Multiple Perspectives on Plant Conservation Biology:

Molecular Phylogeny and Biogeography of the Mammilloid clade (Cactaceae) of Baja California and Adjacent Regions, with Assessment of Extinction Risks to a Selected Species, *Cochemiea halei*, as a Result of Climate Change

by

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ABSTRACT

In the face of the sixth mass extinction on Earth, with the flowering plant family Cactaceae assessed as the fifth most endangered plant or animal family by the International Union for the Conservation of Nature (IUCN), it is imperative that all available tools be used to understand the biodiversity, habitat suitability, climate change impacts and population viability of cacti. Within the Cactaceae, *Mammillaria* Haw and the closely related genus *Cochemiea* (K. Brandegee) Walton of Baja California, Mexico, are species-rich, with 46 regionally endemic taxa, 12 of which have been assessed as threatened or endangered by the IUCN. This study clarifies the evolutionary relationships in the Mammilloid clade, a complex and species-rich clade in tribe Cacteae, and generic circumscription of the genera *Mammillaria* Haw. and *Cochemiea* (K. Brandegee) Walton, estimates divergence times, diversification rates and ancestral ranges and explores habitat suitability and the risk of extinction of a representative species within these genera. The r species, *Cochemiea halei* (K. Brandegee) Walton, a narrowly distributed island endemic, is assessed using species distribution modeling (SDM) and population viability analysis (PVA). SDM in this study includes projections to two climate change scenarios over the next century, using four representative particle concentration pathways, and the PVA uses habitat-specific deterministic and stochastic models. The results of molecular phylogenetic analyses of the Mammilloid cladde restore the genus *Mammillaria* to monophyly via new combinations in the genus *Cochemiea*. The taxa in this study are shown to be of recent origin resulting from rapid diversification and radiation. Geological and climatic forces at multiple scales appear to be responsible for the high degree of biodiversity and endemism of these cacti. SDM shows that *C. halei* is likely to be stranded in its fragmented island habitat, has a facultative adaptation to ultramafic soils, and faces a 21%–53% contraction of its range on the islands under climate change scenarios. PVA suggests that *C. halei* is at increased risk of extinction in response to slight decreases in fecundity and persistence. In general, the perspectives in this dissertation fill several gaps in our prior knowledge of the evolution, biogeography, and conservation pressures of an important, species-rich group of cacti, occurring in a region of high biodiversity and endemism.

DEDICATION

To those friends, family members, and fellow botanists, who have helped me maintain a sense of humor, a sense of proportion, and the ability to think relatively clearly, throughout this challenging and wildly unpredictable endeavor.

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Chapter 1 INTRODUCTION

As evidence mounts that we are witnessing the leading edge of the sixth mass extinction in Earth's history (Barnosky et al. 2011, Peivani 2013, Kolbert 2014, Cafaro 2015, Ceballos et al. 2015, McCallum 2015, Ceballos et al. 2017, Humphreys et al. 2019), the urgent need to understand the evolution, historical distributions, current environmental habitat suitability and population viability of threatened species can be met by the full suite of analytical tools presently available. For that reason, this dissertation uses molecular phylogeny, biogeography, species distribution modeling, climate change projections and quantitative population viability analysis in order to investigate a species-rich, major clade in the Cactaceae.

Cactaceae are the fifth most endangered plant or animal family to be globally assessed to date by the International Union for the Conservation of Nature, and have long been known to be under significant extinction pressure (Anderson et al. 1994, Hernández and Bárcenas 1995, Hernández and Bárcenas 1996, Ortega-Baes et al. 2006, Ortega-Baes et al. 2010, Goettsch et al. 2015, Goettsch et al. 2019). Yet, major taxonomic, biogeographical and conservation management questions remain for the family as a whole and for specific groups within the family (Ortega Baes 2006, Goettsch et al. 2015, Goettsch et al. 2019). This dissertation addresses gaps in our understanding of the evolution and future prospects faced by a diverse, widely distributed, little-studied, and threatened group of cacti.

The clade in the Cactaceae that is the subject of this dissertation, composed in large part of three species-rich genera, *Mammillaria* Haw*.*, *Coryphantha* (Engelm.) Lem. *,* and *Cochemiea* (K. Brandegee) Walton*,* hereafter referred to as "the Mammilloid clade," following its designation as such by Butterworth et al. 2002, and the continued sense of the term in Hernandez-Hernández (2014), has long been a source of taxonomic and phylogenetic confusion (Hunt 1981, Hunt 1984, Butterworth and Wallace 2004, Crozier 2005, Harpke and Peterson 2006, Harpke et al. 2006, Bárcenas et al. 2011, Vázquez-Sánchez et al. 2013). In particular, the species-rich genus *Mammillaria* is clearly non-monophyletic as currently circumscribed, with more than 150 years of taxonomic changes, including segregation into at least 12 smaller genera, and a recent record of molecular phylogenetic analysis confirming non-monophyly (Butterworth and Wallace 2004, Bárcenas et al. 2011, Vázquez-Sánchez et al. 2013).

Mammillaria was first published by British horticulturalist Adrian Hardy Haworth in 1812. In part, taxa transferred to Haworth's new genus had been included in the large genus *Cactus* L., published in 1753 in Linnaeus's *Species Plantarum*. Unbeknownst to Haworth, Stackworth had published a genus of algae named *Mammillaria* in 1809, and, due to the rules of botanical nomenclature which forbid duplicate names, Britton and Rose (1923) used the genus name *Neomammillaria*. The name *Mammillaria* was never actually used in algae taxonomy, however (Staples 2016), and in 1930, *Mammillaria* was conserved for the genus in the Cactaceae by the International Botanical Congress.

Coryphantha was originally circumscribed as a subgenus of *Mammillaria* in 1830, by Engelmann. Lemaire, in 1868, elevated the taxa included therein to the rank of genus, based on the plants having grooves on the adaxial surface of their stem tubercles, and the fact that flowers emerge from new growth, as opposed to *Mammillaria*, where flowers emerge from the previous years' growth. *Cochemiea* was also originally within *Mammillaria*, but segregated by Walton in 1899, due to zygomorphic floral morphology. The research presented in this dissertation has the following general aims:

1). To clarify the previously either unknown or unresolved evolutionary and clade relationships of the Mammilloid clade.

2). To trace, for the first time, the most likely ancestral history, divergence times and diversification rates leading to the current distributions of the Mammilloid clade, in particular to help understand the high rates of peninsular and island endemism.

3). To investigate the environmental variables that correlate most strongly with the habitat of a selected threatened species from the Mammilloid clade and to quantify the likely impacts on the range of this species caused by climate change exposure.

4). To determine if the selected species is at risk of local or global extinction over the next century.

The dissertation is organized to provide increasing detail, from the general investigation of how the taxa in the Mammilloid clade are related to each other and to the Cactaceae as a whole, to the more specific study of where the representative taxon occurs, and why, and what constitutes some of the quantifiable threats it faces.

The Baja California peninsula and adjacent regions are chosen as a geographical constraint that captures aspects of the major clade of cacti studied for three reasons. One is that enduring taxonomic confusion and disagreement among authorities characterizes this clade specifically in this region (Hunt 2006, Rebman and Roberts 2012). The second is that the geological and climatic forces of this region are well-studied, providing extensive support for biogeographical and environmental studies (Dolby et al. 2015). Third, I had extensive prior experience spanning two decades of field work in the region, making continued field work feasible.

Chapter 2 presents a molecular phylogeny of the Mammilloid clade members primarily found in the Baja California region. The main goal of the molecular phylogeny project is to resolve the relationships within this clade, especially by providing clearer resolution than has been recovered in past studies (e.g., Bárcenas et al. 2011) by using, as a source of data, a much larger portion of the plastid genome sequence (plastome) than previous studies. The Baja California members of this clade occur with high rates of peninsular and island endemism (Rebman and Roberts 2012), a large number of taxa within a relatively small geographical area, and unique morphology, and the molecular phylogeny study herein was also designed to better understand the evolutionary relationships of these Baja California clade members in particular.

Chapter 3 presents the results of using multiple methods to clarify the ancestral range of the Mammilloid clade and its biogeographical history in its westward dispersal to the Sonoran Desert and the Baja California peninsula. This chapter is intended to provide deeper understanding of the ancestral origins of the Mammilloid clade members unique to the Baja California peninsula and adjacent regions. How is the Mammilloid clade biogeographically related to the tribe Cacteae, in which it is nested? How long ago did the Mammilloid clade begin to disperse to its current distributions? What are some possible geological and climatic forces that have contributed to the high rates of speciation and endemism in the Baja California members of the Mammilloid clade? In particular, the chapter highlights the distinct biogeography, high diversification rates and recent divergence times of the genus *Cochemiea*, in the expanded sense defined in the molecular phylogeny study in Chapter 2.

Because it is a threatened, narrowly distributed island endemic (Rebman and Roberts 2012, Rebman et al. 2016, IUCN 2019), *Cochemiea halei* (K. Brandegee) Walton was selected for species distribution modeling, climate change impact and population viability studies. Key aspects of the genus *Cochemiea* in Baja California are captured by this species: it is the type species of the original, narrowly circumscribed genus, it is a recently diverging, narrowly distributed island endemic, previously assessed as vulnerable to extinction, and not previously well-studied from an ecological perspective.

Chapter 4 presents the results of species distribution modeling to investigate the environmental variables that correlate to the current distribution of *Cochemiea halei* and to predict likely impacts of climate change exposure on the range of the species.

Chapter 5 employs demographic stage class matrix models, both deterministic and stochastic, to predict the fate of *Cochemiea halei* over the next century, both overall, and in three specified habitat types.

The major findings in the chapters are:

1). The relationships of the subclades of the Mammilloid clade are clarified. The monophyly of the genus *Mammillaria* is recovered by expanding the genus *Cochemiea*, moving all members of a well-supported “Cochemiea clade” out of *Mammillaria* and into an expanded circumscription of the genus *Cochemiea*. Although nested within the former circumscription of *Mammillaria*, *Coryphantha*, a well-supported subclade in the Mammilloid clade, with morphologically distinct characters, is retained as a genus. The evolutionary relationships of several subclades within an expanded genus *Cochemiea* are clarified with strong support values and consistent topologies across multiple analytical methods.

2). The Baja California members of the Mammilloid clade originated in the ancestral range of tribe Cacteae as a whole, namely the Mexican Plateau north of the Trans Mexican Volcanic Belt, and appeared in the Sonoran Desert region approximately 1 million years after the origination of the clade, at 5 million years ago (Ma). Dispersal to the Baja California peninsula occurred simultaneously with continued rifting of the peninsula away from the Mexican mainland, and then several times thereafter, with the Gulf of California not presenting a barrier to dispersal. The divergence times of most of the species of *Cochemiea* are within the last 2 million years, or even more recently. The rate of diversification of the Mammilloid clade is, in general, several times that of the overall mean background rate for angiosperms, and within the Mammilloid clade, the diversification of *Cochemiea* is approximately three times the clade average. Multiple geological events over different timescales are found to be likely drivers of the high rates of peninsular and island endemism and diverse speciation.

3). *Cochemiea halei* has a fragmented suitable habitat, not only between islands but also within varied locales on each island where it occurs. Temperature variables are most strongly correlated with its suitable habitat. The ultramafic, ocean crustal rock on which a majority of individuals occur is a strong constraint on the distribution of the species. *C. halei* is not likely to migrate from its island habitat to the peninsula. Over the next 50 to 70 years, climate change models predict that the species will lose between 21% and 53% of its current range. These factors combined highlight that *C. halei* is at elevated extinction risk.

4). Population viability analysis for *C. halei*, over its entire distribution, as well as in three distinct habitat types, using both deterministic and stochastic methods, also indicates that the species is at elevated risk of extinction over the next century. In particular, the species is sensitive to slight changes in rates of the recruitment of new individuals to the population as well as persistence of established individuals. In all scenarios, lower elevation, drier habitat populations are predicted to decline, with local extinction a strong possibility. The higher elevation populations along the tops of rocky ridges are more likely to remain stable or increase slightly over the next century.

Chapter 5, the last section of the main body of the dissertation, discusses ways in which the molecular phylogeny, ancestral biogeography, species distribution, climate change modeling, and population viability analysis lead to complementary or contrasting inference regarding the evolution, biogeography, and conservation status of the taxa studied.

The structure of the dissertation is in the form of standalone chapters, intended to adhere to the structure of journal articles, although some chapters include more background and detail than one would normally include in an article for publication. The literature review is divided into the introduction for each chapter, and is specific to the research area of that chapter. The literature cited section is comprehensive for all citations in the dissertation.

Chapter 2 MOLECULAR PHYLOGENY OF THE MAMMILLOID CLADE (CACTACEAE) OF BAJA CALIFORNIA AND ADJACENT REGIONS: RESOLVING THE MONOPHYLY OF *Mammillaria* WITH NEW COMBINATIONS IN *Cochemiea*

Abstract

In an effort to resolve more than 150 years of taxonomic confusion, the molecular phylogeny of the Mammilloid clade, including the genera *Mammillaria, Coryphantha* and *Cochemiea* is recovered, including a regionally complete taxon sampling of *Mammillaria* and *Cochemiea* from the Baja California region. Employing the large single copy region of the plastid genome, sequence data is analyzed via maximum likelihood, maximum parsimony and Bayesian inference. The molecular phylogeny is further supported by tracing the ancestral states of three distinctive characters for the sample taxa. The results clarify the evolutionary relationships of these closely related taxa, providing high resolution with generally strong node support values. *Mammillaria* as currently circumscribed is confirmed as non-monophyletic, and the monophyly of the genus is resolved via new combinations in an expanded, monophyletic *Cochemiea.*

Introduction

The flowering plant family Cactaceae Juss., published in 1789, is a well-supported clade within the order Caryophyllales (Hershkovitz and Zimmer 1997, Applequist and Wallace 2001, Nyffeller 2002, Nyffeller and Eggli 2010a, Walker et al. 2018), which, in the most recent comprehensive analyses, was sister to the Anacampserotaceae+Portulacaceae clade (Yang et. al. 2017, Walker et al. 2018). Cactaceae is a New World family with the exception of the Central African tropical epiphyte *Rhipsalis baccifera* (Sol.) Stearn (Anderson 2001). The family is estimated to have originated approximately 35–27 million years ago (Ma), with Hershkovitz and Zimmer, using only ITS sequences (1997), Arakaki et al. (2011) and Hernández-Hernández et al. (2014), using larger data sets, arriving at approximately the same stem age for the family. Cactaceae apparently had an initial period of diversification and dispersal at a rate comparable to other angiosperms, but the family underwent accelerated diversification, including in regard to the clades in this study, with a significant increase in speciation and a rapidly expanded range, from the late Miocene to the present (Crozier 2005, Arakaki et al. 2011, Hernández-Hernández et al. 2014). The causes of this rapid diversification were apparently a combination of increased aridity and reduced atmospheric CO_2, which benefited plants with the combination of stem succulence and Crassulacean Acid Metabolism (CAM) photosynthesis present in cacti (Arakaki et al. 2011).

The history of cactus taxonomy is complex, with both amateur and professional botanists attempting monographs on the entire family, most recently Anderson (2001) and Lodé (2015). Multiple examples of homoplasy (i.e., the repeated evolution of similar morphological traits in distantly related clades) (cf., Majure 2012) and hemiplasy (multiple origins of a character state on a species tree when there is gene tree/species tree discordance and no homoplasy on the gene tree) (Avise and Robinson 2008, Copetti et al. 2017) have contributed to phylogenetic confusion. At the peak of an accumulation of names at the ranks of genus and species, there were more than 15,000 species in 233 genera (Hunt 2016). Currently accepted species number 800–1860, a range that shows enduring disagreement among authorities regarding taxon boundaries (Anderson 2001, Guzmán Cruz et al. 2003, Hernández-Hernández et al. 2011, Hunt 2016, Stevens 2019).

The genus *Mammillaria* Haw. is one of the genera that has received extensive attention in the literature, especially among amateur botanists, although it was professional botanists Britton and Rose, and Buxbaum, who were largely responsible for a proliferation of genera being separated out of *Mammillaria,* and the publication of a large number of species (Britton and Rose 1923, Buxbaum 1951a, 1951b, 1951c, Buxbaum 1954). At least 15 smaller genera have been separated out of *Mammillaria sensu* Haw. (Table 2-1). At the species level, the history is even more complex, with the genus at one time having more than 500 putative species (Hunt 2016). Currently, the accepted number of species is between 164-200 (Hunt 2016), and even at that conservative number, the genus remains one of the most species-rich in Cactaceae (Butterworth and Wallace 2004, Guerrero et al. 2018).

The broadest concepts of *Mammillaria* in taxonomic systems also included the genus *Coryphantha*, first published at generic rank in 1868, after having been recognized by Engelmann as a subgenus of *Mammillaria* in 1856. Morphological characters for *Coryphantha* that are used to separate the genus from *Mammillaria* are the presence of a more or less visible central groove on the adaxial surface of the tubercle, and flowers that emerge from the current year's growth near the apical meristem, as distinct from flowers from previous years' growth in *Mammillaria*, which also feature non-grooved tubercles (Engelmann 1857, Lemaire 1868, Butterworth and Wallace 2004, Dicht and Luthy 2006). Disagreement among experts remains as to the species limits within *Coryphantha*, as well as the level of support for the segregate genus *Escobaria* (Taylor 1986, Anderson 2001, Dicht and Lüthy 2005). Again reflecting the phenotypic diversity of these taxa within tribe Cacteae, several segregate genera have also been recognized as separate from both

Coryphantha (*Cumarinia* Buxb., *Lepidocoryphantha* Backeb, *Aulocothele* Lem., *Glandulifera* Fric and *Rosea* Fric) and *Escobaria* (*Cochisiea* Earle, *Escobesseya* Hester, *Fobea* Fric and *Neobesseya* Britton & Rose). Additionally, several *Coryphantha* species were originally described as *Mammillaria* or, in the case of *Coryphantha salinensis* (Poselg.) Dicht and A. Lüthy*,* as a species of *Echinocactus* Link & Otto.

Britton and Rose (1923) and, later, Buxbaum (1951a-c, 1954) narrowly circumscribed *Mammillaria* and published several segregate genera. Hunt (1997) and Lüthy (1995), working separately, attempted a compromise approach, with a broader circumscription of *Mammillaria* while moving segregate genera back into *Mammillaria* via the recognition of infrageneric series, sections and subgenera (Butterworth and Wallace 2004).

The confused history of *Cochemiea* (K. Brandegee) Walton is relevant here. The type species, originally published as *Mammillaria halei* K. Brandegee (1889), was moved to its own genus by Walton (1899), due to its bilaterally symmetrical, weakly zygomorphic flowers. In 1971, Hunt transferred all *Cochemiea* back into *Mammillaria*, but several authorities since then have retained *Cochemiea* (Bravo-Hollis and Sánchez-Mejorada 1991, Anderson 2001, Rebman and Roberts 2012). Those authors recognized *Cochemiea* as a genus including five species: *C. halei* (K. Brandegee) Walton (the type species), *C. poselgeri* Britton & Rose, *C. pondii* Walton, *C. setispina* J.M. Coult., and *C. maritima* G.E. Linds. Recently, a sixth taxon, *C. thomasii* García-Mor., Rodr. González, J. García- Jim. & Iamonico, from mainland Mexico in Sinaloa, was published (García-Morales et al. 2020). Also relevant: five of the genera segregated from *Mammillaria* occur in Baja California (Table 2-1).

Table 2-1. Genera historically segregated from *Mammillaria sensu* Haw.

Genus	Type	Author(s)	Year
Bartschella*	*B. schumannii*	Britton & Rose	1923
Chilita*	*C. grahamii*	Orcutt	1926
Cochemiea*	*C. halei*	Walton	1899
Dolicothele	*D. longimamma*	Britton & Rose	1923
Ebnerella*	*E. wildii*	Buxbaum	1951
Escobariopsis	*E. sphacelata*	Doweld	2000
Haagea	*H. schwartzii*	Fric	1925
Krainzia	*K. longiflora*	Backeberg	1938
Lactomammillaria	*L. asseliformoides*	Fric	1924
Leptocladia	*L. elongata*	Buxbaum	1951
Leptocladodia	*L. elongata*	Buxbaum	1954
Mammillopsis	*M. senilis*	Weber	1923
Mammilloydia	*M. candida*	Buxbaum	1951
Ohmea	*O. nelsonii*	Buxbaum	1951
Phellosperma*	*P. tetrancistra*	Britton & Rose	1923
Porfiria	*P. coahuilensis*	Boedecker	1926
Solisia	*S. pectinata*	Britton & Rose	1923

*Genera occurring in Baja California.

In regard to the Baja California taxa and relatives in *Mammillaria*, Hunt (1987) retained series *Ancistracanthae* Schumann, and Lüthy (1995, 2001) recognized subgenus *Cochemiea* that was largely congruent with series *Ancistracanthae*, grouped according to a combination of hooked spines and flowers typically larger than other members of *Mammillaria*. Butterworth and Wallace's (2004) molecular phylogeny recovered Hunt's series *Ancistracanthae,* but also showed that it was not monophyletic, due to Hunt's separation of subgenus *Cochemiea*, which is nested within *Ancistracanthae*, as well as the presence of *Neolloydia conoidea* and *Ortegocactus macdougallii* within the clade containing *Ancistracanthae*. Otherwise, Hunt's concept of *Ancistracanthae* and Lüthy's subgenus *Cochemiea* are congruent with the hook-spined *Mammillaria* of Baja California. Amateur botanist Doweld (2000a, 2000b) combined some hook-spined *Mammillaria* into *Cochemiea*, based entirely on seed morphology, but his treatment did not resolve the larger question of the monophyly of *Mammillaria*. In her unpublished doctoral thesis using chloroplast DNA to reconstruct a phylogeny of *Mammillaria* and related genera, Crozier (2005) recommended the transfer of most of Hunt's series *Ancistracanthae* to *Cochemiea*, but this change was never formally implemented.

With the advent of analysis of DNA sequence data, it became more apparent that *Mammillaria* as currently circumscribed was not monophyletic (Butterworth et al. 2002, Butterworth and Wallace 2004, Crozier 2005, Bárcenas et al. 2011, Hernández-Hernández et al. 2011, Vázquez-Sánchez et al. 2013). Butterworth et al.'s Mammilloid clade (2002) contained genera which were historically never published in *Mammillaria*, namely *Ortegocactus macdougalii* Alexander, *Neolloydia conoidea* Britton and Rose, and *Cumarinia odorata* (Boed.) Buxb. Their analysis also showed

Coryphantha and *Escobaria* nested within *Mammillaria* as currently cricumscribed, although the support values for that placement were low. Later studies, for example, Bárcenas et al. (2011) and Vázquez-Sánchez et al. (2013) recovered essentially the same large, well-supported clade, with *Cochemiea, Coryphantha, Escobaria, Ortegocactus, Cumarinia* and *Neolloydia* nested within *Mammillaria* as currently circumscribed.

The monophyly of *Mammillaria* and its relationship to the other Mammilloid clade members has not been resolved, in spite of several molecular phylogenies involving *Mammillaria* between 2002 and the present (Butterworth et al. 2002, Butterworth and Wallace 2004, Crozier 2005, Harpke et al. 2006, Bárcenas et al. 2011, Vázquez-Sánchez et al. 2013). This study has the following goals: 1). Confirmation that the current circumscription of *Mammillaria* is non-monophyletic, using a larger portion of the chloroplast DNA sequences as data than previous studies; 2). Clarification of the relationships within the Mammilloid clade; 3). Determining the level of support for retaining *Coryphantha* and *Escobaria* as separate, monophyletic genera; 4). Investigating whether or not the taxa in the segregate genus *Cochemiea*, recognized by some authorities, form a distinct clade, and if so, if is there support for retaining it at the rank of genus, and; 5). resolving the monophyly of the genus *Mammillaria*, by clarifying its position and boundaries within the Mammilloid clade.

Methods and Materials

Taxon Sampling

Eighty-eight taxa were sampled, including 57 from the genus *Mammillaria* as currently circumscribed, with a nearly complete regional taxon sampling of Baja California and adjacent regions. Among accepted Baja California *Mammillaria*, only a few infraspecific taxa were omitted. Broad sampling across the rest of *Mammillaria* was conducted, based on Butterworth and Wallace's subclade designations, with at least one representative from each of their subclades (2004) (Table 2-2). Also from Butterworth's Clade A, *Neolloydia conoidea*, *Ortegocacus macdougalii* and six species of *Coryphantha* and *Escobaria* were sampled, including the types of both genera (*C. sulcata* and *E. tuberculosa*). An additional seven *Coryphantha*/*Escobaria* not sampled by Butterworth and Wallace (2004) were sampled, as well as *Cumarinia odorata*. Seven taxa were selected from the genera *Acharagma*, *Ariocarpus* Scheidw., *Lophophora* J.M. Coult. *Strombocactus* Britton & Rose and *Turbinicarpus* Buxb. & Backeb as outgroups were selected based on relationships shown in previously published phylogenies (Nyfeller 2002, Butterworth and Wallace 2004, Barcenas et al. 2011, Vázquez-Sánchez et al. 2013) and further verified by a molecular phylogeny of the cactus family carried out by L. Majure using the plastid gene *matK* (L. C. Majure, unpublished data).

Field surveys, including visits to the known type localities, photographs and mapping of the *Mammillaria* of Baja California were conducted approximately every six months for a period of five years, from May 2014 to May 2018. Sources for plant material included cultivated plants from Mesa Garden, the private collection of Dr. Juergen Menzel, the commercial nurseryArid Adaptations (Tucson, AZ), and, whenever possible, field-collected specimens in the Desert Botanical Garden Living Collection. Specimens were keyed out to existing descriptions, using Craig (1945) Hunt (1976, 1987, 2006), Bravo-Hollis and Sanchez-Mejorada (1991), Anderson (2001), and Parfitt and Gibson (2003). All *Mammillaria* included in the analyses came with locality information, including plants from cultivation. All plants from the living collection at the Desert

Botanical Garden also have accession and locality information. Vouchers are deposited at the Desert Botanical Garden Herbarium (DES) (Table 2-2).

DNA extractions, sequencing, assembly and alignment

Total genomic DNA was extracted using a modified CTAB procedure (Doyle and Doyle 1987, Neubig et al. 2014, Majure et al. 2019). DNA was quantitated using a Qubit DNA High Sensitivity fluorometer, with at least 1 ug total DNA extracted per taxon (Invitrogen, Carlsbad CA).

Library preparation and next generation sequencing using genome skimming (cf. Majure et al. 2019) was performed by Rapid Genomics, on the Illumina HiSeq X platform (Rapid Genomics LLC, Gainesville FL). Raw reads (150 bp, paired end) of *Mammillaria prolifera* (Mill.) Haw. were assembled to the large single copy region (LSC) of a *de novo* assembly of the *Cylindropuntia bigelovii* (Engelm.) F.M. Knuth plastome (Majure et al. 2019), using Geneious Prime 2019.1.3 (Biomatters Ltd., Aukland, NZ). Raw reads of *M. prolifera* were then used subsequently to reference map back to the consensus sequence of the LSC of the original reference mapping. A majority consensus sequence was constructed from those reads, and the mapped LSC of *M. prolifera* was then used to reference map the rest of the taxa sampled.

After initial automated alignment in MAFFT v. 7 (Katoh and Kuma 2002), manual refinement and reduction of gaps was conducted in Geneious Prime 2019.1.3 (Biomatters Ltd., Aukland, NZ). All gaps resulting from the alignment process were treated as missing data in subsequent analyses.

Table 2-2. Taxa from the *Mammillaria/Coryphantha/Cochemiea* clade sampled for the phylogenetic analyses.

Name	Clade	BC	Endemic	SA
Mammillaria armillata	**A**	**X**	**X**	**X**
M. albicans	**A**	**X**	**X**	**X**
M. angelensis	**A**	**X**	**X, i**	**X**
M. blossfeldiana	**A**	**X**	**X**	**X**
M. bocensis				
M. boolii	**A**			**X**
M. brandegeei		**X**	**X**	
M. brandegeei gabbii		**X**	**X**	
M. bullardiana		**X**	**X**	**X**
M. capensis	**A**	**X**	**X**	**X**
M. cerralboa	**A**	**X**	**X, i**	**X**
M. dioica	**A**	**X**		**X**
M. estebanensis	**A**	**X**	**X,i**	**X**
M. evermanniana		**X**	**X**	
M. fraileana	**A**	**X**	**X**	**X**
M. goodrichii	**A**	**X**	**X,i**	**X**
M.goodrichii rectispinus	**(A)**	**X**	**X,i**	**(X)**
M. grahamii	**A**			**X**
M. guelzowiana	**A**			**X**
Cochemiea halei	**A**	**X**	**X,i**	
M. heyderi macdougalii				
M. huitzilopotchtli	**F**			
M. hutchisoniana	**A**	**X**	**X**	**X**
M. insularis	**A**	**X**	**X,i (?)**	**X**
M. Columbiana yucatanensis				
M. johnstonii				
M.mainiae	**A**			**X**
C. maritima				
M. multidigitata	**A**	**X**	**X,i**	**X**
M. neopalmeri	**A**	**X**	**X,i**	**X**
M.peninsularis	**F**	**X**	**X**	
M. petrophila	**F**	**X**	**X**	
M. petrophila arida	**F**	**X**	**X**	
M. phitauiana	**A**	**X**	**X**	**X**
C. pondii	**A**	**X**	**X,i**	
C. poselgeri	**A**	**X**	**X**	
M. pottsii	**C**			
M. prolifera	**D**			
M. schumannii	**A**	**X**	**X**	**X**
M. senilis	**E**			
C. setispina	**A**	**X**	**X**	
M. sheldonii				**X**
M. sp. SA		**X**		
M. sp. SL		**X**	**X,i**	
M. sphacelata	**B**			
M. tayloriorum		**X**	**X,i**	
M. tetrancistra	**A**	**X**		**X**
M. thornberi	**A**			**X**
M. viridiflora	**A**			**X**
M. wrightii	**A**			**X**
M. wrightii wilcoxii	**(A)**			**X**
M. yaquensis	**A**			**X**

Clade= from Butterworth and Wallace 2004. BC and Endemic=occurring in Baja California and/or endemic there. i=island endemic. SA=in Hunt's series Ancistracanthae.

Maximum likehood: Using RAxML 8.2.11 on the CIPRES portal (Miller et al. 2010, Stamatakis 2014), the analysis was performed with rapid bootstrapping and rapid hill climbing and a random seed, starting with a random tree, and 1000 pseudoreplicates. A 50% majority rule consensus tree was generated, using trees from all replicates. The best scoring tree based on the log likelihood score was selected for presentation.

Bayesian inference: Model selection was carried out using jmodeltest 2.1.10 (Darriba et al. 2012), running five substitution schemes and testing 40 models. The analysis consisted of two runs with two chains each in MrBayes 3.1.6 (Ronquist and Huelsenbeck 2003) with trees and parameters sampled every 1000 generations. The MCMC sampling procedure was set to 20 million generations, with a stop rule if the average standard deviation of split frequencies fell below 0.001. Post-run analysis was conducted in Tracer 1.7.1 (Rambaut et al. 2018). A maximum clade credibility tree with a 95% confidence interval of posterior probabilities was generated after discarding the first 25% of trees, that is, after the analysis reached stationarity according to analysis in Tracer.

Maximum parsimony: Maximum parsimony analysis was conducted using PAUP* v. 4.0a165 (Swofford 2003). A heuristic search was performed with each replicate having 10 random addition sequences as starting trees. The tree bisection and reconnection (TBR) branch swapping algorithm was used, with maximum reconnection set to eight. A 50% majority rule tree was generated from the 2000 most parsimonious trees.

Morphological analysis: Ten morphological characters were chosen for ancestral state reconstruction using the highest scoring ML tree, in Mesquite v. 3.61 (Maddison and Maddison 2019). The characters were selected based on major distinguishing features traditionally used to separate infrageneric groups in *Mammillaria*, as well as to separate *Mammillaria* from *Coryphantha* (Hunt 1971, Dicht and Lüthy 2005). Those characters were: 1). hooked vs. straight spines, 2). height to width ratio of mature stems, 3). usually ramified versus usually simple stems, 4). lactiferous parenchymal ducts versus watery sap, 5). flower size, 6). grooved versus non-grooved tubercles, 7). the location of flower origination on the stem, 8). spines rigid or flexible, 9). tubercles ovate versus angular or keeled, and 10). stigma lobe length.

Results

The nucleotide alignment used in all of the analyses, with the raw reads from genome skimming for each taxon aligned to the LSC of the plastome of *Mammillaria prolifera*, contained a total of 93,808 characters. Of these, 71,590 were constant (76%) and 22,218 were variable, of which 9,287 characters were uninformative, and 12,931 were parsimony informative characters. High quality percentage of untrimmed bases for the sequences of each taxon ranged from 55% to 85%. Average GC content over the entire alignment was 36%.

The best model of the substitution rate and distribution of nucleotides found using jmodeltest 2.1.10, evaluted by both AIC and BIC scores was GTR+Γ. In the maximum parsimony (MP) analysis, the most parsimonious tree used 31,505 steps. The retention index was 78%, and the rescaled consistency index was 56%. In the maximum likelihood

(ML) analysis, the best bootstrap replicate log likelihood was -427235.8, with a lowest log likelihood of -447452. The average standard deviation of the split frequencies in the Bayesian analysis fell below 0.001 after 3,280,000 iterations. Stationarity was achieved after 810,000 iterations, with a burn in of approximately 25%. Of the 3,280 output trees in the analysis, the first 820 were discarded when calculating the maximum clade credibility consensus tree.

Maximum parsimony, maximum likelihood and Bayesian analysis produced identical topologies with strong support values. ML and MP analysis recovered only one polytomy (three island endemic taxa within the *Cochemiea* clade, see below). Eighty five percent of internal nodes had 90% support or higher in all analyses. Seven out of the total of 66 nodes (approximately 11%) have support lower than 70%.

Clade delineation

A well supported clade, the Mammilloid clade, was recovered composed of *Mammillaria*, *Cochemiea, Coryphantha, Escobaria, Neolloydia, Ortegocactus* and *Cumarinia* (Fig. 2-1). Support values for this clade were at 100% in all three of our analyses. A clade of taxa representing a portion of the genus *Mammillaria* as currently circumscribed, but distinct from both *Coryphantha* and *Cochemiea*, is here referred to as the "*Mammillaria* clade," in recognition of it containing close relatives of the type species.

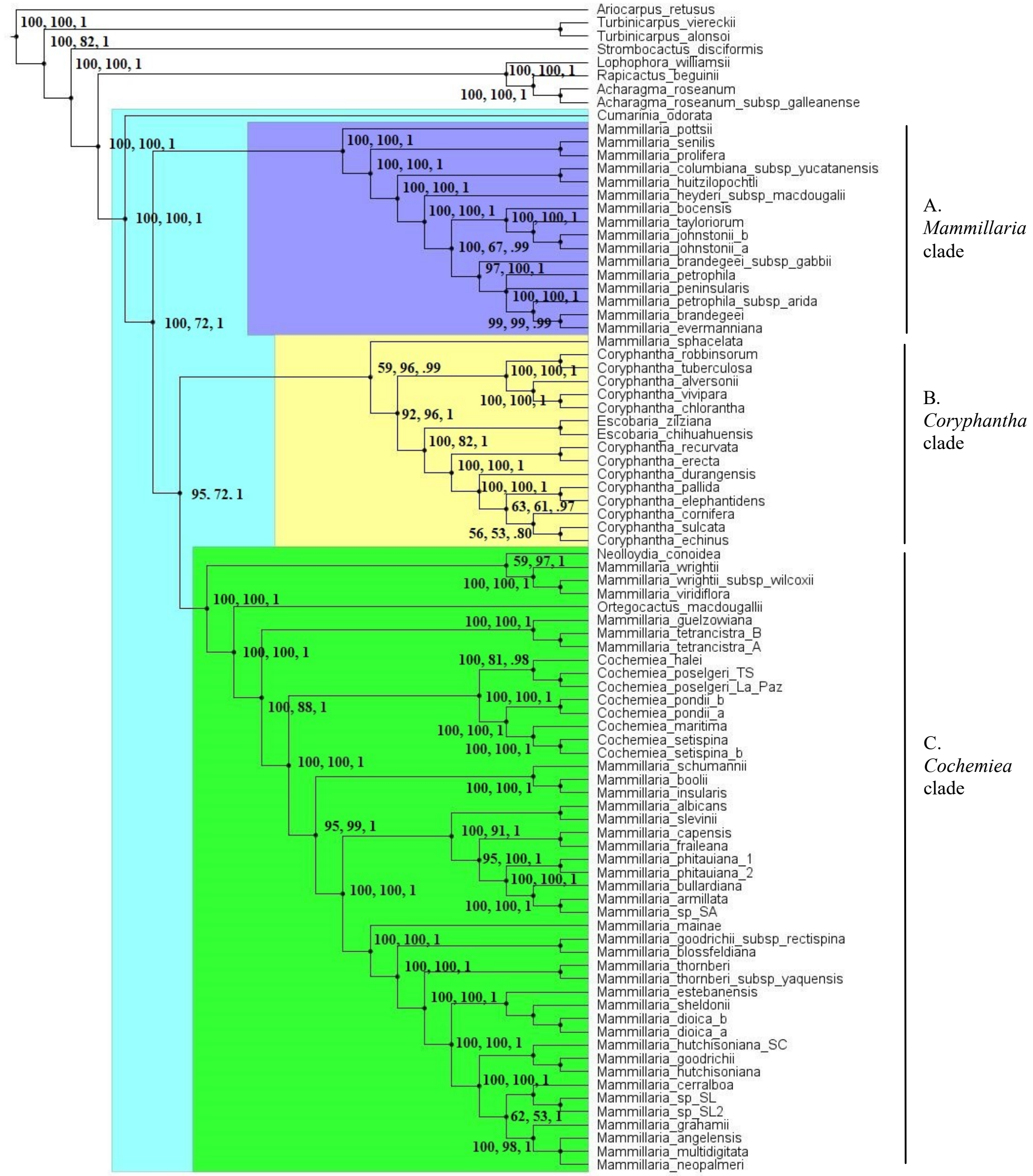


Figure 2-1. Molecular phylogeny of the Mammilloid clade, using the highest scoring maximum likelihood cladogram. Node support values for each internal node show results from a 50% majority rule consensus of 5000 maximum likelihood trees, a 50% majority rule consensus of the 2000 most parsimonious trees, and posterior probabilities from a 95% clade credibility tree from 4000 trees from Bayesian inference. (A) the *Mammillaria* clade, dark blue; (B) the *Coryphantha* clade, yellow, and (C) the *Cochemiea* clade, green. The *Mammillaria*, *Coryphantha* and *Cochemiea* clades with *Cumarinia odorata* compose the Mammilloid clade, light blue.

A clade of many taxa that are included in the current circumscription of the genus *Mammillaria*, but recovered here as distinct, is referred to as "the *Cochemiea* clade," since this clade contains the original genus *Cochemiea sensu* Walton. *Coryphantha* forms a well-supported clade, nested within *Mammillaria* as currently circumscribed,but also containing the species *Mammillaria sphacelatai.* The *Coryphantha* clade is sister to the *Cochemiea* clade.

Within *Coryphantha*, there are two clades representing a distinct separation between a Chihuahuan Desert group and a more western and northwestern group. The Chihuahuan clade also includes *Coryphantha recurvata* (Engelm.) Britton & Rose, a taxon known from northern Sonora and southern Arizona. Otherwise, this clade is represented by taxa that occur farther east and south: *Coryphantha erecta* Lem., *C. pallida* Britton & Rose, *C. elephantidens* Lem., *C. cornifera* Lem., *C. sulcata*, *C. echinus* (Engelm.) Britton & Rose, and *C. durangensis* Britton & Rose (Dicht and Lüthy 2005). This clade also contains two taxa usually placed in *Escobaria*: *Escobaria zilziana* (Boed.) Backb. and *E. chihuahuensis* Britton & Rose. However, these two taxa are sister to the rest of the mostly Chihuahuan clade. The other subclade in *Coryphantha* consists of species from the western Chihuahuan, the transition to the Sonoran Desert, and the Mojave and Great Basin regions. This subclade includes *Coryphantha robbinsorum* (W.H. Earle) A.D. Zimmerman*, Escobaria tuberculosa* (Engelm.) Britton & Rose*, Coryphantha vivipara* Britton & Rose*, Escobaria chlorantha* (Engelm.) Buxb.*,* and *Coryphantha alversonii* (J.M. Coult.) Orcutt.

The *Mammillaria* clade, that is, taxa currently included in the genus *Mammillaria* but with the *Cochemiea* clade removed, shows strong support for Butterworth and Wallace's (2004) clades C-F as a monophyletic group. This clade includes nine taxa from Baja California and adjacent mainland Mexico, but also the more distant *Mammillaria heyderi* Muehlenpf. subsp. *macdougalii* (Rose) L.D. Benson, *M. columbiana* (Britton & Rose) subsp. *yucatanensis* (D.R. Hunt), *M. huitzilopochtli* D.R. Hunt, *M. senilis* Lodd. ex Salm-Dyck, *M. prolifera,* and *M. pottsii* Scheer ex Salm-Dyck.

Acharagma was resolved in a clade with *Rapicactus* Buxb. & Oehme and *Lophophora*, and not as a member of the Mammilloid clade, where it was originally described as an *Escobaria*. *Mammillaria sphacelata,* a taxon that has a confused history in the literature, is recovered here as a member of the *Coryphantha* clade.

The *Cochemiea* clade contains several taxa currently included in the genus *Mammillaria*, as well as *Neolloydia conoidea* and *Ortegocactus macdougalii,* along with the five taxa in the original genus *Cochemiea*. The clade relationships within the *Cochemiea* clade show strong geographically correlated patterns. *Mammillaria wrightii* ssp. *wrightii* and *M. wrightii* subsp. *wilcoxii, M. viridflora* and *Neolloydia conoidea*, none of which occur in Baja, are sister to the rest of the *Cochemiea* + *Ortegocactus* clade. The sub-Trans-Mexican Volcanic Belt, Oaxacan taxon *Ortegocactus macdougalii*, is sister to the rest of the *Cochemiea* clade. A clade consisting of *Mammillaria guelzowiana*, which occurs in the central Mexico, and *M. tetrancistra* (present in Baja Calfironia in the northern, non-peninsular region only; otherwise widespread in the Mohave Desert and the western Sonoran Desert), is sister to the rest of the taxa endemic to Baja or occuring there, with the exceptions of the nearby *Mammillaria mainae* K. Brandegee*,* *Mammillaria grahamii* Engelm. and *Mammillaria sheldonii* (Britton & Rose) Boed of the Sonoran Desert.

Seven well supported subclades were recovered within the *Cochemiea* clade, which was a distinct lineage from *Mammillaria* and sister to the *Coryphantha* clade. Our results show strong support for *Cochemiea* s.s. as a monophyletic group, however, *Cochemiea* s.l. (i.e., the *Cochemiea* clade, Figs. 1-2 and 1-3) makes *Mammillaria* as it is currently circumscribed paraphyletic. Within the old, original genus *Cochemiea*, two distinct lineages were recovered—the southern *Cochemiea poselgeri* and *C. halei* versus the northern *C. pondii, C. maritima* and *C. setispina* complex. *Cochemiea maritima* was universally recovered as more closely related to the peninsular species *C. setispina*, than to the island endemic, *C. pondii* (Fig. 2-3). We were unable to sample the new species, *C. thomasii*, and it remains to be seen what its phylogenetic position is.

The maximum likelihood analysis of ancestral states of synapomorphies for the *Mammillaria, Coryphantha*, and *Cochemiea* clades reinforces the support for these clades. The presence of lactiferous ducts is a diagnostic character for the clade containing the type of *Mammillaria, M. mammillaris* (i.e., *Mammillaria* s.s.; Fig. 4C). Grooved tubercules is a synapomorphy of the *Coryphantha* clade, although they have also evolved convergently in *Neolloydia conoidea* (Fig. 4B). Hooked spines is a synapomorphy of *Cochimiea* s.l. (Fig. 4A), however, that character has also evolved outside of the *Cochemiea* clade in *Mammillaria senilis* (i.e., *Mammillaria* s.s.), and straight spines within the *Cochemiea* clade (found in *Neolloydia conoidea, Mammillaria goodrigii* subsp. *rectipsina*, *Mammillara slevinii* and *Cochemiea halei*) are also convergent, indicating a loss of hooked spines in those taxa (Fig. 4A).

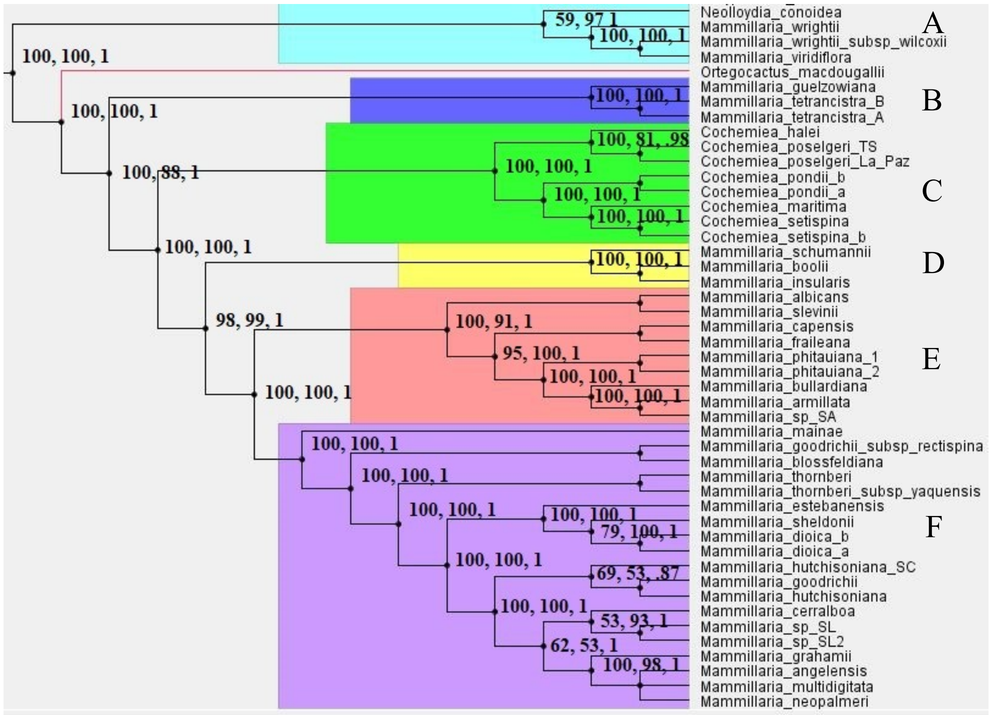


Figure 2-2. Maximum likelihood phylogeny of the *Cochemiea* clade with designation of subclades. (A) *Neolloydia* clade; (B) *M. guelzowiana/M. tetrancistra* clade; (C) *Cochemiea sensu* (K. Brandegee) Walton; (D) *M. schumannii, M. boolii, and M. insularis*; (E) Cape clade, and (F) the Island clade. On the red colored branch, *Ortegocactus macdougallii*. Support values for nodes show the bootstrap support from a 50% majority rule maximum likelihood consensus of 5000 trees, a maximum parsimony 50% majority rule consensus of the 2000 most parsimonious trees, and the posterior probabilities from a 95% clade credibility tree from 4000 trees generated in a Bayesian analysis.

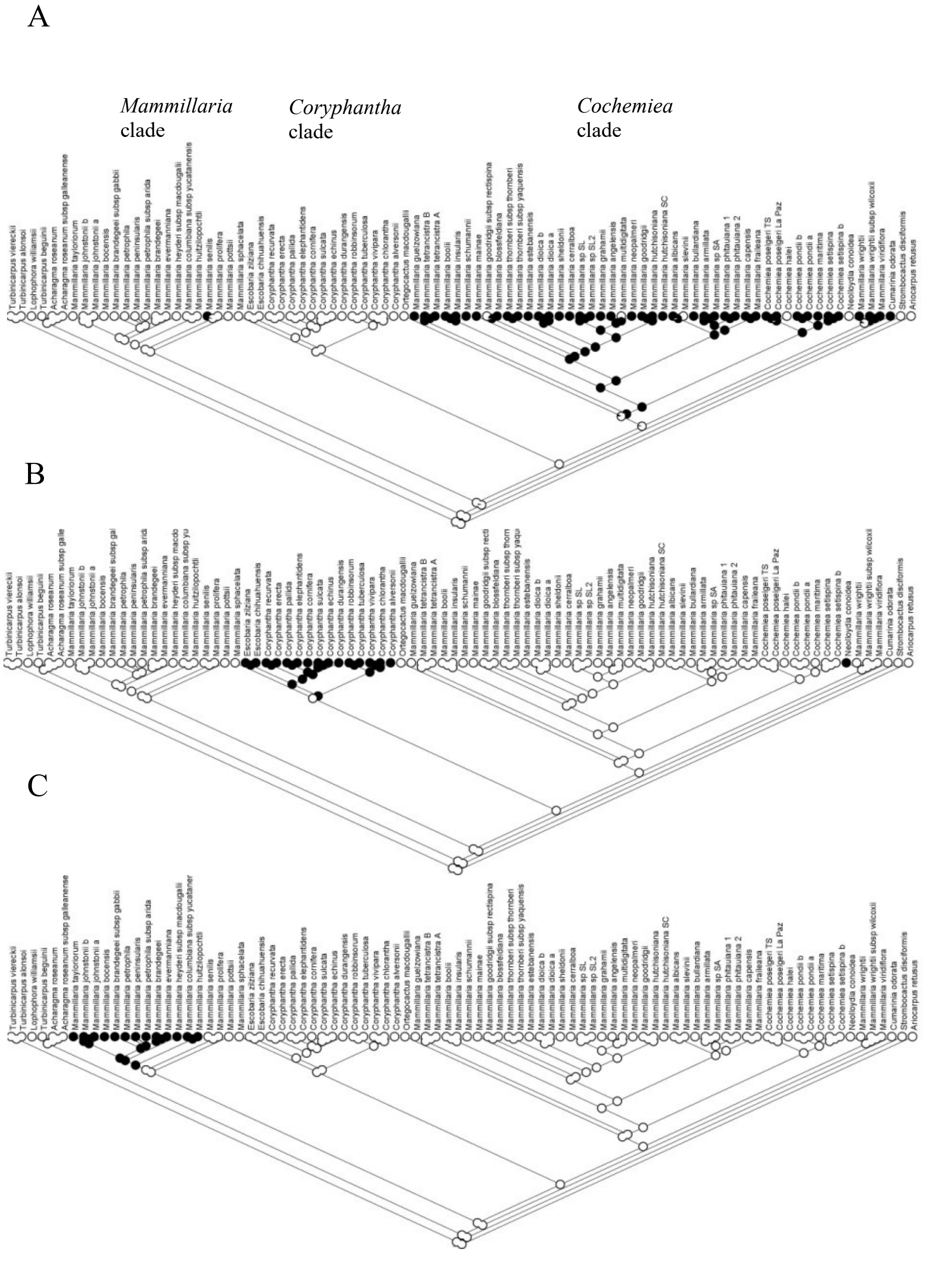


Figure 2-3.**Ancestral states of the three most informative phylogenetic characters for the *Cochemiea* clade, the *Coryphantha* clade, and the *Mammillaria* clade, based on a maximum likelihood analysis.** (A) hooked spines of the *Cochemiea* clade; (B) grooved tubercles of the *Coryphantha* clade; (C) lactiferous ducts of the *Mammillaria* clade.

Discussion

In spite of more than 200 years of taxonomic inquiry and the first molecular phylogenetic studies beginning 20 years ago, the clade relationships in the Mammilloid clade have been unclear, the genus *Mammillaria* has remained unresolved phylogenetically, and circumscription of closely related genera has also been unclear. The results of this phylogenetic analysis provide strong evidence to support a significant recircumscription of the genus *Mammillaria* to resolve longstanding questions. This revision retains monophyly of other genera that are also broadly distinguished by morphological characters.

Resolution of taxonomically problematic taxa

Cumarinia odorata, originally described as a *Coryphantha* (Boedeker 1930), is shown to be a distinct, independent lineage. This taxon is supported here as a monotypic genus and should be retained in *Cumarinia*.

Mammillaria sphacelata Mart. has long been suspected to be neither a *Mammillaria* nor a *Coryphantha* (Orcutt 1926, Hunt 1971, Doweld 2000), and is recovered here as a member of the *Coryphantha* clade. Buxbaum placed *M. sphacelata* in a genus he segregated out of *Coryphantha*, *Leptocladodia.* Doweld (2000) created yet another monotypic genus for this taxon, *Escobariopsis* Doweld. In Butterworth and Wallace (2004), *M. sphacelata* was recovered in a small clade of other unusual *Mammillaria*, including *M. beneckei*, which was itself placed in a segregate genus, *Oehmea* Buxb. (1951a), on account of its larger than usual flowers and large, rough seeds. Further research needs to be carried out to determine if the morphological and molecular characters of *Mammillaria sphacelata* and its related taxa (which were not sampled for this study) would place it under a more broadly circumscribed *Coryphantha*, or if the clade to which *M. sphacelata* belongs may represent a unique lineage.

This analysis indicates little support for retaining *Escobaria* as a genus separate from *Coryphantha*, as currently circumscribed by some authorites. Likewise, the type of *Escobaria, E. tuberculosa*, is deeply nested within *Coryphantha*. More comprehensive sampling from the *Coryphantha* clade of both *Coryphantha* and *Escobaria* species would help to resolve the generic limits in this clade. However, as a strongly supported clade overall, including support from reconstructing the ancestral evolution of adaxial tubercular grooves, the *Coryphantha* clade is clearly separate from both the *Cochemiea* and *Mammillaria* clades.

The *Mammillaria* clade

The *Mammillaria* clade recovered here aligns with Butterworth and Wallace's (2004) clades C–F in their parsimony analysis, as a strongly supported monophyletic group. Lactiferous ducts, producing a latex-like substance when the plants are damaged, support the facile recognition of the clade. Though incomplete, the sampling from the *Mammillaria* clade for this analysis includes nine taxa from Baja California and adjacent mainland Mexico, but also the more distant Sonoran Desert taxa *Mammillaria heyderi* subsp. *macdougalii*, the tropical *Mammillaria columbiana* subsp. *yucatanensis* and *Mammillaria huitzilopochtli* D.R. Hunt, the Madrean *Mammillaria senilis*, and the Chihuahuan *Mammillaria prolifera* and *Mammillaria pottsii*. *M. senilis*, which has hooked spines and unusual flower morphology, presumably an adaptation for hummingbird pollination similar to *Cochemiea*, was once placed in *Cochemiea* by Orcutt. The species was considered unique enough to warrant its own genus, published as

Mammillopsis F.A.C. Weber in 1899. Britton and Rose (1923) and Anderson (2001) speculated that *M. senilis* might be an ancestral mainland Mexico relative of *Cochemiea*, especially because the center of its distribution is in the Sierra Madre Occidental, near Mazatlan in the Mexican state of Sinaloa, directly across the Gulf of California from the Cape Region of Baja. However, the gross morphological similarities between *M. senilis* and *Cochemiea* appear to be another example of homoplasy in the Cactaceae, poking holes in a likely story, as, in spite of its hooked spines and ornithophilous flowers, *M. senilis* is recovered here as a member of the *Mammillaria* clade, not the *Cochemiea* clade.

The Sonoran mainland and Baja peninsular representatives of the *Mammillaria* clade share the general morphology of hemispheric, broader than tall simple stems, straight spines and smaller flowers, with all representatives on the Baja peninsula having lactiferous ducts (Rebman and Roberts 2012). All of the *Mammillaria* clade members on the Baja peninsula are sympatric with one or more members of the *Cochemiea* clade and there is no record of any intermediate forms between these two groups. The same reproductive isolation between these two groups is recorded on the mainland—for example, with the sympatric distributions of *Mammillaria grahamii* and *Mammillaria heyderi* subsp. *macdougallii* in the Sonoran Desert.

Clarifying relationships within the *Cochemiea* clade

Within the *Cochemiea* clade, some relationships from previous studies are confirmed and some contradict prior supposed taxonomic relationships. The close relationship between *Mammillaria tetrancistra* and *Mammillaria guelzowiana* confirms Buxbaum's diagnosis of *M. guelzowiana* (1951b), placing them both (along with the closely related *Mammillaria longiflora*, not sampled here) in the segregate genus

Phellosperma. Doweld (2000) placed *Mammillaria boolii* and *Mammillaria insularis* in *Bartschella*, the monotypic genus created by Britton & Rose (1923) for *Mammillaria schumannii*, entirely on the basis of its circumscissile fruit, that is, dehiscing around the apex of the capsule when ripe. Both *M. boolii* and *M. insularis* have fruit that either are circumscissily dehiscent or that open via a basilar pore, a character otherwise not found in *Mammillaria*, and the three species constitute a well-supported clade.

Mamillaria mainae, (sometimes referred to as *Mammillaria mainiae*, including, for example, in the Flora of North America, yet that orthographic variant has never been officially recognized), is sister to a clade of 15 taxa.

This clade is remarkable for containing five taxa that do not occur in Baja (*Mammillaria mainae* K. Brandegee, *Mammillaria thornberi* Orcutt, *Mammillaria thornberi* Orcutt subsp. *yaquensis* R.T. Craig, *Mammillaria sheldonii* Boed*.,* and *Mammillaria grahamii* Engelm.), as well as six entirely island endemic taxa, spanning islands in the Gulf of California (*Mammillaria cerralboa* Orcutt, *Mammillaria estebanensis* G.E. Linds., *Mammillaria angelensis* R.T. Craig, *Mammillaria multidigitata* Radley) and in the Pacific ocean (*Mammillaria goodrichii* Scheer ex Salm-Dyck, *Mammillaria goodridgeii* var. *rectispina* E.Y. Dawson, *Mammillaria neopalmeri* R.T. Craig and *Mammillaria sp. "SL"*, collected by Alfred Lau and grown in cultivation by Juergen Menzel under "*Mammillaria dioica* f.", with the recorded locality of Isla Magdalena). Hunt (2005) placed *M. sheldonii* as a subspecies of *M. grahamii*, but its close relationship with *M. dioica* is supported in all of the analyses here. Hunt's (2005) diagnosis of *Mammillaria goodridgeii var. rectispina* as closely related to *M. blossfeldiana* is confirmed here. *Mammillaria goodrichii* is most closely related to

Mammillaria hutchisoniana, and if a new combination at the infraspecific level is made, it would place *M. hutchisoniana* as a subspecies of *M. goodridgii*, as the latter name has precedence. Peninsular records (Rebman and Roberts 2012, Hernandez and Gómez-Hinostrosa 2015) of both *Mammillaria hutchisoniana* and *Mammillaria blossfeldiana* exist east of Isla Cedros, the habitat for both *M. goodridgii* and *M. goodridgei* subsp. *rectispina*, which suggests dispersal of the most recent common ancestors of both taxa to the islands (cf. Chapter 3).

Hunt (1997) placed *Mammillaria angelensis* as a subspecies of *M. dioica* K. Brandegee, but our analysis strongly supports a relationship with *M. grahamii*, as is the case with the other two taxa in the "island polytomy," *M. multidigitata* and *M. neopalmeri*. This group, the only polytomy in the ML phylogeny, is not superficially morphologically similar to *M. grahamii* either in stem, spine or flower characters (Craig 1945, Hunt 1997). Both *M. angelensis* and *M. multidigitata* are narrowly restricted island endemics in the Gulf of California, yet separated by a distance of approximately 250 km; *M. neopalmeri* is also an island endemic, but on Guadalupe and San Benito Islands, in the Pacific, near Isla Cedros, 200 km from Isla Angel de la Guarda, with Isla Guadalupe another 320 km to the northwest. Since it is the only polytomy in the phylogeny, it is possible that these three taxa represent a rapid and recent radiation, perhaps a result of long range dispersal by birds. It may be that further study will reduce these taxa to subspecies of *M. grahamii*, but our phylogenetic results are not well enough resolved to make that determination.

Mammillaria hutchisoniana "SC" was collected near Puerto San Carlos, and, for these southern occurrences, Pilbeam (2015) suggested the provisional name "*Mammillaria hutchisoniana* subsp. *australis*." That concept is supported here, with the northerly *M. hutchisoniana* more closely related to *M. goodrichii* than to the *M. hutchisoniana* from Baja California Sur. However, a new combination is not made, pending more research into distinct, diagnosable morphological characters and geographic distributions of these taxa.

Another distinct subclade within the *Cochemiea* clade contains species that are entirely endemic to the Cape Region of Baja. The close relationship of *Mammillaria albicans* with *Mammillaria slevinii* is supported—interestingly, *M. slevinii* was described (Boedeker 1933) as a separate species due to having straight spines and usually simple stems. As is the case with *Cochemiea halei*, this probably shows that hooked spines is a trait that is lost and gained again later, in the *Cochemiea* clade. Another example is *Mammillaria estebanensis*, which sometimes has hooked spines and sometimes straight spines, even within the life span of a single individual (Pilbeam 2018 pers. comm.).

Lüthy (1995) and Hunt (1997) placed *Mammillaria fraileana* as a forma or subspecies, respectively, of *Mammillaria albicans*, but these analyses strongly support *M. fraileana* as a distinct species, most closely related to *Mammillaria capensis*.

The *Cochemiea* subclade, *Cochemiea* s.s., composed of the original taxa in the genus *Cochemiea*, is well supported, with *C. halei* sister to *C. poselgeri*. Those two taxa occur only in Baja California Sur, from San Ignacio in the central peninsula to the Cape Region in the case of *C. poselgeri*. The northern members of the clade are represented by the endemic *C. pondii*, the narrowly distributed *C. maritima* along the Pacific coast approximately 100 km from island distributions of *C. pondii*, and the montane *C. setispina*. Hunt (1997) placed *C. maritima* and *C. setispina* as subspecies of *C. pondii*, but our analysis shows that *C. pondii* is a distinct species, and that *C. maritima* and *C. setispina* are more closely related to each other than they are to *C. pondii*. The analysis here supports retaining the five taxa at the species rank, as they were originally described. There would also be support for making *C. poselgeri* a subspecies of *C. halei* (since the latter name has precedence) and recombining *C. maritima* as a subspecies of *C. setispina*, with *C. pondii* not having any infraspecific taxa. However, this seems unnecessarily complex, given that the biogeographical boundaries of all five taxa are clearly defined.

Cochemiea s.s. is sister to the other clades that are mostly Baja taxa. The strong independence of the *Cochemiea* lineage may account for the floral and other gross morphological differences it displays, characters that made it both the earliest named segregate genus and, unlike the other small genera separated out of *Mammillaria*, still recognized recently as a valid genus by authorities (e.g., Bravo-Hollis and Sanchez-Mejorada 1991, Rebman and Roberts 2012, García Morales et al. 2020).

The monophyly of *Mammillaria*

The most significant findings of this study are in regard to the relationship of the *Cochemiea* clade to the *Mammillaria* clade. Including *Ortegocactus* and *Neolloydia*, there is strong support for recognizing the *Cochemiea* clade at the generic level. If this clade is not recognized as a genus, there are only two other options that preserve monophyly of the clades recovered. The first option would be a greatly expanded concept of *Mammillaria*, which would include all of the taxa in the *Mammillaria* clade, the *Cochemiea* clade, and the genus *Coryphantha*. Given the easily diagnosed morphological characters of the *Coryphantha* clade, namely, a groove on the adaxial surface of the tubercle and flowers emerging from new growth as opposed to older growth, combining this well known clade into *Mammillaria* would make *Mammillaria* s.l. a much more difficult group to recognize, in spite of *Coryphantha* being nested within *Mammillaria* s.l. Likewise, combining all taxa into *Mammillaria* would be disruptive to our current taxonomy of the group, especially considering the large numbers of species of *Coryphantha*.

The other option would require establishing several new, small genera that correspond to the monophyletic lineages near the terminal branches of the phylogeny. Without considering how the *Mammillaria* clade would be segregated due to our incomplete sampling of that large and complex clade, the number of genera that would need to be segregated from *Coryphantha* and the *Cochemiea* clade would be at least 15, with four monotypic genera (*Mammillaria sphacelata*, *Ortegocactus macdougallii*, *Mammillaria mainae* and *Cumarinia odorata*). This would be the only way to retain the original circumscription of *Cochemiea* s.s. at the generic level. None of the genera historically segregated from *Mammillaria* that our analysis recovered as belonging to the *Cochemiea* clade—namely, *Chilita, Ebnerella, Phellosperma* or *Bartschella*—correspond to our subclades. Each of the historical segregates is non-monophyletic, with the exception of the original concept of *Cochemiea* s.s.. Doweld (2000a and b), relying on seed morphology, published an expanded concept of both *Cochemiea* and *Bartschella*, but his placements only align in part with the smaller clades that are strongly supported in all analyses here.

Our solution is to use a middle ground approach, recognizing three major clades at the rank of genus: *Mammillaria*, in the strict sense; *Coryphantha* (here including *Escobaria*, pending a more comprehensive analysis of that clade); and the *Cochemiea* clade (including *Neolloydia* and *Ortegocactus,* which are both strongly supported as within this clade in all analyses). Within the *Cochemiea* clade, the genus name that has priority is *Cochemiea*, published in 1899. As the name with priority, according the International Code of Botanical Nomenclature (ICBN), *Cochemiea* is used here at the rank of genus for all members of the *Cochemiea* clade. Including taxa currently recognized in *Mammillaria, Ortegocactus* and *Neolloydia* (ICBN, Division I, Principle III). Constituting a large, well-supported and coherent clade, this expanded concept of *Cochemiea* resolves many longstanding taxonomic problems, circumscribes a monophyletic *Mammillaria* and preserves *Coryphantha*. Therefore, all of the members of the *Cochemiea* clade are herein transferred to the genus *Cochemiea*. Some taxa in the *Cochemiea* clade were previously combined under *Cochemiea* by Doweld (2000).

Taxonomic Treatment

Taxa previously published in *Cochemiea*:

Cochemiea halei (K. Brandegee) Walton*, Cochemiea pondii* Walton*, Cochemiea poselgeri* (Hildman.) Britton & Rose*, Cochemiea setispina* Walton*, Cochemiea maritima* H.E. Gates ex. Shurly*, Cochemiea thomasii* García-Mor., Rodr. González, J. García- Jim. & Iamonico. *Cochemiea sheldonii* (Britton & Rose) Doweld*, Cochemiea wrightii* (Engelm.) Doweld*, Cochemiea wrightii subsp. wilcoxii* (K. Schumm.) Doweld.

New Combinations in *Cochemiea* s.l.

***Cochemiea armillata* (K. Brandegee) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria armillata* K. Brandegee, Zoe 5:7. 1900

Type. [Mexico], Baja California: San Jose del Cabo. Collected by T.S. Brandegee, s/n. University of California (UC), UC108185

***Cochemiea albicans* (Britton & Rose), Breslin & Majure, comb. nov.**

Basionym: *Neomammillaria albicans* Britton & Rose. 4:138, fig. 152, 1923

Type. [Mexico], no locality information. Collected by J.N. Rose #16842 1911-4-16. US.

***Cochemiea angelensis* (R.T. Craig), Breslin & Majure, comb. nov.**

Basionym: *Mammillaria angelensis* R.T. Craig Mammill. Handb. 165. 1945

Type. R.T. Craig, "material deposited at the Dudley Herbarium at Stanford," (Mammill. Handb. Page 165); probably lost. The Dudley Herbarium closed, and the angiosperm specimens were transferred to The California Academy of Sciences herbarium, but there is no record of *Mammillaria angelensis* there. **Lectotype:**

***Cochemiea blossfeldiana* (Boed.) Breslin & Majure comb. nov.**

Basionym: *Mammillaria blossfeldiana* Boed. Monatsschr. Deutsch. Kakteen-Ges. 3: 209. 1931

Type. [Mexico], Baja California, H.E. Gates, #68, 6-April-1931: CAS0214991

***Cochemiea blossfeldiana* subsp. *rectispina* (Boed) E.Y. Dawson, Breslin & Majure comb. nov.**

Basionym: *Mammillaria goodridgei var. rectispina* E.Y. Dawson Cact. Succ. J. (Los Angeles) 24:80 fig. 46 1952.

Type. [Mexico], Baja California. On hill crests above North Bay, Cedros Island, E.Y. Dawson, 10631, RSA0044443.

Cochemiea boolii **(G.E. Linds.) Breslin & Majure comb. nov.**

Basionym: *Mammillaria boolii* G.E. Linds. Cact. Succ. J. (Los Angeles) 25: 48. 1953

Type. [Mexico] Growing in lava rock on N shoulder of hill which forms N portal of San Pedro Bay. G.E. Lindsay 2220 30-April-1952. CAS 348605.

Cochemiea bullardiana **H.E. Gates, Breslin & Majure comb. nov.**

Basionym: *Neoammillaria bullardiana* H.E. Gates Cact. Succ. J. 6:4 1934.

Type. [Mexico], Baja California, "under giant cactus on sandy plain," H.E. Gates, #68, 10-March-1933: CAS0214877

Cochemiea capensis **H.E. Gates, Breslin & Majure comb. nov.**

Basionym: *Neomammillaria capensis* H.E. Gates, Cact. Succ. J. (Los Angeles) 4: 372.

1933

Type. [Mexico]. Baja California, H.E. Gates, #68, 8-March-1931: CAS0214878

Cochemiea cerralboa **Britton & Rose, Breslin & Majure, comb. nov.**

Basionym: *Neomammillaria cerralboa* Britton & Rose 4: 116. 1923

Type. [Mexico] Gordas Point, 0.5 mile north; Ceralbo Island (sic), L.C. I. M. Johnston

4038, 6-June-1921. NY 385928

Cochemiea conoidea (**(DC.) Britton & Rose), Breslin & Majure, comb. nov.**

Basionym: *Neolloydia conoidea* (DC.) Britton & Rose, Bull. Torrey Bot. Club 1922, xlix.

252

Type. [US] (syntype; as *Neolloydia texensis*) Sanderson, TX. D.T. MacDougal, s/n, December 1920. NY 385922

Cochemiea dioica **(K. Brandegee) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria dioica* K. Brandegee Erythea 5: 115. 1897

Type. [US], San Diego Co., M. E. Jones, 3057, 10-March-1882: NY 385868

Cochemiea estebanensis **(G.E. Linds.) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria estebanensis* G.E. Linds. Cact. Succ. J. (Los Angeles) 39: 31.

1967

Type. [Mexico], Baja California, Isla San Esteban, G.E. Lindsay 3002, 13-January-61: SD00000172

Cochemiea fraileana **(Britton & Rose) Boed., Breslin & Majure, comb. nov.**

Basionym: *Neomammillaria fraileana* Britton & Rose Cactaceae (Britton & Rose) 4: 157.

1923

Type. [Mexico] Baja California, Pichilingue Island, J. N. Rose #16508, 27-March-1911: NY00385931

Cochemiea goodrichii **(Scheer in Salm-Dyck) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria goodrichii* Scheer in Salm-Dyck, Bot. Voy. Herald [Seemann] 7-8: 286, sphalm. 1856 ; Orth. Var.

Type. unknown

Cochemiea grahamii **(Engelm.) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria grahamii* Engelm., Syn. Cact. U. S. 6. 1856 Proc. Amer. Acad.

Arts 3: 262. 1857

Type. [US], In the valley of the Rio Grande, below Donana, Maj. W. H. Emory; C. C. Parry, J. M. Bigelow, C. Wright, A. Schott, s/n., NY00385870

Cochemiea guelzowiana **(Werderm.) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria guelzowiana* Werderm., Z. Sukkulentenk. iii. 356 1928

Type. Original type lost during World War II. **Lectotype:**

Cochemiea hutchisoniana **H.E. Gates, Breslin & Majure, comb. nov.**

Basionym: *Neomammillaria hutchisoniana* H.E. Gates Cact. Succ. J. (Los Angeles) 6: 4. 1934

Type. [Mexico], Baja California, H.E. Gates, #68, 22-July-1933: CAS0214913

Cochemiea insularis **(H.E. Gates) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria insularis* H.E. Gates, Cact. Succ. J. (Los Angeles) 10: 25. 1938

Type. [Mexico], Baja California, H.E. Gates, #68, 5-November-1935: CAS0214897

Cochemiea macdougalii **(Alexander) Breslin & Majure, comb. nov.**

Basionym: *Ortegocactus macdougalii* Alexander, Cact. Succ. J. (Los Angeles) 33: 39. 1961

Type unknown.

Cochemiea mainae **(K. Brandegee) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria mainae* K. Brandegee, Zoe 5: 31. 1900

Type. [Mexico], Sonora, South of Nogales, F. M. Main, #311295, (as isotype): RSA0008919

Cochemiea multidigitata **(Radley & G.E. Linds.) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria multidigitata* Radley & G.E. Linds. Cact. Succ. J. (Los Angeles) 19: 152, latine. 1947

Type. [Mexico], Sonora, San Pedro Nolasco Island, G.E. Lindsay, #499, 24-February-1947: CAS0214984

Cochemiea neopalmeri **(R.T. Craig) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria neopalmeri* R.T. Craig, Mammill. Handb. 267. 1945

Type. [Mexico] (as **neotype**), Isla San Benito del Oeste, Baja California, R.F. Thorne, #58481, 31-January-!985: RSA0006536

Cochemiea phitauiana **E.M. Baxter, Breslin & Majure, comb. nov.**

Basionym: *Neomammillaria phitauiana* E.M. Baxter Journ. Cact. & Succ. Soc. Amer. ii. 472 1931

Type. [Mexico], 30 miles west of Todos Santos, Baja California Sur, E.M. Baxter, s/n, 1930: US00115749

***Cochemiea schumannii* (Hildm.) Breslin & Majure comb. nov.**

Basionym: *Mammillaria schumannii* Hildm. Paul Arendt's Monatsschr. Kakteenk. 1: 125, pl. 8. 1891

Type. [Mexico], (**lectotype,** N. L. Britton & J. N. Rose, "The Cactaceae", Vol. 4, page 58. 1923).

***Cochemiea tetrancistra* (Engelm.) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria tetrancistra* Engelm. Amer. J. Sci. Arts ser. 2, 14: 337. 1852

Type. [US], Arizona, John LeConte, s/n, date unknown: MO-179306

***Cochemiea thornberi* (Orcutt) Breslin & Majure, comb. nov.**

Basionym: *Mammillaria thornberi* Orcutt, W. Amer. Sci. 12: 161. 1902

Type. [US], Arizona, as “possible type,” F.E. Lloyd, s/n, date unknown: NY00385869

***Cochemiea thornberi subsp. yaquensis* R.T. Craig, Breslin & Majure, comb. nov.**

Basionym: *Mammillaria yaquensis* R.T. Craig, Mammill. Handb. 320 (-321). 1945

Type. [Mexico] Rio Yaqui a few miles from Fort Pithaya, as with *Mammillaria angelensis* above, type material was deposited at the Dudley Herbarium. **Lectotype:**

***Cochemiea viridiflora* Britton & Rose** Breslin & Majure, comb. nov.

Basionym: *Neomammillaria viridiflora* Britton & Rose Cactaceae (Britton & Rose) 4: 153. 1923

Type. [US] Arizona, Orcutt. #608, date unknown: NY00385926

Chapter 3 RECENT DIVERGENCE, RAPID DIVERSIFICATION AND MULTIPLE RADIATIONS OF *Cochemiea* AND *Mammillaria* (Cactaceae) IN THE BAJA CALIFORNIA REGION: ACCOUNTING FOR HIGH SPECIES RICHNESS AND PENINSULAR ENDEMISM

Abstract

The *Mammillaria* and *Cochemiea* (Cactaceae) clades of northwestern Mexico and southwestern United States constitute a major component of the angiosperm biodiversity of this region. High species richness is combined with peninsular and island endemism in *Cochemiea,* with 90% of all taxa in that recircumscribed genus endemic to Baja California and adjacent islands. While the main center of distribution of *Mammillaria* is the Sierra Madre Orientalian regions of eastern Mexico into the Coahuilan and Chihuahuan Desert regions, this genus also displays species richness and endemism in Baja California and along the adjacent Sonoran/Sinaloan Gulf of California coast. Past research has suggested that geological and climate heterogeneity at multiple spatial and temporal scales has been important in influencing the floral and faunal biodiversity of Baja California. This study uses a well-supported phylogeny as the basis for reconstructing the historical biogeography, estimating divergence times and finding diversification rate shifts at key nodes for the Mammilloid clade. The likely ancestral biogeographical history and high rate of diversification of the genus *Cochemiea* strongly support its taxonomic circumscription as a clade distinct from *Mammillaria*. We find that the most recent common ancestor of *Cochemiea* became established in the Cape region of Baja California from the Sonoran Desert region, approximately 5 million years ago (Ma), coinciding with the timing of peninsular rifting from the mainland, suggesting a combination of dispersal and vicariance as drivers of endemism. Several dispersal events

to the peninsula from the mainland are indicated, outlining a complex historical biogeography that explains the current distributions of taxa within *Cochemiea*. The diversification rate for *Cochemiea* is estimated to be four to seven times that of the average estimated background diversification rate for angiosperms as a whole, and two to four times that of the Mammilloid clade in which it is nested, characterizing *Cochemiea* as a rapidly speciating clade. Divergence time estimation shows that many of the taxa in *Cochemiea* emerged from common ancestors as recently as 500,000 to 1 million years ago (Ma). Geological and climate forces at multiple spatial and temporal scales are correlated with this rapidly radiating, rapidly diversifying clade.

Introduction

The historical biogeography of the flowering plant family Cactaceae Juss. has been inferred from the current distributions of well-supported clades, with estimates for basal and stem node ages derived from outside the family, since there are no cactus fossil records (Wallace 1995, Hershkovitz and Zimmer 1997, Applequist and Wallace 2001, Edwards et al. 2005, Nyfeller and Eggli 2010 b, Ocampo and Columbus 2010, Barthlott 2015). The family has been presumed to have originated in South America, radiating north after the closing of the Isthmus of Panama, through the tropics into the subtropics of Mexico, and then to its North American distributions (e.g., Barthlott 2015), but a family-wide, well-resolved phylogeny including all major clades and appropriate outgroups has not yet been used to test this biogeographical hypothesis. Similar to other families in the large, diverse order Caryophyllales in which it is nested, Cactaceae show multiple resilient adaptations to a wide variety of arid environments (Buxbaum 1956, Gibson and Nobel 1986, Mauseth 1999, Anderson 2001, Nobel 2002, Soltis and Soltis 2004, Mauseth 2006). The dispersal into the Sierra Madre Oriental and the desert regions of north central Mexico coincides with increasing aridification and the decrease of atmospheric CO_2 in the Late Miocene. Both of these factors have been shown to coincide with rapid dispersal, increased diversification rates and a high rate of speciation in the Cactaceae (Crozier 2005, Arakaki et al. 2011, Vázquez-Sánchez et al. 2013, Hernández-Hernández et al. 2014).

Early estimates of the age of Cactaceae were made based on major geological events, such as the separation of Gondwana during the late Jurassic and early Cretaceous, approximately 145 million years ago (Ma), and the fact that the family is entirely a New World lineage (with the exception of the central African epiphytic cactus, *Rhipsalis baccifera* (Sol.) Stearn). Backeberg (1942, 1977) and Mauseth (1990) conceived of the family as ancient, or at least with a limiting older age ranging from 130 Ma to 90 Ma. Molecular dating of the order Caryophyllales, in which Cactaceae is nested, indicates an origin of 116–104 Ma for that order (Wikström et al. 2001, Anderson et al. 2005, Bell et al. 2010). The lack of a fossil record for Cactaceae introduces additional uncertainty into the time calibration of both stem and crown nodes of phylogenetic trees. Ocampo and Columbus (2010), using node calibration times based on the emergence of volcanic islands in the Hawaiian Island region and molecular phylogenies involving island endemics in the genus *Portulaca* L., arrived at a very recent origin for the suborder Cactineae within Caryophyllales, with this suborder estimated to have emerged only 19.1–3.1 Ma. However, they advise caution in interpreting their results, as their main assumption is that the endemic island lineages did not exist prior to the emergence of the volcanic islands (Ocampo and Columbus 2010). Arakaki et al. (2011) used high-confidence fossils from the Caryophyllales and multiple analyses to arrive at a well-supported inference of a stem age of Cactaceae of about 35 Myr (Arikaki et al. 2011).

This analysis also placed the subclades of Cactaceae in the core Cacteae arising 12 Ma, and the Mammilloid clade (Chapter 2) as emerging 7.6–6.3 Ma (Arikaki et al. 2011), characterizing both the tribe and the Mammilloid clade as relatively recent in the Cactaceae, arising from 23–29 Myr after the origins of the family. Hernández-Hernández et al. (2014) found similar crown ages for Cacteae, at approximately 12 Ma, with the "Mammilloid clade" at 8.6 Ma, as well as a "Core Mammilloid" clade (which corresponds to our Mammilloid clade) at 7.3 Ma. Vázquez-Sánchez et al. (2013) suggested an older origin for Cacteae, at 16 Ma, followed by increased diversification for the Mammilloid clade corresponding to increased aridity in the late Miocene, approximately 6 Ma. That study also found that the Baja Californian distribution of *Cochemiea* (K. Brandegee) Walton resulted from a mid-range dispersal event directly from the Altiplanian region of north central Mexico, but taxon sampling was low in Sonoran and Mohavean examples from the Mammilloid clade, thus possibly obscuring more gradual dispersal from east to west (Vázquez-Sánchez et al. 2013).

The Mammilloid clade has been shown to be sister to a clade in Cacteae containing well-supported, highly morphologically diverse and monotypic or often depauperate genera *Turbinicarpus* Buxb. & Backeb., *Rapicactus* Buxb. & Oehme, *Lophophora* J.M. Coult., *Strombocactus* Britton & Rose, *Obregonia* Fric., *Ariocarpus* Scheidw. *Acharagma* (N.P. Taylor) Glass and *Cumarinia* (F.M. Knuth) Buxb. (Butterworth et al. 2002, Butterworth and Wallace 2005, Hernández-Hernández et al. 2011, Bárcenas et al. 2011, Vázquez-Sánchez et al. 2013, cf. Chapter 2). The gross morphological similarities between *Acharagma* and *Escobaria* led to the type species for *Acharagma, A. roseanum* (Boed.) E.F. Anderson, originally being described as an *Escobaria.* Two genera historically excluded from *Mammillaria sensu* Haw., *Ortegocactus* and *Neolloydia*, were recently shown to be nested in the Mammilloid clade (cf. Chapter 2). The sister clade to the Mammilloid clade is biogeographically restricted without exception to eastern Mexico, through the Sierra Madre Oriental, into the

Chihuahuan and Coahuilan regions. Unlike the Mammilloid clade, this sister clade is not represented by a western dispersal into supposedly more recently forming deserts, such as the Sonoran or Mojavean (Anderson 2001, Vázquez-Sánchez et al. 2013).

Analyses of historical biogeography in Cactaceae have used various methods to infer ancestral ranges for the genera *Pereskia* Mill. (Edwards and Nyfeller 2005), *Opuntia* Mill. (Majure et al. 2012), *Harrisia* Britton (Franck et al. 2013), *Eriosyce* Phil. (Guerrero et al. 2011, Guerrero et al. 2016), *Astrophytum* Lem. (Vázquez-Lobo et al. 2016) and *Cylindropuntia* (Majure et al. 2019). *Astrophytum*, for example, originated in the Altiplanian region of north central Mexico, with two main dispersal events, one to the Coahuila/Chihuahuan subregion and another to the Sierra Madre Oriental (Vázquez-Lobo et al. 2016). This is aone example of a more recent development in the Cactaceae, with the emergence of clades with entirely North American most recent common ancestors (MRCAs). Emergence of major clades with stem nodes that do not have tropical ancestral ranges is reflected in the historical biogeography of the taxa in this study.

The sister clade to the Mammilloid clade in Cacteae has remained in the eastern Altiplanian/Sierra Orientalian/Coahuilan/Chihuahuan Desert region (ASC). However, a radiation of the Mammilloid clade to the Sonoran Desert region (SDR), as well as geographically distant areas such as the Great Basin, the High Plains of western United States, and even as far north as Canada, as well as into the tropics, has significantly expanded the range of the tribe (Arakaki et al. 2011, Vázquez-Sánchez et al. 2013, Hernández-Hernández et al. 2014). Previous studies (e.g., Arakaki et al. 2011) have suggested that the western distributions in Cacteae, including the Mammilloid clade, followed after the estimated formation of the Sonoran Desert, at approximately 8 Mya

(Axelrod 1979), by approximately 1–2 Myr. Although *Coryphantha* (Engelm.) Lem. and *Mammillaria* Haw. still have centers of species richness in the ASC region, there are more western areas of high speciation as well (Fig. 1). In contrast, *Cochemiea* (K. Brandegee) Breslin & Majure has only a few taxa in the east, with *C. macdougallii* (Alexander) Breslin & Majure, *C. conoidea* (Britton & Rose) Breslin & Majure, *C. wrightii* (Engelm.) Breslin & Majure, and *C. guelzowiana* (Werderm.) Breslin & Majure endemic east of the Sierra Madre Occidental. *Cochemiea*'s main centers of species richness are in the Sonoran/Sinaloan regions and on the Baja California peninsula, including its islands (Hernández and Gómez-Hinostrosa 2015).

By exploring phylogroup relationships using the mitochondrial DNA of 12 mammalian, reptilian, avian and amphibian taxa, Riddle et al. (2000) found support for three vicariance events (i.e., the geographical separation of a most recent common ancestor, resulting in independent speciation into two closely related species) that shaped the evolutionary history of the Baja California biota: a mid-Pleistocene mid-peninsular seaway, a late Pliocene northern expansion of the Gulf of California, and a Pliocene seaway isolating the Cape Region. However, in a comprehensive review of geological evidence and its use in biogeographical studies, Wilson and Pitts (2010) emphasize that there remains a lack of consensus regarding the timing of the formation of all of the North American deserts, let alone the geological history of the Baja California peninsula, so that caution in interpreting the timing and the causes of speciation in ancestral biogeographies is in order. In particular, they emphasize the difficulty in separating the effects of geological events such as mountain uplift and peninsular rifting from climatic changes, both of which are likely drivers of biotic distributions and evolution, and which often have complex interactions (Wilson and Pitts 2010).

Only one publication addresses speciation in Cactaceae on the Baja California peninsula, with findings that very recent (< 1 Ma) post-glacial vicariance followed by range expansion and speciation by isolation led to the evolution of *Lophocereus schottii* subsp. *australis* (K. Brandegee) Borg as a distinct entity from its parent species (Nason et al. 2002). A population genetic study of the widespread Baja California taxon, *Stenocereus gummosus* (Engelm.) A.C. Gibson & K.E. Horak, found a likely dispersal route from the peninsula across the Gulf islands to Sonora, an example of support for the hypothesis that the northern Gulf islands have been relatively recent (<1 Ma) "stepping stones" for dispersal of plant species in the region (Cody et al. 1983, Clark-Tapia and Molina-Franer 2003). Whether or not large scale, ancient events such as the peninsular rifting from the mainland that resulted in Baja California, or possible mid-peninsular or Cape region inundation, or effects of glacial/interglacial cycles played a role in the current distributions of *Cochemiea* and *Mammillaria* is unknown.

Contemporary range of *Mammillaria*, *Coryphantha* and *Cochemiea*

The genera *Mammillaria, Coryphantha* and *Cochemiea* have a latitudinal distribution limited to the equator northward. *Coryphantha* is almost entirely distributed from above the Trans-Mexican Volcanic Belt (TMVB) northward, with many taxa marginally entering the United States along the southern border with Mexico, although two species, *Coryphantha vivipara* (Nutt.) Britton & Rose and *Coryphantha missouriensis* (Sweet) Britton & Rose, are widely dispersed to at least as far north as subarctic Canada (Benson 1982), and *Coryphantha cubensis* Britton & Rose is a Cuban endemic (Britton and Rose 1923, Zimmerman and Parfitt 2003, Dicht and Luthy 2005). *Mammillaria* sensu Breslin & Majure contains taxa that have a tropical distribution, including the type species for the genus, *Mammillaria mammillaris* Haw., as well as *M. prolifera* (Mill.) Haw., *M. nivosa* Link ex. Pfeiff., *M. ekmannii* Werderm., and *M. colombiana* Salm-Dyck, with *M. prolifera* and *M. colombiana* subsp. *yucatanensis* (Britton & Rose) D. R. Hunt, sampled in this study. *Cochemiea* sensu Breslin&Majure is most species-rich in the Sonoran Desert region and in Baja California. (Hernandez and Gomez-Hinostrosa 2015) (Fig. 3-1).

Mammillaria occur in the tropics, seasonally dry tropical thornscrub, subtropical xeric zones, xeric desert regions, and mountainous "sky island" habitat (Britton and Rose 1923, Anderson 2001, Zimmerman and Parfitt 2003, Powell and Weedin 2004, Dicht and Luthy 2005, Hernández and Gómez-Hinostrosa 2015). In Mexico, *Coryphantha* is present in tropical to desert habitat, and in the United States, it occurs in a wide range of desert, grassland and temperate zones (Benson 1982, Bravo-Hollis and Sanchez-Mejorada 1995, Zimmerman and Parfitt 2003, Dicht and Luthy 2005). *Cochemiea*, with the exception of two small subclades dispersed geographically, and genetically distant from the core of the genus, occurs in Sonoran thornscrub, coastal Sonora, and reaches its greatest diversification in multiple phytogeographic zones on the Baja California peninsula (Rebman and Roberts 2012, Hernández and Gómez-Hinostrosa 2015).

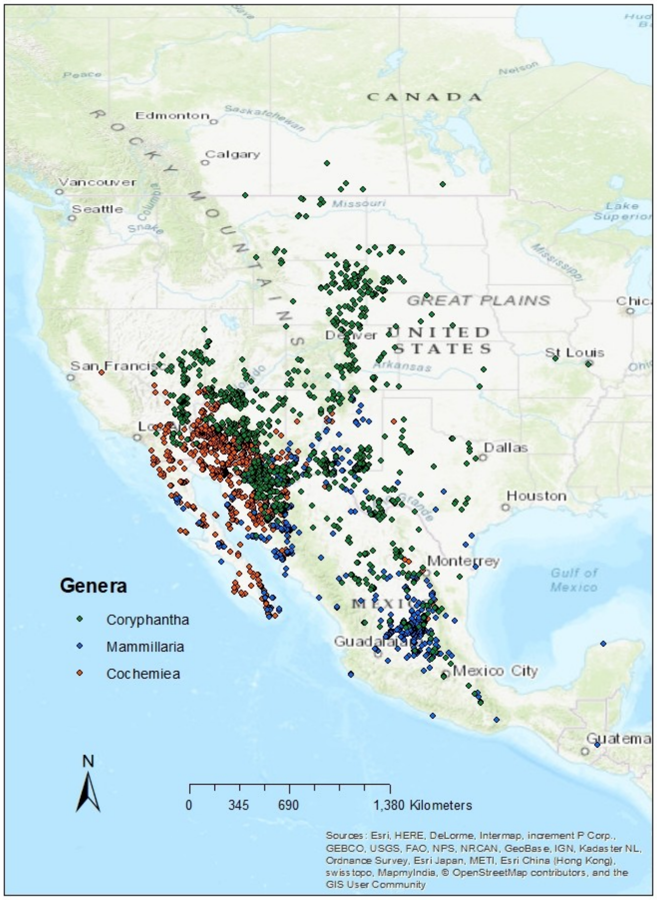


Figure 3-1. Map of current distributions of *Mammillaria*, *Coryphantha*, and *Cochemiea* based on herbarium vouchers with geospatial data. Green squares: *Coryphantha*. Blue squares: *Mammillaria*. Orange squares: *Cochemiea*. Each square represents the geospatial data for a vouchered specimen from SEINet (Southwest Biodiversity Network). Not pictured: eastern tropical and South American distributions of *Mammillaria*, and *Coryphantha cubensis* on Cuba. Basemap copyright ESRI ArcGIS v. 10.1.6.

One of the genetically and geographically distinct lineages in *Cochemiea* occurs in Arizona, New Mexico and Texas (C. *wrightii, C. wrightii* subsp. *wilcoxii* (D.R. Hunt) Breslin & Majure, and *C. viridiflora* (Boed.) Breslin & Majure and *C. conoidea*); another disjunct clade is widely distributed, with two taxa in subtropical Mexico and one taxon from the Sonoran into the Mojave Desert regions (*C. guelzowiana* and *C. tetrancistra*). The distributions of the taxa in *Mammillaria*, *Coryphantha* and *Cochemiea* display adaptation to almost every available habitat from the equator, northward, between the Pacific Coast of North America at approximately -117° to roughly -97° longitude, south of latitude 43°. The most dispersed distributions of vouchered specimens at SEInet or GBIF include *Coryphantha vivipara* at 51° latitude in Saskatchewan, Canada; *Mammillaria eichlamii* at 11.5° latitude in Nicaragua, and *Mammillaria prolifera* at -71° longitude in the Dominican Republic. Four regions in North America have been identified as areas of high species richness in the Cactaceae- the Chihuahuan, Puebla-Oaxacan, Jaliscan and Sonoran-Sinaloan (Barthlott 2015, Hernandez and Gomez-Hinostrosa 2015). In the first three of those regions, *Mammillaria* (including previous circumscriptions of *Cochemiea* s.s.) accounts for the greatest species diversity, with 94, 28, and six species respectively. The main western center of diversity for *Cochemiea* is on the BC peninsula itself, with approximately 25 out of the total of approximately 36 taxa in that clade occurring on the peninsula or its nearby islands (Rebman and Roberts 2012, Barthlott et al 2015, Hernandez and Gomez-Hinostrosa 2015, cf. Chapter 2). The combination of a large extent of occurrence, multiple adaptations to widely varying habitats and high species and morphological diversity, with the estimated origin of only 7-6.3 Ma, suggests a complex biogeographical history and rapid diversification.

Phytogeographic zones of Baja California and adjacent regions

Major climate influences on temperature and precipitation zones of Baja California include the cold California current system, the tropical climate in the Cape Region, the rain and fog shadow in the central desert region of the north, several mountain ranges forming a more or less continuous “spine” down the peninsula at high enough elevations to create “sky islands,” and the hot, dry eastern gulf and island regions (Reimann and Ezcurra 2005). Rebman and Roberts (2012) identified 11 distinct phytogeographic climate zones on the peninsula. The *Mammillaria* and *Cochemiea* of Baja California occur in all of these zones (Hernández and Gómez-Hinostrosa 2015). On adjacent mainland Sonora and Sinaloa, as well as the northern Sonoran/Mojave deserts of the US, the climate is most similar to the Gulf region (Rebman and Roberts 2012). The backdrop of the Sierra Madre Occidental provides a distinct separation between the rest of the mainland distributions of *Mammillaria* and *Coryphantha*, and the mainland Gulf of California Coast (Bye 1995, Luna Vega et al. 2002). Starkly different temperature and precipitation regimes occur between regions separated by small linear distances in Baja California—for example, along the northern Gulf of California coast of the peninsula, in the vicinity of Bahía de Los Angeles, versus the Pacific coast, approximately 80 km west (Rebman and Roberts 2012). Another important example is the hotter, drier Magdalena Plains near Puerto San Carlos in Baja California Sur, and the comparatively cooler and wetter conditions on the Pacific island archipelago in Bahía Magdalena, only approximately 20 km west (cf. Chapter 4).

Goals of this study

We seek to answer the following questions: What is the historical biogeography of the Mammilloid clade? What is the divergence time of the emergence of the Mammilloid clade from the rest of Cacteae, and the timing of the emergence of the individual genera, *Mammillaria, Coryphantha*, and *Cochemiea*? When did *Cochemeia* arrive on the Baja California peninsula, and via what migration route? How many major dispersals to the Baja California peninsula of the ancestors of *Cochemeia* likely occurred? What are some likely geological events, and on what time scale, that have shaped the evolution and current distribution the Mammilloid clade in general and of *Cochemeia* in particular? Does the species richness of *Cochemiea* reflect a high diversification rate? What are the divergence times for the Mammilloid clade emerging from other clades in Cacteae, followed by the timing of the separate clades of *Mammillaria*, *Coryphantha* and *Cochemiea*? What are some likely biogeographical explanations for the high rate of peninsular and island endemism in *Cochemiea*? Using multiple analytical tools combined with a well-supported time-calibrated phylogeny, these investigations will fill a major existing gap in the understanding of the evolution and biogeographical history of important clades in the Cactaceae.

Methods and Materials

Taxa and ancestral ranges

The taxa used in all of the analyses were selected for nearly regionally complete sampling from Baja California and adjacent regions in the genera *Cochemiea* and *Mammillaria*. Sampling of outgroups and *Coryphantha* included at least one representative for each of the known geographical distributions (Rebman and Roberts

2012, Hernández and Gomez-Hinostrosa 2015, Pilbeam 2015). The taxon set is identical to the one used Chapter 2 of this dissertation to reconstruct the phylogeny of Baja California *Cochemiea*, *Mammillaria* and related taxa from adjacent regions.

Three sets of possible ancestral ranges were used in multiple analyses, based on current distributions, following Morrone (2006), Ortega-Baes and Godínez-Alvarez (2006), Vázquez-Sánchez et al. (2013) and Hernández-Hernández et al. (2014). The most disaggregated set included seven regions on the BC peninsula, reflecting current known ranges and endemism, following many of the phytogeographic zones delineated in Reimann and Ezcurra (2005) and Rebman and Roberts (2012), as well as six mainland regions: the tropics below the Trans-Mexican Volcanic Belt, the eastern Altiplanian-Chihuahuan-Coahuilan region, the Sonoran Desert region, the Sierra Madre Occidental, the northern distributions above the Mexican border and the Mojave Desert, with 13 regions altogether. The approach with fewest regions used five general regions: two regions from Baja California (BC north and BC south), the northern distributions into the Great Plains and the Mohave, Sonora/Sinaloa and the eastern region of Mexico. The third approach, which is presented below, divided Baja California into four regions (the California Floristic Province (CA-FP), the Pacific coast south of El Rosario to Todos Santos (PC), the Gulf of California coast including Gulf islands, through the mountains of Baja California to the Central Desert (GC), and the Cape Region of Baja California (CR)), and included the eastern Altiplanian/Sierra Madrean/Chihuahuan region, the Sonoran Desert region, the Sinaloan subtropical thornscrub (SS), and the Mojave Desert region (MDR). (Fig. 3-2). Taxa were assigned to one or more ranges based on their accession data, or, in the case of samples without geospatial data, based on known distributions of vouchered herbarium specimens with known geospatial data, accessed at the Southwest Biodiversity Network (SEINet) and the Global Biodiversity Information Facility (GBIF).

Trees and statistical methods

The data set used for molecular phylogenetic reconstruction was the aligned nucleotide matrix used in Chapter 2 of this dissertation (unpublished data, cf. Chapter 2), a reference guided assembly of raw whole genome 150 bp paired end reads, sequenced on an Illumina HiSeq platform (Rapid Genomics, Gainesville, FL.) assembled to the large single copy region (LSC) of *Mammillaria prolifera* using Geneious Prime 2019 1.3 (Biomatters, Inc. Auckland, NZ, www.geneious.com). Analyses were run in RASP v. 4.1.2 (Yu et al. 2015). Methods used for probabilistic historical biogeographical reconstruction included Bayesian inference for discrete areas (BayAreas) (Landis et al. 2013), statistical dispersal-vicariance analysis (S-DIVA) (Yu et al. 2010), dispersal-extinction-cladogenesis (DEC) (Ree 2005, Ree and Smith 2008) and Bayesian Binary MCMC (BBMC) (Olsson et al. 2006, Sanmartín et al. 2008). Each of these methods uses likelihood estimates of the ancestral ranges of internal nodes on a time calibrated phylogenetic tree, based on stepwise hindcasting from existing ranges. For BayAreas, DEC and BBMC, the starting tree was a 50% majority rule consensus tree of 350 post-burn-in trees derived from a Bayesian analysis in MrBayes v. 3.2.6 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003), using two runs and four chains, the GTR+ Γ model priors and five million iterations, with the average standard deviation of split frequencies less than 0.001 by the end of the run.

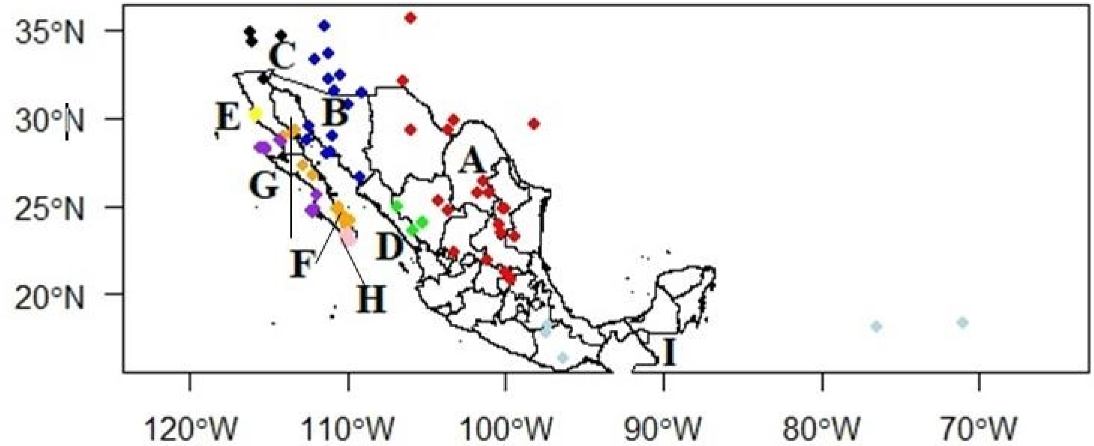


Figure 3-2. Designated ancestral ranges used in the biogeographical analyses, based on current distributions of sampled taxa. Samples of taxa and the geographic areas used in analysis. Each square represents one of the samples used in phylogenetic reconstruction. Taxa are color coded by the region to which they were assigned as their current range, or the primary known distribution, if multiple ranges are known. Pictured in this diagram are nine of the regions used for the reconstruction of ancestral ranges. The regions and colors: (A, red): Altiplanian, Sierra Madre Orientalian, Tamaulipan, Coahuilan and the Chihuahuan Desert Region (ASC), (B, blue): the Sonoran Desert Region (SDR), (C, black): the Mohave Desert region (MDR), (D, green): subtropical Sinaloan thornscrub (SS), (E, yellow): the California Floristic Province (CFP), (F, orange): the Gulf Coast, Gulf islands and Central Desert of Baja California (GC), (G, purple): the Pacific coast and islands of Baja California between El Rosario and Todos Santos (PC), (H, pink): the Cape Region of Baja California (CR), (I, blue): south of the Trans-Mexican Volcanic Belt (TMVB), and other tropical areas.

For S-DIVA, which utilizes a multiple tree sampling method, 2000 random trees were used from 4000 post burn-in trees from the BEAST analysis, which were also used for divergence time estimates (see below). Multiple models were constructed in S-DIVA using highly restricted, moderately restricted and unrestricted range constraints. Tree results were generated in RASP.

Divergence time estimates were performed in BEAST v. 1.10.4 (Drummond and Rambaut 2007, Drummond et al 2012) and its associated software, BEAUti, Log Combiner and Tree Annotator, with post run analysis to test for stationarity and time to burn-in in Tracer v. 1.7.1 (Rambaut et al. 2018). A test of the strict clocklike model was performed in PAUP* v. 4.0a, build 165 (Swofford 2003) using the likelihood ratio of the difference between clocklike and non-clocklike evolution, based on the 50% majority rule Bayesian consensus tree described above. The BEAST run included two taxon groups: nine outgroup taxa in *Ariocarpus, Turbinicarpus, Lophophora*, *Strombocactus* and *Cumarinia*, and the Mammilloid clade, with 79 taxa. Tree priors were set to a mean of 12 Ma for the outgroup taxa and 6.5 Ma for the Mammilloid clade, with a normal distribution (following Drummond 2012), based on well-supported estimated divergence times from Arakaki (2011). Based on the best AIC and BIC scores in jmodeltest v. 2.1.10 (Guindon and Gascuel 2003, Darriba et al. 2012), the GTR+ Γ model for nucleotide substitution was selected, with the three codon positions unlinked. The clock model used was an uncorrelated relaxed clock (Drummond et al. 2006) with a lognormal distribution. Following Drummond (2012), birth-death and Yule pure birth analyses were compared via marginal log likelihood scores, in order to test which coalescent tree prior was more informative. The BEAST run included 20 million iterations with trees sampled every

2000 iterations, from which, excluding trees from the burn in as determined by Tracer, a 95% maximum clade credibility tree was constructed from 4280 trees.

Using 4000 post burn-in trees derived from the above BEAST analysis, an ultrametric 50% majority rule consensus tree was created and used in diversification rate analysis. Accounting for incomplete taxon sampling in outgroups as well as *Mammillaria* and *Coryphantha*, diversification rates and rate shifts over time were estimated in turboMEDUSA v. 0.953 (Alfaro et al. 2009, Brown et al. 2018), implemented in R v. 3.5.1 (R Core Team 2018). Automated optimal model selection, forced birth-death and pure birth (Yule) models were evaluated. The median diversification rate, species turnover rate and 95% confidence interval for the diversification rate of significant rate shifts were chosen to present here.

Ancestral states of three characters in the Mammilloid clade found to be phylogenetically informative (cf. Chapter 2), were traced on the consensus tree used in the historical biogeographical analysis, using Mesquite v. 3.6 (Maddison and Maddison 2019). The selected characters were hooked spines, almost universally characteristic of *Cochemiea* and usually absent in *Mammillaria* as well as almost entirely absent in *Coryphantha*, lactiferous ducts, present in many *Mammillaria*, and adaxial grooves on the tubercles, a trait universal to *Coryphantha*. These characters, out of ten characters tested, were the three highest in relative weight in determining separation between *Cochemiea* and the rest of the Mammilloid clade. Traits were coded as binary in a simple presence/absence scheme for all taxa.

Results

Ancestral range reconstruction and historical dispersal routes

BayAreas, S-DIVA and BBMC methods agreed on ancestral ranges at more than 90% of nodes, with probabilities of a single, most likely ancestral range greater than 60% for more than half of all nodes. The clearest and most well-supported results for ancestral range prediction at all nodes, with the highest probabilities, was provided by the S-DIVA analysis, although the BayAreas results also provided well-supported relative probabilities of the presence of clades at ancestral ranges over time. The most informative results in the S-DIVA analysis were from the regional range set using the disaggregated set of nine ranges.

The S-DIVA analysis shows that the stem node, at approximately 12 Ma, had a 100% probability of originating in the eastern Altiplanian/Sierra Madre Orientalian/Chihuahuan region. (cf., e.g.,Vazquez-Lobo et al. 2016). The emergence of the Mammilloid clade at approximately 8–7 Ma was soon followed by the divergence of the *Coryphantha, Mammillaria* and *Cochemiea* subclades. This clade divergence was followed soon after by ancestral ranges in the Mojave and Sonoran Desert regions.

The *Mammillaria* clade

The MRCA for the *Mammillaria* clade emerged at approximately 8 Ma, with ancestral ranges most likely to be tropical, and eastern Mexico. Dispersal to the Sonoran Desert region is likely to have occurred about 1 Myr after the emergence of the *Mammillaria* clade. Most recent common ancestors (MRCAs) appear for the clade containing *Mammillaria heyderi* subsp. *macdougalii* in the Sonoran Desert region shortly thereafter (< 1 Myr). Several possible ancestral ranges on the Baja California peninsula suggest multiple dispersal, with the ancestral node for the Baja taxa in the *Mammillaria* clade having an equal probability of being the Sonoran Desert region, the Cape Region of Baja California Sur, or the Pacific Coast of Baja California. This change to peninsular ancestral ranges is at approximately 6.5 Ma. *Mammillaria tayloriorum* Glass & R.A. Foster, *M. bocensis* R.T. Craig and *M. johnstonii* Orcutt are most likely to have had origins in the Sonoran Desert region, and have not dispersed since those origins. Early distributions of the *Mammillaria* clade on the Baja California peninsula are likely to have occurred mostly on the Gulf of California Coast and in the Cape Region, with distribution as far north as the California Floristic Province not occurring until approximately 4 Ma. In general, the mainland ancestral nodes remain in the Sonoran Desert region, and the peninsular nodes remain in Baja California, indicating that the Gulf of California may have become a strong barrier to dispersal of *Mammillaria* s.s. (in the sense circumscribed in Chapter 2). The emergence of exclusively Baja Californian ancestral ranges for *Mammillaria* occurs at the Gulf of California coast, approximately from 5–6 Ma. For the taxa in *Mammillaria* s.s. in our sample set, diversification appears to have slowed significantly since approximately 2.5 Ma.

The *Coryphantha* clade

The *Coryphantha* clade arises approximately simultaneously with the *Mammillaria* clade, at 8 Ma. There are probable tropical origins for this clade, with an entirely eastern Mexican ancestral range very soon after these likely tropical origins (<1 Myr later). The dispersal to the Sonoran Desert region and Mojave Desert region occurs approximately 7 Ma, at approximately the same time as the westward migration of *Mammillaria*. A second dispersal west occurs about 1 Myr later, into the Sonoran Desert region. Otherwise, all of the ancestral nodes for *Coryphantha* are located in the Altiplanian/Sierra Madre Orientalian/Chihuahuan region. A major shift occurs at approximately 5 Ma (about 1.5 to 2 Myr after the emergence of the *Mammillaria* and *Coryphantha* clades), when the ancestral range for the genus *Cochemiea* changes from the SDR to the GC and CR of BC. After the jump to the CR of BC, which was approximately 5-6 Ma, the CR and GC play a major role as an ancestral area for the Baja and adjacent *Cochemiea* (Fig. 3-3).

The *Cochemiea* clade

A detailed analysis of the probable ancestral ranges and migration of lineages in the *Cochemiea* clade reveals a complex history (Fig. 3-4). The early Sonoran migration of the more western members of the *C. conoidea* clade— *C. wrightii*, *C. wrightii* subsp. *wilcoxii* and C. *viridiflora*—characterize this subclade as one of the older in *Cochemiea*, otherwise isolated to eastern Mexico, the northern Chihuahuan Desert region. The most recent common ancestor of *Cochemiea* minus this clade shows Sonoran and Mojave Desert ancestral ranges at about 6 Ma. The *C. tetrancistra*/*C. guelzowiana* subclade is similar to the subclade with *C. conoidea*, *C. wrightii. C.wrightii* subsp. *wilcoxii*, and *C. viridiflora*, in that it is a not a very species rich clade, with *C. guelzowiana* still occurring in the eastern Mexican region and *C. tetrancistra*'s most recent common ancestor appearing in the MDR about 6 Ma. Another species that is relictual in the ancestral range is *C. macdougallii*, having an origin of about 8 Ma, at the origination of the entire Mammilloid clade. Also at approximately 6 Ma, at the most recent common ancestor for the Baja California *Cochemiea* plus the subclade containing *C. tetrancistra* and *C. guelzowiana*, the first signs of peninsular ancestral ranges appear, with indications of multiple simultaneous dispersals or vicariance events to the Cape Region, Pacific Coast, and Gulf of California coast of Baja California.

The most recent common ancestor for the primarily BC endemic taxa in *Cochemiea* shows an SS/SDR route to the GC of the peninsula. One of the earliest arrivals on the peninsula is *Cochemiea* in its former, narrowly circumscribed sense, including *C. pondii, C. maritima, C. halei, C. setispina* and *C. poselgeri*. This well-supported clade is likely to have migrated from the Gulf Coast of Baja California to the Pacific Coast and Cape Region about 5.5 Ma, with a north–south split not long after, at 5 Ma. The newly described species, *C. thomasii* García-Mor., Rodr. González, J. García- Jim. & Iamonico, was not sampled for this study. It is located on mainland Mexico, approximately 400 km to the east of the distribution of *C. halei*, with which it has morphological similarities.

Another clade to have early peninsular origins is the Cape Clade, which also arrived on the peninsula via the Sonoran Desert region, to the Gulf of California coast, about 5 Ma. The clade was primarily established as endemic in the Cape Region by 4 Ma. The small clade containing *C. insularis* (H.E. Gates ex Shurly) Breslin & Majure, *C. boolii* (G.E. Linds.) Breslin & Majure, and C. *schumannii* (Hildm.) Breslin & Majure shows a more southerly ancestral range, in the SS.

The Island Clade is the latest to arrive on the peninsula, with ancestral ranges in the Sonoran Desert until 4.5 Ma. With the exception of a probable early migration to the Pacific coast of Baja California by *C. blossfeldiana* (Boed.) Breslin & Majure and subsp. *rectispina* Breslin & Majure, this clade has many nodes with a Sonoran Desert ancestral range, and only developed exclusively peninsular subclades within 1–2 Ma.

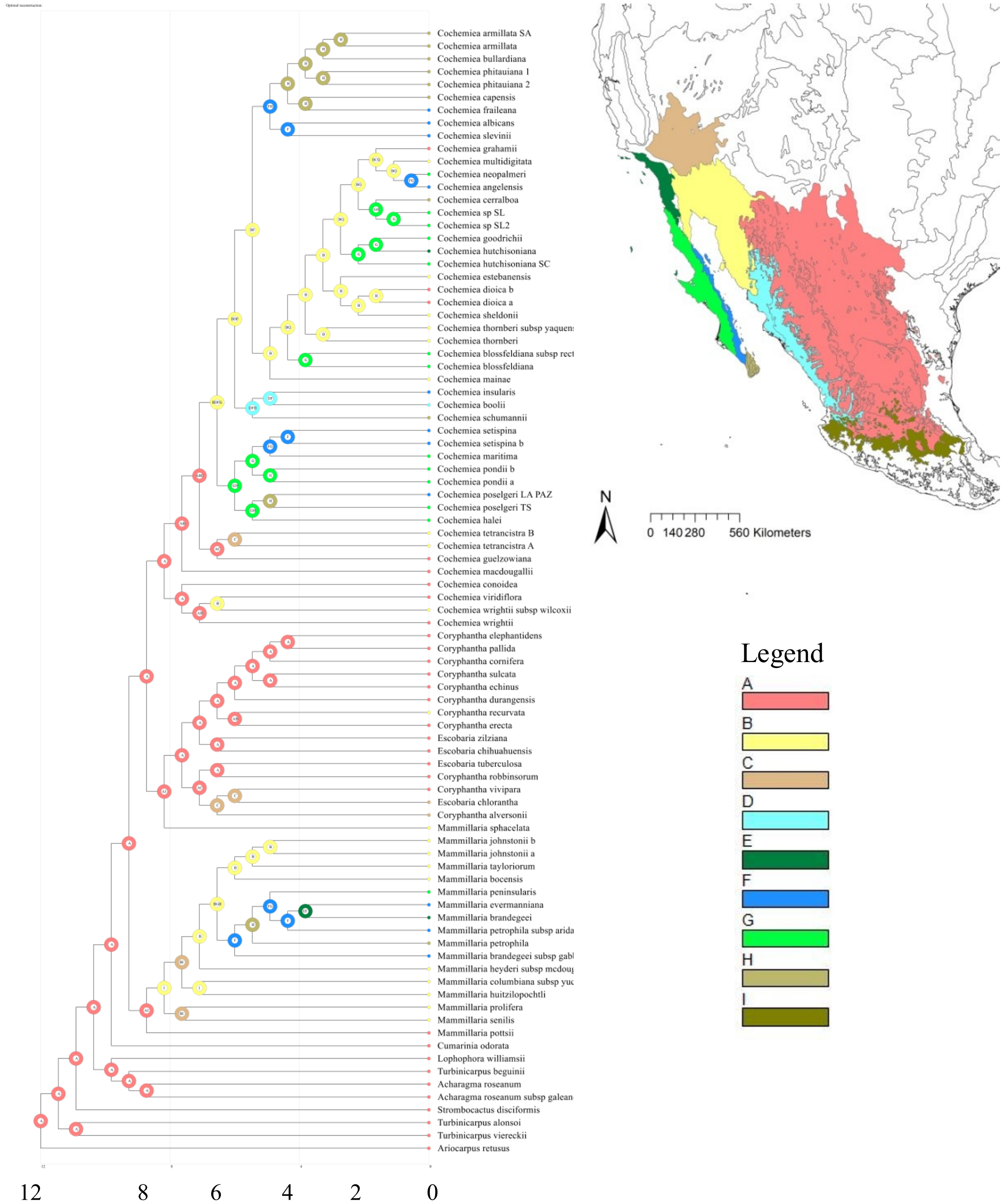


Figure 3-3. S-DIVA analysis of the most likely ancestral ranges for the *Mammillaria*, *Coryphantha* and *Cochemiea* clades. The most likely ancestral ranges in the legend. (A): ASC, (B): SDR, (C): MDR, (D): SS, (E): CFP, (F): GC, (G): PC, (H): CR. The reverse scale at the base of the tree is in millions of years. Nodes with multiple possible ancestral ranges contain the letters of those ranges, but are colored by the most likely ancestral range.

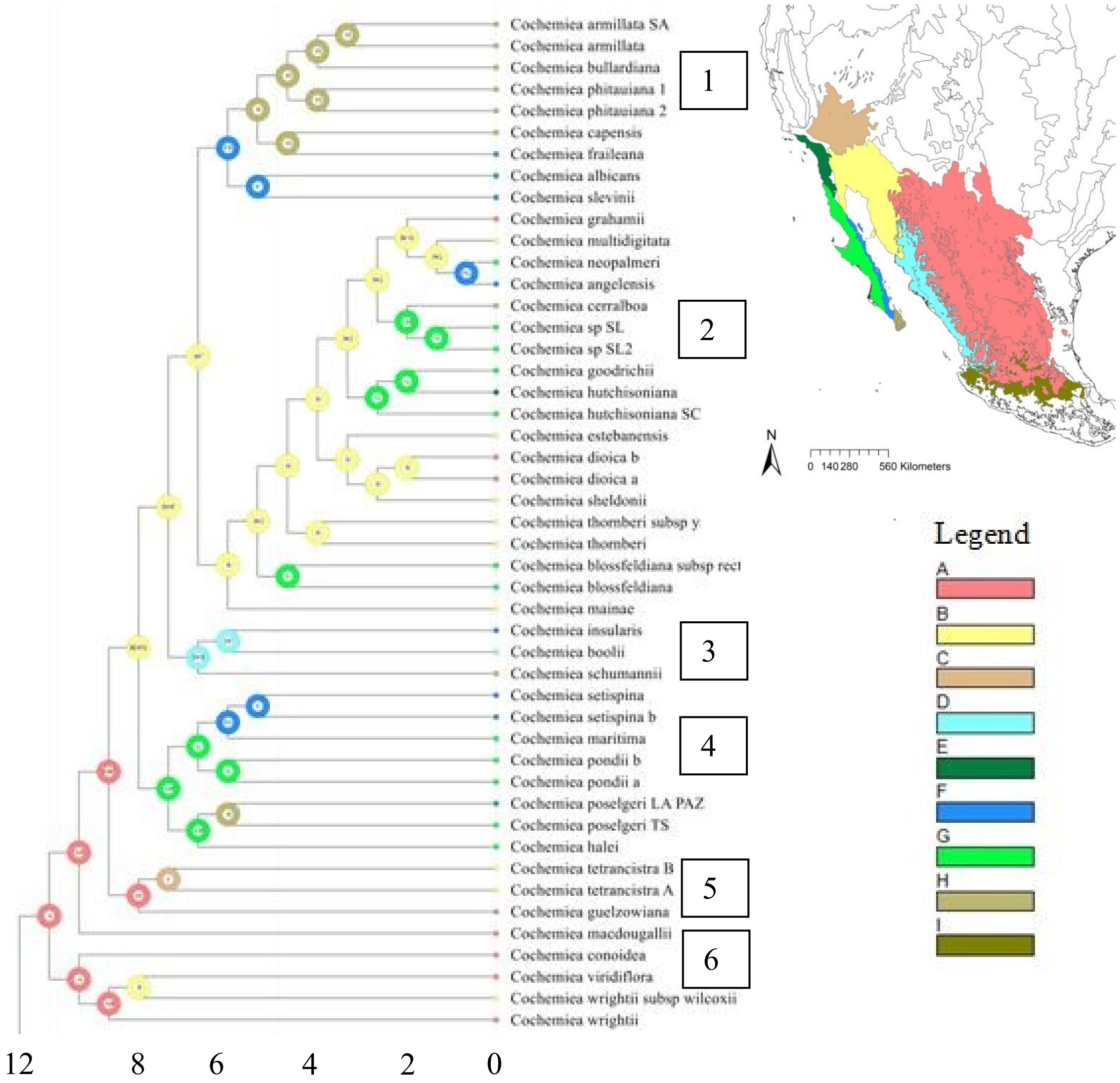


Figure 3-4. S-DIVA analysis of the most likely ancestral ranges of the genus *Cochemiea.* Ancestral ranges reconstructed from S-DIVA analysis. The letters of the most likely ancestral ranges are displayed in the center of each pie chart. The reverse time scale along the base of the tree is in millions of years. (A) ASC; (B) SDR; (C) MDR; (D) SS; (E) CFP; (F) GC; (G) PC; (H) CR; and (I) TMVB. Key to clades: (1) Cape clade; (2) Island clade; (3) *C. schumannii* clade; (4) original *Cochemiea* clade; (5) *C. tetrancistra/guelzowiana* clade and (6) *C. conoidea/C. wrightii* clade.

The Island Clade shows the most varied peninsular ancestral nodes, as well as the most recent speciation events. It is also characterized by extensive mainland distributions of *C. mainae* (K. Brandegee) Breslin & Majure, *C. grahamii* (Engelm.) Breslin & Majure, *C. sheldonii* (Boed.) Breslin & Majure*, C. thornberi* (Orcutt) Breslin & Majure*, C. thornberi* subsp. *yaquensis* (D.R. Hunt) Breslin & Majure, and *C. dioica*, with *C. dioica* being the only one of the group to also occur on the BC peninsula.

Estimated divergence times

Clocklike substitution rates were rejected using a likelihood ratio test between clocklike and non-clocklike evolution in PAUP* v. 4a (p< ,0001). There was no significant difference in marginal log likelihood scores of the birth-death coalescent tree prior or the Yule pure birth model. The results presented here used the Yule model. The BEAST run reached stationarity after six million iterations, out of a toal of 20 million. The BEAST analysis indicates that most of the divergence times of internal nodes agree broadly with Arakaki (2011) and Hernández-Hernández (2014), and that the speciation in *Cochemiea* has occurred rapidly and recently. Relative divergence times generally agree with the S-DIVA and BayAreas estimates of the ages of ancestral ranges. The origin of the Mammilloid clade is recovered as between 7-5 Ma. *Mammillaria* is shown here to have originated after *Coryphantha*, although the predicted node heights overlap for both genera. The most recent common ancestor of *Cochemiea* emerges 500,000 to 1 million years later. The root of *Cochemiea* emerges at approximately 5.5 Ma, roughly simultaneously with the northern distribution of *Cochemiea conoidea*. The island clade emerges approximately 1 million years later, and the Cape clade endemics at approximately 3 Ma. The original *Cochemiea* clade's MRCA emerges also between 3.5

and 2.5 Ma, with the separation between *Cochemiea poselgeri* and *Cochemiea halei* at less than 1 Ma, and the north/south split older than both southern species. Not counting duplicate taxa or subspecies, 16 terminal nodes, approximately 70%, are younger than 1 Ma (Fig. 3-5)

Estimates of diversification rates

The divergence and diversification analysis in turboMEDUSA indicates four shifts in diversification rates. Consistent with estimates of ancestral ranges, dispersal, vicariance and divergence times, the shifts in diversification for the BC and SS/SDR *Mammillaria* and *Cochemiea* indicate accelerated lineage creation over time. The whole taxa set including outgroups also show an increase in diversification dating back to the root node (estimated by MEDUSA as slightly younger than in other analyses above, at 10 Ma). The Chihuahuan Desert *Coryphantha* and the monotypic genus *Cumarinia*, in contrast, have shifts to comparatively lower rates of diversification (Fig. 3-6 and Table 3-1).

Ancestral states of morphological characters

The ancestral states of the three selected morphological characters (hooked spines, lactiferous versus non-lactiferous parenchymal ducts, and adaxial grooves on tubercles) show coincident emergence with diversification rate shifts in two cases. The first is the emergence of lactiferous ducts in *Mammillaria* at approximately the same time at which there was an increase in diversification for the Mammilloid clade as a whole. The second is the emergence of hooked spines in *Cochemiea*, roughly coinciding with the same accelerated diversification.

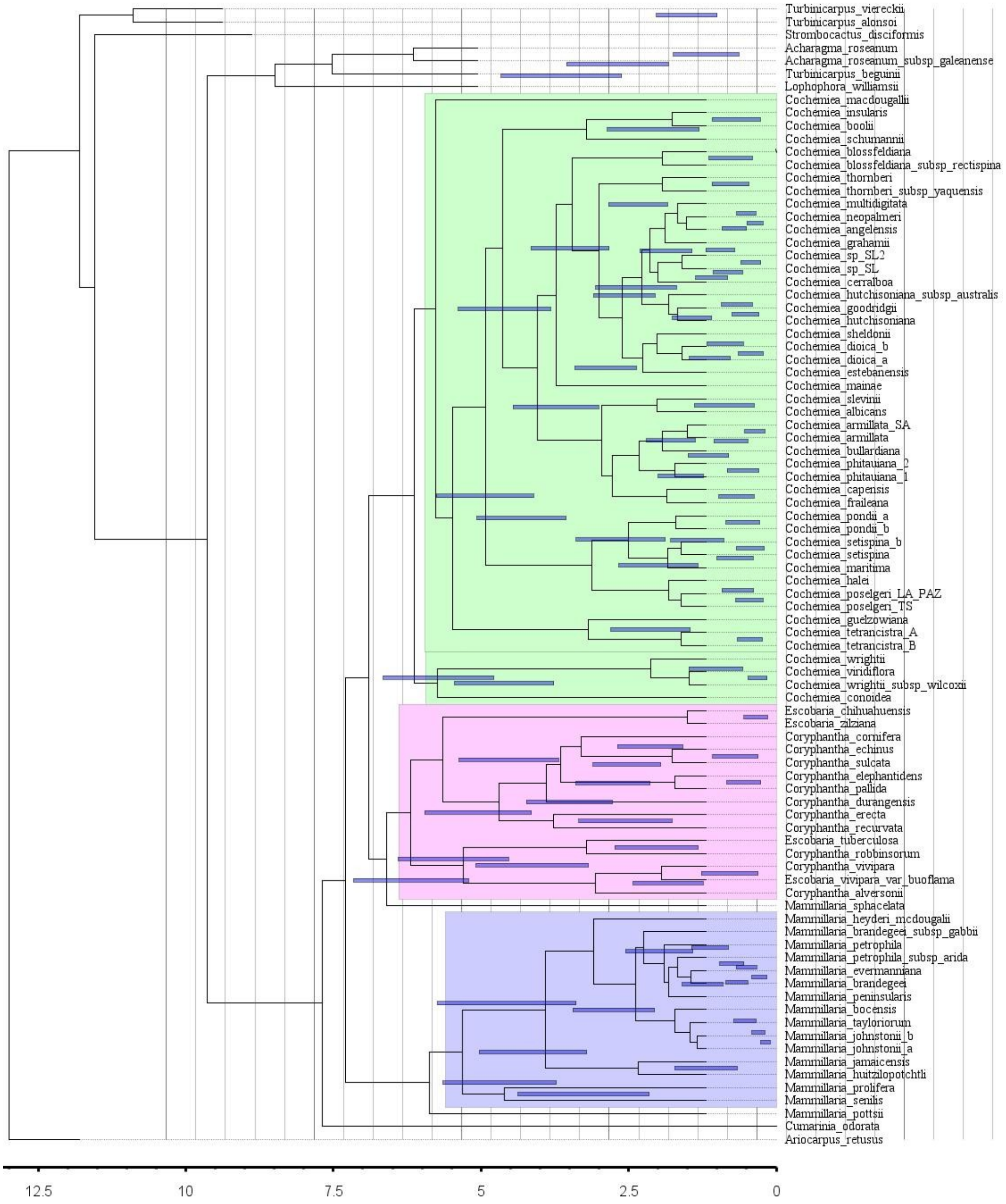


Figure 3-5. Divergence time estimates for the Mammilloid clade showing 95% confidence Interval node heights. Light green: *Cochemiea*. Purple: *Coryphantha.* Blue: *Mammillaria* .The reverse time scale is in millions of years. The tree is a 95% confidence maximum clade credibility tree generated from 4280 trees in BEAST.

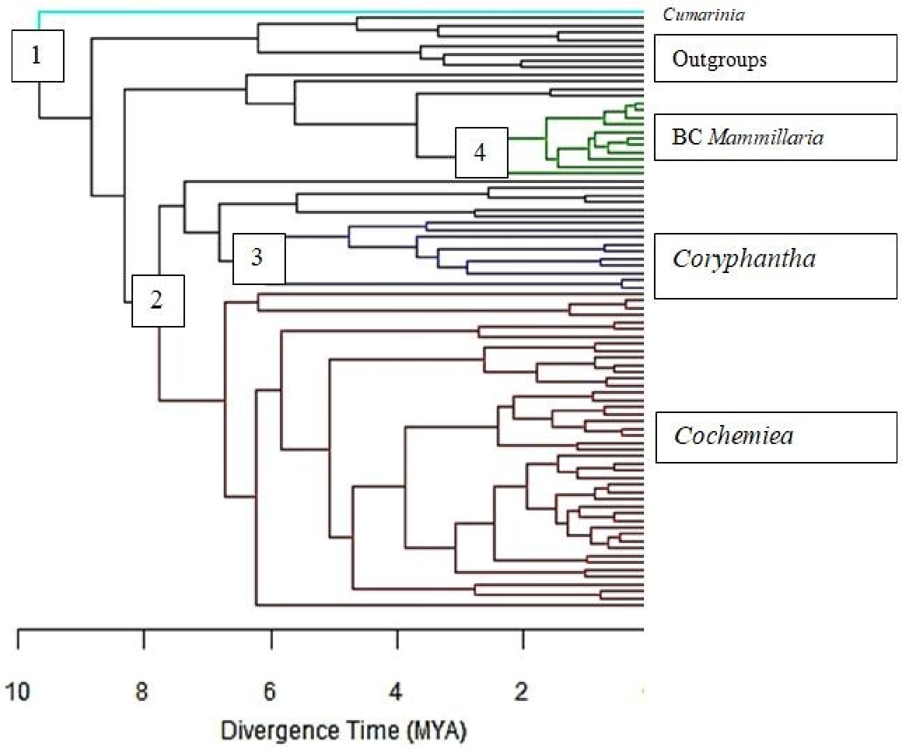


Figure 3-6. The estimated timing of diversification rate shifts for *Cumarinia, Mammillaria*, *Coryphantha* and *Cochemiea*. Nodes with major shifts in diversification as determined by the MEDUSA analysis. Key to nodes: (1) Slowed diversification for the monotypic genus, *Cumarinia*; (2) Increased diversification of the *Cochemiea*+*Coryphantha* clade; (3) Decreased diversification of the *Coryphantha* clade; (4) Increased diversification of *Mammillaria* in the Baja California region.

Table 3-1. Diversification rate shifts for Cacteae, *Cumarinia*, *Cochemiea*, *Coryphantha* and *Mammillaria*.

Shift	Clade/Genus	Age, Ma	Median r	r 95% CI	ε	location
	core Cacteae	13–10	.330	.236–.453	.788	NorthA*
1	*Cumarinia*	13–10	0.00	0.00–.199	na	ASC
2	*Cochemiea*+*Coryphantha*	7–5	.510	.382–.666	na	ASC/SDR/BC
3	*Coryphantha*	5–4	.016	.009–.033	.999	ASC
4	BC *Mammillaria*	2.5–2	1.52	1.16–2.03	na	BC, SS

r = lineages per million years. ε = extinction rate/speciation rate. In cases where ε is "na," MEDUSA's optimal model fit was a pure birth, a.k.a. Yule, model. ASC=Altiplanian/Sierra Madre Orientalian/Coahuilan/Chihuahuan region. SDR= Sonoran Desert Region. BC=Baja California, NorthA= North America, SS=Sinaloan subtropical coast. Note: in a forced birth-death model, ε = .00000015 (not shown in table) for the *Coryphantha*+*Cochemiea* clade, that is, a negligible species turnover rate. The shift for *Coryphantha* indicates a comparatively greatly slowed diversification rate, approximately 2 Myr after an initial increased diversification. *From Arakaki et al., 2011.

Mammillaria developed lactiferous ducts prior to its Baja California migrations, but the timing of the development of hooked spines in *Cochemiea* approximately coincides with the early appearance of the first Baja California clades— the Cape Clade and the five species in the original genus *Cochemiea*. The loss of hooked spines in *Cochemiea* is shown to be a recent event for the five taxa that have straight spines. Adaxial tubercular grooves are estimated to have developed at the same time that *Coryphantha* diverged. The ancestral states for these morphological characters generally trace back to early ancestors, suggesting that these clades have been divergent for almost as long as the Mammilloid clade has been in existence (Fig. 3-7).

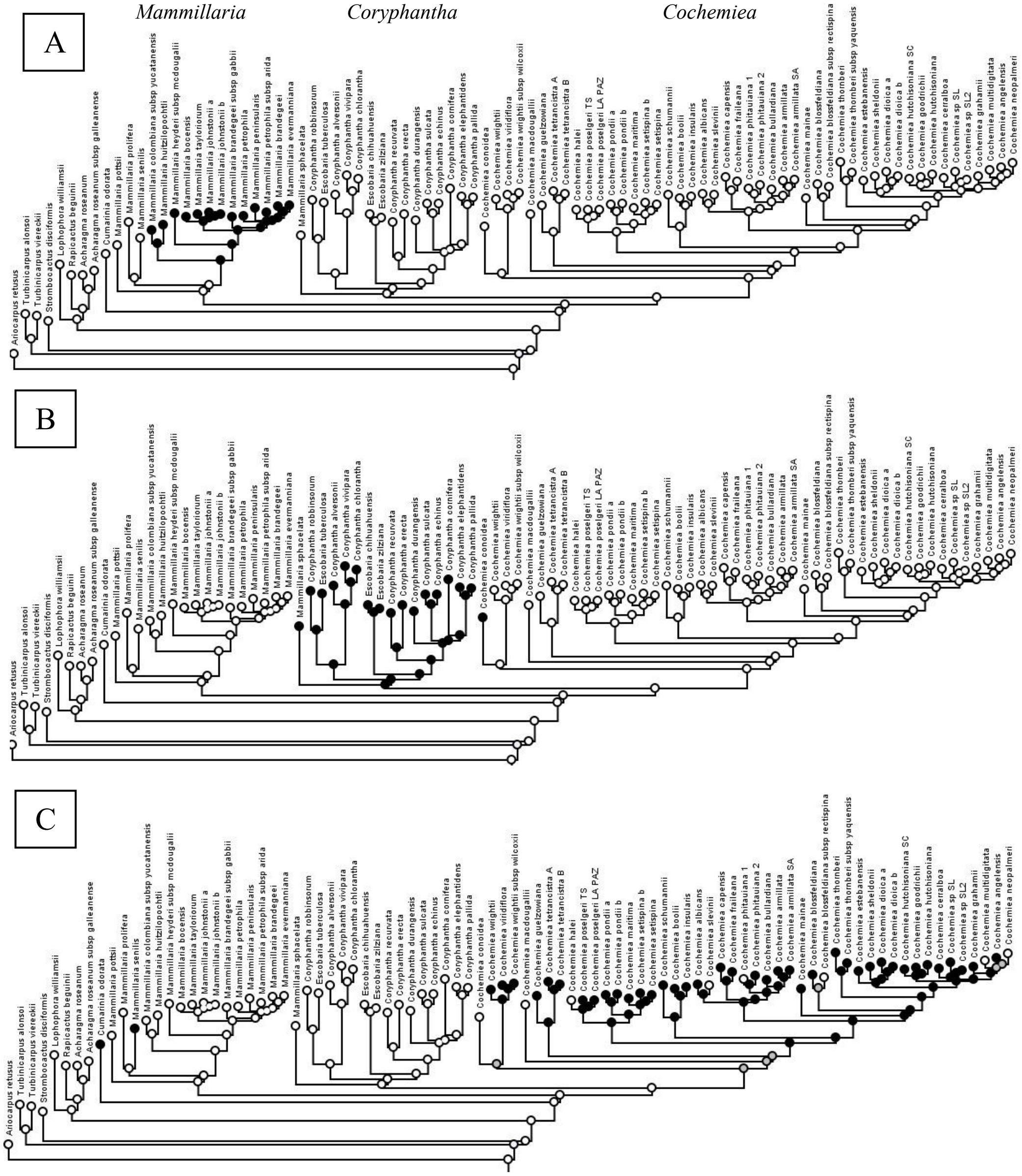


Figure 3-7. Ancestral states of morphological characters traced on a 95% clade credibility Bayesian phylogeny of the Mammilloid clade and outgroups.

The tree used in tracing the ancestral state of characters is the same as that used in estimating the historical biogeography, a 95% clade credibility consensus of 4000 trees generated via Bayesian analysis. Branches are drawn proportional to their length. The characters traced: (A) lactiferous ducts; (B) adaxial grooves on tubercles; (C) hooked spines.

Discussion

The recent and rapid diversification and complex biogeographical history of one of the most species-rich and northwestern clades in the Cactaceae has multiple implications. Earlier results from Arakaki et al. (2011) and Hernández-Hernández et al. (2014) are confirmed, as well as recovering a history that provides time-scaled and biogeographical insight into the molecular phylogeny in Chapter 2. Whereas *Coryphantha* has remained mostly restricted to its earlier ancestral range, the jump from the eastern Altiplanian/Chihuauan ancestral origins of Cacteae and the Mammilloid clade to the Sonoran Desert region, Mojave Desert region and Sonoran/Sinaloan mainland, followed by multiple peninsular speciation events, resulted in *Cochemiea* evolving into a distinct clade, with a uniquely Sonoran/Sinaloan mainland and Baja California extent of occurrence, high species diversity and 90% peninsular endemism. This high diversity and endemism in BC coincides with multiple short and mid-range dispersal and/or vicariance events into markedly different habitats entirely contained on the peninsula or adjacent Sonora/Sinaloa, characterized by unique topography and climate.

Spatial and temporal scales of geological, geographical and climate forces

The plate tectonic actions that caused the separation of the Baja California peninsula from mainland Mexico by rifting are known to have begun more than 30 Ma and are ongoing (Dolby et al. 2015). Hypothetical mid-peninsular seaways, supported by north-south genetic discontinuities, may have formed between 1–2 Ma (Helenes and Careno 1999, Dolby et al. 2015 and the references therein). More recent glacial-interglacial cycles influencing gene flow and/or dispersal find biological support from current high genetic diversity in predicted glacial refugia, high recent gene flow between islands connected to the peninsula at the lowest sea levels, and post-glacial range expansions (Dolby et al. 2015). Multiple geological forces over several time scales have contributed to the high rate of plant diversity and endemism, with 30% of plant taxa endemic to the peninsula (Rebman and Roberts 2012, Dolby et al. 2015). The peninsular endemism of the Cactaceae in general and the genera *Mammillaria* and *Cochemiea* in particular is significant, with 93 out of 130 taxa in the Cactaceae (species and subspecies), or 72%, endemic to the peninsula (Reimann and Ezcurra 2005, Rebman and Roberts 2012). The *Mammillaria* and *Cochemiea* clades taken together have 32 species, 29 of which (91%) are peninsular or island endemics.

Three factors in this analysis support strong effects of peninsular rifting on the evolution of *Cochemiea*. Given that the highest probability for the ancestral range for *Cochemiea* after its dispersal to the Sonoran Desert region is the Cape region of Baja California Sur, via the Gulf of California coast, which is estimated to have been already approximately 200 km distant at about 7 Ma (Bennett 2013), all of the analyses indicate correlation with this separation. The ancestral jump from the eastern Mexico distribution to the Sonoran Desert region is estimated at 7 Ma in the S-DIVA analysis. The root node for *Cochemiea* emerges at 6.5 Ma in the BEAST analysis. A shift toward high diversification rates at approximately 7.5 Ma is predicted by the MEDUSA analysis. Although the shift toward high diversification is estimated by MEDUSA to be about a million years earlier than the other two analyses, this may indicate that increased diversification rates for the MRCA of *Cochemiea* was underway on the mainland, before dispersal to the peninsula.

At the more recent time scale, within *Cochemiea*, there is little support for distinct north-south genetic separation created by mid-peninsular seaways at the species level, as all of the clades show equally likely distributions among taxa located either in the north or south. In fact, more recent nodes between 1-2 Ma for the Island Clade show multiple north-south and south-north ancestral jumps, suggesting that, if a mid-peninsular seaway formed 1-2 Ma, it had little effect on gene flow or dispersal. This is consistent with several mid-range jump dispersals suggested by the ancestral range analysis, where larger geographical barriers than a mid-peninsular seaway seem to have not been a hindrance, especially the highly probable dispersal across a widening Gulf of California.

In the case of the strong north-south split of *Cochemiea pondii*/*maritima*/*setispina* versus *Cochemiea poselgeri/halei*, that disjunction is estimated at approximately 1 Myr older than the putative formation of mid-peninsular seaways in all analyses. The most likely ancestral range for that clade in *Cochemiea* is from the Cape, with a migration to the Pacific coast at about 3 Ma, and then a jump back to the Magdalena Plains and Cape Region for *C. poselgeri* and *C. halei* about 2.5 Ma, with the island dispersal of *C. halei* as recently as 500,000 years ago. It is unknown how incorporating the recently described *C. thomasii* in a biogeographical analysis would affect the ancestral range of the original genus, *Cochemiea.* As a mainland Mexican taxon, located about 400 km east of Bahía Magdalena, *C. thomasii* may represent an older lineage closer to the MCRA of *Cochemiea* s.s., or it may be a more recent distribution back to the mainland from Baja California. In spite of its recent dispersal to the archipelago in Bahía Magdalena, *C. halei* shows a suite of pronounced morphological differences from its sister taxon, *C. poselgeri*, as well as a facultative relationship with serpentine ultramafic ocean crustal rock (cf. Chapter 4). This suggests rapid adaptation to an environment markedly different from both the PC and the CR.

A strong exception to multiple north-south dispersals is the Cape Clade, composed entirely of Cape region or far southern Gulf of California coast endemics. One of the putative trans-peninsular seaways is an inundation that isolated the Cape region as an island for approximately 1 Myr, about 2 Ma, a seaway supported by population level phylogenetic studies of lizards and other vertebrates (Upton and Murphy 1997, Riddle et al. 2000). This hypothesis is supported here by the endemism to the Cape region of the Cape clade and the timing of its establishment as endemic. It may also be that climate plays a role in this endemism, however, since the tropical regime of the Cape region is significantly distinct from adjacent regions to the north. Further research into habitat suitability for the taxa of the Cape region, as well as population-level genetic analysis, would provide more insight into whether the total endemism of this clade is a result of a seaway that isolated the Cape region, a distinct climate, or both.

More recent glacial/interglacial sea level changes could be reflected in multiple east-west dispersals, where lower sea levels would have facilitated trans-Gulf dispersal or north-south dispersal along the Gulf of California and Pacific coasts, via “stepping stone” islands or exposed shoreline. For example, the only polytomy in previous maximum likelihood and maximum parsimony molecular phylogenetic analysis (Chapter 2) is one of three taxa that are close relatives to the mainland-only *Cochemiea grahamii*: *C. multidigitata* (Radley) Breslin & Majure*, C. angelensis* (R.T. Craig) Breslin & Majure, and *C. neopalmeri* (R.T. Craig) Breslin & Majure. Each of these taxa is a restricted, widely dispersed island endemic- *C. multidigitata* on San Pedro Nolasco Island, 16 km from the Sonoran coast, *C. angelensis* on Isla Angel de la Guarda, in the northern Gulf, and *C. neopalmeri* on the San Benitos Islands, in the Pacific, near Isla Cedros. Their estimated divergence is within the past 500,000 years, and this east-west island and cross-peninsular dispersal may be a reflection of dispersal or pollinator routes available at low sea levels, followed by isolation due to interglacial high sea levels. The earliest dispersal is the MRCA of *C. grahamii* and *C. multidigitata,* the taxa that also have the most geographically close ranges. Within approximately 100,000 years, the most likely ancestral range of *C. angelensis* and *C. neopalmeri* is the northern Pacific coast of Baja. Several other island endemics- *C. goodrichii* (Scheer ex Salm-Dyck) Breslin & Majure*,* *C. blossfeldiana* subsp. *rectipsina*, an unnamed taxon on Isla Magdalena, and *C. halei* also on Isla Magdalena, show divergence times in the BEAST analysis approximately coinciding with low sea levels during glacial periods. All of the estimates of dispersal events of less than approximately 500,000 years ago are within the margin of error of the BEAST analysis, however, so are a matter of conjecture. A more detailed historical biogeographical and landscape genetics study at the population level for these island endemics would place their estimated divergence times more exactly, with calibration to recent glacial/interglacial cycles.

Island endemism in the Cactaceae is high in Baja California, both on Gulf of California islands and islands in the Pacific Ocean, with an endemic from the genus *Cochemiea* on nearly every island in the region (Craig 1945, Rebman and Roberts 2012, Pilbeam 2015). Island endemism occurs in four general zones: the northern Pacific islands, the northern Gulf islands, the southern Pacific islands and the southern Gulf islands. There is apparent dispersal both across the peninsula from east to west, and along both coasts of the peninsula, from north to south. One of the more complex patterns in the S-DIVA analysis is in regard to the Island Clade itself- originating in the Cape region of Baja at 5 Ma, with a quick jump to the Sonoran/Sinaloan Gulf coast after only about 100,000 years, another almost immediate transpeninsular jump to the northern Pacific coast of Baja after approximately 100,000 years, then a jump back to the Sonoran/Sinaloan coast at about 3 Ma, with rapid diversification after multiple dispersals back to the peninsula. This zig-zag history over a short time may also account for the island endemism in *Cochemiea*, with ancestors left on islands as stepping stones for frugivorous birds (see below). Again, whether or not inter-glacial cycles facilitated increased dispersal among islands and between the peninsula and islands is a subject of further research.

In summary, the S-DIVA results support the effects of peninsular rifting as a contributing factor to speciation by vicariance, with the possibility of continuing trans-Gulf dispersal after the formation of a wider Gulf; do not show support in *Cochemiea* for mid-peninsular seaways but do suggest the possibility of an insular Cape region, and may show the influence of more recent glacial/interglacial cycles. These geological events driving a complex history of probable vicariance and dispersal, combined with the heterogeneous climate and topography of the peninsula, and the apparent ability of *Mammillaria* and *Cochemiea* to adapt rapidly to novel environments, create a picture of multiple historical abiotic drivers of diversification.

Biotic factors in dispersal and speciation

The most likely mid-to-long range disperser of *Cochemiea* is frugivorous birds. The genus produces large, red fruit, which have been shown to be particularly attractive to birds (Bregman 1988, Carlo et al. 2007). The seeds are contained in sweet, mucilaginous pith, with seeds of *Cochemiea halei*, for example, were observed to remain stuck to paper for more than five months, a pattern of adherence that may lend itself to long range dispersal (Breslin, pers. obsv.). However, even if fruit is ingested, studies have shown that passage through the digestive tract of birds (or mammals), known as endozoochory, has no negative effect on germination, and, in fact, removes inhibitors and can lead to higher rates of germination (Fleming and Sosa 1994, Rojas-Arichiga and Vazquez-Yanes 1999). Although information on how long *Cochemiea* seed is viable is not available, seed from some *Mammillaria* species has been shown to be viable for at least eight years, in habitat (Santini and Martorell 2013). If long term seed viability is a characteristic of *Cochemiea*, this may help account for widespread dispersal across multiple habitats.

Intrinsic barriers to hybridization appear to be present in *Mammillaria* and *Cochemiea* in habitat. No intergeneric hybrids between sympatric *Mammillaria* and *Cochemiea* have been observed, and no intermediate forms are known among the taxa in *Cochemiea*, although the sterile, vegetative characters of some taxa are very similar, which makes definitely identifying intermediate forms challenging in the absence of flowers (Rebman 2019 pers. comm.). In general, members of the genera *Mammillaria* and *Cochemiea* are assumed to be obligate outcrossers, although some species do self pollinate, or occasional individuals are capable of selfing (Craig 1945, Pilbeam 2015). This combination of mostly obligate outcrossing with apparently strong barriers to hybridization and introgression may be another contributing factor to the high species diversity in the genus.

Key innovatons in *Cochemiea*?

One of the main morphological differences between *Cochemiea* and *Mammillaria/Coryphantha* is the presence of hooked spines in *Cochemiea*. Hooked spines are not universally present in *Cochemiea*- *C. halei* always has straight spines as do *C. macdougallii* and *C. conoidea*, and a few of the other taxa in *Cochemiea* are reported to have either hooked or straight spines. Hooked spines are also not always absent in *Mammillaria*- *M. senilis* Lodd. Ex Scheer in this study, for example, has hooked spines (Craig 1945). Hooked spines form as a result of layers of quickly lignifying cells having a differential rate of production, always higher on the adaxial surface (Mauseth 2006, Shlegel 2009). Maximum likelihood analysis tracing the ancestral state for hooked spines suggests that the trait evolved early in *Cochemiea*, from ancestors without hooked spines. A well-supported correlation was found between the emergence of hooked spines and the divergence time of *Cochemiea*. It may be the case that the development of hooked spines is a key innovation in *Cochemiea*, although it is not known what advantage hooked spines confer (J. Mauseth 2019 pers. comm., J. Rebman 2019 pers. comm.). Researchers have speculated that hooked spines aid in dispersal and vegetative reproduction, through attachment to animals and deposition at a distance, or that the hooks function as additional defense against herbivory (Nobel 1985). An additional speculative hypothesis is that hooks condense a higher quantity of atmospheric moisture in fog zones that then drips to the soil surface, increasing available water (Anderson 2001). Future research on hooked spines facilitating increased available water for the root zone would be particularly relevant for Baja California *Cochemiea*, as several areas of diversity along the Pacific coast feature regular fogs (Webb and Turner 2015), and the Pacific coast in particular is shown in our biogeographical reconstruction to be an important ancestral area.

Hernández-Hernández et al. (2014) found that the shift from generalist pollinated flowers to specialist pollination was one of the drivers of increased diversification in Cactaceae in general, in addition to increased aridification and decreased atmospheric CO_2 in the Late Miocene. The presumably hummingbird pollinated flowers of the five taxa in the original, narrowly circumscribed genus *Cochemiea* may represent an important innovation for that clade, but the pollination of these cacti has not been studied. Further research into the pollination syndromes of *Cochemiea* in general would shed more definite light on a possible relationship between species richness, endemism and floral traits.

Diversification rates of the Mammilloid clade

The background diversification rate for angiosperms in general is estimated to be between 0.077 and 0.089 new lineages per million years (Magallón and Sanderson 2007), although more recent studies (e.g., Bell et al. 2010, Tank 2015) have raised doubt about the usefulness or accuracy of a generalized background rate of diversification, due to evidence of repeated cycles of rapid radiation. Regardless of the agreed upon background rate, both *Cochemiea* and *Mammillaria* display high absolute rates of diversification in this study. If the background rates from Magallón and Sanderson (2007) are used for comparison, for example, *Cochemiea* conservatively (i.e., at the lower boundary of the 95% confidence interval) has a diversification rate four times the background, and the *Mammillaria* distributed along the Sonoran/Sinaloan Gulf coast and in Baja, 13 times the background rate. Arakaki et al. (2011) estimated the diversification rate of the

Mammilloid clade as a whole at 0.225 lineage/Myr, and the core cacti at 0 .232 lineage/Myr. Hernández-Hernández et al. (2014) arrived at pure birth estimates of 0.620 (stem)-0.638 (crown) for the taxa in this study. Comparatively, *Cochemiea* has a diversification rate conservatively 1.7 times Arakaki's estimate for the *Mammillaria* clade, and the regional *Mammillaria* of BC and the Sonoran/Sinaloan Gulf coast, about five times that. *Coryphantha* as sampled here, by contrast, has significantly lower diversification rates, at roughly one-tenth to one-half the rate of *Cochemiea,* with a slow-down in diversification estimated to have occurred about 3 Ma. This comparatively lower diversification rate is coincident with *Coryphantha*'s lower species richness in distributions west of the Altiplanian/Chihuahuan region and fewer taxa overall than *Mammillaria*.

Our estimates of high rates of diversification for both *Cochemiea* and the *Mammillaria* local to our study region are consistent with high species diversity and peninsular and island endemism observed in these lineages, especially in consideration of their recent dispersal to the area, complex radiations and recent divergence times.

Conclusion

Detailed multiple and mutually supportive analyses reveal rapid, geospatially complex radiations of the *Mammillaria* and *Cochemiea* clades of northwestern Mexico and the southwestern United States. *Cochemiea* is shown to have developed early, in the Cape region and perhaps initially speciated due to vicariance as a result of peninsular rifting. The drivers of high rates of diversification and endemism are likely to be geological and climate heterogeneity at various spatial and temporal scales on the BC peninsula and the surrounding region. The presence of *Cochemiea* and *Mammillaria* in every available habitat on the Baja California peninsula in particular, combined with their recent arrival to several of their current ranges, suggests a capacity for rapid adaptation to markedly novel but spatially adjacent abiotic conditions. Extensive sympatry between *Mammillaria* and *Cochemiea* as well as within *Cochemiea*, with no evidence of injtergeneric or interspecific hybridization, indicates strong reproductive barriers intrinsic to these plants; this, combined with obligate outcrossing, has probably also driven high rates of speciation. The genus *Cochemiea*, in particular, displays high species richness, a high degree of peninsular and island endemism and rapid diversification. Future research regarding the other genera in Cactaceae with high speciation and endemism on the BC peninsula will place these results in a larger context, and contribute to our understanding of the evolution and biogeography of the Cactaceae as a whole.

Chapter 4 HABITAT SUITABILITY AND PREDICTED HABITAT LOSS OF *Cochemiea halei* (Cactaceae), A THREATENED PACIFIC ISLAND ENDEMIC OF BAJA CALIFORNIA SUR

Abstract

The challenging task of quantifying and ameliorating the threats faced by rare, narrowly restricted endemic plant species in the face of the Earth's sixth mass extinction is more urgent for taxa on islands, which have an elevated extinction risk. *Cochemiea halei* is an island endemic cactus in Baja California Sur, closely related to the more widespread, peninsular species, *Cochemiea poselgeri*, and is of conservation concern, listed as vulnerable on the International Union for the Conservation of Nature Red List and as a species of special concern under Mexican federal law. *C. halei* occurs on the Pacific island archipelago of Islas Magdalena and Margarita in Bahía Magdalena, except for six individuals on the adjacent peninsula, with a known global extent of occurrence of approximately 50 km by 20 km. The oceanic islands where *C. halei* occurs are characterized by rugged terrain, with a climate moderated by the California Current system, and geology consisting mostly of ultramafic crustal rock, as opposed to the sandy plains on the adjacent peninsula. The goals of this study are to 1). understand the current suitable habitat for *C. halei* as predicted by environmental variables; 2). determine if the species is a serpentine endemic or has a facultative relationship with ultramafic soils; 3). predict future trends in the distribution of the species and the relative risk of local and global extinction of the species based on climate change scenarios. We used temperature and precipitation variables 30 arcsecond resolution and a binary classification of soil type, with multiple species distribution modeling methods, to identify important climate and soil conditions driving current habitat suitability. The occurrence of the species is found to be strongly correlated with ultramafic soils, as well as annual temperature range, the mean temperature of the warmest quarter of the year, and a biseasonal summer and winter precipitation pattern typical of the Sonoran Desert. The most important climate predictor for habitat suitability is annual temperature range, one significantly more narrow and with a cooler maximum than on the adjacent peninsula. Within its current extent of occurrence on the islands, the probability of occurrence of the species varies widely, including distinct regions of unsuitable habitat. A combination of temperature, precipitation and soil factors make it unlikely that the species will migrate to the peninsula. The best model of current suitability is used to predict possible effects of four climate change scenarios based on the best case to worst case representative concentration pathways, with projected climate data from two general circulation models, over two time periods. Under climate change, the species is predicted to undergo range contractions of from 21% to 53%, depending on the severity of climate change and duration of exposure to changing climate.

Introduction

Cactaceae are the 5th most endangered plant or animal family to be globally assessed to date by the International Union for the Conservation of Nature (Goettsch et al. 2015). The primary threats to populations of cactus species are thought to be poaching of wild populations for the horticultural trade, small scale farming and ranching, mining operations, and the effects of climate change (Anderson et al.1994, Hernández and Godínez-Álvarez 1994, Oldfield 1997, Bárcenas-Luna 2003, Godínez-Álvarez et al.

2003, Martorell and Peters 2005, Téllez-Valdés and Dávila-Aranda 2003, Ureta and Martorell 2009, Goettsch et al. 2015). Among these threats, increased risk of extinction due to climate change exposure is the least understood (Goettsch et al. 2015). This study aims to help fill this gap, using predictive modeling to anticipate the extinction risk due to current conditions and climate change impacts, faced by a threatened, island endemic cactus.

Temperature and precipitation have been shown to be strong correlates for the distribution of plant species (e.g., Guisan and Zimmerman 2000, Hawkins et al. 2003, Elith and Franklin 2013). Cacti are often narrowly adapted to specific temperature ranges, as well as highly sensitive to seasonal precipitation patterns, such as the bi-seasonal winter/summer precipitation cycles of the Sonoran Desert region, as well as longer precipitation cycles caused by shifts in the California Current and other factors (Gibson and Nobel 1986, Anderson 2001). Islands often have both thermal and precipitation differences from their nearest peninsular or continental land masses, and these factors have been shown to contribute to island endemism and increased risk to island biodiversity (Kreft et al. 2008, Humphreys 2019). Island climates are often significantly distinct from those of adjacent land masses, and, as a result, islands harbor a significant amount of plant biodiversity (e.g., Kreft et al. 2008, Kier et al. 2009), yet island ecosystems also host endemic plant species subject to a rate of extinction 500 to 1000 times higher than the background rate for continental flowering plants (Humphreys 2019).

Ultramafic soils, such as ophiolite, amphibolites, serpentine, and gabbros, predominant in the distribution of *C. halei,* have been shown to drive plant endemism (Kruckberg 1951, Kruckberg 1986, Kazakou et al. 2008, Bothe and Slomka 2017). These soils contain high proportions of heavy metals such as Nickel, Chromium and Manganese, and low quantities of plant nutrients, such as Calcium, Phosphorous and Potassium, and are toxic to most plant species. Consequently, species physiologically adapted to these soils have a competitive edge and are able to colonize areas that other plants cannot (Brady et al. 2005, Harrison et al. 2006, Anacker 2011, Barcenas-Arguello et al. 2017). To date, no studies of habitat suitability of cacti associated with ultramafic soils have been done, and the importance of this substrate to the distribution of *C. halei* is unknown.

Climate change is likely to affect the future distribution of many plant species due to shifts in temperature and precipitation (Bakkenes et al. 2002, Walther et al. 2002, Kelly and Goulden 2008, Urban 2015, Warren et al. 2018). Before 2019, there were very few studies of habitat suitability and the potential effects of climate change in Cactaceae (Téllez-Valdés and Dávila-Aranda 2003, Butler et al. 2012, Martorell et al. 2015, Albuqeurque et al. 2018). In particular, climate projections under all representative concentration pathways (RCPs) of atmospheric "greenhouse gasses" and particulates, show increased mean temperatures ranging from 1.5° C to 4.5° C globally. These temperature increases are projected to coincide with increased aridification, i.e., long term reduction of average soil moisture content, of existing deserts (Collins et al. 2013). Although cacti are adapted to arid conditions, a few prior studies have shown that they are vulnerable to projected changes in both temperature and precipitation under climate change scenarios (Téllez-Valdés and Dávila-Aranda 2003, Butler et al. 2012, Martorell et al. 2015, Albuquerque et al. 2018). The effect of climate change on the future suitable habitat of *C. halei* is unknown, and thus a focus of this study.

Our investigations in this study include identifying the environmental variables that determine the habitat suitability of *Cochemiea halei*. Abiotic correlates for the distribution of rare, narrowly restricted endemic species in general can provide important insight into suitable habitat, possible threats to the persistence of populations, and the potential effects of future climate change (Hawkins et al. 2003, Hijmans and Graham 2006, Franklin 2010, Albuquerque et al. 2011, Albuquerque et al. 2019a, Albuquerque et al. 2019b).

Our specific goals are to investigate: 1) the environmental correlates to the distribution of *C. halei*; 2) whether populations of *C. halei* are more likely to occur on ultramafic soil; 3) whether the species is likely to colonize the peninsula, or if it is more likely to remain isolated on the islands; and 4) the effects of varying levels of climate change on the future range and as a contributor to the risk of local and global extinction of *C. halei* over the next 30 to 50 years. This study will help provide background for urgently needed future analyses of the specific risks faced by narrowly distributed, endemic and endangered cacti.

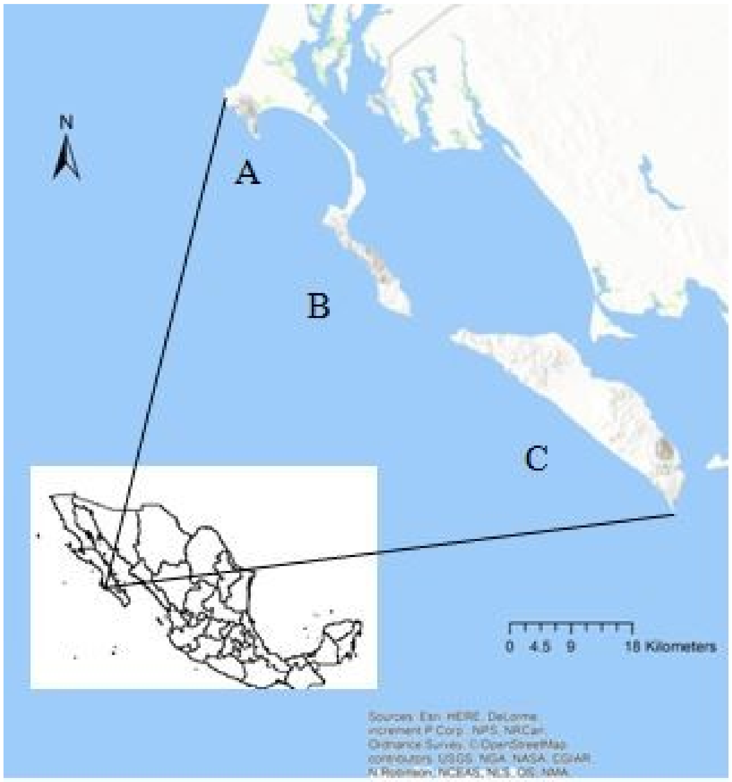
Methods and Materials

The study site

Bahía Magdalena is an ecologically significant embayment along the Pacific coast of the southern Baja California peninsula (Bizzarro 2008). In contrast to the adjacent coastal plains, the island archipelago in Bahía Magdalena is part of the North American cordillera, and has mountainous, rocky terrain as a result (Rangin 1978, Blake et al. 1984, Sedlock 1993) (Fig. 4-1). The islands range in elevation from sea level along the bay coastline to nearly 1000 m. (Blake 1984). Topographical variation on the islands creates heterogeneous terrain, including flats, sand dunes, gravel coastlines and highly eroded arroyos. West-facing cliffs drop to the Pacific, at angles as steep as 90°. These cliffs are predominantly exposed ultramafic rock and gravel (Rangin 1978, Blake et al. 1984, Breslin, pers. obvs.).

The main soil mineralogical composition is serpentine rock and its eroded derivatives or non-ultramafic basalt and sand (Rangin 1978, Blake et al. 1984, Sedlock 1993). The mountainous ridges consist of ultramafic, oceanic crustal rock formed through tectonic plate collisions estimated to have occurred from the Late Jurassic to the Late Cretaceous periods (Sedlock 1993, Zaitsev et al. 2007).

Climate data from WorldClim v. 2.0 for the Bahía Magdalena region shows biseasonal summer and winter precipitation, with autumn and spring being the dry months of the year (Hijmans 2005, Fick and Hijmans 2017). The moderating effects of the California Current system create narrower diurnal and annual temperature ranges, increased precipitation and cooler seasonal averages for the islands than for the adjacent peninsula (Hickey 1979, Bakun 1983, Robinson et al. 2007, Bizzarro 2008, Ulanski 2016). From 2010 to 2018, 13 tropical storms or hurricanes occurred in the study region, with the majority occurring in the hottest month, September (National Hurricane Center; Hurricane Research Division; Central Pacific Hurricane Center).



Sources: Esri, HERE, DeLorme, increment P Corp., NPS, NRCan, Ordnance Survey, © OpenStreetMap contributors, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA

Figure 4-1. Map of the study region showing the islands and location of Bahía Magdalena. The islands in Bahía Magdalena. (A) Cabo San Lazaro; (B) Isla Magdalena; (C) Isla Margarita. Basemap copyright ArcGIS software by Esri. Copyright Esri, inc. All rights reserved.

The vegetation of the Bahía Magdalena region features 18 endemic angiosperm taxa; the endemic cacti represent 33% of the plant endemism in the area (León de la Luz et al 2015). The area is recognized as one of nine regions of high plant endemism in Baja California (Riemann and Ezcurra 2007). The primary vegetative regime is fog crassicaulescent and sarcocaulescent scrub, that is, a combination of leaf and stem succulents, such as the endemic *Agave margaritae* Brandegee and scrub vegetation, generally less than 8 m high (León de la Luz et al. 2015).

Cochemiea halei (K. Brandegee) Walton, the study species, is a mat-forming stem succulent with straight spines and presumably hummingbird pollinated flowers (Craig 1945, Pilbeam 1999) (Fig. 4-2). *C. halei* is of conservation concern, assessed as vulnerable by the IUCN, and protected by Mexican law (IUCN, SEMARNAT). The factors leading to its classification as vulnerable include the narrow geographic range, the low overall population size, and evidence of declining populations. No formal studies of its population viability or quantified risk of extinction have been conducted previously, however (cf. Chapter 5).

Figure 4-2. A flowering specimen of *Cochemiea halei* in habitat on Isla Magdalena.

Survey methods

Occurrence data for *Cochemiea halei* was gathered over four years and eight surveys, in both winter and spring. Random points within the smallest convex polygon around Isla Magdalena and Isla Santa Margarita were generated using ArcMap v. 10.6.1 (ESRI 2019). The random points were used as centers of survey transects (Elzinga et al. 1998, Bonham 2013). In addition to occurrence data, we recorded soil type data and other topographical information, and the latitude and longitude of occurrences was marked using a handheld GPS device (eTrex 30X, Garmin Ltd. Olathe KS). A different surveying technique was employed on Cabo San Lazaro due to the much smaller area of that land mass. At that site, a belt transect method was used, with individuals counted within a 300 m radius along a 3 km segment that covered the entire habitat of *C. halei* (Bonham 2013). The only known peninsular population, with six individuals, was included in all analyses.

Presence points were spatially thinned to a minimum separation of 1 km to reduce sampling bias (Tessarolo et al. 2014, Stolar and Neilsen 2015). A point raster layer of presence/absence locations was generated with 1 km grid squares and multiple records per square were reduced to at most a single record. Point pattern analysis was performed using Ripley's K statistic to measure the degree of spatial correlation of presence/absence records (Baddely 2008).

Environmental variables

To investigate correlations between the distribution of *Cochemiea halei* and its environment, we chose 19 energy and precipitation variables from WorldClim V. 2.0, with averages from 1970 to 2000, at 30 arcsec resolution (a linear distance of approximately 900 m at the equator) (Fick and Hijmans 2017). These variables represent mean annual patterns in temperature and precipitation, annual ranges (seasonality), and extremes or limiting conditions such as the temperature or precipitation of the warmest or coldest quarter (Fick and Hijmans 2017).

Soil type was determined during field surveys using a Munsell soil identification color scale (Munsell Color, Grand Rapids, MI), categorizing soils into ultramafic (2.5Y hue with various color values and chroma) versus either “non-serpentine” (approximately 7.5YR to 10YR) or sand (Roberts 1980). A dense sampling of occurrences of *C. halei* with soil type data was performed to reduce error when interpolating for missing values (Carl and Kühn 2007, Dormann et al. 2007). The soil type data from the field was mapped onto zones of ultramafic versus non-ultramafic substrate, as indicated in the geological map of Isla Magdalena and Isla Margarita by Rangin (1978). The final soil type raster was generated using inverse distance weighted interpolation (Goncalves 2006, Grunwald 2009) in the package gstat in R (Pebesma 2004). The resulting raster was evaluated for degree of error using root mean squared error and 5-fold cross-validation (Goncalves 2006).

Four representative concentration pathways (RCPs) were used in climate change projections: 2.6, representing the best-case future concentration of carbon in the atmosphere, through intermediate levels 4.5 and 6.0, to the worst-case scenario of 8.5, as outlined in the Intergovernmental Panel on Climate Change’s Fifth Assessment Report (IPCC 2013, Liddicoat et al. 2013). The climate data itself was derived from two general circulation models (GCMs). The GCMs used were the Hadley Center Global Environmental Model version 2-ES (HadGEM2-ES) and the Community Climate System Model v. 4 (CCSM4), both of which are frequently used in studies of climate change effects on habitat suitability (e.g., Buison et al. 2010, Bellouin et al. 2011, McQuillan and Rice 2015). The HadGEM2-ES model scenarios include projections of changes in ocean temperature and sea ice, and are especially recommended for use in predicting changes in coastal habitat (Collins et al. 2008, Caesar et al. 2013).

Variable preparation

The reduction of multicollinearity for all variables was performed by constructing a correlation matrix and performing hierarchical cluster analysis (*hclust* R core stats v. 3.2.1), which groups variables according to their mutually related correlations (Benito et al. 2013, Dormann et al. 2013, Sarstedt and Mooi 2014, Albuquerque et al. 2018). A cutoff of 0.5 for Pearson's correlation index was used; all variables correlated higher than 0.5 were discarded (Albuquerque et al. 2018). Biserial correlation analysis, with variables correlated to presence/absence data for *Cochemiea halei*, was performed for all variables below 0.5 (Kraemer 2006, Stolar and Nielsen 2015, Albuquerque et al. 2018). From each cluster of correlated variables as derived from the hierarchical cluster analysis, the variable with the highest correlation to the distribution of *C. halei* was chosen for use in modeling.

Modeling methods

Three methods were used for building models: boosted regression trees (BRT), generalized linear models of the binomial family (GLM) and maximum entropy (Maxent) (Hijmans and Graham 2006, Elith et al. 2008, Franklin 2010). Models used field survey presence and 200 randomly generated pseudoabsence background points (Franklin 1995, Franklin 2010, Elith et al 2010, Elith and Franklin 2013, Phillips and Elith 2013, Guillera-Arriota 2015).

BRT is an iterative machine learning optimization method, in which the deviance residuals from a prior decision tree are used as the data for the next step (called "boosting"); the decision tree building process continues until residual deviance is no longer decreased by iterations (De'ath 2007, Franklin and Miller 2010). Decision trees, the underlying algorithm of BRT, also known as classification and regression trees, perform well with both continuous and categorical variables, and, unlike with GLM, for example, they are robust to a lack of independence among predictors (De'ath 2007, Elith and Leathwick 2009, Elith and Leathwick 2017, Albuquerque 2018).

GLM is a well known regression method that uses maximum likelihood as the measure of the contribution of a variable to a prediction of the "state" of a dependent variable, in this case the binary outcome of presence/absence (Nelder and Wedderburn 1972, Guisan et al. 2002).

Maximum entropy (Maxent) is a machine learning method that employs multinomial logistic regression to estimate the probability of the distribution of a species according to the "maximum entropy" of the distribution, i.e., the most uniform distribution of a species possible given the limits imposed by the predictor variables (Phillips et al. 2006, Elith et al. 2011, Phillips et al. 2017).

For BRT models, evaluation of model performance included measures of residual deviance, k-fold cross-validation and the area under the receiver operator characteristic curve (AUC) (De'ath 2007, Elith and Leathwick 2008). GLM model performance was evaluated with AUC and the adjusted D^2 statistic (a measure of the difference between null deviance and model deviance adjusted for degrees of freedom) and Akaike information criterion (Guisan et al. 2002, Franklin and Miller 2009). Maxent models were evaluated by comparative training and test AUC, and omission on test and training samples against random prediction (specificity-sensitivity curves) (Hijmans 2012, Elith and Leathwick 2017). For each modeling method with each set of variables, a minimum of 50 models were generated and evaluated. The best performing model was selected using the above criteria and is presented below.

Model analysis

Given that the predominant soil type on Isla Magdalena is ultramafic, a soil known to constrain plant distributions, habitat suitability models were generated, in the three methods used, with soil type and without soil type, in order to quantify the importance of soil type as a possible constraint on the distribution of *Cochemiea halei*.

For predictions of current habitat suitability, maps showing the predicted probabilities of presence or absence are presented for the best model with soil type and without soil type. Plots of the partial response of *C. halei* to each of the environmental variables and the proportional contribution of each variable to model performance are also presented.

Climate change scenarios were projected using the best predictive model for current habitat suitability, for the periods 2009-2049 and 2009-2069. Current predicted suitable habitat was subtracted from composite binary presence/absence maps using both general circulation models (GCM's), with range differences counted as "contractions" if a current presence was projected as a future absence, "refuge" if current presences remained presences, and "expansion" if current unsuitable habitat was projected as suitable in the future (Elith et al. 2010, Hatten 2016, Albuquerque et al. 2018). Box plots showing the two most significant environmental predictors and their influence on presence, absence, and predicted range expansion and contraction are presented. The proportion of expansion or contraction of future ranges relative to current habitat suitability were calculated and are shown. Prediction maps are also presented with visualizations of projected expansion and contraction.

Results

Survey results

A total of 1227 records were recorded in the field, with accompanying soil type. After separating occurrence points by a minimum distance of 1 km and removing duplicate records, the occurrence and randomly generated pseudoabsence data set used in modeling consisted of 44 presences and 207 pseudoabsences.

Variable selection

The variables that were below the 0.5 correlation threshold in the cluster analysis but most strongly correlated to the occurrence of *Cochemiea halei* in the biserial correlation analysis were annual temperature range, mean temperature of the warmest quarter, precipitation of the warmest quarter and precipitation of the coldest quarter. These variables, along with soil type, were used in the species distribution models. Annual temperature range differs on the islands versus the peninsula, with island temperature ranges of approximately 20° C and the peninsular range 10° wider at 30° C. Mean temperature of the warmest quarter ranges from 24° C in the northwestern region of Isla Magdalena to approximately 30° C at the lowest elevation in the center of Isla Margarita and on the peninsula. Precipitation during the warmest quarter ranges from 20–40 mm on the islands, except for the highest elevations on Isla Margarita at 70 mm. The majority of peninsular precipitation is also at 70 mm. Precipitation during the coldest quarter is from 20–30 mm on the islands, to slightly over 40 mm on the peninsula (Fig. 4-3).

Modeling results

The three modeling methods of generalized linear models, boosted regression trees and maximum entropy all generated fair to excellent results, as measured by AUC values, with values ranging from 0.80–0.88. Boosted regression trees (BRT) produced the best models, as measured by AUC values, 10-fold cross-validation, model deviance versus null deviance and relevance of information regarding predictors and their contributions to the models. The model results presented below are derived from BRT analysis. The first model presented here is a model that included soil type, which was the best performing BRT model. The map of predicted suitable habitat shows a low probability of colonization of the peninsula, especially to the east of localized, immediately adjacent regions on the western edge of Bahía Magdalena. The highest predicted probabilities on the peninsula are near the town of Puerto San Carlos, where the only known peninsular population occurs. (Fig. 4-4).

Annual temperature range, a simple subtraction of the annual high temperature minues the annual low temperature, has the highest marginal response, which shows a sudden drop in the suitability of habitat for *Cochemiea halei* under an annual temperature range greater than approximately 21.5° C. The optimal mean temperature of the warmest quarter is ranges from 24° C to 26° C, with an increased contribution to occurrence at 26° C, but then a sharp drop off , with temperatures above approximate 26.5° C negatively correlated to occurrence. Precipitation of the warmest quarter is positively correlated with

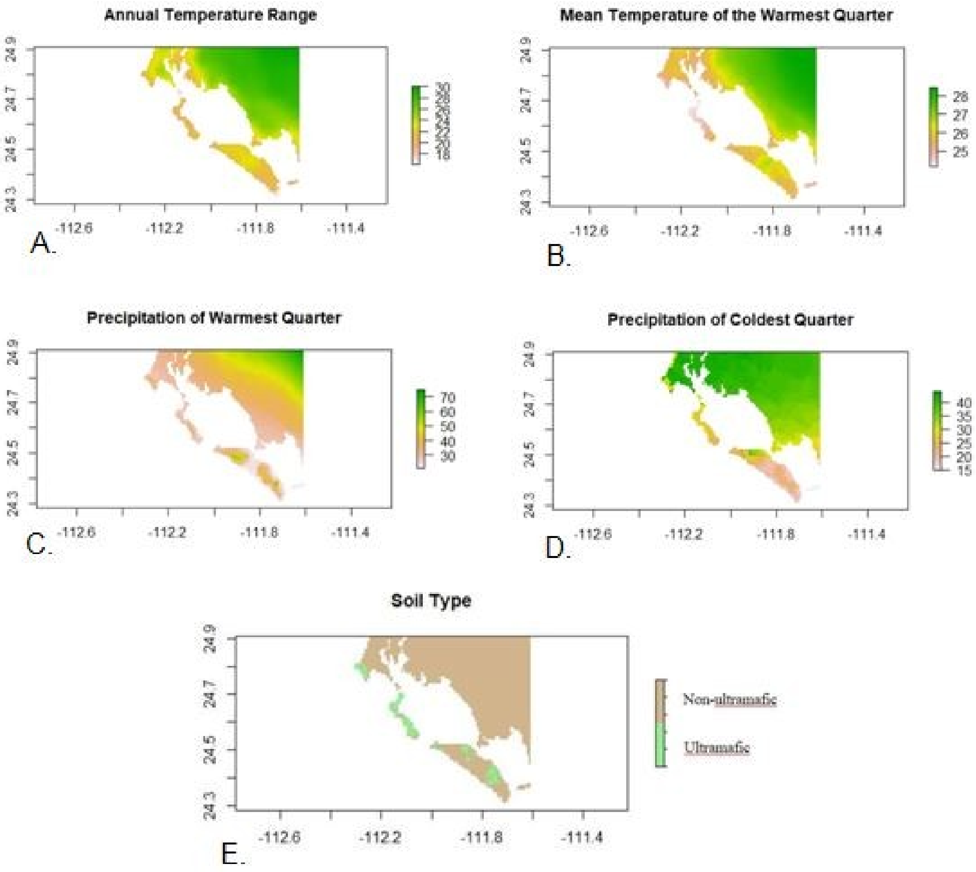


Figure 4-3. Raster maps of the climate and soil variables used in modeling the current suitable habitat of *Cochemiea halei.* (A) annual temperature range;(B) mean temperature of the warmest quarter of the year, July-September; (C) precipitation of the warmest quarter of the year, July–September; (D) precipitation of the coldest quarter of the year, December–February, and (E) soil type. Light green areas are ultramafic soils and tan are all other soil types, including basalt and the sand of the Magdalena Plains on the peninsula. Temperature variables are in degrees C, and precipitation in mm.

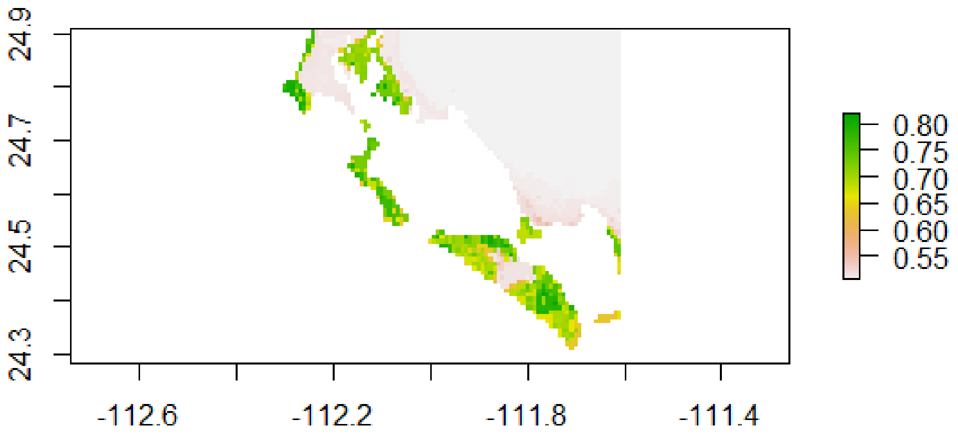


Figure 4-4. Prediction map of currently suitable habitat for *Cochemiea halei*, based on boosted regression tree analysis. The map is of predictions of habitat suitability, on a scale of zero (transparent) to 1 (dark green). The model predictions derive from a BRT method, using WorldClim V. 2.0 data at 30 arcsec resolution. 44 presences and 207 pseudoabsences were used. The following variables were used: annual temperature range, the mean temperature of the warmest quarter (July-September), precipitation of the warmest quarter (July-September), precipitation of the coldest quarter (December-February), and soil type. The model fitted 4950 trees, with a 10-fold cross-validated AUC of 0.88. The parameters used for the boosted regression tree analysis were a tree complexity of 2, a learning rate of 0 .0007, bag fraction of 0 .7 and a step size of 25.

occurrence below 30 mm, but negatively correlated above 30 mm. Precipitation of the coldest quarter shows approximately the same reponse of precipitation of the warmest quarter.

Annual temperature range, a simple subtraction of the annual high temperature minues the annual low temperature, has the highest marginal response, which shows a sudden drop in the suitability of habitat for *Cochemiea halei* under an annual temperature range greater than approximately 21.5° C. The optimal mean temperature of the warmest quarter is ranges from 24° C to 26° C, with an increased contribution to occurrence at 26° C, but then a sharp drop off , with temperatures above approximate 26.5° C negatively correlated to occurrence. Precipitation of the warmest quarter below 30 mm is positively correlated with occurrence, but negatively correlated above 30 mm. Precipitation of the coldest quarter shows approximately the same response of precipitation of the warmest quarter (Fig. 4-5).

The percent relative contributions for each variable to the predictive ability of the model described above show that the most significant predictor is annual temperature range, accounting for nearly 66% of model performance. Thermal energy is a strong predictor of suitable habitat, with the top two temperature predictors accounting for 78.3% of model performance (Fig.4-6).

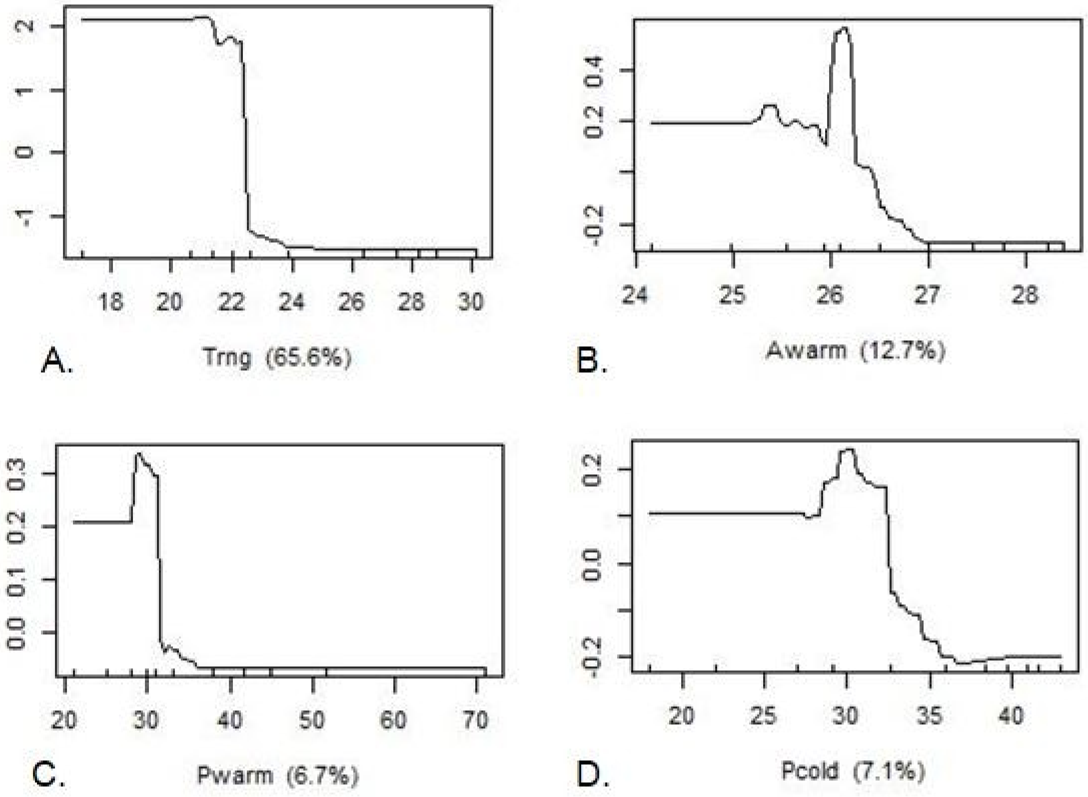


Figure 4-5. Partial response of *Cochemiea halei* to the climate variables used in predicting current suitable habitat. The plots show the marginal response of *C. halei* to each variable. The variables are (A) annual temperature range, (B) average temperature of the warmest quarter, (C) precipitation of the warmest quarter and (D) precipitation of the coldest quarter. The *y*-axis for each plot is on a logit scale, showing the relative impact of values of the variable on the probability of occurrence. The *x*-axis for the temperature variables, A and B, is in degrees C. Precipitation variables, C and D, are in mm. The small tick marks along the *x*-axis in each plot demarcate the deciles of the data.

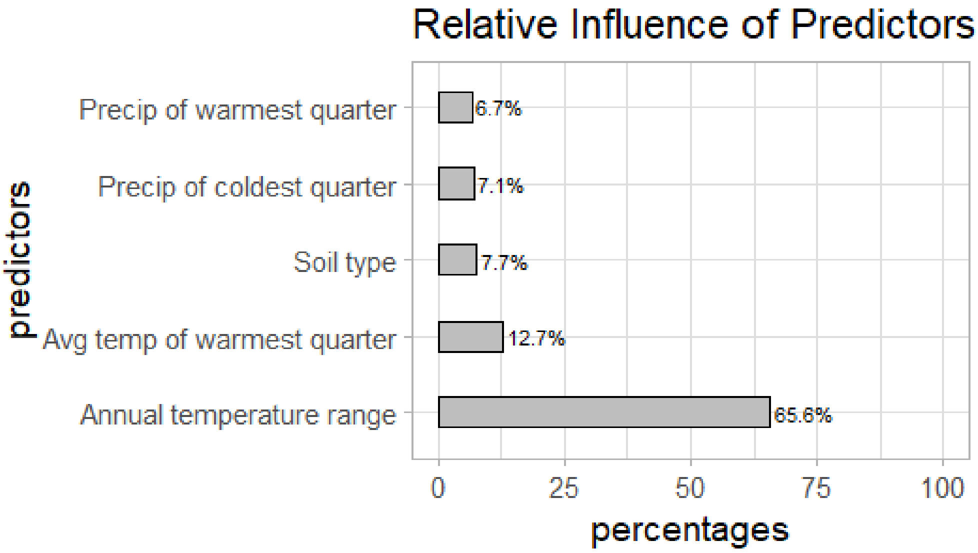


Figure 4-6. The percent influence of each predictor used in boosted regression tree modeling of the current suitable habitat of *Cochemiea haleii.* Percent influence: annual temperature range 65.6%; average temperature of the warmest quarter 12.7%; soil type 7.7%, precipitation of the coldest quarter (December-February) 7.1%, and precipitation of the warmest quarter (July-September) 6.7%.

In order to gauge the impact of soil type on the habitat suitability of *C. halei*, a model was created with the same predictor variables as the above model, but without soil type. The habitat suitability map without soil type shows a higher probability of occurrence on the peninsula, where ultramafic soils do not occur. Higher suitability is also predicted within the islands themselves overall, with a higher saturation in general of suitable habitat. Suitable habitat is also predicted on some pure sand features, such as the sand that connects Isla Magdalena with Cabo San Lazaro. There is also a higher predicted probability of occurrence on basalt and non-ultramafic soil types on the islands. The low, sandy trough in the middle of Isla Margarita, however, remains an area of low suitability, as does the peninsular region to the east of the small footholds predicted for *C. halei*. The 10-fold cross-validated AUC of this model was 0.85, slightly lower than the model with soil type (Fig. 4-7).

The effects of climate change on the range of *Cochemiea halei*

For all projections, loss of between 21%–53% of current suitable habitat is predicted for the species. In the case of the lower representative concentration pathways (RCPs), range contraction is partially offset by expansion into the previously unsuitable habitat. As the climate change scenarios increase in RCP, especially over the longer time period to 2070, expansion is reduced significantly. (Table 4-1).

The range maps showing projected future areas of contraction and expansion for *C. halei* indicate the greatest potential loss of habitat is on Isla Margarita, with regions on that island accounting for 40% to 65% of the total contraction. Only two scenarios predict expansion to the peninsula under the effects of climate change, and in both cases, the predicted new suitable habitat is an isolated patch (Figs. 4-8 and 4-9).

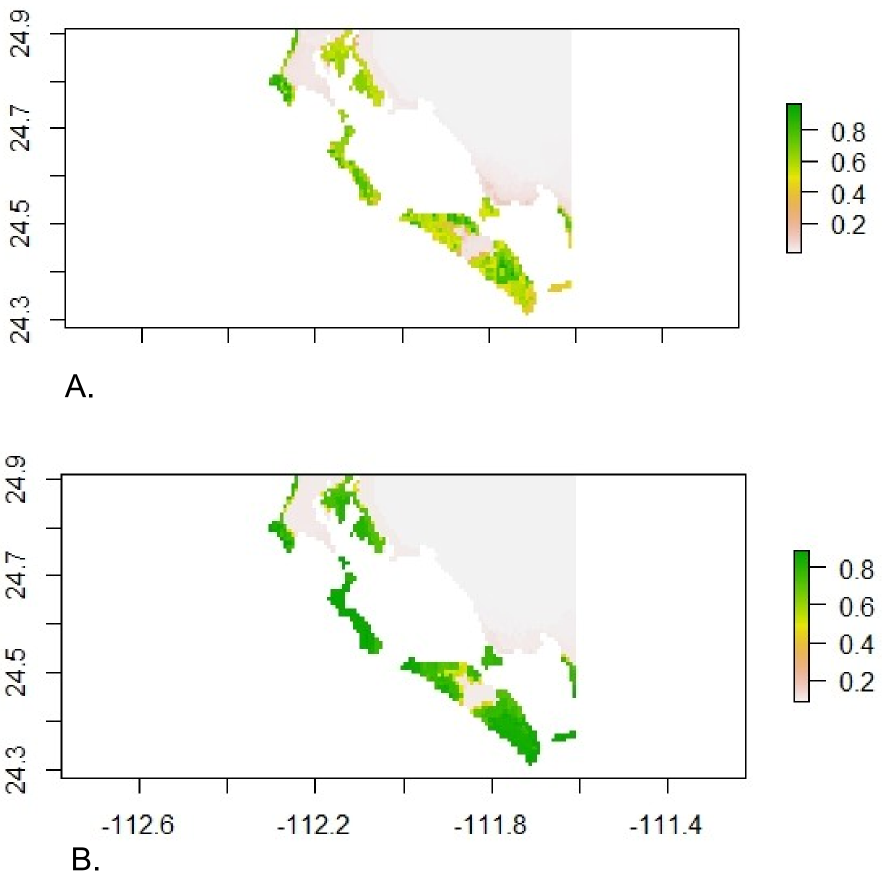


Figure 4-7. Comparison of maps of predictions of current suitable habitat for *Cochemiea halei*, resulting from including soil type and not including soil type in modeling. (A). the prediction map resulting from the best BRT model with soil type, the same results shown in Fig. 4. (B). the map from the best BRT without soil type. Variables are identical in both models except for omission of soil type in model B: annual temperature range, the mean temperature of the warmest quarter (July-September), precipitation of the warmest quarter (July-September), and precipitation of the coldest quarter (December-February). The best model without soil type fitted 2270 trees, with a 10-fold cross-validated AUC of 0.85. The parameters used for the boosted regression tree analysis were a tree complexity of 1, a learning rate of 0.0007, bag fraction of 0.7 and a step size of 15.

Table 4-1. Percent expansion, contraction and net suitable habitat loss for *Cochemiea halei* predicted for two time periods and multiple climate change scenarios.

Time Period	RCP	expansion	contraction	net habitat loss
2050	2.6	19%	-46%	-27%
	4.5	10%	-48%	-38%
	6.0	14%	-47%	-33%
	8.5	25%	-52%	-27%
2070	2.6	29%	-50%	-21%
	4.5	5%	-50%	-45%
	6.0	6%	-50%	-44%
	8.5	2%	-55%	-53%

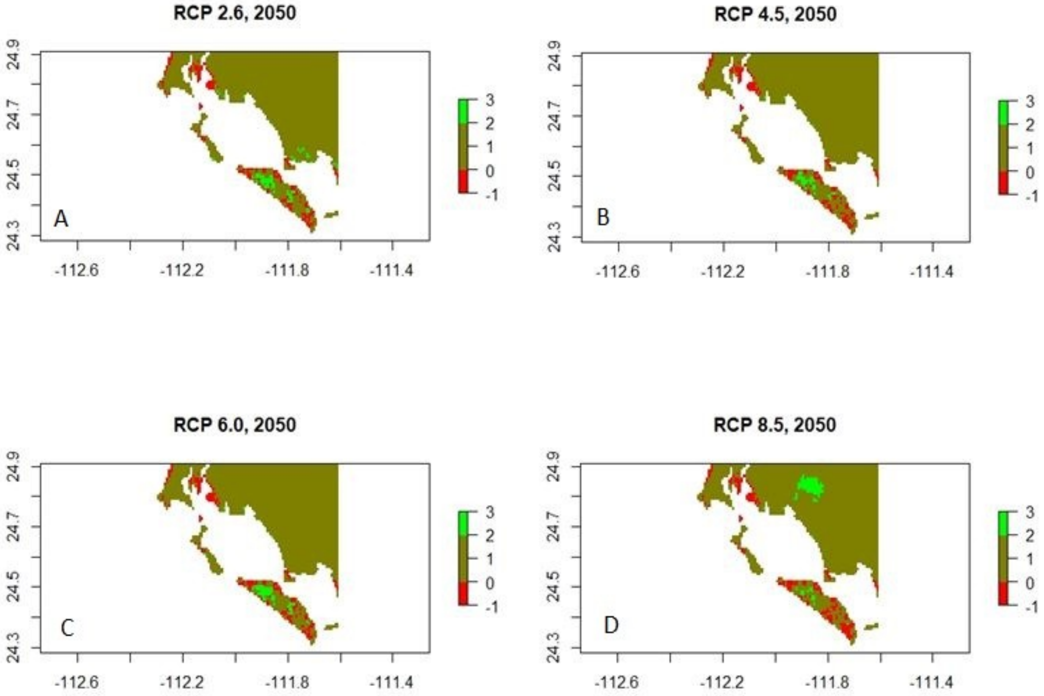


Figure 4-8. Predicted expansion and contraction of the range of *Cochmeia halei* by the year 2050, under four representative concentration pathway scenarios. Light green areas represent projected areas of range expansion (from 2 to 3 on the scale), red areas represent projected areas of range contraction (from 0 to -1 on the scale). Increasing representative concentration pathways (RCP) are indicated at the top of each map; increased RCP corresponds to increased severity of climate change exposure. (A) RCP 2.6; (B) RCP 4.5; (C) RCP 6.0 and, (D) RCP 8.5.

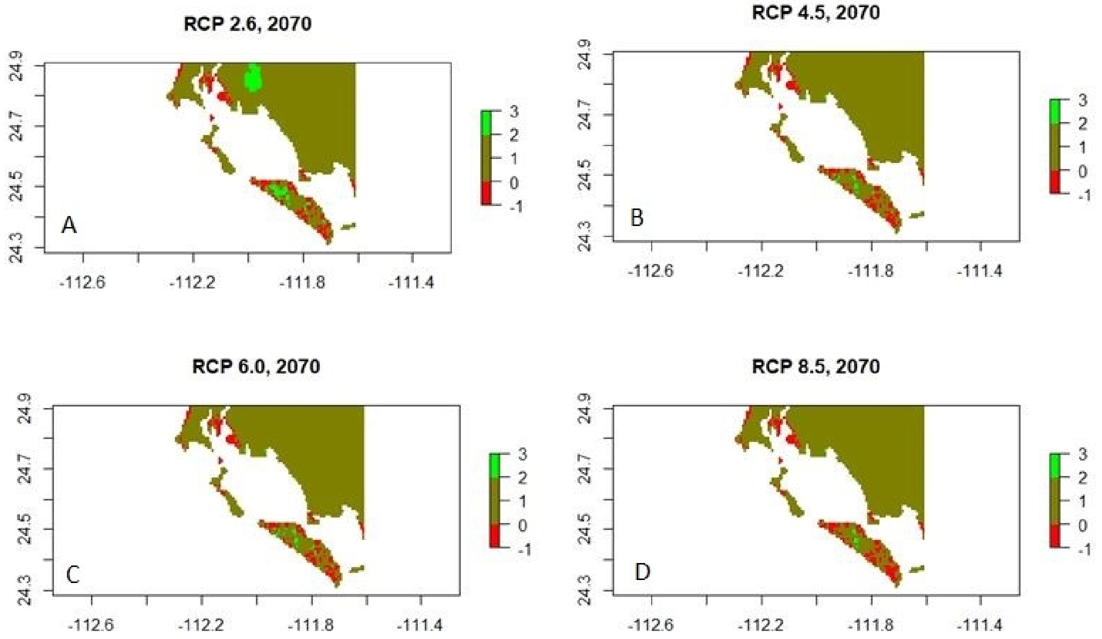


Figure 4-9. Predicted expansion and contraction of the range of *Cochmeia halei* by the year 2070, under four representative concentration pathway scenarios. Light green areas represent projected areas of range expansion (from 2 to 3 on the scale), red areas represent projected areas of range contraction (from 0 to -1 on the scale). Increasing representative concentration pathways (RCP) are indicated at the top of each map; increased RCP corresponds to increased severity of climate change exposure. (A) RCP 2.6; (B) RCP 4.5; (C) RCP 6.0 and (D) RCP 8.5.

Boxplots of the effect of the two most important predictors, annual temperature range and mean temperature of the warmest quarter, on future habitat suitability indicate significant changes for all climate change projections to 2070. The greater variability of annual temperature range for range contraction areas is consistent with the species having more suitable habitat within a narrower temperature range. The significantly higher mean temperatures of the warmest quarter for all projected future areas also contribute tohabitat loss. Predicted areas of expansion also feature higher temperatures, which is a result of temperatures across the study site increasing due to climate change. (Fig. 4-10).

Discussion

We investigated the effects of environmental and soil variables on the distribution of Cochemiea halei, as well as the possible impacts of climate change, using species distribution models. Our results show significant factors affecting the current distribution of the species and potential threats to the persistence of the species in its current geographic location.

The island endemism of *Cochemiea halei* is strongly correlated with both topographical and climate effects. The island archipelago in Bahía Magdalena, the primary suitable habitat for *C. halei*, has significantly different soil and climate from the nearby peninsula. These contrasting conditions are similar in other island habitats near coastal areas along the Pacific Ocean, where conditions are significantly different even a short distance inland (Reimann and Ezcurra 2005, Bizzarro 2008, Ratay et al. 2014).

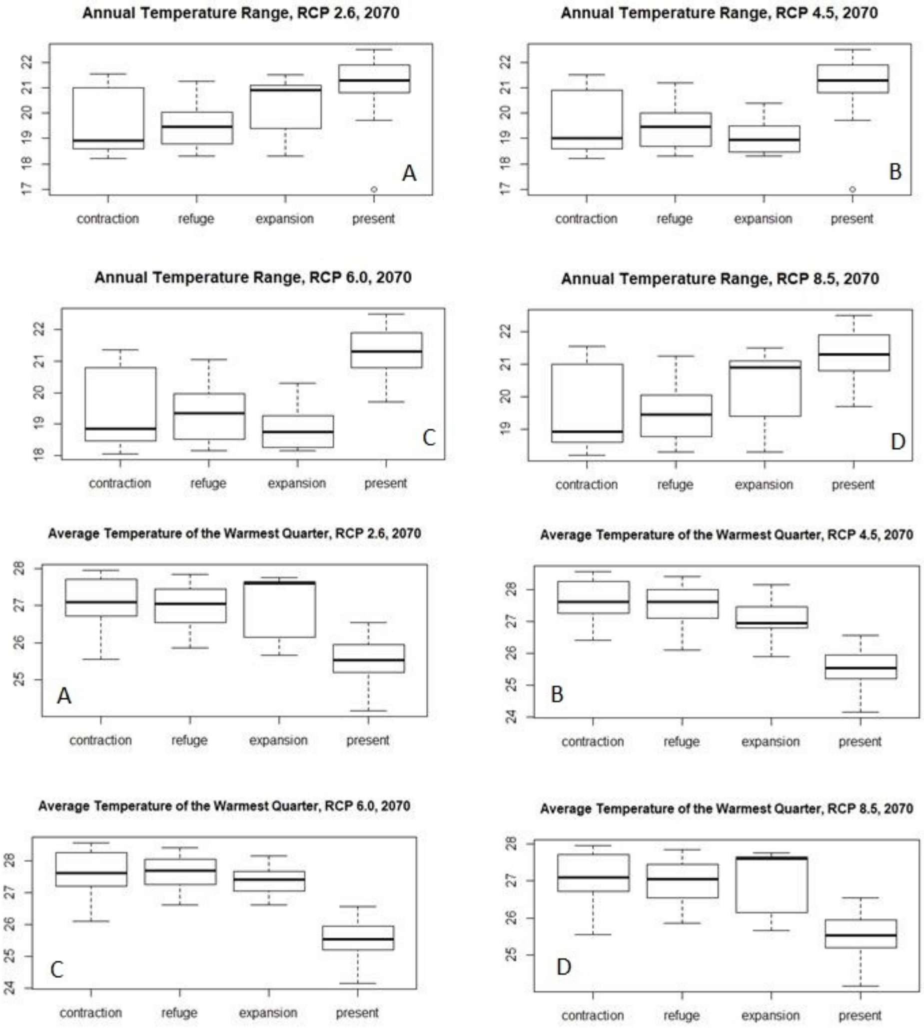


Figure 4-10. Boxplots showing the effect of the two most informative climate variables on the expansion, refuge, and contraction of the range of *Cochemiea halei*, based on four representative concentration pathway scenarios. Each box plot shows the range, 1st quartile, median and 3rd quartile of annual temperature ranges and average temperature of the warmest quarter for each type of predicted future habitat: contraction, refuge, expansion and the present habitat. The *y*-axes are degrees C. All data is from the projections to 2070. (A): RCP 2.6, (B): RCP 4.5, (C): RCP 6.0, (D): RCP 8.5

Cochemiea halei appears to occupy a narrow range of temperature and precipitation correlates. The moderating temperature effects of the California current (Hickey 1979, Huyer 1983, Bakun 1990, Robinson et al. 2007, Ulanski 2016) appear to be important to habitat suitability for the species. The two most influential climate variables in the best model were annual temperature range and the average temperature of the warmest quarter, accounting for approximately 73% of the model's predictive power. Both of these variables show significantly lower values on the islands than on the peninsula, patterns typical of coastal areas moderated by the upwelling of the California current, especially in summer (Bakun 1990). The temperature range on the islands is approximately 10° C narrower than on the peninsula, and the mean temperature of the warmest quarter is 4° C cooler. The bi-seasonal precipitation patterns of the Sonoran Desert region (Shreve and Wiggins 1964) are represented by the influence on model performance of the precipitation of the warmest and coldest quarters. However, precipitation is lower on the islands than inland, during both seasons, with the most significant differences occurring during the warmest quarter. These so-called "microclimate" effects have been shown to drive endemism (Hijmans and Graham 2006, Gogol-Prokurat 2011, Humphreys 2019). With the highest probability of suitable habitat predicted to be within a relatively narrow band of thermal and precipitation parameters, *C. halei* is an example of a species that has a highly localized, well-defined climate response.

In addition to strong climate influences on the current distribution of *Cochemiea* halei, soil type plays an important role. Narrowly restricted endemic plant species, including cacti, have been shown to be strongly dependent on soil types for habitat suitability (Kruckberg 1951, Kruckberg 1985, Kruckberg 1986, Harrison 2006). Several studies of plant distributions have determined the importance of ultramafic soils in particular as a driver of plant endemism (e.g., Kruckberg 1951, Kruckberg 1986, Kazakou et al. 2008, Bothe and Slomka 2017). While *C. halei* does not appear to be an obligate endemic to ultramafic soils, the species is more likely to occur on those soil types, with 60% of occurrences on ultramafic soil. This is similar to other species in the Cactaceae that occur on ultramafic soils, in particular on the islands of Cuba and Puerto Rico (Reyes-Fornet et al. 2019). Obligate and facultative adaptations to ultramafic soils have been shown to provide a competitive advantage for many plant species (Brady et al. 2005, Harrison et al. 2006, Anacker 2011). The model incorporating soil type had stronger predictive performance, and indicated a more fragmented, lower habitat suitability for areas in our surveys where population density was low, suggesting that ultramafic soils are an important constraint on the distribution of the species.

Cochemiea halei's observed establishment on virtually unweathered ultramafic rock and exposed gravel, in addition to lower precipitation on the islands than on the peninsula, suggest that the species is adapted to evaporation of soil moisture and drier conditions, a common characteristic of cacti distributed in rocky environments (Gibson and Nobel 1986). In general, *C. halei* appears to favor cooler, drier habitat, on ultramafic rock and soil, with a moderated annual temperature range, a suite of abiotic predictors that characterize the island habitat in contrast to the nearby peninsula.

Consequently, *Cochemiea halei* is not likely to migrate to the peninsula except for small foothold regions along the peninsular shore. This characterizes *C. halei* as a "stranded" endemic, making its persistence more vulnerable to changes in climate

(Crawford and Stuessy 1997, Cowie and Holland 2006, Stuessy et al. 2014). The only known peninsular population of *C. halei* consists of approximately six individuals limited to a patch of sand measuring 150 m^2. At that site, there is no sign of dispersal in the surrounding area, in spite of the plants being large, seed-bearing and apparently well-established (Gorelick 2007, Breslin pers. obvs.).

The suitable habitat for *Cochemiea halei* is a patchwork of sites even within its narrow range on the islands. Major geographical distinctions within the islands that are illustrated on the prediction map from the model with the best predictive ability (Fig. 4) include two distinct regions on Isla Margarita, zones of less suitable habitat on Isla Magdalena, and a narrow zone of suitability at Cabo San Lazaro, with few areas of on-the-ground connectivity between suitable habitats. Endemic plant species often occur in fragmented habitat with geographical barriers and low connectivity between sites (Rabinowitz 1981, Kotliar and Wiens 1990). As a narrowly restricted endemic, essentially stranded on the islands, this species is at increased risk for stochastic environmental, demographic and genetic setbacks (Ellstrand and Ellam 1993, Lande 1993, Menges 1992, Matthies et al. 2004, Melbourne and Hastings 2008, Mubayi et al. 2019). Even without the impacts of climate change exposure, the species appears to be at elevated risk for local extinction events, population bottlenecks and increased fragmentation.

Climate change

Future climate change scenarios indicate a contraction of *Cochemiea halei*'s overall range of 21% to 53%, depending on the severity of climate change and the length of time the species is exposed to climate change effects. The range contraction reduces suitable habitat on the islands, and the species is unlikely to expand to the peninsula within the climate change conditions and time periods projected here. The unique adaptations of narrowly distributed endemic plant species also make them vulnerable to changing climate conditions, as those adaptations are often in response to significantly different local climates or soil types that are unsuitable for related species (Damschen et al. 2012).

Specifically, each of the climate change scenarios projected in this study indicates a widening of the annual temperature range on the islands, which is significantly correlated with the range contraction. The areas of predicted contraction under all scenarios are lower elevation, mostly bayside, leeward flats. The areas of expansion are mostly into the higher elevation ridges, especially on Isla Margarita. But the opportunity to expand into these higher elevation locales is greatly reduced as climate change becomes more severe, or persists for a longer time period.

Projections under all climate change scenarios are for a higher mean temperature of the warmest quarter, ranging from approximately 3° C to as high as 6° C. Precipitation of the warmest and coldest quarters is projected to decrease by from 10 mm to 15 mm for regions of predicted range contraction. The wider thermal span and the warmer mean temperature from July–September, are factors that, along with reduced precipitation, will contribute to range contraction, driven by hotter, drier climate. Predicted range contractions are consistent with *Cochemiea halei*'s narrow adaptation to an island microclimate.

Conclusion

For the first time, temperature and precipitation correlates are identified that drive the fragmented, highly restricted distribution of an island endemic, vulnerable cactus. We used multiple modeling methods to determine the correlations between topographical and climate variables and the habitat suitability of *Cochemiea halei*, a little-studied, largely island restricted cactus. Our results support the following conclusions: (1) both the moderating effects of Pacific coastal island climate and ultramafic soils unique to the islands strongly determine suitable habitat, which is fragmented, (2) the species is unlikely to disperse to the peninsula, (3) the species has a facultative but not obligate relationship with ultramafic soils, and (4) climate change in all scenarios is likely to contract the range of the species, as a result of greater variability in annual temperature range, higher mean temperatures in the summer and reduced precipitation. Our findings indicate that this narrowly restricted endemic cactus is at increased risk of extinction, and populations should be carefully monitored over at least the next 50 years.

Chapter 5 POPULATION VIABILITY ANALYSIS OF THE ENDANGERED ISLAND ENDEMIC *Cochemiea halei* (Cactaceae): HABITAT SPECIFIC MATRIX POPULATION MODELS AND STOCHASTIC SCENARIOS

Abstract

A species of conservation concern, the island endemic cactus *Cochemiea halei* has unknown demographics and its population dynamics have never been quantitatively studied. The species has been assessed by the International Union for the Conservation of Nature as vulnerable, and only occurs on an archipelago of oceanic islands off the Pacific coast of Baja California Sur, in Bahía Magdalena. Its narrow adaptation to an island climate and ultramafic soils and its highly restricted area of occurrence of approximately 120 km^2 contribute to the vulnerability of the species. Similar to many other narrowly endemic, endangered cacti, *C. halei* is locally abundant but shows very low recruitment of new individuals into the population. Using deterministic and stochastic demographic stage class matrix models, both for the overall population as well as within distinctly different habitat types, we find that *C. halei* has a discrete annual growth rate of less than 1 in many scenarios, indicating a likelihood of declining populations and probable extinction over the next century. In particular, in drier, lower elevation habitat in the rain shadow of the mountainous portions of Isla Magdalena, populations are at risk of extinction. The strongest prospects for persistence of the species over the next century are in higher elevation, ridge top habitats. Stochastic models using a 10% increased probability of recruitment of new individuals and stage class persistence show dramatically improved outcomes for this species in all habitats. However, stochastic projections using an elevated probability of catastrophe years with low recruitment and

increased mortality show that the quasi-extinction probability for the species is above 50% in most cases, even with an unrealistically low threshold population size. The results show a species on the edge of extinction over the next century, sensitive to a narrow range of probabilities of recruitment and persistence, and likely to undergo local extinction events in lower elevation, more xeric habitats.

Introduction

Although often locally abundant, narrowly distributed endemic plant species face unique demographic, environmental and reproductive pressures (Brigham 2003, Lavergne et al. 2004, Lesica et al. 2006). Anthropogenic threats such as farming, ranching and development, as well as poaching by cactus collectors, are the main threats to the long term survival of narrowly distributed, rare cacti (Goettsche et al. 2015). However, slow growing cacti with low reproductive rates, often on unique soil types and within locally isolated climate zones, have been shown to have population dynamics that pose intrinsic or extrinsic, non-anthropogenic threats to persistence (e.g., Contreras and Valverde 2002, Ferrer-Cervantes et al. 2012, Mandujano 2015). As the Earth's biodiversity is under increasing threat, with the apparent advent of the sixth mass extinction in our planet's history (Barnofsky 2011, Kolbert 2014), and with plant species undergoing a rate of extinction as high as 500 times the background extinction rate over the past 250 years (Humphreys et al. 2019), accurately identifying plant species at risk of extinction and attempting to quantify the likely threats has become an urgent task (Humphreys et al. 2019).

Prior demographic population viability studies in the Cactaceae have determined that rare and narrowly adapted cacti have a discrete population growth rate (referred to as lambda, λ) below unity (that is, with a decreasing population), with 15 of 19 published studies indicating a projected population decrease (Table 5-1). This may reflect the tendency of population viability analyses to focus on species that have previously been determined to be at risk, with 17 of the 19 studies addressing cacti assessed as vulnerable, threatened or endangered by the International Union of Conservation of Nature (IUCN).

The number of population survey years in the publications listed ranges from two to 25. Statistical analyses include matrix population, integral projection and generalized linear regression models. In addition to the 19 studies in print, there are more than 30 papers that have been prepared for the Bureau of Land Management and United States Fish and Wildlife Service, in support of recovery plans for federally listed cactus species in the US Endangered Species Act (e.g,, Thomas et al. 2019). The publicly accessible online database, COMPADRE (Salguero-Gomez 2015), a repository of all known plant species studies that have employed structured matrix population models, contains a total of more than 7000 studies at the time of this writing, nearly 50% of which were published after the year 2000. In light of the IUCN assessment of the Cactaceae as the fifth most endangered of all plant and animal families, with one-third of the taxa in the family at risk of extinction over the next century (Goettsch et al. 2015), but only 19 published analyses, there is an urgent need for more population viability analyses of cacti identified as at-risk.

Table 5-1. Selected previous populaton viability studies in Cactaceae.

Species	References
Opuntia rastrera **F.A.C. Weber**	Mandujano et al. 2001
Mammillaria crucigera **Mart.**	Contreras and Valverde 2002
Neobuxbaumia macrocephala **(F.A.C. Weber ex Schum.) E.Y. Dawson**	Esparza Olguin et al. 2002
Harrisia fragrans **Small ex Britton & Rose**	Rae and Ebert 2002
Pachycereus gaumeri **Britton& Rose (as Pterocereus)**	Mendez et al. 2004
Mammillaria magnimamma **Haw.**	Valverde et al. 2004
Stenocereus eruca **(Brandegee) A.C. Gibson and K.C. Horak**	Clark-Tapia et al. 2005
Neobuxbaumia tetetzo **(F.A.C. Weber ex Schum.) Backeb. and** ***Neobuxbaumia mezcalaenis*** **(Bravo) Backeb.**	Esparza Olguin et al. 2005
Mammillaria pectinifera **F.A.C. Weber**	Valverde and Zavala-Hurtado 2006
Echinocactus platyacanthus **Link & Otto**	Jiménez-Sierra et al. 2007
Mammillaria dixanthocentron **Backeb.**	Ureta and Martorell 2008
Mammillaria hernandezii **Glass & R.A. Foster**	Ureta and Martorell 2008
Mammillaria huitzilopochtli **D.R. Hunt**	Flores-Martinez et al. 2010
Coryphantha werdermannii **Boed.**	Portilla-Alonso and Martorell 2011
Echinocereus lindsayi **J. Meyran**	Martorell et al. 2011
Mammillaria gaumeri **(Britton & Rose) Orcutt**	Ferrer Cervantes et al 2012
Sclerocactus mesae-verdae **(Boissev. & C. Davidson) L.D. Benson**	Coles et al. 2012
Astrophytum ornatum **(DC) F.A.C. Weber in Bois.**	Zepeda-Martinez et al. 2013
Harrisia portoricensis **Britton**	Rojas-Sandoval and Melendez Ackerman 2013
Pediocactus bradyi **L.D. Benson**	Shryock et al. 2014
Astrophytum capricorne **F.A.C. Weber in Bois**	Mandujano et al. 2015
Opuntia macrorhiza **Engelm**	Haridas et al. 2015

No prior studies of the population structure, life cycle or risk of extinction of *Cochemiea halei* have been published, and little was known about the species until this Multiple climate change scenarios, projected over the next century, are likely to cause range reduction of 21% –53% for *C. halei* (cf. Chapter 4). Using probabilistic ancestral biogeography based on a well-supported, time calibrated Bayesian molecular phylogeny of the *Mammillaria* and *Cochemiea* clades of Baja California, we found that *C. halei* is a very recent dispersal to the islands in Bahía Magdalena, arriving between approximately 1 million years ago (Ma) to as recently as 250,000 years ago (cf. Chapter 3).

Congruent phylogenetic reconstruction using maximum parsimony, maximum likelihood and Bayesian methods recovered *C. halei* as sister to the widespread peninsular endemic, *Cochemiea poselgeri* (Hildm.) Britton & Rose, which is also the species in *Cochemiea* in closest geographic proximity (cf. Chapter 2, Rebman and Roberts 2012, Hernandez and Gómez-Hinostrosa 2015). There are five taxa in the same clade within the recently expanded genus *Cochemiea* (cf. Chapter 2) that were the original members of a more narrowly circumscribed *Cochemiea*: *C. pondii* (Greene) Walton, *C. maritima* G.E. Linds., *C. setispina* (J.M. Coult.) Walton, *C. poselgeri* and *C. halei*. Among these, the most recently diverging are *C. halei* and *C. poselgeri* (cf. Chapter 3).

Conservation status and threat assessment

Cochemiea halei is assessed by the International Union for the Conservation of Nature (IUCN) as “vulnerable,” (IUCN 2019), and is legally protected in Mexico, listed on the national register of species at risk of extinction, where it is placed in the category “special protection” (SEMARNAT 2010). The species is in the rarity category of “locally abundant in a specific habitat but restricted geographically," as designated by Rabinowitz (1981). Using the Fertig scale (2012), which incorporates seven risk factors for threatened plants with scores ranging from zero (no risk) to 12 (extreme risk), *C. halei* is in the "extremely high risk" category, with a score of eight (Table 5-2). The factors contributing to this at risk status include few populations, using the definition of "population" from Harper (1977), "a spatially defined aggregate of individuals with the potential for gene flow among all individuals," in which case the number of potential populations for *C. halei* ranges from one to approximately six, based on field surveys, although gene flow among geographically separated populations is unknown. The species has a low total population size, N, estimated at 4000 individuals, based on extensive surveying throughout the entire known habitat. *C. halei* is basically "stranded" on the islands, with habitat suitability modeling (cf. Chapter 4) finding that the species is likely to remain an island isolate at least for the next century, with the exception of small foothold sites on the immediately adjacent peninsula. Estimates of fertility, fecundity and establishment to reproductive age are low (see below). The most pressing threat over the next century is climate change, which has been shown to result in range contraction on the islands (cf. Chapter 4).

The goals of this study are to 1) ascertain the demographic structure and vital rates of *C. halei*, 2) determine the habitat-specific and global stage class contributions to the discrete annual growth rate of the species, and 3) estimate the risks of local and global extinction of the species over the next century using deterministic and stochastic demographic matrix model projections.

Table 5-2. Extinction risk assessment for *Cochemiea halei* using the Fertig Scale.

Parameter and reason for threat	Score
Geographic range: local endemic	2
Number of populations: low (fewer than 25)	1
Abundance: low (total population<30,000)	1
Habitat specificity: high (island endemic)	1
Intrinsic rarity: high (low recruitment)	1
Magnitude and immanence of threats: high	1
Population trend: decreasing	1
Total score:	= 8

Methods and Materials

The study species

Cochemiea halei is a highly restricted, locally abundant island endemic, occurring on the island archipelago in Bahía Magdalena, an embayment along the Pacific coast of Baja California Sur. The exception to its island distribution is a single patch of approximately six individual plants near the peninsular fishing town of Puerto San Carlos, 14 km east of the islands (Gorelick 2007, Rebman and Roberts 2012). Although this small patch of plants is probably advanced in age (see below), there are no known signs of dispersal nearby or elsewhere on the peninsula (Gorelick 2007, Hernández and Gómez-Hinostrosa 2015). The total known extent of occurrence (EOO), based on vouchered herbarium records, is approximately 1500 km^2, with an area of occurrence (AOO), i.e., the actual inhabited known range, of approximately 300 km^2 (SEInet, GBIF). Within its AOO, *C. halei* is one of the dominant flowering plant species (Breslin, pers. obs.). Although only 35 occurrences are recorded at GBIF and 12 at SEINet at the time of this writing, we found *C. halei* in most of the habitats on the islands. Population density fluctuates by habitat type, however, with the densest populations found along west to northwest facing slopes and ridge lines. Flat, sandy environments and coastal scrub zones are areas of total or near total absence, as are the steep drop offs along the Pacific-facing coasts of the islands, below a distance of approximately 100 m from the peak of these drop offs.

Cochemiea halei is a stem succulent, usually with dense spines that often completely obscure the stem surface. The following description is combined from Bravo-Hollis and Sanchez-Mejorada (1991), Rebman and Roberts (2012) and my own field records. As in *Mammillaria*, *Cochemiea* has dimorphic areoles, with the spine-bearing areole at the apex of the tubercle, and the flower and stem bearing areole in the tubercular apices. Each spine bearing areole produces 24–28 spines, with one to five central spines 20–30 mm long and several radials, 10–12 mm long. All spines are rigid. Notably, *C. halei*'s central spines are always straight, whereas, in the other members of the original genus *Cochemiea* sensu (K. Brandegee) Walton, and most of the members of its recently expanded genus (36 out of 39 species), the central spines have hooks curving at spine apices adaxially. Stems branch readily, usually basally but occasionally along nearly the entire length. Plants are often highly ramified, and appear to begin branching at a young age, forming dense mats of stems to as much as 3 m across. Stems range from 0.2 to 3 m in length when mature. Stem width, 2–9 cm. Stems are tomentose at the apical meristem. Flowers were observed in the survey months during this study: December, January, April, May and June. Flowers are produced sporadically from axial areoles in prior or past years' growth. Flowers are approximately 5 cm long, scarlet-red, with strongly exerted styles, orange-red stigma lobes appressed to the style, and yellow filaments. Fruit are deeply embedded in the stem for at least a year after formation, exserted from the stem only when ripe, to 2.8 cm in diameter, floral remains persistent. Seeds are about 1 mm in diameter, contained in highly mucilaginous pith, approximately 50 per fruit, but with as many as 100+. Flowers are putatively adapted for hummingbird pollination, but a pollination study for the species has not been done, and during five years and 11 field surveys, the local hummingbird was observed many times (the Baja California endemic *Basilinna xantusii* Lawrence), visiting flowers of *Euphorbia lomelii* V.W. Steinm., and *Fouquieria diguetii* I.M. Johnst., but was never observed visiting *C. halei* flowers.

The study site

Isla Magdalena, on which all of the surveying was conducted for this study, is an oceanic island approximately 20 km due west of the peninsula. All of the following distances were measured to the nearest kilometer using the World Topographical base map and distance measuring tool in ArcGIS v. 10.1.2 (ESRI, inc. 2019). The island, including Cabo San Lazaro, with the intervening Bahía Santa Maria, spans a direct north-south distance of approximately 30 km, from latitude 24.53 to latitude 24.81, and a direct east-west longitudinal distance of approximately 24 km, from -112.05 to -112.30. A straight line approximately bisecting the assembly of the main land mass, Bahía Santa Maria and Cabo San Lazaro is at a bearing of approximately 330° from true north. The island is at its widest at the southeastern region, at 3 km across. The narrowest direct distance across is approximately 0.8 km. The main land mass is approximately 18 km long. Bahía Santa Maria is approximately 13 km long, measured between the rocky headlands at either end of the entrance to the bay. Cabo San Lazaro, at its narrowest east-west distance, is approximately 0.8 km, with its widest point being about 3.7 km. From the northwest end of the cape to the southeast is approximately 7.3 km (Fig. 5-1) The total area of Cabo San Lazaro is approximately 13 km^2 and the total area of the main land mass of Isla Magdalena is approximately 38 km^2. Available habitat for *Cochemiea halei* in this portion of the archipelago is therefore only about 51 km^2. All of the surveys for this population viability analysis were conducted over the 38 km^2 of the main land mass of Isla Magdalena (Fig. 1, D), referred to here as “the island.” The nearby Isla Margarita has highly restricted access due to Mexican military ownership and live ammunition training, and repeat surveying was not possible on that island.

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Figure 5-1. Map of the Bahía Magdalena region, the location of population surveys of *Cochemiea halei.* (A) Cabo San Lazaro; (B) the adjacent peninsula, location of the only known peninsular population of *C. halei*; (C) Bahía Santa Maria, and (D) the main land mass of Isla Magdalena. Locations of habitats for population samples used in the analysis (see results): (1) ridge tops, "Habitat G"; (2) bay side flats; "Habitat F", (3) southeastern xeric flats, "Habitat H". Base map copyright ESRI, Inc. All rights reserved.

Isla Magdalena is a result of plate tectonics, and is a true oceanic island, in spite of being only 14 km from the peninsula. The majority of the island is composed of ultramafic rock, with a ridge of mountains constituting most of the land mass (Blake et al. 1984, Sedlock 1993). A shelf of basalt is at the flat southeastern end of the island. The climate is heavily influenced by the California Current system, so that the ridge tops experience significantly greater atmospheric humidity and lower temperatures than the leeward flats on the bay side of the island and the adjacent peninsula (León de la Luz 2015, cf. Chapter 4). The vegetation regime is scrub with stem succulents, a.k.a. "sarcocaulescent scrub." (León de la Luz 2015).

Survey methods

Initial surveys characterized the habitat types in which *Cochemiea halei* was present, by making an inventory of associated vegetation, aspect relative to the bay or ocean sides of the island and percent cover. Percent cover was estimated with reference to a visual method from Anderson (1986). Habitats with observed distributions of *C. halei* were selected following Mandujano (2015), in this case, using generalized linear models of the Poisson family with habitat types as predictors of stage class abundance instead of ANOVA.

Within the selected habitat types, three approximately rectangular belt transects measuring 1 km by 300 m each were randomly delimited, at a minimum distance of 1 km apart. GPS markers were recorded for the start and end of each transect, as well as at 100 m intervals within each transect, using a handheld eTrek 300 GPS unit (Garmin Technologies, Olathe, KS). Total population counts with number of stems, flowers and fruits for each individual were done within each transect. Surveying was conducted in a point-count method every 100 m, with the exception of within denser populations, where counts were done every 50 m (Elzinga 1998, Bonham 2013). Since presumably young plants are small and were often hidden among rocks or within scrub vegetation, detailed complete coverage surveys were performed over one randomly selected 1 km^2 portion of the transects in each habitat type, to correct for under-detection (Kery et al. 2009, Chen et al. 2013). Detection corrections were applied to Stage I and Stage II counts, and based on the simple probability of under detection as a ratio of complete coverage detection to overall sampling detection. Generalized linear models (GLMs) of total counts and disaggregated stage class counts were used to investigate goodness of fit and dispersion relative to a Poisson distribution, the standard expected distribution for count data (O'Hara 2010). Model fitting was performed in R v. 3.5.1, in the R Studio environment, v. 1.2.1335-1. Regression model diagnostics were performed using the R package DHARMa v. 0.2.0. (Hartig 2018).

Growth rate estimates

Little research has gone into measuring the growth rates of relatively small cacti, in spite of extensive study of the growth rates of large columnar cacti such as *Carnegiea gigantea* Britton & Rose and *Pachycereus pringlei*(S. Watson) Britton & Rose (e.g., Drezner and Lazarus 2008, Drezner 2014, Delgado-Fernández 2016). The growth rate of *C. halei* is not known. In order to attempt to estimate growth rates in different habitats, the apparent production of new tubercles was counted annually in May, on 30 randomly selected individuals within each habitat type. This process was facilitated by the markedly different color of new tubercles, a much lighter green than older tubercles from previous year's growth. Estimates of mean annual tubercle production were made for both flat and low cover as well as mountainous and higher cover habitats. Total counts of tubercles on the longest stems of 30 individual plants were divided by average annual tubercle production to estimate annual growth.

Designation of stage classes

Since the ages of individual plants were unknown, stage classes were chosen as the demographic classes for modeling (Lefkovitch 1965, Caswell 2001, Morris and Doak 2003). Following Vandermeer (1978), the correlation between number of stems and annual seed production (without regard to fecundity) of individual plants was measured to correlate number of stems to fertility. Fruit from 30 randomly selected individuals in each habitat type were counted, and seed was counted per fruit. Simple regression was used to find the correlation between number of stems and estimates for annual average seed production. Stem numbers were binned according to Wand (1997) to determine the optimal number of stage class bins based on number of stems. Since detection in the field of newly germinated plants was not reliable, as *C. halei* seedlings are < 1 cm tall and < 6 mm across for at least the first two years (Steven Brack 2017, personal communication), the smallest stage class included in the analyses was plants with one–two visible stems.

Building the matrix models

We followed the standard procedure for constructing matrix population models from “projection matrices” that include transition probabilities as elements that represent the fate of age or, in our case, stage classes, after each time step, usually one year (Akçakaya 2000, Caswell 2001). The projection matrix is iteratively multiplied by successive dot products of a vector of age or stage class counts. The result is a series of vectors of population counts after time t, the number of iterations. The transition probabilities in the projection matrix are derived from survey data and estimates of each age or stage class contribution to recruitment of new individuals to the population. Conveniently, eigenanalysis of the eigenvectors of the projection matrix yields important measures of the likely fate of a population, since the value of the dominant eigenvector equals λ, the discrete annual population growth rate, and other methods of eigenanalysis yield valuable information about the contribution of each age or stage class to the viability of the population, such as that class's reproductive value and the proportional effect that changes in that class have on λ, called "elasticity". Deterministic models use the same projection matrix for each time step. Stochastic models use either a different projection matrix at each time step, based on random probability, or randomly altered transition rates within matrices. The goal of stochastic modeling is to capture the long term effect of random changes in the environment (Alho 1990, Caswell 2001).

Estimates for the contribution of each stage class to recruitment into Stage I, that is, the fecundity of each stage class, were based on the ratio of estimates of the product of mean stage class fertility (i.e, total annual seed production per stage class times median number of members in that stage class) and the probability of established stage I individuals per year, based on Stage Class I counts (Akçakaya 2000, Morris and Doak 2003, Zavala-Hurtado and Valverde 2003). Estimates of stage class fecundity (i.e., successful establishment of a stage I individual) were adjusted upward by assuming the multi-year persistence of viable seed in the soil, as has been demonstrated for three species of *Mammillaria* (Rodríguez-Ortega et al. 2006). A conservative approach was taken to adjust fecundity so that the resulting 100 year projections of Stage Class I membership were within two standard deviations of the mean of actual survey counts.

After correction for under detection of Stage Classes I and II (the two classes for which there was evidence of under detection), five years of field survey total stage class counts as well as stage class counts per habitat type were used as the basis for estimating transition probabilities. Since the count data was total stage class membership per transect, and not the stage and annual fate of each individual plant, methods to estimate parameters for the projection matrix followed a procedure for an "inverse" problem, that is, given the total stage class counts, finding an optimal projection matrix that would generate that data structure (Caswell 2001). Following Kaplan and Caswell-Chen (1997), Wood's quadratic programming method with a smoothing parameter was used to generate transition probabilities for all projection matrices (Wood 2000, Caswell 2001, Morris and Doak 2003), using quadprog v.1.5-5 (Turlach and Weingessel 2013) and popbio v.2.4.4. packages in R (Stubben and Milligan 2007). The algorithm to estimate a transition probability matrix in the quadprog package is an implementation of Goldfarb and Idnani (1982, 1983). This algorithm is a routine for minimizing the sum of squared deviations between observed stage class counts and the projection matrix that would result in those counts, given a set of constraints on the possible steps between stage classes. The resulting projection matrix is then used in another quadratic optimization routine to estimate a smoothing parameter that minimizes sudden transitions between stages (unlikely in slow growing cacti) but retains the optimal goodness of fit of the original transition matrix (Wood 2000, Caswell 2001). Projection matrices were parameterized for the total stage class counts and for each of three distinct habitats in which surveys were conducted.

Following Caswell (2001) and Mandujano et al. (2015), 95% confidence intervals were generated by unbiased resampling of 1000 bootstrap replicates of the stage class structured population data, generating 1000 projection matrices using the above algorithm, and finding the 95% confidence interval for the discrete growth rate, λ. Deterministic models were projected for 100 years for all of the projection matrices, for the total population as well as each sub-population by habitat type. Eigenanalysis of the eigenvectors of the projection matrices was conducted to determine λ, the reproductive value and elasticity of each stage class. The 100-year projections using the projection matrix with median transition probabilities from 1000 bootstrap replicates were plotted showing the fate of each stage class as well as overall population trends (Caswell 2001).

Stochastic growth rate was estimated using 50,000 iterations for each random probability scenario for each habitat type and for the overall population. Following Alho (1990), Menges (1992) and Caswell (2001), two special case projection matrices were constructed, based on adjustments to the median transition probabilities from the projection matrices used in the deterministic projections. The first was a “bonanza” projection matrix with a 10% annual increase in the probability of each stage class contributing an individual to Stage I, combined with a 10% increased probability of annual survival or transition to the next largest stage class, intended to model periodic Sonoran Desert high winter precipitation events (cf. Polis 1997). The second was a “catastrophe” projection matrix, with a 10% reduction in contributions to Stage I and 10% increased mortality, in order to model years of reduced precipitation (Schwinning et al. 2004, Sponseller 2007, Cable et al. 2008). These adjustments to vital rates were speculative, since the direct impact of increased precipitation or long term drought cycles on *C. halei* is unknown, but estimates follow Polis et al. (1997) as well as Ogle and Reynolds (2004). Quasi-extinction probabilities and time to extinction were estimated for all projection matrices, using 50000 independent stochastic 100-year runs per scenario (Menges 1992, Lande 1993, Caswell 2001, Kaye 2001, Kaye and Pyke 2003, Mandujano 2015).

Results

The total number of individuals of *Cochemiea halei* surveyed annually ranged from 222 to 241, with the high population count in year two (2015) and the low count in year four (2017). The median over five years was 227 individuals, with a standard deviation of 7.54. The survey results show low recruitment to Stage I, but low mortality for all stage classes. The probability of under-detection of Stage Class I was 10% when percent cover was below 15%, and 18% when percent cover was above 15%. Probabilities of under-detection of Stage Class II were 5% with percent cover below 15%, and 9% with percent cover above 15%. These probabilities were used to correct the raw counts for these two classes. The reported counts in all cases are for detection-corrected counts.

A strong correlation between number of stems and seed production was found (Pearson's r=0.90, df=3, *p*<.0001). Five stage classes based on number of stems were designated as follows (Vandermeer 1978, Wand 1997): Stage I: One–two stems, Stage II: three–10 stems, Stage III: 11–19 stems, Stage IV: 20–32 stems, Stage V: 33 or more stems (Fig. 5-2).

Figure 5-2. Photographs of representatives of each of the designated demographic stage classes of *Cochemiea halei*. (A) Stage Class I, one–two stems; (B) Stage Class II, three–10 stems; (C) Stage Class III, 11–19 stems; (D) Stage Class IV, 20–32 stems; (E) Stage Class V, 33 or more stems. (F) shows the typical appearance of the fruit, exserted when ripe.

Box plots of counts by stage class for the five survey years show low recruitment to Stage I, and relatively low survival to Stages IV and V, with Stages II and III being the most abundant. Stage II shows the highest variability. (Fig. 5-3). Stage class count totals for each survey year show the highest standard deviations for Stage Classes I and II, with relatively low variation for the other three stage classes. (Fig. 5-4).

Growth rates resulting in stage class transition, that is, production of new stems, appears to be slow. Mean annual new tubercle production was seven tubercles per stem, with the slowest growth rates found in lower elevation habitats with low percent cover, with mean annual new tubercle production of five. The largest plants, some with stems to nearly 3 m, had a total tubercle count of more than 1000 tubercles from the base of a single stem to the apex, which, assuming an average of seven tubercles a year per stem (as observed in the field over the five years of surveying), would make these large plants approximately 150 years old. However, data was inconclusive regarding whether or not growth rate is age dependent or whether stems on large mats of multi-branched individuals grow more slowly or at differential rates compared to smaller plants with fewer stems.

Three habitats were selected as significant predictors of stage class counts based on regression methods: bay side flats (habitat F) as a predictor of Stage Class IV ($p<0.001$), xeric flats at the southeastern end of the island (habitat H) as a predictor of Stage Class III ($p<0.001$), and ridge tops (habitat G) ($p<0.001$ for all stage classes). The bay side flats of habitat F are characterized by percent cover between 5% and 15%, with generally no hills or slopes steeper than approximately an angle of 10°, and population density for *C. halei* of approximately 0.04 plants per m^2. The xeric flats of

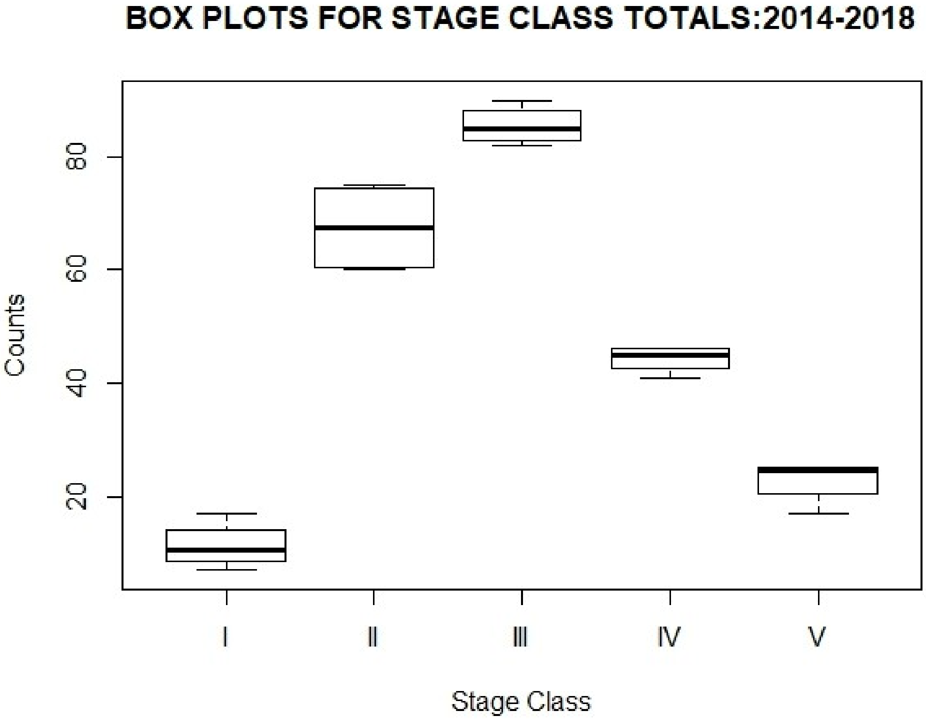


Figure 5-3. Boxplots of demographic stage class counts of *Cochemiea halei* over five survey years, from 2014 to 2018. Box and whisker plots show high and low counts, as well as first quartile, median and third quartile values. Low stage class counts in Stage I, relatively high fluctuation in Stage II, relatively stable populations in Stages III and IV and low counts in Stage V are shown.

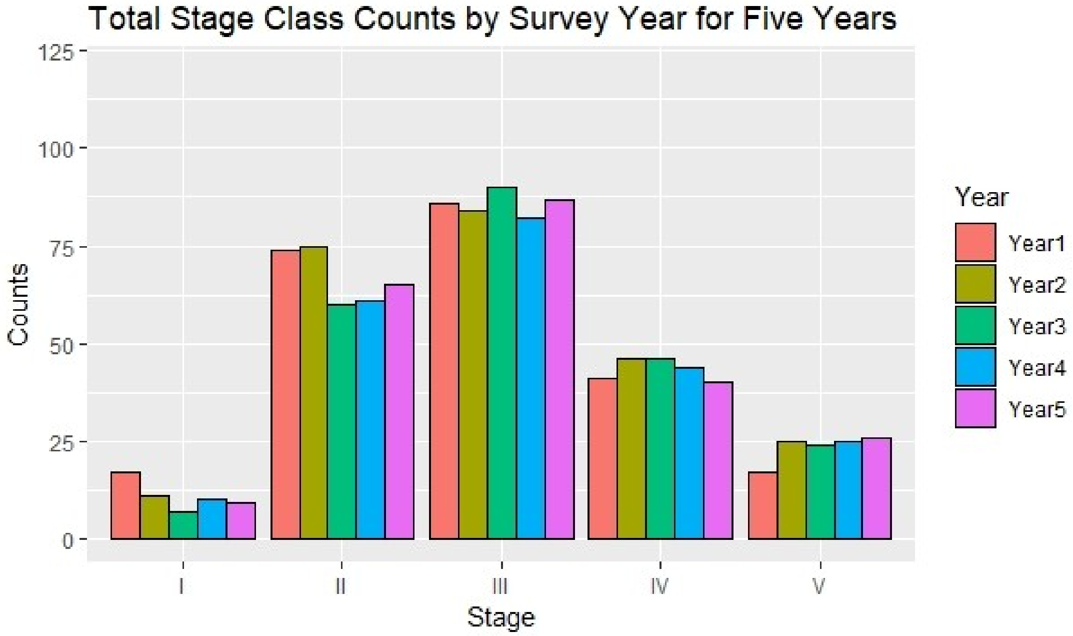


Figure 5-4. Histograms of total stage class counts of *Cochemiea halei* over five survey years, from 2014 to 2018. The *y*-axis is the number of individuals in each stage class, and the *x*-axis is the stage class. The five survey years, 2014–2018, are given in the color coded legend. Standard deviations of stage classes: Stage I: 3.84, Stage II: 7.78, Stage III: 3.03, Stage IV: 2.79, Stage V: 3.66.

habitat H had a percent cover between 0% and 10%, also with few slopes, and a population density of 0.05 plants per m^2. In contrast, the ridge tops of habitat G feature percent cover ranging from 15% to 30%, many rocky slopes at angles as steep as nearly 90°, and a population density of approximately 0.15 plants per m^2. (Fig. 5-5). Stage class counts for the five survey years show that habitats F and H have low recruitment and lower population sizes than habitat G (Fig. 5-6).

As with other cacti, the reproductive dynamics are a combination of high annual seed production, unknown *in situ* germination rates, but very low probability of establishment to persistent size (cf. Contreras and Valverde 2002, Drezner 2005, Ferrer-Cervantes et al. 2012, Mandujano et al. 2015). For example, with high estimates of 50 seeds per fruit and 1200 fruit per year for the surveyed population (approximately four fruits per individual), with 30% of seed viable for an additional year in the soil, there would be approximately 78,000 seeds available annually within the survey population. By comparison, the most abundant Stage Class I (one to two stems) count after correction for under detection was 17 out of 225, or approximately 7.5% of the population, a ratio of only approximately 0.0002 established Stage Class I plants per seed. By contrast, Stage Class II abundance was fairly robust, ranging from 27% to 34% of the total population. As a result, the stage class contributions to Stage I were conservatively estimated to be between 0.01 to 0.03 new Stage Class I recruits per entire stage class per year, based on mean annual fruit production per stage class (cf. Crone 2011).

Figure 5-5. Photographs of the habitat types selected for spatially explicit demographic stage class matrix models of *Cochemiea halei*. (A) hills facing northeast, with low population density; (B) ridge top habitat with high population density, "Habitat G," (C) southeastern basalt flats, "Habitat H." (D) the cliffs facing the Pacific, (E): another example of a ridge top habitat, at the highest point on Isla Magdalena at 660 m, and (F) the bayside flats, with low population density, "Habitat F."

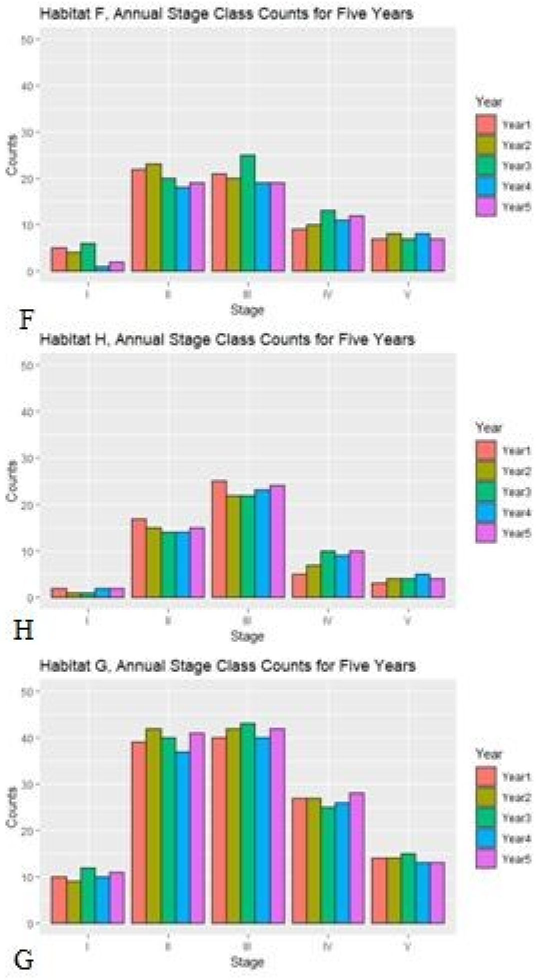


Figure 5-6. Demographic stage class counts by habitat type for *Cochemiea halei* ove3r five survey years, from 2014 to 2018. (F): Habitat F, the bayside flats; (H): Habitat H, the basalt flats at the southeast of the island; (G): Habitat G, ridge tops. Survey years are color coded according to the legend in the margin of the plot of each habitat type. The y-axis is the count of the number of stage class individuals.

Projection matrices for the total counts and the three habitats, using the median transition probabilities from 1000 bootstrap matrices per scenario, show probabilities of stage class persistence between 0.90 and 0.97, and low mortality, between 0.10 and 0.15. Confidence intervals for λ for the total counts in the deterministic models and for habitat H show values on either side of unity, whereas habitat F has all values below unity, predicting population declines for this habitat under current conditions. In all habitats, Stage Class II (three to nine stems) had the highest reproductive value, although with varying proportional effects on contributions to recruitment based on habitat type. Elasticity, a measure of the proportional effect on λ of changes in each stage class, showed variation among habitats, with Stage Class II having the highest proportional effect on growth rate for habitat F, Stage Classes I and II for habitat G, Stage Class III for habitat H, and Stage Class II for the total population. (Figs. 5-7 and 5-8, Table 5-3).

Stochastic models of *Cochemiea halei* showed significant differences in 100-year projected stage class and overall abundance, depending on the frequency of bonanza years (10% increases in fecundity and persistence) versus catastrophe years (10% decrease in fecundity and persistence). When both bonanza and catastrophe years had an equal probability of 0.02, stochastic growth rates were comparable to the growth rates obtained in deterministic projections. When the probability of bonanza years was 0.05 (that is, increased fecundity and survival, likely to occur five times a century), all of the growth rates for all habitats and the total population were above unity. On the other hand, when the probability of bonanza years was reduced to 0.02 (two years out of 100) and catastrophe years was increased to 0.05 (reduced fecundity and survival five times per century), all of the stochastic growth rates were below unity (Table 5-4).

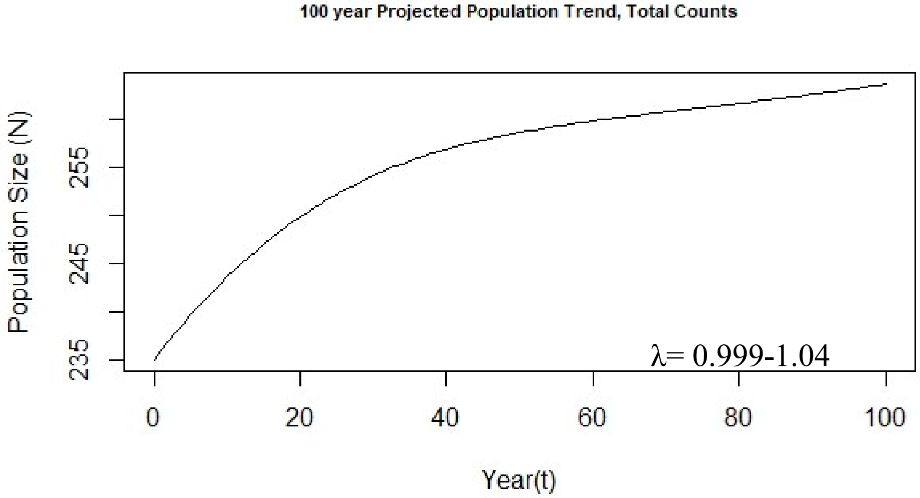


Figure 5-7. 100 year projection from a deterministic stage class matrix model of the overall population trend of *Cochemiea halei* including all habitats. The graphs show the population trajectories of a deterministic 100-year projection for the total population using the projection matrix with median transition probabilities, calculated from 1000 bootstrap replicates. The 95% confidence interval for 1000 bootstrap replicates for λ = 0.999-1.04.

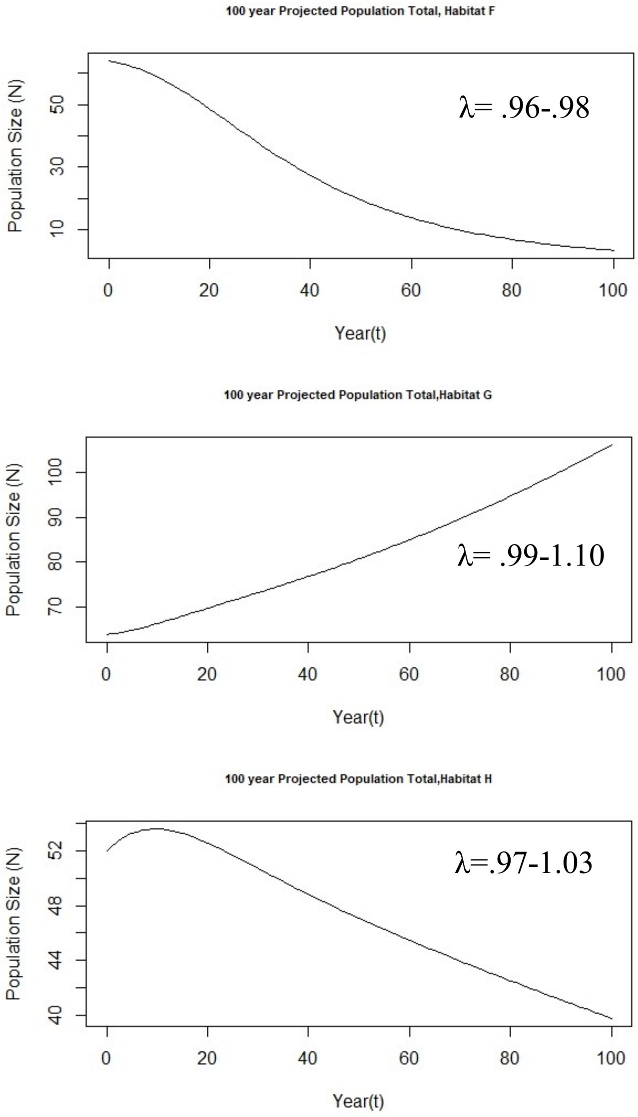


Figure 5-8. 100-year projections of the population trends for *Cochemiea halei* in three different habitat types, based on a desterministic demographic stage class matrix model, with 95% CI lambda values for each habitat type.

Table 5-3. 95% confidence intervals for lambda, reproductive value and highest elasticity for populations of *Cochemiea halei*.

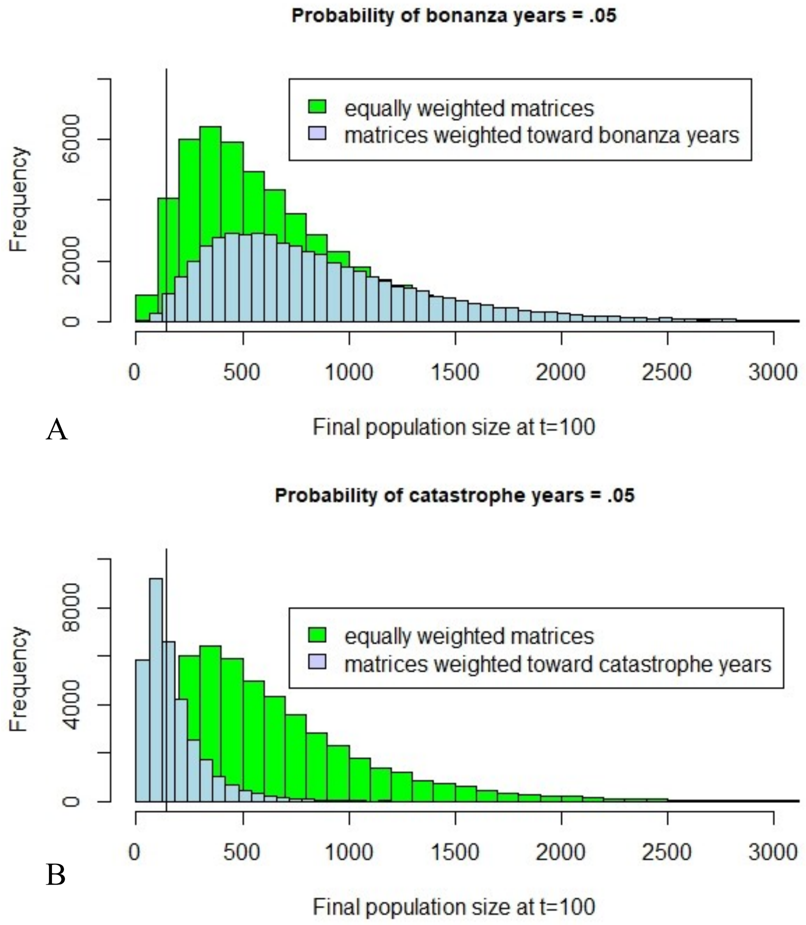
Habitat	95% CI for λ	highest reproductive value	highest elasticity
F	0.96-0.98	Stage II, .84	Stage II, 0.32
G	0.99-1.10	Stage II, 1.18	Stages I and II, 0.35
H	0.97-1.03	Stage II, .87	Stage III, 0.32
Combined	0.99-1.04	Stage II, 1.02	Stage II, 0.34

Table 5-4. Stochastic lambda estimated using varying probabilities of bonanza and catastrophe years, for populations of *Cochemiea halei*.

Habitat type	Stochastic λ, equal probabilities	Stochastic λ, bonanza years, 0.05, catastrophe years, 0.02	Stochastic λ, bonanza years, 0.02, catastrophe years, 0.05
Combined	1.007253	1.031979	0.9730654
F	0.9981862	1.029604	0.9645382
G	1.007626	1.031794	0.9736994
H	1.005612	1.032516	0.9713764

Histograms of the frequencies of the predicted final total population size of *Cochemiea halei*, based on 50,000 stochastic projections with bonanza and catastrophe matrices with equal probabilities of 0.02, compared to either bonanza or catastrophe matrices at a probability of 0.05, show the effects of increased or decreased fecundity and survival. In spite of the projection matrices only being adjusted by a 10% increase or decrease in fecundity and survival rates, an increased probability of bonanza years shifts the majority of the frequencies of final population size to the right of the initial population size of the survey. Also, an increased probability of bonanza years shows possible significant increases in population size, with outliers more than ten times the initial population size. In contrast, the effects of a higher probability of catastrophe years shows a frequency of final population size closer to the initial population size, or smaller. Out of 50,000 runs, 2426 runs (5%) were greater than the initial population size when catastrophe years were more likely. In contrast, when bonanza years were more likely, 37,000 runs (74%) were greater than the initial population size. (Fig. 5-9).

Even with the relative probability of bonanza years at 0.33 (increased fecundity and survival every three years), the quasi-extinction probability for *Cochemiea halei* was 1.0, within the next approximately 50 years, with a threshold population > 400, or roughly one-tenth the current population. On the other hand, with the threshold population below 200, even only a 2% increase in the probability of bonanza years lowered quasi-extinction probability to < 0.20 over the next 100 years. When catastrophe years had a probability of 0.05, a threshold population of 200 resulted in quasi-extinction



Probability of bonanza years = .05

Probability of catastrophe years = .05

Figure 5-9. Population projections for *Cochemiea halei* as a result of 50,000 100-year stochastic projections, using different probabilities of bonanza and catastrophe years. Green bars in both panels represent final population size projections using equal probabilities of catastrophe and bonanza years. (A) frequencies of final population size with bonanza years having a probability of 0.05; (B) frequencies of final population size with catastrophe years having a probability of 0.05. The vertical line marks the initial population size N, from year one of surveys. N=225.

probabilities between 0.70 and 1.0 over the next century. Quasi-extinction probabilities were only reduced to < 0.50 over the next century when the threshold population was lowered to ten individuals, probably an unrealistically low number of individuals.

Discussion

Multiple analyses reveal that *Cochemiea halei* is on the edge of extinction—a species sensitive to differences in habitat type as well as slight changes in fecundity and persistence. In flat habitats on the bay side of Isla Magdalena, with percent cover between 0% and 10%, *C. halei* is vulnerable to local extinction over the next century. On the other hand, in more rugged, higher elevation habitat, with percent cover between 15% and 30%, the species is more likely to persist over the next century. Even in that more favorable habitat, the 95% confidence interval for λ had its lower boundary below unity, signifying a risk of extinction overall.

Climate data from WorldClim v. 2 at 30 arcsec resolution (approximately 1 km^2) indicate that the island climate is significantly distinct from the peninsular climate (Fick and Hijmans 2017, cf. Chapter 4). The most significant drivers of predicted current suitable habitat for *C. halei* are annual temperature range, annual maximum temperature, the precipitation of the warmest quarter (July-September) and the precipitation of the coldest quarter (December-February). In each case, the values for the peninsula and for habitats F and H, the lower elevation, less mountainous habitats with lower percent cover, differ from the data for the ridge tops. Habitats F and H are 15% drier and 20% hotter, collectively, with a wider annual temperature range. Habitat G is cooler, wetter and has a more moderate annual temperature range. Remarkably, within the very narrow spatial range of approximately 51 km^2 on the island, the climate is heterogeneous enough to show distinct patterns of more or less suitable habitat (cf. Chapter 4). It is likely that these landscape scale patterns influence the discrete and stochastic growth rates of the spatially explicit analyses in this study. If so, this would indicate that annual fecundity and persistence of *C. halei* are related to temperature and precipitation, with the most favorable growth rates under pulse precipitation events in what are often cooler winter El Niño years (Polis 1997).

Future climate changes, even under best case scenarios, are likely to reduce the range of *C. halei* (cf. Chapter 4). Given the reality that predicted climate change includes increased temperatures and reduced precipitation, it may be that the scenarios in this study using a higher probability of the catastrophe matrix offer a more realistic picture of the fate of this species. If so, even in the more favorable ridge top habitat, there is a risk of extinction over the next century.

One of the dynamics of narrowly adapted endemics is the development of strategies for persistence in unusual habitats that would be inhospitable for other species, even if they are closely related—yet this same suite of adaptive traits makes narrowly distributed endemics vulnerable to slight changes in conditions (Kruckeberg and Rabinowitz 1985, McNair and Gardner 1998, Bevill and Louda 1999, Wilmé et al. 2006, Damschen et al. 2012). This appears to be the case with *C. halei*, where the risks are related to reduced fecundity and survival. The hedging strategy of low recruitment but slow growth and low mortality is most likely to be an adaptation to long term, stable climate regimes, such as that created by the California Current system, and may reduce resiliency to sudden changes.

Caution in interpreting these results arises regarding the estimates for fecundity and the stage class contributions to Stage Class I. Some studies perform controlled germination experiments *ex situ* and some attempt *in situ* plots to monitor seed germination rates. However, *ex situ* propagation trials over-predict germination rates and are unable to capture rates of actual successful establishment to reproductive age in habitat (Gibson and Nobel 1986, Nobel 2003). Because cactus seed germination and survival to a persistent size is such a rare event in habitat, some *in situ* trials have produced no germination data (e.g., Contreras and Valverde 2002). As a result, fecundity estimates are usually made using an informal Bayesian conceptual framework- given the proportion of the youngest established stage class relative to the total population, and given observed annual seed production, what is the most likely posterior probability for a rate of establishment to persistence? The method used here applies this concept, but also includes tests for rates of fecundity to limit the projection of establishment of Stage Class I plants to within two standard deviations of the mean of the actual survey data. The resulting fecundity estimates may or may not reflect actual biological parameters, but they are conservative, and useful for the goal of the matrix models here, which is to project the future fate of *C. halei* under differing scenarios, under the assumption of a relatively constant Stage Class I membership.

The population size class structure of *C. halei*, where Stage Class I remained small over the survey period, but Stage Class II was relatively abundant, suggests that Stage II (three–nine stems) represents a measure of longer term recruitment, since it is an aggregate of several generations of persistent Stage Class I plants. The dynamic of low establishment but low mortality once established echoes other cactus species for which reproductive patterns *in situ* have been studied (e.g., Drezner 2005, Mandujano et al. 2009). Low mortality for all stage classes also points to dispersal of seed and establishment to Stage II as the segment of the life cycle of *C. halei* that poses the most challenges. Evidence for this pattern with *C. halei* is in the high seed-to-Stage Class I ratio, with a low estimate of at least 10,000 seeds per each Stage I plant, but relatively robust Stage Class II abundance.

Other cautionary notes on the interpretation of the results presented here are related to the survey period, the inverse problem approach and uncertainties regarding the ability of *C. halei* to rapidly adapt to changing conditions, and a lack of biotic data. First of all, the survey period of five years is half the recommended minimum of ten years, proposed by Crone et al. (2011, 2013). Also, using total stage class counts to estimate the probabilities for the projection matrices reduces the resolution of population information. The more standard procedure of tracking the fate of each individual member of a population from year to year may provide more precise estimates of vital rates such as fecundity and mortality (Caswell 2001). It may be that the small sample size, length of the survey period and use of the "inverse problem" method exaggerate the variability of the data. In general, sorting out noise from actual biological signal in matrix population modeling is a challenge (Menges 1992, Crone 2013). In the analyses here, the 95% confidence intervals were relatively narrow, yet the boundaries were, in all cases, on either side of unity for λ, which suggests uncertainty in drawing any definite conclusions about the ultimate fate of the species. The assumption of equal fitness of all surveyed individuals eliminated the possibility of influences of genetic variation on the population. Finally, the biotic dynamic of *C. halei*'s relationship with its putative pollinator, the Baja endemic hummingbird *Baslinna xantusii* is omitted from the analysis, and presents a valuable system for future research.

Conclusion

The results presented herein suggest that, in spite of being apparently successfully adapted to a unique island habitat, characterized by ultramafic soil, extreme weather events, and having low mortality rates, *Cochemiea halei* should be elevated from the vulnerable category to the endangered category by the IUCN and should continue to be monitored, especially under changing climate conditions that may impinge on fecundity and survival. In particular, monitoring should focus on Stage Class II membership for all habitat types and Stage Class III on the southeastern basalt flats, as these classes were consistently shown to have the greatest impact on λ in both deterministic and stochastic models.

Chapter 6 GENERAL CONCLUSIONS

The overarching goal of this project was to clarify the phylogenetic, biogeographic, environmental and demographic aspects of the Mammilloid clade in the Baja California region, with a particular emphasis on the genus *Cochemiea*. Specifically, the research was intended to assist with conservation of members of this clade by clarifying the clade relationships within the Mammilloid clade, placing the Baja California members of the Mammilloid clade in biogeographic context, clarifying the forces that may have led to the high levels of speciation and endemism in the region, and focusing on one narrowly distributed endemic taxon of conservation concern to investigate habitat suitability, climate change impacts and population viability.

Prior to the research conducted here, there were several gaps in our understanding of the Mammilloid clade in general, as well as in the Baja California region:

1). The monophyly of the genus *Mammillaria* was not resolved and its clade relationships within the large Mammilloid clade were unclear.

2). The ancestral biogeography, probable timing and routes of dispersal, diversification rates and divergence times of the Mammilloid clade, especially in the Baja California region, were unknown.

3). Habitat suitability and climate change impacts had never been quantified for a Baja California cactus species, nor for any island endemic cactus species with an association with ultramafic soils;

4). A quantitative population viability analysis of a Baja California cactus had never been conducted.

The molecular phylogeny we present clarifies clade, generic, subclade, species and infraspecific relationships. One of the earliest questions that motivated the molecular phylogeny was: what is the support for retaining the genus *Cochemiea* (K. Brandegee) Walton, s.s.? This study shows strong support for the original genus *Cochemiea* s.s. as a monophyletic group within an expanded concept of *Cochemiea*, and support for *Cochemiea halei* as a well defined taxonomic unit. The phylogeny reveals strong geographical associations for major clades, as well as subclades within the newly circumscribed *Cochemiea*. When combined with biogeography, the picture is further clarified, with the high species richness of *Cochemiea* s.l. in particular shown to be correlated with multiple dispersal events, rapid diversification, recent divergence times, probable vicariance as a result of peninsular rifting, and rapid radiation and adaptation to novel environments.

Certain taxonomic rearrangements, based on our molecular phylogeny, require new assessments of taxon conservation status. The IUCN assessment, based on provisional phylogenies published by Luthy (1995) and Hunt (2006), included *Cochemeia fraileana* (Boed.) Breslin & Majure as a subspecies of *Cochemiea albicans* (A. Berger) Breslin & Majure, although our phylogeny shows strong support for *C. fraileana* as a separate taxon, in need of its own conservation assessment, especially due to its occurrence in close proximity to the expanding urban areas surrounding La Paz, BCS. Similarly, several other taxa in our expanded genus *Cochemiea* were not individually assessed, due to being classified as subspecies, which are sometimes assessed in IUCN global assessments, but were not included for the genus *Mammillaria* s.l. These include: *C. angelensis*, *C. estebanensis*, *C. goodrichii*, *C. blossfeldiana* subsp.

rectispina, and *C. thornberi* subsp. *yaquensis*. Of particular concern, the taxa placed as subspecies of *C. pondii*, namely *C. maritima* and *C. setispina*, are shown in our analyses to have strong support as separate species. Although *C. setispina* is known to be widespread (Rebman, personal communication, 2019), *C. maritima* is a very narrowly distributed coastal endemic and should be assessed, and the conservation status of the island isolated populations of *C. pondii* is not known. Since our climate change modeling results showed significant impacts on the island endemic *C. halei*, especially due to the island climate becoming less moderate and more like the adjacent peninsula, it may be that the Pacific island endemic *C. pondii* will face similar range contractions under climate change scenarios.

The phylogenetic and biogeographic results show *Cochemiea halei* to be the nearest relative to the widespread peninsular species, *Cochemiea poselgeri*, and that it is a very recently divergent taxon, most likely of mid-to-late Pleistocene origin. The habitat suitability modeling reveals that the species is highly localized, its narrow endemism correlated with an island climate and soil that are significantly different from the adjacent peninsula. Climate change, in particular a widening of the annual temperature range and warmer temperatures of the warmest quarter, is correlated with significant range contraction, even within the already narrow and fragmented habitat.

The population viability study corroborated the results of climate change modeling, with similar main areas of predicted range expansion and contraction under climate change. Higher elevation, ridge top habitats were shown to be more likely to persist, while lower elevation coastal, drier habitats will host declining populations. These two regions were also predicted as regions of expansion and contraction, respectively, in the climate change models. Under the more severe climate change scenarios, the availability of higher elevation habitat for expansion is greatly reduced. While deterministic models using current stage class population structure and vital rates show the higher elevation habitat to be refugia for the species in the future, stochastic models showed the strong possibility of declining populations overall, when recruitment and persistence were adjusted slightly downward.

The quantitative habitat suitability modeling, climate change projections and population viability analysis highlight the central importance of performing closer analyses of species of conservation concern where there is little prior data. *Cochemiea halei* is shown to be at elevated risk for extinction over the next approximately 100 years, with population persistence highly sensitive to slight changes in rates of recruitment of new individuals as well as slight adjustments in stage class persistence. These demographic sensitivities, in combination with the current fragmented and narrow distribution of the species and projected range contraction on the islands of between 21% and 53% under climate change, present a picture of a species under extinction pressure. The IUCN category for this species should be elevated from “vulnerable” to “endangered,” based on the species meeting the following criteria, as specified in the IUCN Red List Categories and Criteria, V. 3.1, under which any one of the below criteria categorizes the species as “endangered”:

1. “A3: A population size reduction of ≥50%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer (up to a maximum of 100 years), based on (and specifying) any of (b) to (e) under A1” with the main factor

being A1c: “a decline in area of occupancy, extent of occurrence and/or quality of habitat.”

2. “B1. Extent of occurrence estimated to be less than 5,000 km^2, and estimates indicating at least two of a-c: a. Severely fragmented or known to exist at no more than five locations. b. Continuing decline, observed, inferred or projected, in any of the following: (i) extent of occurrence (ii) area of occupancy (iii) area, extent and/or quality of habitat (iv), number of locations or subpopulations (v) number of mature individuals.”

3. “E. Quantitative analysis showing the probability of extinction in the wild is at least 20% within 20 years or five generations, whichever is the longer (up to a maximum of 100 years).” (IUCN 2012).

Future habitat suitability, climate change and population viability studies of other narrowly distributed peninsular and island endemics of the Baja region in *Mammillaria sensu* Breslin & Majure and *Cochemiea sensu* Breslin & Majure will be able to use this analysis for comparison and may derive useful strategies from the methodology. Of our taxon set representing 46 taxa in *Cochemeia* and *Mammillaria* from Baja California and adjacent regions, 12 were assessed in the IUCN global assessment of Cactaceae as “near threatened” to “endangered,” or 26% of our regional taxa. Given this conservation situation, in combination with many taxa not being assessed, there is much additional work to be done. Even though 70% of the cactus flora of Baja California is within protected areas, our studies showed that, in the absence of direct anthropogenic threats, extinction risks may have been underestimated for taxa in this region. Against a background of clarified phylogenetic, biogeographical, environmental and demographic understanding, the other at-risk members of the Mammilloid clade in this region will be able to be better protected in the future.

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APPENDIX A

SPECIMEN VOUCHERS

Taxa voucher information (collector, herbarium acronym or botanical garden, or commercial nursery/private collection). Material obtained from living collections, commercial nurseries or private collections is cited as: DBG (Desert Botanical Garden, Phoenix, AZ), MG (Mesa Garden, Belen, NM), JM (the private collection of Dr. Juergen Menzel), AA (Arid Adaptations Nursery, Tucson, AZ), CJCN (C and J Cactus Nursery, Vista, CA).

Acharagma roseanum (Boed.) E.F.Anderson — 1956-5611-01 *Cowper* 1076, (DES); ***Acharagma roseanum*** **subsp. *galeanense*** D.R. Hunt — (as *Escobaria roseana var. laui*) LAU 1187, MG, Cult. (DES); ***Ariocarpus retusus*** Scheidw. — DBG 1995-0225-01 *Anderson* 6273, Cult. from wild (DES); ***Coryphantha alversonii*** Orcutt — (as *Escobaria vivipara* var. *alversonii*) SB 1800, MG, Cult. (DES); ***Coryphantha cornifera*** Lem. — DBG 2017-0684-01 (DES); ***Coryphantha durangensis*** Britton & Rose — DBG 1993-0064-10 *Kiel* 8002, (DES); ***Coryphantha echinus*** Britton & Rose — DBG 1995-0125-01 *Slauson* 252, (DES); ***Coryphantha elephantidens*** Lem. — DBG 1955-5362-02 *Mieg* s.n., (DES); ***Coryphantha erecta*** Lem. — DBG 2012-0020-01 *Brack* 508, (DES); ***Coryphantha pallida*** Britton&Rose — DBG 2010-0024-01 *Chvastek* 171, (DES); ***Coryphantha recurvata*** (Engelm.) Britton&Rose — DBG 2018-0728-01, Cult. (DES); ***Coryphantha robbinsorum*** (W.H. Earle) A. Zimmerman — DBG 2016-0386-10, *Radke* s.n., (DES); ***Coryphantha sulcata*** (Engelm.) Britton&Rose — DBG 2017-0685-01, *Majure* 5605, United States, TX (DES); ***Coryphantha vivipara*** (Nutt.) Britton & Rose — DBG 2018-0694-01 *Majure* 6795, United States, NE, (DES); ***Cumarinia odorata*** (Boed.) Buxb. — DBG 2013-0944-01, MG 165, Cult. from wild (DES); ***Escobaria chihuahuensis*** Britton & Rose — DBG 2012-0237-01, Cult. (DES); ***Escobaria vivipara var. buoflama*** (P. Fischer) N.P. Taylor — *Lutz* LZ135, MG, Cult. (DES); ***Escobaria tuberculosa*** (Engelm.) Britton & Rose — DBG 2012-0002-01 *Brack* 428, Cult. from wild (DES); ***Escobaria zilziana*** (Boed.) Backeb. — DBG 2013-0920-01, *Brack* 602, Cult. from wild (DES); ***Lophophora williamsii*** J.M. Coult. — DBG 2017-0586-01, Cult. (DES); ***Mammillaria armillata*** K. Brandegee — *Gates* s.n., JM, Cult. (DES); ***Mammillaria albicans*** (Britton & Rose) A. Berger — *Lau* 1374, MG, Cult. (DES); ***Mammillaria angelensis*** R.T. Craig — DBG 1959-6429-01, *Lindsay* 7186, Cult. from wild (DES); ***Mammillaria blossfeldiana*** Boed. — DBG 2013-0240-01, MG, Cult. from wild (DES); ***Mammillaria bocensis*** R.T. Craig — DBG 1993-0269-10, *Reppenhagen* s.n., Cult. from wild (DES); ***Mammillaria boolii*** G.E. Linds. — DBG 1993-0260-21 *Eggli and Nyfeller* s.n., Cult. from wild (DES); ***Mammillaria brandegeei*** Engelm. ex K. Brandegee — DBG 2013-0422-01 MG 583.2, Cult. (DES); ***Mammillaria brandegeei*** subsp. ***gabbii*** (J.M. Coult.) D.R. Hunt — JM, Cult. (DES); ***Mammillaria bullardiana*** (H.E. Gates) Boed. — *Lau* 1228, JM, Cult. from wild, (DES); ***Mammillaria capensis*** (H.E. Gates) R.T. Craig — *Gates* s.n., JM, Cult. from wild (DES); ***Mammillaria cerralboa*** Orcutt — *Lau* 39, JM, Cult. from wild (DES); ***Mammillaria dioica*** K. Brandegee — DBG 1990-0624-02 *Pinkava* 8804, Cult. from wild (DES), *Lau* 1, JM, Cult. from wild; ***Mammillaria estebanensis*** G.E. Linds. — *Hoxey* 299.2, MG, Cult. from wild; ***Mammillaria evermanniana*** Orcutt — *Gay* ISI-90-16, JM, Cult. from wild; ***Mammillaria fraileana*** (Britton & Rose) Boed. — DBG 1993-0263-10 *Supthut* 7036, Cult. from wild, (DES); ***Mammillaria goodridgii*** Scheer — *Rebman* s.n., JM, Cult. from wild (DES); ***Mammillaria goodridgei*** subsp. ***rectispina*** E.Y. Dawson — JM, Cult. from wild (DES); ***Mammillaria grahamii*** Engelm. — DBG 2016-0061-01, Cult. from wild (DES); ***Mammillaria guelzowiana*** Werderm. — DBG 2017-0173-01 CJCN, Cult. (DES); ***Cochemiea halei*** Brandegee — *Brack* 1662 JM, Cult. from wild (DES); ***Mammillaria heyderi*** Muehlenpf. subsp. ***macdougalii*** (Rose) D.R. Hunt — DBG 2018-0478-01 *Majure* 7054, United States, AZ (DES); ***Mammillaria huitzilopotchtli*** D.R. Hunt — DBG 2013-0222-01 *Otero* 13, Mexico, Puebla (DES); ***Mammillaria hutchisoniana*** (H.E. Gates) Boed. — DBG 1960-6592-02 Cult. (DES), *Reppenhagen* 731, JM, Cult. from wild.; ***Mammillaria insularis*** H.E. Gates ex Shurly — DBG 1992-0773-0103 Cult.; ***Mammillaria jamaicensis*** Areces — DBG 2018-0509-01 *Majure* 7057, Jamaica, Parish Trelawny; ***Mammillaria johnstonii*** Orcutt — *Glass and Foster* 2690, ISI 939, JM, Cult. from wild; *Brack* 432, JM, Cult. from wild; ***Mammillaria mainae*** K. Brandegee — *Glass and Foster* s.n. ISI 832, JM, Cult. from wild; ***Cochemiea maritima*** (G.E. Linds.) D.R. Hunt — DBG 1994-0669-10 *Rebman* 2301, Cult. from wild (DES); ***Mammillaria multidigitata*** Radley ex G.E. Linds. — DBG 1990-0769-02, *Lindsay* s.n., Cult. from wild (DES); ***Mammillaria neopalmeri*** R.T. Craig — DBG 1990 0768 01 *Mueller* s.n., Cult. from wild (DES); ***Mammillaria peninsularis*** Orcutt — *Lau* 46, JM, Cult. from wild; ***Mammillaria petrophila*** K. Brandegee — *Lau* 52, JM, Cult. from wild; ***Mammillaria petrophila*** K. Brandegee subsp. ***arida*** (Rose ex Quehl) D.R. Hunt — JM, Cult. from wild; ***Mammillaria phitauiana*** (Baxter) Werderm. — *Brack* 1259, JM, Cult. from wild, *Lau* 54, JM, Cult. from wild (DES); ***Cochemiea pondii*** Greene — *Lindsay* 550, JM, Cult. from wild, *Lau* 8, JM, Cult. from wild; ***Cochemiea poselgeri*** Hildm. — DBG 1986-0646-21 *Newberry* CN26, Cult. from wild, (DES), DBG 1986-0477-01 *Newberry* 226, Cult. from wild (DES); ***Mammillaria pottsii*** Scheer ex Salm-Dyck — DBG 1991-0616-10 *Kozak, Poole and Ecker* s.n., Cult. from wild (DES); ***Mammillaria prolifera*** (Mill.) Haw. — DBG 2018-0198-01 *Majure* 6584, Dominican Republic (DES); ***Mammillaria schumannii*** Hildm. — DBG 1992-0813-01, Cult. (DES); ***Mammilaria senilis*** Lodd. Ex. Salm-Dyck — *Brack* 497, JM, Cult. from wild; ***Cochemiea setispina*** Engelm. ex. J.M. Coult. — DBG 1959-6430-01 *Lindsay* 7202, Cult. from wild (DES), DBG 1939-0088-01 *Lindsay* s.n., Cult. from wild (DES); ***Mammillaria sheldonii*** (Britton & Rose) Boed. — DBG 1993-0271-10 *Eggli and Nyfeller* 1968c, Cult. from wild (DES); ***Mammillaria slevinii*** (Britton & Rose) Boed. — *Brack* 1251, MG, Cult. from wild (DES); ***Mammillaria sp. SA —*** *Menzel* s.n., JM, Cult. from wild; ***Mammillaria sp. SL —*** *Menzel* s.n., JM, Cult. from wild; *Lau* 44, JM, Cult. from wild; ***Mammillaria sphacelata*** Mart. — DBG 1955-5466-01 *Gates* s.n., Cult. from wild (DES); ***Mammillaria tayloriorum*** Glass & R.A. Foster — *Glass and Foster* 2686, JM, Cult. from wild; ***Mammillaria tetrancistra*** Engelm. — (two collections by Majure, get details); ***Mammillaria thornberi*** Orcutt — DBG 2016 0013 01 *Byrd* s.n., Cult. from wild (DES); ***Mammillaria***

viridiflora (Britton & Rose) Boed. — DBG 1995-1315-10 *Chamberland* s.n., Cult from wild (DES); ***Mammillaria wrightii*** Engelm. — *Brack* 94, JM, Cult. from wild; ***Mammillaria wrightii*** Engelm.subsp. ***wilcoxii*** Toumey ex K. Schum. D.R. Hunt — *Brack* 3, Cult. from wild; ***Mammillaria yaquensis*** R.T. Craig — DBG 2011-0073-01 Cult. (DES); ***Neolloydia conoidea*** Britton & Rose — DBG 1957-5902-01 *Cowper* s.n., Cult. from wild (DES); ***Ortegocactus macdougallii*** Alexander — DBG 2009-006-01, Cult. from wild (DES); ***Strombocactus dicsiformis*** Britton & Rose — ISI 1438, Cult.; ***Turbinicarpus alonsoi*** Glass & S. Arias — *ten Hoeve* 268, JM, Cult. from wild; ***Turbinicarpus beguinii*** (N.P. Taylor) Mosco & Zanov. — DBG 2012-0099-01, Cult.; ***Turbinicarpus viereckii*** (Werderm.) V. John & Riha — DBG 2012-0184-01 *Lau* 1159, Cult. from wild (DES).

BIOGRAPHICAL SKETCH

Peter Breslin made the leap into professional botany after a 25 year career teaching high school mathematics and English. During all of his available vacations and breaks, Breslin traveled to find and photograph rare cacti in habitat, in the Southwest of the United States as well as Sonora and Baja California and Baja California Sur of Mexico. The interest in hard to find, poorly mapped populations of cacti expanded to include a fascination with endemism and biogeography. During a year off from teaching secondary school, Breslin decided to apply to the Environmental Life Sciences Ph.D. program at Arizona State University, where he was accepted in the fall of 2014. Under the advisement of Julie Stromberg and Martin Wojciechowski, with the help of committee members Lucas Majure, Shannon Fehlberg, Fabio Suzart de Albuquerque and Jon Rebman, Breslin pursued in depth research into the *Mammillaria* and *Cochemiea* of Baja California and adjacent regions, using molecular phylogenetics, reconstruction of ancestral biogeography, species distribution modeling and population viability analysis with demographic stage class matrix models. Breslin hopes to work in the research department of a botanic garden, or teach and continue to pursue research in the Cactaceae and other rare and endangered plants in need of conservation.