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Uncovering historical small mammal biodiversity among the Madrean Sky Islands

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Abstract

The Madrean Sky Island Archipelago is a system of 54 mountains with isolated woodland habitat above 1,600 meters, primarily in the Sonoran Desert. These mountains harbor a wide variety of native small mammals spanning 11 families of bats, rodents and shrews. Improved understanding of Madrean Sky Island biodiversity will potentially advance studies of biogeography, phylogenetic relationships, host-symbiont interactions, and processes of community assembly in this ecoregion. However, which species are found in each sky island and how their populations are genetically related remain open questions. To establish the current knowledge baseline, we used voucher specimen geocoordinates and elevations to summarize the extent and timing of past collecting efforts for small mammals in woodland habitats across the Madrean Sky Islands. In total, 97 species of small mammals (39 bats, 54 rodents, 4 shrews) from 9,541 specimens were collected from 1884 to 2023. Of these historical specimens, 79% come from five sky islands (Chiricahuas, Pinalenos, Huachucas, Animas, and Santa Catalinas) and only 25 sky islands in the Madrean system have any recorded specimens. Mexico's 25 sky islands are mostly unsampled (only the San Luis, Sierra dos Ajos, and Sierra La Mariquita have any specimens) and several of Arizona's larger sky islands have fewer than 40 specimens (Galiuros, Canelo Hills, Santa Teresas, Mules, and Dragoons). A large majority of small mammal specimens (87%) were

collected prior to 1980, meaning they were collected without DNA/RNA preservation as a priority. This distributional summary is the current basis for all derived biodiversity knowledge of Madrean Sky Island small mammals, illustrating clear gaps regarding most species of woodland-dwelling bats, rodents, and shrews. This work lays the foundation for future fieldwork and voucher specimen preservation in the Madrean Sky Islands, especially from undersampled mountains where biodiversity assumptions are unconfirmed.

Resumen

El Archipiélago de Islas del Cielo Madreño es un sistema de 54 montañas con hábitats de bosque aislados a más de 1.600 metros de altitud, principalmente en el Desierto de Sonora. Estas montañas albergan una amplia variedad de pequeños mamíferos nativos que abarcan 11 familias de murciélagos, roedores, y musarañas. Mejor comprensión de la biodiversidad de las Islas del Cielo Madreño podría avanzar los estudios de biogeografía, relaciones filogenéticas, interacciones huésped-simbionte y procesos de ensamblaje de comunidades en esta ecorregión. Sin embargo, aún persisten preguntas abiertas acerca de qué especies se encuentran en cada isla del cielo y cómo están genéticamente relacionadas sus poblaciones. Para establecer la base de conocimiento actual, utilizamos las coordenadas y elevaciones de ejemplares testigo para resumir la extensión y la temporalidad de los esfuerzos previos de colecta de pequeños mamíferos en hábitats boscosos en las Islas del Cielo Madreño. En total, se recolectaron 97 especies de pequeños mamíferos (39 murciélagos, 54 roedores, 4 musarañas) de 9,541 ejemplares entre 1884 y 2023. De estos ejemplares históricos, el 79% proviene de cinco islas del cielo (Chiricahuas, Pinaleños, Huachucas, Ánimas y Santa Catalinas) y únicamente 25 islas del cielo del sistema Madreño cuentan con ejemplares. Las 25 islas del cielo de México en su mayoría no han sido muestreadas (solo las San Luis, Sierra dos Ajos y Sierra La Mariquita tienen ejemplares) y varias

de las islas del cielo más grandes de Arizona cuentan con menos de 40 ejemplares (Galiuros, Canelo Hills, Santa Teresas, Mules y Dragoons). La gran mayoría de los ejemplares de pequeños mamíferos (87%) fueron recolectados antes de 1980, lo que significa que se obtuvieron sin priorizar la preservación de ADN/ARN. Este resumen distribucional constituye la base actual de todo el conocimiento derivado sobre la biodiversidad de los pequeños mamíferos de las Islas del Cielo Madrense, e ilustra vacíos claros respecto a la mayoría de las especies de murciélagos, roedores y musarañas que habitan los bosques. Este trabajo establece los cimientos para futuros estudios de campo y la preservación de ejemplares testigo en las Islas del Cielo Madrenses, especialmente en las montañas con escaso muestreo, donde las suposiciones sobre la biodiversidad permanecen sin confirmación.

Keywords: biogeography, Chiroptera, Eulipotyphla, museum specimens, natural history collections, Rodentia, sky islands, species richness.

Introduction

“Mountains—those islands in the sky surrounded by a sea of desert.”

– Edward Abbey (*Desert Solitaire*, 1968: 129)

Envisioning forested desert mountains as ‘sky islands’ dates back to Heald’s (1967) account of Arizona’s Chiricahua Mountains, and Abbey’s (1968) ode to Utah’s La Sal Mountains. The metaphor has inspired generations of naturalists, contributing to the foundations of metapopulation ecology and habitat island biogeography (reviewed in Matthews 2021). The Madrean Sky Island Archipelago, containing the Chiricahuas among other mountains, is globally one of the most extensive of the so-called ‘stepping stone’ archipelagos that connect two mountain chains (Warshall 1995). Spanning between the Colorado Plateau and the Sierra Madre Occidental, the Madrean Archipelago contains somewhere between 40 (Warshall 1995) and 65

(Moore et al. 2013) forested mountains, each one isolated from others by the surrounding Sonoran and Chihuahuan Deserts. Here we present a 54-mountain definition of the Madrean Sky Islands designed for studying woodland-dwelling species relative to the surrounding ‘sea’ of greater aridity (desert grassland and desert scrub; Fig. 1, Table 1).

Intersecting biomes make the Madrean Sky Islands a biodiversity hotspot for plants, insects, birds, mammals, and other taxa (Deyo et al. 2013). However, distributional knowledge of the Madrean biota remains highly incomplete. Historical efforts to characterize species distributions have focused on flora or fauna of the more accessible mountains (e.g. Santa Catalinas, Lange 1960; Moore et al. 2013; Chiricahuas, Duncan 1990; Cahalane 1939); Huachucas, Hoffmeister and Goodpasters 1954; Bowers and McLaughlin 1996). A few individual species have also been studied across multiple mountains (e.g., Mexican Woodrat, *Neotoma mexicana* Sullivan 1994; Canyon Tree Frog, *Hyla arenicolor* Barber 1999; Mexican Jay, *Aphelocoma wollweberi* McCormack et al. 2008; Yarrow’s Spiny Lizard, *Sceloporus jarrovi* Wiens et al. 2019; American Black Bear, *Ursus americanus* Atwood et al. 2011; Gould et al. 2022). Given recent losses of forested habitats in the Madrean Archipelago from fire, logging, and climate change (Williams et al. 2010; Yanahan and Moore 2019), there is growing urgency for a more integrative multi-species and multi-mountain understanding of the region’s biodiversity. Identifying gaps in the historical knowledge of species’ geographical and elevational distributions is therefore a high priority.

An accurate understanding of small mammal biodiversity is particularly imperative in the Madrean region given their potential to serve as zoonotic disease vectors (e.g., hantaviruses: Astorga et al. 2025; lung fungi: Salazar-Hamm et al. 2022) and indicators of ecosystem health (Pearce and Venier 2005; Leis et al. 2008; Russo et al. 2021). Understanding how many species

live in a certain area and how their distributions are influenced by environmental changes can help predict the risk of pathogen spillover into human populations (Olival et al. 2017; Johnson et al. 2020; García-Peña and Rubio 2024). Unfortunately, substantial gaps exist in mammal distributional knowledge across this region. This “dearth of published data” on mammal biodiversity was highlighted for the Madrean Archipelago *ca.* 20 years ago (Koprowski et al. 2005: 412), with particular sampling gaps noted for native species of bats, rodents, and shrews as compared to larger ungulates and carnivores. While the endangered Mount Graham Red Squirrel (*Tamiasciurus fremonti grahamensis*) has been intensively studied (e.g., Merrick et al. 2021; Mahoney and Pasch 2024), most small mammal species in this region are comparatively unknown. The efforts of Findley et al. (1976) and Hoffmeister (1986) in assembling the *Mammals of New Mexico* and *Mammals of Arizona*, respectively, still represent the best distributional knowledge for many Madrean sky-island species despite their outdated taxonomies. Advances in the digitization of museum specimen records over the past two decades now present an outstanding opportunity to revisit prior work on the distribution of Madrean Sky Island small mammals, aiming to set a baseline for future studies.

We seek to address three related questions. First, what is the most functional definition of the Madrean Sky Islands for woodland-dwelling species; i.e., how many separate mountaintop islands does this system contain? Varying answers have been given to this seemingly simple question, calling for a specific geospatial definition. Second, where in the Madrean Sky Islands have small mammal species been historically studied versus not? Museum voucher specimen records are the most reliable means of addressing this question, given that small mammals are cryptic and mostly nocturnal and therefore difficult to identify from photographs. Third, which mountains are historically understudied relative to their size? Here we present evidence of the

114 need for targeted field surveys to fill geographic, elevational, and taxonomic gaps of small
115 mammals in the Madrean Sky Islands.

116 **Methods**

117 *Study system*

118 To define the Madrean Sky Islands study system, we used NASA's ASTER Global
119 Digital Elevation Model (DEM) within ARCGIS Pro v3.1.2 to delimit all areas above 1,600
120 meters (m) in the study region. This elevational cutoff was based on Moore et al. (2013) and
121 roughly corresponds to the lowest elevation of Madrean oak-woodland habitat. The 1,600-m
122 cutoff served as a starting point to isolate the forested mountain areas south of the Superstitions,
123 east of the Baboquivaris, west of the Alamo Hueco and Big Hatchets, and north of the Sierra de
124 Las Guijas. We then performed manual cleanup to refine this delimitation, as follows. First, we
125 eliminated mountain ranges that have less than 1 kilometer squared (km²) area above 1,600 m
126 (i.e., Sierra El Humo and Sierra San Juan). Then, we determined whether contiguous areas of
127 land above 1,600 m constituted separate ranges in the context of the dispersal propensity of small
128 mammals. To resolve any boundary conflicts, we used satellite imagery (Google Earth; Airbus
129 imagery 5/21/2022–11/19/2023) to identify areas of discontinuous oak woodland coverage. For
130 example, while the Galiuro and Winchester Mountains remain continuous in terms of area above
131 1,600 m, a significant gap in oak woodland habitat between them constitutes separating these sky
132 islands. Small, discontinuous fragments of area above 1,600 m were assigned to the nearest sky
133 island if they were within 5 km of each other; otherwise these fragments were eliminated from
134 the study. Using these criteria, we defined 54 isolated forest habitats as constituting the sky
135 islands of the Madrean system and formalized this definition as individual DEM raster and

vector polygon layers (Supplementary Data SD1-SD2; All supplementary data files are available via Github along with relevant R code: https://github.com/uphamLab/RiveraUpham_madreanSmallMammals).

Within this 54-mountain definition, we made one notable exception to separately retain the Canelo Hills and Huachuca Mountains, even though they are continuously connected in terms of both land area above 1,600 m and woodland habitat. The Huachucas reach elevations high enough to maintain pine and mixed conifer forests while the Canelo Hills comprise almost exclusively of oak woodland without elevations above 2,000 m. We reasoned that combining historical records from the steep and heterogenous Huachucas with those from the lower and more uniform Canelo Hills would be misleading. The stark difference in ruggedness as well as the dense historical sampling of the Huachucas relative to the few Canelo Hills specimens also supported this decision (see results).

Specimen records

We summarized natural history specimen records from public databases to assess the historical sampling efforts of small mammals in the Madrean Sky Islands. Searches of the Global Biodiversity Information Facility (GBIF) database (23 January, 2024) allowed us to maximize the number of collections and specimen records included in the study. We focused our searches upon the taxonomic orders of Rodentia, Chiroptera, and Eulipotyphla using a geographic boundary polygon that encompassed the entire study region (bounded at four points: 33.76114, -111.7944; 27.05179, -113.06772; 27.00817, -105.62368; 34.39024, -106.02152). This approach returned 122,324 total specimens (bats: n=21,118; rodents: n=99,844; shrews: n=1,362), including those collected in both lowland and highland habitats. We intersected all specimen

records with the polygons of 54 mountains in the Madrean Sky Islands to filter records to areas above 1,600 m, which reduced the number of specimens to 10,340 total (bats: n=2,260; rodents: n=7,901; shrews: n=179). We also excluded specimens with a coordinate uncertainty of 10 km or greater to maximize both the amount and accuracy of data included in this study, which further reduced the number of specimens to 9,802 (bats: n=2,194; rodents: n=7,429; shrews: n=179). This approach struck a balance between retaining known highland species while excluding known lowland species. Without this uncertainty-based filtering, the coordinates of a strictly lowland species might mistakenly be interpreted to the highest reaches of a mountain (e.g., *Chaetodipus penicillatus* at 2,500 m in the Huachuca Mountains, MSB:Mamm:184809). Among the remaining specimens that had a coordinate uncertainty <10 km, most (n=8,224) lacked any elevation data. To resolve this, we interpolated elevation using the ASTER DEM layer, favoring the interpolated value even among specimens that did have reported elevation data to ensure consistency in subsequent analyses.

A final filtering step removed specimens that were only identified at the genus level, given that this lack of taxonomic certainty may indicate reliability issues with the record. Some specimens lacked a specific identification in GBIF's 'Species' data field, but did contain a complete specific identification in the 'verbatimScientificName' field. For these specimens (n=840, most from University of Michigan Museum of Zoology), we added their verbatim identification to the 'Species' data field for inclusion in our study. For graphing specimen collections over time, we excluded specimens that lacked a date altogether or had been assigned a range of dates spanning multiple years (n=383; typically listed as either January 1st, 1800 or January 1st, 1900). Finally, we updated the taxonomy of the specimens to match that of the Mammal Diversity Database v2.2 (MDD 2025), which included minor spelling changes (e.g.,

181 *Erethizon dorsatus* to *Erethizon dorsatum*), re-assigned genera (e.g., *Aeorestes cinereus* to
182 *Lasiurus cinereus*) and synonymizations (e.g., *Corynorhinus rafinesquii pallescens* to
183 *Corynorhinus townsendii*).

184 *Sampling bias*

185 To identify potential biases of where historical collectors have focused their efforts in the
186 Madrean Sky Islands, we evaluated the ruggedness, area, and elevational profile of each
187 mountain. We calculated the Terrain Ruggedness Index for the individual DEMs, which returned
188 the number of raster pixels in each of 6 ruggedness categories (sensu Riley et al. 1999). We used
189 these pixel counts to generate a weighted average and standard deviation of ruggedness per sky
190 island. To quantify the specimen-area ratio (s/km²) as a measure of “sampling density”, we first
191 intersected the individual polygons with the filtered rodent, bat, and shrew specimen records to
192 identify historical specimens from each sky island individually. Then, we used the attribute table
193 for each mountain’s DEM to calculate the area, multiplying the total number of pixels >1,600 m
194 for each sky island by the size of one pixel in m² (adjusted for longitude and latitude). Lastly, we
195 compared the elevational profiles of mountains using the DEMs to quantify the amount of land
196 area (km²) per unit elevation (m). We applied five vegetation categories to these elevational
197 profiles, following the guidance of Bennett et al. 2004, as follows: oak woodland from 1,600-
198 1,800 m; pine-oak woodland from 1,801-2,200 m; pine forest from 2,201-2,550 m; mixed conifer
199 forest from 2,551-3,000 m; and limber and alpine fir forests >3,000 m (only found in the
200 Pinaleno Mountains). We used these vegetation categories to estimate the total land area
201 available to each habitat type across the sky islands, excluding sky islands that contained less
202 than 1 km² of a given habitat category. Also excluded from these analyses was the highly

203 variable chaparral habitat that occurs between 1,250 m and 2,590 m depending on mountain
204 slope and aspect.

205 **Results**

206 *Study system*

207 Using our definition of the Madrean Sky Islands as containing 54 unique mountain
208 ranges with woodland habitats above 1,600 m, we find that this region encompasses 13,210 km²
209 of isolated habitat within a sea of desert in the Southwestern United States and Northern Mexico
210 (Fig. 1; Table 1). The international border roughly bisects these sky islands, with 25 mountains
211 lying primarily in the state of Sonora (SO) compared to 24 in Arizona (AZ) and 5 in New
212 Mexico (NM). The highest elevations in the Madrean Sky Islands are found at the peaks of the
213 Pinaleno Mountains (AZ) while the largest sky island by area is the Chiricahua Mountains (AZ).
214 The smallest sky island by both maximum elevation and area is Cerro Bacoachi (SO).

215 Comparison of elevational profiles (Fig. 2) reveals that each mountain range varies
216 greatly in slope, aspect, maximum elevation, and total area. For example, the Peloncillo South
217 Mountains (max. elevation=2,095 m, area=921 km²) contain extensive oak woodland habitat and
218 limited pine-oak woodland, but fail to reach the higher elevations needed for mixed conifer
219 forests. On the other hand, the Rincon Mountains (max. elevation=2,646 m, area=265 km²) are
220 less than one third of the area of the Peloncillo South Mountains, yet reach high enough
221 elevations to support mixed conifer forests. In terms of habitat variation, even though the
222 Chiricahua Mountains (max. elevation=2,990 m, area=1752 km²) are 90% larger than the
223 Peloncillo South Mountains overall, the latter contain 48 km² more oak woodland.

224 *Specimen records*

225 After filtering specimen records for quality and locational accuracy, we find that 9,541
226 specimens of small mammals have been collected in the Madrean Sky Islands (Fig. 3). Only 25
227 of the 54 mountains have one or more historical specimen records. Of those, 7,635 specimens
228 were collected in Arizona, 1,761 in New Mexico, and 145 in Sonora (no specimens were
229 collected in the small Chihuahuan regions of the Madrean Sky Islands). In the order Rodentia,
230 we identify 7,228 specimens comprising six families (Cricetidae, Erethizontidae, Geomyidae,
231 Heteromyidae, Muridae, and Sciuridae), 22 genera, and 54 species (Fig. 4). These specimens
232 were collected from 25 sky islands. In the order Chiroptera, we identify 2,135 specimens
233 comprising five families (Molossidae, Mormoopidae, Natalidae, Phyllostomidae, and
234 Vespertilionidae), 20 genera, and 39 species (Fig. 5). These specimens were collected from 20
235 sky islands. Under the order Eulipotyphla, we identify just 178 specimens from one family
236 (Soricidae), two genera, and four species (*Notiosorex crawfordi*, *Sorex arizonae*, *Sorex*
237 *monticolus*, and *Sorex vagrans*) collected from 9 sky islands (see Supplementary Data SD3-
238 SD5).

239 Considering the timing of collecting activity in the Madrean Sky Islands, the earliest
240 specimen was collected in the Huachuca mountains by E. A. Mearns in 1884
241 (FMNH:Mammals:4943) and only 265 specimens were collected across the sky islands before
242 1900. The majority of specimens (5,922; 65%) were collected between 1950 and 1980,
243 encompassing 84% of bats, 59% of rodents, and 48% of shrews ever collected in the Madrean
244 Sky Islands (Fig. 6; Supplementary Data SD6). In the ensuing 43-year period (1981-2023), only
245 1,142 specimens were collected in this region (12% of the total).

Preserved specimens of small mammals from the Madrean Sky Islands are presently housed in 43 different natural history collections, mainly in the southwestern United States. The most extensive of these collections is the Museum of Southwestern Biology (University of New Mexico) with 3,378 specimens, followed by the University of Arizona Museum of Natural History (1,954 specimens), University of Michigan Museum of Zoology (1,090 specimens), and Arizona State University Natural History Collection (394 specimens).

Sampling bias

We find that sky-island area and maximum elevation significantly influence where historical collectors focused their sampling. Collection efforts leading to the preservation of small mammal specimens have been concentrated in a few, large sky islands in the Madrean system, resulting in a positive log-linear relationship between sky-island size and specimens (Fig. 7A; $Y = -3.524 + 1.354X$, $R^2 = 0.3578$, $P = 0.0016$). Similarly, we find a positive linear relationship between the maximum elevation of a sky island and the specimen-area ratio (Fig. 7B; $Y = -3.664 + 0.0017X$, $R^2 = 0.3762$, $P = 0.0011$). Interestingly, we found no significant relationship between the specimen-area ratio and sky-island ruggedness ($R^2 = 0.0791$, $P = 0.1731$), even though ruggedness is positively related to maximum elevation ($R^2 = 0.2901$, $P = 0.0055$). The average specimen-area ratio across all 54 sky islands is 0.32 s/km², or 0.68 s/km² after excluding the 29 mountains without specimens (Supplementary Data SD7-SD8). The most densely sampled sky islands are the Huachucas (3.74 s/km²), Santa Catalinas (2.15 s/km²), Chiricahuas (1.76 s/km²), Pinalenos (1.71 s/km²), and Santa Ritas (1.33 s/km²); only three other sky islands have >1.0 s/km² (the Animas, Alamo Hueco, and Pinal Mountains). We recover notably low sampling density on several large sky islands: the San Luis Mountains (2,515 km², 0.09 s/km²), the Sierra

268 de los Ajos (735 km², 0.12 s/km²), Galiuros (503 km², 0.07 s/km²), and Canelo Hills (423 km²,
269 0.04 s/km²).

270 Discussion

271 The dearth of published research highlighted by Koprowski et al. (2005) has remained a
272 reality for most species of small mammals in the Madrean Sky Islands. However, thanks to two
273 decades of advances in the digitization of museum specimen records, we are now able to
274 synthesize data from 43 natural history collections to identify gaps in the distributional
275 knowledge of this diverse small mammal fauna. The ‘virtual flora and fauna’ of Deyo et al.
276 (2013) was the last attempt to summarize distributional knowledge of taxa across the Madrean
277 Sky Islands, but the surprisingly few records of mammals (n=217) they recovered was likely an
278 artifact of sparse georeferencing efforts at that time. Their work preceded the maturation of
279 integrated databases like VertNet and GBIF (Guralnick et al. 2016; Heberling et al. 2021), which
280 now enable greater synthesis of historical specimen records. In contrast, our search and quality
281 filtering steps revealed 9,541 georeferenced voucher specimens of small mammals (Fig. 3).
282 These specimens are allocated to 97 species from 12 families of bats, rodents, and shrews (Figs.
283 4, 5). The over 40x growth in digitized records from this region illuminates several biases in
284 historical collecting, including 29 of 54 mountains in the Madrean Sky Islands for which no
285 small mammals have ever been vouchered.

286 To put this sampling history in regional context, a study by Jones et al. (2021) in the
287 neighboring Gila Mountains region of New Mexico found 12,505 specimen records from 77
288 species of bats (n≈2,500), rodents (n≈9,250; totals estimated from figures), and shrews across
289 nearly twice the study area (24,383 km² versus 13,210 km² in the Madrean Sky Islands). Both

regions experienced similar peaks of collecting activity prior to 1980, but the large pulse of Gila collecting from 2012-2020 (led by the Museum of Southwestern Biology) differs from the comparatively dormant collecting in the Madrean Sky Islands over the same period (Fig. 6 compared to fig. 6c in Jones et al. 2021). Critically, the paucity of post-1980 specimens from the Madrean Sky Islands means that frozen tissues and holistic specimen preparations are mostly unavailable (both preservation modes were popularized subsequently; Galbreath et al. 2019). Overall, Madrean small mammals have been less extensively studied than those of the Gila Mountains despite the former's ~2x higher density of species per km² (0.0072 versus 0.0032). Recent efforts to re-survey the Santa Catalina Mountains using holistic preservation (2021-2023 led by the Arizona State University Natural History Collections; see Rowsey et al. this volume) have begun bridging this shortfall, but parallel efforts on nearby sky islands are sorely needed.

Digitally defining the mountains of the Madrean Sky Islands was a key step in this study that now enables comparable future studies in this biodiverse region (Fig. 1). Querying how woodland-dwelling taxa of different kinds have responded to past climatic changes in this region, particularly the cycles of forest expansion/contraction since the end-Pliocene (Betancourt et al. 1990), is now more replicable given the included geospatial resource (Supplementary Data SD1-SD2). However, the 54-mountain definition of the Madrean Sky Islands presented here differs from three previous totals: “about 40” in Warshall (1995: 6); “55 ranges/complexes” in Deyo et al. (2013: 296); and “~65 mountain ranges” in Moore et al. (2013: 148). Those differences, and some nuances of our own definition, underscore the inherent subjectivity of dividing a complex, rugged landscape into discrete units. We followed the lead of Moore et al. (2013) in choosing an initial definition of 1,600 m, but then deviated from that work by joining several of the mountains that they also acknowledged were part of ‘Madrean Sky Island complexes.’ The result

better reflects the ability of woodland-dwelling small mammals to disperse through continuous oak woodland (Sutherland et al. 2000; Selonen and Wistbacka 2017). For example, we joined the Patagonia and San Antonio Mountains, which in Moore et al. (2013) appear to only be separated by the U.S.-Mexico international border (Supplementary Data SD9). In the case of the mountain complex consisting of Chiricahua, Pedregosa, Swisshelm, and Dos Cabezas, these ranges are connected by varying degrees of oak woodland and so under that criterion could be considered one unit (as Warshall 1995 chose to do). We chose to join the Chiricahua and Pedregosa Mountains owing to their elevational and forest connectivity above 1,600 m while separating the Swisshelm and Dos Cabezas Mountains since they lack such elevational connectivity. Satellite imagery does show sparse oak woodland growth below 1,600 m connecting these latter two mountains from the Chiricahuas (Google Earth; Airbus imagery 5/21/2022–11/19/2023), but we reasoned that this thin forest likely presents a strong enough dispersal barrier to warrant separate mountain recognition.

We found clear patterns of uneven among-mountain sampling of small mammals across the Madrean Sky Islands that makes accurate biodiversity assessments difficult. Past collecting efforts have concentrated mainly on 8 sky islands that collectively contain 87% of known rodent, bat, and shrew specimens. These more densely sampled mountains all contain >1.0 specimens/km² (Fig. 7A), consistent with the expectation of positive specimen-area relationships if larger mountains attract more collecting efforts. However, the comparatively sparse sampling of other large sky islands (e.g., San Luis and Sierra de los Ajos in Mexico, Galiuros and Canelo Hills in the U.S.) indicates that mountain area is not the only factor explaining historical collecting. Indeed, the maximum elevation of a mountain is also strongly associated with increased sampling density (Fig. 7B), perhaps in part owing to the development of paved roads

to areas above 1,600 m on some of the taller mountains (e.g. the Pinaleños, Santa Catalinas, and Santa Ritas). Road accessibility, a known bias in biodiversity surveys (Kadmon et al. 2004; Monsarrat et al. 2019), was likely critical in promoting surveys of mountains with established roads. Yet roads may also threaten biodiversity by promoting land conversion (Bennett 2017; Barrientos et al. 2021). Thus, sky-island access roads may paradoxically be associated with both increased biodiversity knowledge (as measured in specimens and resulting publications) and potential threats, a tradeoff that land managers must closely consider.

Even for sky islands with comparatively dense historical sampling, small mammal diversity is still likely underestimated. For example, the Huachuca Mountains have the highest sampling density of any Madrean Sky Island at 3.67 s/km², yet over a century of fieldwork on the mountain failed to find the Cliff Chipmunk (*Neotamias dorsalis*) until a breeding population was identified in 2007 (Cudworth and Koprowski 2010). Furthermore, a 2023 field survey of the Santa Catalina Mountains (2.15 s/km²) identified the first specimen of the Fulvous Harvest Mouse (*Reithrodontomys fulvescens*) ever recorded on that sky island (Rowsey et al. this volume). We suggest that the status of the Madrean Sky Islands as a ‘biogeographic crossroads’ (Spector 2002) raises the likelihood that additional species at the northern or southern edge of their distributions have gone undetected on multiple mountains. Surveying elevational gradients across adjacent sky islands may present a useful test of the hypothesis that species have ‘rare edges and abundant cores’ (Brown 1984; Martin et al. 2024). Future work that mitigates the identified sampling biases for small mammals may be able to accomplish this goal.

Comparing elevational profiles among sky islands shows striking heterogeneity in the extent of different forest types across mountains (Fig. 2), suggesting that biodiversity knowledge gained from one sky island might not apply to all others. For example, the Peloncillo South and

Patagonia Mountains have similar maximum elevations (2,095 and 2,200 m, respectively) but the former contains ~4.5x more forested area than the latter across a sloping oaken plateau. These disparate elevational profiles are associated with more total specimens (587 vs. 95, respectively) and more apparent species diversity in the former than the latter (27 rodent, 19 bat, and 1 shrew species compared to 12, 5, and 0). While this positive correlation between sky-island area and species richness is consistent with Frey et al. (2007), no systematic method exists for identifying which species will be lost and which will be retained as the sky-island area shrinks. Hence, we expect each additional sky island for which the resident small mammal fauna is surveyed adds value to the total biodiversity knowledge of the Madrean system.

Potential biases in our study pertain to three issues: the accuracy of digital specimen records, unevenness in digitization efforts, and the historical methods used to obtain those specimens. First, while online biodiversity data aggregators like GBIF have advanced the ability to synthesize specimen records globally (Heberling et al. 2021), GBIF data requires careful validation to correct errors and outdated taxonomies (Zizka et al. 2020). Because 94% of the specimens in our study's initial download predate the widespread use of handheld GPS devices (Kumar and Moore 2002), their coordinate data presumably came from secondary georeferencing using field notes and locality descriptors to assign latitude and longitude. Our filtering based on coordinate uncertainty thresholds aimed to alleviate specious records in the dataset, but this approach still relies on the accuracy of initial georeferencing (Murphey et al. 2004). Second, unevenness among natural history museums in the extent and accuracy of specimen digitization is another source of bias. Although the GBIF search returned relevant results from most major collections, we found that expected specimens from the American Museum of Natural History (AMNH) were completely absent. We identified 921 small mammal

specimens from a direct search of the AMNH Mammal Collection that were likely collected above 1,600 m in the Madrean Sky Islands (based on the locality data field), but georeferencing these specimens was beyond the scope of our study and unlikely to alter the main findings (a majority of specimens are from the Chiricahuas, Pinalenos, Santa Catalinas, and Huachucas, see Supplementary Data SD10). Lastly, the lack of transparency regarding which trapping techniques were used to capture specimens on each sky island presents another bias. For example, mountains surveyed using Museum Special snap traps may yield greater diversity and abundance of small mammals per trapnight than those using Sherman live traps (Eulinger and Burt 2011). The unevenness of bat-netting efforts is another potential bias; however, bat specimens were recovered from most of the same mountains as non-volant taxa (Fig. 3) and bats and rodents have had roughly parallel specimen accumulation curves through time (Fig. 6). The apparent rarity of shrews likely reflects the infrequent use of pitfall traps, drift fences, and other methods (Maddock 1992), rather than actual low abundances in the Madrean Sky Islands.

Taxonomic changes and historical difficulties in identifying small mammals present other challenges to this study. The external measurements that are often used to differentiate related species can be prone to error, potentially leading to misidentification (Blackwell et al. 2006). Indeed, in our review of specimen records, we identified 11 species whose identification requires further investigation (Supplementary Data SD11). For example, the 18 specimens identified as *Leptonycteris curasoae* in the Madrean Sky Islands are presumably either *L. nivalis* or *L. yerbabuenae*, given that *L. curasoae* is endemic to Colombia and Venezuela (Cole and Wilson 2006), but making this determination would require physically examining those specimens (all housed in the MSB Mammal Collection). Similarly, our dataset includes 1 specimen of *Peromyscus beatae*, a species of deer mouse native to central Mexico with no known distribution

in the Mexican portion of the Madrean Sky Islands (Álvarez-Castañeda et al. 2017), indicating that this specimen may be a misidentified individual of *P. boylii* (Tiemann-Boege et al. 2000). So too with the 11 specimens of *P. truei* that are recorded from sky islands in Arizona (Chiricahuas and Santa Catalinas) when their known distribution is thought to be restricted to the Animas Mountains of New Mexico south into the Sierra Madre Occidental (Hoffmeister 1981; Cook 1986). Investigation is needed to determine if these specimens constitute a modern range expansion, historical undersampling, or previous misidentification. These issues highlight the steadfast importance of museum specimens as physical records, each one providing a critical opportunity to revisit such issues, collect new data (e.g., measurements, DNA sequences), and thereby gain new insights even hundreds of years later.

Overall, we find that woodland-dwelling small mammals are surprisingly understudied throughout the Madrean Sky Islands. These forested mountains exist at the crossroads of the Nearctic and Neotropical biogeographic realms, which presents a diverse natural laboratory of repeated forest isolation and reconnection for studying how ecological and evolutionary processes unfold (Marshall 1957, Warshall 1995, Spector 2002, Koprowski et al. 2005, Deyo et al. 2013, Moore et al. 2013). We find that only 8 of the 54 mountains have had substantial historical sampling of voucher specimens, and 29 mountains are apparently still unsampled. The multiplicity of threats now impacting this region from fires, drought, and human disturbance signals an imperative to document basic biodiversity patterns across the sky islands (Misztal and Hansen 2013; Peters et al. 2018; Yanahan and Moore 2019; Love et al. 2023). Geopolitical conflicts such as the construction of a steel wall along the US-Mexico international border, bisecting as many as six sky islands, also impact biodiversity in this region. This wall directly blocks dispersal routes for larger mammals and indirectly impacts smaller mammals via

increased light pollution, human presence, and road infrastructure (Harrity et al. 2024; Marín and Koprowski 2025). Increased fire severity, notably in more mesic and high elevation biomes, has also played a role in the degradation of sky island habitat, which has the potential to decrease diversity among small mammal communities (O'Connor et al. 2014; Villarreal et al. 2019; Culhane et al. 2022). Therefore, future studies should focus on elevational sampling in un- or under-sampled sky islands, particularly in Mexico where only two mountains (San Luis, Sierra de Los Ajos) have digital records of >10 small mammal specimens. So too should future studies focus on cryopreserving tissues and preparing holistic specimens (*sensu* Galbreath et al. 2019) since even the comparatively well-sampled sky islands mostly lack post-1980 collection efforts. Having multiple thoroughly sampled elevational gradients in the Madrean Sky Islands would enable replicated tests of which factors are the most important determinants of species richness (Chen et al. 2017) and metacommunity structure (Presley et al. 2012), two long-standing eco-evolutionary questions. Finally, work is needed to query the population-genetic histories of montane small mammals in this system, particularly how differing dispersal abilities affect gene flow between conspecific populations on different mountains. Apt candidates for this research would be some of the most common sky-island species in museums, such as *Peromyscus boylii* or *Corynorhinus townsendii*.

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453 **Supplementary Data**

454 Supplementary Data SD 1.—54 individual sky island vector polygon shape layers and
455 supporting files for use in GIS software.

456 Supplementary Data SD 2.—54 individual sky island DEM raster layers and supporting
457 files for use in GIS software.

458 Supplementary Data SD 3.—Table of all Chiroptera specimens included in the study with
459 original GBIF data fields as well as columns added during the study (e.g., Species_MDD).

460 Supplementary Data SD 4.—Table of all Eulipotyphla specimens included in the study
461 with original GBIF data fields as well as columns added during the study (e.g., Species_MDD).

462 Supplementary Data SD 5.—Table of all Rodentia specimens included in the study with
463 original GBIF data fields as well as columns added during the study (e.g., Species_MDD).

464 Supplementary Data SD 6.—Combined table of all specimens included in the study with
465 the exception of specimens that lacked a date altogether or had been assigned a range of dates
466 spanning multiple years (n=383).

467 Supplementary Data SD 7.—Data matrix summarizing area, mean ruggedness, maximum
468 elevation, and specimen counts for each sky island.

469 Supplementary Data SD 8.—Raw area and ruggedness data for each sky island.

470 Supplementary Data SD 9.—Changes made to the mountains included in the Madrean
471 Sky Islands compared to Moore et al. 2013.

472 Supplementary Data SD 10.—Table of specimens from the American Museum of Natural
473 History that are likely relevant to the study, but lack geocoordinates.

474 Supplementary Data SD 11.—List of 11 species found in the Madrean Sky Islands that
475 need further examination. These observations fall outside of the currently understood ranges of

476 these species. Both *P. truei* and *P. difficilis* are known to occur on specific sky islands, however,
477 some specimens have been reported outside of these known mountains, warranting additional
478 verification. Specimens of *L. ega* and *M. keenii* likely belong to *L. xanthinus* and *M. evotis*
479 respectively, but verification of specimens is needed in those cases as well.

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669 **Tables**

670 **Table 1.**—List of all 54 mountains in the Madrean Sky Islands region as defined in this study,
 671 with the label numbers corresponding to Figure 1.

672

Label	Mountain	Area above 1,600 meters (km ²)	Maximum elevation (m)
1	Superstition	43.28	1902
2	Pinal	144.36	2392
3	Santa Teresa	327.76	2497
4	Santa Catalina	414.78	2806
5	Galiuro	501.57	2322
6	Pinaleño	747.2	3267
7	Peloncillo North	40.30	1982
8	Peloncillo Central	38.11	1982
9	Rincon	264.10	2646
10	Winchester	234.28	2315
11	Dos Cabezas	218.99	2485
12	Baboquivari	69.59	2262
13	Sierrita	24.12	1887
14	Santa Rita	341.77	2869
15	Whetstone	183.10	2331
16	Little Dragoon	39.81	2037
17	Dragoon	252.40	2275
18	Swisshelm	83.45	2181
19	Chiricahua	1769.87	2990
20	Peloncillo South	903.55	2095
21	Animas	739.77	2598
22	Little Hatchet	35.47	2017
23	Big Hatchet	109.32	2542
24	Alamo Hueco	89.17	2090

Label	Mountain	Area above 1,600 meters (km ²)	Maximum elevation (m)
25	Atascosa	11.09	1948
26	Patagonia	201.43	2200
27	Canelo Hills	416.09	1968
28	Huachuca	357.84	2875
29	Mule	265.56	2241
30	Pajarito	8.89	1800
31	Sierra Chivato	192.43	2195
32	Sierra San Jose	123.24	2539
33	Sierra La Ceniza	13.61	1822
34	Sierra de Embudos	24.31	1921
35	San Luis	1722.44	2515
36	Sierra Avispas	5.39	1746
37	Sierra Cibuta	43.72	2079
38	Sierra El Pinito West	52.24	2264
39	Sierra La Mariquita	239.50	2500
40	Sierra de los Ajos	719.64	2616
41	Sierra La Madera	38.22	2044
42	Sierra Azul	296.54	2452
43	Sierra El Manzanal	28.70	1919
44	Cerro Bacoachi	3.79	1707
45	Sierra San Antonio	112.39	2213
46	Sierra Buenos Aires	94.70	2474
47	Sierra El Pinito East	37.42	2230
48	Cerro Bellotal	35.63	1942
49	Sierra Purica	11.50	1925
50	Sierra La Sandia	137.04	2179
51	Sierra Jacaral	224.80	1908
52	Sierra Aconchi	37.43	2190
53	Sierra de Oposura	133.79	2345

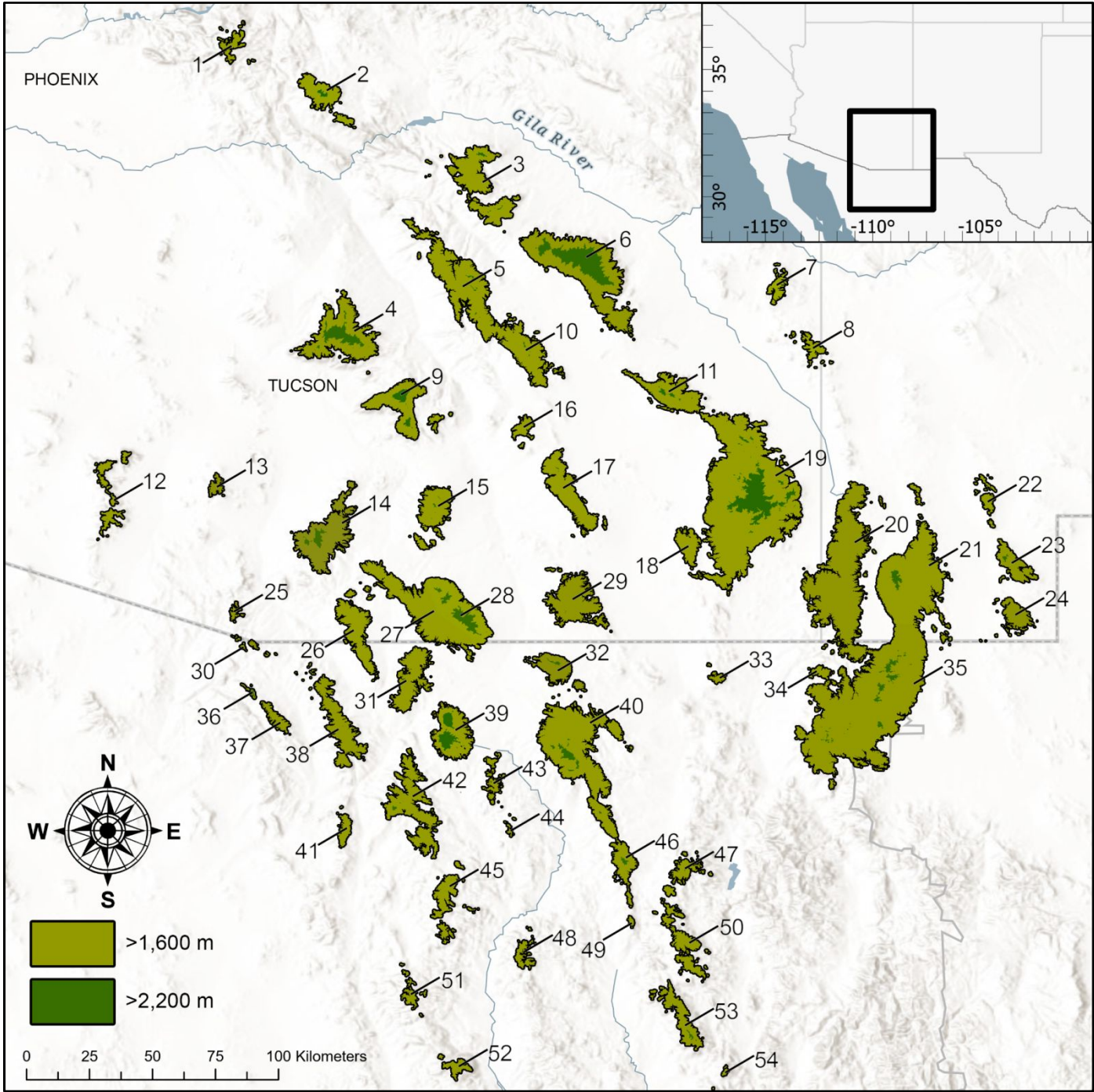
Label	Mountain	Area above 1,600 meters (km ²)	Maximum elevation (m)
54	Sierra de Las Guijas	4.11	1823

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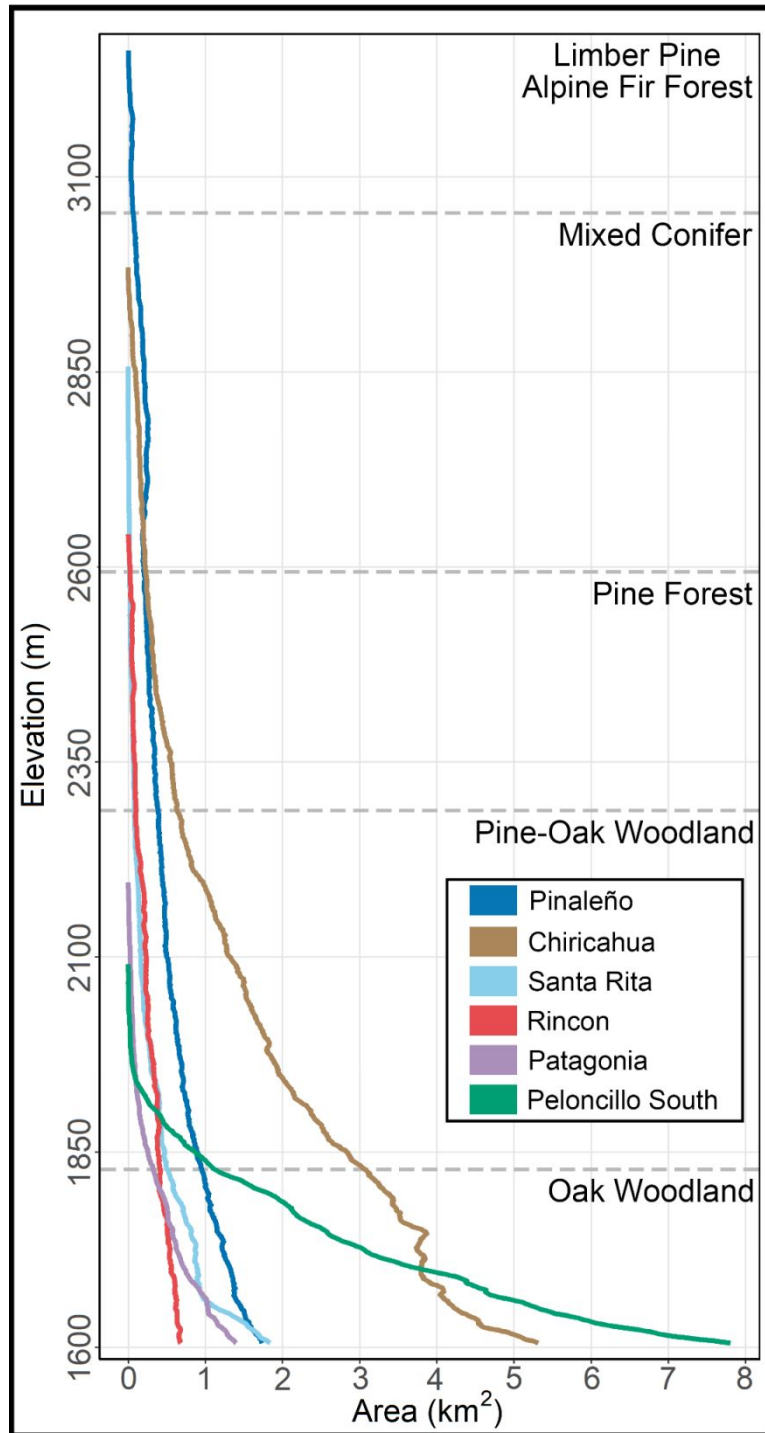
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Figures

Fig 1

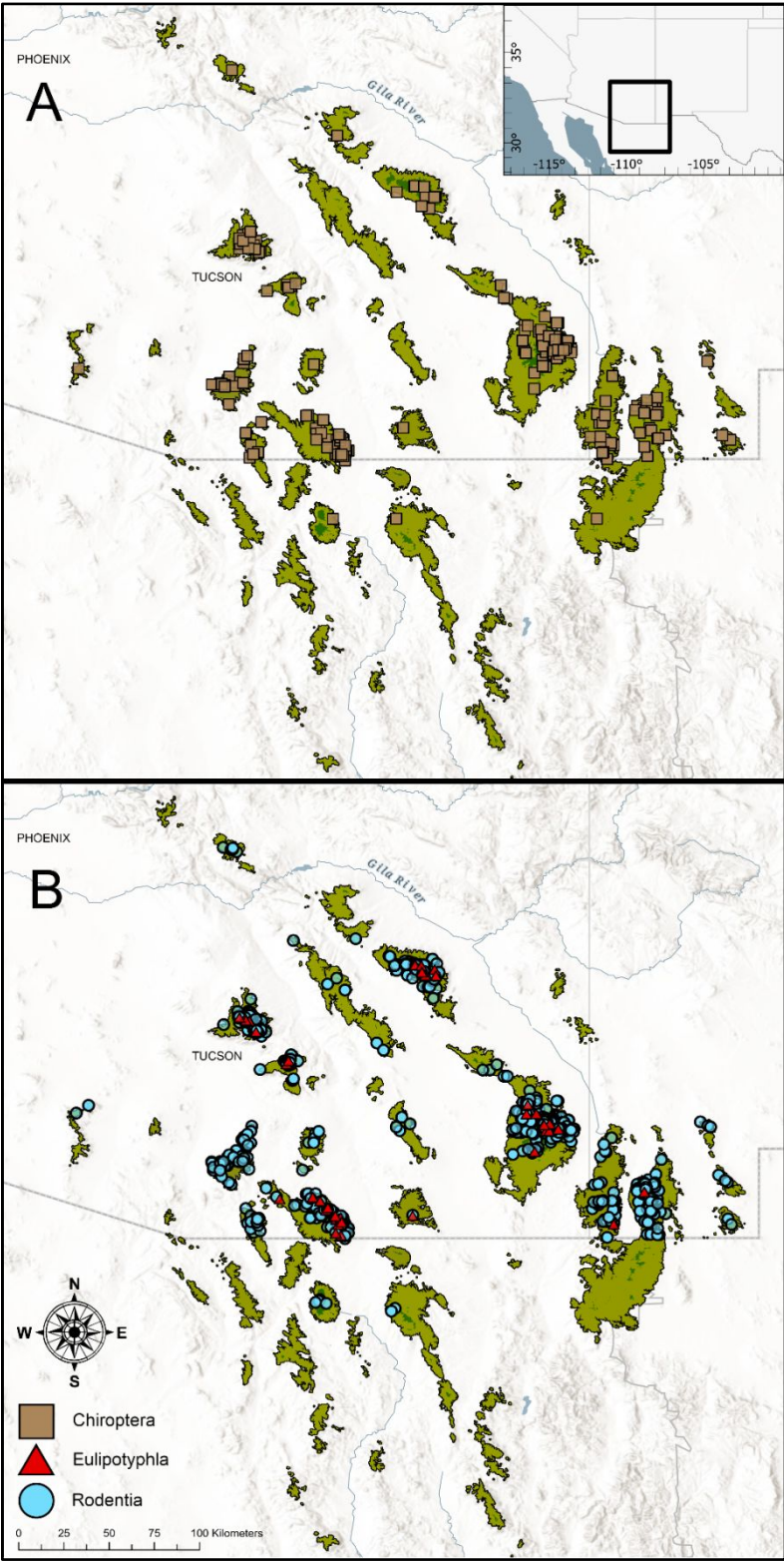


677 Fig. 2



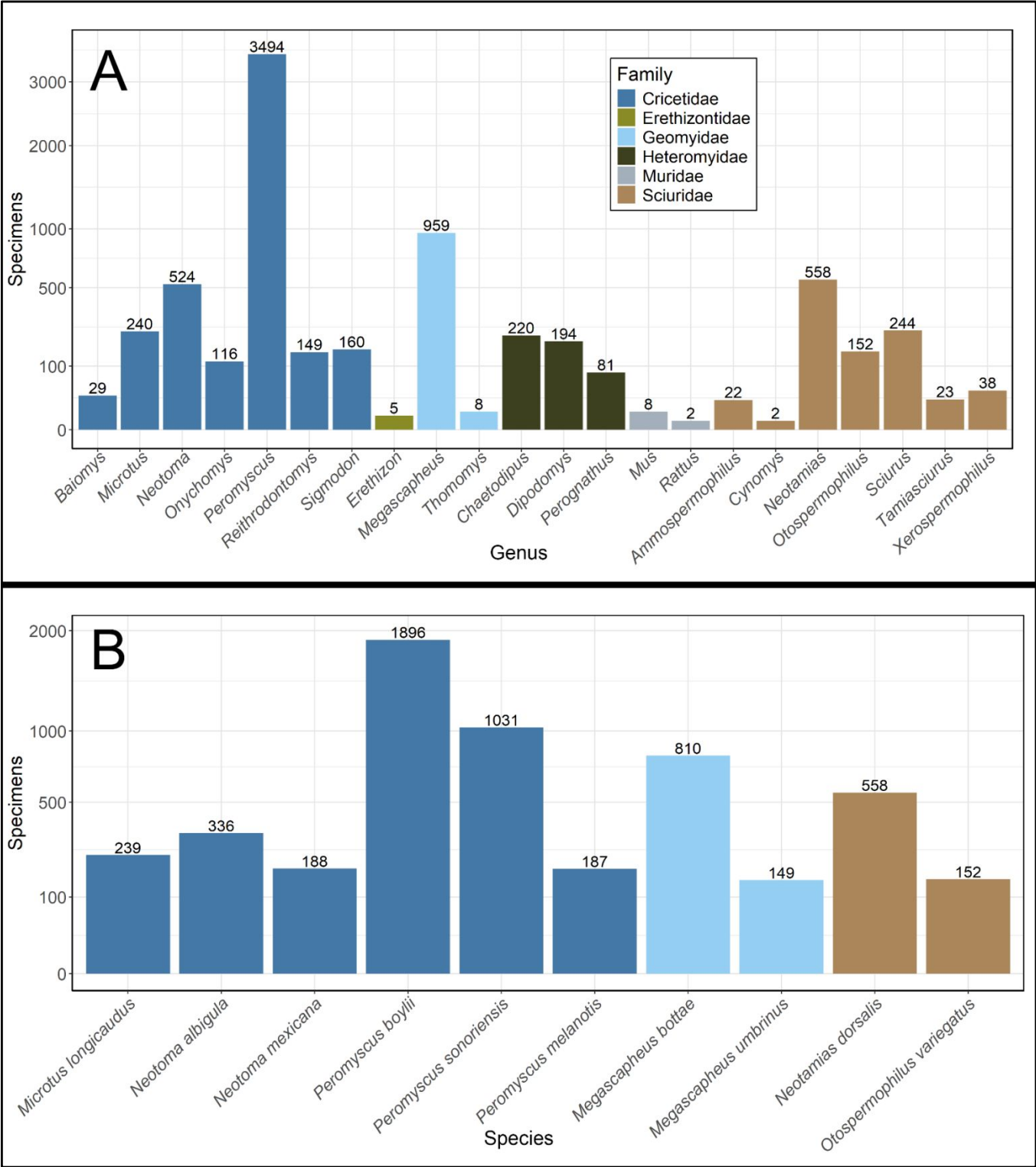
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679 Fig 3.



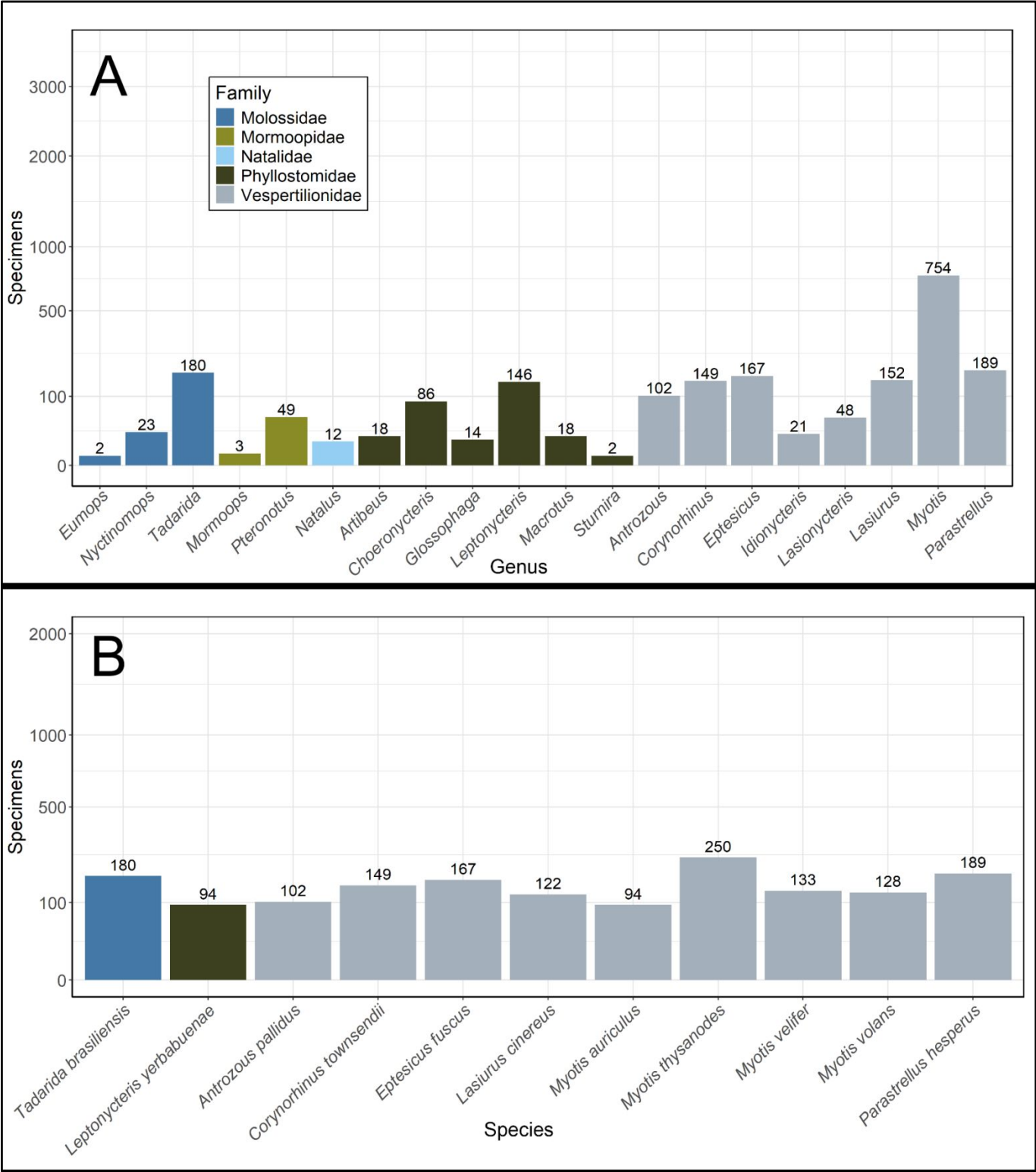
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681 Fig 4.



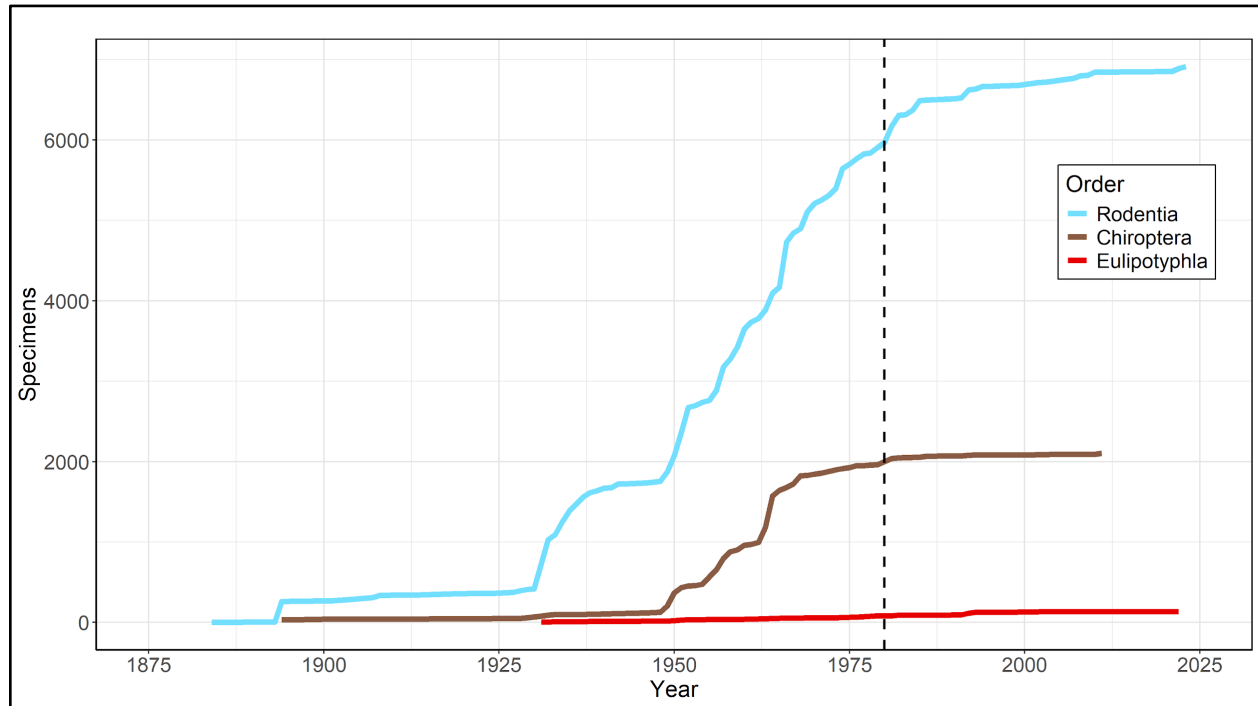
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683 Fig 5.

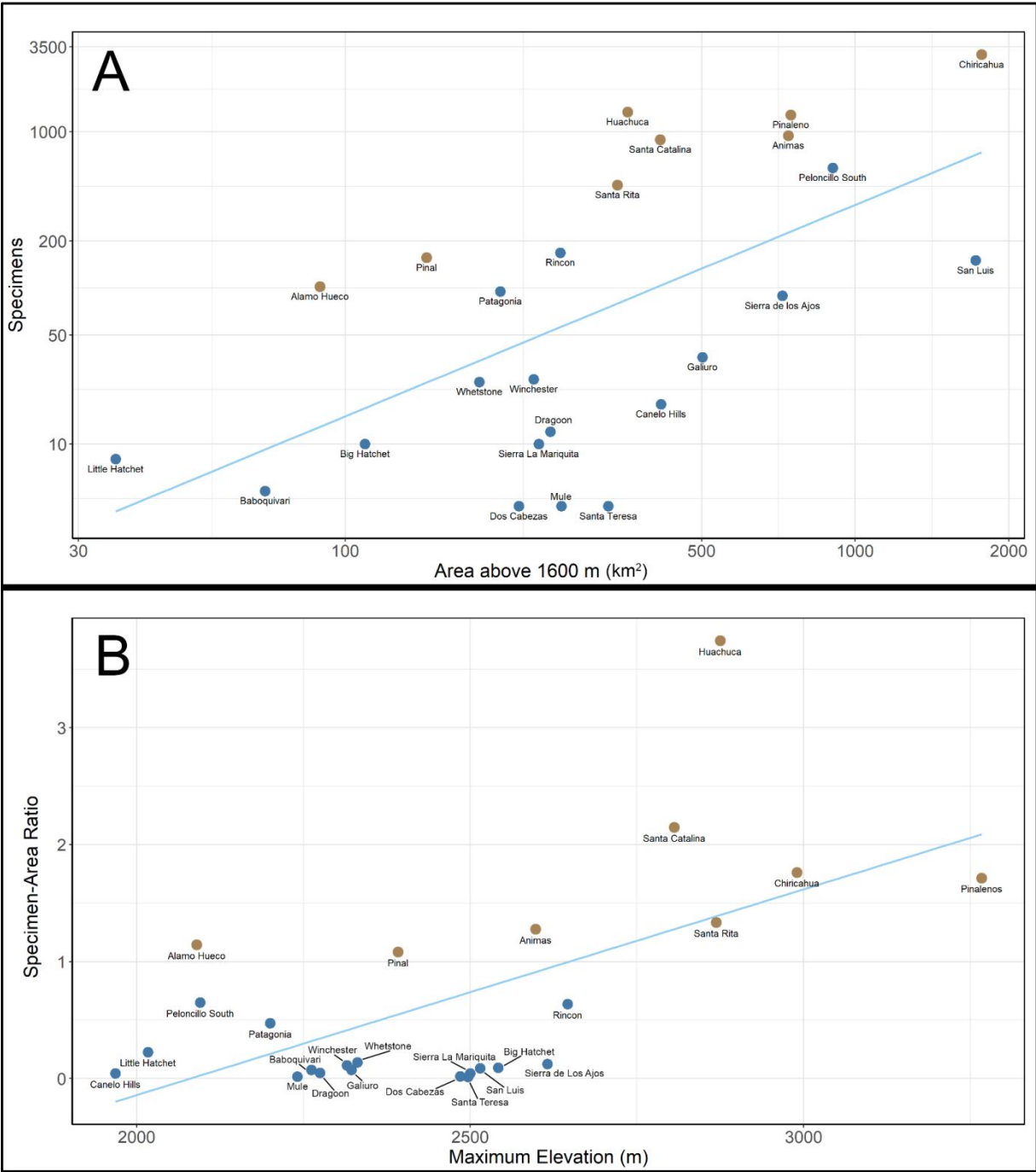


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685 Fig 6.



687 Fig 7.



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Figure Legends

Fig 1.—Map of the Madrean Sky Island region showing the 54 mountains defined in this study, with numbered labels corresponding to Table 1. The Colorado Plateau lies directly North of the figure and the Sierra Madre Occidental lies South/Southeast of the figure.

Fig 2.—Elevation per unit land area above 1,600 m for six mountains in the Madrean Sky Island region of Arizona. The five ecoregions are overlaid with their typical upper range limit relative to elevation.

Fig 3.—Historical voucher specimens sampled from areas greater than 1,600 m in the Madrean Sky Islands, as separated by (A) Chiroptera, and (B) Eulipotyphla and Rodentia.

Fig 4.—Frequency of rodent specimens sampled at >1,600 m in the Madrean Sky Islands (A) by genus with colors corresponding to taxonomic families, and (B) by the 10 most frequently sampled species. Both charts are on a square root scale.

Fig 5.—Frequency of bat specimens sampled at >1,600 m in the Madrean Sky Islands (A) by genus with colors corresponding to taxonomic families, and (B) by the 10 most frequently sampled species (*Leptonycteris yerbabuenae* and *Myotis auriculus* are equally the 10th most common). Both charts are on a square root scale.

Fig 6.—The accumulation of specimens over time across Chiroptera, Rodentia, and Eulipotyphla. The colored lines begin where the first specimen for each order was collected (1884, 1894, and 1931 respectively) and the vertical dashed line indicates the year 1980.

Fig 7.—(A) Biases in historical sampling as measured by the number of small mammal specimens relative to mountain area above 1,600 meters. Both axes are shown on a log₁₀ scale, indicating a multiplicative relationship between sky-island area and number of specimens. (B) Biases in historical sampling as measured by the density of sampling relative to sky-island

712 maximum elevation on a linear scale. In both panels, the 29 sky islands without any historical
713 specimens were excluded and sky islands with a specimen-area ratio greater than 1 are shown in
714 brown.

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