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# Linking patterns of intraspecific morphology to changing climates

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## Abstract

**Aim:** This study examines how climate shaped *Microtus californicus* (Rodentia: Arvicolinae) ecomorphology throughout the Quaternary. It tests three hypotheses: (a) climate corresponds with consistent shape variation in *M. californicus* dentition; (b) Quaternary warming and drying trends caused *M. californicus* morphotypes to predictably shift in range through time and (c) Quaternary warming and drying led to predictable changes in tooth morphological variation. Finally, we discuss how shifts in climate-linked morphological variation may affect the potential of *M. californicus* to react to future climate change.

**Location:** Western United States.

**Taxon:** *Microtus californicus* (Peale, 1848).

**Methods:** Geometric morphometrics and partial least squares analyses were used to discern how climate contributes to consistent variation in the shapes of the *M. californicus* lower first molar (m1), validated for the full toothrow. We further corroborate this relationship, reconstructing precipitation at fossil localities using m1 morphology and comparing those values to palaeoclimate-model-derived precipitations. Disparity analyses and a MANOVA were performed to examine changes in variation and whether a shift in tooth shape occurred through time.

**Results:** *Microtus californicus* m1 and toothrow shapes are narrower and more curved in cooler, wetter climates. Morphology-based palaeoclimate reconstructions align with model-based palaeoclimate estimations. When time averaging is accounted for, *M. californicus* demonstrates a 12% reduction in variation from fossil to present-day specimens, and these changes in tooth shape correspond with climate-related morphotypes.

**Main conclusions:** As California became drier and hotter since the late Pleistocene, *M. californicus* dental morphology generally tracked these changes by adapting to the consumption of rougher vegetation in drier environments. This resulted in the loss of some high-precipitation morphotypes, indicating that ecomorphology, often observed at the species and community levels, translates to intraspecific variation and dynamically changes in response to changing climates. The loss of climate-linked morphological variation since the late Pleistocene may limit the ability of *M. californicus* to respond to future changes in climate. These findings portend that other species may have experienced similar losses in adaptability.

## KEYWORDS

California, climate change, dental morphology, functional trait, geometric morphometrics, intraspecific variation, *Microtus californicus*, palaeontology, partial least squares, Quaternary

## 1 | INTRODUCTION

In the face of dramatically changing climates, species will be forced to move, adapt or face extinction. Species traits will determine the capacity of a species to move or adapt. The distribution of traits within an ecosystem is fundamentally controlled by environmental factors including climate (e.g. temperature, precipitation) and biotic interactions (e.g. food resources, predation, competition), and the functional interplay between them (Polly et al., 2011). Ecological morphology, or ecomorphology, describes the relationship between an individual's morphology and its ecological role (Norton, Luczkovich, & Motta, 1995). There are many studies that examine how morphological traits vary with climate at the species or community level. However, few examine how population-level climate-linked trait dynamics change over time. For example, the body sizes of both snakes and mammals are closely tied to local temperatures (Damuth et al., 1992; Head et al., 2009; Smith, Betancourt, & Brown, 1995), and the mammal molar proportions relate to local aridity (Evans, 2013; Fortelius et al., 2002). Correlations between climate and morphology can indicate the relative importance of specific environmental variables on an organism's physiology.

Climate-linked intraspecific variation can reveal a species' potential to survive as climate changes. Species with high intraspecific variation generally have larger population sizes (Mimura et al., 2017) and higher potential for being able to adapt to change (Herrando-Pérez et al., 2019). However, even if a species has high phenotypic variation, that variation is not necessarily relevant to a particular stressor or may not be accessible to allow adaptation. When assessing a species' adaptability to climate change, the spatial distribution, mobility and type of intraspecific variation are crucial. Here, we examine the extent to which intraspecific ecomorphological relationships dynamically reflect changing environments.

We introduce a method that uses partial least squares (PLS) and geometric morphometric shape analyses to identify climate-linked morphologies, characterize climate-linked variation and identify the dynamics of intraspecific responses to climate change through time. We demonstrate this method by examining the molar and upper tooththrow morphologies of *Microtus californicus* (the California vole; Peale, 1848). We explore the factors that affect distributions at different taxonomic scales using a rich palaeontological record to provide historical context. We trace how climate-linked variation has changed throughout the Holocene as climates in the western U.S. have become warmer and drier. To understand how climate has historically influenced intraspecific variation, several questions must be explored: (a) Are climatic variables related to the modern pattern of ecomorphological variation? This can be the first clue that climate is driving changes in variation. (b) As climate shifted in the past, did morphotypes track those shifts? If so, the association between the

two becomes stronger and can suggest the nature of their relationship. (c) Do climatic shifts result in an overall change in the amount of variation present? Answering these questions creates a picture of past and present intraspecific variation. They also provide a contextual understanding of the current state of a species and demonstrate the potential of the species to react to future climate change.

## 2 | STUDY SYSTEM

### 2.1 | *Microtus californicus*

We address these questions by examining the California vole, *Microtus californicus* (Rodentia: Arvicolinae; Peale, 1848), an excellent study species because its teeth are abundant in the Quaternary fossil record and are identifiable to the species level using discriminant shape analyses (McGuire, 2011; McGuire & Davis, 2013). *M. californicus* is abundant in present-day ecosystems of western North America (Conroy et al., 2016), where it influences the structure of ecological communities by differentially consuming plant species (Borchert & Jain, 1978; Conroy & Gupta, 2011) and serves as food for predators (Huntly, 1991). Prior research has found that precipitation is important for determining this species' range (Church, 1966; McGuire & Davis, 2013), and this species generally lives in the drier regions of the west coast of North America. In fact, previous research has demonstrated a correlation between present-day geographical clines and the shape of its lower first molar (m1; McGuire, 2010). Because geographical clines roughly correlate with climatic clines across California, m1 shape in this species may be driven by changes in climate (McGuire, 2010).

Here, we test the hypothesis that m1 and tooththrow shape are consistently associated with mean annual temperature (MAT) and mean annual precipitation (MAP) across the range of *M. californicus*. We use m1 specimens because they are commonly found as isolated elements in the fossil record. However, we also sought to ensure that a single, small, isolated tooth does not exhibit a spurious relationship with climate. Thus, we also examine the entire upper tooththrow to validate the pattern of shape change and the correlation between climate and tooth shape. For both m1 and tooththrow analyses, we use landmark geometric morphometric analyses in conjunction with PLS analyses to determine whether temperature and precipitation, and separately latitude/longitude, relate to the PLS axes of shape variables.

### 2.2 | Fossil localities

Using geometric morphometrics and discriminant analyses, we have previously identified 101 *M. californicus* Quaternary

fossil m1s from seven California localities: Emery Borrow (E), Montezuma (M), McKittrick Brea (Mc), Pacheco 2 (P), Palos Verdes (PV), Prune Avenue (PA) and Samwell Cave (S) (Figure 1; Table S1; McGuire, 2011; McGuire & Davis, 2013). These fossil specimens are used to test how temperature and precipitation influence morphology using the following logic: First, we document a relationship between climate and morphology in present-day specimens. We then determine whether the same pattern prevails in the fossil specimens, by determining whether trends in fossil morphologies agree with previously published palaeoclimatic proxy data and palaeoclimate data from the last 21 ka derived from CCSM3 downscaled palaeoclimate models (Collins et al., 2006; Lorenz, Nieto-Lugilde, Blois, Fitzpatrick, & Williams, 2016) and from 21 to 300 ka using Oscillayers (Gamisch, 2019).

Palynological data, palaeolimnology, *Neotoma* (packrat) mid-den evidence and CCSM3 palaeoclimate models suggest that southern California has become drier since 9 ka. This implies that morphotypes now found in wetter areas should have prevailed there in the past. Northern California and Oregon have

had no change in precipitation or have become wetter over the same time period (Boxt, Raab, Davis, & Pope, 1999; Collins et al., 2006; Diffenbaugh & Ashfaq, 2007; Gamisch, 2019; Kirby, Lund, Anderson, & Bird, 2007; Lorenz et al., 2016; Mock & Brunelle-Daines, 1999; Thompson, Schultze-Lam, Beveridge, & DesMarais, 1997). Since the Last Glacial Maximum (21 ka; LGM), each of the included fossil localities (except Samwell cave, which includes only Holocene specimens) has undergone warming and drying (Figure 1; McGuire & Davis, 2013). We therefore anticipate that dental morphotypes found at each fossil locality in the past should be distinct from the modern morphotype found there today, should generally reflect drying trends throughout Southern California and the Bay Area and should reflect specific changes in climate as assessed by palaeoclimate proxies and model-based palaeoclimate reconstructions.

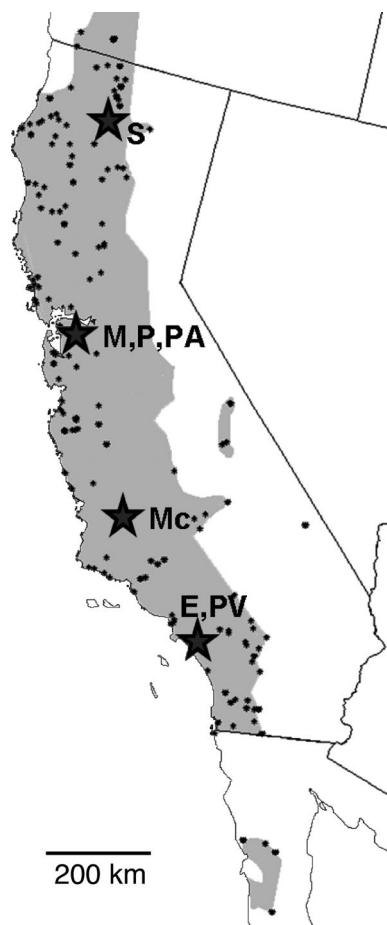
### 3 | MATERIALS AND METHODS

#### 3.1 | Morphological and climate data

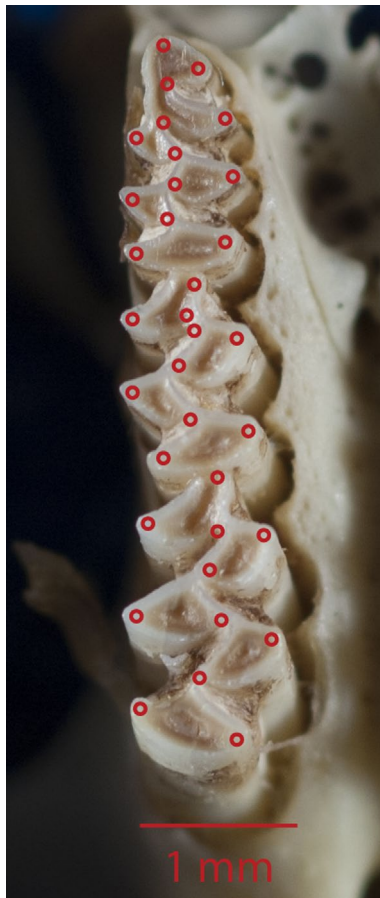
We analysed 101 fossil m1s, 307 modern m1s and 361 modern upper tooththrow specimens of *M. californicus*. Fossil specimens from the seven localities are housed at the University of California Museum of Palaeontology (UCMP; Berkeley, USA) or the Los Angeles County Museum of Natural History (LACM; Los Angeles, CA; Figure 1; Table S1; McGuire & Davis, 2013). Modern specimens are from the Museum of Vertebrate Zoology (MVZ; Berkeley, USA) and were evenly sampled from throughout the species' range, with a male and female specimen selected from each county and subspecies designation (Figure 1 & Table S2). Specimens were photographed using a Nikon D70s and AF Micro-NIKKOR 60 mm f/2.8D macro lens ensuring, and best practices for small-specimen photography were followed (Fox, Veneracion, & Blois, 2020).

Left m1s and upper left tooththrows were digitized on Tiff images using tpsDig 2.10 (Rohlf, 2006), designating 21 landmarks and 15 semilandmarks for the m1s (after McGuire, 2011 semilandmark placement) and 34 landmarks for the tooththrows (Figure 2). Semilandmark curves were drawn and initially subsampled by length using tpsDig 2.10 (Rohlf, 2006). They were slid using bending energy in tps Relative Warps 1.45 (Rohlf, 2007) and subsampled again in tps Utility 1.40 (Rohlf, 2008).

Generalized Procrustes analysis (GPA) was performed separately on the m1 and tooththrow specimens. GPA superimposes landmark configurations and corrects for non-shape variation. To determine present-day temperature and precipitation values, each modern specimen and fossil locality was mapped using ArcGIS 9.3 (ESRI, Redlands, CA, USA; Figure 1). Modern MAT and MAP layers with 30 arc-second spatial resolution were downloaded from the WorldClim 1.9 dataset (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; <http://www.worldclim.org>). Present-day (1950–2000) climate data were then extracted for each modern specimen and fossil locality.



**FIGURE 1** *Microtus californicus* range map. Map of California and surroundings overlaid by the present-day range of *M. californicus* in light grey. Modern specimens used are indicated by small black asterisks and listed in Table S2. Fossil localities are indicated by large stars. Letters correspond with locality names and data listed in Table S1



**FIGURE 2** Placement of 34 landmarks on the upper right tooththrow of *Microtus californicus*

Each fossil locality has an associated age range (Table S1). For each fossil locality, we examined the palaeoprecipitation that the site experienced across its associated age range. Palaeoclimate data for dates ranging from 21 ka to present, were extracted from downscaled CCSM3 data (Collins et al., 2006; Lorenz et al., 2016) sampled at 100-yr intervals. For dates older than 21 ka, palaeoprecipitation data were derived from Oscillayers (Gamisch, 2019) and sampled every 10 ka. These intervals reflect the temporal resolution of the climate data.

### 3.2 | Climate morphotypes

Climate morphotypes were established using only modern specimens. Using the 'geomorph' 3.0.6 package in R (Adams, Collyer, Kaliontzopoulou, & Sherratt, 2016), a two-block PLS analysis was employed, separately for m1 and tooththrow specimens. This technique creates new linear combinations of the multidimensional variables, called singular axes, that maximize the covariation between dependent and independent variables (McGuire, 2010; Rohlf & Corti, 2000). This process reduces the dimensionality of the specimens' associated independent climate and dependent shape variables (i.e. partial warp scores), establishing climate and shape singular

axes, coefficients of covariation between them, and singular vectors indicating the relative importance of temperature versus precipitation in PLS outcomes. All climate variables were normalized to mean = 0 and SD = 1 for these analyses. To determine the validity of these outcomes, permutation tests were performed in which PLS was repeated 100 times, each time randomly pairing instances of the climate and shape variables.

Deformation analyses were then created to determine the relative tooth shape change along the first singular climate axis for m1 and, separately, tooththrow specimens. Warp diagrams show the amount and aspect of shape variation that occurs between the specimens. A Spearman's rank correlation was then performed to determine whether the relationship between the m1 and climate, as determined by each specimen's PLS score, is similar to the relationship identified between the tooththrow and climate.

### 3.3 | Examining relationships through time

The PLS relationship established using modern m1 specimens was used to estimate past precipitation values based on fossil m1 morphology. We used a *t*-test to determine whether morphologically estimated precipitation values were significantly different from modern precipitation values at each locality in JMP 8.0 (SAS Institute). Morphologically derived palaeoprecipitation estimates were visually compared to model-derived palaeoprecipitation estimates from across the entire range of age uncertainty for each fossil locality. Model-derived palaeoprecipitation and morphologically predicted palaeoprecipitation data are likely drawn from different temporal resolutions, represent different variance distributions, and therefore violate any statistical tests for comparison. However, by comparing the range of precipitation values that the fossil specimen might have experienced with morphologically derived palaeoprecipitation estimates, we can identify whether the trends agree.

### 3.4 | Structure of modern and Quaternary variation

The variances in overall m1 shape were compared between fossil and modern specimens. Due to geographical sampling limitations, fossil localities do not fully sample Pleistocene and Holocene morphological variation, whereas modern sampling was performed across the entirety of species' range. This effect should decrease variation in fossil samples with respect to modern ones. However, fossil localities also are time-averaged, which has the opposite effect on variation. Hunt (2004) demonstrated that in small mammals, time averaging over 100,000 years results in a 3% decrease in variation from fossil to modern populations. If fossil specimens represent the maximum estimated timespan across all sites, 300,000 years (Table S1), then a 9% decrease in variation from fossil to modern populations would be expected given no overall change in variation.

To determine whether the mean m1 shape changed through time, Manovaboard 6.4 (Sheets, 2006b) was used to perform a one-way

MANOVA on shape variables as grouped by age (modern or fossil). DisparityBox 6i (Sheets, 2006a) was used to examine variation in overall m1 shape in fossil and modern specimens. DisparityBox uses disparity calculations established by Foote (1993), comparing the distance of each specimen to the centroid of that group of specimens ( $d$ ):  $\text{Variation} = \sum(d_i^2)/(N - 1)$ . In all, 200 bootstraps (resampling with replacement) were performed to determine the confidence intervals for each variation calculation.

## 4 | RESULTS

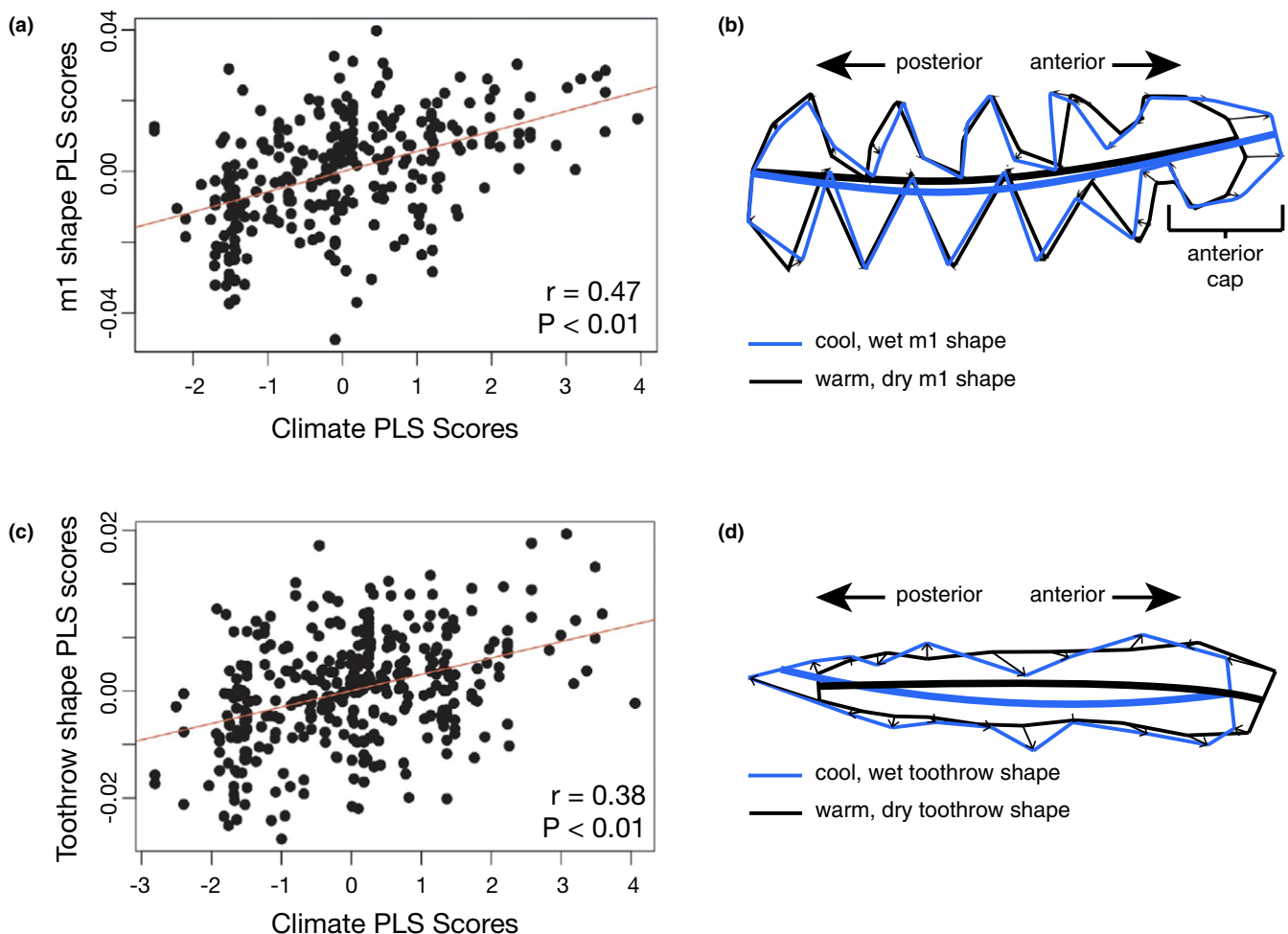
### 4.1 | Climate ecomorphology

We find significant positive covariation between the first singular PLS axes of climate and of the m1 shape (Figure 3a; PLS regression,  $r = 0.47$ ;  $p < 0.01$ ) and tooththrow shape (Figure 3c; PLS regression,  $r = 0.38$ ;  $p < 0.01$ ). Mean annual precipitation carries a greater weight than MAT in driving these patterns. The predictive power of

the PLS is significantly higher than expected by chance (Permutation test,  $p < 0.01$ ).

From deformation analyses, it is evident that m1s and tooththrows are relatively straight and stout in warmer and drier (high temperature and low precipitation) climates and curved and gracile in cooler and wetter (low temperature and high precipitation) climates. This trend is particularly evident towards the anterior cap of the m1 (Figure 3b) and the middle of the tooththrow (Figure 3d). Furthermore, the orders of m1 and tooththrow specimens along their respective first PLS climate axes are highly correlated (Spearman's rho,  $\rho = 0.99$ ;  $p < 0.01$ , Figure 4). This indicates a very similar relationship between m1 shape and climate and between tooththrow shape and climate, providing an independent validation of the relationship.

While PLS cannot confidently estimate the precipitation experienced by a single fossil specimen, it can provide a reliable estimate when considered across local populations. At each fossil locality, it establishes a range of values that is representative of that population overall. Morphologically estimated precipitation values for fossil localities generally indicated more precipitation in the past than in the present (Figure 5, blue boxes). Past estimated precipitation values



**FIGURE 3** PLS-determined relationships between climate and *Microtus californicus* tooth shape (a) and (b) and tooththrow shape (c) and (d). PLS regressions (a) and (c) were performed using a two-block PLS analysis. Deformation diagrams of shape extremes (b) and (d) demonstrate shapes from cool, wet climate extremes (blue) to warmer, drier climate extremes, as indicated by arrows connecting the shapes. Centre lines depict differences in tooth curvature between climate extremes

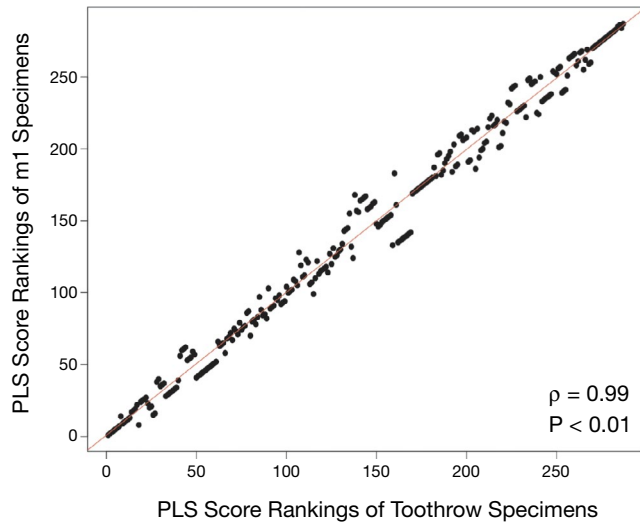


were significantly higher than modern precipitation values ( $t$ -test,  $p < 0.01$ ) for Prune Avenue, Palos Verdes, Pacheco 2, McKittrick and Emery Borrow; indistinguishable for Montezuma ( $t$ -test,  $p = 0.47$ ); and significantly lower for Samwell Cave ( $t$  test,  $p < 0.01$ ). The distribution of values generally overlaps with that of palaeoprecipitation values sampled from the youngest age range of a site (Figure 5, green boxes) for all sites except Montezuma. However, palaeoprecipitations reconstructed from dental morphology at Prune Avenue and

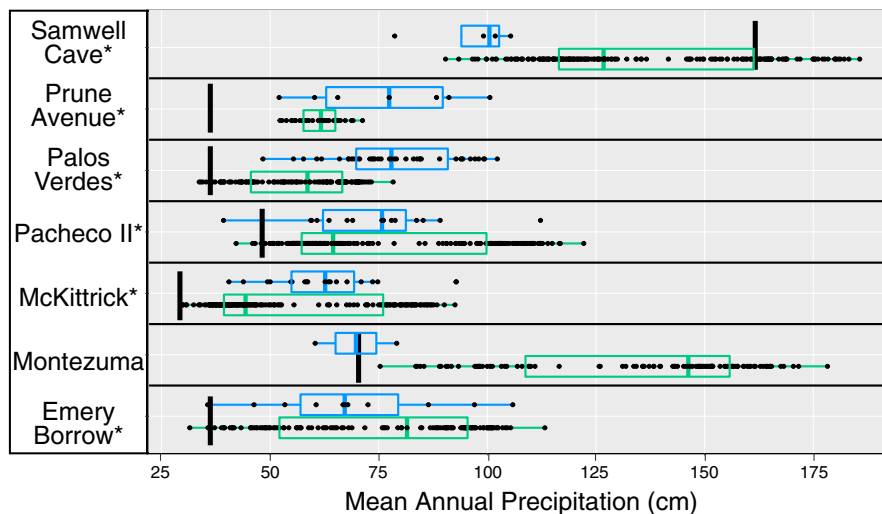
Palos Verdes both predict some wetter climate values than those based on climate models. Notably, Samwell Cave, which is in northern California (Figure 1), has become wetter through time, as predicted by climate models (Figure 5).

## 4.2 | Structure of modern and Quaternary variation

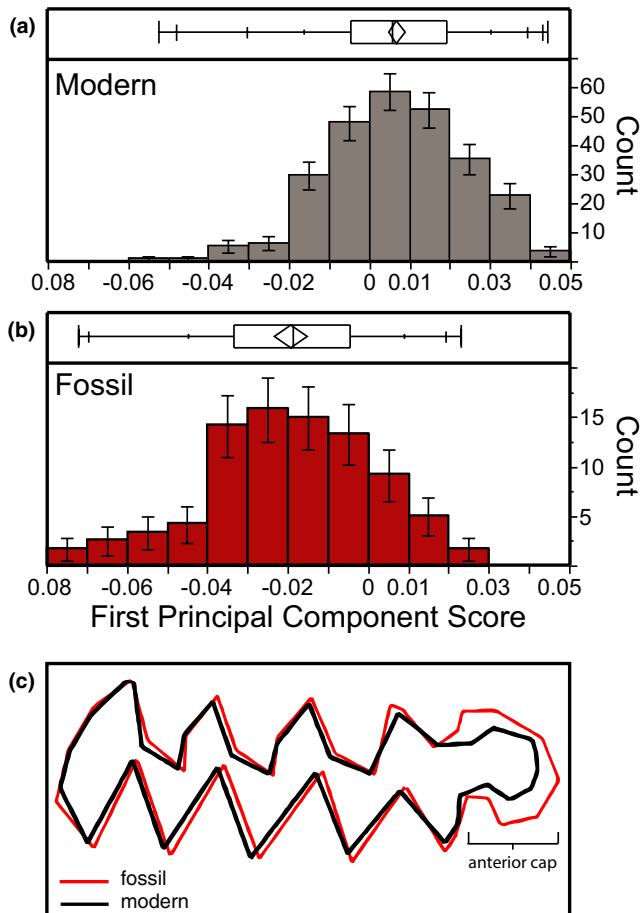
Fossil and modern *M. californicus* demonstrated a difference in overall mean m1 shape (MANOVA,  $p < 0.01$ ). Fossil specimens come from seven geographical locations throughout the range of the species, whereas modern specimens were selected from over 150 locations across its entire known range. Given large number of modern specimens, we are certain that they approximate the morphological variation present in the species today. However, the fossil specimens very likely missed some aspects of morphological variation historically present in some populations. Nevertheless, fossil specimens had 21% higher variance than modern specimens (Foote disparity,  $p < 0.01$ ), more than twice the amount that would be expected due to the time averaging over 300 ka (9%). Given that the fossil specimens have considerably patchier geographical sampling than the modern specimens, this is likely an underestimation of the actual loss of variation through time. The distribution of shape values along the first principal component demonstrates a change in the mean and difference in variance between the modern (Figure 6a) and fossil (Figure 6b) specimens. The deformation diagram indicates the relative shape change along the first principal component from fossil to modern specimens (Figure 6c). Fossil molars demonstrate relatively more rounded, high-domed anterior caps than the modern specimens, a similar pattern to that seen between high- and low-precipitation morphotypes (Figure 3b).



**FIGURE 4** Spearman's rank analysis of specimens with both m1 and toothrow data. Each specimen, represented by a data point, was ranked based upon its environmental/climate variable PLS score along the first singular PLS axes from the toothrow (x-axis) and m1 (y-axis) analyses. The resultant plot contains a least-squares regression line



**FIGURE 5** Box plots of morphologically estimated precipitation (top row; blue) and CCSM3 precipitation estimates from across the stratigraphic extent of the fossil site (bottom row; green). The midline of the box represents the mean, the leading and end edges of the box are 25th and 75th quartiles, respectively, and the whiskers represent the 95% confidence interval of the mean. Black vertical lines indicate present-day mean annual precipitation values at each fossil locality. Asterisks (\*) indicate that morphologically estimated precipitation significantly differs from modern values. Morphology-based precipitation estimates overlap considerably with CCSM3-estimated precipitation for all sites except for Montezuma, for which estimates do not differ from modern



**FIGURE 6** Distributions of modern (a) and fossil (b) first principal components of m1 tooth shape with standard error whiskers and quartile box plots above. Mean is shifted to the left ( $p < 0.01$ ) and variance is greater ( $F < 0.01$ ) in fossil specimens relative to modern specimens. Relative m1 shape change between fossil and modern specimens along the first principal component (c)

## 5 | DISCUSSION

Our findings demonstrate that ecomorphology, often observed at the species and community levels, translates to intraspecific variation and dynamically changes in response to changing climates. In *M. californicus*, we find that m1 shape is correlated with modern climate (Figure 3a). In particular, in cooler, wetter regions the anterior cap is more robust and complex, and the overall curvature of the tooth is greater (Figure 3b). This curvature scales up, reflecting the overall curvature of the whole tooththrow (Figures 3d and 4), indicating that this pattern is the result of a more extensive jaw phenotype. The pattern also holds through time. When we reconstruct palaeo-precipitations using tooth shape, the predicted precipitations are different from modern values at each site and within the range of expected palaeo-precipitations (Figure 5). In fact, we anticipate that this strategy could be used to refine the ages of the fossils collected at the sites. For example, the age of the Montezuma site is uncertain, collecting as the result of active channel deposits (Wolff, 1973). The

fossil m1s from Montezuma seem more likely to represent modern specimens than fossil specimens, indicating that these are likely to be relatively recent specimens. When examining morphological variation through time, we see a reduction in morphological variation of 21% from fossil to modern specimens and a corresponding shift in mean shape from having more robust to more gracile anterior caps (Figure 6), paralleling the shape trends between wetter and drier morphotypes (Figure 3b). The consistent covariation between *M. californicus* m1 and tooththrow shape and climate, the agreement between the morphologically derived and model-derived palaeo-precipitation, and the loss of morphotype variation all demonstrate that climate is a driving factor in the overall intraspecific structure of dental variation.

The change in jaw and tooth shape from wet-environment morphotypes that are curved to dry-environment morphotypes that are straight (Figure 3) likely reflect the differences in food sources available in these different habitats. Indeed, the nitrogen and oxygen signatures of *M. californicus* individuals significantly correlate with aridity, likely as the result of both physiological changes from water stress and ecological dietary changes (Crumsey, Searle, & Sparks, 2019). In grasslands, the predominant habitat of *M. californicus*, precipitation correlates with overall productivity and the relative abundance of grasses and forbs (Murphy, 1970; Pitt & Heady, 1978; Zavaleta, Shaw, Chiariello, Mooney, & Field, 2003). Differences in the relative roughness of the grasses and forbs growing under different precipitation regimes affect many aspects of dental morphology, including hypsodonty (Fortelius et al., 2002) and number of molar lochs (Evans, 2013). It is therefore quite conceivable that it could drive a change in jaw and tooth curvature. Notably, *M. californicus* populations with straighter, stouter molars are likely able to better process the tough grasses found in dry environments. Furthermore, it is likely that tooth and jaw shape is part of a broader precipitation-dependent trait complex.

*Microtus* tooth shape develops very early in the life of the organism and changes very little throughout ontogeny (Markova, Smirnov, Kourova, & Kropacheva, 2013). Because morphology is established early and intraindividual variation far exceeds individual variation, it is unlikely that biomechanical differences in food processing result in phenotypically plastic jaw and tooth differences. This suggests that differences in the tooth shape are more likely the result of environmental filtering (Polly, 2003). However, detailed analysis of the phenotype-genotype relationship would be necessary to confirm the genetic fidelity of jaw and tooth shape in this species, as there is still the potential that intergenerational plasticity could affect dental variation.

The dynamics of *M. californicus* intraspecific variation have the potential to affect its ability to adapt to changing climates. Although a change in molar and jaw morphology itself may not be sufficient to reduce fitness, it may be representative of more integral climate-related adaptations. Models project that California will become warmer over the next 100 yrs, and that precipitation will increase in the north and decrease in the south (Meehl et al., 2007). As 21% of m1 variation has been lost, likely consisting of the highest-precipitation morphotypes, increases in precipitation could challenge some northern populations as precipitation regimes exceed the scope of the variability that remains in this species. Furthermore, it

is unclear whether the southern populations can endure additional reductions in precipitation, beyond the arid conditions that these populations have previously experienced. Although this species is currently abundant, continued monitoring is recommended, especially for endangered populations such as *M. californicus scirpensis* (Neuwalde, 2002), which lives in relatively arid regions.

Quaternary climate change reduced the phenotypic variation of *M. californicus*, setting the stage as we move into a period of even more rapid climate change. Botkin et al. (2007) refer to the discord between the predicted rise in endangered species resulting from present-day climate change and the relatively few species that became extinct during previous glacial-interglacial transitions as the 'Quaternary conundrum'. However, when we examine how the past has set the stage for the present and a future that includes unique climatic conditions, the conundrum disappears. As evidenced by *M. californicus*, it is likely that in many species experienced a reduction in variation and population restructuring caused by earlier Quaternary change. These changes may limit their ability to adapt in the future. This overall reduction in variation has left the species in a more vulnerable position than it was in during the Pleistocene. The fact that *M. californicus*, a species that is abundant in modern and past California ecosystems, has experienced drastic reductions in morphological variation should increase our wariness about the possible status of many other species that are less abundant and potentially less resilient.

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## DATA AVAILABILITY STATEMENT

Files containing tooth and tooththrow landmark data are available as .tps files on Dryad (<https://doi.org/10.5061/dryad.v15dv41tk>).

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## BIOSKETCHES

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Author contributions: JM conceived of and planned all analyses, performed most analyses, and wrote the manuscript. DL performed all upper jaw analyses, contributed relevant writing and figures, and significantly edited the manuscript.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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