Morphological variation in pectoral girdles of deer mice (genus *Peromyscus*)

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ABSTRACT

The genus *Peromyscus* (deer mice), comprising 83 recognized species that inhabit a wide range of Nearctic regions, is an important group of organisms for studying variation across a large geographic distribution. While *Peromyscus* are scratch diggers — using their forelimbs to break up substrate before pushing it backward with their hindlimbs — there is variation in digging speed and burrow structure that exists between habitats and taxonomic groups. Despite the large literature on *Peromyscus* biology, little is known about the morphological differences between these groupings that could potentially explain the behavioral variation seen in *Peromyscus*. To address this gap, we analyzed the structure and variation of the pectoral girdle using x-ray computed tomography (CT) datasets across the genus *Peromyscus* using natural history collections (NHCs). Using CT images from over 109 individuals and 40 species of *Peromyscus* from the University of Michigan Museum of Zoology (UMMZ) and the Museum of Southwestern Biology (MSB), we segmented and collected nine linear measurements across the forelimbs (humerus, radius, ulna, hand, and scapula) to examine and quantify variation in pectoral girdle morphology across the genus. We grouped individuals by ecoregion, species group, and sex, and statistically compared forelimb morphology of individuals across groups. We also analyzed bioclimatic variables using each individual's locality to determine how temperature and precipitation best explain PC scores. Our results revealed several significant

morphological differences between groupings, particularly between those from warmer climates (e.g., North American deserts) and cooler climates (e.g., eastern temperate forests). Humerus length, scapula length, and scapula height were the main limb measurements driving differences between groups. Additionally, certain bioclimatic variables representing extreme seasonal weather had a strong influence on PC scores. For instance, PC1 is best explained by the mean temperature of the driest quarter (bioclim9), with greater temperatures representing longer humerus and scapula lengths relative to other forelimbs. This study offers valuable insights into how pectoral girdle morphology varies in *Peromyscus*, based on both ecological and taxonomic distinctions.

Keywords: adaptation, burrowing, ecoregion, forelimbs, habitat, natural history, species group, specimen, x-ray computed tomography

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INTRODUCTION

Natural history collections (NHCs) are the libraries of life, serving as the archive of humanity's knowledge of the biodiversity known on our planet (Lister 2011). The voucher specimens housed in NHCs provide spatiotemporal snapshots of an organism, making them essential for understanding the extent of biodiversity and its evolution over time. NHCs have traditionally been used in morphological and taxonomic analyses for comparing organisms and studying potential connections between them (Hilton, Watkins-Colwell and Huber 2021). With the addition of x-ray computed tomography (CT) to the biodiversity scientists' toolkit, voucher

specimens deposited in NHCs are primed to support a reinvigoration of older biological disciplines, such as anatomy (Hilton, Watkins-Colwell and Huber 2021; Blackburn *et al.* 2024). Similar to genomics, the volume of CT data and the breadth of questions that can be answered with that data are immense, and they have aided in the expansion of newer disciplines such as functional anatomy and biophysics (Blackburn et al., 2024). A clear example is the openVertebrate (oVert) Thematic Collections Network, which provides a digital collection of 3D specimen data that researchers use to study form-function relationships and comparative anatomy (Blackburn *et al.* 2024). Through the collaboration of many NHCs and support from federal funding agencies, CT datasets from voucher specimens have been produced at scale and are now available to facilitate large-scale morphological comparisons of species across a broad geographic distribution (Hipsley *et al.* 2020; Blackburn *et al.* 2024).

Morphological analysis has been employed to address numerous questions related to variation. Forelimb morphology, in particular, provides a wealth of insights into locomotion and behavioral differences among mammals. Fossorial and semi-fossorial mammals have undergone multiple adaptations that aid in their digging ability (Kley and Kearney 2007). For example, the most common form of digging in mammals, called scratch digging, involves rapid strokes of the forefeet to loosen the substrate and simultaneous kicks with their forefeet to move the substrate back (Kley and Kearney 2007). Modifications in the forelimbs and pectoral girdle are adapted for digging speed and force (Kley and Kearney 2007). Some examples of this may include robustness of the humerus and radius, the long acromion process in the scapula, the long olecranon process, and the short length of the humerus and metacarpal (Kley and Kearney 2007; Elissamburu and de Santis 2011).

One mammalian group that may offer valuable insights into these types of forelimb modifications is the genus *Peromyscus* (deer mice). The genus *Peromyscus* currently comprises 83 described species (ASM 2025), which are widely distributed across various environments in North America, including deserts, forests, and montane ecosystems (Blair 1950). The robust distribution of *Peromyscus* provides an ample opportunity for studying variation across different habitats (Bedford and Hoekstra 2015a). During extreme temperatures, *Peromyscus* rely on either shelter from their environment, such as vegetation, or must create their own refuge through burrowing (Hu and Hoekstra 2017). Depending on the habitat, burrowing is a necessity for many *Peromyscus* species, such as *P. polionotus*, which inhabit open, sandy areas with little vegetation, unlike species that live in heavily vegetated habitats (Hu and Hoekstra 2017). The morphological consequences of these varying habitat-induced behaviors are widely unknown.

To study different habitats across a wide distribution, ecoregions remain essential. Ecoregions, defined by the United States Environmental Protection Agency (EPA) and the Commission for Environmental Cooperation (CEC), are areas where various geographical and ecological features are similar (Commission for Environmental Cooperation 1997). Ecoregions have historically been used in ecosystem management, the development of water quality standards across different habitats, and the creation of conservation goals (Omernik 1995). Using ecoregions to group similar ecological areas allows for large-scale comparative analyses of these distinct regions. Past studies have differentiated *Peromyscus* species distributions based on geographical features in a similar fashion to how ecoregions are characterized (Wilson 1967). Researchers can use such methods to compare *Peromyscus* morphology according to their associated ecoregion.

In addition to ecoregions, *Peromyscus* species groups are also important to consider when studying morphology. Species groups are informal taxonomic groups used to represent groups of species with close phylogenetic relationships (Blair 1950). In *Peromyscus*, species groups have been historically used to compare evolutionary relationships and speciation within the paraphyletic genus (Blair 1950). There are currently 14 recognized species groups, including the addition of the *hooperi* group, compared to the original 13 recognized by Musser and Carleton (2005) (Bradley *et al.* 2007). In large genera, such as *Peromyscus*, species groups enable researchers to conveniently analyze and categorize multiple species that share similar habitats, behaviors, and evolutionary relationships. This enables comparison among groups to identify broad ecological and morphological patterns.

Lastly, sex is another important factor that may affect *Peromyscus* morphology. *Peromyscus* are typically sexually dimorphic in terms of body size, which may impact forelimb morphology (Schulte-Hostedde, Millar and Hickling 2001). To account for size when comparing bone measurements, past studies have reduced measurements to relative proportions by dividing the measurements by the geometric mean (Mosimann 1970). Dividing by the Euclidean length instead is mathematically analogous and provides a vector-based normalization, emphasizing proportional differences relative to body size.

The primary goal of this study is to compare forelimb morphology across the genus *Peromyscus* while accounting for differences by ecoregions, species groups, and sex in order to understand how pectoral girdle morphology is shaped by *Peromyscus* ecology. To accomplish this goal, we leveraged CT data generated from museum voucher specimens to digitally separate and extract (i.e., segment) the pectoral girdle and compare its size and shape among individuals of different species. We hypothesize that there is a difference in *Peromyscus* pectoral girdle

morphology as a function of their environment. We predict that *Peromyscus* species occurring in warmer climates would exhibit longer appendages as would be predicted by Allen's rule (Allen 1877). In addition, we predict that *Peromyscus* species living in ecoregions where burrowing is a necessity for shelter (e.g., open, sandy environments) will have more robust pectoral girdles. We also hypothesize that there will be a morphological signal at the taxonomic level. Burrowing behavior has been shown to differ among *Peromyscus* species based on field observations, where some species rely heavily on burrowing (e.g., *P. polionotus* of the *maniculatus* group) and others have not been shown to burrow (e.g., *P. perfulvus* of the *melanophrys* group) (Hu and Hoekstra 2017). Such behavioral differences between species groups could be reflected in their morphology. The extent of forelimb morphological variation across different *Peromyscus* species groups has been largely understudied. This study provides a comprehensive analysis of pectoral girdle morphology in *Peromyscus*, offering insights into ecological and taxonomic effects on morphology.

METHODS

Specimens Examined.—We examined 109 whole-body, fluid-preserved adult specimens from the University of Michigan Museum of Zoology (UMMZ) and the University of New Mexico Museum of Southwestern Biology (MSB) (see Supplementary Appendix 1). Our dataset included 40 different *Peromyscus* species, accounting for 13 of 14 *Peromyscus* species groups across North America (see Fig. 1). The *hooperi* species group was removed from the study due to insufficient specimen availability. We attempted to include at least 5 to 6 specimens per species group with approximately an even number of males and females. Specimen locality and sex were obtained from collection records on VertNet from UMMZ and MSB.

X-Ray Computed Tomography (CT).—Specimens were CT scanned using a Nikon XT H 225 ST μCT scanner with the scanning parameters of 85 kilovolts, 200μ-amperes, 250 millisecond exposure time, and 1601 radiograph images at 2x frame averaging. Most datasets were produced from the NSF-funded FuncQEE project (Award # 1902105). Additional datasets were produced to increase taxonomic coverage. 3D segmentations of the humerus, ulna, and radius were completed for 81 individuals using VGSTUDIO MAX. For time purposes, some specimens were only measured and not segmented, which did not impact the data, as the same points where the measurements were taken were accessible without segmentation using the raw 3D skeleton.

Morphological Measurements.—Morphological measurements were collected using the methods in Iwaniuk et al. (1999). The humerus, radius, ulna, olecranon, ulnar shaft, third metacarpal, third phalanx, and scapula were measured for each individual (see Fig. 2). Linear measurements were completed using VGSTUDIO MAX's Polyline Length tool. The topmost and bottommost points of each bone were used to measure its length. We collected each measurement three times and averaged the three measurements, following standard UMMZ procedures for CT datasets. This approach helps reduce human error when selecting measurement points.

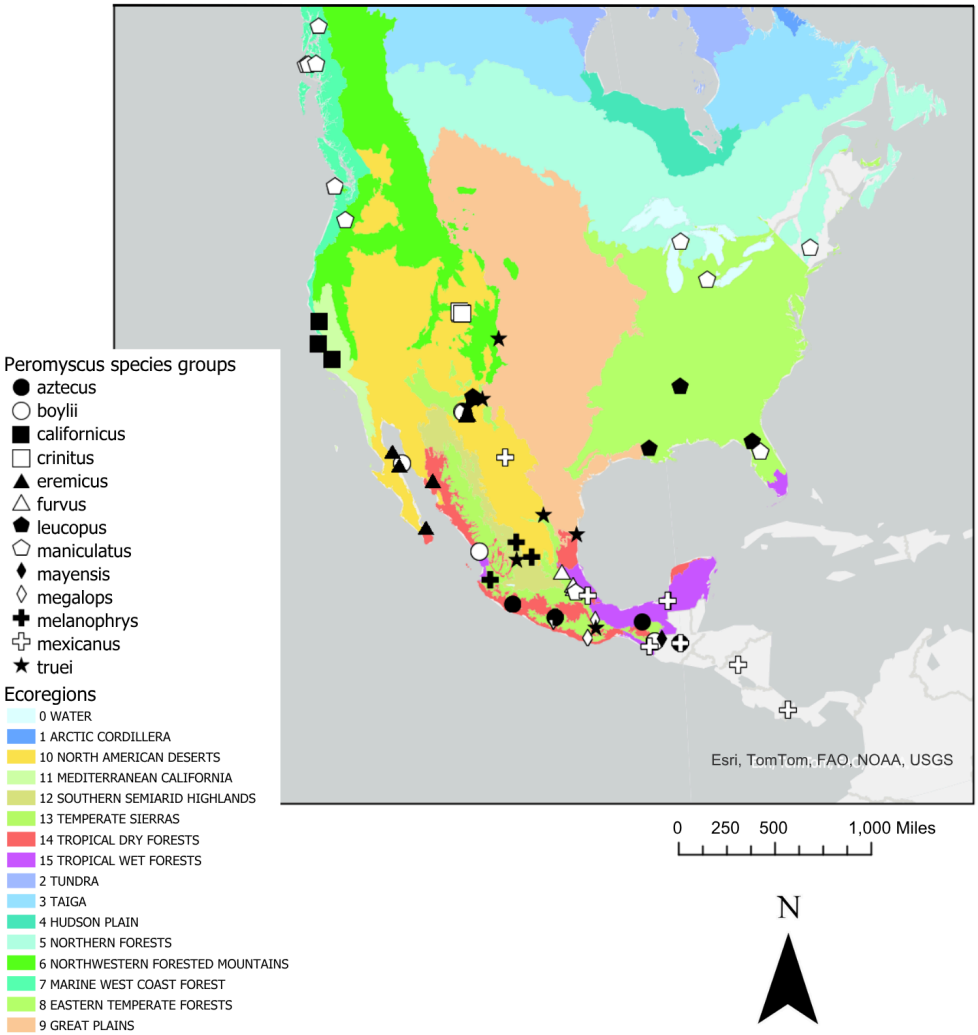


Fig. 1. Localities of *Peromyscus* individuals used in the study across different ecoregions.

Each individual is defined by their species group.

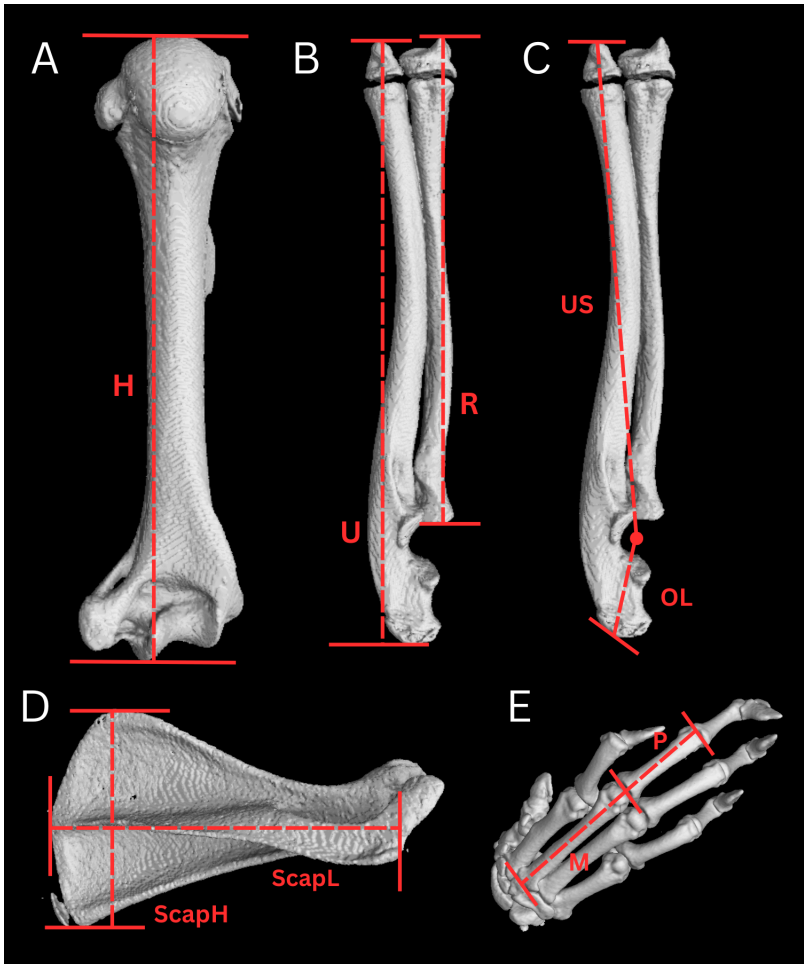


Fig. 2. Linear measurements for each bone. A) Humerus (H) length measurement. **B)** Ulna (U) and radius (R) length measurements. **C)** Olecranon (OL) and ulnar shaft (US) length measurements. **D)** The scapula height (ScapH) and length (ScapL) measurements. **E)** The third metacarpal (M) and respective proximal phalanx (P) length measurements. Detailed descriptions are found in Iwaniuk et al. (1999).

Ecological Definitions.—Ecoregions were defined using the Commission for Environmental Cooperation (CEC)'s Level I ecoregion descriptions and maps (see Table 1) (Commission for Environmental Cooperation 1997). *Peromyscus* species were assigned to particular ecoregions based on distribution maps and taxonomy publications from Mammalian

Species and the Global Biodiversity Information Facility (GBIF) (see Fig. 2). For species with distributions across multiple ecoregions, the most overlapping ecoregion was chosen. Temperate sierras and tropical dry forests were combined into a singular ecoregion category in this study due to their geographic similarity (see Fig. 1). Both ecoregions contain the eastern and western Sierra mountains, volcanic rock, high plant diversity, and seasonal heavy rainfalls (Commission for Environmental Cooperation 1997).

Table 1. Ecoregion descriptions and abbreviations (Commission for Environmental Cooperation 1997)

Ecoregion	Abbrev.	Description
North American deserts	NAD	Arid to semi-arid deserts with extreme seasonal temperatures
Southern semi-arid highlands	SSAH	Semi-arid climate with valleys, hills, and plains from the volcanic sierras
Marine West Coast forests	MWCF	Rocky, temperate rainforests along the coast
Eastern temperate forests	ETF	Dense forest cover with high seasonality
Temperate Sierras/Tropical dry forests	TSTDF	Sierra mountains and dense forests with intense rainfall and volcanic rock
Mediterranean California	MC	Warm and mild Mediterranean climate with dense shrubs, mountains, and plains
Tropical wet forests	TWF	Tropical rainforest with less than three dry months

Statistical Analyses.—We examined whether forelimb measurements varied significantly by species group, ecoregion, and sex using a multivariate framework. Paleontological Statistics (PAST) and R were used to conduct a principal component

analysis (PCA), multivariate analyses of variance (MANOVAs), and a linear discriminant analysis (LDA) using the averages of each bone measurement (Hammer, Harper and Ryan 2001). The PCA enabled us to identify the main factors contributing to variation within *Peromyscus* morphology. Additionally, PC scores per specimen are proxies for the overall shape of each specimen (Teta et al. 2022) because the first few PCs provide orthogonal dimensions that enable us to quantify shape. For example, Teta et al. (2022) used PCA scores of *Abrothrix hirta* specimens as descriptors of shape to quantify cranial variation independent of size. The LDA allowed us to discriminate between groups based on morphological measurements, and the MANOVAs tested whether our groupings were significant. All measurements were row-normalized (all values are divided by their Euclidean length) before conducting each statistical analysis to account for length differences among each bone and variation in body size among individuals, rendering measurement values relative to each other.

We used Spatial Analysis in Macroecology v4.0 (SAM) to visualize PC scores based on the latitudes and longitudes of specimens in the study (Rangel, Diniz-Filho and Bini 2010). SAM allowed us to compare PC scores across the *Peromyscus* distribution and test if there was any spatial correlation associated with *Peromyscus* morphology via Moran's *I* tests for each PC score. A Moran's *I* test is an analysis that tests for spatial autocorrelation, indicating whether values are similar or dissimilar based on proximity to each other (Moran 1950). Moran's *I* tests were conducted at 12 distance classes ranging from 181.619 km to 5492.51 km.

To assess different environmental variables in the context of our data, we used WorldClim (Fick and Hijmans 2017). WorldClim offers a global database of 19 different

bioclimatic (bioclim) variables. We used the R package geodata to extract all 19 bioclim variables from WorldClim at a spatial resolution of 2.5 minutes based on individual specimens' latitudes and longitudes (Fick and Hijmans 2017). We then used the corresponding bioclim variables as covariates and implemented the combined bioclim and soil types covariates into regression tree analyses for the first three PCs to determine which variables or groupings best explained our PC scores.

Spearman correlations.—We used Spearman correlations to test for relationships between the first three PCs and all 19 bioclimatic variables (Xia and Shen 2024). Such analyses do not assume normality of the data and capture relationships that may not be perfectly linear (Schober, Boer and Schwarte 2018). We presented these findings in the form of a Spearman correlation heatmap using R (Xia and Shen 2024). Blue values represent a positive relationship, while the red values represent a negative relationship between two variables. Testing for multicollinearity allows us to identify highly correlated predictor variables, thus avoiding redundancy and improving the interpretability of the data.

Regression Trees.—Regression trees are robust nonparametric algorithms that do not have assumptions on the normality or multicollinearity of the datasets (Muñoz and Felicísimo 2004). This approach is based on decision trees that follow a dichotomous yes-no system. They split a specific group or value into two choices to explain the variable of interest (e.g, PC scores). The first split indicates the best explanation for the variable of interest. Multiple splits are followed until all the variation is accounted for (De'ath and Fabricius 2000). Furthermore, this approach is valuable as it is capable of capturing nonlinear relationships in the datasets implemented (Urban 2002). Regression

trees were used to determine the best environmental predictors of our morphological PC scores (shape) following the framework of Teta et al. (2022).

RESULTS

Multivariate Analyses of Morphological Variation.—We conducted a PCA to examine variation across multiple bone measurements, allowing us to visualize how individuals were distributed according to ecoregion, species group, and sex. The first three PCs explained 56.54%, 17.52%, and 14.38% of the variance (total 88.45%). For the PCA, we used the two principal components with the highest variance (PC1 and PC2) as the axes to visualize the distribution of each grouping (see Fig. 3 and Supplementary Fig. 1). All groupings were highly overlapping, indicating no clear separation of groups. According to the PC loadings plot, humerus length and scapula size (both length and height) contribute positively to PC1 the most (see Fig. 4), meaning those with higher PC1 scores appear to have longer humeri and larger scapulae. For PC2, humerus, metacarpal, phalanx, and scapula length contributed positively to PC2 values, while scapula height is negatively driving them. For PC3, humerus length contributes positively to its values, and scapula length negatively affects it. PCs 1-3 were used in subsequent analyses as they accounted for a strong majority of the variance and represented biologically meaningful axes of forelimb variation.

To further analyze humerus and scapula variation based on the results from the PCA, we compared average humerus length, scapula length, and scapula height across different ecoregions without row-normalizing the measurements (see Supplementary Fig. 2). No row-normalization allowed us to capture both shape and size differences. Greater values in all three bone measurements were seen in *Peromyscus* from Mediterranean California (MC), southern

semi-arid highlands (SSAH), temperate Sierras/tropical dry forests (TSTDF), and tropical wet forests (TWF). Additionally, using CT data and segmentations, pectoral girdles were compared across the *Peromyscus* species group phylogeny (see Fig. 5). Despite 3D visualizations of the data, differences between forelimb morphology are not visually discernible and require in-depth statistical analyses to examine.

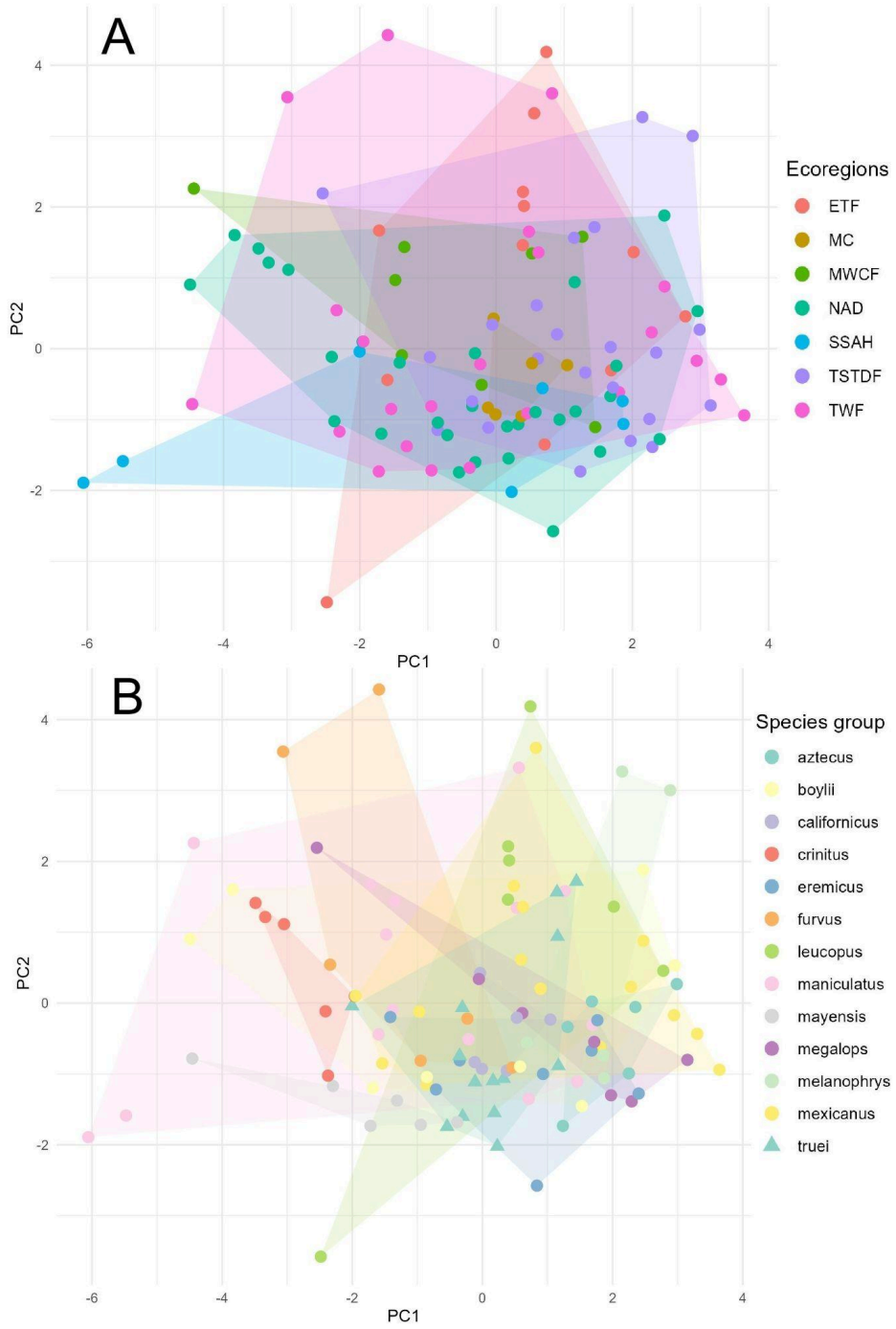


Fig. 3. Principal component analysis (PCA) of *Peromyscus* forelimbs with groupings of ecoregions (A) and species group (B). PC1 and PC2 explain 56.54% and 17.52% of the total variance, respectively. See Supplementary Fig. 1 for PCA with sex grouping.

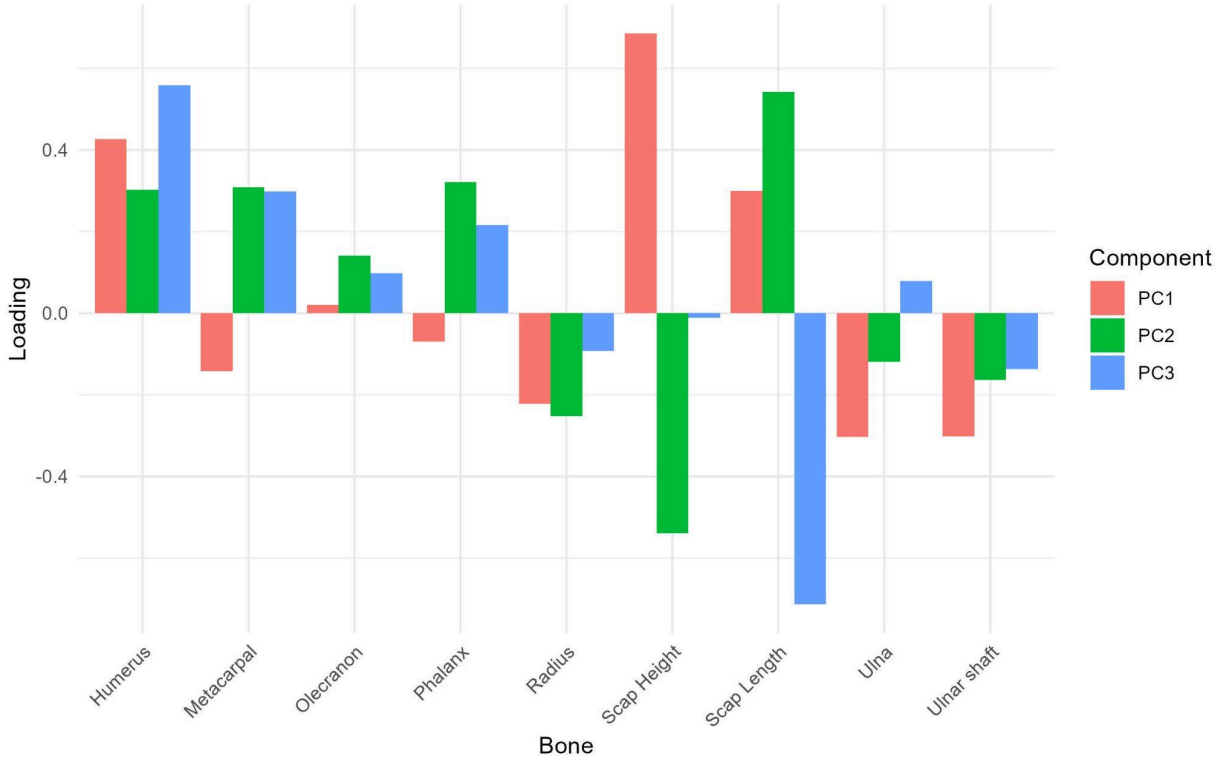


Fig. 4. PC loadings plot of all *Peromyscus* forelimb measurements.

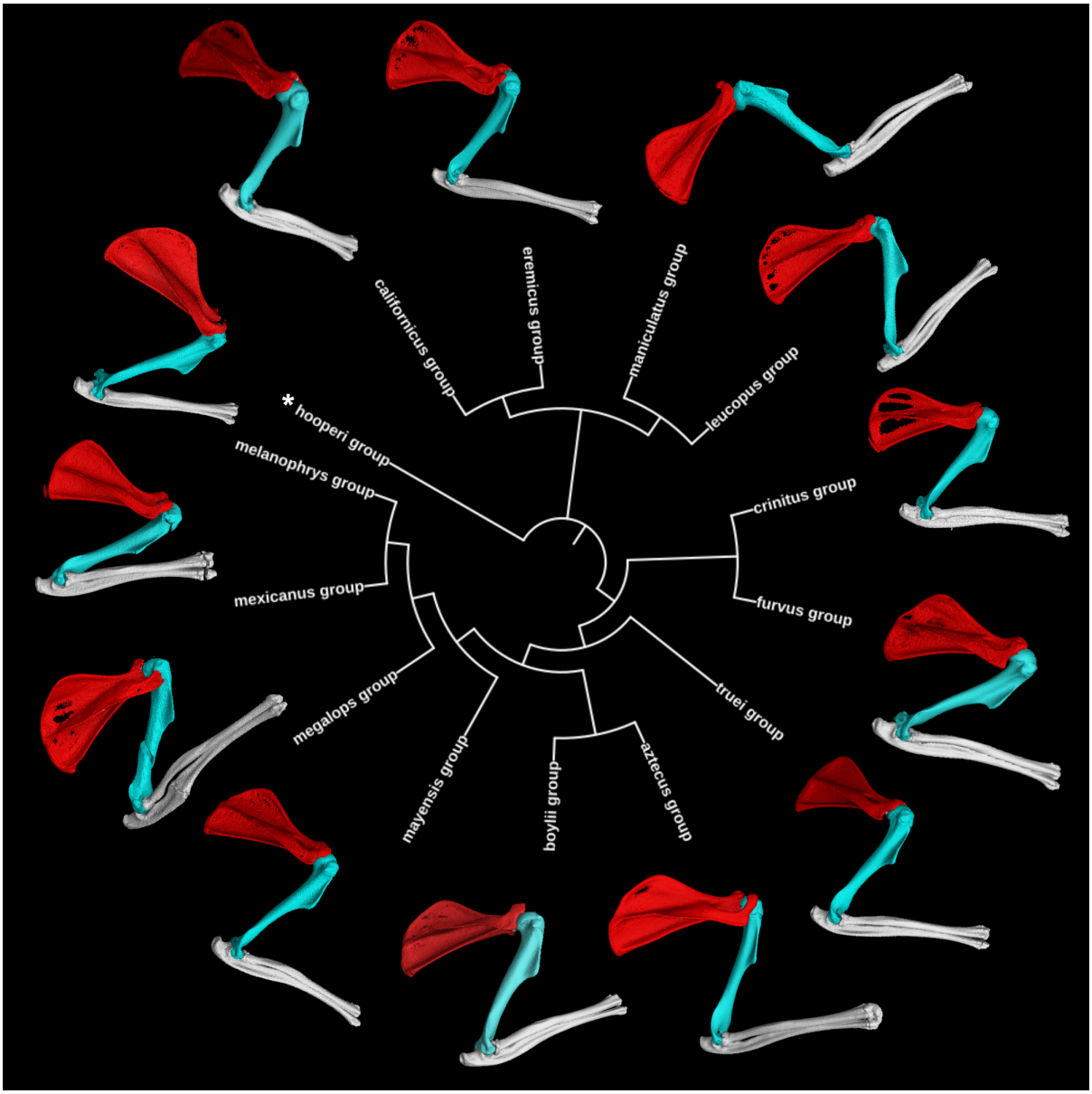


Fig. 5. Forelimb character trait variation of *Peromyscus* species groups mapped on mitochondrial cytochrome-b phylogeny. The phylogeny was produced using cytochrome-b sequences from GenBank and mapped using NGPhylogeny.fr and Interactive Tree of Life (iTOL) (Katoh et al. 2019; Lemoine et al. 2019). The branch lengths are arbitrary. Forelimb morphological variation is not visually discernible and requires statistical analyses to observe subtle differences. *the *hooperi* group was excluded due to the limited availability of specimens.

We also conducted an LDA to assess whether ecoregion, species group, and sex groupings could be distinguished based on forelimb measurements. The first three linear discriminants explained 37.66%, 25.68%, and 18.96% of the variance, respectively (82.30%). Plotting of the first two dimensions of LDA also showed many overlapping groups (see Fig. 6 and Supplementary Fig. 3). LDA loading scores revealed many of the bone measurements negatively driving LD1 while positively driving the other LDs (see Fig. 7). Compared to the PCA, the radius and ulna seem to have more influence over the LDs compared to the scapula for the PCs, forearm length plays a greater role in distinguishing groups than shoulder or upper arm morphology. For ecoregions, 47.71% of individuals were correctly classified. 57.80% of individuals' species groups were correctly classified, and 65.14% of individuals' sexes were correctly classified. These results indicate that ecoregions may not produce substantial separation in forelimb morphology, whereas species group and sex show moderate differentiation among individuals. Subtle differences between groups may exist within *Peromyscus*.

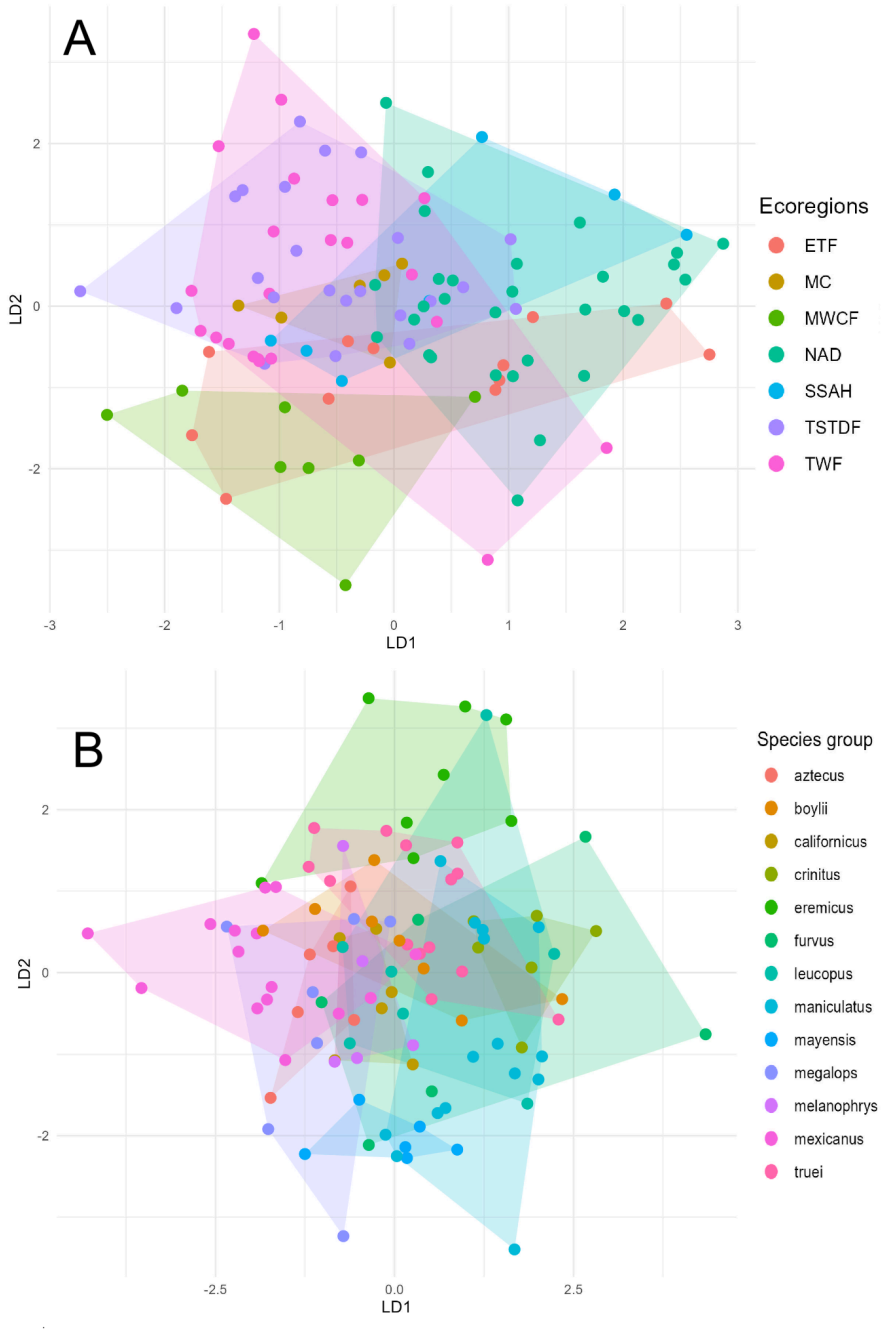


Fig. 6. Linear discriminant analysis (LDA) of *Peromyscus* forelimbs with groupings of ecoregions and species group. See Supplementary Fig. 2 for LDA with sex grouping.

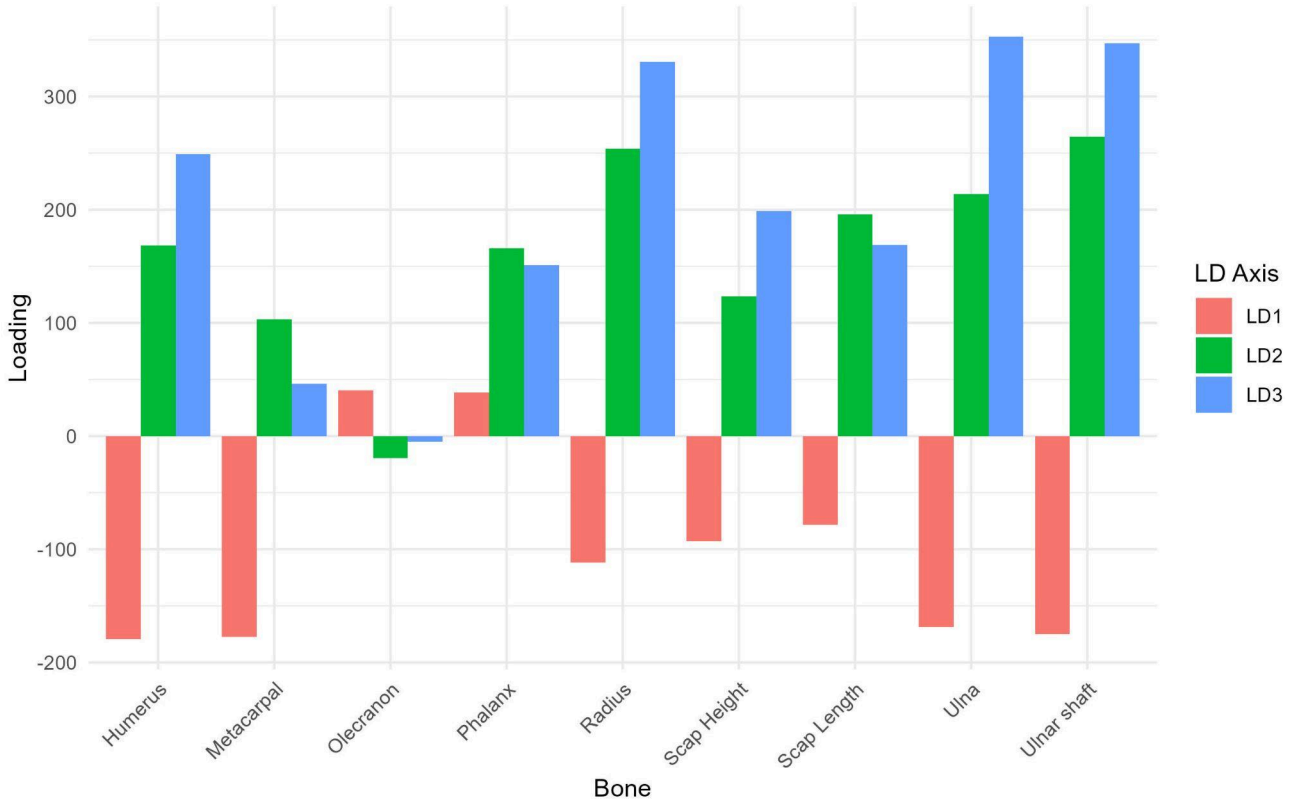


Fig. 7. LD loadings plot of all forelimb measurements.

The MANOVA analyses showed significant differences among five ecoregions and six species groups. Ecoregion pairs involving North American deserts (NAD), marine west coast forests (MWCF), eastern temperate forests (ETF), tropical wet forests (TWF), and temperate sierras/tropical dry forests (TSTDF) were the only ecoregion groups to have significant differences (Wilks' $\lambda = 0.253$, $F(54, 483.9) = 2.77$, $p < 0.001$) (see Supplementary Table 1). The MANOVA between species groups had even fewer significant pairings, with the *mexicanus* species group having the most (Wilks' $\lambda = 0.065$, $F(108, 653.2) = 2.76$, $p < 0.001$) (see Supplementary Table 2). However, when considered together, the *Peromyscus* specimens examined in this study did not show significant sexual dimorphism based on the MANOVA (Wilks' $\lambda = 0.891$, $F(9, 99) = 1.34$, $p = 0.226$).

Spatial Autocorrelation.—Significant Moran's *I* values in PCs 1-3 occurred at multiple distance classes. For PC1, significant positive values were observed at 181.619 m ($I = 0.083$, $p = 0.016$) and 2300.282 m ($I = 0.093$, $p = 0.003$). Significant negative values were observed at 538.12 m ($I = -0.094$, $p = 0.016$) and 2620.03 m ($I = -0.116$, $p = 0.006$). For PC2, only two significant values occurred at 823.375 m ($I = 0.142$, $p = <0.001$) and 2992.922 m ($I = -0.161$, $p = <0.001$). PC3 had significant positive values at the shortest distances of 181.619 m ($I = 0.188$, $p = <0.001$), 538.12 m ($I = 0.143$, $p = <0.001$), and 823.375 m ($I = 0.132$, $p = <0.001$) and significant negative values at the longer distances of 1718.066 m ($I = -0.124$, $p = 0.001$), 2620.03 m ($I = -0.192$, $p = <0.001$), and 2992.922 m ($I = -0.146$, $p = <0.001$). Standard error across all Moran's *I* values ranged from 0.034 to 0.039. Despite the first three PCs showing some significant Moran's *I* values, the shape of the correlograms is nearly flat, as most points are close to zero (see Supplementary Fig. 4). These findings show that there is no strong or consistent spatial distribution, suggesting weak spatial autocorrelation. This indicates that the forelimb shape of individuals does not strongly depend on their spatial proximity.

Spearman correlations.—According to the Spearman correlation heatmap, the first three PCs were mainly positively correlated with bioclimatic variables (see Fig. 8). PC1 had high positive correlations with bioclims 1, 6, 8, 9, 11, and 15, suggesting longer humeri and larger scapulae are associated with greater mean temperatures during different extreme months (e.g., coldest month, wettest quarter). Strong negative correlations were observed for PC1 in bioclims 4, 14, and 17, indicating that individuals with longer humeri and larger scapulae tend to occur in areas with lower temperature seasonality and lower precipitation during the driest periods. For PC2, there were not many strong positive correlations, yet there were moderate negative correlations between PC2 and bioclims 3 and 15, indicating a possible correlation between PC2,

isothermality, and seasonality. In PC3, strong positive correlations were seen in bioclims 12, 13, and 16, showing a possible correlation between PC3 and precipitation. A strong negative correlation was also observed in bioclim7, indicating a relationship between PC3 and temperature extremes. These patterns highlight potential multicollinearity between the first three PCs and bioclimatic variables.

Regression Trees.—The regression trees show variables that affect values in PCs 1-3 (see Fig. 9 and Supplementary Fig. 5). PC1 was mainly defined by bioclim9 (mean temperature of the driest quarter), bioclim6 (minimum temperature of the coldest month), and bioclim3 (isothermality). PC2 was mainly influenced by bioclim14 (precipitation of the driest month), bioclim5 (maximum temperature of the warmest month), and bioclim2 (mean diurnal range). PC3 was driven by bioclim16 (precipitation of the wettest quarter), bioclim7 (temperature annual range), and four of the ecoregion distinctions (three of which had significant MANOVA values). Latitude did not seem to play a role in affecting PC scores (see Fig. 9 and Supplementary Fig. 6).

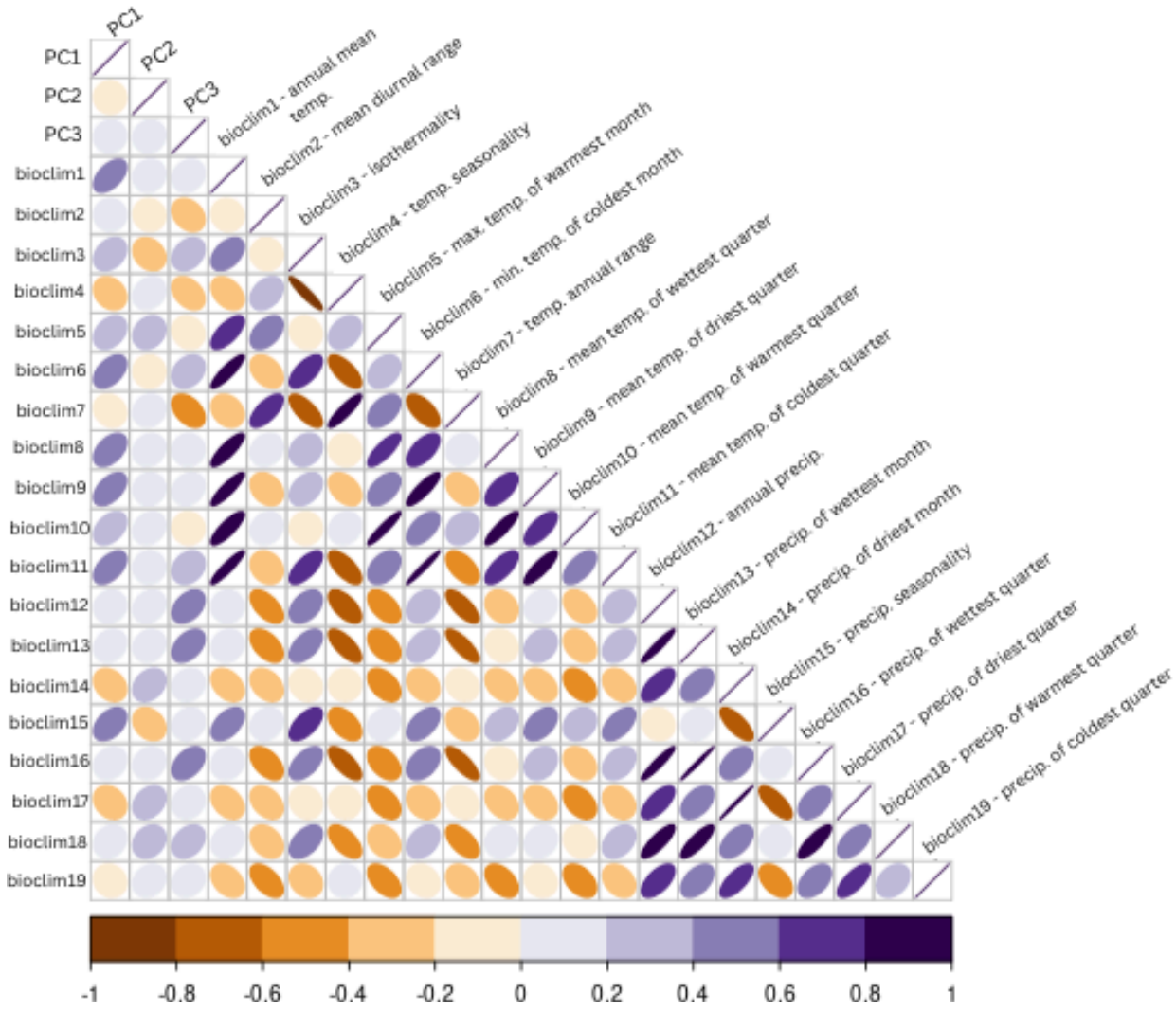


Fig. 8. Spearman correlations heatmap of PCs 1-3 and all 19 bioclimatic variables (Fick and Hijmans 2017)**.**

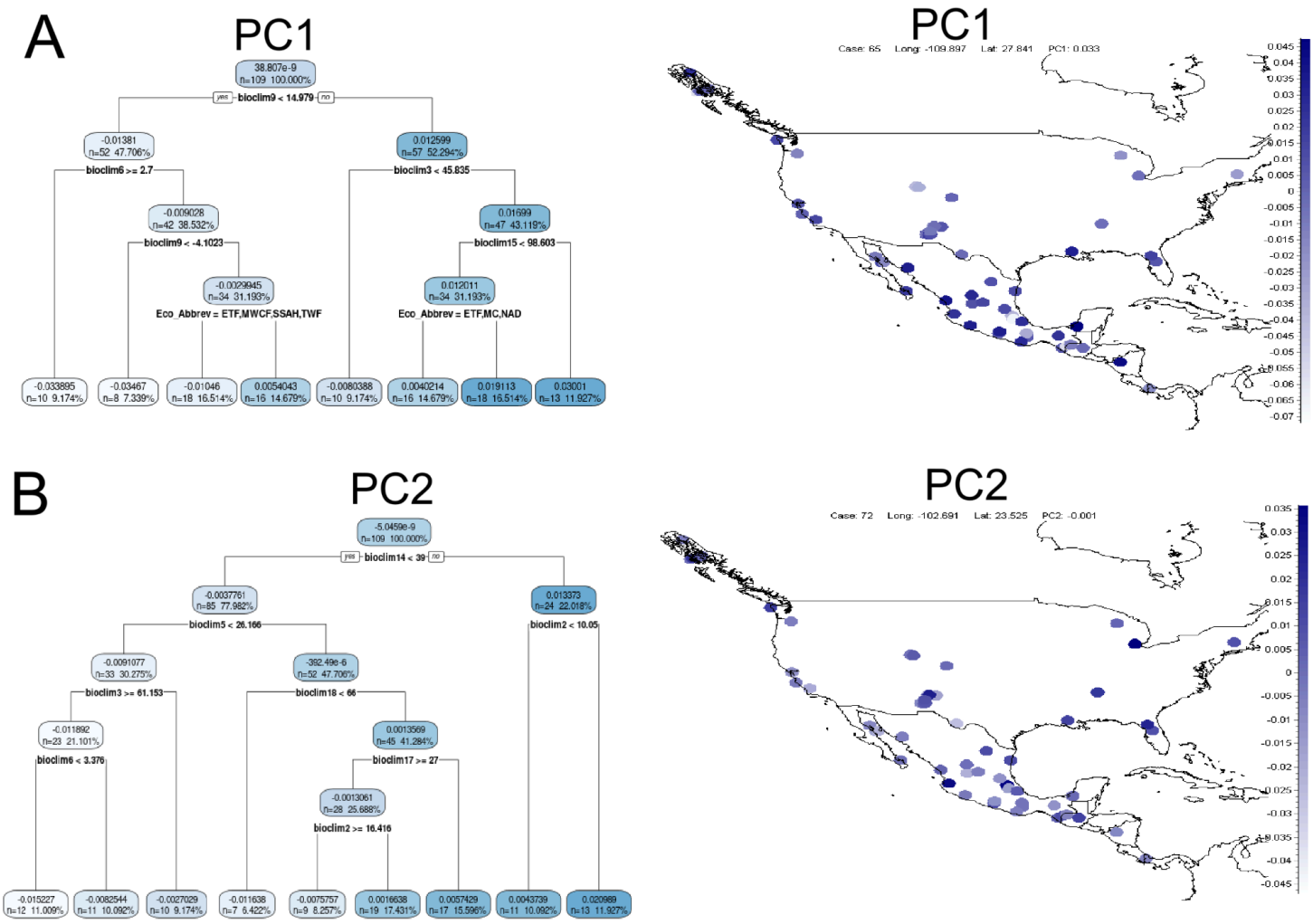


Fig. 9. Regression trees and spatial distributions for PCs 1 and 2. See Supplementary Figs. 5 and 6 for the regression tree and spatial distribution of PC3.

DISCUSSION

Understanding how pectoral girdle morphology varies across the genus *Peromyscus* provides insight into a possible basis of burrowing adaptations and the relationship it has with different environmental factors (Hu and Hoekstra 2017). *Peromyscus*'s large distribution allows us to observe morphological variation across many habitats with varying climate, substrate, and geological features. This study aids in filling in gaps of research when it comes to *Peromyscus*

morphology affecting their digging behavior and adds to the growing body of literature addressing mammalian morphological adaptations to burrowing and environmental impacts on morphology.

From our PCA loadings, humerus and scapula size are the main morphological features driving PC values. Seen in PC1, representing 56.54% of variance, scapula height and humerus length had the highest PC loadings of 0.69 and 0.43, respectively. In PC2, representing 17.52% of variance, scapula length and scapula height had the highest PC loadings of 0.54 and -0.54, respectively. In PC3, representing 14.38% of variance, scapula length and humerus length had the highest PC loadings of -0.71 and 0.56, respectively. Scapula and humerus size primarily drive the major axis of pectoral girdle morphological variation in our dataset. This supports the idea that scapula and humerus size and shape are most representative of pectoral girdle adaptation to burrowing in scratch diggers (Kley and Kearney 2007). The scapula restricts the rotation of the humerus, which is important for having a greater force while digging (Kley and Kearney 2007). However, future research should consider separating groups based on *Peromyscus* that do not burrow from those that do to test functional anatomy tied to burrowing behavior explicitly.

Other mammals also exhibit different forelimb morphology in terms of digging adaptations (Kley and Kearney 2007; Samuels and Van Valkenburgh 2008; Costes *et al.* 2022; de Oliveira, da Silva Netto and Tavares 2025). In Western European moles (genus *Talpa*), which have a largely subterranean lifestyle, shorter forelimbs are beneficial for stronger and faster digging abilities (Costes *et al.* 2022). These forelimb adaptations have been noted to be the main structure used for digging and locomotion (Costes *et al.* 2022). Additionally, in oryzomyine rodents, significant scapula morphological differences were observed between groups of varying locomotive lifestyles and species within the genus *Cerradomys* (de Oliveira, da Silva Netto and

Tavares 2025). Widened scapular blade and anterior subscapularis ridge promote forelimb rotation and adductive actions of *C. goytaca,* facilitating greater strength and flexibility while climbing (de Oliveira, da Silva Netto and Tavares 2025). These studies represent how forelimb morphological adaptations seen in mammals respond to locomotive needs. In our dataset, the scapula and humerus were the main bone measurements driving PC scores. In the case of PC1, larger PC1 values meant more robust humeri and scapulae, which are essential for providing stronger digging forces in mammals. Therefore, the strong influence of the humerus and scapula on PC scores highlights a possible adaptive association between these bone measurements and burrowing in *Peromyscus*.

The LDA follows a similar pattern to the PCA. There was much overlap between our different groupings, suggesting that distinctions between groups may be more subtle. However, the radius, ulna, and humerus were observed to be the main measurements driving LD scores. In LD1, representing 37.66% of variance, humerus, metacarpal, and ulnar shaft length had the highest LD loadings of -179.42, -177.22, and -175.09, respectively. In LD2, representing 25.68% of variance, ulnar shaft and radius length had the highest LD loadings of 264.72 and 253.86, respectively. In LD3, representing 18.96% of variance, the ulnar shaft, ulna, and radius length had the highest LD loadings of 352.92, 347, and 330.85, respectively. The difference between the measurements driving PC scores vs. LD scores reveals that the humerus length and scapula size may vary the most across the whole dataset, while the radius and ulna length best explain the variation between groups of *Peromyscus*. The length of the radius and ulna and their proportions to other bones have been observed to be indicators of different types of locomotion, such as distinguishing between fossorial, arboreal, terrestrial, and semi-aquatic mammals (Ito and Endo 2025). Studies have shown that some species of *Peromyscus* (e.g., *P. californicus*) are poor

diggers and display behaviors of semi-fossoriality (Weber and Hoekstra 2009). Future research should investigate forelimb morphology by type of locomotion in *Peromyscus* species.

Despite PCA and LDA showing strong overlap in the data, there are subtle morphological differences between some of the ecoregion groups and species groups as detected by the MANOVA. The ecoregions NAD, MWCF, ETF, TWF, and TSTDF were the only ecoregions to have significant differences between them and other ecoregions, including between each other. These MANOVA results could indicate a difference in *Peromyscus* morphology between individuals that live in warmer climates (i.g, NAD, TWF, TSTDF) compared to those that live in colder/highly seasonal climates (i.g, MWCF, ETF). Significant MANOVA results between warmer climates could indicate that temperature alone is not solely responsible for the observed morphological differences. Moreover, we observed non-significant MANOVA values when comparing morphological differences among sexes. Although rodents are often sexually dimorphic in body size, the degree of dimorphism in our dataset may not be sufficient to produce differences in limb measurements between sexes (Schulte-Hostedde, Millar and Hickling 2001). However, further analyses should consider comparing differences between sexes per species to account for *Peromyscus* species, which may show stronger signs of sexual dimorphism.

The weak spatial autocorrelation found in our Moran's *I* test and mapping of the PCs across our study area indicates that ecological groupings (i.e., ecoregion) may be defining pectoral girdle morphology more than geographic proximity (e.g., latitudes, longitudes). Differences between habitats could drive variation within *Peromyscus* forelimbs due to substrate, climate, and behavioral disparities as a response to the environment.

Along those lines, forelimb morphology has been observed to be adaptive in fossorial mammals depending on the environment's substrate (Siciliano-Martina, Guerra and Veech 2023).

Differences in substrate could be used to explain differences between ecoregion groups in *Peromyscus*. For example, in hispid cotton rats (*Sigmodon hispidus*), individuals that lived in sandy soils had seven times more burrows than those that lived in compact clay soils (Shump 1978). Sandy soils have also been shown to have less complexity than clay soils for small mammals (Laundre and Reynolds 1993), making it easier to facilitate burrowing. Differences in substrate may drive these behavioral adaptations to the environment, possibly impacting pectoral girdle morphology. Moreover, in kangaroo rats (genus *Dipodomys*), specialized forelimb morphology (i.e., robusticity of the olecranon) was seen in *D. elator*, a species that primarily lives in a denser substrate environment of clay (Siciliano-Martina, Guerra and Veech 2023). This indicates that denser substrates could promote forelimb adaptations for enhanced burrowing in these environments. These differences in substrate and morphology could explain the morphological differences we see between different ecoregions in *Peromyscus*. For instance, the MANOVA pairing between ETF and NAD was significant. Temperate forests typically have hard rock near the surface and an accumulation of clay in their soils (Adams *et al.* 2019). The deserts usually have dry, sandy substrates, including dunes (Commission for Environmental Cooperation 1997). The energetically efficient sandy substrate of the deserts could promote burrowing in *Peromyscus* compared to the denser substrate of the temperate forests, leading to pectoral girdle morphological adaptations. However, lab-reared *Peromyscus* species were found to exhibit the same digging patterns compared to their wild counterparts, suggesting that digging ability may be heritable rather than environmental (Hu and Hoekstra 2017). However, differences between individuals that have evolved in different environments could still exist (i.e., those that live in sandy soils may show morphological traits that are different from those living in rock substrates, reflecting adaptations to these different environments).

Another possible explanation could be that our morphological data are in support of Allen's rule. Allen's rule states that animals living in warmer latitudes tend to have longer appendages for better heat dissipation (Allen 1877). We observed, on average, longer humeri and scapulae were seen amongst *Peromyscus* species living in MC, SSAH, TSTDF, and TWF. These areas have an annual temperature range of 12 to 29°C and an annual precipitation range of 200 to 3,000 mm (Commission for Environmental Cooperation 1997). We also saw the *mexicanus* species group, a group that typically inhabits warmer climates, being more significantly different from other groups based on our MANOVA. These ecoregions are typically hot and humid climates where having more surface area is necessary for releasing excess body heat. Temperature differences between climates could enforce a selective pressure on *Peromyscus* limb morphology.

Our regression trees further support this idea. For PC1, our results indicate that temperature during extreme climate stress (i.e., driest quarter, coldest month) could explain variation within *Peromyscus* morphology. For PC2, temperature and precipitation during extreme hot and dry seasons were driving regression tree analyses. Lastly, PC3 had more broad results, with scores being mostly determined by precipitation seasonality, annual temperature range, and large-scale ecoregions. These harsh seasonal climates affecting the PCs could indicate a need for burrowing, such as protecting themselves from extreme weather events. In warmer climates, such as deserts, with less forest coverage, fewer places for shelter, and higher temperatures, there may be a greater need to burrow for *Peromyscus*, suggesting that these unfavorable conditions enhance the need to burrow (de Oliveira, da Silva Netto and Tavares 2025). *Peromyscus* may rely mainly on burrowing to maintain thermoregulation (Kinlaw 1999). Burrows protect against extreme temperatures and dry climates, which is necessary for fossorial or semi-fossorial

mammals in arid environments. Due to this behavior change, the hotter climate could exert a selective pressure for adaptations that enhance digging in *Peromyscus*. In colder climates, vegetation and tree cover provide shelter and shade for *Peromyscus* species, reducing the need for burrowing to cooler temperatures (Kinlaw 1999).

Additionally, the phylogeny of *Peromyscus* is largely debated (Bradley *et al.* 2007; Platt *et al.* 2015). Being a paraphyletic genus, many *Peromyscus* species groups have been noted to diverge from other genera such as *Megadontomys*, *Neotomodon*, *Habromys*, *Osgoodomys*, and *Isthmomys* based on cytochrome-b sequences (Bradley *et al.* 2007). This makes the evolution of *Peromyscus*' forelimb morphology less clear, and additional morphological variation could be found between species groups with the addition of these taxa. Future studies should control for phylogenetic proximity, as more closely related individuals are expected to share more similar traits.

CONCLUSION

The genus *Peromyscus* is an excellent study system for understanding how morphology differs across a wide distribution (Bedford and Hoekstra 2015b). Our results demonstrate subtle morphological differences in the pectoral girdles between taxonomic groups (i.e., species groups) and *Peromyscus* species living in different ecoregions. Because of their availability in NHCs, additional and more extensive study of this group of mice would prove invaluable to further our understanding of large-scale adaptation and evolution in widely distributed taxa. Although we used a large number of datasets representing a majority of the species in the genus, more individuals per species are needed for better resolution of the morphological variation within *Peromyscus*. In addition, because of known paraphyly in the genus *Peromyscus* (sensu lato)

(Platt *et al.* 2015), a reassessment of these data with additional taxa is warranted to fully understand the variation within this genus. Geometric morphometrics should also be considered for addressing shape differences among the forelimbs.

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SUPPLEMENTARY DATA

Supplementary Appendix 1. Complete list of all *Peromyscus* specimens used in the study. Specimens are organized by species group and then alphabetically by species. The total number of specimens examined for each species group is given. Specimens are located in the University of Michigan Museum of Zoology (UMMZ) and the University of Mexico's Museum of Southwestern Biology (MSB).

Species group	# of specimens	Species and collection #
aztecus	6	*P. aztecus evides* UMMZ113740, UMMZ113741 *P. oaxensis* UMMZ109095, UMMZ122508 *P. spicilegus* UMMZ110695, UMMZ110700
boylii	8	*P. boylii* MSB74714, MSB74725 *P. levipes* UMMZ118346, UMMZ118350 *P. simulus* UMMZ109042, UMMZ109047 *P. stephani* UMMZ116581, UMMZ116582
californicus	6	*P. californicus californicus*

Species group	# of specimens	Species and collection #
		UMMZ109703, UMMZ109704, UMMZ178720 *P. californicus parasiticus* UMMZ103725, UMMZ103726, UMMZ103727
crinitus	6	*P. crinitus auripectus* MSB109317, MSB109322, MSB109323, MSB109324, MSB109353, MSB115514
eremicus	8	*P. eremicus* MSB263585, MSB263594 *P. eva* UMMZ117250 *P. guardia harbisoni* UMMZ116548, 116553 *P. interparietalis interparietalis* UMMZ116554, UMMZ116557 *P. merriami merriami* UMMZ116576
furvus	6	*P. furvus* UMMZ110712, UMMZ110713, UMMZ110714, UMMZ113077, UMMZ113078, UMMZ113762
leucopus	7	*P. gossypinus* MSB81569, MSB81570 *P. gossypinus gossypinus* UMMZ103747, UMMZ103750 *P. leucopus* MSB87786, MSB89757 *P. leucopus leucopus* UMMZ115693
maniculatus	15	*P. keeni* UMMZ57845, UMMZ57846, MSB195201, MSB221428, MSB221540, MSB221554, MSB231922, MSB311969 *P. maniculatus bairdii* UMMZ167788 *P. maniculatus gracilis* UMMZ167892, UMMZ170383 *P. melanotis* UMMZ112996, UMMZ112997 *P. polionotus rhoadsi* UMMZ79957, UMMZ79963

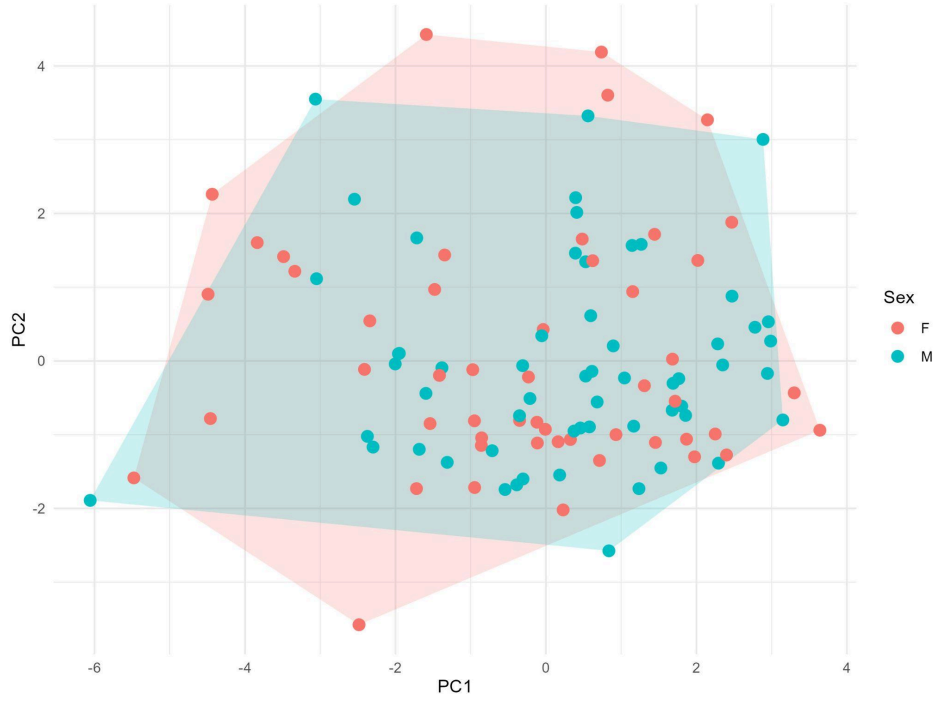
Species group	# of specimens	Species and collection #
mayensis	6	*P. mayensis* UMMZ117911, UMMZ117912, UMMZ117913, UMMZ118340, UMMZ118342, UMMZ118339
megalops	7	*P. megalops auritus* UMMZ109058, UMMZ109059, UMMZ109061, UMMZ109066 *P. melanocarpus* UMMZ113760 *P. melanurus* UMMZ118369, UMMZ118370
melanophrys	5	*P. melanophrys consobrinus* UMMZ117240, UMMZ120997 *P. melanophrys melanophrys* UMMZ110720 *P. perfulvus* UMMZ101271, UMMZ101272
mexicanus	15	*P. grandis* UMMZ122515 *P. guatemalensis* UMMZ118352, UMMZ118356 *P. gymnotis* UMMZ117270, UMMZ117271 *P. mexicanus mexicanus* UMMZ113073, UMMZ133074 *P. mexicanus saxatilis* UMMZ117015, UMMZ117019 *P. nudipes* MSB262156, MSB262207 *P. yucatanicus* UMMZ120779, UMMZ120782 *P. zarhynchus* UMMZ101721, UMMZ101722
truei	14	*P. collinus* UMMZ113004, UMMZ113008 *P. difficilis difficilis* UMMZ101273, UMMZ101274 *P. gratus* MSB82342, MSB82343 *P. nasutus* UMMZ56763, UMMZ56765 *P. ochraventer* UMMZ113070, UMMZ113071 *P. truei*

Species group	# of specimens	Species and collection #
		MSB28596, MSB28597
		P. truei zapotecae
		UMMZ109126, UMMZ109131

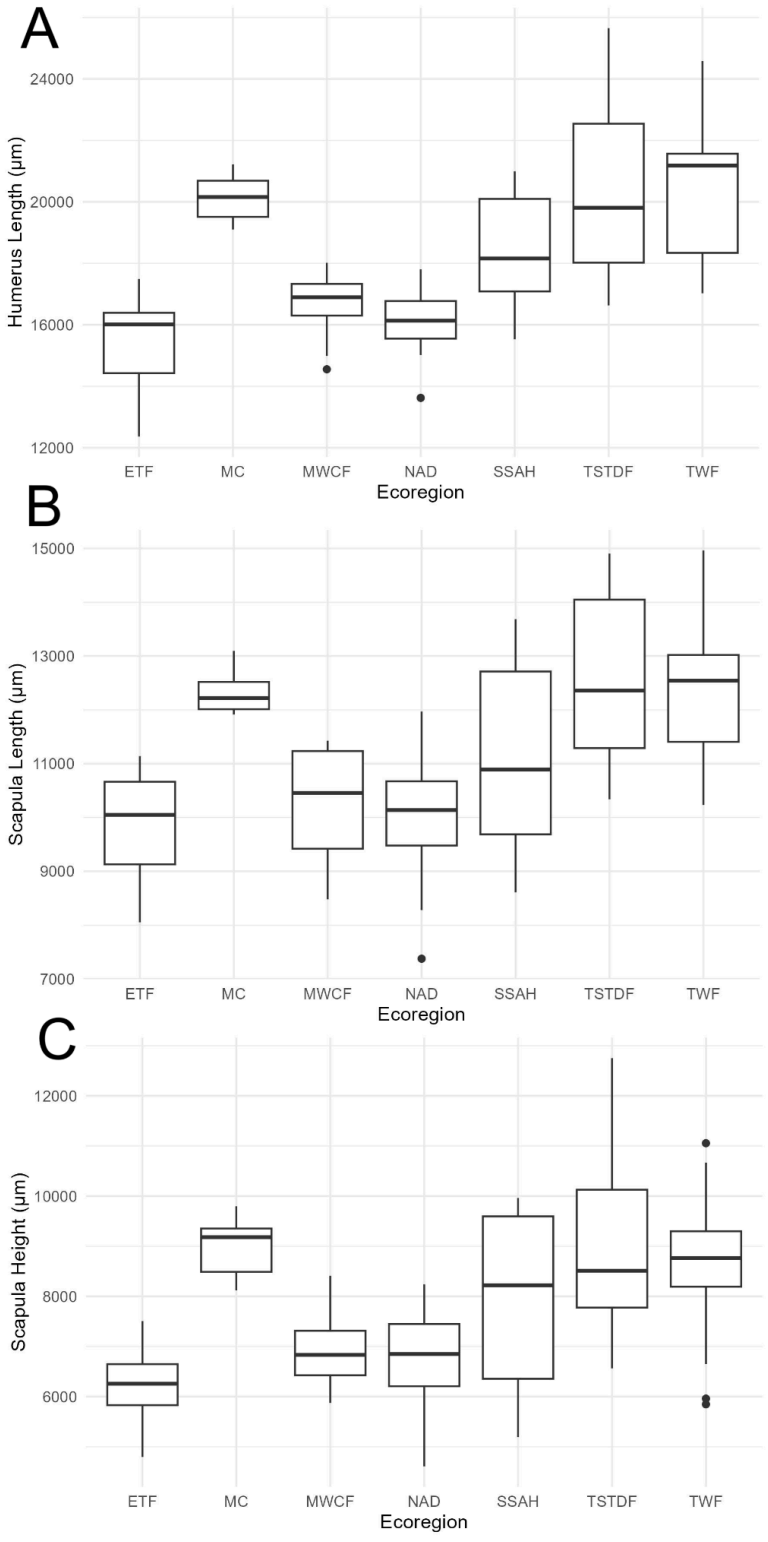
Supplementary Appendix 2. Complete list of all *Peromyscus* individuals used in creating the phylogenetic tree (see Fig. 5). These individuals were used strictly for their cytochrome-b sequence and were not involved in any of the morphological analyses. Sequences were taken from the National Center for Biotechnology Information (NCBI) Nucleotide.

Species	GenBank Accession	Basepairs (linear DNA)
P. maniculatus	PP746695.1	1144
P. boylii	PP746696.1	1144
P. truei	PP746697.1	1144
P. leucopus	AF131926.1	1143
P. eremicus	AY322503.1	1143
P. melanophrys	AY322510.1	1143
P. crinitus	AY376413.1	1143
P. megalops	DQ000475.1	1143
P. mexicanus	AY376425.2	1143
P. mayensis	DQ836300.1	1143
P. hooperi	DQ973103.1	1143
P. californicus	FJ716218.1	1143
P. aztecus	FJ214683.1	1143

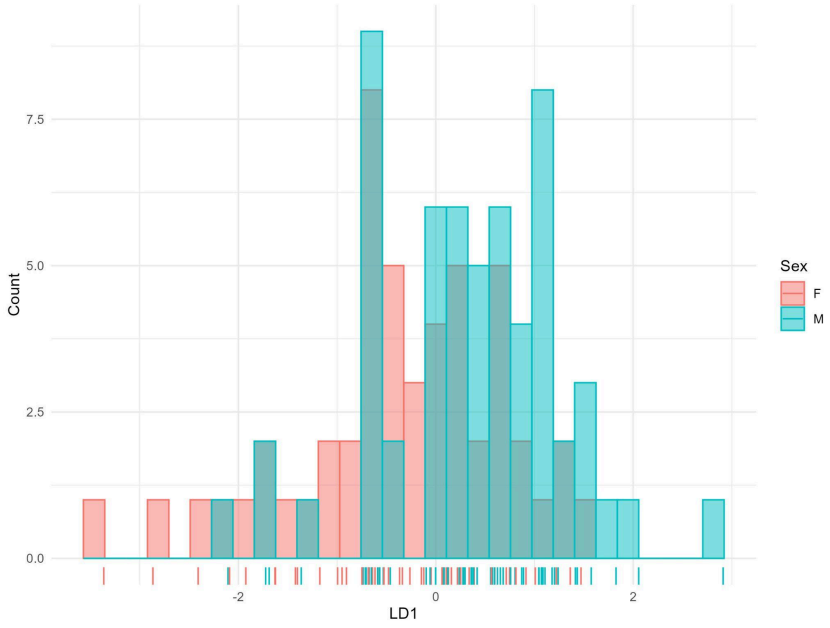
Species	GenBank Accession	Basepairs (linear DNA)
P. furvus	KT965004.1	1117



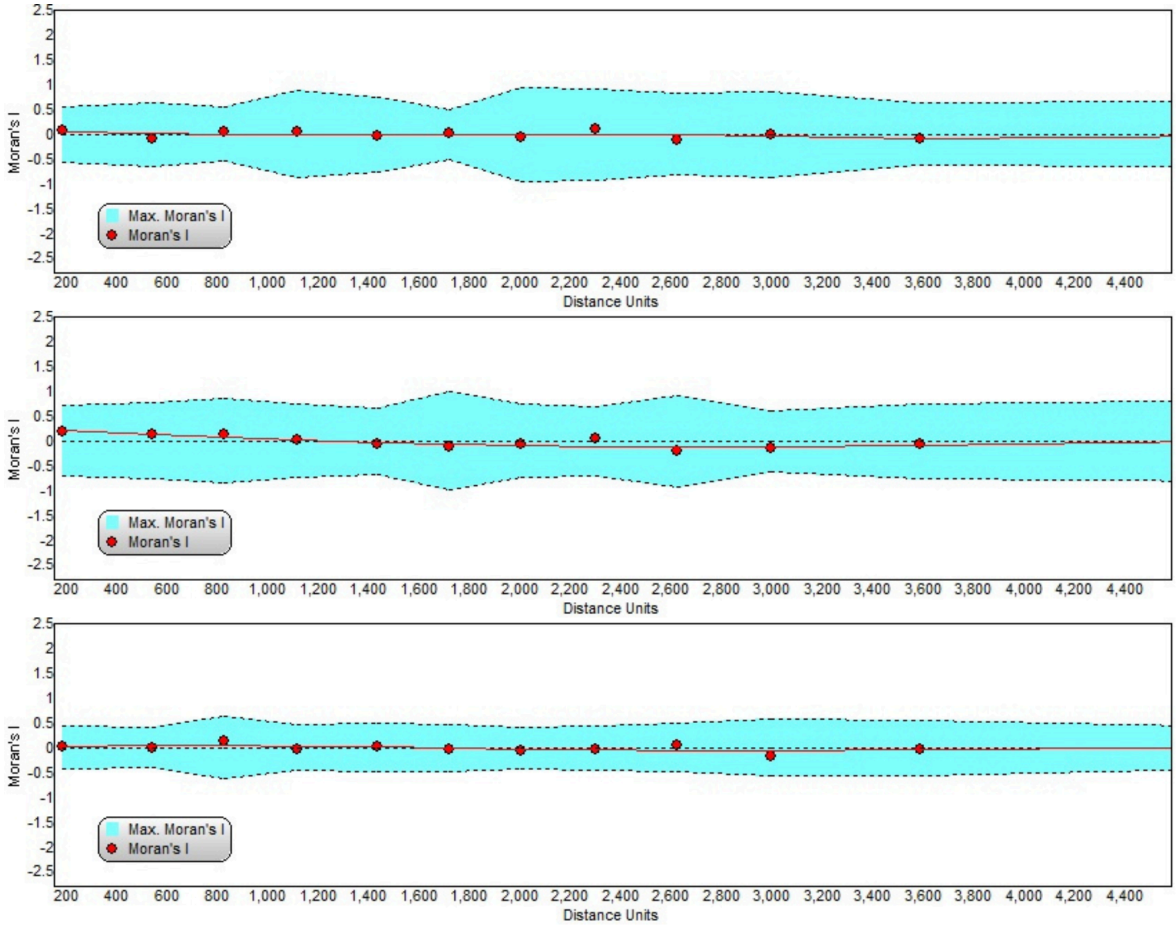
Supplementary Fig. 1. Principal component analysis (PCA) of *Peromyscus* forelimbs across sexes. See Fig. 3 for the PCA across ecoregions and species groups.



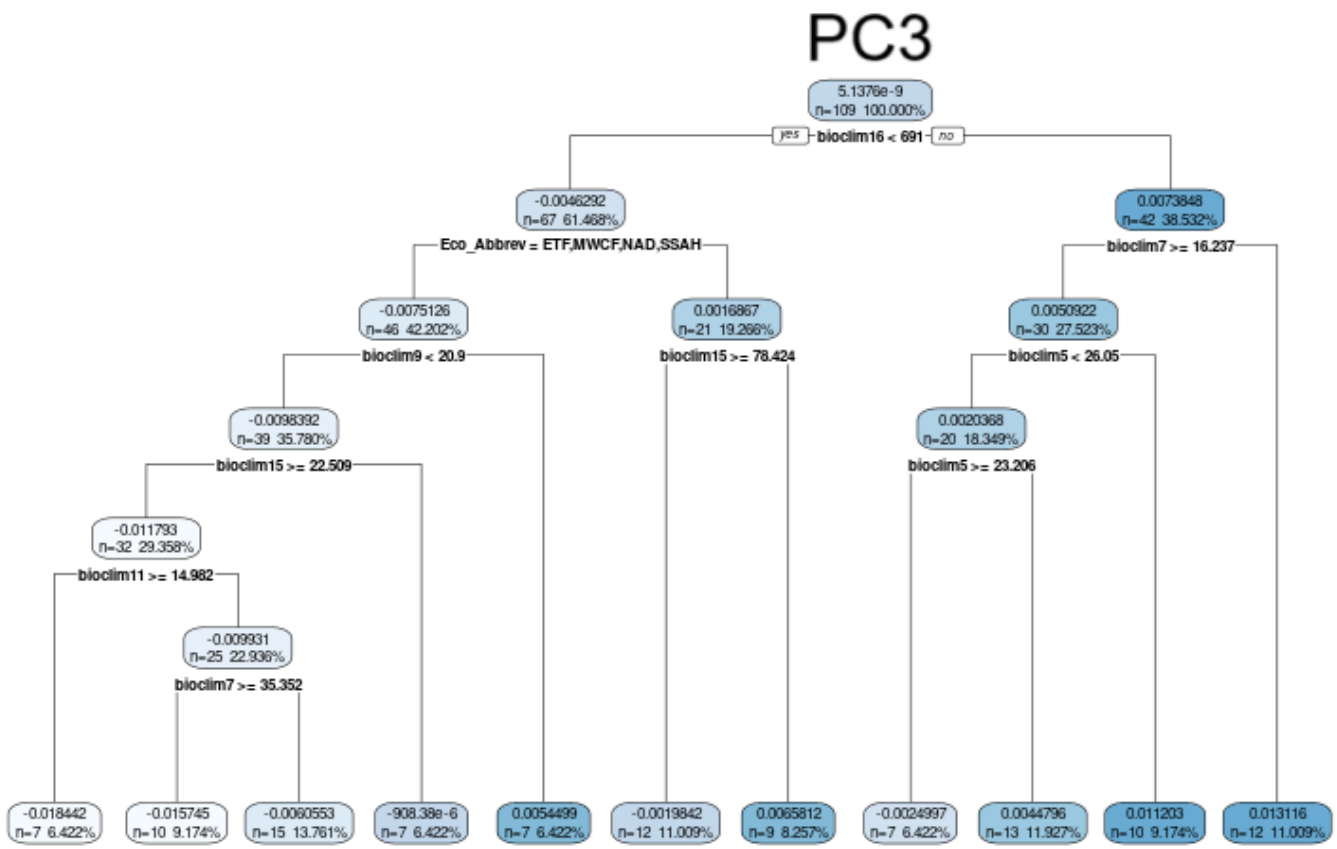
Supplementary Fig. 2. Humerus length (A), scapula length (B), and scapula height (C) variation across different ecoregions.



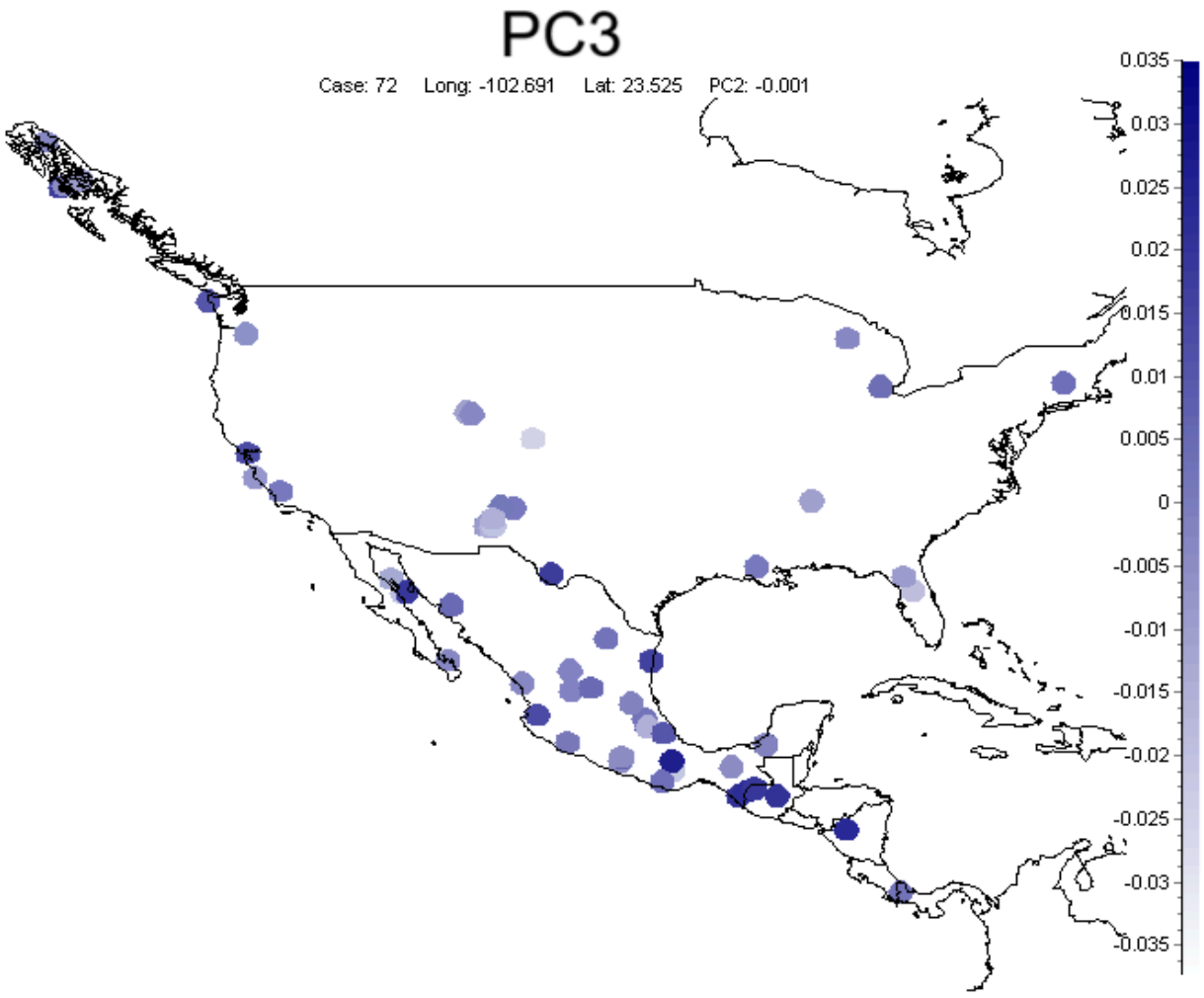
Supplementary Fig. 3. Linear discriminant analysis (LDA) of *Peromyscus* forelimbs across sexes. See Fig. 6 for the LDA across ecoregions and species groups.



Supplementary Fig. 4. Correlogram of Moran's *I* test for PCs 1-3. Red dots indicate Moran's *I* values across various spatial distributions, while the blue area indicates values where the null hypothesis (there is no spatial autocorrelation) would be accepted.



Supplementary Fig. 5. Regression tree for PC3. See Fig. 9 for regression trees of PCs 1 and 2.



Supplementary Fig. 6. Spatial distribution of PC3. See Fig. 9 for the spatial distributions of PCs 1 and 2.

Supplementary Table 1. MANOVA results across ecoregions. See Table 1 for ecoregion abbreviations.

	1.	2.	3.	4.	5.	6.	7.
1.NAD	-						
2.SSAH	.16	-					
3.MWCF	**.00**	.38	-				

4.ETF	**.01**	.27	.16	-			
5.TSTDF	**.01**	.12	**.01**	**.04**	-		
6.MC	.19	.87	.76	.36	.64	-	
7.TWF	**.00**	.19	**.04**	**.02**	.69	.65	-

Supplementary Table 2. MANOVA results across species groups

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
1.*truei*	-												
2.*maniculatus*	**.03**	-											
3.*leucopus*	.36	.48	-										
4.*melanophrys*	.19	.30	.84	-									
5.*mexicanus*	**.00**	**.00**	.05	.16	-								
6.*boylii*	.16	.14	.41	.92	.06	-							
7.*megalops*	.21	.11	.56	.91	.36	.55	-						
8.*californicus*	.69	.34	.69	.96	.26	.78	.94	-					
9.*aztecus*	.24	.15	.79	.98	.38	.67	.86	.88	-				
10.*furvus*	.49	.90	.86	.94	.06	.80	.71	.93	.77	-			
11.*eremicus*	.39	**.01**	.33	.56	**.01**	.48	.24	.50	.43	.46	-		
12.*mayensis*	.07	.19	.45	.84	**.04**	.43	.71	.89	.74	.80	.19	-	
13.*crinitus*	.41	.51	.77	.83	**.02**	.60	.49	.78	.65	.98	.51	.70	-