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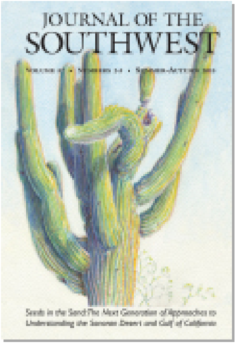

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> The biota of the lands has had a restless place and has endured displacements, inundations, extinctions, and has been forced into migrations with the coming and going of the sea, with the submergence or emergence of mountains, and with the concomitant changes of local climate. Close study of the plant and animal life, when directed by a correlating intelligence, should reveal a course of evolution, expressed jointly by plant and rock, hardly equaled in plant geography.
>
> —Howard Scott Gentry (1949:82)

Introduction

For almost a century the Baja California peninsula (Peninsula), Gulf of California (Gulf), and broader Sonoran Desert region (figure 1) have drawn geologists and biologists alike to study its unique physical and evolutionary processes (e.g., Wittich 1920; Darton 1921; Nelson 1921; Johnston 1924; Beal 1948; Durham and Allison 1960). The challenge remains to untangle the long, intricate, and at times enigmatic geological and climatological histories that have shaped the high levels of endemism and biodiversity observed in the region today (Van Devender 1990; Grismer 2000; Riddle et al. 2000).

Evolutionary theory argues that areas of endemism are generated through increased speciation rates or an unusual capacity to sustain species whose populations go extinct elsewhere. Areas with such high levels of unique biodiversity also demand conservation effort to preserve the underlying evolutionary processes and mitigate the extinction risk posed to species with limited ranges (Myers et al. 2000). Endemism rates

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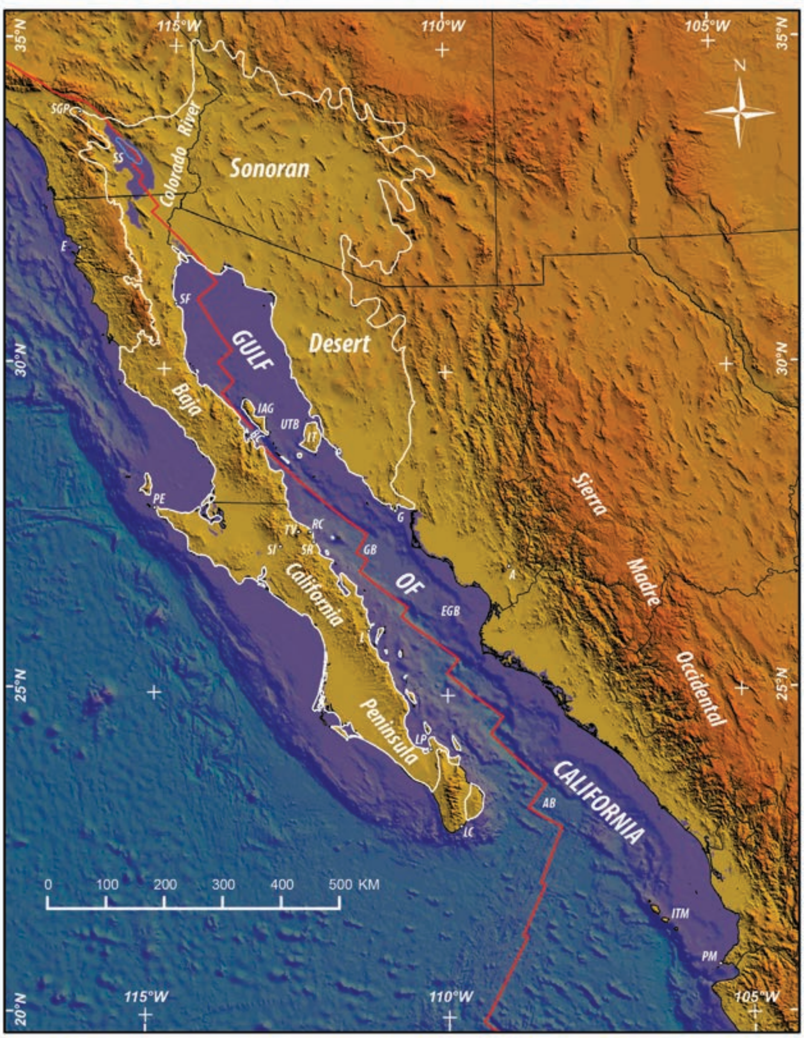


Figure 1: Physiographic map of the Gulf of California–Salton Trough–Sonoran Desert regions of western North America. Outline of Sonora Desert in white. Towns: E-Ensenada, SF-San Felipe, G-Guaymas, SR-Santa Rosalía, SI-San Ignacio, A-Alamos, L-Loreto, LP-La Paz, LC-Los Cabos. Places: SGP-San Gorgonio Pass, SS-Salton Sea, BC-Ballenas Channel, PE-Punta Eugenia, TV-Las Tres Virgenes volcanoes, RC-La Reforma Caldera, PM-Punta Mita. Islands: IAG-Isla Ángel de la Guarda, IT-Isla Tiburón, ITM-Islas Tres Marías. Marine Basins: UTB-Upper Tiburón basin, GB-Guaymas basin, EGB-East Guaymas basin, AB-Alarcon basin. All geographic analyses and maps use base map elevation data from the Shuttle Radar Topography Mission (SRTM) [http://srtm.usgs.gov/].

for reptiles and plants reach 54% and 30%, respectively, along the Peninsula (Grismer 2002; Brusca et al. 2005; Riemann and Ezcurra 2005; Munguía-Vega 2011; Rebman and Roberts 2012), and the Gulf is one of the world's marine diversity hotspots (Roberts et al. 2002). Yet, after almost a century of investigation into the geology, climate, and biology of this region, questions of timing and causality between these perspectives remain. In this article we attempt to unite the wealth of knowledge that remains divided along disciplinary lines, bridge their perspectives, and guide future study. To do so we include examples from the emerging field of geogenomics, in which large-scale genetic data inform geological hypotheses (Baker et al. 2014). The interdisciplinary nature of this effort is founded on the belief that through a synthetic approach incorporating plate tectonics, fossils, climate, ecology, and genetics we can better answer the long-standing questions about the physical history and origins and patterns of biodiversity surrounding the Gulf of California.

Reviews with varying scopes and emphases have summarized previous geological and biological work (Case and Cody 1983; Atwater and Stock 1998; Helenes and Carreño 1999; Case et al. 2002; Oskin and Stock 2003a; Riddle et al. 2000; Hafner and Riddle 2005; Lindell et al. 2006; Riddle and Hafner 2006). This contribution presents geological and climatological processes with the biological patterns they are hypothesized to create, under an explicit discussion of the timescales on which these phenomena occur. Geological processes are organized into three tiers (figure 2, table 1) based on the typical duration of the process. First-order processes fundamentally shape the landscape and take the longest to occur (>5 million years [Myr]). These processes involve plate tectonics, such as continental rifting of the Peninsula away from Mainland Mexico (Mainland). Second-order processes are physical land-sea interactions with local effects that occur on the timescale of 3–1 Myr, such as seaways that may have flooded low passes across the Peninsula. Third-order processes are predominantly climatic phenomena that occur on the shortest timescales of tens to hundreds of thousands of years (kyr). In theory, impacts of third-order events are only observable during or relatively soon after the event ends as the resulting biological signal may be temporary. By contrast, first-order events such as tectonic rifting may isolate a population, which becomes a separate species observable long after the process ends, yet may be difficult to observe over a short period during the event. These three categories are not absolute nor should be interpreted as such, but will prove useful in organizing the variables at play when correlating the histories of this region (table 1).

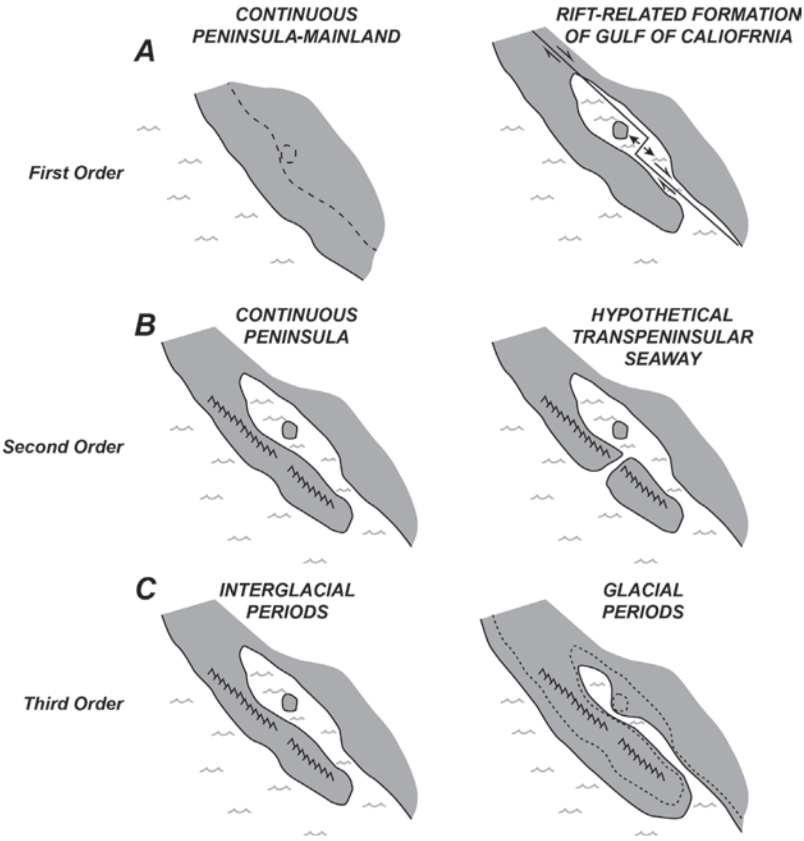
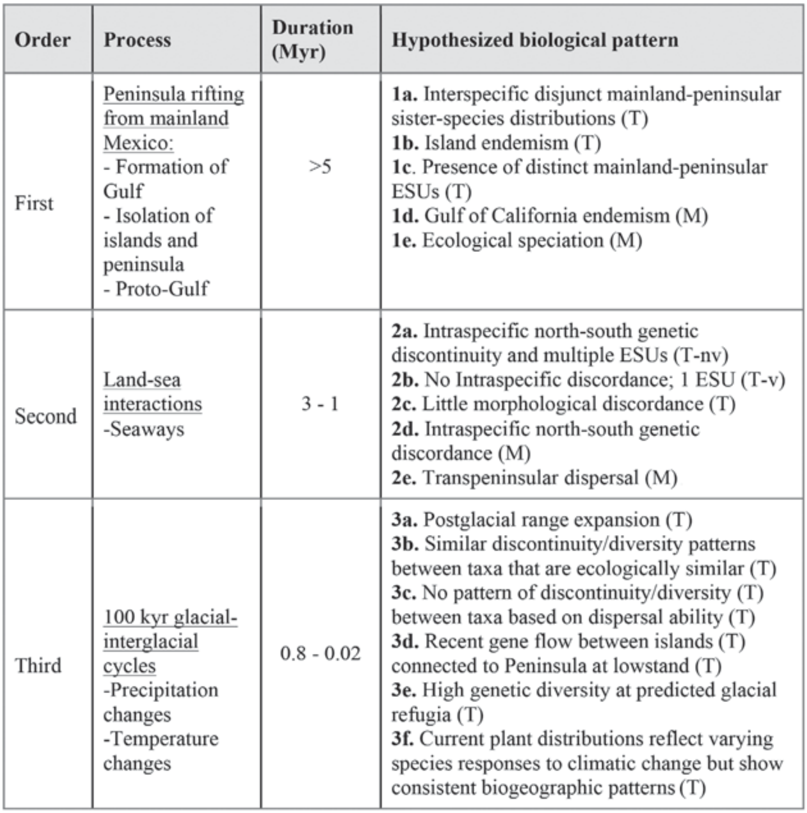


Figure 2: Schematic depictions of geologic/climatic processes evaluated in this study. (A) Rifting of the Baja Peninsula and formation of the Gulf. (B) Formation of transpeninsular seaways. (C) Sea-level lowstand associated with glaciations.

New contributions presented here address well-documented hypotheses. First, a topographical analysis evaluates the feasibility of proposed midpeninsular seaways, both middle Miocene and Plio-Pleistocene in age, by estimating the vertical tectonic uplift rates required for topographic passes to host seaways at these times, and comparing these rates to those documented along the Baja California peninsula. Second, a novel mapping technique visually summarizes previous terrestrial genetic patterns for peninsular taxa to assess regions of high and low biodiversity. Third, the first full listing of plant species shared between the Mainland and Peninsula is presented with preliminary analysis of geographic patterns. Fourth, distribution and speciation of marine species are presented as new, independent lines of evidence to assess the proto-Gulf embayment and midpeninsular seaway hypotheses. Finally, we offer a discussion of sampling schemes, biological study systems, datasets, and analyses most informative for future work.

Table 1. *Geological processes organized by tier (first order, second order, third order) with duration of each and corresponding biological hypotheses for the events given. Biological patterns for Evolutionary Significant Units (ESUs) are specific to marine (M), terrestrial (T), terrestrial non-volant (T-nv), or terrestrial volant (T-v) species. Hypothesis numbers (e.g., 2a) are used throughout the text.*



Order	Process	Duration (Myr)	Hypothesized biological pattern
First	Peninsula rifting from mainland Mexico: - Formation of Gulf - Isolation of islands and peninsula - Proto-Gulf	>5	**1a.** Interspecific disjunct mainland-peninsular sister-species distributions (T) **1b.** Island endemism (T) **1c**. Presence of distinct mainland-peninsular ESUs (T) **1d.** Gulf of California endemism (M) **1e.** Ecological speciation (M)
Second	Land-sea interactions -Seaways	3 - 1	**2a.** Intraspecific north-south genetic discontinuity and multiple ESUs (T-nv) **2b.** No Intraspecific discordance; 1 ESU (T-v) **2c.** Little morphological discordance (T) **2d.** Intraspecific north-south genetic discordance (M) **2e.** Transpeninsular dispersal (M)
Third	100 kyr glacial-interglacial cycles -Precipitation changes -Temperature changes	0.8 - 0.02	**3a.** Postglacial range expansion (T) **3b.** Similar discontinuity/diversity patterns between taxa that are ecologically similar (T) **3c.** No pattern of discontinuity/diversity (T) between taxa based on dispersal ability (T) **3d.** Recent gene flow between islands (T) connected to Peninsula at lowstand (T) **3e.** High genetic diversity at predicted glacial refugia (T) **3f.** Current plant distributions reflect varying species responses to climatic change but show consistent biogeographic patterns (T)

METHODS

Geology

To analyze the feasibility of a midpeninsular seaway in the geologic past, we constructed topographic profiles for the two lowest topographic passes in the midpeninsular region (section 1.1.3). The pass elevation (maximum elevation of each transect) reflects the minimum amount of uplift (positive vertical movement) required for the region to have flooded in the past. We calculated the rate of tectonic uplift necessary to achieve this change and compared it to uplift rates documented around the Gulf of California rift.

Phylogenetic Diversity

Using 85 studies of terrestrial taxa along the Peninsula (table S1), we created a GIS database with the geographic coordinates of sampling locations corresponding to each Evolutionary Significant Unit (ESU), which describes deep or significant genetic divergence for haploid (i.e., mitochondrial DNA in animals, chloroplast DNA in plants) and/or diploid markers (i.e., nuclear DNA). An ESU is a group of individuals that has been isolated from other individuals (conspecifics) for long enough to exhibit meaningful genetic divergence (Ryder et al. 1988), and contribute substantially to the ecological or genetic diversity of a taxon as a whole. Following Moritz (1994), ESUs must be reciprocally monophyletic for mtDNA (mitochondrial DNA) supported by bootstrap/posterior probability values (e.g., a phylogroup with ≥ 0.80 statistical support) and/or exhibit significant divergence of allele frequencies at nuclear loci (e.g., $Fst \geq 0.2$), or be statistically supported by Bayesian assignment tests.

We generated a convex polygon for each ESU with more than one sampling locality to represent the spatial extent of each group. The density, or overlap, of ESUs was measured over a 10-km x 10-km grid. We generated maps by taxonomic group, marker ploidy, and dispersal ability. Species that barely enter the northern part of the Peninsula and show phylogeographic structure north of the 33°00’N associated with the Transverse Range discontinuity in California (e.g., Chatzimanolis and Caterino 2007) were excluded unless their southern distribution reached the 30°00’N latitude on the Peninsula.

We constructed a frequency distribution from the geographical location of the genetic discontinuities in the Peninsula for a subset of 52 taxa, as described in detail in Munguía-Vega (2011). Genetic discontinuities are areas along the Peninsula separating two distinct ESUs. Given the shape and orientation of the Peninsula, we divided the analysis by latitude. A first analysis included discontinuities covering $\leq$ 1°20’00” latitude (narrow discontinuities) that could be confidently assigned to a single degree of latitude. With a chi-square goodness-of-fit test, the resulting distribution was compared against a null hypothesis of uniformly distributed genetic discontinuities ($X^2 = 20.22$, df = 10, $P = 0.027$). Since only a fraction of discontinuities adhered to the definition of narrow discontinuities ($N = 19$ taxa), the geographic location of all observed genetic discontinuities $\leq$ 3°00’00” latitude (broad discontinuities) was also estimated for the 52 taxa and superimposed to further explore the regions that showed a higher density of genetic discontinuities.

Plant Distribution Patterns

We assembled several lists to identify plant species co-occurring between the Peninsula and state of Sonora, Mexico. The list of Sonoran plants was assembled from the following regional floras: the Midriff Islands (Wilder 2014), Isla Ángel de la Guarda (Moran 1983a; Wilder 2014), the Guaymas region (unpublished checklist last edited in February 2014 from Dr. Richard Felger), and Río Chuchujaqui for the Alamos region (Van Devender et al. 2000). We cross-referenced this list against peninsular species documented in Sierra Libertad (Wehncke et al. 2012), the central Gulf coast of the Peninsula (Cody et al. 1983; Turner et al. 1995), and the Cape region of Baja California Sur (Lenz 1992).

The cross listing yielded 526 plant taxa present on the Mainland and Peninsula (table S2). All available herbarium records for these taxa were downloaded from the SEINet herbarium database (Southwest Environmental Information Network [SEINet] 2014), resulting in ca. 165,000 georeferenced herbarium records that matched the taxonomic name in addition to all known synonyms of the input list (table S2). These distribution records were merged with the input table in the R programming environment and multiple shape files were created. We used GIS to determine distributions throughout the Sonoran Desert and mapped species exhibiting one of four patterns from the high number of records (>165,000) and shared species (526). Baja California plant distributions are underrepresented due to incomplete digitization pojects and restricted data sets during the period of the development of this paper.

1. First-Order Processes—Peninsular Rifting from Mainland Mexico

1.1. Geological Processes

1.1.1. Formation of the Modern Gulf of California

Rifting apart a previously contiguous continent fundamentally alters the landscape. Stretching and thinning Earth's crust, lowering its surface, and forming alternating valleys and ridgelines (e.g., Basin and Range) can cause climate heterogeneity and fragment existing populations. Prolonged rifting can lower Earth's surface below sea level, enabling flooding of marine waters that may serve as barriers to gene flow in terrestrial organisms, and as dispersal corridors for marine species. A notable example of this process is the rifting of the African and South American continents to form the proto-Atlantic Ocean (Wegener 1912). This rifting event isolated species on both rift margins of the Atlantic Ocean (Africa and South America) in the Mesozoic era (ca. 130 Ma), forming separate species. Similar geological processes have recently initiated in the Gulf (figure 3) and may be controlling intra- or inter-specific genetic patterns, widespread speciation events, and changing species distributions between the Mainland and Peninsula.

Rifting began in northwestern Mexico as early as ca. 30 Ma (Ferrari et al. 2013), stretching Earth's crust and forming small Basin and Range-style valleys in eastern Sonora, Sinaloa, and Nayarit. The location of active rifting gradually migrated westward and concentrated in the Gulf sometime after ca. 12.3 Ma (Atwater and Stock 1998). At this time, the Pacific plate began sliding northwest along the San Andreas Fault system away from the Mainland. Unlike in California where Pacific–North America relative plate motion is parallel to the plate boundary (the San Andreas Fault), relative plate motion in the Gulf is oblique to the plate boundary. As a result, the Gulf consists of a stepped pattern of short spreading centers connected by transform (strike-slip) faults (figure 2A).

The modern Gulf gradually flooded northward, as recorded in sedimentary rocks containing marine fossils from near the southern mouth of the Gulf up to near San Gorgonio Pass in southern California. In the southern Gulf, evidence for marine conditions exists as early as 10 Ma at Punta Mita near Puerto Vallarta (Gastil and Krummenacher 1978), ca. 8–7 Ma on Islas Tres Marías (Carreño 1985; McCloy et al. 1988), and ~7.5–7 Ma near Los Cabos (Carreño 1992; Molina-Cruz 1994), which may represent a local embayment of the Pacific Ocean

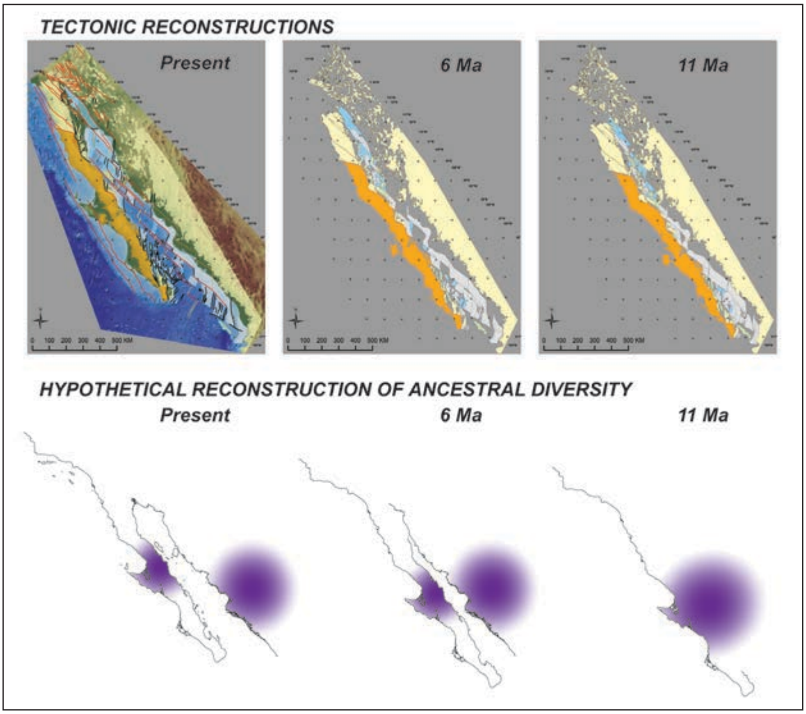


Figure 3: Plate tectonic reconstruction maps back to Miocene time (upper row) reconstruct motion on faults to restore the past positions of fault blocks around the Gulf of California. Polygons are areas of continental crust, colored by relative amounts of extension and thinning due to continental rifting (yellow, unextended; gray, moderately extended; blue, highly extended). Baja California microplate is colored orange for clarity. See Bennett et al. (2013b) for more details and animations of this plate tectonic reconstruction. Lower row schematically shows where an 11-Ma hypothetical ancestral biodiversity center (purple) would be today due to plate tectonics.

instead of a full-fledged Gulf at that time. Farther north, correlative marine salt deposits near Santa Rosalía (Holt et al. 2000) and in the offshore East Guaymas basin (Miller and Lizarralde 2013) provide evidence for inundation at a slightly later time, ca. 7 Ma.

During the same period that the southern Gulf flooded (ca. 10–7 Ma), the northern Gulf and Salton Trough regions show no evidence for marine conditions, as rift valleys were filling with nonmarine sediments in coastal Sonora (Darin 2011; Bennett et al. 2013a), northeastern Baja California (Lewis 1996; Seiler et al. 2010), and in the Salton Trough area (Dorsey et al. 2011) at that time. A stack of unique volcanic ash deposits, now located in coastal Sonora, on Isla Tiburón, and in northeastern Baja California, correlate across the northern Gulf (Oskin et al. 2001) and are not associated with marine conditions. Correlation of these ash deposits is based on several similarities, including their ages, lithology, geochemistry, thickness, and unique paleomagnetic direction (see Bennett 2013 for detailed summary). Restoring outcrops of these ash deposits to their locations ca. 6 Ma requires moving Baja California back to the southeast ~250 km (figure 3), a similar distance to what extrapolation of modern-day plate tectonic rates would predict (Oskin and Stock 2003b).

At ca. 6.3 Ma, fossil-rich marine sediments first record flooding at several locations in the northern Gulf and Salton Trough (summaries in Oskin and Stock 2003a; Bennett 2013). This flooding event is exceptional, with the northernmost 400–500 km of the Gulf flooding synchronously, 6.3 ± 0.1 Ma, from southwestern Isla Tiburón to San Gorgonio Pass in southern California. With this event the modern Gulf took form and was quite distinctive in shape, only ~50 km wide and up to ~1,400 km long (figures 1 and 3). Flooding of the northern Gulf coincides with, and is attributed to, the full development of the Pacific–North America plate boundary in both time and space. These tectonic events provided a mechanism for the subsidence (lowering of Earth's surface) required for marine flooding (figure 2A; Oskin and Stock 2003b). Rifting and subsidence continued and the Colorado River began draining into the Gulf by 4.1 Ma (Dorsey et al. 2007; House et al. 2008; McDougall and Miranda-Martinez 2014). A detailed plate tectonic reconstruction (figure 3) is the most up-to-date paleotectonic view of how the Peninsula, Gulf islands, and shoreline evolved through time (Bennett et al. 2013b), which provides visual-spatial context for discussions of how geological and climatic processes may impact biodiversity in the region (Bennett et al. 2013b).

1.1.2. Proto-Gulf Hypothesis

Although the inundation of the modern Gulf is well documented, the presence, extent, timing, and cause of an older proto-Gulf embayment are debated. If an earlier incarnation of the Gulf existed (i.e., the proto-Gulf embayment), it could have initiated biological processes, such as speciation, much earlier than effects imparted by the modern Gulf (section 1.2.3). The geological and biological interpretations of the proto-Gulf hypothesis differ, and will be treated separately (for biological evidence see section 1.2.2). In the geological literature, Moore and Buffington (1968) first hypothesized a late Miocene proto-Gulf of California marine basin to explain an area of anomalously old oceanic crust offshore Puerto Vallarta at the entrance (mouth) of the Gulf. The proto-Gulf concept was later expanded to include faulting related to continental rifting and evidence of marine sedimentary rocks from the northern and central parts of the Gulf ca. 15–5 Ma (e.g., Karig and Jensky 1972; Gastil et al. 1979) and was envisioned as a Gulf of varying sizes, as large as the distance from Puerta Vallarta to the Lower Colorado River (e.g., Moore 1973). With increased knowledge of plate tectonic (e.g., Atwater 1970) and subduction zone history (e.g., Hausback 1984) in northwestern Mexico, the proto-Gulf term was used differently (e.g., Stock and Hodges 1989; Gans 1997; Fletcher et al. 2007). The proto-Gulf began to specifically refer to the tectonic period beginning ca. 12.5 Ma with the transition from subduction to oblique rifting, and ending at ca. 6 Ma, when the Pacific–North America plate boundary became localized in the Gulf. Thus, conceptions of a proto-Gulf have evolved in the geological literature.

Evidence for a middle Miocene embayment in the northern Gulf has been reported, which calls upon an older (pre-11-Ma) incarnation of the Gulf of California. One group of studies documented marine conditions ca. 13–11 Ma on southwest Isla Tiburón (Smith et al. 1985; Gastil et al. 1999), which marks the only terrestrial exposure of marine strata of supposed proto-Gulf age. However, recent reexamination of these marine strata indicates that the oldest marine deposits on Isla Tiburón are actually 6.4 to 6.1 Ma (Bennett 2013), consistent with the regional flooding event ca. 6.3 Ma (Oskin and Stock 2003a). Another group of studies documented middle Miocene marine microfossils in cuttings from deep oil exploration wells throughout the Salton Trough and northern Gulf (Helenes et al. 2009) and interpreted the specimens to be *in situ* (in the original place of deposition). Helenes et al. (2009)

suggest these specimens are evidence for a pre-11-Ma proto-Gulf embayment and that marine waters might have fed this proto-Gulf from the Pacific Ocean across what is now the Baja California peninsula near the towns of Santa Rosalía and San Ignacio (Helenes and Carreno 1999) through a midpeninsular seaway (see section 1.1.3). However, the sediments hosting these microfossils are chemically and mineralogically similar to the diagnostic, quartz-rich rocks of the Colorado Plateau (Jiménez 2013) that are eroded and transported by the Colorado River, which first reached the Gulf of California between 5.7 and 4.1 Ma (Dorsey et al. 2007; House et al. 2008). This suggests that these middle Miocene (pre-11-Ma) microfossils were eroded from older middle Miocene marine sediments elsewhere and included in these younger, late Miocene sediments.

Though uncontested *in situ* middle Miocene marine strata within the Gulf region have not been found, the mere presence of reworked middle Miocene marine microfossils (e.g., McDougall 2008; Helenes et al. 2009) requires that marine conditions existed somewhere nearby during middle Miocene time and deposits from this unidentified source contributed the reworked fossils into late Miocene marine basins. Three hypothesized origins of middle Miocene strata exist (for a detailed review, see Bennett 2013). The first is from deposits related to a middle Miocene proto-Gulf embayment, similar to what Helenes and Carreño (1999) proposed, where marine waters were fed eastward from the Pacific Ocean, because southern (Gulf entrance) and northern (Los Angeles basin) connections to the Pacific are doubtful (Helenes and Carreño 1999). The second hypothesized source is a shallow embayment northeast of and parallel to the modern-day Gulf, within Sonora and Sinaloa, behind a NW-SE oriented chain of middle Miocene volcanic centers (Fenby and Gastil 1991; Smith 1991; Helenes and Carreño 1999; Bennett 2013). However, no outcrops of middle Miocene marine strata have been observed here; only nonmarine strata of this age have been documented in this region (Herman and Gans 2006; Darin 2011; Bennett et al. 2013a). Also, the regionally extensive ash deposit outcrops of the 12.5-Ma tuff of San Felipe and the 6.4-Ma tuffs of Mesa Cuadrada (Bennett and Oskin 2014) never overlie marine sediments, which suggests nonmarine conditions throughout northwestern Mexico when these volcanoes erupted. A third hypothetical source is from the continental shelf on the Pacific side of the southernmost Peninsula, where middle Miocene marine strata were exposed to wave-base erosion during late Miocene time (Brothers et al. 2012) and could have contributed middle

Miocene specimens into the northern Gulf of California. Each of these scenarios requires further exploration (see section 1.3).

1.1.3. Geological Assessment of Middle Miocene Midpeninsular Seaways

The existence of a middle Miocene proto-Gulf embayment in the general region of the modern-day northern Gulf requires a sea-level connection to the Pacific Ocean. Because a southern (via Gulf mouth) or northern (via L.A. basin) connection to the Pacific Ocean is unlikely, some other low-lying region is required to feed marine water from the Pacific into a hypothesized proto-Gulf embayment. Helenes and Carreño (1999) proposed a middle Miocene midpeninsular seaway (referred here as San Ignacio) located through the San Ignacio area. We identify an additional low topographic pass (Agua Armada) as another candidate that may have hosted a middle Miocene midpeninsular seaway. Due to the absence of a middle Miocene marine sedimentary rock record in the two proposed midpeninsular seaway paths, we evaluate the feasibility of these two hypothetical midpeninsular seaways through analysis of topographic data (figure 4) and comparison to published tectonic uplift histories.

Vertical topographic changes to the midpeninsular region since middle Miocene time include faulting, local inflation from magma chambers, deposition of volcanic rocks, and differential erosion. The rates of these processes vary over short distances and render determination of high-resolution paleo-topography difficult. The process of regional-scale rift flank uplift (uplift of the margins surrounding a rift) can affect larger regions (e.g., Mueller et al. 2009) and is likely to be the main driving cause of the 400 ± 200 m of vertical tectonic uplift observed along the crest of the central Peninsula (Mark et al. 2014). This rift flank uplift is attributed to intense crustal extension and localized oceanic spreading in the rift axis to the east (Mueller et al. 2009) and constrained to have occurred between ~6 and 3 Ma (Mark et al. 2014).

The more frequently cited potential pass (San Ignacio) is located through the town of San Ignacio and branches in the east around Las Tres Virgenes volcanoes and La Reforma caldera, connecting to the Gulf near Punta Santa Ana in the north and/or Santa Rosalía in the south (figure 4C). These branches may have been a single path as the intervening area may have been much lower prior to the 1.2-Ma and younger

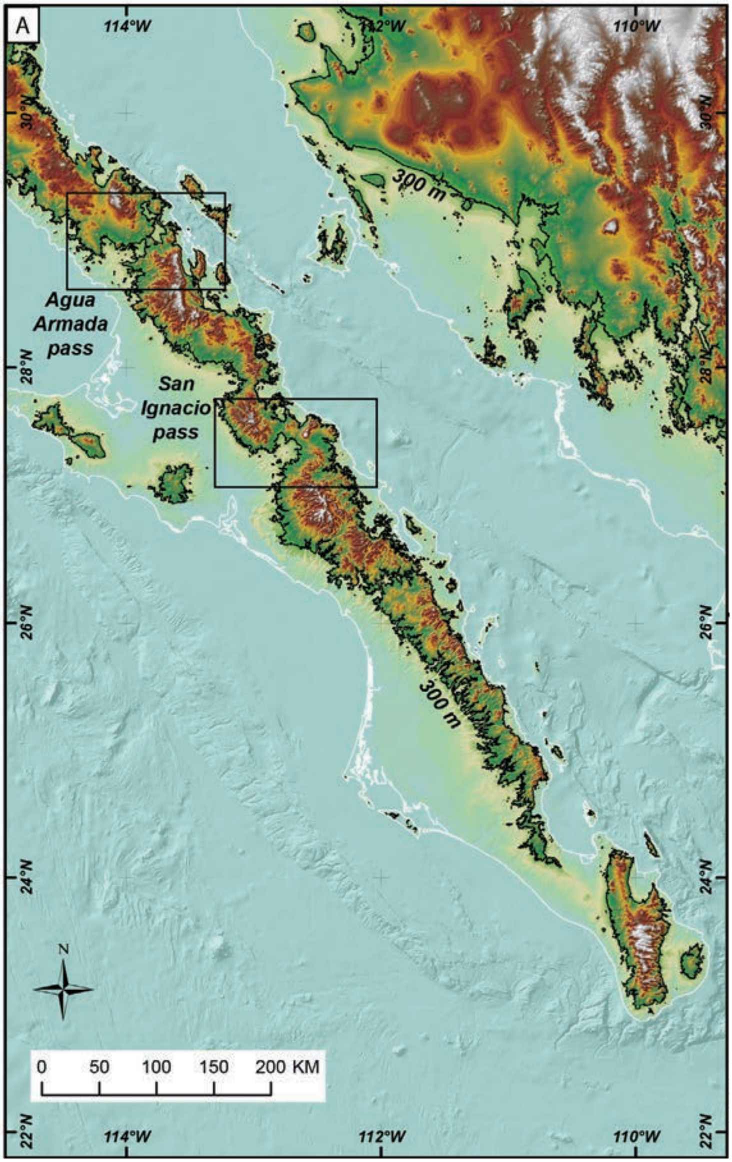
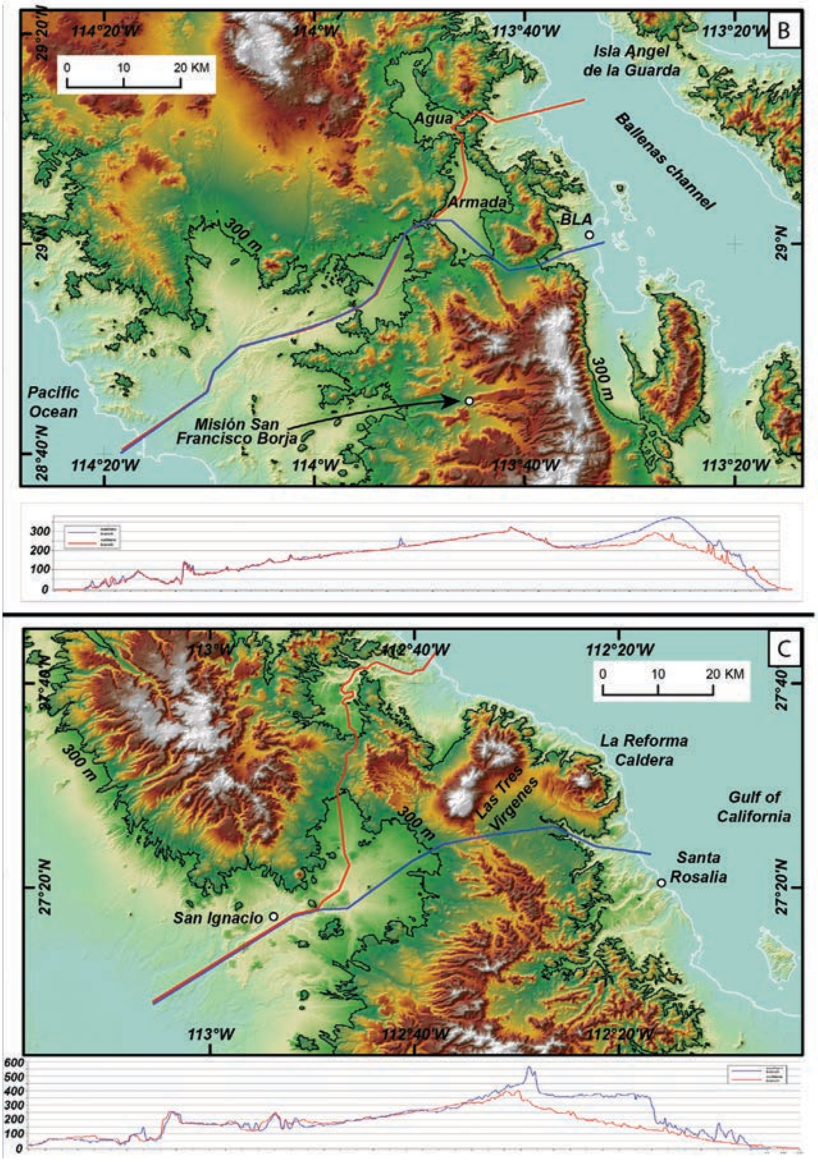


Figure 4: Topographic analysis of seaways across the Baja California peninsula. Modern shoreline in white. (A) Regional topography of the Peninsula with 300-m elevation contour (black line). (B) A broad topographic pass with a pass (maximum) elevation just over 300 m exists in the Agua Armada region. The northern branch (red) is lower than the southern branch (blue), which has a secondary, eastern pass over 350



m. BLA, Bahía de Los Angeles. (C) A broad topographic pass also exists in the San Ignacio region. The northern branch (red) has a pass elevation near 400 m. The southern branch (blue) has a pass elevation just over 550 m. The northern branch appears to be more feasible than the southern branch, as it is ~150 m lower than the southern branch.

eruptions that built the volcanic hills of Las Tres Virgenes and La Reforma (Garduño-Monroy et al. 1993; Schmitt et al. 2006). The northern branch of this San Ignacio path has a pass elevation near ~400 meters above sea level (masl) and the southern is ~550 masl (figure 4C). The southern path appears to cross a NW-SE oriented normal fault with possibly ~100 m of down-to-the-northeast fault motion during Quaternary time, which may contribute to its relatively higher modern elevation. If these branches of the San Ignacio pass were at sea level during latest middle Miocene time (~12 Ma) and were uplifted ~6–3 Ma (e.g., Mark et al. 2014) uplift rates of ~0.1–0.2 mm/yr are required over that ~3-Myr period to uplift this pass to its modern-day elevation.

We identify a second SW-NE oriented potential pass (Agua Armada) through the Agua Armada region, with a pass elevation just over 300 masl (figure 4B). This pass may be more feasible for flooding than the more frequently cited San Ignacio pass because of its relatively lower elevation. About 25 km south of the Agua Armada pass (figure 4B), Wittich (1920) observed fossil-rich dune deposits at ~400-m elevation near Misión San Francisco Borja (San Borja). If these dunes were deposited as part of a middle Miocene shoreline and are now at ~400 m, then the nearby 300-m-high Agua Armada pass could have been flooded in middle Miocene time. If this pass (~300 m) was at sea level during latest middle Miocene time and was also uplifted ~6–3 Ma, uplift rates of ~0.1 mm/yr during that time are required to uplift this pass to its modern-day elevation. If uplift occurred over a longer period of time (e.g., ~12–3 Ma), slower rates of uplift would be required to bring both the San Ignacio and Agua Armada passes to their modern-day elevations.

The uplift rates required for the San Ignacio and Agua Armada passes to have hosted a middle Miocene seaway are within the uplift rates (0 to 0.3 mm/yr) observed along the northwestern Baja coastline (Mueller et al. 2009). Thus, these uplift rate estimates suggest that a middle Miocene seaway through Agua Armada is plausible. This is further supported by 400 ± 200 m of modeled uplift at the peninsular drainage divide (Mark et al. 2014). However, importantly, Mueller et al. (2009) observed that uplift rates along the western Peninsula coastline decrease from ~0.1 mm/yr to near 0 mm/yr just north of Isla Ángel de la Guarda, signifying that the magnitude of rift flank uplift may have been smaller at the latitudes of San Ignacio and Agua Armada. From these geological observations, topographic analysis, and comparison to the timing and rates of vertical tectonic uplift, it is feasible that these passes could have hosted transpeninsular seaways that connected a middle Miocene proto-Gulf embayment to the Pacific Ocean. However, direct geological evidence, such as marine sedimentary rocks of middle Miocene age, is required to confirm any transpeninsular hypothesis. Additionally, this evidence does not speak to the location and size of a middle Miocene embayment, only that transpeninsular seaways in this region were possible at this time.

1.1.4. Midriff Islands

The Midriff Islands are an archipelago stretching across the central Gulf, comprising islands with heterogeneous and distinct geologies. Some are fragments of continental crust similar to the Peninsula and Mainland that originated from the rifting of the Peninsula and flooding of the Gulf (Ángel de la Guarda, San Lorenzo, Tiburón, San Pedro Nolasco). Other islands are volcanic (e.g., San Esteban, San Pedro Mártir, Tortuga) and formed from accumulation of volcanic deposits that breached sea level after the modern Gulf formed. Their physical size ranges across four orders of magnitude from the largest island (Isla Tiburón, ~1,200 km^2) to small rocky outcrops.

In the northern Gulf, evidence from volcanic rocks (Oskin et al. 2001; Oskin and Stock 2003b) and submerged continental shelves on both rift margins (offshore Sonora/Tiburón and northeastern Baja California) suggest the modern shorelines were separated by ~30 km until 6.4–6.1 Ma (Bennett 2013). Such narrow gaps were likely devoid of marine water until the 6.3-Ma flooding event, which would have then isolated island species (section 1.2.2). From plate tectonic restorations of the Baja California peninsula back to the southeast (Bennett et al. 2013b), the lateral extent of marine deposits interpreted to be middle Miocene by Helenes et al. (2009) appears too extensive in offshore geophysical data (e.g., Mar-Hernández et al. 2012) for the space available (~30 km) during middle Miocene time. Geological and geophysical observations from offshore basins (e.g., Aragón-Arreola and Martín-Barajas 2007; Mar-Hernández et al. 2012) indicate marine conditions have continuously existed in the Lower Tiburón and Upper Tiburón basins between Isla Tiburón and the Puertecitos area of Baja California since at least ca. 6 Ma. Similar observations from the Lower Delfín basin suggest that the short, northwestern shoreline of Isla Ángel de la Guarda disconnected from Baja California slightly later, ca. 3.3–2 Ma (Aragón-Arreola and

Martín-Barajas 2007). The timing of formation for the narrow Ballenas Channel, which separates Ángel de la Guarda from Baja California, is less well known, but the development of a major strike-slip fault in the Channel likely occurred ca. 3.3–2 Ma (Nagy and Stock 2000; Stock 2000). Finally, isolation of Isla Tiburón from coastal Sonora has likely been transient, with the island connected to the Mainland by land bridges during periods of low sea level (Lambeck and Chappell 2001; Davis 2006; Felger and Wilder 2012; section 3).

1.2. Biological Patterns

1.2.1. Speciation between the Mainland and Peninsula and Endemism (Hypotheses 1a–1d)

Given enough time, a vicariant event that physically divides and isolates a population so the daughter populations no longer interbreed will produce two distinct species as those new populations drift independently and adapt to different environments (Wiley 1988). Given the age of Gulf flooding (8–7 Ma in the south, ca. 6.3 Ma in the north), species with low dispersal potential that cannot interbreed across the Gulf are expected to have started speciating in late Miocene time (hypothesis 1a; see table 1 for hypotheses). Species-level designations of disjunct or widely separated sister lineages have been proposed for several taxa, including gopher, bull, and pine snakes (Rodriguez-Robles and De Jesus-Escobar 2000), crotaphytid lizards (McGuire et al. 2007), desert rodents (Riddle et al. 2000), and spiders (Crews and Hedin 2006), to name a few. The iconic Baja Californian succulent plant, cirio (boojum, *Fouquieria columnaris*), is sister to all other members of Fouquieriaceae, likely due to its isolated evolution on the Peninsula (Schultheis and Baldwin 1999). These studies hint at a widespread pattern of vicariant speciation between the Mainland and Peninsula, which contributes to higher biodiversity. Additional genetic and morphological studies are needed to reveal whether Mainland-Peninsula rifting instigated speciation in species with higher dispersal potential such as plants and birds (hypothesis 1c).

Following rift-related speciation (or at least vicariance), new species are narrowly distributed on an isolated peninsula, which is ideal for generating high levels of endemism, as documented to a stronger effect on islands (Kier et al. 2009). By conservative estimates, over 6,000 species of plants and animals exist on the Peninsula, 30% of which are endemic

(Riemann and Ezcurra 2005; Rebman and Roberts 2012). Of 856 invertebrate species, only tenebrionid beetles, bees, ants, scorpions, and butterflies have been well studied and 30.7% of those studied are endemic. Mammals have 42 species (19% endemic) and reptiles have 96 species (33.3% endemic; see Munguía-Vega 2011 for summary).

The Pacific and Gulf islands host 115 species of reptiles, of which almost half (42.6%) are endemic. Forty-five species of mammals are present on Gulf islands (excluding bats) with a 48.8% endemism rate. Endemism levels are far lower in volant (able to fly or glide) species such as birds and plants, which can likely disperse between islands (Case and Cody 1987; Wilder 2014, and see Rebman 2002 for review of island plants) (the most isolated island, San Pedro Mártir, is only ~50 km from either coast). In Gulf waters, there are 766 documented invertebrate taxa endemic to the Gulf (Brusca et al., 2005). The Gulf is also host to the world's smallest cetacean, the vaquita (*Phocoena sinus*), which is near extinction, and the region provides important spawning and nursery habitat for many fishes and marine mammals.

Ancestral levels of biodiversity that existed before rifting and northward translation of the Peninsula should be considered (for a reconstructed example, see figure 3). For instance, if the region already hosted high levels of biodiversity, then rifting of that region and isolation of the Peninsula and islands would have led to much higher levels than if the region had been species poor prior to rifting. Additionally, movement of the Peninsula northwest over the past few million years could have shifted temperature and rainfall gradients, and should be considered when evaluating modern species distributions and historical barriers. Moreover, while vicariance models of speciation are most commonly applied in this region due to its tectonic and topographic complexity, we must also note the potential for sympatric speciation. For example, adaptation of individuals toward different traits (e.g., food type) may divide a population over time as individuals segregate by those traits and hybrids formed between them are selected against (Maynard Smith 1966). Therefore, even in scenarios where vicariance is likely, similar ecological or sympatric speciation processes may also be occurring.

1.2.2. Biological Evaluation of a Proto-Gulf (Hypothesis 1d)

For geologists, the precise details of how, when, and where a proto-Gulf embayment might have formed are contentious and still under investigation. For biologists, however, these details are less important than the biological patterns they would affect regarding speciation and geographic distributions. The concept of a middle Miocene proto-Gulf embayment is relatively new to biological work (e.g., Hurtado et al. 2010; Dolby et al. 2012); it could have isolated individuals of marine species from their ancestral ranges, potentially leading to vicariant speciation in many taxa. Recent work indicates that speciation ages between Gulf-endemic and non-endemic sister species within the east Pacific bay gobies (estuarine-nearshore marine fishes) cluster between 16 and 10 Ma (Ellingson 2012; Ellingson et al. 2014). This timing coincides with the proto-Gulf embayment hypothesized by Helenes et al. (2009); however, this genetic analysis cannot provide geographic information for where the potential embayment would have existed. Such a biological scenario requires an embayment that continuously persisted from the middle Miocene until the modern northern Gulf flooded ~6.3 Ma, and requires it then physically connected with the modern Gulf to account for modern geographic distributions of these fishes. No evidence presently exists for marine deposits between 11 Ma and ~6.3 Ma, but this theoretical embayment could have produced the middle Miocene marine sediments discussed in section 1.1.2. A middle Miocene—or proto-Gulf—embayment is the most parsimonious explanation for these speciation data. Alternatively, the onset of middle Miocene upwelling in the east Pacific could have played a role, but how this would cause synchronous speciation among Gulf endemics is unclear (Jacobs et al. 2004). Replication of these phylogenetic results with other Gulf endemics and integration with the existing geological framework are needed.

1.2.3. Modern Gulf Influence on Marine Biodiversity (Hypothesis 1e)

Flooding of the modern Gulf 8–6 Ma expanded available marine habitat in the eastern Pacific. Although paleo-oceanographic details of this region since late Miocene time are not well constrained, many have argued that the modern Gulf exerts unique selection pressures on its inhabitants relative to the Pacific for several reasons. First, the Gulf is sheltered from the strong waves driven by the fetch of the Pacific Ocean. Second, tides in the Gulf are notoriously high, reaching 7 m in the north (Roden 1964). Third, sea surface temperatures fluctuate annually up to 16°C in the Gulf compared with <2°C in the Pacific (Ellingson 2012).

Fourth, islands in the Gulf mark localized regions of seasonal upwelling (Zeitzshel 1969). Finally, since the Colorado River first drained into the Gulf ca. 4.1 Ma until twentieth-century damming, it discharged significant volumes of freshwater and sediment into the northern Gulf. When the large Colorado Delta ecosystem formed it offered unique habitat to which delta endemics adapted (Swift et al. 2011). Many species also thrived in the new, extensive riparian habitat (Leopold 1949). Therefore, the abiotic conditions in the Gulf are more seasonally and annually variable than those in the Pacific, and combine to form a unique habitat likely to impart divergent selection pressures. Over time these factors may cause differentiation, and perhaps ecological speciation between Gulf and Pacific marine populations (e.g., Littler and Littler 1981).

1.3. Tectonic Rifting-Associated Hypotheses: Future Work

To test whether rifting of the Peninsula caused speciation in more highly dispersive lineages, such as plants (hypotheses 1a, 1c), additional plant phylogenies are needed at the inter-specific level. The null expectation is that speciation events are distributed evenly throughout a phylogenetic tree between the base and tips. If speciation events within the phylogeny cluster in age and significantly deviate from the null evenly distributed model, then one may infer an external mechanism (i.e., rifting) contributed to that pattern. Phylogenies for plant families Anacardiaceae, Cactaceae, and Fabaceae, with Mainland-Peninsula sister species, would be appropriate for such an analysis. Additionally, trans-Gulf species pairs would provide an opportunity to calibrate the rate of evolution for genes used in other work where time calibration is elusive and reveal interspecific differences in diversification times.

If a proto-Gulf embayment existed and caused the observed diversification of east Pacific bay gobies between 16 and 10 Ma, then one would expect to observe similar synchronous speciation in other taxonomic groups between Gulf-endemic and non-endemic sister species (assuming similar levels of dispersal and population differentiation). Constructing age-calibrated phylogenies of groups with Gulf-endemic and non-endemic taxa is the most direct way to address this question (Magallón 2004; Rutschmann 2006). If similar patterns of parallel speciation and timing are observed in other groups (fish, mollusks, arthropods) with different ecological affinities it would support vicariant speciation via a marine embayment because ecological or environmental mechanisms would be expected to affect such taxa differently. Also, applying different rate-based reconstruction methods is needed (e.g., Drummond et al. 2006; Drummond and Suchard 2010) to determine how robust the east Pacific bay gobies diversification ages are to the assumptions of different evolutionary models. Also, because the existence of a middle Miocene proto-Gulf embayment relies upon a connection to the Pacific Ocean, geologists should locate direct geological evidence of middle Miocene deposits in the San Ignacio or Agua Armada passes to evaluate whether conditions at this time in these regions were marine or nonmarine.

One could evaluate whether ecological speciation is occurring in marine taxa between the modern Gulf and Pacific by focusing on specific traits thought to be under divergent selection pressures between the two habitats, such as body size, and larval or metabolic characteristics that might associate with different salinity or temperature regimes. Differences in gene expression levels across environments can be assessed using RNAseq (transcriptomics), which sequences the messenger RNA produced from the genome to infer how highly expressed a set of genes is with the assumption that genes will be expressed at different levels in different environments (Wang et al. 2009). This method has been used to study hypoxia tolerance in the goby *Gillichthys mirabilis* (Gracey et al. 2001). Additional “common garden” experiments using RNAseq could be used to determine whether any observed physiological differences in expression levels are fixed differences between the populations or plastic, meaning the expression patterns of a population can change in response to the environment.

2. SECOND-ORDER PROCESSES— LAND-SEA INTERACTIONS

2.1. Geological Processes

2.1.1. Geological Assessment of Plio-Pleistocene Midpeninsular Seaways

Over a decade of phylogeographic study has revealed repeated patterns of genetic discordance in topographically low regions along the Peninsula (Riddle et al. 2000; Murphy and Aguirre-León 2002; Hafner and Riddle 2011), but any geological evidence to explain such isolation remains elusive (Lindell et al. 2006; Brusca 2015). Biologists have attributed this vicariance to transient Plio-Pleistocene age transpeninsular seaways that connected the Gulf to the Pacific Ocean through these narrow passes (figure 2B), temporarily isolating northern and southern terrestrial populations. For seaways to have existed through passes now hundreds of meters above sea level requires that the pass was at sea level when the isolation occurred and has since uplifted, possibly due to its proximity to the rift zone (e.g., Mueller et al. 2009; Mark et al., 2014). Two commonly cited locations for these seaways are (1) the Isthmus of La Paz and (2) the midpeninsular region near the towns of San Ignacio and Santa Rosalía. The proposed midpeninsular seaway locations are similar to that suggested by Helenes et al. (2009) for a ca. 12-Ma seaway that would have connected to a proto-Gulf embayment (see sections 1.1.2 and 1.1.3).

No obvious modern barriers to gene flow exist at these locales, and due to a paucity of alternative explanations (but see Gottscho 2014), seaways remain the favored explanation for the genetic discontinuities observed (Hafner and Riddle 2011). The La Paz seaway is thought to have ended ca. 3 Ma, and would not have significantly affected dispersal of marine species because of its proximity to the entrance of the Gulf, but would have isolated terrestrial taxa. For a review of the La Paz seaway see Gentry (1949) and Murphy and Aguirre-Léon (2002).

The midpeninsular seaway is thought to have flooded ca. 2–1 Ma based on the amount of genetic divergence between northern and southern populations and assumed strict molecular clock mutation rates. A Plio-Pleistocene midpeninsular seaway explanation has gained favor in the biological literature because it accounts for dozens of genetic discordance patterns between northern and southern peninsular populations in one explanation. In the Santa Rosalía area the marine Plio-Pleistocene Santa Rosalía formation and rocks of similar age extend inland, reported at elevations as high as 340 masl (Ortlieb 1978). If this observation is accurate, it could support a midpeninsular seaway hypothesis, suggesting that this region was ~340 m lower during Pleistocene time. Alternatively, marine rocks at these coastal sites could be explained by a local inundation of the Gulf during a sea-level highstand, and therefore do not necessitate, though are consistent with, a midpeninsular seaway.

The principal challenge to the Plio-Pleistocene hypothesis arises from the lack of physical or geological evidence (Lindell et al. 2006); no 2- to

1-Ma sedimentary deposits have been discovered in the purported regions despite reconnaissance missions (e.g., Darton 1921; Beal 1948; Wilson 1948). Lack of sedimentary evidence indicates either that the seaway did not exist, or the sediments were deposited and subsequently eroded. Another major challenge to the Plio-Pleistocene midpeninsular seaway hypothesis comes from geologic data that constrain the timing of uplift that formed the high, east-facing topographic escarpment along the spine

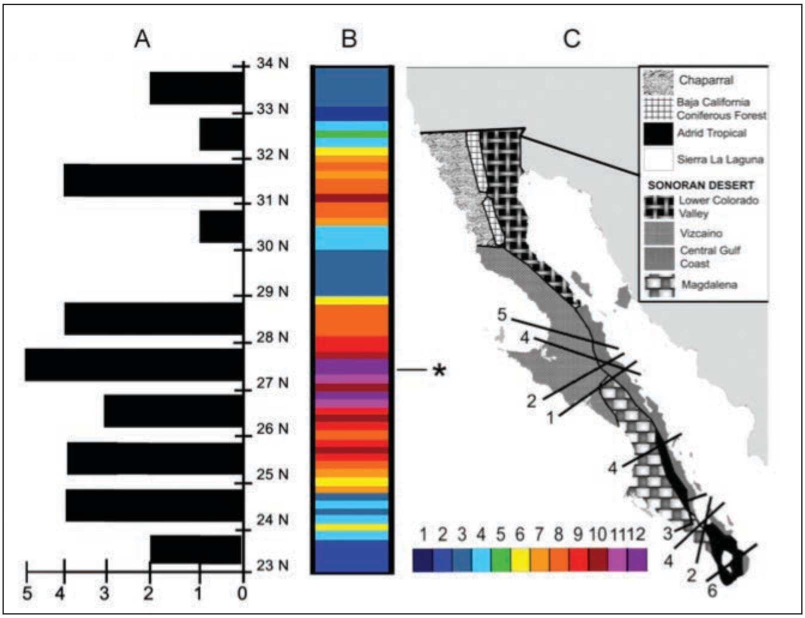


Figure 5: Latitudinal distribution of genetic discontinuities (regions separating two distinct ESUs) along the Baja California peninsula for a subset of 52 taxa analyzed by Munguía-Vega (2011). (A) Frequency of narrow discontinuities (spanning less than 1°20' latitude) in 19 taxa; (B) frequency of narrow and broad (spanning less than 3°0' latitude) discontinuities in 52 taxa, plotted with a resolution of 0°10' latitude; (C) phytogeographic regions on the Peninsula (following Shreve and Wiggins 1964; Wiggins 1980) and approximate location of the discontinuities suggesting the seaways as depicted by different authors. References for the location of proposed seaways: (1) Upton and Murphy 1997, (2) Nason et al. 2002, (3) Alvarez-Castañeda and Patton 2004, (4) Lindell et al. 2005, (5) Crews and Hedin 2006, (6) Lindell et al. 2008. Asterisk indicates area between 27°20' and 27°30'N with 14 genetic discontinuities, the largest value observed in the Peninsula.

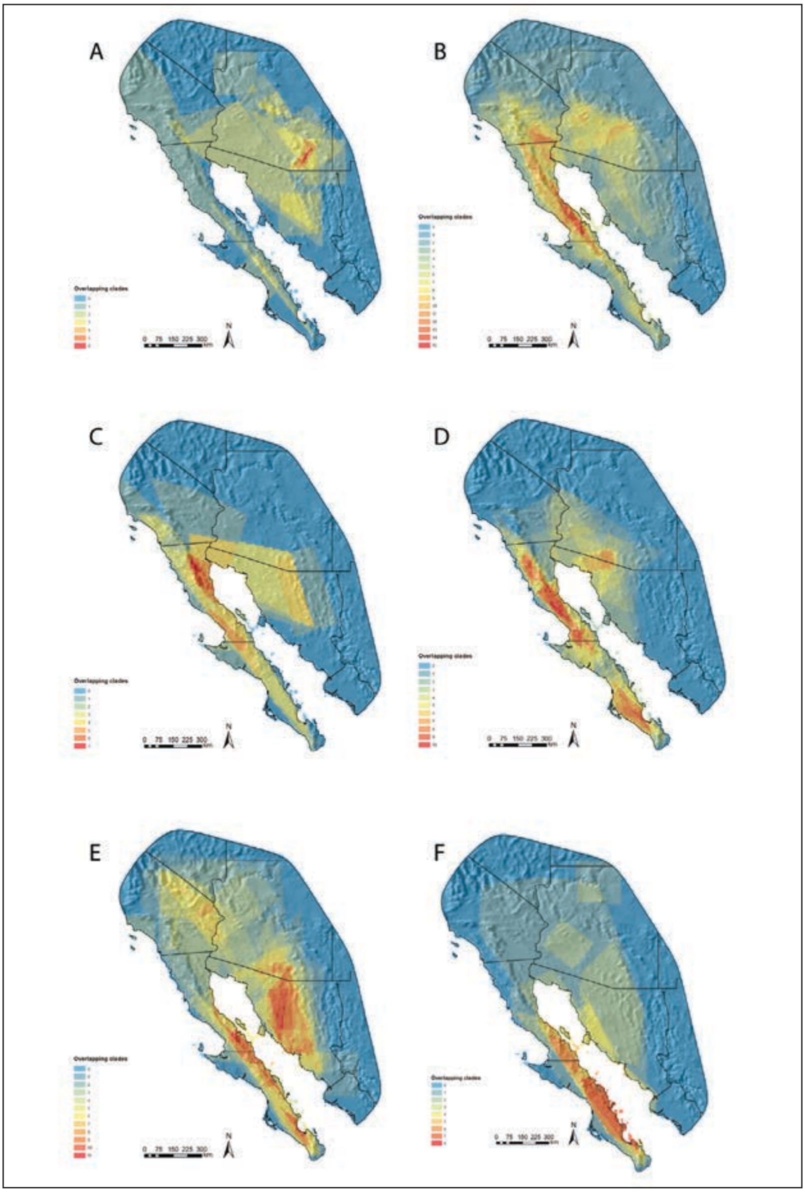


Figure 6: Phylogenetic diversity data illustrating spatial overlap of ESUs from genetic markers (both haploid and diploid) for different taxa: (A) amphibians, N = 4 taxa; (B) reptiles, N = 32 taxa; (C) birds, N = 8 taxa; (D) mammals, N = 14 taxa; (E) invertebrates, N = 21 taxa; (F) plants, N = 6 taxa.

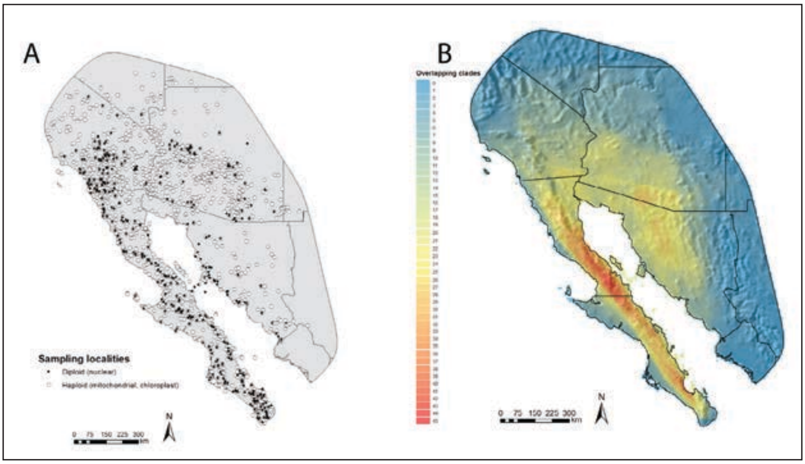


Figure 7: (A) Sampled localities for genetic markers across all taxa with haploid (open circles) and diploid (closed circles) data (N = 85 taxa). (B) Phylogenetic diversity data illustrating spatial overlap of ESUs from genetic markers (both haploid and diploid) for all taxa (N = 85 taxa). See tables S1 and S2 for details on taxa.

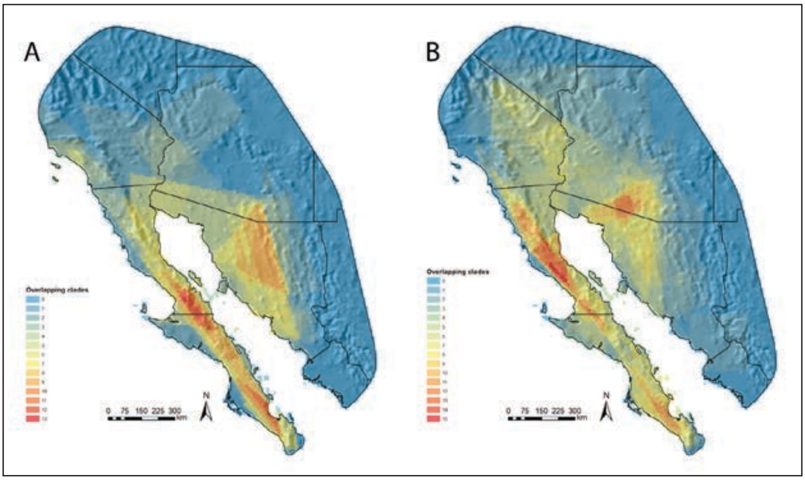


Figure 8: Phylogenetic diversity data illustrating spatial overlap of ESUs from genetic markers (both haploid and diploid) for (A) volant animals, N = 22 taxa, and (B) non-volant animals, N = 57 taxa.

of the Peninsula. Near Loreto, ~15- to 6-Ma lava flows west of the Peninsula's topographic spine have been uplifted and incised, recording a history of vertical tectonic uplift (Mark et al., 2014). Younger lava flows (~3 Ma to recent) have subsequently flowed into these uplift-related canyons. These findings indicate that the majority of vertical tectonic uplift occurred ~6–3 Ma and preclude the possibility that a younger (~2- to 1-Ma) seaway flowed across the central Baja California peninsula since the region had already reached significant elevation. Thus, it is challenging to explain the observed Plio-Pleistocene genetic discordance with a midpeninsular seaway hypothesis.

2.2. Biological Patterns

2.2.1. Genetic Evidence for Midpeninsular Vicariance (Hypotheses 2a, 2b, 2c)

While the geological uplift history makes a 2- to 1-Ma transpeninsular seaway unlikely, this seaway hypothesis motivated much of the terrestrial phylogeographic research in the region. We will review the results of this work generally and formalize the seaway-associated hypotheses.

The meta-analysis presented here of phylogeographic studies along the Peninsula confirms previous work that species exhibit a high degree of geographical structure concentrated in this area (Riddle et al. 2000; Hafner and Riddle 2005; Lindell et al. 2006; Riddle and Hafner 2006; Leache et al. 2007, Munguía-Vega 2011). The frequency of narrow genetic discontinuities departs significantly from a null expectation of uniform geographic distribution over the Peninsula (figure 5A; Munguía-Vega 2011), but the spatial overlap of ESUs is not consistent across organismal groups (figure 6).

Analyses incorporating all previous genetic studies (both haploid and diploid markers) reveal the area of largest phylogenetic diversity in the entire Sonoran Desert is the high-elevation peninsular region between 28°N and 30°N latitude (figure 7B). The northern boundary of this diverse area (30°N) has been previously identified as a region with a high density of genetic discontinuities spanning less than 3° latitude (observed in 52 taxa here; Munguía-Vega 2011; figure 5B). At 30°N, the desert transitions to Mediterranean climate and marks a dramatic change in modern vegetation (Vanderplank et al. 2014). Conservation principles and the Coriolis effect limit the southward migration of the jet stream to ~30°N regardless of the climate state (Minnich et al. 2014), and might explain the northern extent of the diversity center seen in these analyses. The area of highest phylogenetic overlap (and thus likely highest genetic diversity) for non-volant animals is located around 30°N latitude (figure 8B). The area of highest overlap for volant animals is between 28°N and 29°N (figure 8A). Whether this difference is random or indicates that different mechanisms limit the northern limit of diversity for these two groups is unclear.

The number of ESUs observed within taxonomic groups negatively correlates with the ability of individual species to disperse, as expected (Dawson 2001; Soltis et al. 2006; but see Patarnello et al. 2007). Among taxa, reptiles show the largest average number of ESUs per group for haploid markers (3.32; table S1, figure S1C), whereas the lowest was observed within birds (1.57). For diploid markers, largest values were observed for invertebrates (2.75) and lowest for birds (1) (table S2, figure S2G). Within animals, volant animals showed lower levels of genetic structure (average 2 ESUs per taxa for haploid markers) compared to non-volant animals (2.98) (figure S3), but this pattern was not observed for diploid markers (table 2).

Genetic discontinuities in this midpeninsular region in our meta-analysis are broader than authors previously suggested, and vary latitudinally by taxonomic group (figure 6). Both San Ignacio and Agua Armada passes, which were suggested sites of Plio-Pleistocene transpeninsular seaways, are narrow (35–40 km between the northern and southern 400-m contours). The expectation from flooding of these passes is that low-dispersal species (e.g., rodents, reptiles) would be genetically discordant (different) on either side of the barrier (hypothesis 2a), and that high-dispersal species (birds, wind-dispersed plants) would disperse over the barrier and exhibit no genetic discordance (hypothesis 2b). In contrast to this expectation, plants exhibit the greatest genetic discordance in this region (figure 6F). Additionally, both volant (figure 8A) and non-volant animals (figure 8B) exhibit discordance in the middle of the Peninsula.

Importantly, these spatial analyses are only as robust as the sampling density on which they are based, and it is likely many of these studies have sampling schemes that preclude fine-scale geographic interpretation. The average number of sampled localities included in each study is 20, but ranges from 8 (birds) to 40 (reptiles) (table 2). Because the length of the Peninsula is ~1,200 km, 10 sampling locations distributed evenly along a longitudinal transect yield only 1 sample per 120 km. For comparison, the distance between the Agua Armada and San Ignacio seaway passes is only ~65 km. This lack of spatial resolution should be considered when drawing inferences from such data and should guide sampling efforts for future studies.

2.2.2. Marine Patterns and the Midpeninsular Seaway (Hypotheses 2d, 2e)

Riginos (2005) uncovered a north-south genetic discontinuity to varying degrees in five nearshore fishes in the western Gulf, and other studies revealed similar patterns (Stepien et al. 2001; Hurtado et al. 2013). North-south genetic discordance was interpreted as consistent with a midpeninsular seaway, which would have produced a break in otherwise contiguous habitat for nearshore inhabitants. However, fishes with pelagic larval phases can often disperse well. For instance, given a 30-day larval duration, strong Gulf currents can transport larvae up to hundreds of kilometers from the source (Munguía-Vega et al. 2014; Soria et al. 2014), suggesting that even in the presence of a seaway, larvae should likely have maintained genetic connectivity. Also, the precise geographic site of discordance differs between species, which might be expected given species-specific factors governing post-barrier gene flow. Alternatively, the midpeninsular region marks a zone of ecological transition that may better explain these results. The midpeninsular seaway passes (Agua Armada and San Ignacio) are located between present-day northern and southern seasonally driven gyres in the Gulf (Lavin et al. 1997; Marinone 2003) and are currently characterized by cooler temperatures at least half the year (Lluch-Cota et al. 2007). The site of discordance is also near the Midriff Islands where seasonal upwelling occurs (Zeitzshel 1969), and roughly coincides with the northern extent of mangrove habitat in the western Gulf (Whitmore et al. 2005; Aburto-Oropeza et al. 2008). Therefore, any of these ecological factors could produce or contribute to a north-south genetic discordance in the absence of a seaway.

2.3. Land-Sea Interactions: Future Work

More detailed reconstructions of past topography in the midpeninsular region would improve our understanding of land-sea interactions and enable biological interpretations to progress in a geologically feasible framework. Additionally, geologists can use available volcanic dates in

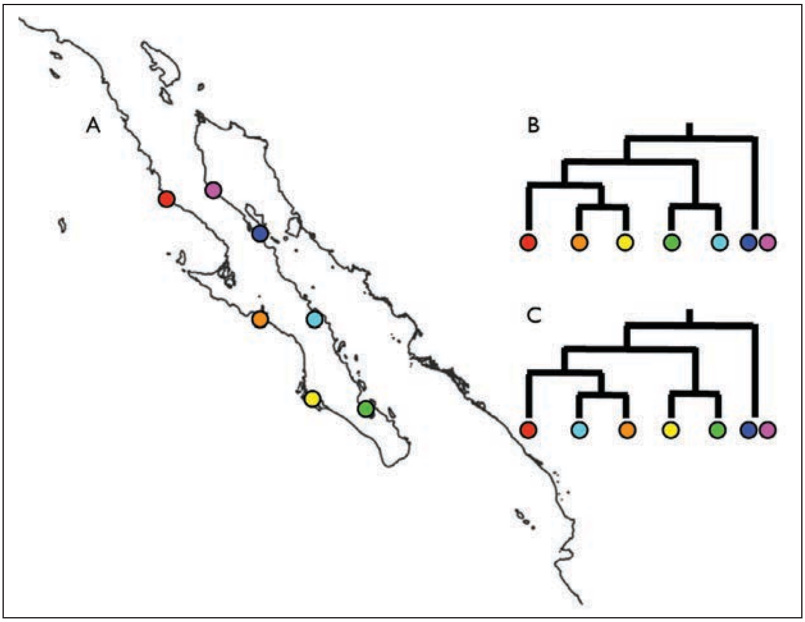


Figure 9. (A) Map of the Baja California coastal marine populations with each population's genetic identity denoted by color (red to violet Hypothesized topologies are presented under two different dispersal scenarios: (B) a null isolation by distance model and (C) topology expected with addition of gene flow through a midpeninsular seaway.

the region to evaluate candidate regions where Plio-Pleistocene strata may be exposed in these passes, which would provide more direct evidence regarding any seaway or regional flooding at this time.

For biological interpretations, it is necessary to learn whether the differences observed between patterns of haploid and diploid markers (figures S1, S2; see section 4.2) are due to mutation rate or marker characteristics (e.g., effective population size). If differences were due to mutation rate it would mean the isolating event was biologically relevant and nuclear (diploid) markers generally evolve too slowly to record the event. If, however, discordance in the mtDNA (mitochondrial DNA) lineages results from the fact that mtDNA records events more readily due to its haploidy and single-parent inheritance, it might indicate that the event, though widespread taxonomically, may not have been as significant as previously thought. Developing robust nuclear datasets with resolution similar to mtDNA could clarify whether this signal is observable in diploid markers. Single Nucleotide Polymorphisms (SNPs) or sequence data through targeted approaches, such as the quickly evolving flanking regions of ultraconserved elements (Faircloth et al. 2013), restriction associated DNA (Miller et al. 2007), or introns, may give comparable nuclear data. Using taxa for these studies that previously exhibited mtDNA discordance provides a natural comparison. Additionally, genetically underrepresented groups (e.g., amphibians, birds) should be prioritized in future studies.

It is possible to use marine taxa to further test the midpeninsular seaway hypothesis. Rather than preventing gene flow along the western coastline of the Gulf as previously studied, for some marine species a transpeninsular seaway would have facilitated gene flow and/or dispersal between the Pacific and Gulf, which today is limited or entirely inhibited for many species by prohibitively warmer southern waters (Bernardi et al. 2003). Under a null hypothesis with no seaway, isolation by distance around the Peninsula is expected, where genetic relatedness between populations is primarily a function of coastal distance between them (figure 9B). The alternative hypothesis includes dispersal facilitated between the Gulf and Pacific Ocean through a midpeninsular seaway. Under this experimental hypothesis, individuals adjacent to the seaway region along the Gulf and Pacific coasts are more closely related than under the null hypothesis (figure 9B compared to 9C). The relatedness of seaway-adjacent populations can be assessed topologically in tree reconstructions, through assignment tests, or via metrics such as Fst (fixation index). If the alternative hypothesis is supported, it would provide independent support for the midpeninsular seaway hypothesis that is less confounded by terrestrial ecological factors (see section 3.2).

3. Third-Order Processes— 100-kyr Glacial-Interglacial Cycles

3.1. Climatic Phenomena

3.1.1. Climate History

The middle Miocene climate transition (14.2–13.8 Ma) is observed in isotope records from deep-sea sediments, which record a dramatic cooling episode of 6–7°C (Shevenell et al. 2004), marking the onset of long-term cooling during which Antarctica's ice volume dramatically grew (Zachos et al. 2001). During the middle Miocene, coastal upwelling intensified along California (White et al. 1992), which imparted a tempering effect on regional climate, delivering cool, nutrient-rich waters that promote primary production and summer fog (for review of biological responses, see Jacobs et al. 2004). Upwelling intensification also led to a general aridification of the western coast, permitting more arid-adapted species over time and the precursor community to the Sonoran Desert (Axelrod 1979), which existed by 8–5 Ma. In late Miocene (11.6–5.3 Ma), offshore sea surface temperatures increased substantially from a winter minimum of 10°C to 17°C by the earliest Pliocene (Barron 1973). Sea surface temperatures off the California coast were still several degrees warmer than today during the early Pliocene warm period (Dekens et al. 2007), beginning 4.6 Ma and ending ~3 Ma with the onset of northern hemisphere glaciations, driven primarily by cyclical changes in Earth's axis and orbit around the sun. Between ca. 3 and 0.8 Ma northern hemisphere glaciations occurred with a 41-kyr periodicity, after which the periodicity increased to 100 kyr, yielding larger temperature and sea-level fluctuations (Mudelsee and Schulz 1997). During these later glaciations, sea levels lowered 100–150 meters below sea level (mbsl), dramatically changing island footprints and forming some land bridges (figure 2C). Since the last glacial maximum (LGM) ca. 20 ka (thousand years ago), temperatures have increased, with slightly higher than present temperatures at the start of the Holocene (ca. 10 ka). Temperatures decreased during the middle Holocene Climate Optimum, which also brought drier conditions in some places (Steig 1999), but the Mexican monsoon climate continued.

3.1.2. Future Climate Change Predictions

Climate change research predicts globally increased temperatures, regional aridification, and increased frequency and/or magnitude of extreme weather events (e.g., droughts, floods, storms) and a rise in mean sea level by 2100 (IPCC 2012). Although the details of how these effects will manifest on the Peninsula and the Sonoran Desert are uncertain, trends are suggested. Some (though not all) Complex General Circulation Models predict El Niño Southern Oscillation (ENSO) activity will increase in strength or become more frequent (Collins et al. 2010). Bakun (1990) proposed that if climate change increased the strength of alongshore winds, then coastal upwelling would intensify along the California coast, increasing both nutrient availability for primary producers and coastal summer fog, which is an additional water source for coastal vegetation in rain-limited climates. The Gulf of California, however, might limit the offshore-onshore temperature disparity by moderating the land-sea temperature disparity and thereby limit or prevent such an increase in summer fog. Lower annual precipitation, primarily through decreased winter rainfall, is predicted, along with lower snowpack volume in high-altitude regions that will melt earlier in the year (Seager and Vecchi 2010). Under increased temperature and decreased precipitation expectations, Ecological Niche Modeling predicted extensive turnover (>30% of species modeled) for those species living on the Peninsula (Peterson et al. 2002). If accurate, the ecosystem constituents observed today might be different in the future, which is of particular concern for endemic species that would have to migrate or face extinction. High-altitude chaparral communities, by contrast, are suggested to be relatively impervious to future climate change (Minnich et al. 2014). Finally, damming and diversion of river waters has already had a marked impact, particularly in the Colorado River delta, which has lost most if not all of the freshwater and sediment discharge it previously had (Brusca 2015), with significant impacts on biology (Kowalewski et al. 2000). Any future regional aridification will further perturb this highly modified hydrographic state, the consequences of which are difficult to predict, but will be challenging for the artisanal fishermen and coastal towns that depend on the Gulf's productivity.

3.2. Biological Patterns

3.2.1. Glacial-Interglacial Vegetation Changes

Significant differences exist between the vegetation during glaciations and what we observe today. Desert scrub, the dominant Sonoran Desert vegetation type today, probably existed for only 10% to 20% of the Pleistocene, unlike open woodland vegetation, which was widespread for ca. 80% to 90% of glacial periods (Van Devender 2002). Fossil packrat middens (*Neotoma* sp.) document expansion of temperate and mesic or moderate moisture-adapted trees and shrubs into desert elevations since the last glacial maximum (LGM) ca. 20 ka (Betancourt et al. 1990), though midden data may be biased toward mesic-adapted species in rocky areas, thus overestimating climate-associated change (Minnich et al. 2014). In the Arizona Upland subdivision of the Sonoran Desert (300–1,550 masl), single-leaf pinyon-juniper woodlands with shrub live oak and Joshua tree dominated during the LGM. Desert trees and scrub plants fully established by 9 ka, when the summer rainfall climate regime was established. More subtropical associated desert plants (e.g., paloverde, saguaro) didn't arrive until 4.5 ka (Van Devender 1990; Metcalfe 2006), and the Sonoran Desert established its present-day boundaries ca. 6 ka (Thompson and Anderson 2000).

On the Peninsula, pinyon-juniper and chaparral species probably extended about 400 km south of their current distributions ca. 10 ka, while the mid-Peninsula may have experienced the Mediterranean climate of southern California and northern Baja California today (Metcalfe 2006) with almost no areas of pure desert vegetation north of 27°N (Holmgren et al. 2011). Lake sediment cores from Laguna Chapala and Laguna Seca in the northern Peninsula support a change from wetter to drier conditions during the early to middle Holocene (Davis 2003; Metcalfe 2006; Roy et al. 2010). Packrat middens from Sierra San Pedro Mártir 650–900 masl record the expansion downslope of chaparral species during the latest Pleistocene followed by their rapid replacement by Sonoran Desert species during the early Holocene (Holmgren et al. 2011). Cataviña (640–680 masl) and San Fernando middens suggest a pinyon-juniper woodland/chaparral in the LGM was replaced by mesquite, and then cactus by middle Holocene ca 5 ka (Van Devender 2002; Metcalfe 2006). In the mid-Peninsula (Sierra San Francisco) a 10.2-ka midden preserves *Juniperus californica* and other chaparral species (laurel sumac, *Malosma laurina*; Baja manzanita, *Arctostaphylos peninsularis*; American wild carrot, *Daucus pusillus*) at 780 masl, suggesting a mild Mediterranean climate 5°C to 6°C cooler with at least twice the winter precipitation of today (Rhode 2002). These cooler conditions in the southern Peninsula are further supported by chaparral communities isolated on high mountain peaks south of 28°N (Moran 1983b).

While desert scrub expanded and the chaparral/woodland vegetation contracted to higher elevations and latitudes toward their current distributions ca. 11 ka, small, isolated areas of mesic environments remained in sheltered canyon oases (Arriaga and Rodriguez-Estrella 1997) and montane habitat above 800 masl throughout the Peninsula (Moran 1983b; Minnich et al. 2014).

3.2.2. Climate, Refugia, and Genetic Discontinuities (Hypotheses 3a–3e)

Glacial refugia are populations that survive glaciations and harbor the majority of the modern genetic diversity within a species (Hewitt 2000, but see Petit et al. 2003). The location, nature, and expansion from refugia on the Peninsula remain unclear.

Northern (Nason et al. 2002) and southern (Garrick et al. 2009) expansion from refugia has been observed along the Peninsula in arid-adapted succulent plant taxa, though the southern expansion results may instead result from differential pollination rates. Instead of unidirectional postglacial migration, topographic relief along the Peninsula may have provided an array of microclimates that hosted refugia during the LGM (Garrick 2010; hypothesis 3c). This view is supported by our analyses showing that areas of highest genetic (phylogroup) overlap correspond to high-elevation ranges in the Peninsula, Sonora, and southern Arizona (hypothesis 3e; figures 7B, S1B, S2B). If the concentration of phylogroups corresponds with historical refugia, then volant animals were located farther south than non-volant animals, both on the Mainland and on the Peninsula. The locations, however, are different for each animal taxonomic group (figure 6); reptile diversity centers between 28°N and 30°N in high elevations of the Peninsula. In contrast, maximum diversity overlap for birds is north of 30°N at higher elevations, and in the lowlands of the lower Colorado Valley east of the mountains. For mammals, the highest diversity centers between 28°N and 30°N at lower elevations west of the mountains, and in the Magdalena plains north of La Paz. Invertebrates and plant patterns were more similar than any other groups and included higher elevations around 28°N latitude and in Baja California Sur (hypothesis 3b). This observation supports ecological co-associations, which are constraints imposed by biotic interactions between insects, herbivores, parasites, and their host plants where one group cannot thrive without the other and vice versa (Garrick et al. 2013). It is therefore expected that distributions (and thus diversity patterns) of such groups are similar. In summary, if individuals retreated to mountainous regions during glaciations, it could create areas of low ESU overlap in the topographically low regions between mountains that could resemble a historical barrier, like a seaway.

Discontinuities for some peninsular species have been explained by regions of poor habitat quality and low density of individuals (e.g., Leache and Mulcahy 2007; Garrick et al. 2009). When species encounter ecological gradients or abrupt changes in climate individuals may adapt to local environments (Grismer 2002), as suggested elsewhere (Lapointe and Rissler 2005; Davis et al. 2008). The strong 30°N non-volant genetic discontinuity (northern diversity limit) corresponds with the transition between the cool, mesic California coastal scrub and chaparral vegetation, and the arid, temperate Vizcaíno region at the start of the Sonoran Desert (figure 5C). This climatic transition is the southern extent of the jet stream, which was likely stable throughout Pleistocene glacial-interglacial cycles (section 2.2.1; Minnich et al. 2014). Climatic stability may have contributed to the high levels of endemism in the California Floristic Province–Sonoran Desert transition zone (Vanderplank et al. 2014) as seen in other Mediterranean regions (Cowling et al. 2014). In other areas, such as California, transition zones between animals and plants known or suspected to hybridize are also located across such climatic gradients (Remington 1968). Another example of regional climate anomalies is the Vizcaíno peninsula (Punta Eugenia), which diverts cold upwelling Pacific waters offshore and marks the transition to increased summer rainfall in the south (Minnich et al. 2014). This transition zone coincides geographically with the midpeninsular discontinuity. Depending on when this phenomenon began, it may have contributed to the midpeninsular genetic discontinuity, or to differential selection pressures across this transition zone that could produce a discontinuity over time. Another alternative, more recently posited hypothesis attributes such biological transition zones to Pacific fracture zones (Gottscho 2014).

Climate-driven ecological gradients may have limited the migration of individuals at intermediate elevations such as mountain passes. Distributions of well-adapted animal subspecies contracted and expanded with different vegetation types during glacial fluctuations (Van Devender 2002). Some desert scrub inhabitants from the Sonoran Desert, such as reptiles (*Sauromalus obesus*, *Uta stansburiana*, *Aspidoscelis* [*Cnemidophorus*] *tigris*, *Trimorphodon biscutatus*, *Hypsiglena torquata*, *Lichanura trivirgata*), an amphibian (*Bufo punctatus*), and mammals (*Dipodomys merriami*, *Neotoma lepida*, *Chaetodipus baileyi*, *Thomomys bottae*, *Peromyscus* sp., *Ammospermophilus* sp.), were found in LGM–early Holocene woodland packrat middens from California and Arizona (Mead et al. 1983; Van Devender 1990). Such occurrences indicate many desert animals were not restricted to southern refuges during glacial periods but remained *in situ*. These observations suggest the phylogeographic patterns observed for some desert reptiles and mammals may not have arisen from extinction and recolonization from southern refugia, but by adaptation to different areas with divergent selection pressures (Davis et al. 2008). A packrat midden from the Lower Colorado River basin (>55 ka) showed a mixture of woodland and desert species that might have survived in small, separate populations within dry patches of woodlands, opposing the traditional concept of desert refugia (Holmgren et al. 2014).

The absence of a desert refugium in the rain shadow of the Sierra San Pedro Mártir (one of the most arid regions of the Sonoran Desert) and the individualistic nature of species' responses to climatic change (Whittaker 1953; Van Devender 1977; Huntley 1991) suggest the concept of a desert refugium should be reconsidered. It seems unlikely that a community of arid-adapted taxa resembling modern Sonoran Desert communities existed during glacial periods. Instead, arid-adapted taxa may have segregated by niche and assembled at the onset of modern climatic conditions ca. 6 ka to form the communities we now term the Sonoran Desert.

3.2.3. Plant Distribution Patterns (Hypothesis 3f)

To define the biogeographic patterns and links between the Peninsula and Mainland we identified plant species co-distributed between them. Through assembly of trans-Gulf floristic listings, georeferenced herbarium patterns for 526 disjunct taxa (table S2) were mapped and four biogeographic patterns were identified.

Widespread taxa (*N* = 346; table S2): The majority of species shared between the Peninsula and Mainland are widely distributed throughout the Sonoran Desert, and generally extend far beyond the boundaries of the desert. Most have long-range dispersal syndromes and produce a widespread biogeographic pattern.

Northern taxa (*N* = 20; figure 10A; table S2): A group of predominantly temperate species wraps around the northern head of the Gulf. They are lowland desert species (e.g., *Ephedra aspera* and *Peucephyllum shottii*) or occur primarily at higher elevations (e.g., *Crossosoma bigelovii*, *Rhus kearnyi*, and *Sideroxylon leucophyllum*).

These species may have been distributed above 32°N and dispersed southward to the Peninsula and Sonora. Many of these species are on the Peninsula and Midriff Islands across the Gulf, but remain confined to the northwest corner of Sonora. The horseshoe distribution pattern resembles that of ring species complexes, which is a unique form of speciation in which the terminal populations (those most distant) are

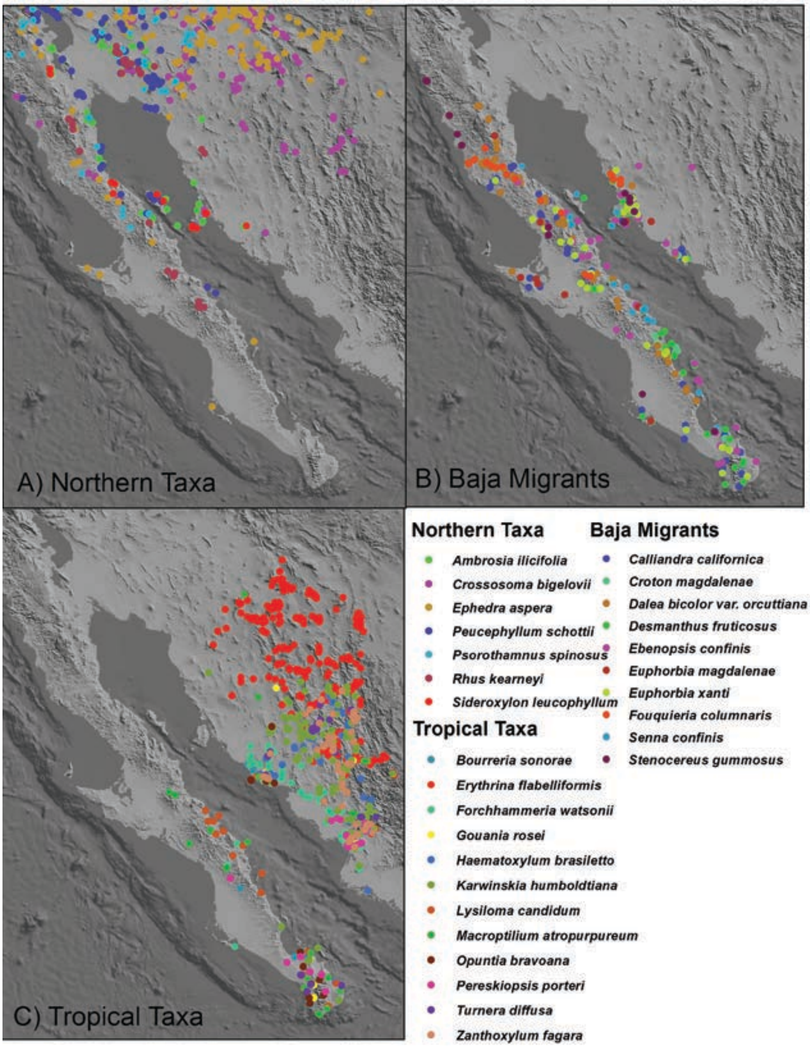


Figure 10: Three distribution patterns are shown, including (A) northern taxa, distributed in a horseshoe pattern around the head of the Gulf, (B) Baja migrants, widely distributed throughout the Peninsula, Midriff Islands, and very limited in Sonora, and (C) tropical taxa, which have southerly distributions with varying northern limits. Sample dots are color-coded according to species (bottom right panel).

reproductively isolated, but remain genetically connected through the intervening populations (Irwin et al. 2001, 2005). For example, Baja California and Arizona/Sonora populations of the *Agave deserti* complex (Navarro-Quezada et al. 2003) are reciprocally monophyletic and the Gulf is a reproductive barrier (Gentry 1978). If such trans-Gulf gene flow at the southern range of such a species is absent, studies into whether ring speciation is occurring and its prevalence among species with this distribution pattern might be of interest.

Baja migrants (*N* = 48; figure 10B; table S2): First identified by Cody et al. (1983), a sizable group of plants is broadly distributed over the Peninsula, across the Midriff Islands, and narrowly on the Sonoran coast. Unlike the northern taxa group, these species are not distributed north, or around the head, of the Gulf.

A hypothesis for the origin of this pattern is that species migrated from the Peninsula to the Mainland via the Midriff Islands. Previous work shows that the Mainland clades, when present, often nest within peninsular ones (Clark-Tapia and Molina-Freaner 2003; Garrick et al. 2009, but see Fehlberg and Ranker 2009). Sea-level lowstands associated with glaciations would have increased island footprints and could have facilitated this gene flow.

Tropical taxa (*N* = 112; figure 10C; table S2): Species with tropical affinities are clustered to the south on either side of the Gulf in Sonora near Guaymas/Alamos and the Cape region of Baja California Sur. These taxa have varying northern limits as they follow the foothills of the Sierra Madre Occidental on the Mainland or the peninsular range in Baja California.

The southern boundaries of the Sonoran Desert are near Guaymas, Sonora (27°55'N), and farther south at the Cape region in Baja California Sur (23°32'N). These areas have mean annual precipitation of 200–400 mm, of which more than half arrives as summer rain (Cody et al. 1983), and might account for the large number of tropically affiliated plants shared across the Gulf.

3.3. Climatic Patterns: Future Work

Future work should test whether the absence of genetic overlap of species in the topographically low midpeninsular region is due to montane glacial refugia or abiotic clines with north-south differential local adaptation, among other hypotheses. If the northern and southern mountains hosted glacial refugia, then within-species genetic diversity should be highest in those regions and decrease toward low-lying regions, and display a strong spatial pattern. Analyses using haplotype networks, or new spatially explicit genetic software programs such as BioGeoBEARS (Matzke 2013), may offer insight given enough data and proper spatial sampling. Such programs can model or test different historical biogeographic scenarios and, given the genetic data, indicate a most probable history. Performing such analyses comparatively on previously studied species would reveal whether this history is shared. The role of local adaptation to abiotic clines could be tested through gene expression or genome methylation studies, which would reveal genes that are differentially expressed between northern and southern populations across numerous taxa. This information would provide specific genes and physiological pathways that are facilitating local adaptation to abiotic factors such as temperature and precipitation.

Our analysis shows strong geographic, taxonomic, and genetic marker biases in previous phylogeographic work that should be improved in future studies (table S1). Sonora is the least sampled area in the Sonoran Desert, particularly for diploid markers (figure S2A). More studies of birds, plants, and amphibians should be included as they compose 9%, 7%, and 5% of the total studies, respectively. Studies using nuclear markers are lacking (only 25.8%), and genetic overlap of distinct ESUs is most commonly observed in studies using haploid markers (compare figures S1 and S2). Even microsatellite data are largely absent, and it is a widely used approach to assess postglacial expansion patterns (e.g., Heuertz et al. 2004). Studies in the Sonoran Desert region have yet to incorporate next-generation sequencing technologies and genomic analyses (e.g., O'Neill et al. 2013). Such methodologies (McCormack et al. 2013) should be applied to desert-woodland/chaparral transition zones such as the La Rumerosa or Magdalena-Cucurpe to infer the histories of modern desert edge communities. Exemplar taxa in the sky island relictual habitats could also be investigated to see if these regions are, in fact, stable over Pleistocene time. Finally, ancient DNA from packrat middens would provide an ancient analogue to modern conditions, perhaps with the ability to assess historical biogeographical patterns as a comparison to today.

4. CONCLUSIONS

4.1. Summary of Findings

Rifting of the Baja California peninsula from Mainland Mexico and formation of the Gulf of California produced speciation of terrestrial taxa (e.g., reptiles, amphibians, arachnids) that do not disperse around or across the Gulf. More species-level genetic work is needed to address whether similar divergence occurred frequently in highly dispersive groups (e.g., plants and birds). The high degrees of insular, peninsular, and Gulf endemism stem from this rifting combined with subsequent isolation. Flooding of the modern Gulf (ca. 6 Ma) created new marine habitat that likely exerts different selection pressures on its marine inhabitants compared to the Pacific Ocean, and may be a source of ecological speciation, though explicit testing is required. The proto-Gulf hypothesis of an old (ca. 15- to 12-Ma) marine embayment differs in detail between biology and geology. Geological evidence for its location and cause is lacking, but reworked middle Miocene marine microfossils and synchronous speciation of Gulf endemic and non-endemic sister species of east Pacific bay gobies may suggest the presence of a middle Miocene marine embayment somewhere in northwestern Mexico. The precise location, size, and shape of such an embayment remain unknown.

Physical evidence for midpeninsular seaways is absent and recent uplift estimates indicate these passes may have been floodable during middle Miocene time, but are unlikely to have flooded during the Plio-Pleistocene. Additional support against Plio-Pleistocene seaways comes from our analyses showing that north-south midpeninsular genetic breaks are also observed in highly dispersive taxa, which would probably have been able to disperse over such a barrier. We offer alternative explanations for the ubiquitous north-south discordance pattern observed: (1) Stability and range of microhabitats afforded in montane regions to the north and south may have afforded glacial refuges so populations were repeatedly isolated, or (2) there was differential north-south adaptation to temperature and precipitation gradients; each of these explanations would explain why midpeninsular valleys exhibit low ESU overlap.

Four plant species distribution patterns are uncovered that may originate from rifting and/or postglacial migration. Future genetic studies should focus on these species to understand connections between the Mainland and peninsular portions of the Sonoran Desert. Packrat midden data indicate that glacial refuges probably did not resemble modern Sonoran Desert communities. Instead, response to climatic events may be much more individualistic and less community oriented (except for obligate or co-associated species). We suggest the opportunities to advance this knowledge are in application of large nuclear and ancient DNA data.

Finally, the analyses performed herein reveal a major bias toward taxonomic group (reptiles and mammals) and mtDNA (table 2). We suggest that, to differentiate between competing hypotheses and eliminate confounding variables, these patterns be reevaluated with nuclear data, for which several methods are suggested (section 2.3). Additionally, alternative approaches using topographical analysis and marine species would provide novel, independent perspectives on long-debated hypotheses.

4.2. Caveats and Concerns of Mitochondrial Genetics

Genetic discontinuities decrease quickly, independent of a population's size, after gene flow is restored between temporarily isolated populations (Irwin 2002). However, the non-recombining (i.e., it acts as a single gene) nature and single-parent inheritance pattern of the mitochondrion can make this discontinuity observable much longer in mitochondrial than nuclear DNA (Rubinoff et al. 2006). Therefore, the lasting discordance observed among many taxa along the Peninsula may be biased by a heavy reliance on mtDNA.

Another caveat is that since the mitochondrion does not recombine, mtDNA-based interpretations may reflect a gene lineage and not necessarily the true history of the populations. In the absence of several independent markers, stochastic coalescence processes may drive patterns and interpretations in the absence of a "real" biological signal. Munguía-Vega (2011) demonstrated that mtDNA discontinuities can arise spontaneously if the migration rate is only one successful migrant per generation between populations. As an example, reciprocal mitochondrial monophyly could arise (assuming one generation per year) in just 20,000 years (e.g., since the LGM, Andrews and Barry 1978), with a census size of 400,000 individuals (e.g., Ne = 20,000, 5% of census size), without any physical barrier. These findings signify that continuously distributed species with restricted dispersal can form genetic discontinuities in regions where migration has never been completely impeded, and therefore an impassable physical barrier is not always required.

Another process that may be occurring in some species is reinforcement, in which permanent biological barriers such as low hybrid fitness, incompatibility of alleles, and postzygotic isolation mechanisms limit interbreeding between previously isolated populations (Crews and Hedin 2006). The hybrids form in the zone of secondary contact (i.e., purported seaway region), the width of which is proportional to fitness of the hybrids. In this case, strong selection pressure against hybrids would be required to explain the narrow north-south genetic discontinuity, but this could be aided by ecological gradients imparting divergent selection regimes during isolation (Barton and Hewitt 1985; Phillips et al. 2004; Macholan et al. 2007). Whether selection against hybrids in the secondary contact zone would affect so many taxa similarly is uncertain, and the general absence of morphological diversification has termed this "cryptic" divergence.

4.3. The Assumption of Parsimony

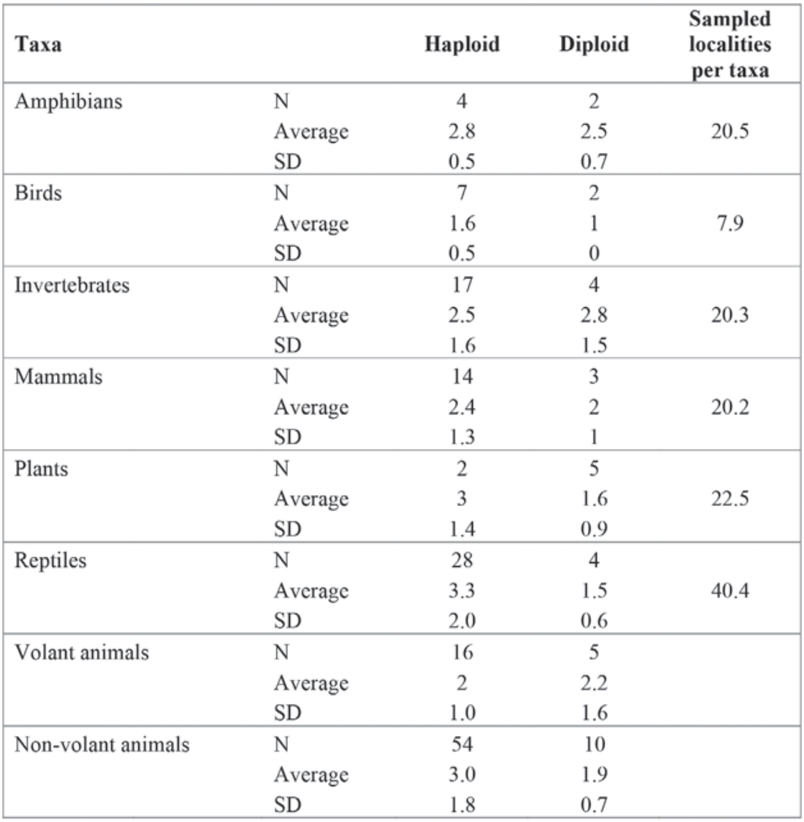
Parsimony, the assumption that the simplest explanation is most likely, is among the most widely used assumptions in biology, yet its veracity and appropriateness are rarely testable. To date, researchers have favored parsimonious explanations where a single event (i.e., a seaway) is used to explain dozens of intra-specific patterns of diversity and discordance among co-distributed species (as theory advises). However, this review suggests that a single discrete explanation is sometimes insufficient to account for the patterns observed, many species with complex histories may not be shaped by a single barrier, and that barrier or event may not affect all species similarly. The actual biodiversity patterns can result from different underlying factors operating at different times and locations that result in similar phylogenetic patterns (i.e., pseudocongruence) (Lapointe and Rissler 2005; Feldman and Spicer 2006; Riddle and Hafner 2006; Soltis et al. 2006; Chatzimanolis and Caterino 2007). This vicariance explanation also highlights what may have been a reluctance to call on ecological factors as primary agents in isolation and diversity patterns along the Peninsula.

As a region with complicated tectonic and climatic histories, the Gulf of California and broader Sonoran Desert constitute a setting where the assumption of parsimony in interpreting evolutionary patterns should be reconsidered.

4.4. An Interdisciplinary Future

Significant debates have persisted in geology regarding existence and nature of a proto-Gulf of California, timing and details of modern Gulf formation, and translation and structure of the Peninsula through time. Similar debates within biology regarding presence of a midpeninsular seaway, the role of abiotic gradients, and Pleistocene refugia have continued as well. Widespread biological patterns, however, are usually the genuine result of physical or climatic processes (e.g., seaways, rifting, glacial-interglacial oscillations), and can thus be used to inform the nature of such underlying events even in the absence of physical evidence or reason to search. Biological patterns, however, can also arise from random

Table 2. *Average number of ESUs, sample size (number of taxa, N) and standard deviation (SD) for taxonomic groups, haploid and diploid markers, and average number of sampled localities per taxon.*



Taxa		**Haploid**	**Diploid**	**Sampled localities per taxa**
Amphibians	N	4	2	20.5
	Average	2.8	2.5	
	SD	0.5	0.7	
Birds	N	7	2	7.9
	Average	1.6	1	
	SD	0.5	0	
Invertebrates	N	17	4	20.3
	Average	2.5	2.8	
	SD	1.6	1.5	
Mammals	N	14	3	20.2
	Average	2.4	2	
	SD	1.3	1	
Plants	N	2	5	22.5
	Average	3	1.6	
	SD	1.4	0.9	
Reptiles	N	28	4	40.4
	Average	3.3	1.5	
	SD	2.0	0.6	
Volant animals	N	16	5	
	Average	2	2.2	
	SD	1.0	1.6	
Non-volant animals	N	54	10	
	Average	3.0	1.9	
	SD	1.8	0.7	

or biotic factors, in which case geological evidence can rule out competing external mechanisms, and remains the only source for absolute dating. Each discipline provides an opportunity for independent knowledge and evaluation that should be used to advance the understanding within each field, particularly when faced with conflicting evidence within a discipline. In light of the emerging field of geogenomics and a broad emphasis on interdisciplinary research, our review suggests that to move such debates forward and construct a holistic understanding, synthetic, cross-disciplinary research is not just innovative, but necessary. ✥

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