UNIVERSITY OF CALIFORNIA
RIVERSIDE

Correlates of Plant Biodiversity in Mediterranean Baja California, Mexico.

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Plant Biology

by

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August 2013

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Acknowledgements

First and foremost I acknowledge my advisor, Exequiel Ezcurra, for his patience, kindness and excellence in mentoring. Similarly Richard Minnich and Norman Ellstrand of my committee have both been highly supportive and academically nurturing and I am most grateful. I remain indebted to my long-term mentors Lucinda McDade and Richard Felger for their ongoing support; and for academic counsel throughout the last three years I sincerely thank the following individuals who have contributed importantly to my academic formation: Jon Rebman, Naomi Fraga, Alan Harper, Bart O'Brien, Steve Junak, Jose Delgadillo, Hugo Riemann, Tom Oberbauer and Phil Rundel. For archeological and malacological information I am grateful to Tom Demare, Jerry Moore, Margaret Conkey, Hans Bertsch, Carlos Figueroa, Enah Fonsecca and Matthew Des Lauriers.

I am grateful to my lab-mates Benjamin Wilder, Alejandra Martinez and Andrew Semotiuk who have been my friends and colleagues. I thank Andrew Sanders and Teresa Salvato for their generous assistance with all herbarium activities. Nicki Rorive, Deidra Kornfeld, Maria LaBarrie and Henry Gutierrez have each been enormously kind and helpful. Robert Graham, Woody Smith and Aapris Frisbie generously assisted with soil samples and soluble isotope analyses; James Sickman facilitated the Carbon Isotope analyses. I also thank the 2012 Graduate Student Association for their patience with my travel schedule.

For funding I am profoundly grateful to the Jiji foundation, who made it possible for me to spend the third year of my research in the field, and to Jim Riley who graciously gave stipend funding for research expenses in 2012 and 2013. I am also grateful to Saul Alarcon and Terra Peninsular A.C., for providing office space and a community in Ensenada; the Cabrillo Marine Aquarium for field trips to the Pacific Islands in 2012 and 2013; Rancho Santa Ana Botanic Garden and the San Diego Natural History Museum for office space, resources, and a thriving research community; and to Jim Folsom and Huntington Botanical Gardens for their collaboration and comradeship.

My deep appreciation is expressed to O'Malley Miller and the Miller Family Charitable Trust; and Wade Killifer and Club La Misión of San Vicente, for the resources that made the phenology study feasible. I am grateful to Heriberto Arauz for his tireless assistance throughout the project. I thank the following friends and landowners for their generosity in permitting the installation of the weather stations and visitation: Pedro Verduzco, Izaias Rudamedkin, Guadalupe Panyagua, and Jose Gabino Covarrubias. Thanks to Francisco Jose del Toro Guerrero and Terra Peninsular. A.C. for assistance with figure iii, 2.3, and 3.1.

For assistance with fieldwork I am grateful to:
Adriana Romero, Alan Harper, Alex Rudametkin, Asunsción Soler, Barbara Eisenstein, Bart O'Brien, Ben Wilder, Bernardo Alps, BJ Ledyard, Carlos Figueroa, Carol Baird, Cesar Garcia, Charlie DeLaRosa, Chris Mankey, Cody Coyotee Howard, Diane Alps,

Domingo Flores, Elisabet Whencke, Eulogio Lopez, Fred Roberts, George Simancas, Giandiego Campetella, Horacio Moncada, Isabel Granillo, Jesus Loya, Jim Riley, Joan Citron, John Case, John Trager, Jorge Alcantar, Jorge Flores, Jorge Montiel, Jorge Ochoa, Jose Alonso Villareal, Josue Campos, Karen Zimmerman, Larry Fukuhara, Luis Barragan, Matt Guilliams, Maximo Velasquez, Paul Cipolla, Pauline Hughes, Raul and Caroline Aguiar, Raul Arce, Romulado Ortiz, Sandy Valderrama, Sarah Ratay, Sean Lahmeyer, Sergio Mata, Steve Pietrolungo, Tom Mulroy, Wally Boggess, and Xavier Lopez.

I thank my parents, Penny and John Vanderplank, for their lifelong support of all my endeavors, and Familia Sanchez for welcoming me into their home and family during my Riverside years. I thank Captain Jim (Rambo) Hughes and the crew of the Cortez (Hopper, Rooster, Chuck and Jake) for providing the perfect office space for completion of this dissertation, and for their friendship throughout the process.

The text of this dissertation in part, is a reprint of the material as is appears in Vanderplank, S. 2013. Endemism in an ecotone: from Chaparral to Desert in Baja California, Mexico. *In:* C. Hobhom (ed.) 2013. *Vascular Plant Endemism.* Springer-Verlag. In Press.

Dedication

I dedicate this thesis to Dr. Alan Harper, for his tireless efforts to conserve land in Baja California, and his support of my endeavors in research and conservation of a place that is so dear to us both.

ABSTRACT OF THE DISSERTATION

Correlates of Plant Biodiversity in Mediterranean Baja California, Mexico.

by

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Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, August 2013
Dr. Exequiel Ezcurra, Chairperson

Northwestern Baja California is an area of exceptionally high local endemism, nestled at the southernmost end of the California Floristic Province (CFP), one of the world's mediterranean-climate regions. The ecotonal position between the CFP and the central deserts of the Baja California Peninsula reflects the transition of the major climatic regimes. This area appears to have been more climatically stable than adjacent areas, and the local endemism along the coast is largely the result of the persistent marine layer, which buffers temperature extremes and maintains moisture during the drier months of the year. The driving hypothesis of this dissertation is that long-term climatic stability provided by the cold coastal upwelling of the California Current (driven in turn by the large-scale circulation of the seas) has buffered climatic conditions along the coast, reducing species extinctions and allowing adaptive processes leading to high levels of endemism in the local flora. The high productivity of the coastal upwelling has also had an impact on local plant diversity through the impact of prehistoric shell middens on soil heterogeneity: Ocean deposits (aragonite shells) extracted by indigenous people have added to landscape complexity and increased biological diversity along the coast. Shell middens are scattered along the coast, and idiosyncratically change soil conditions and the resultant plant communities. Shell middens consistently increase native plant diversity, but with very different species compositions, overlapping conservation priorities for archeology and biodiversity. The climate-buffering effect of the coastal currents can be evaluated in the flowering dynamics of the local plant communities: Plant phenology is predominantly controlled by season and available moisture. Fogs dampen seasonality in flowering times and plants flower for longer time periods at the coast, allowing probable mechanisms for speciation. This stability is consistent with the high levels of endemism that can be seen along the coast, and in microclimate effects on phenology along the inland-to-coast gradient. Conservation of coastal habitats in this southern edge of the California Floristic Province is of elevated importance due to the refugium effect of the marine layer, and the presence of archeological sites that increase biodiversity.

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Preface

Mediterranean climates (hot dry summer and mild wet winters) are found in five regions of the world (Fig. i). Each of these regions has an equator-ward transition into arid summer-rainfall deserts near the 30th parallel, which creates a major phytogeographic ecotone with a mix of mediterranean and desert adapted species (Vaks *et al*. 2006; Dean & Milton 2000; Rundel *et al*. 1998; Bahre 1979). Four of the five regions have a cold offshore current, which generates summer fogs that increase available moisture in the dry season (Fig. ii). Ironically, it is the marine inversion coupled with fogs that create the west-coast deserts. These regions of fog-desert and transition to mediterranean climate are unique globally, with each continent exhibiting significant areas of local endemism that are among the worlds biodiversity hotspots (Myers *et al.* 2000).

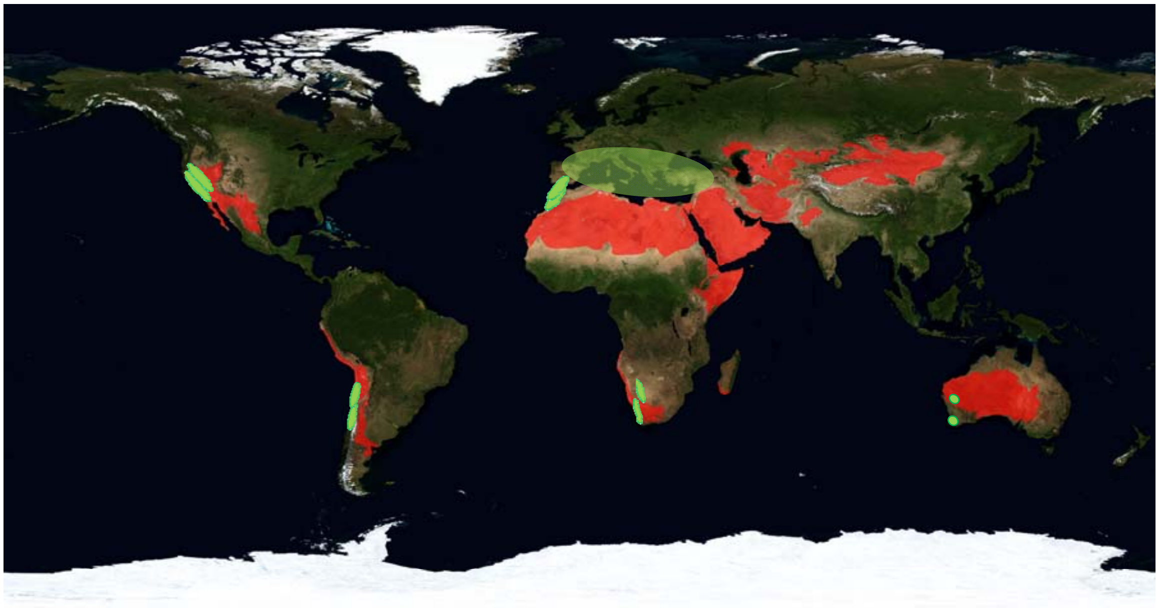

Fig. i. World map; Green polygons are approximate mediterranean climate regions, red areas are deserts (adapted from Ezcurra & Mellink 2013). Note the similarity of latitude in the mediterranean climate regions.

Ecological dynamics of the mediterranean-climate regions of the world have stimulated global collaborative research since the development of the International Biological Program in the 1970s and some milestone publications have resulted from these large-scale efforts (Cody & Mooney 1978; Di Castri *et al.* 1981; Ehleringer & Mooney 1983; Di Castri 1991). Regions of mediterranean climate are known to have inordinately high biodiversity as compared to other areas of similar latitude, making each of them a global biodiversity hotspot (Cowling *et al.* 1996, Myers *et al.* 2000). This biodiversity has recently been shown to be more closely related to climatic stability and reduced rates of extinction, than a rapid diversification during the development of the mediterranean climate (Lancaster & Kay 2013; Sniderman *et al.* 2013).

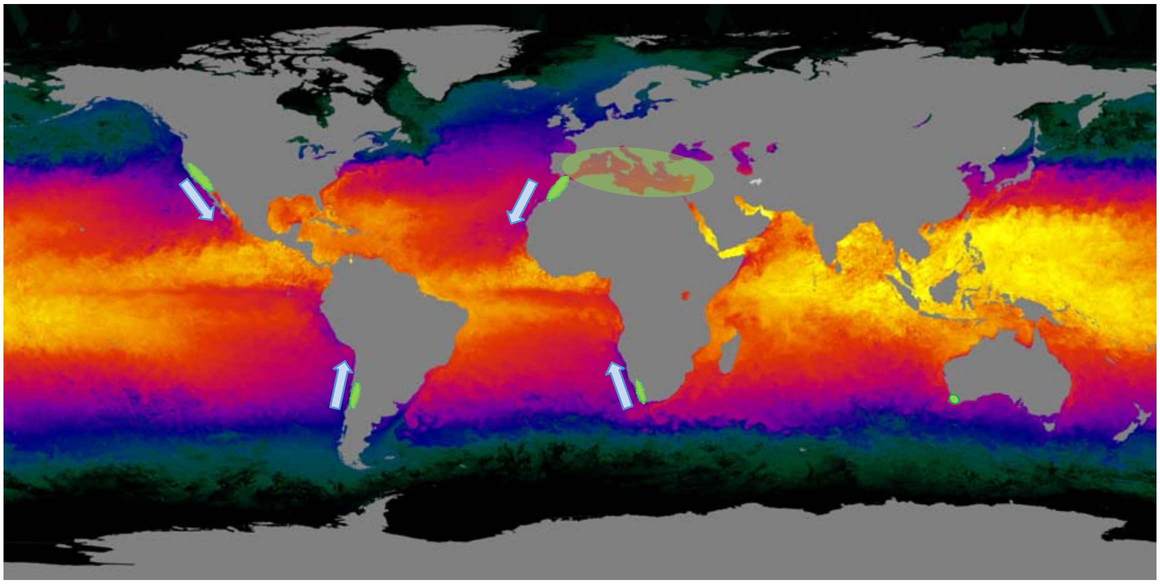

Fig ii. Green shapes are approximate mediterranean climate regions of the world, base map shows sea surface temperatures; blue arrows indicate directions of off-shore currents that cause coastal upwelling (adapted from Ezcurra and Mellink, 2013).

The California Floristic Province (CFP) (Fig. iii) is the mediterranean climate region of North America, a set of coastal, winter-rain habitats that start in the wet forests of the Pacific Northwest and transitions into the central desert of Baja California, Mexico, in the south (Minnich and Franco Vizcaíno 1998). There are several ecotones on the peninsula of Baja California (Fig. iv) that almost all exhibit elevated species richness and/or endemism. The mediterranean-desert ecotone is home to high levels of both plant species richness and local endemism. A closer look at the distribution of these endemics (Riemann & Ezcurra 2007) shows a coastal belt of endemic species between the 30th–32nd parallels (Fig. iv).

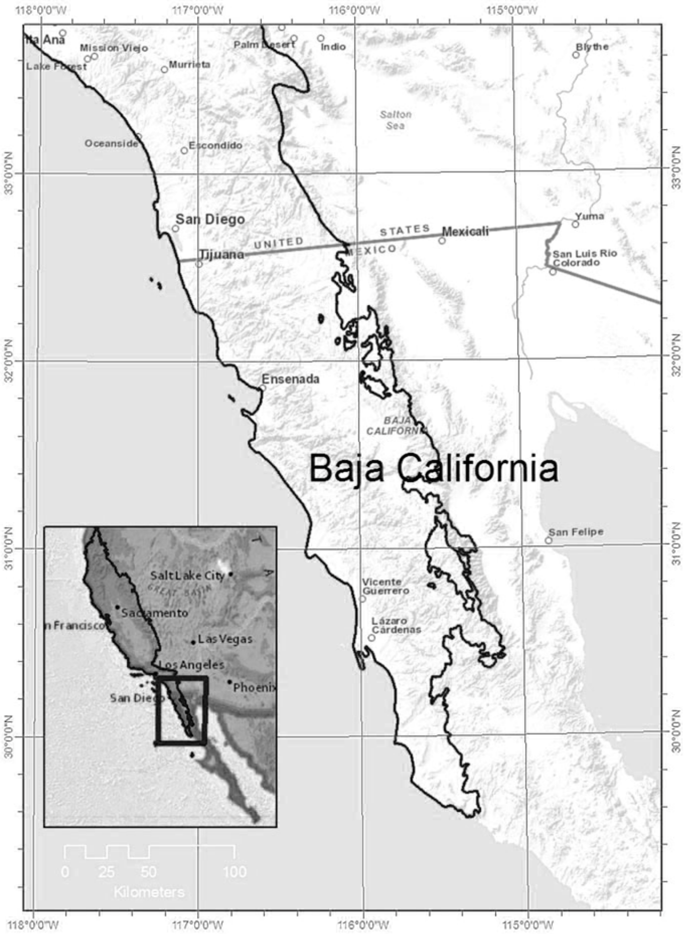

Fig iii. California Floristic Province (inset) and area of study outlined in black.

Ecotones are commonly areas of high species richness chiefly due to the presence of species from both adjacent ecoregions. In some large geographic ecotones high biodiversity may also be the result of localized endemism (Fig. v).

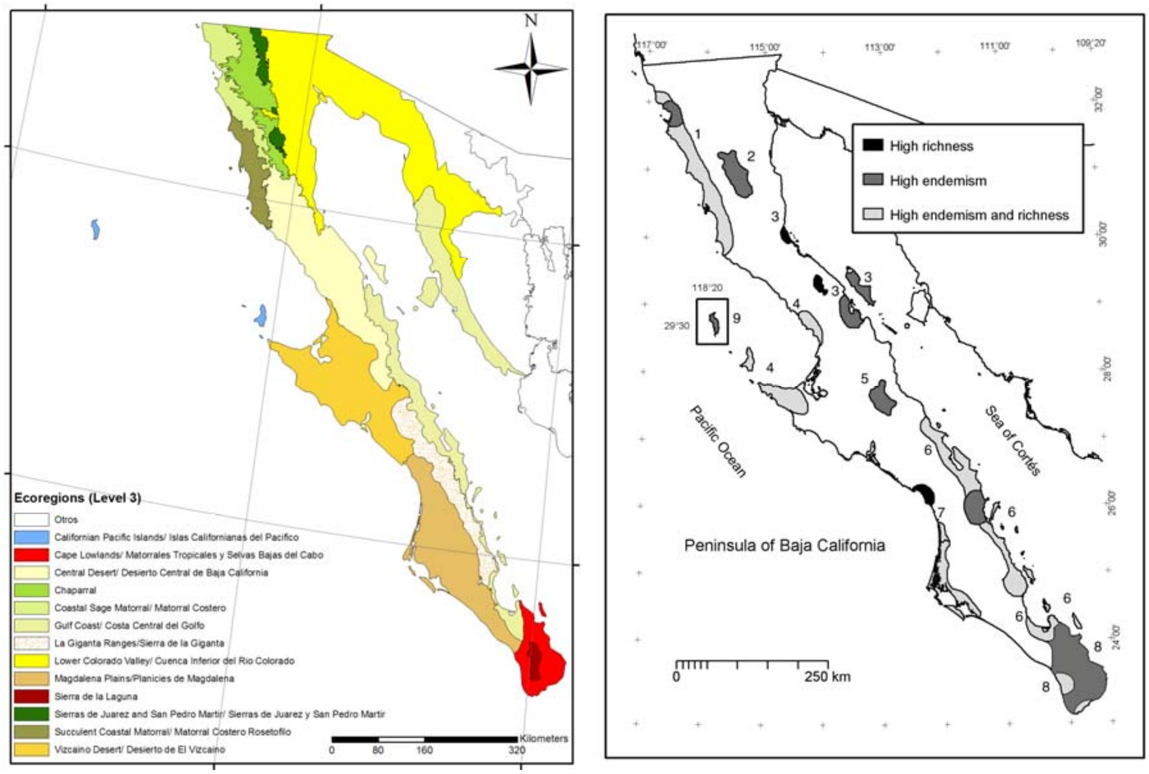

Fig iv. Ecoregions of the peninsula of Baja California and areas of richness and endemism (left from Garcillan *et al.* 2010, right from Riemann & Ezcurra 2007).

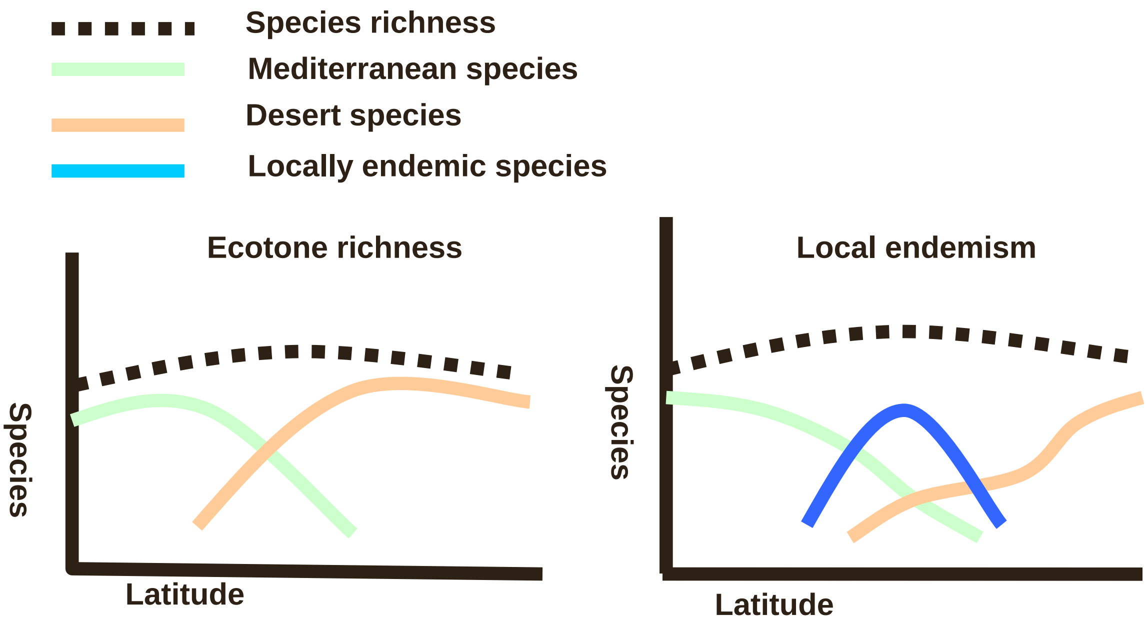

Fig. v. Source of ecotone richness. Left graph shows expected sources of ecotone richness; right graph shows actual sources of ecotone richness.

The plants of this region currently have no protected areas at the state or federal level, and are conserved only in private protected areas (including two natural reserves (ca. 22,000 acres) owned by the non-profit organization Terra Peninsular, A.C.), and through UMA's (Unidades de Manejo Ambiental para la Conservacion) which offer sustainable use easements for activities such as hunting. As demonstrated by Riemann & Ezcurra 2005, there is an urgent need for conservation of this under-studied region of exceptional species endemism. This thesis attempts to document some of the causal factors of endemism and species richness in this highly impacted area of rapid urban expansion.

"The transition region between the chaparral and desert in Baja California is a particularly critical one in which many isolated endemics....can be found"
Raven & Axelrod (1995)

The leitmotif of this dissertation is – what are the oceanic influences on the distribution of plant biodiversity and endemism found in the coastal ecotone of Northwestern Baja California?

The distribution of endemism in the ecotone strongly suggests oceanic influences on the vegetation. To better understand how land-ocean dynamics influence biodiversity in mediterranean Mexico, and the origins of this hotspot of biodiversity, I present novel data on the climatic, pre-historic and phenological patterns that influence the biodiversity seen today. This dissertation treats sources of biodiversity in three separate chapters that have been individually prepared for publication in peer-reviewed journals or books.

Chapter 1: Land-ocean dynamics as drivers of endemism and how water has shaped the modern flora: *"Endemism in an ecotone: from Chaparral to Desert in Baja California, Mexico"*

Chapter 2: Pre-historical human activity and landscape complexity: *"Biodiversity and Archeological Conservation targets connected: Aragonite shell middens increase floristic diversity and landscape heterogeneity on the forgotten peninsula"*

Chapter 3: Land-ocean dynamics and variations in plant flowering times: *"Coastal Fogs, Plant Phenological Dynamics and Refugia in Mediterranean Mexico"*

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Chapter 1:

Endemism in an ecotone: from Chaparral to Desert in Baja California, Mexico

Introduction

Vegetation patterns on a global scale are primarily determined by climate. The mediterranean climate of coastal California and the first true desert conditions in western North America are thought to have originated during the late Miocene and the Pliocene, 5–10 million years ago, with the most recent migration of warm-desert vegetation becoming extensive approximately 12,000 years ago, after the end of the last glacial period (Frenzel 2005; Raven & Axelrod 1978; Axelrod 1978). Regional geography also has a significant impact on plant distributions; when the Baja California peninsula broke away from mainland Mexico new barriers to plant migrations was formed. The peninsula is recognized as a center of unique biodiversity, largely due to its isolation from the mainland (Garcillán *et al.* 2010). The northwestern region of the peninsula has a mediterranean climate and chaparral vegetation, but to the south and east lies the Sonoran Desert, with vegetation adapted to some of the hottest conditions in the Americas.

This case-study is focused in the region between parallels 30 and 33 in Baja California, Mexico (Figure 1). Along the Pacific Coast of North America a mediterranean climate prevails, resulting in a phytogeographic region known as the California Floristic Province (CFP) stretching from southern Oregon to northern Baja California. The mediterranean climate is characterized by hot dry summers and cool wet winters. Differences in the air temperatures in the troposphere cause jet stream winds to sweep across the Pacific Coast. In North America the moisture-laden jet stream passes over land, its strength has a positive correlation with the latitudinal temperature gradient (Minnich *et al.* 2000). A rainfall gradient from winter to summer precipitation is clearly observed as one moves southward along the peninsula of Baja California (Caso et al. 2007; Minnich *et al.* 2000; Hastings & Turner 1965; Aschmann 1959; Shreve 1936). Mean monthly temperatures vary little across northwestern Baja California (13ºC, or 55ºF, in winter and 23ºC, or 73ºF, in summer in the north at Tijuana, and 14ºC, or 57º F, in winter and 24ºC, or 75ºF, in summer to the south at El Rosario). Rainfall is not predictable in the ecotone and the evapotranspirative balance varies significantly between seasons and between years. The Sierra de Júarez and the 3,000-m high Sierra de San Pedro Mártir form the spine of the peninsular ranges that act as a barrier to westerly winds, creating mediterranean winter rains from the coast to the crest of the sierra, and rainshadow of Sonoran Desert to the east. The southern end of the Sierra de San Pedro Mártir meets the relatively low relief of the central desert and that region coincides with the shift from mediterranean climate to arid and semi-arid climate near the 30th parallel. That break in the topography allows north-westerly winds to blow across the peninsula moving moisture quickly across the landscape into the Gulf of California and the Mexican mainland, resulting in reduced precipitation in the peninsula.

The California Floristic Province (CFP) has been designated as a global biodiversity hotspot, an area of high endemism that has been heavily impacted by human activity

(Myers et al. 2000). The CFP, home to 2,125 endemic vascular plants, originally occupied 324,000 square kilometers. Today only 80,000 square kilometers – less than 25%, remain naturally vegetated (Myers et al. 2000). The Baja California portion of the CFP is home to around 1,800 native vascular plant species, with almost half being rare, threatened, or locally endemic in the region. O'Brien et al (in press) evaluated all plant taxa within the CFP of Baja California, scoring them for rarity and endemism, and documenting 172 plant taxa entirely endemic to the region (ca. 10% of the native flora) and an additional 67 near-endemic species. These 239 species represent more than 11% of total endemism for the entire CFP in an area that is less than 5% of the size of the total province. Minnich & Franco-Vizcaino (1998) using aerial photos produced the first vegetation map of northwestern Baja California that shows major vegetation assemblages and areas of land clearing.

Cowling et al. (1996) examined the flora of California and other mediterranean climate regions and speculate that speciation arises from disruptive selection and is strongly driven by fire and climate change. Fire suppression is less practised in Baja California compared to California, and studies comparing areas on either side of the border have shown dramatic changes in fire dynamics as a result of fire suppression in California (Minnich 2006; Minnich & Chou 1997). As a result of reduced fire suppression (stable fire interval and more frequent disturbance regime), the chaparral plants of Baja California may be more actively undergoing speciation processes, and perhaps more resistant to extinction. Within northwest Baja California there are two primary areas of high plant endemism: the mountain ranges, and the coastal plain between Ensenada and El Rosario (Riemann & Ezcurra 2007). The influence of the relatively cold California current results in a persistent stable marine layer and fogs that dominate coastal climate most of the year (Vanderplank 2011a). The effect of the current is strongest during the warm months of the year with persistent fogs buffering evapotranspiration. Unique habitats have been identified within this region – namely the Maritime Succulent Scrub, noted for its high numbers of rosette-forming taxa that harvest moisture from the heavy coastal fogs (Martorrel & Ezcurra 2002; Minnich & Franco-Vizcaíno 1998; Rundel 1972). There are also small areas of Maritime Chaparral that favor non-sprouting evergreen sclerophyllous species adapted to longer intervals between fire cycles and increased moisture from fog than inland areas (Minnich *et al.* 2013).

The low relief coastal plain between Ensenada and El Rosario is an area of exceptionally high endemism in the state of Baja California (Garcillán et al 2010; Riemann & Ezcurra 2007). As a result of strong climate gradients, this region may be key to species migrations under changing climate regimes. It seems to be a hotbed of speciation and an important species refugium because the coastal fog mitigates the changing precipitation and temperature patterns (Minnich 2007). El Niño events typically favor higher winter rainfall and dense spring flowering events; but many years are very dry (Minnich *et al.* 2000). The flora responds rapidly to local weather, which in turn affects all higher trophic levels, causing pulses in the availability of resources (Minnich 1985). The coastal plain has relatively little variation in elevation, but minor topographical features and underlying edaphic conditions have a strong effect on floristic composition. A rich patchwork of species assemblages within the same broad vegetation belt is also observed along the California coast. Microclimatic conditions appear to have a strong influence on plant distributions and putatively relict vegetation associations are fragmented throughout the Californias, and in particular in northwestern Baja California (Minnich & Franco-Vizcaíno 1998; Peinado et al 1994; Delgadillo 1998; Raven & Axelrod 1978). The occurrence of micro-endemics in northwest Baja California suggests that plant distributions are not homogeneous and thus unlikely to be entirely controlled by broad climatic and latitudinal effects.

Primary hypothesis

The coastal area between Ensenada and El Rosario appears to have been a plant species refugium with a more stable climate than the adjacent regions to the north and south. This hypothesis assumes that the area has had a climatic transition near the 30th parallel for most of the Quaternary. During glacial periods the climate was cooler and wetter north of the 30th parallel and cooler south of the 30th parallel. Glacial periods dominate 90% of the time during the last million years, interglacial periods being brief interludes (Benson *et al.* 1997; Minnich *et al.* 2013). Thus rainfall gradients increased in glacial periods and decreased in brief interglacial periods. These climate patterns may have contributed to a flora that is rich in both paleotaxa (maintained by the relatively stable climate through time) and neo-endemic taxa that appear to have radiated in response to changing climate not severe enough to cause extinction. The most significant refugium is seen along the coast where fog buffers variation in climate, especially temperature and evapotranspiration.

How water availability shapes plant communities

In the present interglacial northwestern Baja California experiences relatively extreme short-term precipitation variation, ranging from severe drought to major flooding events (Minnich *et al.* 2000). Heavy rainfall events (largely ENSO-driven) also create vernal pools. Historical data from stable isotope records indicate that in this region the moist glacial (Pleistocene) climates gradually transitioned into moist Holocene climates, with shifts in the source of precipitation (Minnich *et al.* 2013; Bartlein 1998).

The degree of endemism in northwestern Baja California suggests that the amplitude of climatic change has not been as large as that in the adjacent regions. The plant communities of northwest Baja California are dynamic and, while some species have migrated, others have remained in situ and evolved in a locally changed climate regime. The ability for plants to respond to climatic change is probably more limited in long-lived slow-growing species such as tree species as compared to shorter-lived herbaceous species due to length of generation times. Climatic control of phenology (variation in flowering time with local weather) may be a key control of gene exchange that drives plant evolution and extirpations.

There are numerous putatively ancient paleoendemic taxa in northwestern Baja California (Raven and Axelrod 1978). These paleotaxa are often assumed to have undergone niche conservatism through time, suggesting that they occupy microclimates that are remnants of paleoclimate. The southern side of the rugged transverse range along the seismically active Agua Blanca fault just south of Ensenada is a local high rainfall region due to orographic lift of this mountain range. The transverse range harbors many of these paleotaxa. Small-scale topography and microclimates have a significant effect on species distributions with spatial diversification from increased terrain complexity. For example, conditions in a canyon (e.g., one about 20 m deep) will greatly alter the vegetation found on either side of the canyon walls and exposed ridges (which also differs from the wetter areas at the canyon bottom). Such canyons often support populations of narrow endemics and disjunct taxa. Diversity of microhabitats and niches offers greater opportunity for refuge to the micro-endemic species of the region, hence the paleo-nature of many of the plants in the ecotone. Similarly, the large islands of Guadalupe and Cedros, offshore west Baja Californa, have sharply reduced evapotranspiration and drip precipitation from fog allows relict populations of pines (*Pinus radiata*; Axelrod 1980) to persist. The absence of fossil packrat middens (due to humid climate; see Betancourt et al. 1990) in this region makes reliable identification of paleoendemics challenging. The absence of close relatives suggests a long lineage in taxa such as *Adenothamnus*, and less obviously in monotypic genera such as *Xylococcus* and *Ornithostaphylos* (Francisco 2001).

In the same region there are also several genera with relatively numerous closely related species occupying small, often allopatric, ranges (e.g., *Arctostaphylos, Astragalus, Ceanothus, Dudleya*), which might be considered neoendemics or species undergoing adaptive radiations. Several species of *Hazardia* in northwest Baja California form a "patchwork quilt" when their ranges are mapped. Although largely not sympatric, each species borders the other, occupying a small geographic region. This pattern alludes to a common origin and perhaps an adaptive radiation event in their evolutionary history. These occurrences provide supportive evidence that the ecotone has been a refugium through times of global climate change, fostering both ancient lineages and more recent species diversifications. The buffering effect of fog may have been a significant factor in the provision of climatic refugia for plants under changing climate.

Drought-avoidance strategies and plant physiognomies

Throughout the peninsula of Baja California there is great variation in rainfall both spatially and temporally (Minnich *et al.* 2000; Hastings and Turner 1965). Studies by Franco-Vizcaíno (1994) show that even within the arid desert province to the south, floristic composition continues to vary southward along the gradient from winter to summer rainfall. The frequency and intensity of rainfall events affects soil properties and plant species composition (Shreve 1951). The unpredictability of water in this region has resulted in a suite of different drought-adaptations in the flora. Throughout this precipitation gradient a variety of life-strategies are observed.

There has been much debate concerning the southern limit of the CFP in Baja California, with some authors excluding the Maritime Succulent Scrub. The debate is arbitrary partly due to the difficulty of classifying the vegetation, as an increasing number of succulent plants are seen southward and more mesic plants become increasing scarce. The botanical community generally recognizes the southern limit of the CFP at the 30th parallel near El Rosario, due to terminal orographic effects at the southern Sierra de San Pedro Martír (Garcillán *et al.* 2010; Minnich & Franco-Vizcaíno 1998; Thorne 1993). The map of Minnich & Franco-Vizcaino (1998) shows the extent of the maritime succulent scrub on the southernmost coastal plains of the CFP. Studies on the flora of San Quintín and Colonet also highlight the predominant contingent of the CFP flora in this region (Vanderplank 2011a,b; Harper *et al.* 2010).

Forrest Shreve (1936) published a seminal paper observing the precipitation gradient and the transition in the vegetation of the ecotone region between Ensenada and El Rosario in NW Baja California. In particular he noted the increased number of succulent species as one moves south, combined with decreasing numbers of chaparral species, and the increase in locally endemic taxa that are adapted to this small area with its unique climate. Shreve also commented on the nature of this ecotone and the increased heterogeneity of vegetation and life-forms, and therefore of the landscape. Minnich & Franco-Vizcaíno (1998) analyzed Jesuit missionary reports on the flora of the region and conclude that there is no compelling evidence that the vegetation of this region has changed since Spanish contact in 1768.

Many of the drought-tolerant physiognomies of the northwest Baja California ecotonal plants have phenological phases that correlate directly to precipitation, with varied responses depending on the timing, intensity and duration of rainfall events. The phenological plasticity of the ecotone plants correlates with rainfall and fog moisture, often producing growth pulses that vary in magnitude with the availability of water.

Annual plants: This strategy represents the ultimate in opportunism for plants in an area of uncertain rainfall. After sufficient rainfall these species germinate rapidly, often flowering and fruiting very quickly without necessarily becoming large (Felger 2000). In northwestern Baja California these species are often showy with flowers and/or reproductive organs that may be larger than the vegetative structures. In areas of summer rainfall a contingent of C4 summer annuals, which are better adapted to a very rapid growth and high temperatures, appear following rains (Mulroy & Rundel 1977). The ecotone region has mostly winter annuals due to summer drought.

Trees with permanent access to water: Several broad-leaved deciduous tree species in northwestern Baja California survive the dry warm late-summer–early fall weather by forming roots deep into perennial water sources (e.g., cottonwood *Populus fremontii*, sycamore *Platanus racemosa*, coast live oak *Quercus agrifolia*). During Pleistocene times these trees species were likely more widespread in perennial water-courses (Minnich 2007). Currently they are largely restricted to permanent streams, and areas where bedrock pushes aquifers to the surface. The role of mycorrhizal fungi also enables some of these species to survive in bedrock that roots cannot penetrate but does not prevent the fungal hyphae reaching the water table (Allen 2009). These tree species are generally wind pollinated and dispersed, with predictable flowering times. Putative paleo-endemics, such as *Brahea armata*, and *Pinus muricata*, fall into this category in northwestern Baja California .

Evergreen chaparral: The evergreen sclerophyllous shrubs of California's chaparral exhibit a suite of characteristics that make them highly tolerant of seasonal (late summer and early fall) drought. Small, tough, leaves with short internodes have strong stomatal controls and high cuticular resistance to reduce water-loss (Keeley & Keeley 1988; Minnich 1985; Hanes 1977). Their evergreen habit allows them to respond quickly after rainfall events and flower/fruit profusely. The large amounts of organic matter that these plants accumulate make them highly fire-prone in dry weather (Keeley 1977). Eventually the evapotranspirative ratio is so high that fire weather results in regular burns (Minnich 2006). As such, the distribution of the chaparral and its evolutionary history are tightly linked to the history of fire (Minnich 2006). Chaparral ecotone endemics include various parapatric species of *Arctostaphylos* and *Ceanothus*, genera which appear to still have high potential for speciation. There are also several putative paleo-endemic large woody shrubs (e.g., *Ornithostaphylos, Xylococcus*, and *Arctostaphylos* species such as *A. australis*).

Succulent plants: Succulence a well-known strategy for dealing with the pressures of increasingly arid conditions and drought. In combination with CAM (crassulacean acid metabolism) photosynthesis, this strategy is a particularly effective for resisting high radiant loadings and irregular precipitation. There are an increasing number of species in the Cactaceae and Crassulaceae at the southern end of the CFP, many of which are locally endemic (e.g., *Ferocactus fordii, Echinocereus maritimus, Mammillaria louisae*). Unique adaptations are seen in *Mammillaria brandegee*i, a locally endemic species that actually has its vegetative body underground, exposing on the top of the plant at the soil surface. During drought it actually shrinks down into the soil, where the microclimate is much more equitable.

Drought deciduousness: Particularly common in the coastal scrub are drought-deciduous species, seen among many narrowly endemic habitat dominants (e.g., *Ambrosia chenopodifolia, Aesculus parryi, Bahiopsis laciniata, Fraxinus trifoliata*). The number of months a plant is without leaves varies depending on local weather conditions. Drought deciduousness is often combined with other drought-tolerant strategies, e.g., succulent stems and drought-deciduous leaves (*Euphorbia misera*).

Stem succulents and rosettes: The Maritime Succulent Scrub has a dominant element of rosette-forming plants e.g., the near-endemic *Agave shawii* subsp. *shawii* and various locally endemic *Dudleya* species. In Spanish it is known as the ‘Matorral Costero

Rosetofilo' or rosetophyllous coastal scrub. These rosette-forming plants have been shown to be efficient fog harvesters (Martorell & Ezcurra 2002).

Geophytes/underground storage organs (culms, bulbs, tubers, etc): Although there are few true bulbs in the region (excepting a few species of wild onion and mariposa lily), there are several species that have some kind of under-ground storage organ (e.g., *Dichelostemma pulchellum, Marah macrocarpa, Jepsonia parryi*). These species avoid hot dry spells, remaining underground until soil moisture reaches levels appropriate to stimulate growth, yet there a very few, if any, endemic taxa with underground storage organs as their primary drought adaptation.

Some taxa have multiple strategies. Of particular note are some of the most narrowly restricted taxa – three *Dudleya* species that grow in areas with different lithologies on Colonet mesa (Harper et al 2010). All three are *Hasseanthus*-complex *Dudleya* species that are drought-deciduous with underground storage organs (rhizomes), and above-ground leaves are succulent and pseudo-rosetophyllous.

Plant distributions: rarity and endemism

In reviewing the work of Grime (1977), Kruckeberg & Rabinowitz (1985) note that many plants that are adapted to environmental extreme (e.g., serpentine endemism, halophytes) appear to be restricted to these extreme habitats only by competition or exclusion by other species in more favorable habitats (i.e., many halophytes can grow in non-saline conditions, but appear to be out-competed in normal conditions). These processes highlight the role that repeated disturbances (e.g., fire) or stress (e.g., basic soils) will have on selecting for the composition of a vegetation type. Frequent disturbance increases the spatial extent of favorable habitat for many species. There is evidence that early colonizing species are much less likely to go extinct and endemic species in mature communities are much more susceptible to catastrophic events and human activities (Kruckeberg & Rabinowitz 1985).

Vanderplank (2011) found no correlation between the local and global abundance of taxa in the ecotone (i.e., a plant that was globally scarce was equally likely to be rare, frequent or abundant locally, as was a cosmopolitan species). This places most endemics in the 'locally abundant but restricted geographically' or 'constantly sparse and geographically restricted' categories (Rabinowitz 1981). Stebbins (1980) states that the primary cause of localized endemism is adaptation to a localized ecological factor and Kruckeberg & Rabinowitz (1985) note that narrow endemics are most often members of distinctive communities or singular habitats. This statement is difficult to verify globally. The number of narrow or micro-endemics in the ecotone that are seemingly not restricted to a harsh environment or highly specific micro-habitat is noteworthy.

Qian (1998) showed that globally, along the latitudinal gradient, generic richness shows a striking increase with decreasing latitude. Many authors have attributed the high endemism and biodiversity at low latitudes to long-term climatic stability, suggesting that

Rapoport's rule (species range increases with latitude) is a product of the increase in the amplitude of climatic oscillations towards the poles (Ghalambor *et al.,* 2006, Mourelle & Ezcurra 1997; Stevens 1989; Janzen 1967). As such, other areas of high climatic stability such as the CFP would be expected to have increased levels of endemism. Smaller climatic shifts allow the survival of paleoendemics, and diverging gene pools (neoendemics) are able to proliferate. Using change in mean annual temperature since the last glacial maximum Jansson (2003) showed that areas that have experienced the largest temperature changes today have lower endemism in mammals, birds, reptiles, amphibians and vascular plants (robust to area, latitude, extent of former glaciation and oceanic island syndrome). It is however important to note that this spatial evidence is not temporal evidence and these species may not have evolved in-situ.

If one compares the ecoregions of Baja California with the hotspots of endemism and species richness for the peninsula (Garcillán et al 2010; Riemann & Ezcurra 2007), we see that where each ecotone occurs there is a peak in species richness. Peaks in local endemism are only occasionally seen in these ecotones, suggesting that the presence of an ecotone alone is not responsible for the elevated levels of endemism. Consistent with patterns seen in northwest Baja California, Sorrie and Weakley (2001) show that topography may be a minor consideration in endemism; for example, the coastal plain of Florida has <250 m relief yet the state is second in endemism only to California. Endemism in ecotones is not well-studied but often a peak in endemism is seen in ecotones. The forest-savannah ecotone in Africa has been shown to be important to divergence and speciation (Smith et al., 1997; 2005).

Recent research on the biotic interactions between desert plants has revealed that facilitation as a mutualism evolved between taxa from the Quaternary (nurse plants) and taxa from the Tertiary that were adapted to wetter conditions, but persist as a result of the nursing effects of more recently derived lineages (Valiente *et al.* 2006). Facilitation is asserted to have saved many species from extinction during times of climatic change at the end of the Tertiary, and facilitation is often facilitated by a few key-stone 'nurse' species (Verdú & Valiente 2008). Wangler & Minnich (1996) showed that post-fire recruitment of pinyon pine (*Pinus monophylla*) requires mature shrubs as nurse-plants. Surprisingly the generalist nurses are often the most abundant species in the community, providing strong resistance to extinction for the dependent species. This facilitation also allows niche conservatism in ancient lineages and increases phylogenetic diversity in plant communities (Valiente & Verdú 2007). Alternatively, in closely related species, facilitative mutualisms can turn into competition in times of stress of changing climate (Valiente & Verdú 2008, Verdú *et al.* 2010).

The literature on the flora of California far exceeds that available for Baja California, and gives some insight into the origins of the present endemism and diversity (Thorne & Viers 2009; Vandergast *et al.* 2008; Richerson & Lum 2008; Viers *et al.* 2006; Stebbins & Major 1965). Recently, Kraft *et al.* (2010) found that distributions of neoendemics in California correlate poorly to climate and topography. Endemics of the western edge of deserts were very young species, with most endemism found in habitats that have undergone post-pleistocene isolation or climatic change; sky islands with wetter climates have the greatest diversity of endemics.

Jansson (2009) stresses the relevance of emerging information on historical climate change that can be used to study microrefugia of Pleistocene climate oscillations. The heterogeneous environment of the ecotone in Baja California lends itself to the concept of microrefugia and studies of the likelihood of microrefugia in this zone should be pursued. Diadema (2009) found that glacial refugia are climatically stable areas that are determined by complex historical and environmental factors. Refugia are priorities for the long-term conservation of species and genetic diversity, representing ‘phylogeographical hotspots’ especially under changing climate regimes.

Migrational convergence occurs when generalist species move from one climate to another (Minnich 2013; 2007; 1985). Ackerly (2009) reviews the factors affecting the age and origin of California and mediterranean vegetation, and introduces the concepts of synclimatic (with climate) migration, resulting in niche conservatism (as documented by Kelly & Goulden 2008); and anticlimactic (not following climate) migration which often results in adaptive evolution. As such, species that moved with climate have conserved niches, species that did not move fast enough had to adapt (also see Minnich 2007). Ackerly (2009) points out that survival may be heavily dependent on biotic contexts and for those species not migrating with the climate it may be the presence or absence of competition from new species arriving (or not) that dictates whether a species survives the new regime (rather than it being wholly necessary to ‘adapt’ to the new climate). The successful ‘adaptive’ response may simply be factors that are barriers to dispersal of other species. This may be even a depleted gene pool in the potentially competing taxa. Ackerly states “By this logic, the greatest opportunity for adaptive evolution will occur on the trailing edge of species ranges during episodes of climate change, as changing conditions kill off the existing vegetation”. Assuming there will always be a ‘trailing edge’ near the 30th parallel due to the position of the jet stream and its physical limits, one can tentatively hypothesize that the ecotone will always be a hotspot of potential for adaptive evolution under any climate change regime.

Conclusions

Since the southern extent of mediterranean climate does not pass further south than the 30th parallel, it is likely that there has long been a transition in the vegetation near the 30th parallel in northwestern Baja California, corresponding to the southern limit of winter precipitation originating from the west. It follows that plant taxa ranging through this region would be unable to follow synclimatic migration routes, and thus migration in the ecotone is likely to have been anticlimactic (favoring adaptive radiations). The arid southern end of the CFP may hold more relictual diversity and more neo-endemic lineages than other regions of the CFP due to the climatic stability offered by the marine layer.

There are many putatively ancient ‘paleoendemic’ taxa in the ecotone region (Raven & Axelrod 1978); but the absence of fossil packrat middens or any other macrofossil records, and a dearth of detailed fossil and molecular information for the region, makes identification of paleoendemics challenging. There are also several genera in the ecotone that have many closely related species occupying small allopatric ranges (e.g., *Astragalus*, *Dudleya, Hazardia,*), which might be considered neoendemics. I hypothesize that the 30th parallel ecotone has been a refugium through times of global climate change, fostering both ancient lineages and neoendemics. The presence of cold currents and the the resultant marine layer are likely to be stable, suggesting that the ecotone will remain a refugium, with low rates of extinction. Future research should look at range sizes of endemics in Baja California to allow mapping and phylogenetic distance analyses. The effect of species interactions remains unstudied, and nurse plant effects are little-known in this region. It seems probable that similar processes may be active in the ecotone, and perhaps other undiscovered interspecific processes are contributing to the distributions of the narrow endemics.

Water plays a vital role in the distribution of plants in the ecotone of northwest Baja California, and other dryland systems. Life-strategies, distributions, trophic interactions, phenological timings and evolutionary histories are strongly linked to patterns in water availability, and systems for drought-tolerance. Future research should address the resource-pulses caused by sporadic rainfall events and their effects on the entire ecosystem.

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Chapter 1 Figures

Fig. 1.1 California Floristic Province (*red polygon*), Baja California and region of case study (*red polygon* south of latitude 33°N).

Figure 1.2**.** Succulent Maritime Scrub, near Cerro Solo, on the coast of northwestern Baja California (Photographed by Sean Lahmeyer).

Figure 1.3. Endemic palm *Brahea armata* (Arecaceae) in the southern Sierra San Pedro Martir of Baja California. This area experiences light grazing and fires.

Chapter 2:

Biodiversity and archeological conservation targets connected:

Aragonite shell middens increase floristic diversity and landscape heterogeneity on the forgotten peninsula

Abstract

Natural and Cultural Heritage sites frequently have non-overlapping or even conflicting conservation priorities, as human impacts have often resulted in local extirpations and reduced levels of native biodiversity. The predictable winter rains of NW Baja California over thousands of years have weathered calcium from the clam shells deposited by the PaiPai and Kiliwa people in middens along the coast. The release of this calcium has changed soil properties, remediated sodic and saline soils, and resulted in a unique microhabitat that harbors very different plant assemblages to those of the surrounding matrix. Native biodiversity and landscape heterogeneity are significantly increased on these shell middens. Protection of this cultural landscape will encourage both archeological and biodiversity conservation. On the forgotten peninsula, natural and cultural heritage priorities are overlapping and mutually beneficial.

Introduction

The preservation of archeological sites does not always overlap with the conservation of biodiversity. The United Nations Educational Scientific and Cultural Organization (UNESCO) separates cultural heritage sites and natural heritage sites at the core of its goals and missions: of 981 heritage sites, 759 are cultural, 193 natural, and only 29 (2.65 %) have mixed properties (www.unesco.org). Cultural conservation and biodiversity conservation have overlapped in the sustainable use of natural resources (Timmer & Juma 2005); but shared targets of elevated conservation importance for both archeological and biodiversity priorities are still few.

People have harvested coastal resources for more than 150,000 years, and have impacted populations of shellfish dating back more than 23,000 years (Rick & Erlandson 2009; Jackson *et al.* 2001). In the coasts of the Americas, hunter-gatherers exploited coastal ecosystems leaving behind shell mounds, or middens, which form microhabitats for distinct biotic communities. Humans were significant components of coastal ecosystems for millennia, blurring the boundaries between the natural and anthropogenic worlds deep into human prehistory (Rick & Erlandson 2009).

The Pacific coast of North America is littered with shell middens from a variety of indigenous peoples whose long-term occupation of the coast resulted in heavy marine deposits on land. The Seri people (one of the most robust-and intact indigenous communities in northern Mexico – and retaining considerable traditional knowledge) apply common indigenous names to over 150 species of mollusks, and still rely heavily on shellfish as part of their subsistence (Bertsch & Moser 2011). Coastal disturbance and development has destroyed many coastal middens in California, but many still remain in Baja California, Mexico, although development pressure is increasing (Moore 2006).

Human inhabitation of the Baja California Peninsula, often referred to as ‘the forgotten peninsula’ by archeologists, began more than 11,000 years ago (Des Lauriers 2010; Laylander & Moore 2006). Occupation was transient, migratory, involving large distances and small (> 30 people) family groups (Moore 2012, Hyland 1997). People moved freely from mountains to sea, often relying heavily on marine resources for protein. In Baja California, the harvesting of shellfish (clams, mussels, and abalone) is evidenced in the presence of large middens, defined by the presence of discarded shells, soil, archeological artifacts, and sometimes charcoal (Mudie & Lelievre 2012). After thousands of years, many of these shell middens have become mounds of calcium-rich soil that provide new habitats for plants (Fig. 2.1; Felger 2007).

The Pai-Pai and Kiliwa people of northwestern Baja California (among the last indigenous language speakers of the region) did not leave pyramids, temples, or permanent structures (Meigs 1935). Their homes were often ephemeral and their lifestyle transitory (Moore 1999; 2012; Figueroa 2009), but their middens, dotted across the landscape often many kilometers inland (Moore 2001; Meigs 1935; 1938), are some of the most significant archeological sites in the region. Moore (2001; 1999) dated many of the middens in the San Quintín region, and records regular occupation from the first half of the sixth millennium into historic times with the majority of middens being 3–5,000 years old.

The shell middens found in northwestern Baja California can broadly be separated into two types—calcitic and aragonitic. Calcitic species are nacre-forming bivalves found chiefly on exposed rocky foreshores (e.g., California mussel, *Mytilus californianus*, and Black abalone *Haliotis cracherodii*) with layers of calcite and sheet nacre (or mother-of-pearl, a mix of calcite bonded by protein). Aragonitic species are found mostly on sandy beaches with strong surf (predominantly Pismo clam *Tivela stultorum*); their shells have lamellar layers of aragonite but no calcite or nacre (Coan *et al.* 2000). In calcitic species calcium is tightly bound by thin layers of protein, and the shells degrade extremely slowly, whereas aragonitic species have shells that decompose much more readily and release calcium carbonate into the environment (Harper 2000; Fig. 2.2).

In the mediterranean climate region of Baja California, where winter rainfall is sufficient for soil development and weathering of shells, the effect of these prehistoric middens on contemporary vegetation is noticeable along low sedimentary coasts (Vanderplank 2010). As early as 1938, Meigs suggested that studies on the vegetation of the middens of NW Baja California could uncover patterns of movements of people historically, and/or successional patterns in the flora, because he observed the presence of *Ambrosia chenopodiifolia* (syn. *Franseria chenopodiifolia*) on recent midden sites. His observation may be related to agave pit-roasting remains, because this species often dominates on burnt soil. Similar vegetation changes between middens and the surrounding vegetation matrix are not so clearly observed along rocky shores where middens are made up mostly of nacreous calcite shells.

The leading hypothesis of this study is that the concentrated prehistoric deposition of aragonitic shells impacts the contemporary distribution of native plants. To investigate the relationship between current plant distributions and past human occupation, we compared the flora of two major midden complexes in NW Baja California to their surrounding soil matrices. We further hypothesize that historical human activity has increased environmental heterogeneity, resulting in increased plant diversity and a more complex species assemblage. We also analyze the conservation value of past human disturbances, by investigating whether human activity has positively enhanced landscape heterogeneity and native plant species richness, making conservation priorities for biodiversity and archeological sites overlapping and mutually beneficial.

Methods

Site selection

Two extensive midden complexes from PaiPai and Kiliwa people in NW Baja California were identified at sites where extensive archeological investigation had already been conducted (Colonet and San Quintín; Fig. 2.3). Exact localities of the study sites are not presented here at the request of the National Institute of Anthropology and History of Mexico (INAH), due to the sensitive nature of archeological sites. Three midden complexes were selected in the Colonet region, for a total of 11 middens; and four in the San Quintín region, for a total of 15 middens. Midden sampling was conducted with specific prerequisites for site selection. Criteria included: Suitable distance from the ocean (i.e., not directly adjacent) with matrix vegetation on all sides; sizable ancient middens; aragonite shell middens; stable plant communities present; and the presence of a fine-grain soil matrix.

Floristic analysis

Two-meter wide belt transects were run parallel to the coast (north to south) along the entire length of each midden (from 20 to 200 m in length). Matrix control transects of the same length were laid both coastward and inland of each midden to control for edge effects and distance from the coast. For each belt transect, all perennial species were listed (and their abundance quantified using cover estimates.) Percentage of aragonite shell visible at the midden surface was recorded, together with percentage of bare ground as a measure of total vegetative cover.

To examine the distribution of perennial species across all samples and both sites, a non-standardized principal components analysis (PCA) was conducted for the two sites individually and combined, using each transect as a sampling unit. Jackson's (1993) Broken Stick Distribution model was used to test for significant axes. Overall species richness on and off middens for each sample unit was calculated, and averaged across transects. The preference of any given species for the midden habitat compared to the matrix was evaluated by calculating the species frequency in middens and outside middens, and comparing both binomial frequencies by means of a *t*-test using a Bonferroni correction for multiple comparisons.

Soil analysis

A saturated paste extract was obtained from soil samples on and off middens at three sites in Colonet and four sites in San Quintín. In the extract solution, electric conductivity (EC) was measured with a portable EC meter and water-soluble cations were quantified using ICP (Inductively Coupled Plasma) analysis in the UCR soil science laboratory.

To verify the accuracy of EC as an estimation of total dissolved salts in the soil solution, we correlated our EC measures with the ICP estimation of total cations, and found an almost perfect linear relationship between both measures ($r = 0.996$; $n = 14$; $P < 0.0001$). To test for soil sodicity, we transformed our cation dataset to Sodium Adsorption Ratio (SAR) values, using the standard soil-science formula $\mathrm{SAR} = \mathrm{Na}/\sqrt{([\mathrm{Ca}+\mathrm{Mg}]/2)}$, where the variables Na, Ca, and Mg represent the concentration of the respective elements in meq/L. The SAR ratio index measures the activity of sodium as a dispersant on soil clay particles relative to the flocculation effect of the bivalent ions calcium and magnesium.

Results

Floristic data:

Despite the proximity of the two study regions, they are almost entirely different in their floristic composition (both on the middens and in the surrounding matrix). The only species found significantly on both midden complexes was *Marah macrocarpa*, an abundant globose succulent with a wide geographic range. The almost complete floristic disjunction between both regions was captured by the PCA of the whole data matrix, in which the first axis (explaining 37% of the total variance) separated the two study regions into two very distinct clusters, highlighting the fact that the plants of the middens have no commonalities between the two regions.

The PCA for each region separately had only one statistically significant axis that explained 30% of total floristic variance in Colonet and 34% in San Quintín. In both regions, these floristic axes correlated very strongly with the amount of shell cover in the soil (r = 0.89, P=0.0003 in Colonet, and r = 0.84, P=0.0001 in San Quintín; Fig. 2.4). Floristic variation, as summarized by the PCA axes, was strongly related to the amount of shell in the site.

Ordering the species by their PCA scores, we obtained for both regions a list of the species that preferentially colonize middens, on the one hand, and of those that are found chiefly off-middens, on the other (Table 2.2 for Colonet and Table 2.3 for San Quintín). According to the t-test on their binomial frequencies in- and off-middens, sixteen species were found in San Quintín showing a significant preference for middens, while five showed a significant preference for the matrix. In Colonet, in contrast, only five species were found with a significant preference for middens and five with a preference for the matrix.

Significant differences in species richness on and off middens were found at both sites. San Quintín had highest species richness on the middens themselves, whereas the Colonet middens had lower richness than the surrounding matrix (Fig. 2.5). Both sites host a very different flora on the middens as compared to their surrounding vegetation matrix, and significantly demonstrates the effect of middens on overall species diversity in both regions.

Site-specific differences

Each region had midden complexes with distinct characteristics. San Quintín middens were raised up to 3 m higher than the surrounding matrix, apparently from sand trapped by shell piles. Shells are almost exclusively aragonite, and vegetation is taller than on the surrounding matrix. Colonet middens are almost flat with much lower quantities of shell visible at the soil surface, and a small percentage of calcite shells visible in addition to aragonite shells. Matrix soils appear to have more clay than the silty soils of San Quintín, and burnt soils suggests agave roasting may have taken place at some midden sites, although it may also be a result of recent fire. Vegetative cover on the middens at Colonet is also distinctly taller than in the surrounding matrix. Despite lower species richness on the Colonet middens (as compared to matrix) vegetative cover was often seen to be tallest on the midden (data available upon request).

Soil data

In the low-lying, floodable soils of San Quintín the presence of shell middens had a very large effect on soil salinity. Matrix soils were strongly saline, with a mean conductivity of 34,400 µS/cm, while midden soils were non-saline, with mean conductivity around 790 µS/cm (in agricultural science, the conventionally accepted threshold for saline soils is 4,000 µS/cm). In the higher elevation mesa of Colonet, removed from the flood zone, no significant differences were observed in electrical conductivity between matrix and midden soils, both showing an average of around 120–140 µS/cm (Fig. 2.6; Table 2.4).

Sodicity in the soil, measured as the Sodium Adsorption Ratio (SAR) of the saturated paste extract solution, had a similar trend. In the floodable matrix soils of San Quintín sodicity was extremely high, with a mean SAR value of 89, while midden soils were non-sodic with mean SAR around 2.5 (the conventionally accepted SAR threshold for sodic soils is 13). In Colonet a generally similar, but less pronounced pattern was observed. Mean SAR values were 7.4 in matrix soils, and 1.7 in middens, but this difference was only marginally significant ($P = 0.1$) because of relatively high standard errors.

Discussion and significance

Calcium in coastal soils

The beneficial effects of calcium added onto saline and sodic soils are well known (Buol *et al.* 2011). The bivalent calcium cations displace other soil cations and significantly change soil characteristics, flocculating soil particles, giving the soil a porous structure, and promoting the leaching of salts. In contrast, sodium cations cause soil particles to deflocculate and disperse, giving sodic soils a lack of internal structure and poor drainage that create difficult conditions for plant growth and promote salinization (Brady & Weil 2007). The effect of aragonite shells as a soil amendment agent was strikingly visible in the San Quintín region, where both dissolved salts and sodicity in the middens were only a small fraction (2–3%) of the concentration in the matrix.

Our data suggest that the release of calcium, as a causative agent of soil modification, is the main factor driving the differential colonization of middens by native plants. The differences observed between our two study regions show that the impacts of the middens themselves are matrix-dependant and the effect of calcium varies with the original soil conditions. It is noteworthy that adjacent coastal desert regions in the peninsula also harbor extensive middens, but the lack of soil development (sandy soils) and steady rainfall for weathering have failed to produce similarly visible effects during the same timescale.

Floristic patterns

Matrix species in San Quintín are all salt-marsh species. Matrix species in Colonet are maritime succulent scrub species, with a high number of local endemics. Midden species in San Quintín are maritime succulent scrub with a strong desert influence and a surprising number of succulent plants, perhaps related to the sandy soil of the midden. Midden species in Colonet are mediterranean-climate species that are abundant elsewhere in the regional landscape. Middens in the Colonet region were sometimes adjacent to vernal pools, which are another key conservation target for biological diversity.

There are opposite trends in species richness between the two sites. In San Quintín richness is greatly elevated on the middens, whereas in Colonet richness is lower on middens. The addition of the calcium has a divergent effect on the soil matrix in these two communities, and present vegetation. It is unequivocal that the human harvest of marine invertebrates leaves a trail of environmental transformation that increases native diversity and landscape heterogeneity. At the same time species colonization of middens in different habitats is not predictable because each soil type responds differently to the addition of calcium, resulting in different plant communities. The deposition of aragonite shells did not promote the occurrence of calciphiles (calcium-loving species). Instead, it is the formation of a more heterogeneous landscape, driven by the footprint of prehistoric human activities, which promotes species richness at each site.

Soil-vegetation interactions

There are considerable differences in the middens of the two study regions, including microterrain (raised or flat), quantity of shell, soil type, and salinity. The shared effect of shell at both sites allows us to discount the mounding effects as the single source of the observed floristic change. Shell quantity at the two regions varied markedly, and their impact was different in each: Small amounts of surface shell (3–5%) were enough to significantly impact floristic composition at Colonet, whereas 20% shell at San Quintín was not enough to yield a marked floristic difference from the matrix. The role of factors such as type and duration of human occupation, whether or not cooking fires took place and roasting pits were made, and the age of the individual middens, is unclear. The lack of dated middens at Colonet prohibits age comparison but Figueroa (2009) hypothesizes that site occupation may have been more impermanent and transient than at adjacent regions due to the lack of fresh water.

The prehistoric footprint

The impact of aragonite shell middens on soil conditions and plant communities is evidence that the historical activity of indigenous people has augmented the native plant biodiversity. The cultural landscape is more heterogeneous, favoring unique plant assemblages within the matrix-midden mosaic. Recent studies have shown that in the San Quintín region the percentage of endemic and rare plants is strongly correlated with overall plant species richness (Vanderplank 2010). Therefore we can expect an increase in the number of endemic and rare plants that grow in the cultural landscape of the broader region due to increases in species diversity provided by the midden mosaic.

Previous evidence of human impacts increasing biodiversity has only been reported in light of indigenous management of the land e.g., via burning or ‘gardening’ (Gadgil *et al.* 1993). This is the first example of past human activities inadvertently benefitting terrestrial biodiversity as a result of harvesting marine life and altering soils. In the future, the vegetation of the middens may continue to change with increasing amounts of calcium carbonate being released into the soil as shells decompose. Middens will continue to maintain a distinct flora to that of the surrounding matrix, maintaining landscape heterogeneity and native plant richness, even if the floristic composition varies through time. Long-term monitoring of middens may inform our understanding of plant ecology in soils where shell is being continually eroded. In deeper timescales we may see a similar effect in middens of calcite shells that decompose more slowly than aragonite.

Shell middens in NW Mexico have been previously proposed to have great potential for ecotourism and educational purposes (Tellez-Duarte *et al.* 2001). The value of conserving biodiversity in areas of traditional management and simultaneously conserving native cultures has long been recognized (Furze *et al.* 1996; Timmer & Juma 2007), but conservation of abandoned archeological sites has been more challenging. The surviving indigenous people of Baja California have been largely displaced (relocated to the north). The Kiliwa people who inhabited San Quintín now number approximately 50 individuals, living along Arroyo León south of Valle de la Trinidad, with just 5 native speakers. The PaiPai, who inhabited Colonet now number approximately 350 people living in two communities (in Valle de la Trinidad and Sierra de Juárez) (http://bajacomunidad.org/tribes/). To preserve their history and the rich biodiversity that results from their ancestral stewardship we hereby propose additional protection and vigilance be given to the shell middens of NW Baja California.

In conclusion, our study shows that in these regions priorities for the conservation of archeological sites and terrestrial biodiversity are overlapping and complementary in their targets (fig 7). Conservation efforts focused on the local natural and cultural heritages will mutually benefit from increased protection of archeological shell middens.

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Chapter 2 Figures:

Figure 2.1. Aragonite shell middens in San Quintín allow the growth of non-halophytic plants such as jojoba and cholla, which do not prosper in the saline soils of the matrix. Note the decomposed shells of pismo clams and the flakes from hand-tools visible on the soil surface.

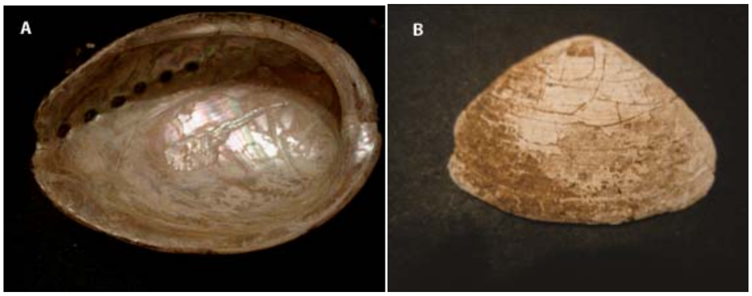

Figure 2.2 (a & b). Abalone shells, with nacreous calcite layers (a) decompose more slowly than clam shells with aragonitic layers (b).

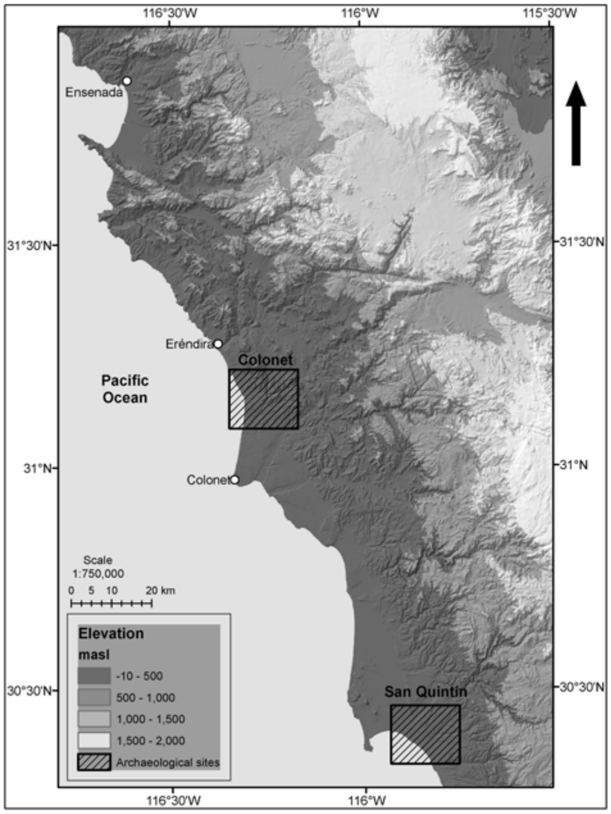

Figure 2.3. Study regions (Colonet and San Quintín) on the Pacific Coast of Baja California.

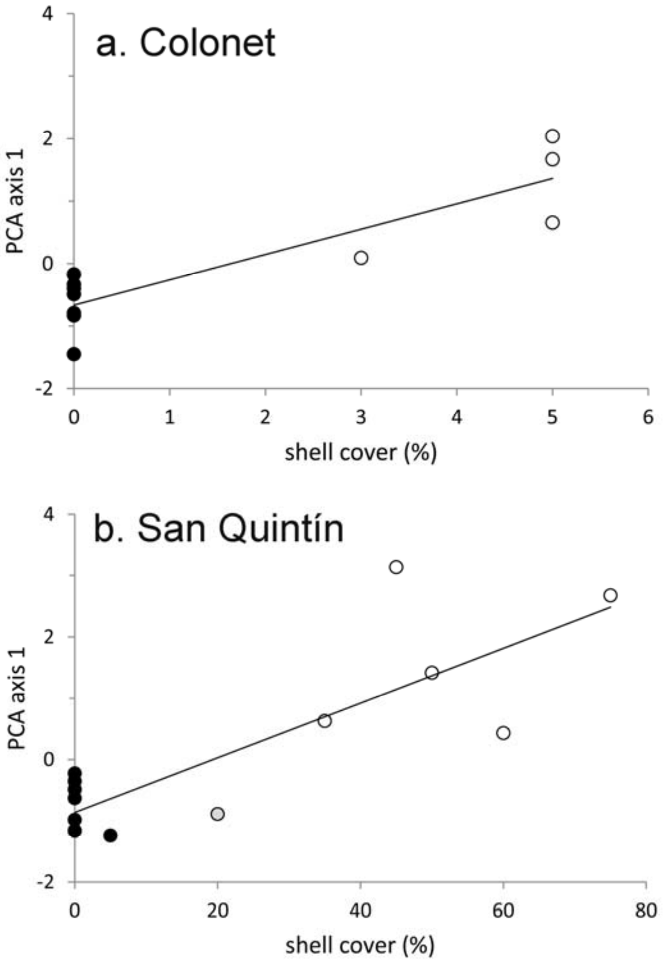

Figure 2.4 (a & b). Correlation between floristic variation (first PCA axis) and surface shell cover for (a) Colonet ($r = 0.89$, $P < 0.0001$) and (b) San Quintín ($r = 0.84$, $P < 0.0001$). Matrix (off-midden) transects are indicated by black dots, on-midden transects by white dots. An atypical midden transect with low shell cover is indicated by a gray dot. The species significantly associated with the floristic axes, i.e., the matrix and midden species for each region, are listed in Table 2.1.

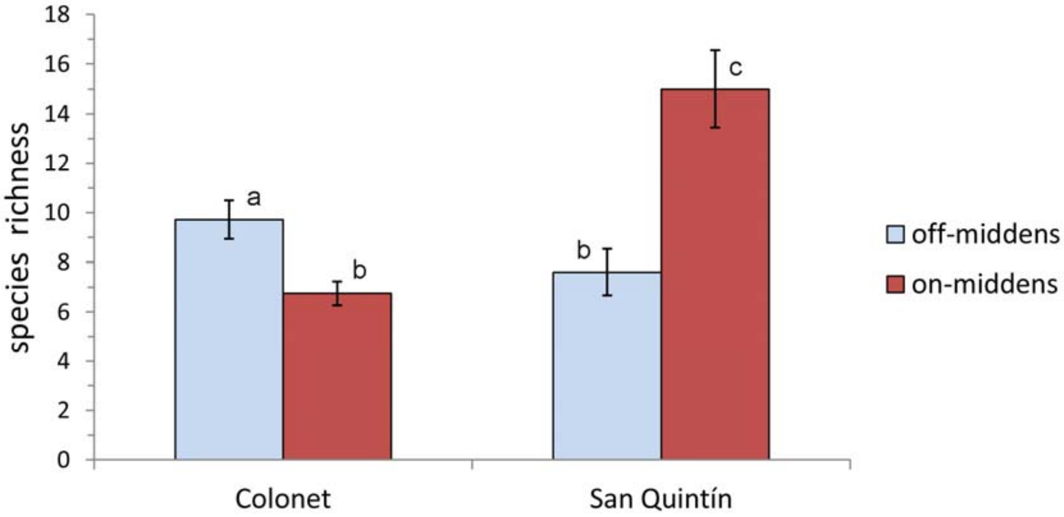

Figure 2.5. Floristic richness on- and off-middens in Colonet and San Quintín. Bars labeled by different letters are significantly different according to a *t*-test ($P < 0.01$).

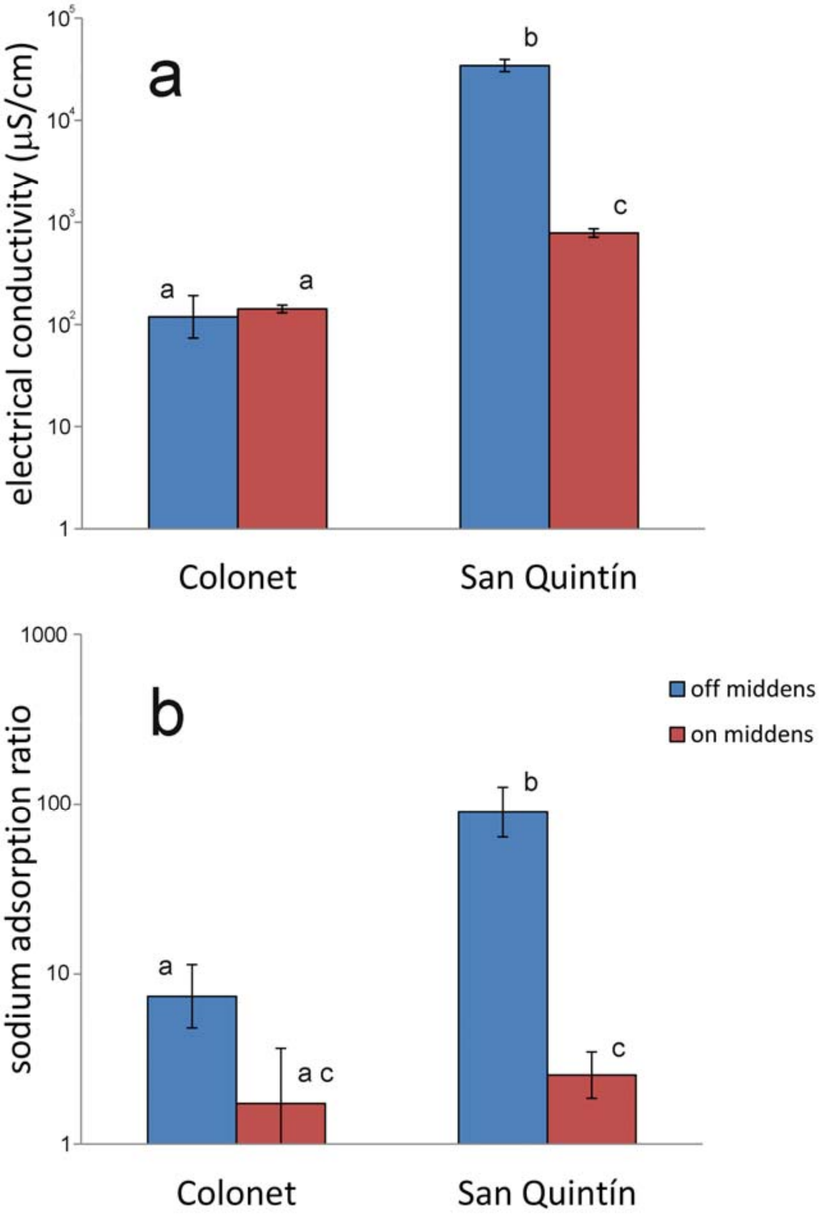

Figure 2.6. (a) Electrical conductivity and (b) Sodium Adsorption Ratio off- and on-middens in Colonet and San Quintín. Note that, in order to keep all data points within a visually comparable scale, the vertical axis was log-transformed in both plots. In each graph, bars labeled by different letters are significantly different according to a *t*-test ($P < 0.01$).

Figure 2.7. Following the precedence of neighboring California, the coastal middens of the forgotten peninsula are being destroyed by expanding agriculture and urbanization.

Table 2.1

San Quintín	**Colonet**
Matrix species	
Frankenia salina	*Dudleya ingens*
Juncus acutus	*Hazardia ferrisiae*
Sarcocornia pacifica	*Acmispon glaber*
Atriplex barclyana	*Rosa minutifolia*
Arthrocnemum subterminale	*Eriogonum fasciculatum*
Midden species	
Gambelia juncea	*Rhus integrifolia*
Astragalus trichopodus	*Astragalus trichopodus*
Lycium californicum	*Euphorbia misera*
Artemisia californía	*Marrah macrocarpa*
Echinocereus maritimus	*Encelia californica*
Ephedra californica	
Dudleya cultrata	
Aesculus parryii	
Atriplex canescens	
Sphaeralcea ambigua	
Cylindropuntia prolifera	
Ferocactus fordii	
Cylindropuntia californica	
Mirabilis laevis	
Atriplex julacea	
Mammillaria dioica	

Table 2.1. List of species with significant affinities for middens or matrix sites in Colonet (C) and San Quintín (SQ). We selected species that had both (a) significantly high or low axis loadings in the PCA, and (b) differed significantly in their frequency in middens as compared to the matrix according to a *t*-test on the binomial frequencies. In order to avoid errors derived from multiple comparisons, we used a Bonferroni correction with a probability threshold of $P = 0.001$ (SQ) and $P = 0.003$ (C).

Table 2.2.

Family	Scientific name	frec out	frec in	Preference
Agavaceae	*Agave shawii*	0.9	0.8	
Anacardiaceae	*Rhus integrifolia*	0.3	0.8	**in**
Asteraceae	*Hazardia ferrisiae*	0.4	0.0	**out**
Asteraceae	*Artemisia california*	0.9	0.8	
Asteraceae	*Isocoma menzeisii*	0.1	0.3	
Asteraceae	*Encelia californica*	0.0	0.8	**in**
Cactaceae	*Echinocereus maritimus*	0.3	0.0	
Cactaceae	*Ferocactus viridescens*	0.6	0.0	**out**
Cactaceae	*Mammillaria dioica*	0.6	0.3	
Crassulaceae	*Dudleya ingens*	1.0	0.5	**out**
Crassulaceae	*Dudleya attenuata*	0.3	0.0	
Cucurbitaceae	*Marah macrocarpa*	0.0	0.3	**in**
Ephedraceae	*Ephedra californica*	0.4	0.0	**out**
Euphorbiaceae	*Euphorbia misera*	0.0	0.5	**in**
Fabaceae	*Acmispon glaber*	1.0	0.3	**out**
Fabaceae	*Astragalus trichopodus*	0.0	0.3	**in**
Polygonaceae	*Eriogonum fasciculatum*	1.0	0.3	**out**
Polygonaceae	*Eriogonum fastigiatum*	0.1	0.0	
Rosaceae	*Rosa minutifolia*	1.0	0.5	**out**
Simmondsiaceae	*Simmondsia chinensis*	0.9	0.8	

Table 2.2. Species frequencies in and out of middens at Colonet. Preference is shown in or out of middens only for taxa that were statistically significant according to a *t*-test.

Table 2.3.

Family	Taxon	frec out	frec in	Preference
Anacardiaceae	*Toxicodendron diversilobum*	0.1	0	
Anacardiaceae	*Rhus integrifolia*	0	0.2	**in**
Asteraceae	*Isocoma menzeisii*	0.7	0.8	
Asteraceae	*Helianthus niveus*	0	0.2	**in**
Asteraceae	*Ambrosia chenopodifolia*	0	0.2	**in**
Asteraceae	*Artemisia california*	0	0.4	**in**
Cactaceae	*Lophocereus schottii*	0	0.2	**in**
Cactaceae	*Stenocereus gummosus*	0	0.2	**in**
Cactaceae	*Echinocereus maritimus*	0	0.4	**in**
Cactaceae	*Cylindropuntia prolifera*	0	0.4	**in**
Cactaceae	*Ferocactus fordii*	0	0.6	**in**
Cactaceae	*Cylindropuntia californica*	0	0.6	**in**
Cactaceae	*Mammillaria dioica*	0	0.4	**in**
Chenopodiaceae	*Sarcocornia pacifica*	0.9	0.4	**out**
Chenopodiaceae	*Atriplex watsonii*	0.5	0.4	
Chenopodiaceae	*Atriplex barclyana*	0.2	0	**out**
Chenopodiaceae	*Arthrocnemum subterminale*	0.2	0	**out**
Chenopodiaceae	*Allenrolfia occidentalis*	0.1	0	
Chenopodiaceae	*Suaeda cf. nigra*	0.3	0.6	
Chenopodiaceae	*Atriplex canescens*	0	0.4	**in**
Chenopodiaceae	*Atriplex julacea*	0.1	1	**in**
Crassulaceae	*Dudleya cultrata*	0.3	1	**in**
Cucurbitaceae	*Marah macrocarpa*	0	0.2	**in**
Ephedraceae	*Ephedra californica*	0	0.2	**in**
Euphorbiaceae	*Euporbia misera*	0	0.2	**in**
Fabaceae	*Astragalus trichopodus*	0	0.4	**in**
Frankeniaceae	*Frankenia salina*	0.7	0.2	**out**
Sapindaceae	*Aesculus parryii*	0	0.2	**in**
Juncaceae	*Juncus acutus*	0.6	0.2	**out**
Malvaceae	*Sphaeralcea ambigua*	0	0.4	**in**
Nyctaginaceae	*Mirabilis laevis*	0	0.4	**in**
Plantaginaceae	*Gambelia juncea*	0	0.6	**in**
Poaceae	*Distichlis spicata*	0.9	0.8	
Poaceae	*Distichlis littoralis*	0.7	0.8	
Simmondsiaceae	*Simmondsia chinensis*	0	0.2	**in**
Solanaceae	*Lycium brevipes*	0.8	0.6	
Solanaceae	*Lycium andersonii*	0	0.2	**in**
Solanaceae	*Lycium californicum*	0.5	1	**in**

Table 2.3. Species frequencies in and out of middens at San Quintín. Preference is shown in or out of middens only for taxa that were statistically significant according to a *t*-test.

Table 2.4.

		EC	Ca	K	Mg	Na	total	sodicity
Colonet	Matrix	146.67	0.76	0.33	0.45	7.12	8.65	8.71
Colonet	Midden	143.33	1.10	0.40	0.42	1.69	3.61	3.04
S-Quintin	Matrix	35250.00	66.69	12.07	144.08	916.60	1139.45	109.23
S-Quintin	Midden	797.50	13.66	2.11	4.58	8.14	28.49	2.95

Table 2.4: Mean soil Electrical Conductivity (EC), and water-soluble cations (used to calculate sodicity) for midden and matrix sites at each region. EC is measured in μS/cm, all cations are measured in meq/L, sodicity is measured as a ratio.

Chapter 3:

Coastal Fogs, Plant Phenological Dynamics and Refugia in Mediterranean Mexico

Abstract

Coastal sage scrub is most diverse at the southernmost extreme of the California Floristic Province, a biological diversity hotspot, with high local endemism and outstanding conservation value. It is also an area with two steep moisture gradients, one from rainfall (N-S), and one from coastal fogs (W-E) buffering climate. Phenological timing in perennial shrubs of mediterranean climates has been shown to vary with available moisture. We installed five weather stations across the moisture gradients and monitored phenology at each from 2010-2013. A principal components analysis of the data demonstrates a seasonal pattern in regional flowering times, but distinct differences in local weather and phenology between the five study-sites. Three flowering syndromes are revealed in the flora: (a) water-responders or spring bloomers, (b) day-length responders or fall-blooming taxa, and (c) aseasonal bloomers that show no strong seasonal affinity. The two moisture gradients are the strongest drivers of flowering times (rainfall and fog). Coastal sites showed lower variation in phenological space than inland sites, where phenological seasonality is dampened by ocean-derived moisture. The presence of the marine layer from cold ocean currents extends and buffers perennial plant phenology, and this probable driver of local endemism highlights the necessity of coastal conservation.

Introduction

During most of the Tertiary period much of what is now Mexico and the American Southwest was covered by a type of low-canopy temperate vegetation called by Daniel Axelrod (1958) the “Madro-Tertiary” flora. During the Quaternary, these ecosystems gradually contracted and fragmented, giving way to the modern drylands of more tropical affinities that expanded in North America (Lancaster & Kay 2013; Minnich 2007; Rzedowski 1973; Axelrod 1950). Relatively large extensions of these formerly widespread temperate communities remain in the Californian Floristic Province (CFP), a global biodiversity hotspot, where their presence has been associated with mediterranean climates with moist winters and dry summers (Ackerly 2009; Myers *et al.* 2000; Raven & Axelrod 1978).

Mediterranean ecosystems around the world are particularly diverse, and seem to display a springtime flowering peak during the transition from the cool wet winters into the hot dry summers, at a time when mild spring temperatures and winter-accumulated soil moisture generate optimal conditions for plant growth (Cowling *et. al.* 1996). Prior studies have shown the existence of similar “mediterranean-type” vegetation outside winter-rain areas that do not display a peak in spring flowering like their winter-rain counterparts but rather show peak flowering during the summer monsoon (Sniderman *et al.* 2013; Verdú *et al.* 2002; Peñuelas *et al.* 2002; Barbour & Minnich 1990; Minnich 1985). It appears that spring flowering in mediterranean vegetation is a phenomenon that can be modulated or even triggered by available moisture. Recorded climatic anomalies seem to support this hypothesis: For example, Minnich (1985) looked at the impacts of an unusual summer rainfall event in southern California that occurred with Hurricane Doreen, and found that species that normally flower only in winter were able to put on new leaves and flower profusely after the summer rain. Studies show that, even in more mesic mediterranean-climate regions, rainfall has a stronger influence than temperature or daylength on reproductive phenology (Peñuelas *et al.* 2004; 2002).

Coastal sage scrub, an assemblage dominated by facultatively deciduous low shrubs, reaches its highest floristic diversity in northwestern Baja California, due to long-term climatic stability in the region (Westman 1981, Axelrod 1978). This area has undergone small climatic change compared to other regions of coastal sage scrub. Further north, the increased rains during the last glacial maximum made vegetation shifts disruptive and chaparral was found to the coast (Minnich *et al.* 2013; Minnich 2007). The composition and diversity of coastal sage scrub species has been shown to be most strongly related to summer temperatures (Westman 1981). The marine layer of northwestern Baja California reduces temperature and evapotranspiration and as a result has the richest coastal sage scrub assemblages in North America. The climatic stability of coastal fogs has long been seen to affect plant phenology; historical accounts from the 1800s note the extended (earlier and later) flowering of annual plants along the coast (Minnich 2010, p.143). Yet there have been no previous studies on the perennial phenology of the coastal sage scrub.

The southernmost extreme of the CFP along the Pacific coast of North America (located in Baja California, Mexico), harbors coastal sage scrub in areas of very low precipitation. It is generally accepted that this southernmost ecotone of the CFP is largely maintained by the marine layer (low temperature, high humidity and low clouds), associated with the cold coastal upwelling of the California Current. These fogs buffer the low rainfall regime as the CFP transitions into the Sonoran Desert (Axelrod 1978; Raven & Axelrod 1978). In Baja California, no studies have examined the dynamics of fog in these coastal ecosystems and its variation as a function of the proximity to the ocean. We hypothesize that coastal fog has a decisive influence on plant flowering phenology, and that oceanic influence plays a central role in the long ecotonal transition of the CFP along the Pacific coast of Baja California.

The driving question in our study was: How does phenological timing vary wish available moisture in evergreen shrubs at the southern dry edge of the California Floristic Province? Within this general problem, we asked three relevant questions: (a) Are there general flowering patterns in the regional flora and can local perennial species be classified into simple phenological categories? (b) Can significant climatic variation be detected between sites within the larger region, and what are the main factors driving between-site variation? And, (c) what are the phenological differences between sites in this geographic ecotone, and can these differences be tied to differences in site-specific weather patterns?

The Study Region

This study focuses on the southernmost extreme of the California Floristic Province, in the mediterranean-to-desert ecotone in Baja California, Mexico, where environmental conditions begin to transition into those of the typical coastal desert of the Vizcaíno peninsula. One of the most important characteristics of this ecotone is its high species richness and the presence of a large number of narrowly endemic species (Riemann & Ezcurra 2007; 2005).

Endemism: One of the intriguing properties of this ecotone is the presence of a band of coastal endemism. Along the flat coastal plains of northwestern Baja California between parallels 30 and 31.5, is one of the areas of highest endemism in the State of Baja California (Garcillán *et al.* 2010; O'Brien *et. al.* in press). Microclimatic conditions appear to have a strong influence on the distribution of endemics, and putatively ancient vegetation associations are fragmented in northwestern Baja California (Delgadillo 1998; Peinado *et al.* 1994; Raven & Axelrod 1978).

Gradients and ecotonal variation: NW Baja California is an area of strong environmental gradients where the mediterranean climate meets the desert ecosystems of the central peninsula of Baja California. Mean annual rainfall drops sharply from 280 mm in Ensenada (lat 31° 52') to 140 in San Quintín (lat 30° 25'). Forrest Shreve (1936) noted the precipitation gradient and the transition in the vegetation, with an increased number of succulent species as one moves south, combined with decreasing numbers of Mediterranean species and an increase in locally endemic taxa.

Ocean influences: A second gradient is seen in the flora that relates to distance from the coast. In the coastal plain, fog appears to buffer the low winter rainfall regime, promoting the growth of “nebulophytes” (rosette-forming plants that are able to capture fog; Martorell & Ezcurra 2002; Rundel 1972). The regional vegetation is dominated by drought-deciduous and sclerophyllous plants that respond rapidly to pulses in moisture availability (Franco-Vizcaíno 1994; Minnich 1985; Shreve 1936).

The Pacific coast of NW Baja California offers an ideal system to study the effect of environmental variables such as rainfall, fog, and temperature on ecosystem dynamics. Firstly, as stated above, the precipitation gradient and the fog gradient vary in a nearly-orthogonal manner; the first decreases chiefly from north to south, while the second decreases inland, from east to west. Secondly, the high levels of endemism in this ecotone provide a suite of study species from a broad range of evolutionary lineages, which can help to compare phylogenetic signals in the data. Lastly, the relatively undisturbed habitats of the region (particularly as compared to California) allow a fine scale analysis that can avoid confused data signals from large numbers of invasive species or from human-induced disturbance.

Methods

Weather data

Five weather stations were installed, spanning a 140-km north-south winter rainfall gradient (high to low) from 31.57 to 30.52 degrees of latitude (Fig. 3.1). The weather stations (HOBO microstations, Onset Computer Corporation, Bourne, MA) record hourly data on temperature, relative humidity, and total rainfall each hour (in the third year of the project a leaf-wetness sensor was installed at each station and the data were correlated to relative humidity, to corroborate the usefulness of the latter as a proxy for fog moisture and dew drop).

Hourly data were transformed to daily means of temperature and humidity, and daily totals, in the case of rainfall. Daily values were averaged in turn into monthly means for temperature and humidity, and monthly cumulative totals for rainfall. The monthly values were averaged across the three years of our study period, to obtain a descriptive trend of weather patterns in each site. Additionally, a time-series analysis was conducted on the daily temperature and humidity averages, by fitting the first harmonic of a Fourier series to detect the existence and magnitude of periodic oscillations (Bloomfield 2000).

Phenological data

Each weather station became the center of a study site having an area of ca. one km^2. Within each study site, all perennial shrubs were identified (herbarium specimens at

RSA). Phenological data was collected for all 86 taxa. Native spring ephemerals were combined into a single data-set (Table 3.2 for a list of all taxa). Data was collected every six to eight weeks from March 2010 to January 2013, for a total of 17 sampling events. Data was initially recorded intensively (estimated abundances and intensities for each species) and after the first year a simplified ordinal scale for data collection was developed based on observed flowering intensities, from a value of 1 for low flowering intensity to 3 for peak bloom (>75% of the population in full flowering), and a zero score for species not flowering (Table 3.3). For each site we developed a time-series data matrix with sampling dates (columns) and species (rows), showing the flowering score of each species at each date.

Isotope analysis

Leaf samples of fall-blooming species were sent to the UCR Facility for Isotope Ratio Mass Spectrometry to quantify δ^{13}C, a measurement that can distinguish between C4 and C3 photosystems. Stable carbon isotopic compositions were expressed as delta values relative to the VPDB standard (Vienna Peedee belemnite), following the USGS guidelines (USGS40, http://isotopes.usgs.gov/lab/referencematerials/USGS40.pdf).

Data Analysis

In order to analyze the time-trajectory of phenological samples across dates, we used Principal Component Analysis (PCA) of the raw (i.e., non standardized) dates × species matrices. We used the broken-stick distribution to test for significant axes (i.e., axes that possess more variation than can be expected by chance, see Jackson 1993). We then used the resulting axes (a linear combination of species flowering times) to test their scores against external climatic and environmental variables using linear models.

We performed two distinct analyses. In the first analysis, aimed at finding the general phenological dynamics for the region as a whole, all sites were combined together to obtain a regional 17 dates × 86 species matrix, and an average score of flowering intensity was taken across all five sites in order to get a general measure of flowering phenology across the gradient. For the second analysis, we maintained the individuality of the different sites. To do so, we eliminated from our analysis all the species that were present in less than four sites and retained only the regionally common taxa (16 in total). We then performed two PCA analyses. In the first one, the 17 dates were repeated across the five sites to create a matrix of 16 species × 85 dates-nested-within-sites. For the second analysis, the 16 species were repeated across the five sites creating a matrix of 17 dates × 80 species-nested-within-sites. In the first analysis we analyzed the differences in the time-trajectories of the sites in the phenological space defined by the flowering of the regionally common species. For the second analysis we analyzed the dispersion of the clusters produced by each species in the five different sites.

In order to obtain a quantitative measure of seasonality, we first converted all observations to Julian days (sequential day counts), taking the spring equinox as the origin. We then converted these dates into angles, which measure the angular position (φ)

of the earth in its orbit around the sun. Using the sine and the cosine of the Julian time, each date can be uniquely recognized by its position in a rectangular coordinate system. The sine of φ measures the winter-to-summer solstice axis: for the summer solstice, $\sin(\varphi) = 1$, for the winter solstice, $\sin(\varphi) = -1$. Similarly, the cosine of φ measures the spring-to-autumn equinox axis: for the spring equinox, $\cos(\varphi) = 1$, for the autumn equinox, $\cos(\varphi) = -1$.

Results

Regional flowering pattern

According to the broken-stick test, two significant PCA axes were found for the combined sites matrix. The analysis showed a strong cyclical dynamics of the pooled regional data from March 2010 to January 2013. Time-specific data points showed a circular trajectory in flowering times, or "phenological space," that is clearly visible in the first two multivariate axes (Fig. 3.2). Axis 1 separated spring sampling dates to the right from late summer and fall dates to the left. Axis 2, in contrast, separated late-spring and early-summer dates above, from winter dates below. In agreement with this interpretation, axis 1 was significantly correlated with the spring-to-autumn transform of time, while axis 2 was significantly correlated with the summer-to-winter component ($r^2 = 0.86$ and $r^2 = 0.83$, respectively; see Fig. 3.2a and 3.2b).

An analysis of the loadings of all species in these two axes allowed us to make a first characterization of phenological strategies of the regional flora, which we classified into

(a) spring bloomers (positive loadings on axis 1); (b) fall bloomers (negative loadings on axis 1) (c) species that showed good flowering during the study but did not show a consistent flowering time, classified as aseasonal or opportunistic bloomers. The list of species derived from this regional analysis is presented in Table 3.1.

All fall-blooming species showed δ^{13}C values in their leaves consistent with a C3 photosynthetic metabolism (Table 3.4). The values ranged between −24 and −32, within the range of the value for C3 plants, which is approximately −28, and removed from the expected value for C4 plants, which is ca. −13.

Climatic gradients

All sites showed a similar seasonal trend in both monthly precipitation and mean temperatures (Fig. 3.3). There was a marked effect of the ocean as a temperature buffer, as mean summer temperatures were higher at the inland sites than at coastal ones (4.5°C higher in August). Total precipitation was significantly and positively correlated with latitude (multiple $r^2 = 0.95$, $n = 5$, $P = 0.04$; Fig. 3.4a). Relative humidity (a proxy for the effect of coastal fogs) showed a marked general inland-to-coast gradient: The distance to the coast of each site was negatively correlated with mean annual air humidity ($r = -0.88$, $n = 5$, $P = 0.04$; Fig. 4b). Additionally, there was a strong interaction between seasonal trends in air humidity and the proximity to the ocean: Inland sites showed maximum humidity values in winter and a generally dry air in summer, while coastal sites maintained high levels of air humidity in summer, when the marine layer from the cool

California Current creeps onto land in the form of summer fogs. Data from the two most extreme sites (Santo Tomás, an inland and our northernmost site, with high rainfall and low fog, and San Quintín, our southernmost and most coastal site, with low rainfall and high fog) clearly show the buffering effect that the marine layer has on summer temperatures and relative humidity (Fig. 3.5).

Between-site variation in phenology

The PCA of all the sites separated showed very similar patterns as that of the first analysis, performed on the pooled dataset: Each site showed an annual circular trajectory in flowering times, with axis 1 separating spring samples to the right from fall samples on the negative side, and axis 2 separating late-spring and early-summer samples from the rest of the cluster. Within this general seasonal trend, not all sites varied with similar amplitude. Some coastal sites, like San Quintín or La Misión, showed lower variation in phenological space relative to the other, more inland, sites, Santo Tomás, Covarrubias, and La Joya. This result seems to be mostly related to proximity to the ocean and the influence of the marine layer. We found a significant and negative correlation ($r = -0.91$, $n = 5$, $P = 0.03$; Fig. 3.6a) between the standard deviation of each site along axis 1 (a measure of fall-to-spring phenological variation) and mean relative humidity for each site, demonstrating that phenological variation and seasonality is dampened by the proximity to the coast and the ocean-derived moisture (Fig. 3.6a). As with the pooled dataset, all sites also showed a significant correlation between axis 1 and the spring-to-autumn signal ($r = -0.94$, $n = 5$, $P = 0.02$; Fig. 3.6b). The slopes of the regression lines were different;

the more inland sites had greater slopes, and hence a stronger response to seasonality than the coastal sites. The coastal sites showed lower flowering intensity in spring compared to inland sites, but maintained some flowering during summer when inland sites were largely dormant (Fig. 3.6c), showing that seasonality of phenology is buffered by proximity to the coast.

Between-species variation in phenology

The species-nested-within-sites PCA also yielded a similar result to the pooled-data PCA: spring-flowering species to the right of axis 1, and fall-flowering plants on the left. Notably, fall taxa had a significantly lower variance along axis 1 than the spring bloomers, indicating that flowering in fall-bloomers is in general more synchronous than in spring bloomers ($F_{(46,14)} = 3.09$, $P = 0.01$; Fig. 3.7). Axis 2 places on the positive side of the axis plants with long duration of flowering, such as *Eriogonum fasciculatum*, which start flowering in spring but keep on producing flowers late into the summer.

Discussion

Phenological dynamics at a regional scale

The multivariate analysis showed that most of the statistically significant phenological variation observed (axis 1 of the PCA) is driven by the spring-to-fall seasonal flowering gradient. Axis 2 was mostly due to the long flowering duration of *Eriogonum fasciculatum*, a spring bloomer that continues well into the summer. Based on their seasonal behavior, species can be divided into three groups according to their dominant phenological trends and their position along axis 1 of the PCA:

Spring bloomers (water responders). A group of species flowered in spring, when winter-accumulated moisture is abundant and temperatures begin to rise (Table 3.1). This group includes many deciduous species, such as deerweed (*Acmispon glaber*), California sunflower (*Encelia californica*), San Diego sunflower (*Bahiopsis laciniata*), and goosefoot (*Ambrosia chenopodiifolia*), but also includes other non-deciduous life-forms, such as the sclerophyllous jojoba (*Simmondsia chinensis*), the bushrue *Cneoridium dumosum*, the globose cactus *Mammillaria dioica,* and *Ephedra californica*, a leafless perennial. Although most of these water responders are insect-pollinated, some, such as *Ambrosia chenopodiifolia*, *Simmondsia chinensis*, and *Ephedra californica* are pollinated by wind.

Phenological response to abiotic environmental factors is individual to each species (Bowers & Dimmit 1994; Rathcke & Lacey 1985). Despite a shared response to available moisture cues, there was a high degree of variability in onset, duration and synchrony across species. Accordingly, the phenological patterns in the rainfall-responder species show variation in lag-times synchrony and duration of flowering.

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

If a plant is able to cope with the summer and fall drought, off-season flowering can have important advantages. On the one hand, by flowering at a time when few other species are in bloom, the plant can more effectively attract pollinators while reducing inter-specific pollen transfer. On the other hand, seed dispersal pressures may also play a selective role on flowering times. In wind-dispersed Asteraceae, producing seeds in fall —a normally windy time of the year— may enhance dispersal and reduce the risk of seed-bank predation, as seeds are released shortly before the onset of winter rains.

Aseasonal bloomers. These species do not display a strong seasonal pattern, despite their frequent flowering. Within this group a distinction can be made between truly aseasonal species whose individuals flower more or less continually throughout the year, and species whose individuals flower for short periods of time, but in which different individuals may flower at different times. In the second group, the individuals themselves may display a canalized flowering period, but their asynchronous pattern makes the species aseasonal at a population level. Thus, this general syndrome may in fact be a grab-bag of different strategies, expressed either at the population or at the individual level.

Species without distinct flowering patterns have been shown to be associated with aseasonal climates (Rathcke & Lacey 1985, Gentry 1974) and, interestingly, many of these taxa are present (often uniquely present*) at the San Quintín site, which is the foggiest year-round (e.g., *Helianthus*, Ribes*, Nicotiana*, Peritoma, Rhus, Malosma, Stephanomeria,* and *Euphorbia*). The majority of the species in this category have fleshy and/or vector-dispersed fruits. It is possible that seed dispersal in these taxa is placing a selective pressure on year-round reproduction, or conversely that plasticity of phenology favors vector-dispersal of fruits. Low synchrony (low levels of flowering throughout a long flowering season) may help some individuals to avoid temporal bouts of predation from specific insects (Elzinga *et al.* 2007).

Perhaps the most surprising appearance in this category of aseasonal bloomers is *Gutierrezia californica* a drought-deciduous herbaceous perennial, that normally initiates flowering in spring. In NW Baja California it was found flowering almost every month of the year. The two short-lived taxa, the invasive *Brassica tournefortii* and native annual/biennial *Stephanomeria dieguensis* were strongly aseasonal in their flowering, behaving as opportunistic species. Succulent species such as *Myrtillocactus* and *Agave*, and the large woody shrubs in *Rhus* and *Malosma* all have canalized-flowering individuals but aseasonal populations. They are also found in a variety of environments without fog mitigation of drought, and the individuals seem to be responding to water availability on a very fine scale.

Weather patterns in the regional gradient

The rainfall patterns of the broader region are strongly influenced by ENSO cycles, and the severity of the rainfall gradient is caused primarily by the orographic lift of winter storms caused by the transverse range between Ensenada and Santo Tomas (Minnich *et al.* 2000; Gonzalez *et al.* 2010). Our weather monitoring system revealed the large effect that the proximity to the ocean has on climatic traits in this region. Average air humidity and fog decrease rapidly as a function of distance to the coast, while peak summer temperatures increase along the same gradient. Coastal environments, in short, have milder summer temperatures and receive larger amounts of ocean-derived moisture than inland sites. On top of this east-west gradient, there is also a latitudinal rainfall gradient in which mean annual precipitation decreases from north to south at a rate of ca. 1 mm per km. The environmentally buffering effect of the California Current is highest in summer, when climate in the inland sites is hot and dry but when the summer fogs bring moisture and cooler temperatures to the coastal ecosystems.

Between-site differences in phenological variation

The multivariate analyses for all sites taken as separate samples confirmed the importance of the spring-to-fall seasonal flowering gradient as the major driver of plant phenology. This general trend varies significantly from site to site: Sites near the coast and under a stronger influence of coastal fogs showed lower variances along the multivariate phenological axes than sites further inland. Axis 1 was significantly related to seasonality in general, but the slope of the relationship between this axis and the spring-to-fall time gradient was significantly higher for inland sites than for coastal sites. This again confirms the more buffered and stable nature of coastal ecosystems. Available moisture derived both from rain and fog seems to control phenology in the region, but fog seems to play an extremely important role in phenological variation between sites.

The lower variance along axis 1 of fall bloomers in the PCA (repeating species in rows according to their abundance in the different sites at each date), indicates more synchronous flowering in autumnal bloomers. Since fall tends to be the driest time of the year, this trend suggests that, while spring flowering is generally triggered by local moisture availability, fall flowering of Asteraceae such as *Baccharis sarothroides* and *Ericameria palmeri* seems to be more dependent on photoperiod.

Conclusions

The southern edge of the California Floristic Province is an area of high local endemism and outstanding conservation value. With strong gradients both N-S and E-W, this large geographic ecotone harbors a unique endemic flora. Within a generalized spring-driven cyclic phenological pattern, important differences occur between species and between sites. Some deep-rooted Asteraceae growing in arroyos or low-lying areas maintain a fall-blooming phenology, while other species seem to flower opportunistically according to local conditions. At a community level, sites near the coast have significantly milder environmental conditions than inland sites. The thermally-buffering effect of the coastal current induces cooler summers, while the marine layer brings frequent fogs to coastal plains.

Our data showcase the large-scale influence of ocean currents and coastal upwelling on the concentration of a large number of endemic species of land plants. The land-ocean linkages are clear drivers of plant phenology: the presence of fog from the cold California current creates a local weather pattern that to a large extent controls flowering in the region. Physical data suggest that ocean currents have been stable for millions of years, so one can assume heavy fogs in the presence of high radiant loadings through deep time. The presence of these fogs thus may well have had a strong role in the creation of species refugia and the survival many endemic species found here.

In that sense, it is important to note that many of the local endemic or near-endemic taxa correspond to obvious fog-adapted lifeforms, such as succulent rosettes (*Dudleya* spp., *Agave shawii*) or densely-spined cacti (*Bergerocactus emoryi*). Fog is playing a critically-important role in the extension of the southern range limit of many CFP species by ameliorating the lack of rainfall in this gradient. Similarly, the inland fog limit is likely to define the inland (eastern) range limit of many taxa.

The main finding, that fog and the marine layer strongly affects plant phenologies, provides insight into the natural history of this region, and identifies a probable driver of endemism that should be given serious consideration in conservation planning. Although our climate is changing, fog will continue to form along the coast in warm weather and buffer temperature increases, creating a climatic refugium for biodiversity in future, and significantly elevating the importance of coastal conservation.

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Chapter 3 Figures

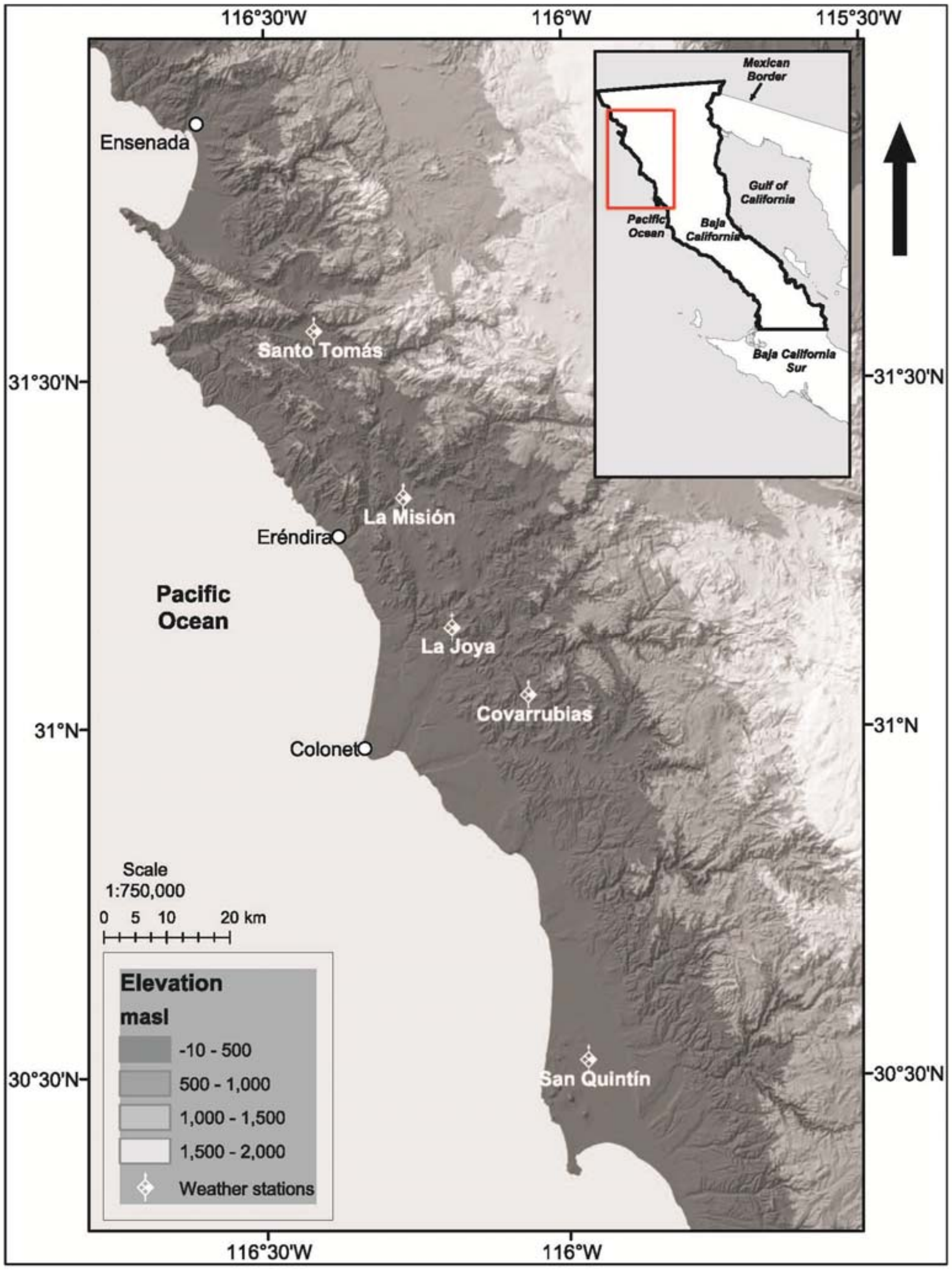

Figure 3.1. Map to show location of weather stations and study sites on the Baja California Peninsula.

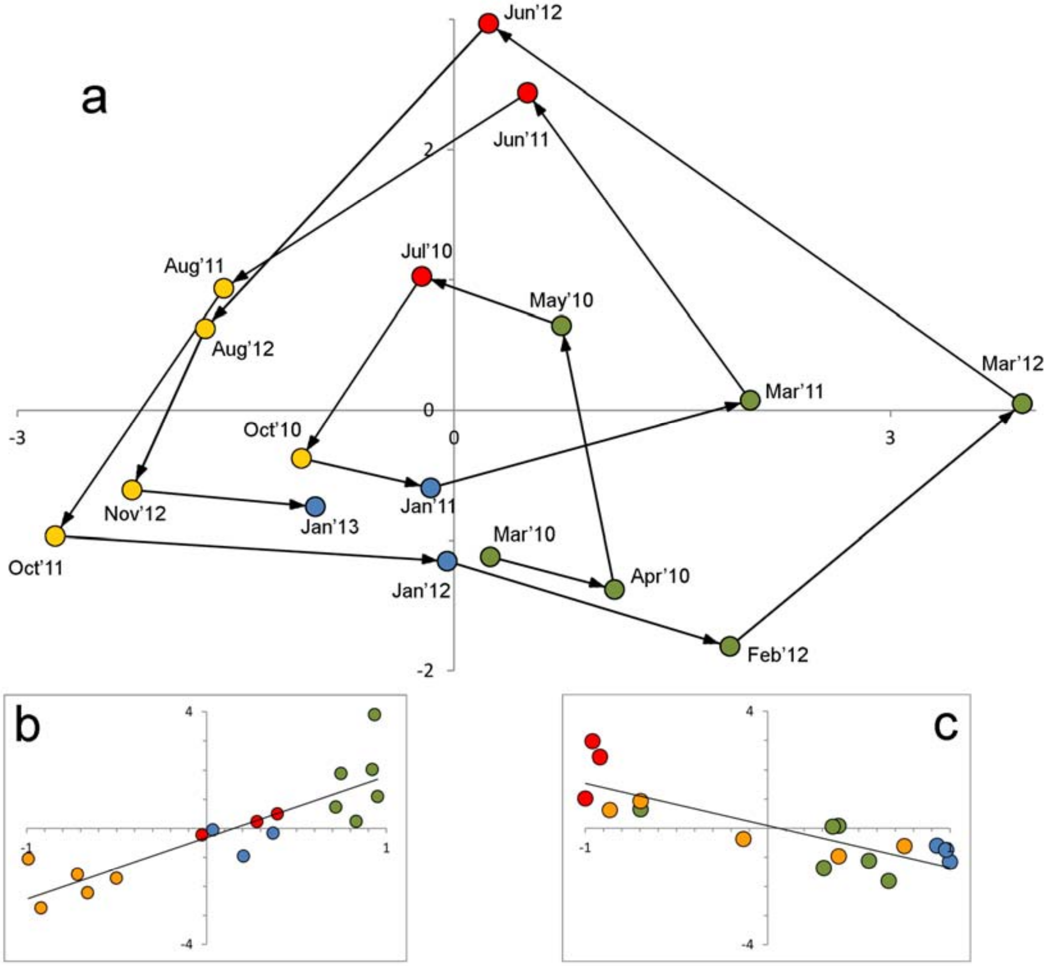

Figure 3.2. (a) Principal component biplot showing the trajectory of all sites together in phenological space. Each dot corresponds to a different sampling date, and arrows join succeeding dates. Species arranged according to their PCA loadings along axis 1 are presented in Table 3.1. (b) Correlation between axis 1 and the spring-to-fall time vector. (c) Correlation between axis 2 and the summer-to-winter time vector.

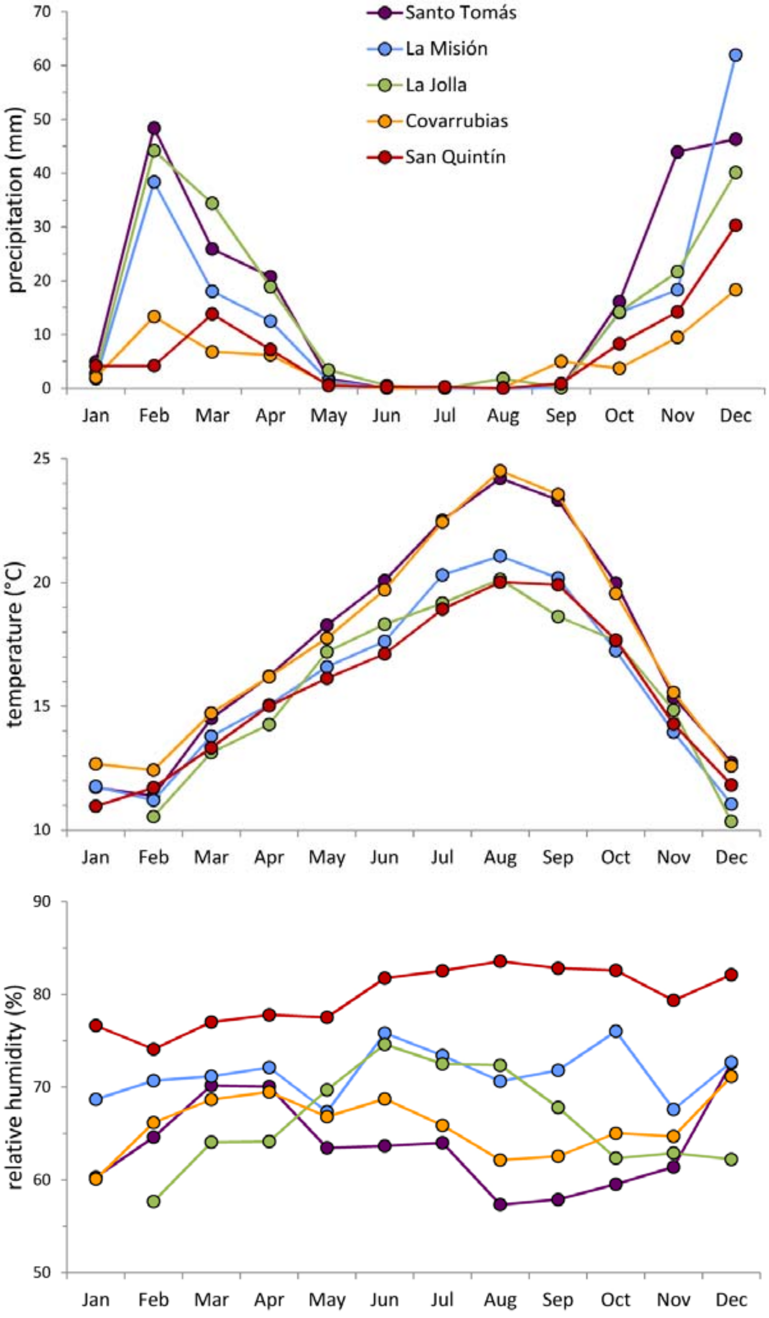

Figure 3.3. (a) Mean monthly precipitation (mm), (b) monthly-averaged daily air moisture content (%), and (c) mean monthly temperature (°C) for the five sites studied.

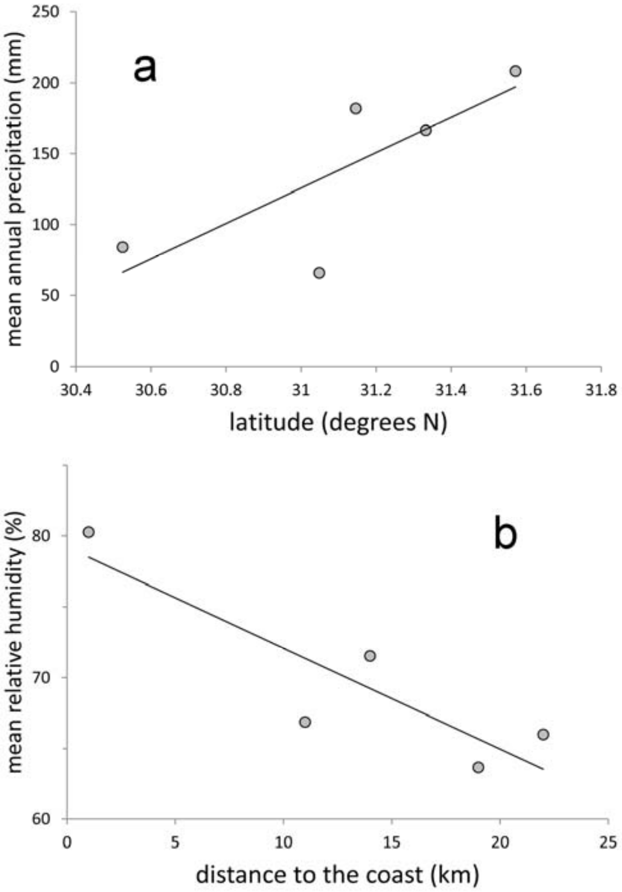

Figure 3.4. (a) Correlation between latitude and mean annual precipitation, and (b) correlation between mean air moisture and distance from the coast for the five study sites.

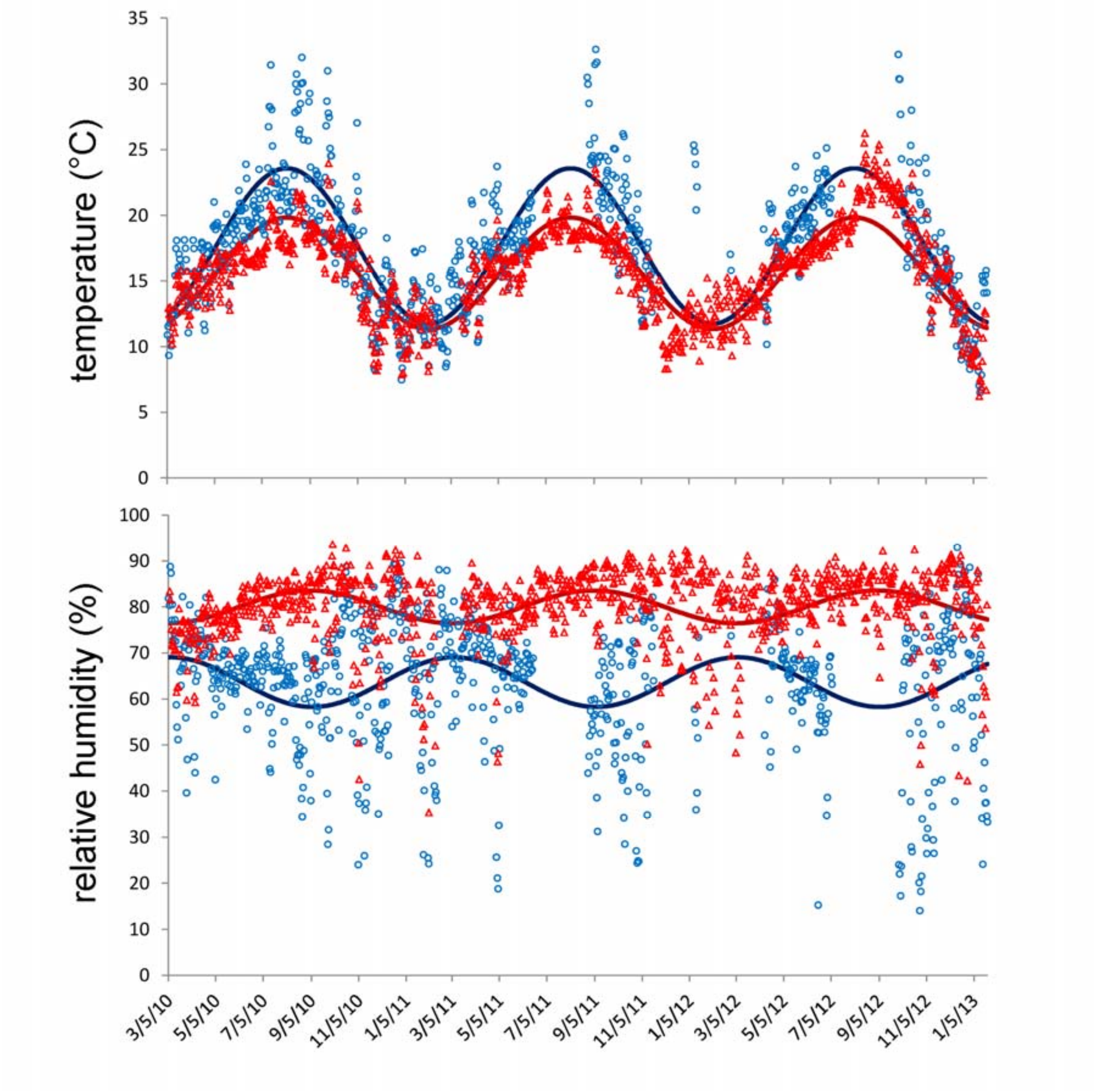

Figure 3.5. (a) Mean daily air moisture content (%), and (b) mean daily temperature (°C) for two study sites in the extremes of our study gradient: Santo Tomás, a relatively rainy inland site, and San Quintín, a more arid but coastal site subject to frequent fogs. The sinusoidal lines show the periodic trend captured by the first harmonic of a Fourier series (in all cases, the variance explained by the periodic trends was highly significant; $P < 0.0001$).

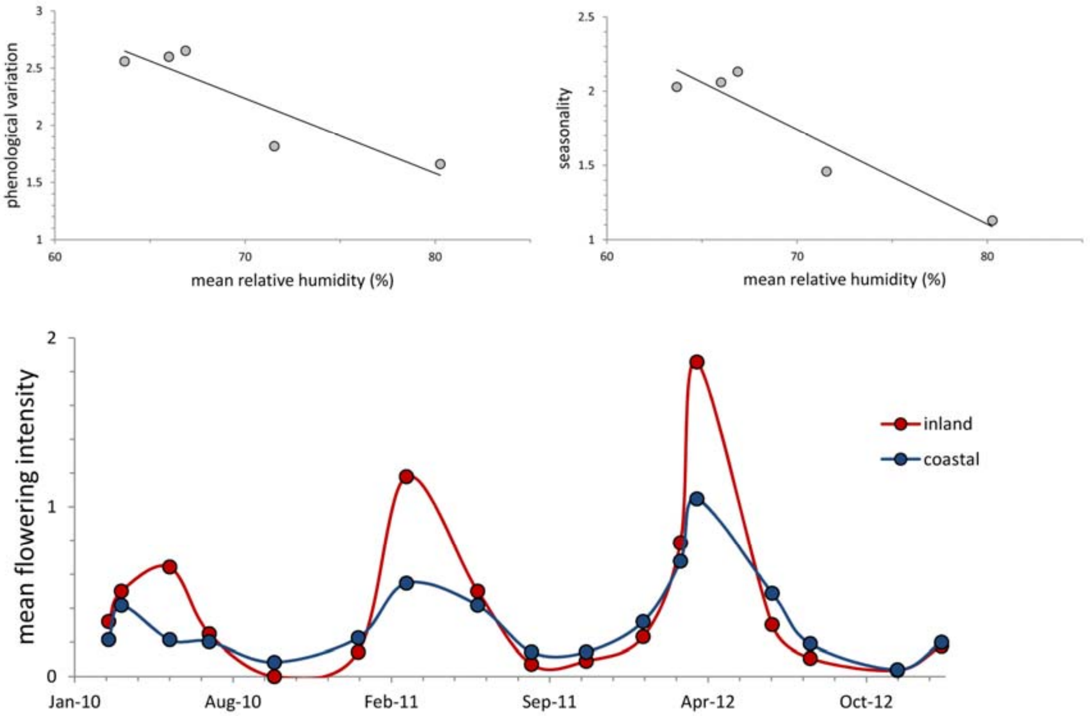

Figure 3.6. Dates-nested-within sites PCA: (a) Correlation between the standard deviation of the each site's scores along axis 1 (a measure of seasonal variation) and mean relative humidity at each site (a measure of fog incidence). (b) Slopes of the regression line between each site's scores along axis 1 and the spring-to-fall time vector (the higher the slope, the stronger the phenological variation along seasons), correlated against fog-derived humidity. (c) Average flowering intensity of spring-blooming plants in inland sites and coastal sites, during the three years of our study. Coastal sites, which receive more fog, have lower seasonal variation than inland sites, which display marked phenological differences between spring and late summer.

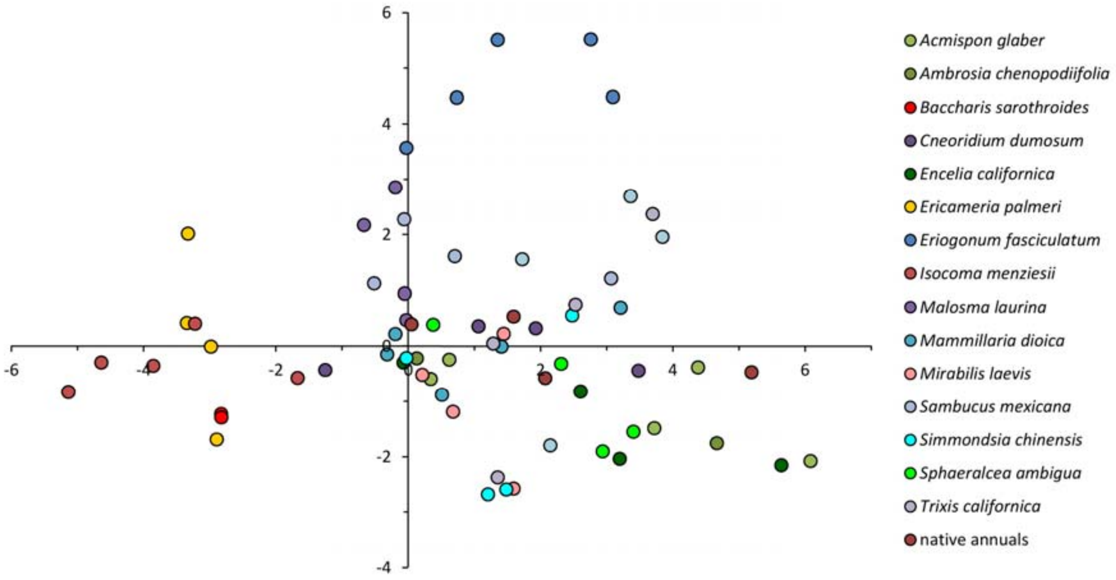

Figure 3.7. Species-nested-within-sites PCA: species-plot for axis 1 against axis 2. Axis 1 separates spring bloomers (right) from late-summer and autumn-bloomers (right). Axis 2 shows species with long flowering duration that extend from spring into summer (e.g., *Eriogonum fasciculatum*). Note the higher dispersion of spring bloomers compared to late-summer and autumn bloomers.

Table 3.1

Family	Scientific name	Life-form	Pollination syndrome	Fruit type
Spring bloomers (water responders) High on axis one				
Fabaceae	***Acmispon glaber***	**H**	**Vector**	**Dry**
	Native annual species	**A**	**Vector**	**Dry**
Asteraceae	***Encelia californica***	**H**	**Vector**	**Wind dispersed**
Malvaceae	***Sphaeralcea ambigua***	**H**	**Vector**	**Dry**
Asteraceae	***Bahiopsis laciniata***	**H**	**Vector**	**Dry**
Asteraceae	***Trixis californica***	**H**	**Vector**	**Wind dispersed**
Polygonaceae	***Eriogonum fasciculatum***	**E**	**Vector**	**Dry**
Amaranthaceae	***Ambrosia chenopodiifolia***	**H**	**Wind**	**Dry**
Rutaceae	***Cneoridium dumosum***	**Dd**	**Vector**	**Dry**
Fabaceae	*Astragalus trichopodus*	**H**	**Vector**	**Dry**
Simmondsiaceae	***Simmondsia chinensis***	**E**	**Wind**	**Dry (large)**
Convolvulaceae	*Calystegia macrostegia*	**V**	**Vector**	**Dry**
Cactaceae	***Mammillaria dioica***	**Ss**	**Vector**	**Fleshy**
Adoxaceae	***Sambucus mexicana***	**Dd**	**Vector**	**Fleshy**
Nyctaginaceae	***Mirabilis laevis***	**H**	**Vector**	**Dry**
Rubiaceae	*Gallium nuttallii*	**H**	**Vector**	**Dry**
Ephedraceae	*Ephedra californica*	**E**	**Wind**	**Dry**
Fall bloomers (off-season flowering) Low on axis one				
Grossulariaceae	*Ribes tortuosum*	**Dd**	**Vector**	**Fleshy**
Asteraceae	*Hymenoclea monogyra*	**E**	**Wind**	**Wind dispersed**
Asteraceae	*Hazardia berberidis*	**E**	**Vector**	**Wind dispersed**
Asteraceae	*Baccharis salicifolia*	**E**	**Wind**	**Wind dispersed**
Apocynaceae	*Asclepias subulata*	**H**	**Vector**	**Wind dispersed**
Asteraceae	***Baccharis sarothroides***	**E**	**Wind**	**Wind dispersed**
Asteraceae	***Ericameria palmeri***	**E**	**Vector**	**Wind dispersed**

Family	Scientific name	Life-form	Pollination syndrome	Fruit type
Asteraceae	***Isocoma menziesii***	**E**	**Vector**	**Wind dispersed**
Aseasonal flowerers (abundant but close to 0 on axis one)				
Nyctaginaceae	*Nicotiana glauca*	**E**	**Vector**	**Dry**
Cactaceae	*Myrtillocactus cochal*	**Ss**	**Vector**	**Fleshy**
Plantaginaceae	*Gambelia juncea*	**E**	**Vector**	**Dry**
Brassicaceae	*Brassica tournefordii*	**A**	**Vector**	**Dry**
Asteraceae	*Stephanomeria dieguensis*	**A**	**Vector**	**Wind dispersed**
Agavaceae	*Agave shawii*	**Rs**	**Vector**	**Dry (large)**
Anacardiaceae	*Rhus integrifolia*	**E**	**Vector**	**Fleshy**
Asteraceae	*Helianthus niveus*	**E**	**Vector**	**Dry**
Asteraceae	*Gutierrhizia californica*	**H**	**Vector**	**Wind dispersed**
Brassicaceae	*Peritoma arborea*	**Dd**	**Vector**	**Dry (large)**
Euphorbiaceae	*Euphorbia misera*	**Dd**	**Vector**	**Fleshy**
Anacardiaceae	***Malosma laurina***	**E**	**Vector**	**Fleshy**

*Bold scientific name indicates that the species was also included in the second PCA of dominant species only.
** *Life-form categories:*Stem succulents (Ss); Rosette succulents (Rs); Vines (V); Drought-deciduous perennials (Dd); Evergreen perennials (E); Perennial herbs/herbaceous perennials (H); Annuals (A)

Table 3.1. Species belonging to the three dominant phenological syndromes. Life form, pollination syndrome and fruit type are included for each taxon.

Table 3.2.

Family	Scientific name
	Native spring ephemerals
	Non-native spring ephemerals
Adoxaceae	***Sambucus mexicana***
Agavaceae	*Agave shawii*
Alliaceae	*Allium peninsularae*
Amaranthaceae	*Atriplex canescens*
Amaranthaceae	*Atriplex julacea*
Anacardiaceae	***Malosma laurina***
Anacardiaceae	*Rhus integrifolia*
Apocynaceae	*Asclepias subulata*
Apocynaceae	*Sarcostemma arenarium*
Asteraceae	***Ambrosia chenopodifolia***
Asteraceae	*Artemisia californica*
Asteraceae	*Baccharis salicifolia*
Asteraceae	***Baccharis sarothroides***
Asteraceae	***Bahiopsis laciniata***
Asteraceae	*Conyza bonariensis*
Asteraceae	***Encelia californica***
Asteraceae	***Ericameria palmeri***
Asteraceae	*Gutierrhizia californica*
Asteraceae	*Hazardia ferriseae*
Asteraceae	*Hazardia berberidis*
Asteraceae	*Helianthus niveus*
Asteraceae	*Hemizonia fasciculata*
Asteraceae	*Hymenoclea monogyra*
Asteraceae	***Isocoma menziesii***
Asteraceae	*Iva haesiana*
Asteraceae	*Perityle emoryi*
Asteraceae	*Porophyllum gracile*
Asteraceae	*Pseudognaphalium biolettii*

Asteraceae	*Centaurea melitensis*
Asteraceae	*Stephanomeria* spp.
Asteraceae	***Trixis californica***
Brassicaceae	*Brassica tournefordii*
Brassicaceae	*Isomeris arborea*
Cactaceae	*Bergerocactus emoryi*
Cactaceae	*Cylindropuntia californica*
Cactaceae	*Cylindropuntia prolifera*
Cactaceae	*Ferocactus viridescens*
Cactaceae	*Mammillaria dioica*
Cactaceae	*Myrtillocactus cochal*
Cactaceae	*Opuntia cf. littoralis*
Cactaceae	*Stenocereus gummosus*
Convolvulaceae	*Calystegia macrostegia*
Crassulaceae	*Dudleya anthonyi*
Crassulaceae	*Dudleya cultrata*
Crassulaceae	*Dudleya cf. edulis*
Crassulaceae	*Dudleya ingens*
Crassulaceae	*Dudleya pulverunlenta*
Curcurbitaceae	*Marah macrocarpa*
Ephedraceae	*Ephedra californica*
Euphorbiaceae	*Acalypha californica*
Euphorbiaceae	*Croton setigerus*
Euphorbiaceae	*Euphorbia misera*
Fabaceae	***Acmispon glaber***
Fabaceae	*Astragalus trichopodus*
Grossulariaceae	*Ribes tortuosum*
Hydrophyllaceae	*Eriodictyon sessilifolium*
Hydrophyllaceae	*Phacelia ixoides*
Lamiaceae	*Salvia apiana*
Lamiaceae	*Salvia munzii*
Malvaceae	***Sphaeralcea ambigua***

Malvaceae	*Sphaeralcea fulva*
Nyctaginaceae	*Mirabilis laevis*
Oleaceae	*Fraxinus parryi*
Onagraceae	*Camissonia cf. califonica*
Onagraceae	*Camissonia crassifolia*
Plantaginaceae	*Gambelia juncea*
Plantaginaceae	*Penstemon spectabilis*
Polygonaceae	***Eriogonum fasciculatum***
Polygonaceae	*Eriogonum fastigiatum*
Polygonaceae	*Harfordia macroptera*
Ranunculaceae	*Clematis pauciflora*
Rhamnaceae	*Rhamnus crocea*
Rosaceae	*Adenostomma fasciculata*
Rosaceae	*Heteromeles arbutifolia*
Rosaceae	*Prunus fremontii*
Rosaceae	*Rosa minutifolia*
Rubiaceae	*Gallium nuttallii*
Rutaceae	***Cneoridium dumosum***
Sapindaceae	*Aesculus parryi*
Simmondsiaceae	*Simmondsia chinensis*
Solanaceae	*Datura wrightii*
Solanaceae	*Lycium andersonii*
Solanaceae	*Lycium brevipes*
Solanaceae	*Nicotiana glauca*
Solanaceae	*Physalis crassifolia*

Table 3.2: All plants at the five weather stations. (Bold font denotes species in analysis 2)

Table 3.3.

	1 individual or <10%	10–75%	>75% of population
Early flower	1	2	2
Mid flower	1	2	3
Late flower	1	2	2.5

Table 3.3: Categories of flowering intensity and abundance (based on natural breaks in field data from year 1).

Table 3.4.

Sample ID	**Sample Weight (mg)**	**%C**	**δ^{13}C ‰ vs VPDB**
Ericameria palmeri	1.084	46.43	−30.21
Hazardia ferrisiae	1.498	47.33	−31.76
Baccharis salisifolia	1.406	49.91	−30.38
Ambrosia monogyra	1.163	44.65	−30.10
Baccharis sarothroides	1.410	53.55	−24.55
Euphorbia misera	1.189	36.97	−28.84
Peritoma arborea	1.340	42.46	−26.54
Isocoma menziesii var. menziesii	1.102	42.34	−30.54

Table 3.4: δ^{13}C of leaf samples from summer-blooming species.The δ^{13}C ‰ vs VPDB ratio in C3 plants is approximately −28, and C4 plants are approx. −13. This indicates that all plants sampled displayed C3 photosynthesis.

Conclusions

The Pacific Ocean has an enormous influence on ecological dynamics and biological diversity in the coastal mediterrnean ecosystem of northwestern Baja California. Ocean currents control water availability in the form of coastal fogs that both provide additional water and mitigate moisture losses from radiant loadings, creating refugia and areas of reduced climatic change that can stimulate adaptive evoluntionary change.

Marine influences on landscape diversity are seen as a direct result of pre-historical human harvesting of shellfish and the subsequent shell deposition onto land. Aragonite shells have weathered sufficiently during the last 5,000 years to show marked impacts on terrestrial plant distributions. As shell decomposition continues we can expect to see continued changes in the flora that occupies these deposits, continually providing a different microhabitat to the surrounding matrix which increases landscape heterogeneity.

Conservation planning in this region should give elevated importance to the preservation of coastal lands, particularly within the fog-reach zone. Additional protection of shell middens is warranted in order to protect both the rich human history of the peninsula and the present and future biodiversity of these sites that increase landscape complexity.

Climate change considerations

In considering plant conservation and the creation of natural reserves, the impacts of the marine layer on local weather and resultant biodiversity should be taken into careful consideration. Although some climate models have been developed for this region none of the climatic modelling included fog, snow, or wind, which are extremeley important factors in determining local water availability and resultant plant occurrences.

The cold California current is likely to be persistent, forming coastal fogs whenever solar radiation is high. Therefore, we can expect fog to ammeliorate extreme events of heat and drought along the coast in future. Coastal regions thus are likely to harbor many species that may be extripated further inland. Coastal lands therefore are of greatly increased importance to plant conservation in a changing climate.

Although the cold current may be the saving grace for many coastal species, other ocean phenomena may have negative implications for terrestrial biodiversity in a changing climate. Many authors predict an increase in ENSO extremes in coming years that may well result in flash floods, heat waves, and perhaps wetter conditions that allow invasive species to penetrate in from the North. An additional and complicated consideration for coastal conservation is the probability of rising sea-levels. There is little data available to help us understand the likelihood and speed of plant migrations in future conditions.

Final thoughts

Conserved coastal lands in northwestern Baja California could also offer a perfect opportunity for plants to continue to evolve and adapt to a changing climate. As Ackerly (2009) said: "*..the greatest opportunity for adaptive evolution will occur on the trailing edge of species ranges during episodes of climate change, as changing conditions kill off the existing vegetation"*. The position of this ecotone, near the 30th paralell, suggests that it will continue to be an extremely important transitional area and the range limit for several taxa from the north and south. As such, it is an important gene-bank for wide-ranging species, and an essential conservation hotspot for its local endemics.

In conclusion, conservation of coastal ecostystems is of the utmost importance in northwestern Baja California, where the California Floristic Province meets the Mexican Deserts, and oceanic influences leave a rich mosaic of native and narrowly endemic plants.