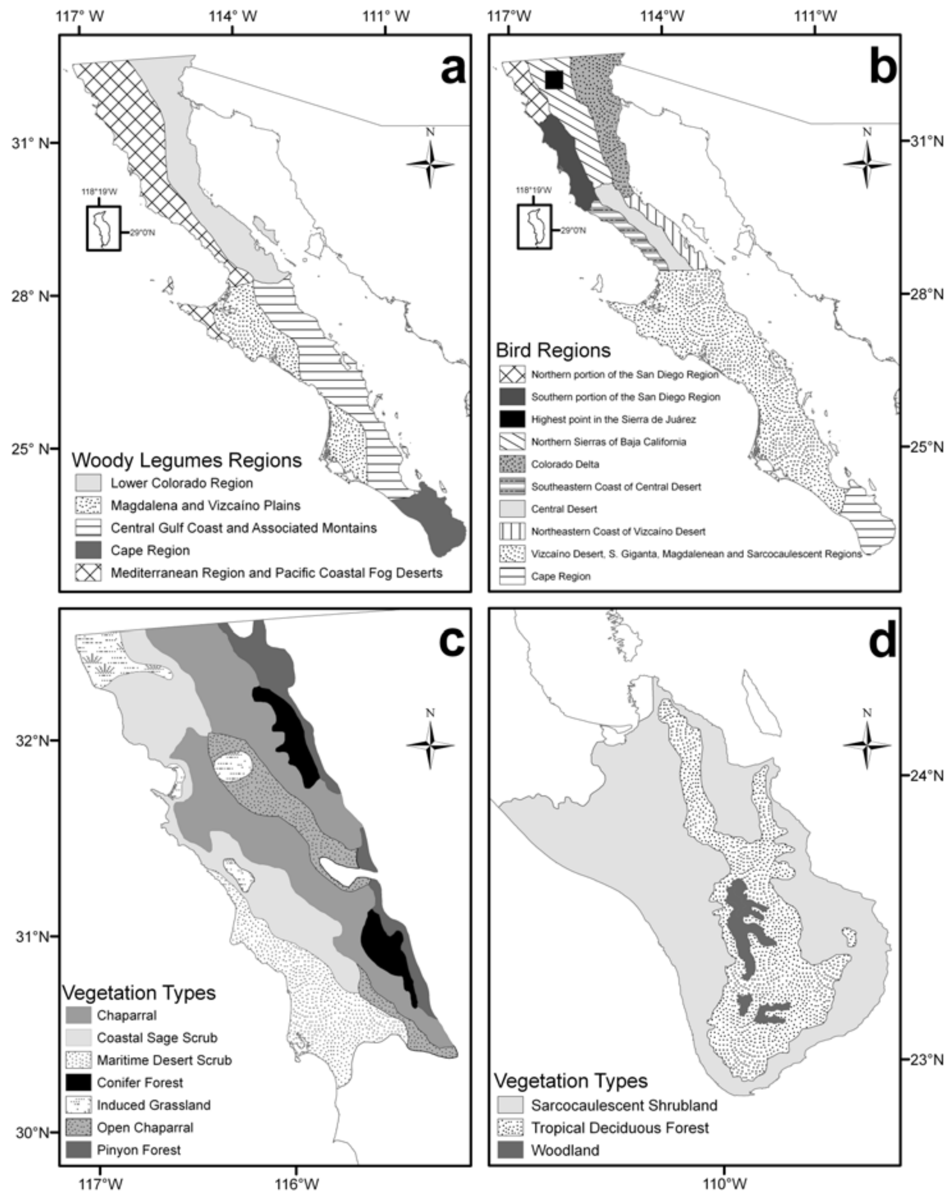


*Figure 9. Further biological regionalizations: (a) woody legume regions (Garcillán and Ezcurra 2003), (b) bird regions (Rojas-Soto, Alcántara-Ayala, and Navarro 2003), (c) vegetation types in northwestern Baja California (Minnich and Franco-Vizcaíno 1999), and (d) vegetation types of the Cape Region (León de la Luz, Pérez Navarro, and Breceda 2000).*

the Cape Region at the southern end, driven by summer rains), and the Desert Region lying in between, with varying proportions and highly unpredictable amounts of both winter and monsoon precipitation patterns.

Furthermore, all the studies identify quite clearly the three main factors that influence the biogeographic variation of the peninsula: (a) the 1,300 km-long latitudinal span of the peninsula that bridges the seasonal, winter-moist, and temperate California Floristic Region to the hot, tropical deciduous forests of the Cape (fig. 1c); (b) the divergent marine influences on the two coasts, which maintain a cool, foggy climate on the Pacific side while the gulf coast is washed by the warm waters of the Sea of Cortés (fig. 1b-d); and (c) the mountainous peninsular backbone that introduces altitudinal cooling as a third environmental gradient and strengthens the coastal differences through the rain shadow effect, making the gulf slope distinctly different from the Pacific side, while the high sierras between the two, fed by atmospheric moisture from cool ascending air, harbor relatively lush forests and green scrubs (fig. 1a). These three axes of climatic variation—long latitudinal span, strong east-west contrasts in climate, and pronounced topography—form the core of all the different biogeographic subdivisions that have been proposed for the peninsula by different authors.

Substantial consensus exists also on sub-regionalization within these three general regions. A robust general agreement is found with regard the sub-regionalization of the non-desert regions, that is, the Mediterranean and Cape regions. Three main ecoregions are defined inside each one, based fundamentally on altitude and coastal influence: coastal scrub, chaparral, and conifer forests in the Mediterranean region, and sarcocaulescent scrubs, tropical dry forests, and montane forests in the Cape region.

In the case of the large Desert Region there are also important consensuses. First, most researchers have described a significant north-south biological change occurring in the middle of the peninsula, around 28° N latitude, separating the Central Desert ecoregion in the north (the boojum tree desert) from the Vizcaíno Desert south of this boundary. Second, based on the contrasting marine and climatic influences on the peninsular coasts, it is generally accepted that two distinct desert areas lie on the two sides of the peninsula: to the west, on the Pacific side, under the cold and foggy influence of the California Current, two very flat ecoregions appear to be well defined and recognized by most researchers: the Vizcaíno Desert and the Magdalena Plains, differentiated in turn by their varying proportions of seasonal precipitation (winter rains are higher in the Vizcaíno than in the Magdalena desert). On the warmer gulf side, two distinct ecoregions having stronger continental influence from the mainland have been repeatedly recognized by researchers: The San Felipe Desert, the peninsular extension of the Lower Colorado Desert, and the Central Gulf Coast Desert, a narrow fringe of coastal land characterized by late-summer rains, or *chubascos,* that arrive from the south. Finally, most biogeographic studies single out as a distinct ecoregion occupying a mountain corridor that runs parallel to the coast of the Gulf of California the Sierra de la Giganta, whose distinct richness in tropical species, which thrive in its warm, protected, and relatively moist slopes, has long been recognized.

Despite these overwhelming areas of agreement, some aspects still remain under discussion, especially the exact boundaries of the transitions between ecoregions. Except in the cases where topography defines a sharp transition (e.g., the steep escarpment separating the Mediterranean Region from the San Felipe Desert) the limits between ecoregions are normally diffuse gradients of biological change, and—quite expectedly—different researchers studying different taxa with different methods will not always reach the same results. More than well-defined border lines we should think of gradual, and often blurry, transition zones.

In spite of these relatively minor differences, there is deep agreement among the majority of the regionalizations proposed for the Baja California peninsula. Remarkably, this common biogeographical outline was delineated by Edward Nelson in 1921 and refined by Forrest Shreve thirty years later. In times when biogeographical work was mostly done on horseback with little more in the way of tools than boots, tents, and field notebooks, these two extraordinary naturalists showed how the combination of a firm commitment, acute capacity for observation, creative intelligence, and a profound sense of place and wonder is capable of generating a deep understanding of the forces that drive the distribution of life-forms on Earth.

Building upon Nelson's acute understanding of topography and large-scale patterns, Shreve's classification of desert communities based on the external morphology of the dominant plants reflects his brilliant understanding of a very significant underlying pattern. In the Baja California drylands, the functional morphology of the stem seems to be the leading factor determining the abundance and distribution of desert plants, modulating their capacity to capture light, store water and nutrients, survive droughts, and explore their immediate environment. Shreve's classification showed an uncanny foresight into future advances in ecophysiology and a genius for understanding the underlying causes of biological distributions. His definition of ecological regions seems to be based on accurate descriptions of the way natural selection and evolution have adapted the predominant morphologies and life-forms to the harsh desert environments.

The Sonoran and Baja California deserts' large variation in winter/summer rainfall patterns, continentality, temperature regime, and land-bridge connections have all contributed not only to their large floristic diversity, but also to their wondrous wealth of life-forms and adaptations (Shreve 1937; Shreve and Wiggins 1964; Wiggins 1980; Rzedowski 1991). We want to end this paper with a tribute to Edward Nelson and Forrest Shreve, and the many others who followed them and were inspired by their views of life. ✥

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