

ABSTRACT

PHYLOGENETIC ASSESSMENTS FOR CALIFORNIA'S HIGHEST RISK MAMMALS

Anthropogenic activities have severely impacted much of the life on Earth. To protect and preserve our remaining natural areas, conservation biology has traditionally focused on the impacts of humans on natural systems. Recently, conservation biology has incorporated phylogenetic metrics to better understand the evolutionary value of imperiled species. All extinctions include the loss of some biological value, but extinctions of many closely related species result in a disproportionate loss of evolutionary history relative to the same number of extinction events among distantly related species. Mammals are one of the most well-studied groups in phylogenetics, making them ideal candidates for evaluating the loss of evolutionary history that accompanies extinction. I use data collected from a published phylogeny on California's native terrestrial mammals to investigate the relationships between conservation status, as a proxy for extinction risk, and phylogeny. I examined the potential losses of phylogenetic diversity and disparity by calculating the change in Phylogenetic Diversity (PD) and Net Relatedness Index (NRI) when species with elevated extinction risks were pruned from the California mammalian tree of life. These analyses reveal that the potential loss in PD and NRI is equal to or even lower than expected from a random loss of the same predicted number of species. These results are consistent with global trends for mammals, but show how this global pattern is also present at some regional scales, which is not always the case in previous investigations.

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December 2018

PHYLOGENETIC ASSESSMENTS FOR CALIFORNIA'S
HIGHEST RISK MAMMALS

by
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A thesis
submitted in partial
fulfillment of the requirements for the degree of
Master of Science in Biology
in the College of Science and Mathematics
California State University, Fresno
December 2018

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ACKNOWLEDGMENTS

I would like to thank Shelby Moshier and Michael Bravo for their support in data organization and collection for this project. Lastly, I would like to acknowledge the support of the Division of Research and Graduate Studies at California State University, Fresno for supplying the grants that helped make the dissemination of these results possible.

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INTRODUCTION

Modern humans have drastically altered the planet over the last 200 years, ushering in a unique period of Earth's history – the Anthropocene epoch (Crutzen 2002). One impact of human activities is a rapid increase in the rate of species extinctions, potentially causing the sixth mass extinction in Earth's history (Wake and Vredenburg 2008). Mass extinctions are multifaceted; at the most basic level, they involve the loss of more than 75% of all species on the planet (Barnosky et al. 2011). Not every species is equivalent; extinctions can be viewed in terms of their ecological (Fowler 2010), economic (reviewed in Cardinale et al. 2012), and evolutionary (Jablonski 2001) impacts. The evolutionary impacts of Earth's last five mass extinctions have been well explored (Jablonski 2005), but the potential sixth mass extinction is often described in terms of its ecological and economic consequences (Cardinale et al. 2012) rather than the potential evolutionary implications (Raup 1979, Heyer et al. 1988). The evolutionary diversity of species can be represented as the tree of life – a single trunk representing common ancestry that flows into major branches representing Kingdoms and Phyla, all the way through smaller branches (Families), twigs (Genera), and tips that represent individual species. If a subset of species on that tree is lost at random with respect to its placement on the tree (phylogeny), most major branches, and thus most evolutionary diversity, remain preserved (Mace et al. 2003). Nee and May (1997) revealed that 81% of phylogenetic branch length remained when 95% of species were removed, but only when the 5% remaining were randomly distributed across the phylogenetic tree. Understanding phylogenetic history is important because when extinction is phylogenetically non-random, entire branches on the tree of life can be lost, dramatically reducing evolutionary diversity and the ability to adapt to

future changes (Purvis and Hector 2000). The evolutionary dimension of biodiversity is one that conservation biologists are working to incorporate with economic and ecological dimensions to maximize the conservation of all facets of biodiversity (Wilson and Perlman 2000).

Mammals represent a major branch on the vertebrate tree of life and have been shown to disproportionately influence the ecology of the systems they inhabit (Roemer et al. 2009, Davidson et al. 2012). California is part of a global biodiversity hotspot (Calsbeek et al. 2003), which includes unique mammal diversity. It is also host to approximately 200 of the 440 mammal species native to the United States and has the highest mammal diversity in the continental US (Stein et al. 2002). The evolutionary diversity of mammals is well known (Davies et al. 2008), as are extinction risks (Purvis and Hector 2000a, Cardillo et al. 2005, Cardillo et al. 2006). However, these disparate sources of information have not been combined to ask the following question: What are the potential evolutionary and phylogenetic implications of current mammalian extinction risk in California?

Conservation status assessments often vary in assessments of the same species (Arponen 2012, Reece et al. 2013, Reece and Noss 2014). I collected conservation status listings from five systems: The International Union for the Conservation of Nature (IUCN; see Rodrigues et al. 2006), the Federal and California Endangered Species Acts (Barbour and Kueppers 2012), the global and state Conservation Status Assessments (Regan et al. 2004). I performed the analyses under each metric of extinction risk and under a summary statistic that averages across all six metrics.

I sought to determine the phylogenetic diversity (genetic difference and evenness) and disparity (mean genetic distance) amongst California's mammals by determining whether species (and subspecies; see Appendix A) with higher at-risk

statuses are non-randomly distributed on the mammalian phylogenetic tree. If status is correlated with relatedness in the phylogeny, then phylogenetic diversity and disparity will change significantly when these species are removed from the tree of life. As reviewed in Veron et al. (2017), global extinction risk does tend to be phylogenetically clustered, but the pattern varies by taxon and region. Global mammalian extinction risk does not show a strong pattern of phylogenetic clustering (Huang et al. 2012), but this pattern has not been investigated based on the conservation statuses of Californian mammals or across metrics of extinction risk beyond the IUCN (Rodrigues et al. 2006), which can be subjective (Mace and Lande 1991, Cassini 2011).

LITERATURE REVIEW

Anthropogenic Extinctions

The richness and abundance of species, populations, and genes is a fundamental dimension of biodiversity that directly impacts the functioning of ecosystems (Chapin et al. 1997). In the past 200 years, human impacts have permanently changed the earth, ushering in a new era, the Anthropocene. Anthropogenic activities have created unique consequences for biodiversity, causing many plant and animal species to be at risk of extinction. Specifically, anthropogenic activities associated with large-scale agriculture (Phalan et al. 2011), forestry (Newton 2007), and urbanization (McKinney 2002) are large contributors to extinction events and native biodiversity loss (see Pellet et al. 2004, Pauchard et al. 2006). The shared consequences of these anthropogenic activities consist largely of overexploitation, changes in land use (agricultural and urban), invasive species, and environmental pollution (Lande 1998).

The impacts of biodiversity loss have been well-studied, and above all, the overexploitation of resources is the largest driver of biodiversity loss globally (Maxwell et al. 2016). Overexploitation can be described as the harvesting of wild resources at a rate that cannot be mediated by natural regrowth. Maxwell et al. (2016) summarized that 6,241 of 8,688 threatened and near-threatened species around the globe are currently affected by overexploitation for commerce, recreation, and substance. The dangers of these impacts become more threatening as humans continue to push the boundaries of wild areas.

As the global human population surpasses 7.6 billion people, natural areas are rapidly being repurposed for agricultural and urban needs. Recently, 1.53 billion hectares of land were dedicated for agricultural purposes (Foley et al.

2011), while urban centers are expected to expand to 0.18 billion hectares by 2030 (Seto et al. 2012). In the process of global human expansion, populations of native species have been destroyed, fragmented, or translocated, leading to drastic implications for global biodiversity (Rands et al. 2010). This drastic change in land use has led to 70% of the remaining forest cover being within 1km of the forest's edge. The loss of ecosystem function coupled with forest fragmentation reveals a considerable loss of resident biodiversity by 13-75% (Haddad et al. 2015).

The future of global ecosystem productivity and biodiversity in remaining wild areas will be heavily dependent on the area and quality of the habitat fragments that remain (Haddad et al. 2015). The effectiveness of these areas will be dependent on the quality, connectivity, and total area remaining in each patch of wilderness. As human development breaches the final barriers of wilderness, increased invasive exchanges, including invasive species and diseases, are to be expected (Cohen and Carlton 1998, Mooney and Cleland 2001). This increase in biotic exchange has been associated with elevated extinction risk in native species (Rodda et al. 1997, Gurevitch and Padilla 2004, Pimentel et al. 2005) and biodiversity loss (Molnar et al. 2008).

Environmental pollution is an additional concern for future extinctions and biodiversity loss (Maxwell et al. 2016). A side effect of large-scale agriculture and domestic and industrial development is the pollution byproducts generated by them. These pollutants have been well-documented in sediments (Cohen et al. 1993), runoff in water (Brodie et al. 2012), and contaminant presence in the air (Newman 1979). More recently, the negative effects that environmental pollution has on biodiversity have become an important area of study (Terlizzi et al. 2005). Anthropogenic activities have made severe impacts around the earth, affecting

wildlife biodiversity and ecosystem efficiency, both directly and indirectly. As anthropogenic activities continue to influence the world around us, extinction events become more prevalent, and conservation biologists will have a greater responsibility to investigate this unique period in Earth's history to alleviate potential extinction events in the next century.

Conservation Biology

Conservation is a crisis-driven discipline of biology. As species become more 'at-risk' of extinction, conservation biology serves to investigate the implications of these predicted extinctions. Although extinctions are a natural part of the evolutionary process, anthropogenic extinctions reveal idiosyncratic economic, ecological, and evolutionary consequences. Conservation planning is constantly being refined to minimize biodiversity loss through the preservation of select areas through conservation actions (Pressey and Cowling 2001), but conservation biology has traditionally focused on economic and ecological aspects of preservation at the species level. Though these aspects are important to conservation implementation, I argue that they do not paint the whole picture of the ecosystems and the services they provide. Here, I emphasize the importance of phylogenetics in the field of conservation biology. It is important to understand the phylogenetic dimensions of extinctions and extinction risk to implement useful conservation policies and ensure the survival of species and the preservation of the tree of life.

This study utilized phylogenetic systematics to evaluate the evolutionary history for the Californian native, terrestrial mammals. This recent style of conservation assessment provides additional information that is based upon the

traditional approaches of describing extinction risk (reviewed in Cardinale et al. 2012).

Phylogenetic Assessments for Conservation Biology

Conservation assessments continuously evolve, and methods of evaluating biodiversity loss improve (Egoh et al. 2007). In recent years, phylogenetics have been utilized to incorporate evolutionary history into conservation assessments (Crandall et al. 2000) and the conservation community has emphasized the importance of phylogenetic outlooks in conservation biology (Hartmann and Steel 2006, Minh et al. 2006). Purvis et al. (2005) emphasized three areas of insight provided by phylogenetics in conservation biology that act a basis for understanding phylogenetics as a metric for conservation biology. These foci include delimiting units and currencies of biodiversity assessments, record keeping for evolutionary processes, and creating a framework for understanding how anthropogenic exploitation affects biodiversity. In this thesis, I addressed the first area of insight: delimiting currencies for understanding phylogenetic biodiversity. I incorporated this area of insight by assessing the diversity and disparity of California's mammals in the phylogenetic context.

By delimiting currencies in phylogenetic assessments, management plans can look outside the traditional scope of focusing on entire species. Phylogenetic assessments solve this issue by providing extra units of biodiversity measurement, such as evolutionary significant units (Moritz 1994) and currencies (Faith 1992a).

With all the benefits of including phylogenetic methods into conservation assessments, they do have shortcomings. Phylogenetic assessments may lack the evolutionary information necessary for providing valuable conservation assessments (Purvis et al. 2005, Winter et al. 2013) because of uncertain

assumptions of evolutionary relationships (Shooner et al. 2018). Recently however, there has been a swell of scientific justification for conserving all components of biodiversity, including the preservation of evolutionary information (Mace and Purvis 2008, Santamaria and Mendez 2012, Winter et al. 2013), since the loss of species will inevitably lead to a loss of evolutionary diversity (Purvis et al. 2000, Mace et al. 2003).

Evaluating Evolutionary History

There are at least two common approaches for assessing evolutionary diversity (Type II biodiversity indices *sensu* Vellend 2011): phylogenetic diversity and evolutionary distinctiveness. Phylogenetic diversity accounts for variance in the richness and evenness of species present on a phylogenetic tree and is important in understanding the total amount of evolutionary history in any given phylogeny (Faith 1992b). Evolutionary distinctiveness is used to quantify the number of relatives of a species, and how phylogenetically distinct they are. Here, I utilized phylogenetic diversity to investigate the diversity of traits across an entire phylogeny for a community-based approach. Alternatively, evolutionary distinctiveness is often utilized to measure the distinctiveness of species, and does not fit well into the context of the question presented in this thesis.

Vanewright et al. (1991) proposed ‘phylogenetic diversity’ (PD) as a novel variable for conservation biology. Phylogenetic diversity is essential for maintaining genetic uniqueness throughout the tree of life, and preserving unique features developed in these select lineages (Pellens and Grandcolas 2016). The increasing threat of the sixth mass extinction event puts pressure on the conservation biology community to maintain standardized methods for evaluating

conservation priorities and threats in the phylogenetic context (Faith 1992a, Webb 2000, Webb et al. 2002).

Assessing phylogenetic disparity is another common method of evaluating evolutionary diversity in the context of conservation. Phylogenetic disparity measures how distinct, on average, any two lineages in the phylogeny are from one another (Webb et al. 2002). Disparity and diversity are important for differentiating between a phylogeny with many species that are closely related (high diversity and low disparity) and one with deep divergences among clades but few species (high disparity, low diversity) (Gould 1991, Foote 1997). Phylogenetic disparity can be used to address a phylogeny within larger community structures (Webb et al. 2008) including net relatedness index (NRI) and nearest taxon index (NTI; Webb et al. 2002). Both metrics have been widely used to determine the phylogenetic distinctiveness within communities (Winter et al. 2013). Net Relatedness Index (NRI) is used to assess relatedness on a longer time scale, whereas NTI reflects a more finely-scaled relatedness. I used NRI to address the mean pairwise distance to reflect the phylogenetic structure across the entire phylogeny (Webb 2000) rather than NTI, which calculates the mean of the branch lengths connecting species to their relatives (Webb et al. 2002). By utilizing NRI, I was able to measure the extent of clustering or evenness of taxa within a phylogeny to understand the evolutionary relatedness of species (Webb et al. 2002).

Relevance

Conservation biology focuses on preserving biodiversity (Winter et al. 2013), and the impacts of biodiversity loss are complex on local and global scales (Duffy et al. 2007, Cardinale et al. 2012). Conservation biology advances

alongside interdisciplinary fields (Berkes 2004) by incorporating new methodologies such as phylogenetics (Bininda-Emonds et al. 2000, Cardillo et al. 2005, Purvis et al. 2005). Phylogenetic applications have steadily increased in conservation biology over the last decade in terms of their applicability for investigating processes such as extinction (Purvis et al. 2000), invasive species (Winter et al. 2009), and ecosystem functions and services (Faith et al. 2010, Srivastava et al. 2012).

As the literature surrounding conservation biology accumulates, phylogenetic perspectives on biodiversity loss are continuously updated. It is well-known that species are not equal in terms of their evolutionary histories (Pellens and Grandcolas 2016) and now conservation biology has shifted more attention to evolutionary history.

In this study, I addressed conservation biology through two metrics (PD and NRI) to investigate the evolutionary relationships of endangered species in terms of conservation biology. These metrics of conservation evaluation have been used in previous studies but have never been utilized in the context of California's mammalian phylogenetic tree of life. This research will add to the foundation of evolutionary-based conservation efforts and will provide insight on the evolutionary values of California's native terrestrial mammals for species in need of conservation action.

METHODOLOGY

Taxonomic Data

I compiled taxonomic data on California's native terrestrial mammalian species from the IUCN Red List, California Department of Fish and Wildlife (CDFW), NatureServe, and the American Society of Mammalogists (ASM). I removed all non-native species from the dataset. I decided to remove Cetaceans from the phylogeny because they are not year-round residents to the California coastline. After I removed these individuals, the dataset consisted of 168 taxa.

Binning Species

I collected status rankings from five different assessments: Global Conservation Status Assessment (GCSA), State (SCSA), Federal U.S. Endangered Species Act (ESA), California Endangered Species Act (CESA), and the IUCN Red List. Because conservation status for the same species may vary across different assessment systems, rankings were translated from categories such as "Vulnerable" and "Threatened" into a number scheme to calculate Extinction Risk Scores (ERS) for the taxa within each scheme, similar to Reece and Noss (2014). Extinction Risk Scores were ranked from 6 to 1 by order of increasing extinction risk. Non-threatened and species with insufficient data were scored with the largest numeric values possible for that conservation assessment (Table 1). To anecdotally depict the variation in status of the same species across all five assessments, I conducted pairwise regressions of each assessment using numerical categories as given in Table 1 (see Results).

From Table 1, conservation agencies consist of Global/State Conservation Assessment (GSA/SCSA), Endangered Species Act (ESA), California Endangered Species Act (CESA), and the International Union for the Conservation of Nature

Table 1. Extinction Risk Scores (ERS) for five conservation agencies.

	GCSA	SCSA	ESA	CESA	IUCN
No Risk	6 -G1	6 -S1	5 -Data Deficient	5 – Data Deficient	5 – Data Deficient
Low Risk	5.5 - G1.5	5.5 - S1.5	4 - None	4 - None	4 - Least Concern
Medium Risk	5 - G2	5 - S2	3 - Proposed	3 - Proposed	3 - Near Threatened
	4 - G3	4 - S3	Threatened	Threatened	
	3 - G4	3 - S4	2 - Threatened	2 - Threatened	2 - Vulnerable
	2 - G5	2 - S5			
High Risk	1 - G6	1 - S6	1 - Endangered	1 - Endangered	1 - Endangered/Critically Endangered

(IUCN). Species were grouped into High-, Medium-, Low-, and No-risk groups based on rankings from 1 to 4, and 1 to 6. Higher ranking numbers are associated with lower extinction risk for each conservation agency. Numbers to the left of the hyphens are the standardized risk scores, whereas the numbers and words to the right of each hyphen are the risk category names provided by the corresponding agency.

The five conservation assessments I incorporated do not use the same classification scheme to depict extinction risk. I made the five assessments comparable by classifying taxa into High-, Medium-, Low-, and No-Extinction risk categories as given in Table 1. Species that were classified as “Data Deficient,” “S1,” or “G1,” have very low extinction risk and were not included in these treatments. I repeated these analyses on each of the five conservation assessments independently using the High, Medium, and Low categories in Table 1.

Generating the Phylogeny

The phylogeny was adapted from a previously published supertree that contained over 4,500 species found across the world (Bininda-Emonds et al. 2007). I trimmed the original tree down to the 168 native terrestrial Californian species using the ‘geiger’ (Harmon et al. 2008) ‘phytools’ (Revell 2012), and ‘picante’(Kembel et al. 2010) packages in the program R v3.1.1 (R Core Team 2017).

Calculating PD and NRI

I removed species of special concern according to bin type (High, Medium, Low), for each conservation agency (ESA, CESA, GCSA, SCSA, IUCN), using the picante package in R. This allowed me to analyze how extinction risk was distributed within the mammalian phylogeny. Each analysis consisted of three hierarchically structured species removals and calculations. First, I removed species binned in High, then High+Medium, and finally High+Medium+Low extinction risk. Phylogenetic diversity was measured by using the metric of PD (Faith 1992b, Faith and Baker 2006) and disparity was assessed using the NRI (NRI; Webb et al. 2002). Phylogenetic Diversity (PD) was derived from the phylogeny by summing a group of branch lengths using the minimum distance between nodes. I calculated NRI through R using the *predictABEL* (Kundu et al. 2011) package. This method scores mean pairwise phylogenetic distance of taxa within a clade relative to the rest of the tree. I was then able to describe the phylogenetic diversity of California’s mammals by comparing PD and NRI metrics to those for the tree of all mammals in the dataset.

I created a null distribution for each treatment by running 1,000 randomized simulations for each PD and NRI assessment to determine whether the

phylogenetic distribution of extinction risk was randomly distributed across the tree phylogeny for the conservation assessments. I considered the PD or NRI calculation for each treatment to be significantly different from the null distribution when it fell outside of the null distribution. The *predictABEL* package in R includes this statistical test and automatically tested for significance in the NRI assessments.

RESULTS

Taxonomic Data

After compiling these taxonomic data, I determined the distribution of species by habitat and taxonomic family. These findings revealed a large and relatively even spread in each of these categories (distribution of habitat types given in Figure 1). Rodents were the largest group on the order level consisting of 55% of the total number of taxa in the phylogeny. Herbivores were the largest diet type group in the dataset and made up 63% of the total number of individuals in the phylogeny.

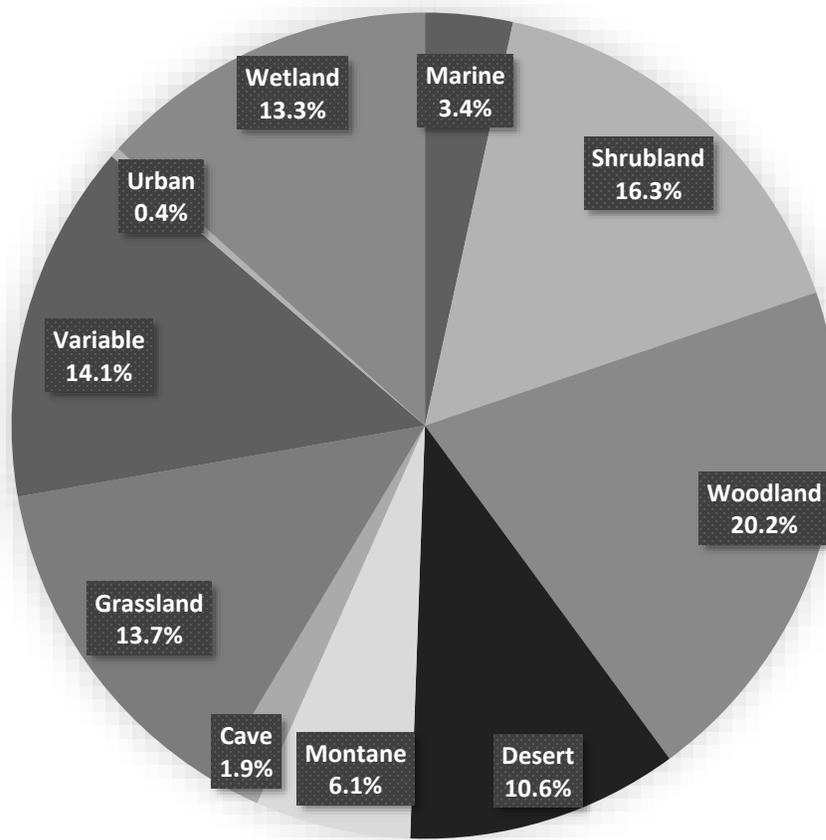


Figure 1. Distribution of habitat type across all taxa for a dataset of 263 taxa. Habitat data were collected from the IUCN Red List and cross referenced with the California Department of Fish and Wildlife (CDFW). Taxa that were listed with two or more habitat types were classified as “variable.”

Binning Species

The conservation status of species varied heavily across assessment types. The boxplots of the High/Medium/Low ERS score spread revealed a large amount of variance across assessments for High and Low species scores (Figure 2). I observed considerably fewer Medium scores for species across all conservation assessment types, although the standard deviation of this group was higher than the High and Low boxplots (Figure 2). The IUCN, ESA, and CESA had a similar spread of High-, Medium-, and Low-risk evaluations across species. However, both the global CSA and state CSA rankings listed more species as being High-risk compared to the other three assessments. Medium risk rankings were the least common across all assessment types.

When I regressed numerical scores between all pairwise combinations of assessment system, I observed high correlation between the State (SCSA) and Global (GCSA) Conservation Status Assessment scores ($R^2=.73$) and the US (ESA) and California (CESA) Endangered Species Act scores ($R^2=.30$) (Figure 3). The p-values for each regression were <0.05 for each assessment comparisons for all regressions ($\alpha=0.05$). The correlations I tested remained significant even after performing a Benjamini-Hochberg correction (Benjamini and Hochberg 1995) on each comparison. Most assessments showed a weak correlation with a slightly positive slope, except for the comparisons between the IUCN and Global CSA, and the IUCN and State CSA, which both had negative slopes.

The assessment of habitat type revealed non-significant association between extinction risk categories (see Table 1) and habitat type, population trend, population fragmentation, and diet type (see Appendix B). The chi squared test for habitat type compared to the High, Medium and Low bins I used in this study was non-significant ($p > .99$; Table B.1) as were the values for population trend ($p > .70$; Table B.2), diet type ($p > .37$; Table B.3), and population fragmentation ($p > .98$; Table B.4).

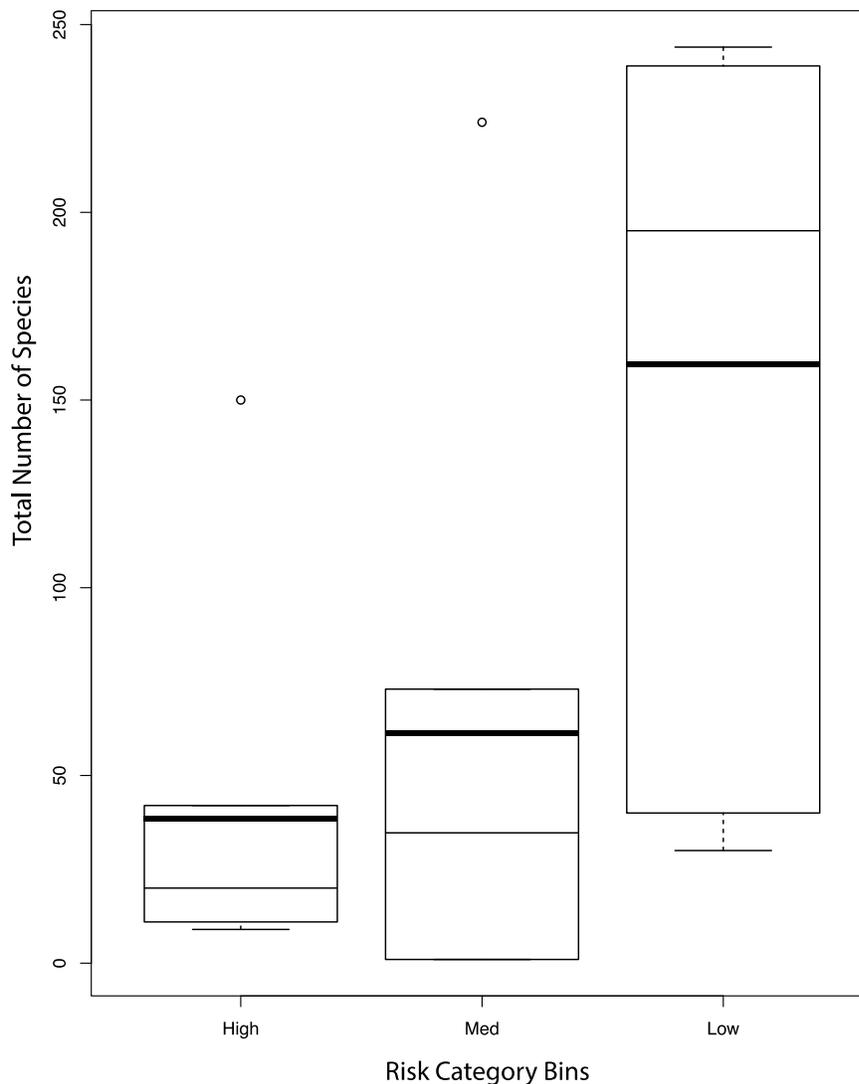


Figure 2. Comparison of all bins for all five conservation assessments. This boxplot depicts the variance for all taxa across all five assessment types that were binned into High, Medium and Low extinction risk categories. The y-axis 'Total Number of Species' accounts for the total number of taxa registered cumulatively across all conservation assessments; therefore, every species is accounted for five times. Error bars designate minimum and maximum number of species listed in each category. The thin black bars represent median, and the thick black bars represent the mean of each category. Points located above the High and Medium bins represent outlier conservation assessments (State Conservation Status Assessment, and Global Conservation Status Assessment, respectively).

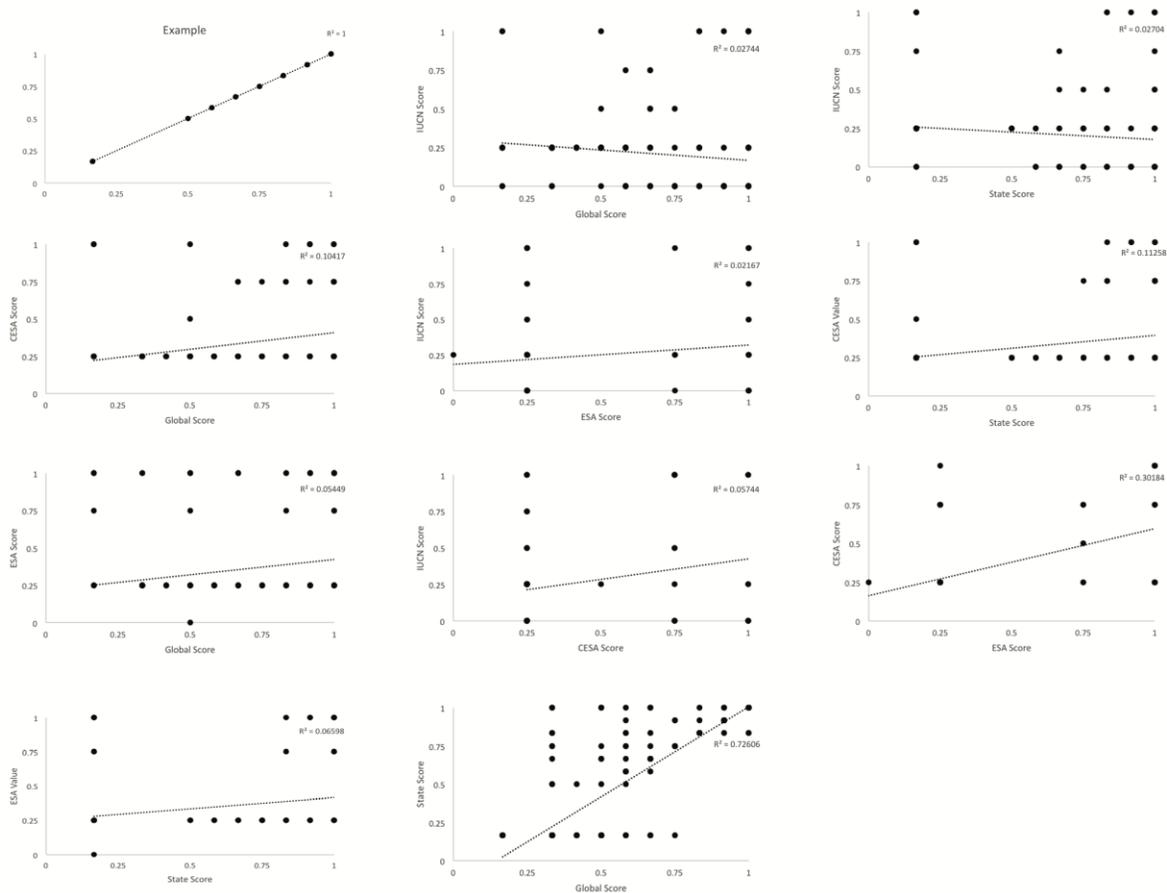


Figure 3. Pairwise comparisons for all taxa assessed for extinction risk by the International Union for the Conservation of Nature Red List (IUCN), Endangered Species Act (ESA), California Endangered Species Act (CESA), Global Conservation Status Assessment (GCSA), and the State Conservation Status Assessment (SCSA). All comparisons were standardized on a scale from 0 to 1, with the value of one corresponding with the most elevated level of extinction risk. The top left plot shows a hypothetical relationship between two different assessment types, which are perfectly correlated with an R squared value of 1. There were low levels of correlation across all assessment comparisons apart from the GCSA/SCSA ($R^2=.73$) and ESA/CESA ($R^2=.30$) plots.

Generating the Phylogeny

This phylogeny was adapted from the original supertree (Bininda-Emonds et al. 2007) using the “drop.tip” function from the “phylo” package in R. This phylogeny was produced using FigTree v1.4.3. Each taxonomic order was designated with an identifying color (Figure 4).

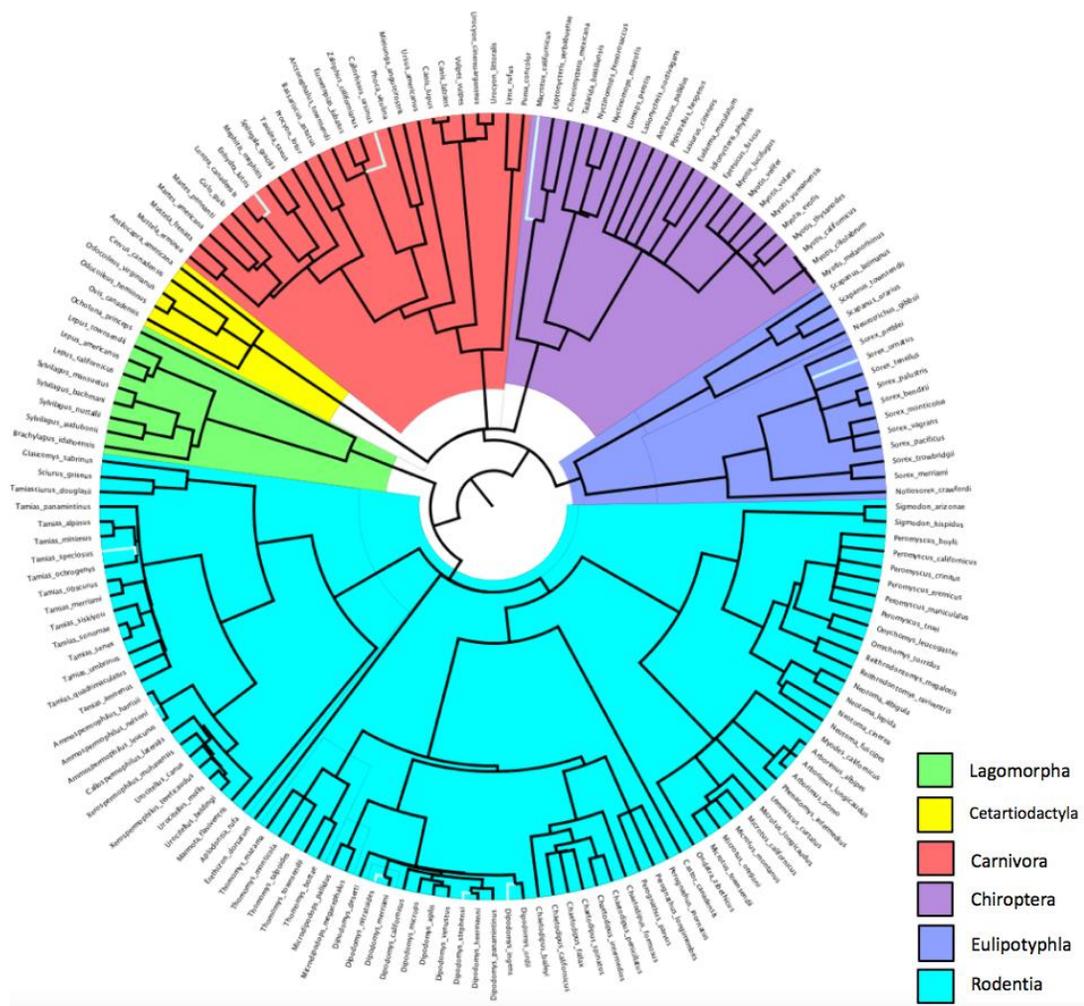


Figure 4. A phylogenetic tree showing the extinction risk in California’s mammals. This phylogeny consists of 168 native, terrestrial mammals and depicts a removal of taxa within the highest risk categories from the Global Conservation Status Assessment (CSA). I culled all nine taxa listed as “Endangered” from the tree and highlighted their branches with white bars. Extinction risk in this cull was phylogenetically random and revealed no significant difference from 1000 iterations of the random culls of the same number of species.

Calculating PD and NRI

In nearly every assessment, PD was highly conserved after removing at-risk species, with PD dropping an average of 19.1% in the phylogeny, with no incidence of a loss of PD significantly greater than the null distribution of PD values.

I calculated that 7% of the total number of native terrestrial mammals have elevated extinction risk according to the IUCN. When these species are trimmed from the phylogeny, PD dropped by 2.2%. Comparatively, when I ran 1,000 random iterations with the same percentage loss, the average loss of PD was 11.2%. The loss of PD for this treatment was not significantly greater than what would be observed from a random loss of the same number of species (Figure 5). I observed similar trends in other treatments. When species in the High-risk categorization scheme for GCSA were removed from the phylogeny, PD dropped by 1.3% (16.3% in the control). The largest decrease in PD occurred when species in the High SCSA bin were trimmed from the tree, with an observed PD loss of 50% (51% PD loss in the control). Though these percentage losses of PD were considerable, they were not significantly different in comparison to a random loss of the same species for any of these assessments. Lastly, when the species from the High bin were trimmed from the ESA and CESA lists, PD dropped by 3.8% (19.4% in control) and 1.2% (17% in control), respectively. The loss of PD in the High-risk treatment for ESA and CESA resulted in significantly lower losses of PD than were observed in null distribution. Removal of species categorically ranked by the IUCN as experiencing population trend or population fragmentation resulted in modest and statistically non-significant losses of PD (Table 2). I observe a consistent trend whereby species at elevated extinction risk were more distantly related to each other than were species selected at random, resulting in slightly lower losses of evolutionary diversity than control groups.

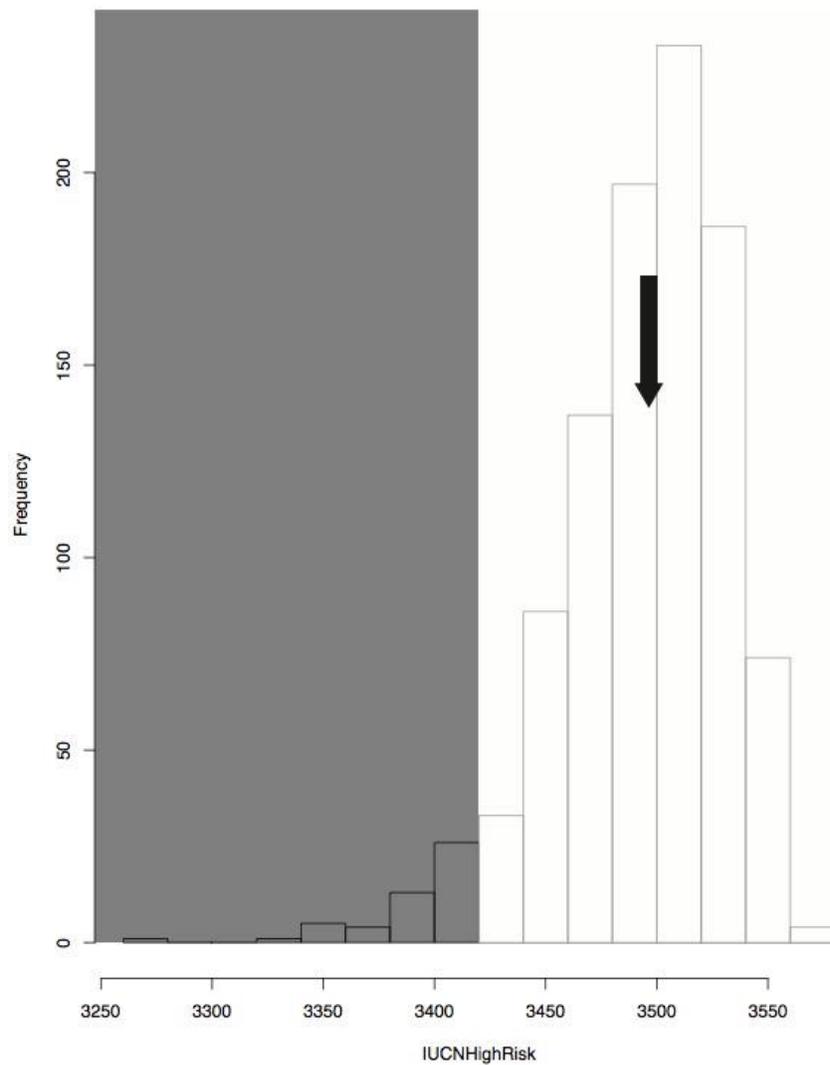


Figure 5. Histogram depicting the distribution of expected and observed PD (see black arrow) when IUCN Endangered species are removed from the phylogeny. The histogram is a null distribution of 1000 repetitions when the same number of random species are removed from the tree. I binned species into High, Medium+High, and Low+Medium+High extinction risks and iteratively removed those species to calculate PD. I then iteratively removed the same number of species, randomly, to determine if extinction risk is phylogenetically random. The area of no shading represents no significantly greater loss of PD than what would be randomly lost; gray shading represents the area where PD loss would be significantly greater than randomly expected. The black arrow is the observed PD value.

Table 2. Observed changes in Phylogenetic Diversity (PD) for the phylogeny of California's mammals (n=168).

Treatment	# Taxa Removed	PD	% of Total PD
Total PD	-	3449	100%
CSA-G_{HIGH+MED+LOW}	149	892	26%
CSA-G_{HIGH+MED}	123	1487	43%
CSA-G_{HIGH}	5	3405	*99%
CSA-S_{HIGH+MED+LOW}	137	1266	37%
CSA-S_{HIGH+MED}	120	1638	47%
CSA-S_{HIGH}	114	1729	50%
ESA_{HIGH+MED+LOW}	21	3282	*95%
ESA_{HIGH+MED}	20	3295	*96%
ESA_{HIGH}	18	3319	*96%
CESA_{HIGH+MED+LOW}	12	3380	*98%
CESA_{HIGH+MED}	12	3380	*98%
CESA_{HIGH}	6	3411	*99%
IUCN_{HIGH+MED+LOW}	14	3339	*97%
IUCN_{HIGH+MED}	6	3415	*99%
IUCN_{HIGH}	9	3375	*98%
Population Trend	21	3205	*93%
Population Fragmentation	13	3332	*97%

From Table 2, subscripts (High, Med, Low) represent at-risk species bins that were removed from that treatment. Five systems of assessing extinction risk include Conservation Status Assessments at the global (CSA-G) and state levels (CSA-S), the US Endangered Species Act (ESA), the California Endangered Species Act (CESA), and the International Union for the Conservation of Nature (IUCN). I also performed treatments on species with negative population trends and evidence of population fragmentation, both assessed by the IUCN. Asterisks designate a statistically significant deviation from the null distribution of PD values for the same number of species removed at random with respect to extinction risk. In all cases reported here, the loss of PD was significantly less than expected, indicating no phylogenetic clustering of extinction risk.

Like the results for PD, I observed no significant loss in NRI when high-risk species were removed from the phylogeny (Table 3). Net Relatedness Index was measured using the average mean phylogenetic distance (MPD), measuring the mean phylogenetic distance between each possible pair of taxa within each phylogeny. Mean phylogenetic distance was conserved across all treatments with an average MPD value of 166.1 (s.d. = 1.1) for this phylogeny.

In Table 3, NRI was calculated using the methods from Webb et al. (2002) to calculate NRI using mean phylogenetic distance (MPD). Subscripts (High, Med, Low) represent at-risk species bins that were removed from that treatment.

Table 3. Net Relatedness Index (NRI) for the phylogeny of California's mammals (n = 168).

Treatment	# Taxa Removed	NRI
Total MPD	-	164
CSA-G_{HIGH+MED+LOW}	149	167
CSA-G_{HIGH+MED}	123	167
CSA-G_{HIGH}	5	166
CSA-S_{HIGH+MED+LOW}	137	169
CSA-S_{HIGH+MED}	120	168
CSA-S_{HIGH}	114	165
ESA_{HIGH+MED+LOW}	21	166
ESA_{HIGH+MED}	20	166
ESA_{HIGH}	18	166
CESA_{HIGH+MED+LOW}	12	166
CESA_{HIGH+MED}	12	166
CESA_{HIGH}	6	166
IUCN_{HIGH+MED+LOW}	14	166
IUCN_{HIGH+MED}	6	166
IUCN_{HIGH}	9	166
Population Trend	21	167
Population Fragmentation	13	167

CONCLUSION

Discussion

I incorporated current records of extinction risk, life history traits, and habitat type with phylogenetic comparative methods to determine if California's mammals are prone to phylogenetically clustered extinctions. I found no evidence to support a phylogenetic clustering of extinction risk in terms of phylogenetic diversity or disparity. Until now, no phylogenetic analysis for the extinction risk for California's native terrestrial mammals has been published. Overall, I found that categorization schemes consistently selected branches with shorter lengths than would be expected if drawn randomly. This phylogenetic analysis reveals that the potential loss in PD is generally lower than expected from a random loss of the same number of species. Still concerning, however, is that between 9.2 – 38.5% of California's terrestrial mammalian species have elevated extinction risk, with an associated loss of 1.9 – 14.3% of phylogenetic diversity (as measured by PD). Because the loss of PD and NRI was phylogenetically random, the results suggest these losses are not exacerbated by phylogenetic clustering.

Phylogenies are important tools that interpret the evolutionary histories of species and can be utilized for managing the future of conservation biology (Davies et al. 2008). The literature on evolutionary history and extinction risk suggests that future extinction events may impact the tree of life more severely than if extinctions were random (Nee and May 1997, Purvis et al. 2000b, Parhar and Mooers 2011), but this pattern varies by taxonomic group and geography. As reviewed extensively in Veron et al. (2017), mammals show phylogenetically clustered extinction risk for carnivores (Kuntner et al. 2011), but not for primates (Arregoitia et al. 2013) and these patterns varied geographically. Similarly, plants

show sometimes contradictory patterns of phylogenetically clustered extinction risk globally (Vamosi and Wilson 2008), but not always regionally (Schwartz and Simberloff 2001, Lozano and Schwartz 2005, and Davies et al. 2011) Although estimating extinction risk in relation to phylogenies is not a new concept, this facet of conservation biology is diversifying to include geographic and trait information into phylogenetic comparative studies (see Isaac et al. 2005). Fritz et al. (2009) investigated the effects of anthropogenic threats and biological traits across the globe using phylogenetic comparative methods and observed strong geographical variation in the influence of traits on risk for larger species living in tropical regions on a regional scale. Furthermore, Arregoitia et al. (2013) investigated the associations of lineage age, clade sizes, evolutionary disparity and extinction risk predicted by the IUCN Red List and observed no significant prevalence for older, slower evolving species and extinction risk. Given the lack of a general or global pattern, this study fits nicely into the suggestions of Veron et al. (2017) that future studies focus on regional taxonomically limited assessments of the phylogenetic distribution of extinction risks.

Assessing Extinction Risks

I observed low correlation across extinction risk assessments, except for global and state levels CSA and the ESA and CESA (see Harris 2012 for a comparison of IUCN and ESA, see Reece and Noss 2014 for a detailed comparison of CSA, ESA, CCVI, and IUCN). Specifically, I observed that the Global and State CSA assessment types ranked species considerably higher than their counterparts. Changes in conservation status can be influenced across conservation agencies because of changes in human knowledge of species over time (Quayle and Ramsay 2005, Ramesh et al. 2017), by research parameters and

by varying assessment methods (see Burgman 2002) as well as differing priorities and funding availability. Dirzo et al. (2014) and others have emphasized the importance of measuring defaunation relative to extinction, or the idea that population declines may be a better loss-of-biodiversity metric to assess than the number of extinctions, or by extension, extinction risk as assessed in the study. I noted a lack of phylogenetic clustering of population decline and fragmentation (as assessed by the IUCN). These results are consistent with both traditional metrics of extinction risk and those based solely on declines in population size or anthropogenic habitat fragmentation.

Less Phylogenetic Diversity Lost than Expected?

I observed significant differences in PD for the phylogeny for 13 of 18 treatments. These differences in PD were all significantly lower than what would be expected if the same number of species were removed randomly, revealing a tendency for the removal of shorter branch lengths. Since loss of total PD in both phylogenies was marginal across all treatments, it seems unlikely that entire clades would be lost if these at-risk species go extinct. Consistent with previous investigations of phylogenetic conservatism in mammals (Cooper et al. 2011), I suggest that extinction risk, or that traits that underlie it, are not phylogenetically conserved for California's terrestrial mammals.

Future Research Directions

The analyses in this thesis reveal the relationship between conservation statuses and extinction risk by relating the phylogenetic diversity and disparity of California's mammalian tree of life. The scope of this study aimed to understand the implications of conservation application on the state level. However, natural communities expand beyond arbitrary state lines. The methodologies used in this

study could be further applied to smaller and larger regional scales. California's endemic species are a subset of the phylogeny presented here, and further assessments on their conservation statuses and phylogenetic histories would offer another phylogenetic perspective that is limited to California. Additionally, including phylogenetic information for more species within a larger region, such as those along the west coast of the United States or within the Pacific Southwest (Region 8 of the U.S. Fish and Wildlife Service), would likely follow with trends of larger scale conservation assessments (Cooper et al. 2011, Veron et al. 2017).

Forward-looking extinction risk assessments associated with land use change, sea level rise, and climate change have revealed threats to biodiversity in other systems (Reece et al. 2013, Reece and Noss 2014). Combining these forward-looking approaches into a single assessment (see Standardized Index for Vulnerability and Value Assessment [SIVVA] in Reece and Noss 2014) may provide a robust and flexible framework for extinction risk assessments for California's mammalian phylogeny.

Finally, species' current geographic ranges have been used in conservation assessments (Anderson and Martinez-Meyer 2004, Rattis et al. 2018) to determine the scale dependence of habitat predictors. In the past, natural history determined the occurrence and distribution of species when other data were lacking (Anderson and Martinez-Meyer 2004). Future work could incorporate the shifts of species' historical and modern distributions to anticipate the future environmental losses of California's mammals. The combination of scale adjustments, forward-looking assessments, and historical distribution records will bolster the phylogenetic assessments of California's mammalian species presented in this study.

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APPENDICES

APPENDIX A: 'SPECIES/SUBSPECIES' PHYLOGENY
RESULTS

In addition to the assessments on California's terrestrial mammals, I collected data on the subspecies of California's species and performed similar analyses as previously described. The results were not qualitatively different between analyses restricted to full species and analyses that included full and subspecies, thus I report primarily on analyses of the full species tree, excluding subspecies. I clarify the difference between these two phylogenies by distinguishing them as the 'Species' (n=168) and 'Species/Subspecies' (n=263) phylogenies.

One tree was reconstructed to include all 263 taxa in the dataset. This tree has an additional 95 tips that represent subspecies, which were not present in the original supertree, thus I denote this as the 'species/subspecies' phylogeny. I used taxonomy to determine placement and fixed each subspecies node to be .01 million years apart from the parent species to coincide with the wake of the last glacial maximum nearly 12,000 years ago. I chose .01mya as the branch lengths for subspecies because the climate change in that period caused large shifts in many species geographic distributions (Holt 1990). I assume these changes in geographic distributions either gave rise to these modern subspecies or represent a very conservative most recent possible divergence time.

The 'species/subspecies' (263 species and subspecies phylogeny were successfully adapted from the original supertree (Bininda-Emonds et al. 2007) using the "drop.tip" function using the "phylo" package in R. Both trees (figures 3 and 4) were produced using FigTree v1.4.3. In nearly every assessment, the 'species/subspecies' PD was highly conserved after culling treatments with PD dropping an average of 14.1% for the 'species/subspecies' phylogeny

In both phylogenies, the largest loss in 'species/subspecies' PD was observed in global and state CSA assessments in High and Medium bins. I

observed no general significant trend in NRI for either phylogeny. Mean phylogenetic distance was conserved across all metrics with an average MPD value of 164.3 (s.d. = 1.2) for the 'species/subspecies' phylogeny.

I calculated that 7% of the total number of native terrestrial mammals have elevated extinction risk according to the IUCN. However, when these species are trimmed from the 'species/subspecies' phylogeny, PD dropped by 2.4%. Comparatively, when I ran 1000 random iterations with the same percentage loss, PD dropped by 3.3%. When species in the High-risk categorization scheme for global CSA (32.4% of total species) were culled from the phylogeny, 'species/subspecies' PD dropped by 8.6% (1.9% in the control). The largest decrease in 'species/subspecies' PD occurred when species in the High state CSA bin (38.5% of total species) were trimmed from the tree, with an observed PD loss of 14.3% (32.1% PD loss in the control). Though this percentage loss of PD was considerable, it was not significant in comparison to a random loss of the same species. Lastly, when the species from the High bin were trimmed from the ESA (13% of total) and CESA (9.2% total) lists, 'species/subspecies' PD dropped by 3.8% (4.4% in control) and 1.9% (2.0% in control), respectively. The loss of PD in the High cull for ESA and CESA was significantly different (over dispersed) from the random loss of the same number of species

APPENDIX B: ADDITIONAL STATISTICS

I tested the goodness of fit (chi-squared tests) between different potential factors to extinction risk (habitat type, population trends, diet type, and population fragmentation) across the five conservation agencies. Across each chi-squared test I observed no significant difference between the observed distributions of extinction risk to what would be expected if these were randomly distributed.

Habitat type was divided into ten categories: Coastal, Shrubland, Woodland, Desert, Montane, Cave, Grassland, Urban, Wetland, and Variable. Species having two or more predominant habitat types were categorized as variable (e.g., *Canis latrans*). I then ran a chi-square test on the extinction risk of all species across all five categorization schemes for each habitat type to determine if extinction risk was significantly associated with habitat type. The chi squared tables consisted of 26 rows (see Tables B.1-B.4). I tested for significance at $p < 0.05$ for the entire chi squared table.

Population trend was categorized into four classifications: Decreasing, Stable, Increasing, and Unknown. Species with decreasing population trends were removed from the tree in this analysis.

Population fragmentation was categorized by presence or absence, except for species that had no data available, in which case they were classified as “unknown.” Species with population fragmentation were removed from the tree for this treatment.

Table B.1. Chi squared table for habitat type and conservation status bins.

	Marine	Shrubland	Woodland	Desert	Montane	Cave	Grassland	Variable	Urban	Wetland
GCSA H	0	0	1	0	0	0	0	0	0	0
GCSA M	4	30	25	16	13	3	24	27	1	20
GCSA L	0	0	1	0	0	0	1	1	0	1
SCSA H	0	4	2	0	0	0	0	0	0	2
SCSA M	1	2	4	2	1	0	5	7	0	3
SCSA L	3	24	21	14	12	3	20	21	1	16
ESA H	0	3	3	0	0	0	1	2	0	1
ESA M (Delisted)	0	0	0	0	0	0	0	1	0	0
ESA M (Threatened)	0	0	1	0	0	0	0	0	0	1
ESA M (P Threat)	0	0	0	0	0	0	0	0	0	0
ESA M (P End)	0	0	0	0	0	0	0	0	0	0
ESA M (Candidate)	0	0	0	0	0	0	0	0	0	1
ESA L	4	27	23	16	13	3	24	25	1	18
CESA H	0	1	1	0	0	0	1	0	0	0
CESA M (Delisted)	0	0	0	0	0	0	0	0	0	0
CESA M (Threatened)	0	1	2	0	0	0	0	1	0	1
CESA M (P Threat)	0	0	0	0	0	0	0	0	0	0
CESA M (P End)	0	0	0	0	0	0	0	0	0	0
CESA M (Candidate)	0	0	0	0	0	0	0	0	0	0
CESA L	4	28	24	16	13	3	24	27	1	20
IUCN H (CE)	0	0	0	0	0	0	0	0	0	0
IUCN H (E)	0	1	4	0	0	0	0	0	0	0
IUCN M (NT)	0	1	0	0	0	0	0	2	0	2
IUCN M (VU)	0	0	0	0	0	0	1	1	0	1
IUCN L (LC)	4	28	23	16	13	3	23	25	1	18
IUCN (DD)	0	0	0	0	0	0	1	0	0	0

Table B.1 Conservation agencies used in this table include the International Union for the Conservation of Nature Red List (IUCN), Endangered Species Act (ESA), California Endangered Species Act (CESA), Global Conservation Status Assessment (GCSA), and the State Conservation Status Assessment (SCSA). Bins are grouped into High (H), Medium (M) and Low (L) risk groups and compared across 10 habitat types listed by the IUCN. The chi squared test for habitat type compared to the High, Medium and Low bins was non-significant ($p > .99$).

Table B.2. Chi squared table for population trends and conservation status bins

	Increasing	Stable	Unknown	Decreasing
GCSA H	0	0	1	0
GCSA M	2	67	69	25
GCSA L	1	1	1	1
SCSA H	0	2	6	0
SCSA M	0	11	11	3
SCSA L	3	55	54	23
ESA H	0	2	6	2
ESA M (Delisted)	0	1	0	0
ESA M (Threatened)	0	0	1	1
ESA M (Proposed Threatened)	0	0	0	0
ESA M (Proposed Endangered)	0	0	0	0
ESA M (Candidate)	0	0	0	1
ESA L	3	65	64	22
CESA H	0	0	3	0
CESA M (Delisted)	0	0	0	0
CESA M (Threatened)	0	0	4	1
CESA M (Proposed Threatened)	0	0	0	0
CESA M (Proposed Endangered)	0	0	0	0
CESA M (Candidate)	0	0	0	0
CESA L	3	68	64	25
IUCN H (Critically Endangered)	0	0	0	0
IUCN H (Endangered)	0	2	3	0
IUCN M (Near Threatened)	0	3	1	1
IUCN M (Vulnerable)	0	1	1	1
IUCN L (LC)	3	62	65	24
IUCN (DD)	0	0	1	0

Table B.2. Conservation agencies used in this table include the: International Union for the Conservation of Nature Red List (IUCN), Endangered Species Act (ESA), California Endangered Species Act (CESA), Global Conservation Status Assessment (GCSA), and the State Conservation Status Assessment (SCSA). Bins are grouped into High (H), Medium (M) and Low (L) risk groups and compared across four population trends listed by the IUCN. The chi squared test for population trends compared to the High, Medium and Low bins was non-significant ($p > .70$).

Table B.3. Chi squared table for diet type and conservation status bins.

	Herbivore	Insectivore	Omnivore
GCSA H	1	0	0
GCSA M	103	43	17
GCSA L	2	2	0
SCSA H	5	3	0
SCSA M	10	14	1
SCSA L	91	28	16
ESA H	9	1	0
ESA M (Delisted)	1	0	0
ESA M (Threatened)	1	1	0
ESA M (Proposed Threatened)	0	0	0
ESA M (Proposed Endangered)	0	0	0
ESA M (Candidate)	1	0	0
ESA L	94	43	17
CESA H	3	0	0
CESA M (Delisted)	0	0	0
CESA M (Threatened)	5	0	0
CESA M (Proposed Threat)	0	0	0
CESA M (Proposed End)	0	0	0
CESA M (Candidate)	0	0	0
CESA L	98	45	17
IUCN H (CE)	0	0	0
IUCN H (E)	5	0	0
IUCN M (NT)	4	1	0
IUCN M (VU)	2	1	0
IUCN L (LC)	94	43	17
IUCN (DD)	1	0	0

Table B.3. Conservation agencies used in this table include the: International Union for the Conservation of Nature Red List (IUCN), Endangered Species Act (ESA), California Endangered Species Act (CESA), Global Conservation Status Assessment (GCSA), and the State Conservation Status Assessment (SCSA). Bins are grouped into High (H), Medium (M) and Low (L) risk groups and compared for three diet types listed by the IUCN. The chi squared test for diet type compared to the High, Medium and Low bins was non-significant and diet type ($p > .37$).

Table B.4. Chi squared table for population fragmentation and conservation status bins.

	Present	Not Present	Unknown
GCSA H	0	0	1
GCSA M	17	93	53
GCSA L	0	3	1
SCSA H	0	5	3
SCSA M	1	17	7
SCSA L	16	74	45
ESA H	2	5	3
ESA M (Delisted)	0	1	0
ESA M (Threatened)	0	1	1
ESA M (Proposed Threatened)	0	0	0
ESA M (Proposed Endangered)	0	0	0
ESA M (Candidate)	1	0	0
ESA L	14	89	51
CESA H	1	2	0
CESA M (Delisted)	0	0	0
CESA M (Threatened)	0	3	2
CESA M (Proposed Threatened)	0	0	0
CESA M (Proposed Endangered)	0	0	0
CESA M (Candidate)	0	0	0
CESA L	16	91	53
IUCN H (CE)	0	0	0
IUCN H (E)	1	3	1
IUCN M (NT)	0	5	0
IUCN M (VU)	1	1	1
IUCN L (LC)	15	86	53
IUCN (DD)	0	1	0

Table B.4. Conservation agencies used in this table include the: International Union for the Conservation of Nature Red List (IUCN), Endangered Species Act (ESA), California Endangered Species Act (CESA), Global Conservation Status Assessment (GCSA), and the State Conservation Status Assessment (SCSA). Bins are grouped into High (H), Medium (M) and Low (L) risk groups and compared for three possible categories of population fragmentation listed by the IUCN. The chi squared test for the presence of population fragmentation compared to the High, Medium and Low bins was non-significant ($p > .98$).