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Authors: Fleischner, Thomas L., Floyd, M. Lisa, Rack, Jessie, Hanna, David, Blevins, Karen, et al.

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The Mogollon Highlands Ecoregion of the American Southwest: A Neglected Center of Ecological Diversity

Thomas L. Fleischner,[1,6] M. Lisa Floyd,[1] Jessie Rack,[2] David Hanna,[1] Karen Blevins,[3] Bruce Christman,[4] and Andrew T. Holycross[5]

[1]Natural History Institute
[2]Department of Biological Sciences, Northern Arizona University
[3]Independent Geospatial Technologies Consultant
[4]Herpetological Conservation, LLC
[5]Arizona State University – Biodiversity Knowledge Integration Center

[6]Corresponding author: tom@naturalhistoryinstitute.org; 928-863-3232

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ABSTRACT

The Mogollon Highlands of Arizona and New Mexico is a uniquely biodiverse ecoregion that has been previously neglected by scientific studies. Here, we delineate, map, and describe the area, and focus on two taxonomic groups—snakes and conifers—to exemplify the region. The Mogollon Highlands Ecoregion (MHE), as described here, has potential to serve as a center of adaptation to changing climate. This, combined with its inherently high biodiversity, merits its consideration as a conservation priority. We document the diversity and distribution of snakes in the MHE: 39 species were found, a species richness on par with the Madrean Archipelago (sky islands) of Arizona and New Mexico, a region known for its high snake diversity. The MHE is also home to unique conifer diversity, with elevated levels of endemism and genetic exchange. We recommend consideration of the MHE as a uniquely diverse region, and a high conservation priority.

Index term: biogeography; conifer diversity; landscape conservation; Mogollon Highlands Ecoregion; snakes

INTRODUCTION

To be effective, conservation efforts should protect biological and ecological diversity at multiple levels of organization (Trombulak et al. 2004), from very small (genetic) to very large (ecosystems and landscapes). Biodiversity is most effectively maintained by protecting larger areas (Soulé 1985; Noss and Cooperrider 1994), especially in cases where heterogeneous landscapes feature high gamma (regional scale) diversity and include sites of high alpha (within-habitat) diversity (spatial scales of diversity *sensu* Whittaker 1960, 1972). Strategies for long-term protection of biodiversity under the changing conditions of climate change have remained remarkably consistent over the past three decades (Noss 2001; Heller and Zavaleta 2009; McLaughlin et al. 2022).

Conservation potential is strengthened when protected landscapes provide gradients of environmental factors such as elevation, precipitation, and temperature, as such conditions allow for shifts in species ranges. Similarly, connectivity with continental-scale corridors (such as north–south trending mountain ranges) optimizes opportunities for population shifts when physical conditions change (Hunter et al. 1988; Ranius et al. 2023). Connectivity and climate corridors—pathways that connect warmer to cooler areas less impacted by human activity—offer efficient opportunities for ecological adaptation to climate change (Lawler 2009; Lawler et al. 2020). Conservation biologists have called for identifying "climate change refugia"—areas that are sufficiently buffered from climate change as to enable persistence of species and other valued resources, as during climate upheavals in the paleoecological past (Morelli et al. 2016). A recent analysis of this approach (Saunders et al. 2023) suggests that the southwestern United States, and particularly the Rocky Mountains and the Sierra Madre Occidental of México, represent potential high-priority climate change refugia.

In the American Southwest (especially Arizona), biological attention has been focused largely on the canyon country of the Colorado Plateau and the especially well-studied Sonoran Desert. This has been facilitated, in part, by the largest research universities and government agencies (e.g., USGS, USFS, and cooperative parks study units at Northern Arizona University in Flagstaff, Arizona State University in Tempe, University of Arizona in Tucson, and the University of Utah in Salt Lake City). The continental-scale ecotonal transition zone that connects the Colorado Plateau and the Sonoran Desert, much of it along the 200-mile-long escarpment known as the Mogollon Rim, has accommodated biological studies, often addressing autecological or ethological questions (e.g., Barber et al. 1998; Dobbs and Martin 1998; Martin and Martin 2001), but has remained less known than the Plateau country to the north and the low deserts to the south. In an analysis of herbarium records for the western United States, for example, all counties of this transitional zone were "under-collected" (Taylor 2014). This transition zone has tended to be viewed as a line—the boundary between two other places—and has been overlooked as a distinct region worthy of consideration at the landscape level.

We have identified this area as the Mogollon Highlands Ecoregion (MHE) (Fleischner et al. 2017). Here, we make the case that the MHE deserves recognition as a distinct and important ecological region in its own right, not just as a transitional zone between two long-recognized regions (Colorado Plateau and Sonoran Desert). Given its location and the evidence of prior research, we argue that the MHE represents one of the most biodiverse regions in North America —an ecological treasure that the scientific community has largely failed to recognize. As a result, this region has been undervalued in the realm of conservation strategy.

The MHE represents an ecologically fascinating North American transition zone of continental importance. This dramatic landscape of escarpments, canyons, mesas, deserts, and high conifer forests is a land of high biological and ecological diversity. It is where the Sonoran Desert of the Basin and Range Province meets the redrock canyon country of the Colorado Plateau and the Southern Rocky Mountains, and where the northern limits of some species coexist with the southern limits of others. In the Mogollon Highlands, the mega-diversity of Meso-America, and the Sierra Madre in particular (DeBano et al. 1995), has direct access into North America. As Felger and Wilson (1995) pointed out more than two decades ago, this Apachian/Madrean region is a "neglected center of biodiversity." More recently, it has been referred to as a "biodiversity hotspot" in reference to herpetology (Bezy and Cole 2014). Davis et al. (1997) highlighted the region as a notable center of endemism in North America.

The core of this region is what the World Wildlife Fund (WWF) named the "Arizona Mountain Forest" (Ricketts et al. 1999). WWF concluded this region had regionally outstanding biological distinctiveness, due to relatively high species richness and endemism. The Mogollon Highlands largely coincides with The Nature Conservancy's "Arizona-New Mexico Mountains" ecoregion (Marshall et al. 2006), although, as defined here, the Mogollon Highlands extends beyond these montane forests to include parts of adjacent, interwoven communities. As we recognize it, the Mogollon Highlands coincides with the northern portion of the "Apache Highlands" of The Nature Conservancy; however the Apache Highlands extends far south, including the Madrean "Sky Islands" and into the Sierra Madre Occidental of Sonora and Chihuahua, Mexico (Turner et al. 2005).

Portions of the Mogollon Highlands have been referred to, inconsistently, by many names (e.g., "Arizona Central Highlands," "Arizona Transition Zone"), yet the area remains relatively ill-defined relative to its southern counterpart, the Sonoran Desert, and its northern neighbor, the Colorado Plateau. This region roughly aligns with the interface of two great physiographic provinces of the American West: the Basin and Range and Colorado Plateau (Hunt 1967). Due to great geologic diversity (Nations and Stump 1996), the Mogollon Highlands present dramatic topographic diversity, varying several thousand feet in elevation, and including a series of deep canyon systems that drain off the Colorado Plateau and emerge into the low Sonoran Desert. The MHE contains the highest density of springs in Arizona (Stevens 2018).

The region's positioning at a continental-scale biogeographic crossroads contributes to its high ecological diversity. The southern extent of the Rocky Mountains intersects the eastern portion of the Mogollon Highlands. All four of North America's deserts connect directly with the region: the Great Basin Desert to the north, the Mojave to the west, and the Sonoran and Chihuahuan to the south. Some species (e.g., *Juniperus osteosperma* and *J. scopulorum*) reach their southern extent here, while Sierra Madrean species (e.g., alligator juniper [*Juniperus deppeana*], Emory oak [*Quercus emoryi*], red-faced warbler [*Cardellina rubifrons*]) reach their northern boundaries. Additionally, some Great Plains species (e.g., blue grama [*Bouteloua gracilis*], thirteen-lined ground squirrel [*Spermophilus tridecemlineatus*], gray catbird [*Dumetella carolinensis*]) reach their western extent here while the eastern extent of some shrubs (e.g., *Rhus ovata*) lies in this region.

This rich merging of biotas owes much to larger-scale climatic patterns. The Southwestern Climate Pattern—typified by winter and summer precipitation, separated by spring and fall droughts —is influenced by both mid-latitude and subtropical atmospheric circulation regimes (Sheppard et al. 2002; Sellers 2008). One specific consequence of this atmospheric confluence is a bi-seasonal precipitation pattern (Lowe 1964), which, in turn, leads to higher botanical diversity as plant phenologies can be oriented around one or both seasons. As a result, floristic affinities extend both north and south (McLaughlin 2008).

The Mogollon Highlands includes five of the North American life zones described by Merriam (Lowe 1964; Phillips et al. 1989). It represents an interfingering of 11 of the 26 biotic communities in the southwestern United States and northwestern Mexico (southern Utah to northern Sinaloa, Pacific Coast to New Mexico), as described by Brown (1994). Because of this confluence of habitats, the MHE encompasses much of the plant diversity of Arizona, which has the third highest plant species richness of any state (Stein et al. 2000). The regional diversity is amplified even more due to punctuation by linear ribbons of riparian forest—one of the highest productivity habitats in North America. These lush green corridors concentrate wildlife, and include some of the highest biodiversity (alpha diversity) sites in North America (Johnson et al. 1977; Ohmart and Anderson 1982; Fleischner 1999). (Because of their limited geographic extent, however, riparian zones do not appear as distinct "communities" in our analysis.) Based on these observations, the MHE accords with criteria for high priority conservation consideration. In a report by the National Biological Service, two community types in the Mogollon Highlands region were identified as "endangered ecosystems," defined as those in 85–95% decline: old-growth ponderosa pine (*Pinus ponderosa*) forest, and Southwest riparian forests (Noss et al. 1995).

The ongoing ecological health of the Mogollon Highlands is especially important in this age of rapid climate change. This area of dramatic elevational gradients, at a continental-scale biogeographic crossroads, can yield understanding of the capacity for species and ecological communities to adapt to global climate change. Based on these factors, we posit that the

MHE is a center of biological and ecological diversity, worthy of recognition and protection.

Accurate mapping of species diversity is essential for the identification of areas of high conservation priority (Andermann et al. 2022). Having established the boundaries of the MHE (see Methods), we commenced biological analysis of portions of the flora and fauna within it. There are significant challenges in clarifying species diversity in several important taxa—for example, vascular plants—due to chaotic taxonomic revisions that render comparisons between data sets problematic. Highly mobile animals, such as birds, present in the Mogollon Highlands in various seasonal patterns, can confuse geographic analysis.

As a primary example, we focus here on snake diversity in the MHE. In a recent comprehensive review, Holycross and Mitchell (2020) thoroughly documented the snake fauna of Arizona. Their work demonstrates that biotic communities in Arizona each have their own relatively distinct herpetofauna (see also Holycross et al. 2022). Snake species distributions are limited by a number of environmental factors such as precipitation, surface temperature, soil type, or elevation (Schall and Pianka 1978) and are often constrained by landscape features such as canyons, mountains, or rivers (Brown et al. 2020). Because of the high-quality data available from this ongoing research, this taxon offers the ideal starting point for corroborating the biological importance of the MHE. Given the ecological diversity of available habitats in this region, directly resulting from its ecotonal character, we predict higher snake diversity in the MHE compared with other regions of comparable size in the contiguous United States.

METHODS

Mapping

The MHE boundary was conceptualized using (1) prior delineations (such as the Arizona Transition Zone physiographic data and EPA Level IV ecoregions of Griffith et al. 2014); (2) the distribution and overlap of selected taxa (especially woody plants, reptiles, and selected herbaceous plants) in ellipse analyses; and (3) thoughtful discussion and tracking of the overlap of various taxa from the Rocky Mountains, the Madrean and Sonoran regions, and the east and west as well. For ellipse analyses, locations of selected plant and animal species occurrences were downloaded from the SEINet (Southwest Environmental Information Network) database and from the Global Biodiversity Information Facility (GBIF). These locations were plotted in ArcGIS and "Directional Distribution (Standard Deviation Ellipse)" ellipses were mapped using the Directional Distribution tool in ArcMap (Mitchell 2005; Allen 2009). Parameters were set at 1 standard deviation. These ellipses describe the spatial trend of plant species ranges; these ellipses were combined and areas of overlap identify zones of high species diversity.

As a "highlands," an important initial delineator of this region was elevation. A lower elevational at 1067 m (3500 feet) above sea level was isolated from a digital elevation model. As a transitional zone between high deserts and mountains of the Colorado Plateau to the north and the low deserts and basins of the Sonoran Desert south, it runs along the Mogollon Rim escarpment bisecting central Arizona. The northern boundary was initially based upon representative ecoregions defined by the EPA Level IV (Griffith et al. 2014) and Arizona Transition Zone physiography (Peirce 1985). The boundary was modified to expand into areas where ecoregions were thought to be inclusive of the Mogollon Highlands (i.e., containing a suite of species with transitional characteristics) or contracted where ecoregions were deemed exclusive (i.e., where the ecoregion better exemplifies the high deserts and mountains to the north or the low deserts to the south). ArcGIS was used for this analysis, resulting in a polygon feature class that identified the spatial extent of this region.

With a preliminary boundary in place (Fleischner et al. 2017), we turned our attention to refining the boundary (recognizing that defining boundaries of non-discrete systems is somewhat subjective). While we were confident that the southern boundary was well-delineated (3500 foot contour = 1067 m), the northern and eastern boundaries contained areas and drainages that required further input from additional criteria.

We sought input from many colleagues, including biologists, geologists, and wilderness travelers, and developed rubrics for the inclusion/elimination of questionable areas. We relied significantly on National Hydrologic Data from USGS, focusing on Level 12 watersheds (http://nationalmap.gov/standards/nhdstds.html). We used a combination of watershed boundaries that drain into the Mogollon Highlands area *and* contain vegetative or faunal elements shared with the greater Mogollon Highlands. In general, when our boundary includes a piece of a different physiographic province (Peirce 1985) *and* the biota are inconsistent with that of the Mogollon Highlands, we excluded that portion of the landscape (e.g., San Francisco Peaks and upper Sycamore Canyon). The similarity of plant taxa across three areas of questionable affinity along the northern boundary was investigated using similarity indices of vegetation (Ellenberg and Mueller-Dombois 1974). Thus, using these similarity indices, watersheds in question were compared and were included if the comparative indices supported a similarity with MHE vegetation and they were excluded if the indices captured an area of dissimilar vegetation (i.e., captured vegetation characteristic of more northern ecoregions or biotic provinces).

Finally, we turned our attention to the southeastern boundary in New Mexico, an area well known to one coauthor (BC), who made suggestions of additions to the boundary based on faunal (snake) habitats and physiographic ecoregions. The decision was made to extend the boundary east of Continental Divide (the previous boundary) to include the Black Range, an area that has vegetation and faunal continuity with the Gila Wilderness at the 1676 m (5500 foot) elevation contour.

We modified the 20 "ecoregions" of Griffith et al. (2014) that are found within the boundary of the MHE by, first, renaming them, for the sake of clarity, as *communities*. These 20 communities, along with their characteristic geology, soils, dominant plant species, and other habitat characteristics are summarized in Appendix 1. All plant taxonomy accords with APG IV nomenclature.

Snake Diversity and Distribution in the MHE

Records from the Arizona and New Mexico portions of the Mogollon Highlands were obtained independently. For the Arizona portion of the Mogollon Highlands, we extracted data within the Mogollon Highlands isopleth from a database we compiled to build the range maps in *Snakes of Arizona* (Holycross et al. 2020a). For the New Mexico portion of the Mogollon Highlands, we extracted data from the VertNet database, as well as collections of the Gila Center for Natural History at Western New Mexico University and the Museum of Southwest Biology at the University of New Mexico, primarily by plotting the stored coordinates then running an overlay query for those observations that fell within the Mogollon Highlands Ecoregion boundary. For those observations without coordinates, a selection set was generated based upon county values that intersected the Mogollon Highlands boundary. We temporarily assigned these observations coordinates at the center of the New Mexico portion of the Mogollon Highlands Ecoregion, and then georeferenced them from within the ArcGIS Online environment by the contributor (BC) most familiar with that portion of the New Mexico herpetofauna. He also reviewed and verified the plots of all records that he did not personally georeference.

Because of the different methods used to construct the maps in each state, the New Mexico portion is based on records gathered from only a subset of the institutions that were queried in Arizona. In Arizona, we queried many smaller collections (national park units, small college collections, and other institutions that do not participate in VertNet). Snake locations were overlain on the MHE community polygons to extract the species of snakes that have been recorded in each habitat.

Snake taxonomy used here follows that used in Holycross and Mitchell (2020) and Holycross et al. (2022); however, in several cases this taxonomy is controversial. As applied to this analysis, these include recognition of *Crotalus cerberus* and *C. viridis*, *Crotalus molosssus* and *C. ornatus*, *L. californiae* and *L. splendida*, as well as *Lampropeltis knoblochi* and *L. pyromelana* as separate species. In each of these cases, these taxa were formerly recognized as single polytypic species and split based on phylogenetic studies that have been questioned for a variety of cogent reasons (see PDF supplement to Holycross et al. 2022 and Holycross and Mitchell 2020 for relevant citations). However, in all cases, definitive evaluations of species boundaries in these taxa using more appropriate data, sampling, and analyses have yet to be published. We have elected to continue to use these names (with reservation), in the interest of consistency and stability, but recognize that definitive evidence of speciation is lacking in all four cases. Whether the splits above represent speciation events or not, they do represent significant intraspecific diversity as recovered in phylogenetic analyses. In only three of these cases would use of the alternative taxonomy affect the diversity metrics reported here (recognition of *L. knoblochi* as a species separate from *L. pyromelana* does not affect our diversity metrics, as *L. knoblochi* is extralimital to the MHE).

Gymnosperm Diversity in the MHE

To evaluate the diversity of gymnosperm taxa occurring in the MHE, we searched both Seinet (SEINet Portal Network 2023) and World Flora Online (2023). We compared the species richness in the MHE with a polygon of identical size and shape farther north in Arizona that has the Mogollon Rim as its southern boundary. We extracted all records for Pinaceae and Cupressaceae within the MHE and this parallel polygon. While taxonomic designations, especially at the subspecies level, are continually in revision, we used the same rubric to accept or reject synonyms in both areas; we accepted the latest taxa designated by World Flora Online (2023), and we eliminated taxa that occurred only as plantings or cultivars in nonnative landscapes.

RESULTS

Our refined map of the MHE is represented in Figure 1. The MHE covers 70,490 km^2 of highly diverse terrain spanning elevations above 1061 m (3500 feet) in a south-east trending arc through central Arizona and western New Mexico (Figure 1). The diverse landscapes of this Ecoregion support 20 communities. Vegetation and habitat characteristics of these 20 communities are summarized in Appendix 1.

The most extensive communities in the MHE are three types of conifer forests, five types of woodlands primarily dominated by conifers, oaks and other perennial shrubs (interior chaparral), six types of grasslands and tablelands, and six high deserts and basins; winding through each of these is riparian vegetation. The region overlaps small upland areas of Mohave, Sonoran, and Chihuahua desert origin.

We identified 2223 vouchered observations representing 39 species of snakes in the Mogollon Highlands (Appendix 2). Three *Thamnophis* records and one *Salvadora* record were not assigned to species. Both of these genera are represented by more than one species with the Mogollon Highlands and cannot be assigned to a species without examining the specimens. The number of recorded snake species varied considerably across the Mogollon Highlands communities with records lacking for six communities (Table 1). Variability among communities in the number of records is likely due to several factors: areal representation of the community within the Mogollon Highlands, rugged terrain inhibiting travel, lack of public access (e.g., on some tribal lands), and remoteness from population centers. Clearly, areal representation (km^2) in the Mogollon Highlands is a critical factor; the six communities lacking records altogether were among the eight smallest communities. Interestingly, the Low Mountains and Bajadas community was represented by only 95.4 km^2 and yielded only 7 snake records, but was among the best sampled and highest diversity communities in metrics controlling for community area (records/km^2 and species/km^2). After controlling for community size (area in km^2), the communities capturing the highest snake

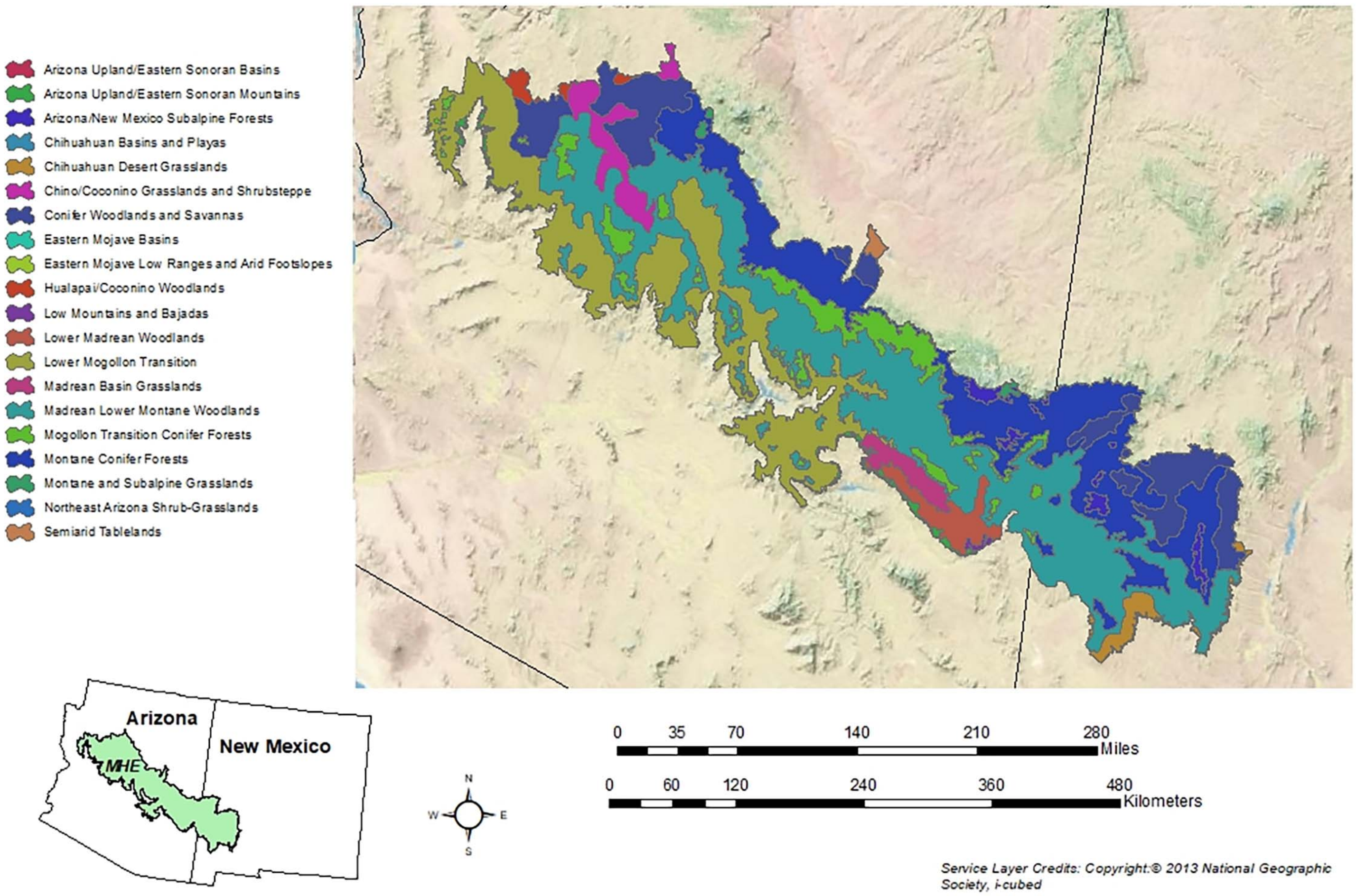

Figure 1.—The Mogollon Highlands Ecoregion, showing 20 component communities.

diversity were (in descending order) (1) Arizona Upland/Eastern Sonoran Basins, (2) Low Mountains and Bajadas, (3) Chihuahuan Deserts and Grasslands, (4) Lower Mogollon Transition, (5) Montane and Subalpine Grasslands, and (6) Madrean and Lower Montane Woodlands. Several of these communities (1, 2, and 5) rank highly in this metric because although relatively few species were documented within them, they are also represented by relatively few km^2 in the MHE. The majority of the communities contributing the most to absolute diversity are relatively low-elevation habitats along the southern boundary of the MHE, as expected when assaying an ectothermic taxon.

Snakes Endemic to the Mogollon Highlands

Of particular note are two species of snakes that are endemic, or nearly endemic, to the Mogollon Highlands: the Mogollon narrow-headed gartersnake (*Thamnophis rufipunctatus*) and the Arizona black rattlesnake (*Crotalus cerberus*). The Mogollon narrow-headed gartersnake (*T. rufipunctatus*) is an aquatic specialist and restricted to the upper watersheds of the Gila River in the Salt, Verde, and San Francisco rivers in Arizona and the San Francisco and Upper Gila rivers in New Mexico. (Holycross et al. 2020b). It is found in Conifer Woodlands and Savannas, Lower Madrean Woodlands, Lower Mogollon Transition, Madrean Lower Montane Woodlands, Mogollon Transition Conifer Forests, and Montane Conifer Forests where it is restricted to perennial streams at elevations ranging from ~700 to 2430 m (Rossman et al. 1996). *Thamnophis rufipunctatus* is listed as threatened under the U.S. Endangered Species Act (USFWS 2014). Precipitous decline has been recorded in this species in recent years, likely because of its high degree of habitat specialization and its diet—which is almost exclusively fish (Hibbitts et al. 2009).

The Arizona black rattlesnake (*C. cerberus*) is nearly endemic to the MHE. Outside of the Mogollon Highlands, populations of *C. cerberus* are found only in peripheral isolated mountain ranges and canyons (Holycross et al. 2020a; Nowak et al. 2020). This rattlesnake occurs most often in high-elevation woodlands, usually in riparian areas, and is associated with a variety of ecoregions, including Arizona/New Mexico Subalpine Forests, Chino/Coconino Grasslands and Shrubsteppe, Conifer Woodlands and Savannas, Low Mountains and Bajadas, Lower Madrean Woodlands, Lower Mogollon Transition, Madrean Basin Grasslands, Madrean Lower Montane Woodlands,

Table 1.—Snake diversity and frequency by community type in the Mogollon Highlands Ecoregion.

	Area (km^2)	# records	# species	records/km^2	species/km^2
Arizona Upland/Eastern Sonoran Basins	5.8	19	8	3.286	1.383
Arizona Upland/Eastern Sonoran Mountains	691.5	7	6	0.010	0.009
Arizona/New Mexico Subalpine Forests	849.4	4	3	0.005	0.004
Chihuahuan Basins and Playas	0.5	0	0	0.000	0.000
Chihuahuan Desert Grasslands	865.8	52	14	0.060	0.016
Chino/Coconino Grasslands and Shrubsteppe	1991.9	45	12	0.023	0.006
Conifer Woodlands and Savannas	7494.8	134	19	0.018	0.003
Eastern Mojave Basins	0.4	0	0	0.000	0.000
Eastern Mojave Low Ranges and Arid Footslopes	15.0	0	0	0.000	0.000
Hualapai/Coconino/Woodlands	432.6	0	0	0.000	0.000
Low Mountains and Bajadas	95.4	7	7	0.073	0.073
Lower Madrean Woodlands	1463.4	19	11	0.013	0.008
Lower Mogollon Transition	14,177.7	683	29	0.048	0.002
Madrean Basin Grasslands	950.6	20	14	0.021	0.015
Madrean Lower Montane Woodlands	22,551.8	804	33	0.036	0.001
Mogollon Transition Conifer Forests	4214.4	99	11	0.023	0.003
Montane and Subalpine Grasslands	179.3	7	1	0.039	0.006
Montane Conifer Forests	14,317.5	327	16	0.023	0.001
Northeast Arizona Shrub-Grasslands	1.2	0	0	0.000	0.000
Semiarid Tablelands	192.6	0	0	0.000	0.000

Mogollon Transition Conifer Forests, and Montane Conifer Forests (Hulse 1973; Jones 1988; Nowak and Schofer 2006; Griffith et al. 2014; Holycross et al. 2022). It is most commonly found at elevations from 900 to 3000 m (Nowak et al. 2020).

Gymnosperm Diversity in the MHE

A survey of the literature, accepting native species and subspecies designations as reported in SEINet Portal Network (2023) and World Flora Online (2022), suggests a high diversity of gymnosperm species relative to other southwestern ecoregions. The MHE contained 15 accepted species or subspecies in the Pinaceae (pines and firs) and 11 species or subspecies in Cupressaceae (junipers and cypress), while the same-size adjacent polygon to the north had 10 species or subspecies in Pinaceae and 8 species or subspecies in the Cupressaceae (World Flora Online 2022; SEINet Portal Network 2023).

DISCUSSION

The Mogollon Highlands Ecoregion merits consideration as a prominent, unique, high biodiversity transition zone of North America—not merely as the neglected edges of other provinces. Moreover, regions with significant elevational gradients, and with broad interpenetration of numerous ecological communities, represent living laboratories for adaptation to ecological and climatic change. The MHE is ideally suited for ongoing studies of adaptation to a changing Earth, and provides an important conservation opportunity.

The snake database serves as a starting point for evaluating the biogeographic affinities and patterns of distribution of a portion of the Mogollon Highlands fauna. There are four main lines of evidence that illustrate the biogeographic affinities and patterns in the MHE. First, the Mogollon Highlands exists at the nexus of several ecoregions, each with a relatively distinct herpetofauna (Holycross et al. 2022). Although largely peripheral to the Mogollon Highlands, these ecoregions—Sonoran Desertscrub, Mohave Desertscrub, Great Basin Desertscrub, Plains and Great Basin Grassland, Semidesert Grassland, Rocky Mountain Subalpine Conifer Forest, and Subalpine Grassland—contribute to the diversity of the Mogollon Highlands snakes. For example, *Crotalus pyrrhus*, which is associated with the xeric rocky environs of the Sonoran Desert, is included in the biota of the Highlands because portions of this desert are represented within the southern margin of the western Highlands. Likewise, *Lampropeltis triangulum*, which is primarily associated with Plains and Great Basin Grassland found to the north of the Highlands, is represented because pockets of this community persist within its boundaries.

Second, the proximity of the Cochise Filter Barrier contributes to diversity from east to west across the Mogollon Highlands. The Cochise Filter Barrier is a region that (very generally) follows the spine of the Peloncillo Mountains from the Sierra Madre in Mexico up to the Mogollon Highlands. This region serves or served as a barrier to gene flow for closely related organisms (including many amphibians and reptiles) distributed both east and west of it. Historically, separate subspecies of several species of snake have been recognized on either side of the Cochise Filter Barrier, although recently, many have been elevated to full species status. While some of these elevations are controversial, it is clear that the barrier contributes to diversity in the region. One example is the presence of both *Crotalus molossus* and *Crotalus ornatus* within the Mogollon Highlands. Only recently recognized as a separate species, *C. ornatus* is only present in the far eastern portion of the Mogollon Highlands.

Third, the steep elevational gradient present within the Mogollon Highlands contributes to diversity. Species limited in

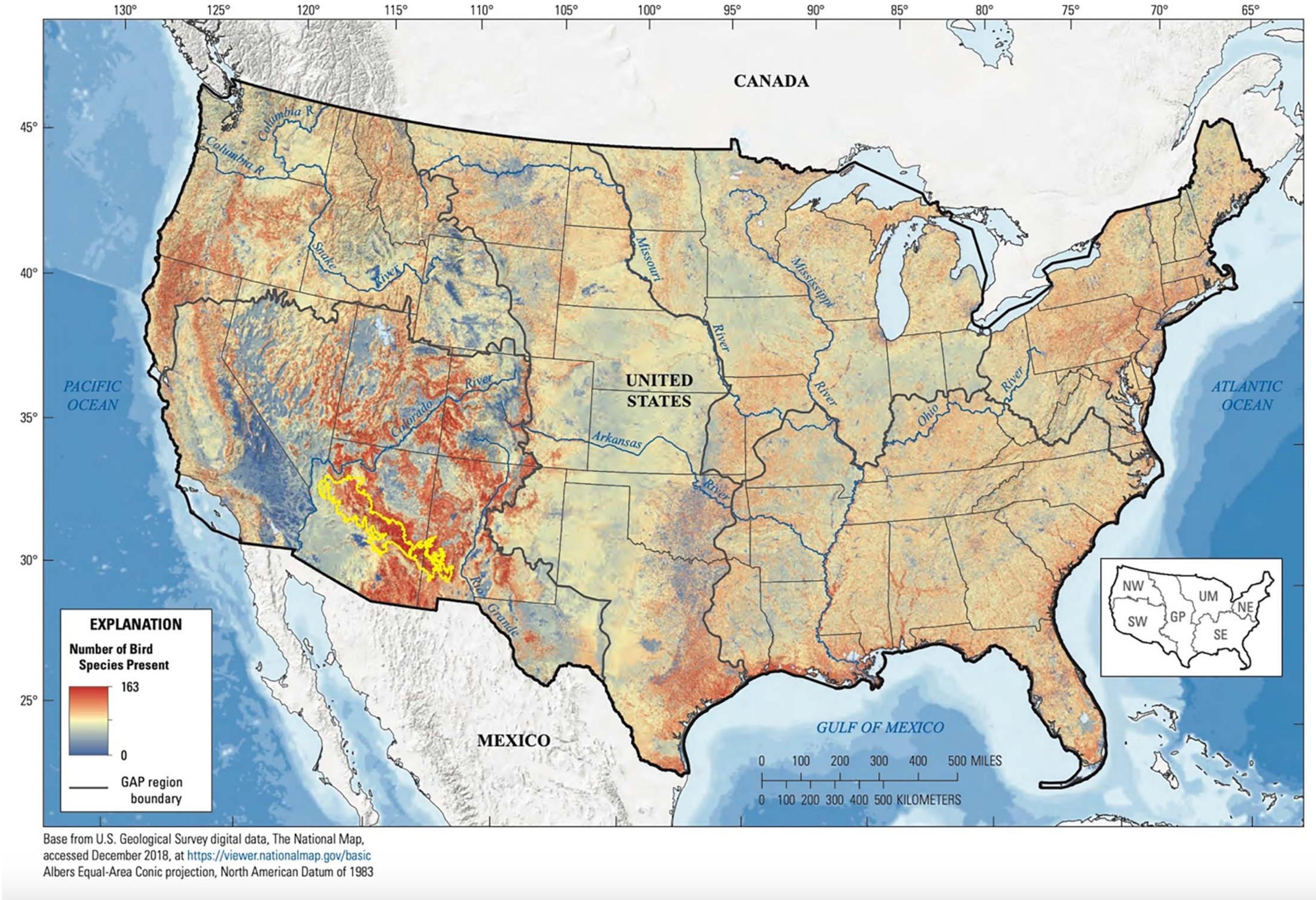

Figure 2.—Bird species richness in the coterminous United States, derived from species habitat distribution models (from Gergely et al. 2019: p. 14.). Mogollon Highlands Ecoregion outlined in yellow.

their elevational distribution can be found at the ends of this broad elevational gradient within the bounds of the Highlands. Examples among the snakes include *Phyllorhynchus decurtatus* (generally limited to low elevations) and *Lampropeltis pyromelana* (generally limited to relatively higher elevations).

Finally, the dissected nature of the highlands contributes to the diversity of the region. Large canyons carved by major rivers are lined by biotic communities associated with lower elevations, creating a unique mosaic of communities. These incursions of low-elevation habitat explain the presence of species like *Crotalus atrox* along the Salt River at a location very near the geographic center of the Mogollon Highlands.

We documented 39 species of snakes within the boundaries of the Mogollon Highlands. For comparison, Bezy and Cole (2014) documented 35 species of snakes in the Madrean Archipelago of southern Arizona and New Mexico. While their methods of constructing species lists differ from ours (their criteria being stricter in some senses), the Madrean Archipelago is often heralded for its herpetological diversity. These data support our prediction that the snake diversity of the Mogollon Highlands Ecoregion is on par with that of that of the Madrean Archipelago and, by extension, on par with, or higher than, many other regions (Bezy and Cole 2014; Holycross and Mitchell 2020).

Our findings on snake diversity supplement previous knowledge on biodiversity of other taxa. There are more species of butterflies (Lepidoptera: Rhopalocera) in the Central Arizona Highlands—essentially, the Arizona subset of the MHE—than in most American states (McNally 2020). Recent analysis (Gergely et al. 2019) shows that the highest bird habitat diversity in the coterminous United States is centered in the MHE (Figure 2). The MHE is also an area of great botanical importance due to elevated levels of endemism and genetic exchange between species, as exemplified by the rich diversity in the gymnosperms. Included in the MHE are gymnosperms that approach the limits of their geographic distributions, for example, *Juniperus deppeana*, alligator juniper (MHE is northern limit, with a few fingers reaching north of the Mogollon Rim) and *Pinus edulis* and *Juniperus osteosperma* (MHE is the southern limit).

An important group of gymnosperms of the Mogollon Highlands are the cembroid pines, including many of the piñon pine species. The most widespread piñon pine in the Mogollon Highlands, known variously as *Pinus edulis* var. *fallax* (Little

1968; Felger et al. 2019), *Pinus* × *fallax* (Buck et al. 2023), or *Pinus fallax* (elevated to species level by Montes et al. 2019, 2022), is tolerant of higher temperatures and lower moisture than other closely related piñon species. Here, we call this species the Mogollon Highlands piñon, *Pinus* × *fallax* (after Buck et al. 2023), to call attention to its narrow distribution and unique characters. Long known for its varying needle number (typically one needled with some two-needle fascicles), it was thought that the Mogollon Highlands piñon arose from hybridization of the more northern two-needled *Pinus edulis* and the Great Basin one-needled *P. monophylla* (e.g., Lanner 1974a, 1974b). However, recent genetic studies using nuclear DNA and chloroplast origin show that this piñon is a hybrid, sharing genes of *P. edulis* (Colorado piñon) and *P. californarium*, a one-needled species that occurs today well west, on California hillsides (Buck et al. 2023). Today it occupies hotter and drier habitats than either of its parents (i.e., 12 mm less rainfall and 2–4°C higher temperatures). It is a stable morphotype, shows less heterozygosity than might be expected of hybrids (Buck et al. 2023), and has been found in packrat middens from 48,000 y ago (Cole et al. 2013). As such, novel gene combinations in this piñon make it well adapted to the transitional shrub-rich habitats of the Mogollon Highlands through its ability to tolerate aridity and slightly higher temperatures than its parental genotypes. These novel gene combinations may well be reintroduced into the parent populations by backcrossing in the future, heightening the importance of this Mogollon Highlands hybrid. The resilience of this piñon pine can, in part, be attributed to its hybrid status; between 1985 and 2000, woodlands increased in extent in the Mogollon Highlands, and have declined only slightly since (0.3–0.8%), despite drought and low levels of beetle infestations (Rodman et al. 2022). In contrast, recent climate shifts have had more severe impacts on *Pinus ponderosa* (ponderosa pine) forests of the Mogollon Highlands, as warming and drying conditions approach the physiological limits for this species, which now occurs as "trailing edge" forests (Huffman et al. 2020). Landscape-scale analyses have shown climate and wildfire-related declines since 2000, favoring the oak components of the forest such that a shift is seen from pine forest to the more xeric pine-oak (Rodman et al. 2022).

The Mogollon Highlands Ecoregion, then, represents a center of ecological diversity significant on regional and continental scales. This is clearly exemplified by the data presented here on exceptional snake diversity, and by the unusual convergence of conifer species, including endemism and genetic recombination not observed elsewhere. Recognition of the ecological importance of this ecoregion is long overdue. We believe that—especially in an age of rapid climate change—the MHE should be valued and protected as a remarkable center of biodiversity, a home to taxa with a unique array of adaptations, and an area of great biological potential, with so much yet to be understood.

SUMMARY

- The MHE is a previously unrecognized center of ecological diversity, stemming from its location at a biogeographic crossroads, and great elevational and topographic variation, with climatic influences from mid-latitudes and subtropics.
- Due to the unusually comprehensive database for snake distributions in the MHE, we used this taxon to test our assertion that the biogeography of the MHE was highly diverse, with species from multiple sources. Snake diversity (39 species) in the MHE was on par with that of the Madrean Archipelago (Sky Islands region), which is known for high snake diversity.
- The MHE also represents an area of great botanical importance, due to its elevated levels of endemism and genetic exchange between species.
- Because of its high biodiversity and its capacity for climate change adaptation, the MHE should be considered high priority for conservation.

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Thomas L. Fleischner is Senior Advisor & Director Emeritus of the Natural History Institute, Faculty Emeritus at Prescott College, and a past Chair of the Natural History Section of the Ecological Society of America. His work has highlighted the need for a rejuvenation of natural history, in the natural sciences and in society at large. He is the author or editor of four books, most recently, Nature, Love, Medicine: Essays On Wildness and Wellness and The Way of Natural History.

M. Lisa Floyd (aka Lisa Floyd-Hanna) is a professor emeritus of environmental studies at Prescott College and a Research Affiliate at the Natural History Institute in Prescott, Arizona. She received a BS in Biology and an MS in Botany from University of Hawaiʻi, and a PhD in Evolutionary Ecology from the University of Colorado. For four decades she has conducted research on reproductive biology and ecological process, including fire history and dynamics, in Colorado and Arizona forests and woodlands.

Jessie Rack was, until recently, Program Director of the Natural History Institute, and is currently Assistant Teaching Professor of Biological Writing at Northern Arizona University. She earned a PhD in Ecology & Evolutionary Biology from the University of Connecticut, where her research investigated how aquatic salamander larvae differentiate between predators on the basis of chemical cues. She has also taught writing in the Princeton Writing Program and is an AAAS If/Then Ambassador, a prestigious national award that honors contributions from female scientists and enables them to serve as STEM role models for young women.

David Hanna is emeritus instructor of Environmental Studies at Prescott College and a Research Affiliate of the Natural History Institute in Prescott, Arizona. He received his BA in Natural History from Fort Lewis College and an MS from Antioch University. His research has applied GIS technology to numerous projects including vegetation mapping and fire histories in the southwestern United States.

Karen Blevins is an independent contractor in the Geospatial Technologies industry. She has worked in private industry as a GIS Analyst and was the Geospatial Technologies Program Director at Mesa Community College for over 17 years. Karen led the geodatabase and mapping component of Snakes of Arizona.

Bruce Christman is a Conservation Herpetologist working as a private consultant in collaboration with state, federal, and private entities involved in furthering conservation and recovery of T&E herp species in New Mexico.

Andrew T. Holycross is a professor at Mesa Community College, adjunct faculty in the Biodiversity Knowledge Integration Center at Arizona State University, and a Research Affiliate at the Natural History Institute in Prescott, Arizona. He is an editor of Snakes of Arizona *and an author of* A Field Guide to Amphibians and Reptiles in Arizona *(2nd edition).*

LITERATURE CITED

Allen, D.W. 2009. GIS Tutorial II: Spatial Analysis Workbook. ESRI Press, Redlands, CA.

Andermann, T., A. Antonelli, R.L. Barrett, and D. Silvestro. 2022. Estimating alpha, beta, and gamma diversity through deep learning. Frontiers in Plant Science 13. <https://doi.org/10.3389/fpls.2022.839407>

Barber, P.M., T.E. Martin, and K.G. Smith. 1998. Pair interactions in red-faced warblers. Condor 100:512–518.

Bezy, R.L., and C.J. Cole. 2014. Amphibians and reptiles of the Madrean Archipelago of Arizona and New Mexico. American Museum Novitates 3810:1–24.

Brown, D.E., ed. 1994. Biotic Communities: Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City.

Brown, D.E., R.D. Babb, and C.H. Lowe Jr. 2020. Biotic communities. Pp. 9–30 *in* A.T. Holycross and J.C. Mitchell, eds. Snakes of Arizona. ECO Publishing, Rodeo, NM.

Buck, R., D.O-D. Vecchyo, C. Gehring, R. Michelson, D. Flores-Rentería, B. Klein, A.V. Whipple, and L. Flores-Rentería. 2023. Sequential hybridization may have facilitated ecological transitions in the Southwestern pinyon pine syngameon. New Phytologist 237(6):2435–2449.

Cole, K.L., J.F. Fisher, K. Ironside, J.I. Mead, and P. Koehler. 2013. The biogeographic histories of *Pinus edulis* and *Pinus monophylla* over the last 50,000 years. Quaternary International 310:96–110.

Davis, S.D., V.H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A.C. Hamilton. 1997. Centres of plant diversity: A guide and strategy for their conservation. Vol. 3. The Americas. IUCN Publications Unit, Cambridge, UK.

DeBano, L.F., P.F. Ffolliott, A. Ortega-Rubio, G.J. Gottfried, R.H. Hamre, and C.B. Edminster, tech. coords. 1995. Biodiversity and management of the Madrean Archipelago: The sky islands of southwestern United States and northwestern Mexico. RM-GTR-264, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Dobbs, R.C., and T.E. Martin. 1998. Variation in foraging behavior among nesting stages of female red-faced warblers. Condor 100:741–745.

Ellenberg, D., and D. Mueller-Dombois. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York.

Felger, R.S., J.T. Verrier, K. Kindscher, and X.R.H. Khera. 2019. Field Guide to the Trees of the Gila Region of New Mexico. University of New Mexico Press, Albuquerque.

Felger, R.S., and M.F. Wilson. 1995. Northern Sierra Madre Occidental and its Apachian outliers: A neglected center of biodiversity. Pp. 36–51 *in* L.F. DeBano, P.F. Ffolliott, A. Ortega-Rubio, G.J. Gottfried, R.H. Hamre, and C.B. Edminster, tech. coords. Biodiversity and management of the Madrean Archipelago: The sky islands of southwestern United States and northwestern Mexico. RM-GTR-264, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Fleischner, T.L. 1999. Keeping the cows off: Conserving riparian areas in the American West. Pp. 64–65 *in* T.H. Ricketts, E. Dinerstein, D. M. Olson, C.J. Loucks, W. Eichbaum, D. Della-Sala, K. Kavanagh, P. Hedao, P.T. Hurley, K.M. Carney, et al., eds. Terrestrial Ecoregions of North America: A Conservation Assessment. World Wildlife Fund/Island Press, Washington, DC.

Fleischner, T., D. Hanna, and L. Floyd-Hanna. 2017. A preliminary description of the Mogollon Highlands ecoregion. Plant Press [Arizona Native Plant Society] 40(2):3–6.

Gergely, K.J., K.G. Boykin, A.J. McKerrow, M.J. Rubino, N.M. Tarr, and S.G. Williams. 2019. Gap Analysis Project (GAP) terrestrial vertebrate species richness maps for the conterminous U.S. U.S. Geological Survey Scientific Investigations Report 2019–5034. <https://doi.org/10.3133/sir20195034>

Griffith, G.E., J.M. Omernik, C.B. Johnson, and D.S. Turner. 2014. Ecoregions of Arizona (poster). USGS open file report 2014-1141. <https://doi.org/10.3133/ofr20141141>

Heller, N.E., and E.S. Zavaleta. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142:14–32.

Hibbitts, T.J., C.W. Painter, and A.T. Holycross. 2009. Ecology of a population of the narrow-headed garter snake (*Thamnophis rufipunctatus*) in New Mexico: Catastrophic decline of a river specialist. Southwestern Naturalist 54:461–467.

Holycross, A.T., K. Blevins, and K.L. Kabat. 2020a. Species distribution maps. Pp. 682–719 *in* A.T. Holycross and J.C. Mitchell, eds. Snakes of Arizona. ECO Publishing, Rodeo, NM.

Holycross, A.T., T.C. Brennan, and R.D. Babb. 2022. A Field Guide to Amphibians and Reptiles in Arizona. 2nd ed. Arizona Game and Fish Department, Phoenix.

Holycross, A.T., and J.C. Mitchell, eds. 2020. Snakes of Arizona. ECO Publishing, Rodeo, NM.

Holycross, A.T., E.N. Nowak, B.L. Christman, and R.D. Jennings. 2020b. *Thamnophis rufipunctatus* (Mogollon narrow-headed gartersnake). Pp. 440–455 *in* A.T. Holycross and J.C. Mitchell, eds. Snakes of Arizona. ECO Publishing, Rodeo, NM.

Huffman, D.W., M.L. Floyd, D.P. Hanna, J.E. Crouse, P.Z. Fulé, A.J.S. Meador, and J.D. Springer. 2020. Fire regimes and structural changes in oak-pine forests of the Mogollon Highlands ecoregion: Implications for ecological restoration. Forest Ecology and Management 465:118087.

Hulse, A.C. 1973. Herpetofauna of the Fort Apache Indian Reservation, east central Arizona. Journal of Herpetology 7:275–282.

Hunt, C.B. 1967. Physiography of the United States. W.H. Freeman, San Francisco, CA.

Hunter, M.L., Jr., G.L. Jacobson Jr., and T. Webb III. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. Conservation Biology 2:375–385.

Johnson, R.R., L.T. Haight, and J.M. Simpson. 1977. Endangered species vs. endangered habitats: A concept. Pp. 68–79 *in* R.R. Johnson and D.A. Jones, tech. coords. Importance, preservation, and management of riparian habitat: A symposium. RM-GTR-43, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Jones, K.B. 1988. Distribution and habitat associations of herpetofauna in Arizona: Comparisons by habitat type. Pp.109–128 *in* R.C. Szaro, K.E. Severson, and D.R. Patton, tech. coords. Management of Amphibians, Reptiles, and Small Mammals in North America. RM-GTR-166, USDA Forest Service, Fort Collins, CO.

Lanner, R.M. 1974a. Natural hybridization between *Pinus edulis* and *Pinus monophylla* in the American Southwest. Silvae Genetica 23:108–116.

Lanner, R.M. 1974b. A new pine from Baja California and the hybrid origin of *Pinus quadrifolia*. Southwestern Naturalist 19:75–95.

Lawler, J.J. 2009. Climate change adaptation strategies for resource management and conservation planning. Annals of the New York Academy of Science 1162:79–98.

Lawler, J.J., D.S. Rinnan, J.L. Michalak, J.C. Withey, C.R. Randels, and H.P. Possingham. 2020. Planning for climate change through additions to a national protected area network: Implications for cost and configuration. Philosophical Transactions of the Royal Society B 375:20190117.

Little, E.L. 1968. Two new pinyon varieties from Arizona. Phytologia 17:329–342.

Lowe, C.H. 1964. Arizona's Natural Environment: Landscapes and Habitats. University of Arizona Press, Tucson.

Marshall, R., M. List, and C. Enquist. 2006. Ecoregion-based conservation assessments of the southwestern United States and northwestern Mexico: A geodatabase for six ecoregions, including the Apache Highlands, Arizona-New Mexico mountains, Colorado Plateau, Mojave Desert, Sonoran Desert, and southern Rocky Mountains. Prepared by The Nature Conservancy, Tucson, AZ.

Martin, P.R., and T.E. Martin. 2001. Behavioral interactions between coexisting species: Song playback experiments with wood warblers. Ecology 82:207–218.

McLaughlin, B.C., S.A. Skikne, E. Beller, R.V. Blakey, R.L. Olliff-Yang, N. Morueta-Holme, N.E. Heller, B.J. Brown, and E.S. Zavaleta. 2022. Conservation strategies for the climate crisis: An update on three decades of biodiversity management recommendations from science. Biological Conservation 268:109497.

McLaughlin, S.P. 2008. Vascular flora. Pp. 120–140 *in* P.F. Ffolliott and O.K. Davis, eds. Natural Environments of Arizona: From Deserts to Mountains. University of Arizona Press, Tucson.

McNally, P. 2020. Butterflies of the Central Arizona Highlands. ECO Publishing, Rodeo, NM.

Mitchell, A. 2005. The ESRI Guide to GIS Analysis. Vol. 2. ESRI Press, Redlands, CA.

Montes, J.R., P. Peláez, A. Willyard, A. Moreno-Letelier, D. Piñero, and D.S. Gernandt. 2019. Phylogenetics of *Pinus* subsection *Cembroides* Engelm. (Pinaceae) inferred from low-copy nuclear gene sequences. Systematic Botany 44:501–518.

Montes, J.R., P. Peláez, A. Moreno-Letelier, and D.S. Gernandt. 2022. Coalescent-based species delimitation in North American pinyon pines using low-copy nuclear genes and plastomes. American Journal of Botany 109:706–726.

Morelli, T.L., C. Daly, S.Z. Dobrowski, D.M. Dulen, J.L. Ebersole, S.T. Jackson, J.D. Lundquist, C.I. Millar, S.P. Maher, W.B. Monahan, et al. 2016. Managing climate change refugia for climate adaptation. PLOS One 11(8):e0159909.

Nations, D., and E. Stump. 1996. Geology of Arizona. 2nd ed. Kendall/Hunt, Dubuque, IA.

Noss, R.F. 2001. Beyond Kyoto: Forest management in a time of rapid climate change. Conservation Biology 15:578–590.

Noss, R.F., and A. Cooperrider. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington, DC.

Noss, R.F., E.T. LaRoe III, and J.M. Scott. 1995. Endangered ecosystems: A preliminary assessment of loss and degradation. Biological Report 28, US Department of the Interior, National Biological Service, Washington, DC.

Nowak, E.M., and J.X. Schofer. 2006. Initial surveys to locate Arizona black rattlesnakes (Crotalus viridis cerberus) in Arizona national parks and monuments. Report to Western National Parks Association, US Geological Survey, Southwest Biological Science Center, Colorado Plateau Research Station, Flagstaff, AZ.

Nowak, E.M., M. Amarello, and J.J. Smith. 2020. *Crotalus cerberus* (Arizona black rattlesnake). Pp. 511–528 *in* A.T. Holycross and J.C. Mitchell, eds. Snakes of Arizona. ECO Publishing, Rodeo, NM.

Ohmart, R.D., and B.W. Anderson. 1982. North American desert riparian ecosystems. Pp. 433–479 *in* G.L. Bender, ed. Reference Handbook on the Deserts of North America. Greenwood Press, Westport, CT.

Peirce, H.W. 1985. Arizona's backbone: The Transition Zone: Fieldnotes [Arizona Bureau of Geology and Mineral Technology] 15(3):1–6.

Phillips, A.M., III, D.A. House, and B.G. Phillips. 1989. Expedition to the San Francisco Peaks: C. Hart Merriam and the Life Zone concept. Plateau 60:19–30.

Ranius, T., L.A. Widenfalk, M. Seedre, L. Lindman, A. Felton, A. Hämäläinen, A. Filyushkina, and E. Öckinger. 2023. Protected area designation and management in a world of climate change: A review of recommendations. Ambio 52:68–80.

Ricketts, T.H., E. Dinerstein, D.M. Olson, C.J. Loucks, W. Eichbaum, D.A. DellaSala, K. Kavanagh, P. Hedao, P. Hurley, K. Carney, et al. 1999. Terrestrial Ecoregions of North America: A Conservation Assessment. World Wildlife Fund/Island Press, Washington, DC.

Rodman, K.C., J.E. Crouse, J.J. Donager, D.W. Huffman, and A.J.S. Meador. 2022. Patterns and drivers of recent land cover change on two trailing-edge forest landscapes. Forest Ecology and Management 521:20449.

Rossman, D.A., N.B. Ford, and R.A. Seigel. 1996. The Garter Snakes: Evolution and Ecology. University of Oklahoma Press, Norman.

Saunders, S.P., J. Grand, B.L. Bateman, M. Meek, C.B. Wilsey, N. Forstenhaeusler, E. Graham, R. Warren, and J. Price. 2023. Integrating climate-change refugia into 30 by 30 conservation planning in North America. Frontiers in Ecology and the Environment 21:77–84.

Schall, J.J., and E.R. Pianka. 1978. Geographical trends in numbers of species. Science 201:679–686.

SEINet Portal Network. 2023. Accessed 28 Apr 2023 from <http//: swbiodiversity.org/seinet/index.php>.

Sellers, W.D. 2008. Climate. Pp. 26–39 *in* P.F. Ffolliott and O.K. Davis, eds. Natural Environments of Arizona: From Deserts to Mountains. University of Arizona Press, Tucson.

Sheppard, P.R., A.C. Comrie, G.D. Packin, K. Angersbach, and M.K. Hughes. 2002. The climate of the US Southwest. Climate Research 21:219–238.

Soulé, M.E. 1985. What is conservation biology? BioScience 35:727–734.

Stein, B.A., L.S. Kutner, and J.S. Adams. 2000. Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press, New York.

Stevens, L. 2018. Springs ecosystem ecology and stewardship: History and future. Springs Ecosystem Science: 2018 Symposium. Springs Stewardship Institute and the National Park Service, 4–6 June 2018, Flagstaff, AZ. Accessed 10 Aug 2023 from <https://docs.springstewardship.org/SpringsSymposium2018/Stevens_Keynote.pdf>.

Taylor, D.W. 2014. Large inequalities in herbarium specimen density in the western United States. Phytoneuron 53:1–8.

Trombulak, S.C., K.S. Omland, J.A. Robinson, J.J. Lusk, T.L. Fleischner, G. Brown, and M. Domroese. 2004. Principles of conservation biology: Recommended guidelines for conservation literacy from the Education Committee of the Society for Conservation Biology. Conservation Biology 18:1180–1190.

Turner, D., R. Marshall, C. Enquist, A. Gondor, D. Gori, E. Lopez, G. Luna, R. Paredes A., C. Watts, and S. Schwartz. 2005. Conservation priorities in the Apache Highlands Ecoregion. Pp. 375–379 *in* G.J. Gottfried, B.S. Gebow, L.G. Eskew, and C.B. Edminster, comps. Connecting mountain islands and desert seas: Biodiversity and management of the Madrean Archipelago II. RMRS-P-36, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

[USFWS] U.S. Fish and Wildlife Service. 2014. Endangered and threatened wildlife and plants; Threatened status for the northern Mexican gartersnake and narrow-headed gartersnake. Federal Register 79(130):38678–38746.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279–338.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

World Flora Online. 2022. Accessed 10 Dec 2022 from <http://www.worldfloraonline.org/>.

Appendix 1.—Characteristics of vegetation, topography, and elevation of ecological communities in the Mogollon Highlands Ecoregion.

Community	Elevation	Topography	Representative Species
Grasslands and Tablelands (6)			
Chino/Coconino Grasslands and Shrub-Steppe	1272–1909 m (4200–6300 ft)	Open valleys, flats, and low relief plateaus.	Vegetation is a mix of semi-desert grasslands, semi-desert shrub-steppe, and sagebrush shrublands that include grasses *Bouteloua gracilis* (blue grama), *B. eriopodia* (black grama), *Elymus elymoides* (bottlebrush squirreltail), *Heterostipa comata* (needle-and-thread), and *Ericoma hymenoides* (Indian ricegrass). Shrubs include *Atriplex canescens* (fourwing saltbush), *Krascheninnikovia lanata* (winterfat), *Artemisia bigelovii* (Bigelow sagebrush), and *Ephedra* spp. (Mormon tea).
Montane and Subalpine Grasslands	2273–2909 m (7500–9600 ft)	Mountain basins, valleys, and flat terrain.	This vegetation is characterized as grasslands, with patches of evergreen or deciduous forest, and occasional herbaceous wetlands. Grasses include *Festuca arizonica* (Arizona fescue), *Danthonia parryi* (Parry's oatgrass), *Muhlenbergia montana* (mountain muhly), *Blepharoneuron tricholepis* (pine dropseed), and occasionally *F. idahoensis* (Idaho fescue). Forests may have *Populus tremuloides* (quaking aspen), *Abies concolor* (white fir), *Pseudotsuga menziesii* (Douglas-fir), and *Pinus ponderosa* (ponderosa pine).
Northeast Arizona Shrub-Grasslands	1455–1894 m (4800–6250 ft)	Gently sloping to irregular and dissected plateaus, irregular plains and valleys, mesas, buttes, and badlands.	Vegetation is characterized by shrubs including *Atriplex confertifolia* (shadscale), *A. canescens* (fourwing saltbush), *Ephedra* spp. (Mormon tea), *Coleogyne ramosissima* (blackbrush), and grasses *Ericoma hymenoides* (Indian ricegrass), *Bouteloua eriopodia* (black grama), *B. gracilis* (blue grama), *Hilaria jamesii* (galleta), and *Sporobolus airoides* (alkali sacaton).
Madrean Basin Grasslands	1030–1713 m (3500–5653 ft)	This habitat includes the upper portions of level to rolling valley plains, sloping alluvial fans, and some low hills.	Vegetation is characterized by semi-desert grasslands with *Bouteloua eriopodia* (black grama), *Hilaria mutica* (tobosa), *B. curtipendula* (sideoats grama), *Scleropogon brevifolius* (burro grass), *Bothriochloa barbinodis* (cane beardgrass), *Erogrostis intermedia* (plains lovegrass), *B. hirsuta* (hairy grama) and *Muhlenbergia* spp. (muhly grasses), *Hilaria belganeri* (curly mesquite grass), and *Hopia obtusa* (vine mesquite grass). Interspersed shrubs or trees include *Prosopis* spp. (mesquite), *Isocoma tenuisecta* (burroweed), *Yucca* spp. (yucca), *Agave* sp. (agave), *Dasilyron wheeleri* (sotol), *Ephedra* spp. (Mormon tea), *Mimosa* spp. (mimosa), and *Fouquieria splendens* (ocotillo) and cacti as minor components of the grasslands.
Chihuahuan Desert Grasslands	954–2206 m (3500–7280 ft)	By definition, the Mogollon Highlands includes portions of this habitat above 3500 feet, where plateaus, high intermountain basins, alluvial fans, and bajadas occur.	At the low elevations, vegetation is characterized by *Bouteloua gracilis*, *B. grisea*, *B. curitpendula* (blue, black, and sideoats grama), *Sporobolus* sp. (dropseeds), and *Muhlenbergia porteri* (bush muhly), with scattered *Larrea tridentata* (creosotebush), *Acacia* sp. = *Vachellia*, *Senegalia* (acacias), *Nolina microcarpa* (beargrass), and species of cacti. In ancient lakebeds and alluvial areas, we find *Bouteloua.grisea* (black grama), *Hilaria mutica* (tobosa), and *Flourensia cernua* (tarbush). Scattered *Yucca* spp. (yuccas), *Agave lechuguilla* (lechuguilla), *Dasylirion wheeleri* (sotol), and *Juniperus* sp. (junipers).
Semi-arid Tablelands	515–2295 m (5000–7575 ft)	Mesas, plateaus, cliffs, canyons, and valleys.	This vegetation is a mix of shrub and grassland with *Sporobolus airoides* (alkali sacaton), *Atriplex confertifolia* (shadscale), *A. canescens* (fourwing saltbush), *Bouteloua eriopodia* (black grama), *B. gracilis* (blue grama), *B. curtipendula* (sideoats grama), *Ericoma hymenoides* (Indian ricegrass), *Hilaria jamesii* (galleta), *Pascopyron smithii* (western wheatgrass), *Ericameria nauseosus* (rubber rabbitbrush), and *Krascheninnikovia lanata* (winterfat). Some scattered *Juniperus* sp. (juniper) and piñon-juniper (*Pinus* sp.–*Juniperus* sp.) woodland.
Woodlands and Transitions (5)			
Hualapai/Coconino Woodlands	1272–2048 m (4200–6760 ft)	Plateaus, mesas, mountains, cliffs, and rolling uplands, with some narrow valleys and canyons.	Trees include *Juniperus osteosperma* (Utah juniper), *Pinus edulis* var. *edulis* (Colorado piñon), *and P.* × *fallax* (Mogollon Highlands piñon), all shrubs including *Purshia stansberiana* (Stansbury cliffrose), and grasses *Hilaria jamesii* (galleta), *Bouteloua gracilis* (blue grama), *B. curtipendula* (sideoats grama), *Pascopyron smithii* (western wheatgrass), *B. eriopodia* (black grama), *Hestperostipa comata* (needle-and-thread), *Elymus elymoides* (bottlebrush squirreltail), and *Poa fendleriana* (buttongrass). Shrubs include *Atriplex canescens* (fourwing saltbush), *Krascheninnikovia lanata* (winterfat), *Ephedra* sp. (Mormon tea), and *Quercus turbinella* (scrub oak).
Madrean Lower Montane Woodlands	1273–2121 m (4200–7000 ft)	A topographically diverse habitat of hills, low mountains, and deep canyons.	This woodland is unique in that it supports the Mogollon Highlands piñon *Pinus* × *fallax* as well as represents the southern edge of several juniper species (*Juniperus osteosperma* and *J. monosperma*) and the northern extent of alligator juniper (*J. deppeana)*. Numerous oaks occur here including *Quercus grisea* (gray oak), *Q. emoryii* (Emory oak), and *Q. gambelii* (Gambel oak). At some middle elevations, a chaparral community beneath the trees with shrubs such as *Ceanothus greggii (*desert ceanothus), *Cercocarpus montanus* (alderleaf mountain mahogany), *Q. turbinella* (scrub oak), *Arctostaphylos* sp. (manzanitas), and *Mimosa aculeaticarpa biuncifera* (catclaw mimosa). Other areas are open grasslands with mixed gramas and scattered oaks or junipers and, at the highest elevations, *Pinus ponderosa* (ponderosa pine) and *Quercus* sp. (oaks).

Appendix 1.—Continued.

Community	Elevation	Topography	Representative Species
Conifer Woodlands and Savannas	1515–2545 m (5000–8400 ft)	High plateaus, low mountains, and numerous canyons.	This vegetation is characterized by *Juniperus osteosperma* (Utah juniper), *J. monosperma* (one-seed juniper), *Pinus edulis* (piñon pine), *Purshia stansburyana* (Stansbury cliffrose), *Fallugia paradoxa* (Apache plume), *Atriplex canescens* (fourwing saltbush), *Ephedra torryana* (Mormon tea), and includes grasses *Stipa comata* (needle-and-thread), *Bouteloua curtipendula* (sideoats grama), *B. gracilis* (blue grama), *B. eriopoda* (black grama), *Koeleria macrantha* (Junegrass), *Hilaria jamesii* (galleta), *Elymus elymoides* (squirreltail), and *Poa fendleriana* (muttongrass). *Pinus ponderosa* (ponderosa pine), *Muhlenbergia montana* (mountain muhly), and *Festuca arizonica* (Arizona fescue) may occur at higher elevations.
Lower Madrean Woodland	1212–2416 m (4000–7975 ft)	Low- to mid-elevation mountain ridges, slopes, and hills.	This vegetation is characterized as Madrean encinal or evergreen oak woodlands and Madrean juniper-piñon woodland. *Quercus* species are well-represented, including *Quercus emoryi* (Emory oak), *Q. hypoleucoides* (silverleaf oak) and *Q. rugosa* (netleaf oak), and *Q. arizonica* (Arizona white oak), *Q. grisea* (gray oak), *Pinus* × *fallax* (Mogollon Highlands piñon), *Pinus discolor* (border piñon), and *P. cembroides* (Mexican piñon), *Juniperus deppeana* (alligator juniper), *J. monosperma* (one-seed juniper), *Arbutus arizonica* (Arizona madrone), *Robinia neomexicana* (New Mexico locust). Understory grasses of *Bouteloua gracilis* (blue grama), *B. curtipendula* (sideoats grama), *B. hirsuta* (hairy grama), *Schizachyrium scoparium* (little bluestem), and *Eragrostis intermedia* (plains lovegrass). Several species of cacti, including *Opuntia* spp. and *Agave* spp., are found here. Riparian vegetation is dominated by *Populus fremontii* (Fremont's cottonwood) and *Platanus wrightii* (Arizona sycamore). *Salix* spp. (willows) are well developed in this habitat.
Lower Mogollon Transition	909–1515 m (3500–5000 ft)	Hills and low mountains, deep canyons, and a few broader valleys.	This habitat supports desert scrub, semi-desert grasslands, and chaparral communities. Semi-desert grasslands include *Hilaria mutica* (tobosa), *Bouteloua eripodia* (black grama), and *Aristida* spp. (three awns), with a mix of scattered *Agave* spp. (agaves), *Yucca* spp. (yuccas), *Dasyliron wheeleri* (sotol), *Opuntia* spp., *Gutierrizea sarothrae* (broom snakeweed), and *Prosopis* spp. (mesquite). Chaparral areas include *Quercus turbinella* (scrub oak), *Cercocarpus montanus* (mountain mahogany), *Arctostaphylos* spp. (manzanita), *Eriogonum leptophyllum* (shrubby buckwheat), *Ceanothus greggii* (desert ceanothus), *Purshia tridentata* (cliffrose), deerbrush, *Rhus trilobata* (skunkbush), and *Garrya wrightii* (Wright's silktassel), with scattered desert shrubs. In open chaparral stands or after burns, grasses include native *Bouteloua* spp. (gramas) and the invasive grasses *Eragrostis intermedia* (plains lovegrass) and *Bromus rubrum* (red brome).
Forests (3)			
Arizona/New Mexico Subalpine Forests	2575–3828 m (8500–12633 ft)	High mountains with moderate to steep slopes.	This vegetation is characterized by *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (corkbark fir), *Picea pungens* (blue spruce), *Abies concolor* (white fir), and *Populus tremuloides* (quaking aspen), with some *Pseudotsuga menziesii* (Douglas-fir) at lower elevations. In the understory, *Juniperus communis* (dwarf juniper), *Symphoricarpos montanus* (snowberry), *Ribes cernuum* (wax currant), *Salix* spp. (willow), *Muhlenbergia montana* (mountain muhly), *Bromus carinatus* (mountain brome), and *Koeleria cristata* (Junegrass).
Montane Conifer Forests	1818–3261 m (6000–9784 ft)	High plateaus, open low mountains, and high mountains with steep slopes, numerous canyons.	Vegetation is characterized by *Pinus ponderosa* (ponderosa pine), *Juniperus scopulorum* (Rocky Mountain juniper), *J. monosperma* (one-seed juniper), or *J. osteosperma* (Utah juniper), with *Pseudotsuga menziesii* (Douglas-fir), *Pinus strobiformis* (southwestern white pine), *Abies concolor* (white fir), and *Populus tremuloides* (quaking aspen) at higher elevations. *Picea pungens* (blue spruce) can occur in cool moist canyons. Understories include *Quercus gambelii* (Gambel oak), *Artemisia tridentata* in the northern reaches, and *Cercocarpus montanus* (mountain mahogany), *Festuca arizonica* (Arizona fescue), *Bouteloua gracilis* (blue grama), *B. curtipendula* (sideoats grama), *Blepharoneuron tricholepis* (pine dropseed), *Muhlenbergia montana* (mountain muhly), *Koeleria macrantha* (Junegrass), and *Elymus elymoides* (bottlebrush squirreltail).
Mogollon Transition Conifer Forests	1636–2333 m (5400–7700 ft)	Plateau escarpments with steep slopes, high hills and low mountains, and some deep canyons.	This habitat contains woodlands and forests unique to the Mogollon Highlands bioregion. This shrub-rich forest type is characterized by a codominant mixture of trees and tall shrubs, the diverse shrub component distinguishing it from ponderosa pine forests of the Mogollon Rim area and north. Trees include *Pinus ponderosa* (ponderosa pine), scattered *P. chihuahuaensis* (Chihuahuan pine), *Juniperus deppeana* (alligator juniper), *Pinus* × *fallax* (Mogollon Highlands piñon), evergreen oaks such as *Quercus hypoleucoides* (silverleaf oak), *Q. rugosa* (netleaf oak), and *Q. emoryi* (Emory oak) in the southeastern areas, *Cercocarpus montanus* (mountain mahogany), *Ceanothus fendleri* (Fendler's ceanothus), *Arctostaphylos* sp. (manzanita), and *Garrya wrightii* (Wright's silktassel). Grasses include *Bouteloua gracilis* (blue grama), *B. curtipendula* (sideoats grama), and *Poa fendleriana* (muttongrass).

Appendix 1.—Continued.

Community	Elevation	Topography	Representative Species
High Deserts and Basins (6)			
Arizona Upland/ Eastern Sonoran Basins	454–1091 m (3500–3600 ft)	Flat to gently sloping basins and valleys, bajadas, alluvial fans, plains, eroded washes, stream terraces, and floodplains.	*Larrea tridentata* (creosotebush) and *Ambrosia dumosa* (white bursage) dominate. Upper bajadas have *Carnegia gigantea* (saguaro), *Parkinsonia microphylla* (foothills paloverde), *Olneya tesota* (desert ironwood), *Ambrosia deltoidea* (triangle-leaf bursage), *Fouquieria splendens* (ocotillo), *Prosopis glandulosa* (honey mesquite), *Acacia* sp. = *Vachellia*, *Senegalia* (acacias), *Opuntia* spp., and *Muhlenbergia porteri* (bush muhly). *Yucca brevifolia* (Joshua tree) occur northwest of Wickenburg.
Arizona Upland/ Eastern Sonoran Mountains	454–1363 m (3500–4500 ft)	Hills and low mountains that occur above our 3500 ft cutoff are included in the Mogollon Highlands.	The vegetation is characterized as desert scrub with *Carnegiea gigantea* (saguaro), *Parkinsonia microphylla* (foothills paloverde), *Larrea tridentata* (creosotebush), *Ambrosia deltoidea* (triangle-leaf bursage), *Lycium* spp. (wolfberry), *Muhlenbergia porteri* (bush muhly), *Aristida* spp. (three-awn grasses), *Opuntia* spp. (pricklypear), *Cylindropuntia fulgida* (jumping cholla), *Fouqueria splendens* (ocotillo), and *Sphaeralcea* spp. (globe mallows). *Olneya tesota* (desert ironwood) may occur at lower elevations.
Eastern Mojave Basins	485–1273 m (3500–4200 ft)	Flat to gently sloping basins and valleys with bajadas, alluvial fans, plains, eroded washes, stream terraces, and floodplains. A few isolated hills and buttes occur.	This vegetation is characterized by *Larrea tridentata* (creosotebush), *Ambrosia dumosa* (white bursage), *Opuntia* spp. (pricklypear) and *Cylindropuntia fulgida* (cholla), *Yucca* spp., *Ephendra viridis* (Mormon tea), and *Coleogyne ramosissima* (blackbrush). Grasses are sparse, with some *Hilaria rigida* (big galleta), *Muhlenbergia porteri* (bush muhly), and *Ericoma hymenoides* (Indian ricegrass). Some areas are nearly barren of vegetation. A few *Yucca brevifolia* (Joshua tree) at higher elevations. Riparian areas with *Salix* sp. (willows), *Prosopis glandulosa* (mesquite), and exotic *Tamarix chinensis* (tamarisk).
Eastern Mojave Low Ranges and Arid Footslopes	545–1653 m (3500–5456 ft)	Hills and low mountains, mesas, alluvial fans, and occasional lava flows make up this habitat, which extends well below the elevation cutoff for Mogollon Highlands.	Vegetation is characterized by scattered *Larrea tridentata* (creosotebush), *Ambrosia dumosa* (white bursage), *Yucca brevifolia* (Joshua tree), *Y. elata* (soaptree yucca) and other yucca species, *Coleogyne rammosisima* (blackbrush), *Krascheninnikovia lanata* (winterfat), *Ephedra viridis* (Mormon tea), *Mendora spinescens* (spiny menodora), *Hilaria rigida* (big galleta), *Ericoma hymenoides* (Indian ricegrass), and *Festuca annua* (annual fescue). On rocky sites cacti including *Cylindropuntia echinocarpa* (silver cholla) and *Opuntia basilaris* (beavertail). As in all deserts, annual species flourish from the seed bank when precipitation is abundant.
Low Mountains and Bajadas	900–1655 m (3500–5400 ft)	This habitat type occurs on the Gila River floodplain. The terrain is hilly.	Scattered *Juniperus* spp. on the upper elevations. *Platanus wrightii* (Arizona sycamore) and *Salix* species occur along waterways. In dry areas, *Dasylirion wheeleri* (sotol), Yucca spp., *Fouquieria splendens* (ocotillo), *Opuntia* spp. (pricklypear), *Prosopis glandulosa* (honey mesquite), *Acacia greggi* = *Senegalia greggi* (catclaw acacia), and scattered perennial grasses.
Chihuahuan Basins and Playas	787–1085 m (3500–3580 ft)	Deep depressions or grabens filled with sediment to form flat to rolling basins. Broad valleys with alluvial fans, dissected fan terraces, valley slopes, and the Gila River floodplain.	This vegetation is characterized by desert scrub with *Larrea tridentata* (creosotebush), *Flourensia cernua* (tarbush), *Atriplex canescens* (fourwing saltbush), scattered cacti, as well as scattered *Prosopis* sp. (mesquite) and *Vachellia* or *Acacia* sp. = *Vachellia*, *Senegalia* (acacias). Sparse, scattered grasses include *Bouteloua gracilis* (blue grama), *Muhlenbergia porteri* (bush muhly), *Sporobolis airoides* (alkali sacaton), *S. cryptandrus* (sand dropseed), and *Digitaria californica* (Arizona cottontop). Along the Gila River: *Populus fremontii* (Fremont's cottonwood), the stately *Platanus wrightii* (Arizona sycamore), and *Salix* spp. (willow), as well as patches of the invasive *Tamarix pentandra* (tamarisk).

Appendix 2.—Snake species (n = 39) found in the Mogollon Highlands Ecoregion, with community occurrences.

Family	Species	MHE Community Occurrence
Boidae	*Lichanura roseofusca*	Madrean Lower Montane Woodlands, Lower Mogollon Transition
Colubridae	*Arizona elegans*	Madrean Lower Montane Woodlands, Lower Mogollon Transition, Arizona Upland/Eastern Sonoran Basins
	Diadophus punctatus	Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Woodlands, Lower Mogollon Transition, Montane Conifer Forests, Mogollon Transition Conifer Forests, Low Mountains and Bajadas
	Gyalopion canum	Madrean Basin Grasslands, Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Mogollon Transition
	Hypsiglena chlorophaea	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Lower Montane Woodlands, Lower Mogollon Transition, Arizona Upland/Eastern Sonoran Basins
	Hypsiglena jani	Chihuahuan Basins and Playas, Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Montane Conifer Forests
	Lampropeltis californiae	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Basin Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Mogollon Transition
	Lampropeltis pyromelana	Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Transition, Montane Conifer Forests, Mogollon Transition Conifer Forests
	Lampropeltis splendida	Madrean Lower Montane Woodlands
	Lampropeltis triangulum	Chino/Coconino Grasslands and Shrub-Steppe
	Masticophis bilineatus	Madrean Basin Grasslands, Madrean Lower Montane Woodlands, Lower Mogollon Transition, Arizona Upland/Eastern Sonoran Mountains, Low Mountains and Bajadas
	Masticophis flagellum	Madrean Lower Montane Woodlands, Lower Mogollon Transition
	Masticophis taeniatus	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Basin Grasslands, Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Mogollon Transition, Montane Conifer Forests, Mogollon Transition Conifer Forests, Arizona Upland/Eastern Sonoran Basins
	Phyllorhynchus decurtatus	Lower Mogollon Transition
	Pituophis catenifer	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Basin Grasslands, Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Woodlands, Lower Mogollon Transition, Montane Conifer Forests, Mogollon Transition Conifer Forests, Arizona Upland/Eastern Sonoran Basins, Low Mountains and Bajadas
	Rhinocheilus lecontei	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Basin Grasslands, Conifer Woodlands and Savannas, Lower Mogollon Transition, Arizona Upland/Eastern Sonoran Basins
	Salvadora grahamiae	Madrean Basin Grasslands, Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Woodlands, Montane Conifer Forests, Mogollon Transition Conifer Forests
	Salvadora hexalepis	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Basin Grasslands, Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Mogollon Transition, Montane Conifer Forests, Arizona Upland/Eastern Sonoran Basins, Low Mountains and Bajadas
	Sonora semiannulata	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Basin Grasslands, Madrean Lower Montane Woodlands, Lower Mogollon Transition
	Tantilla hobartsmithi	Madrean Lower Montane Woodlands, Lower Madrean Woodlands, Lower Mogollon Transition
	Tantilla nigriceps	Madrean Lower Montane Woodlands
	Thamnophis cyrtopsis	Chino/Coconino Grasslands and Shrub-Steppe, Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Woodlands, Lower Mogollon Transition, Montane Conifer Forests, Mogollon Transition Conifer Forests, Arizona Upland/Eastern Sonoran Mountains
	Thamnophis elegans	Chino/Coconino Grasslands and Shrub-Steppe, Montane and Subalpine Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Woodlands, Lower Mogollon Transition, Arizona/New Mexico Subalpine Forests, Montane Conifer Forests, Mogollon Transition Conifer Forests
	Thamnophis eques	Madrean Basin Grasslands, Madrean Lower Montane Woodlands, Lower Mogollon Transition, Mogollon Transition Conifer Forests
	Thamnophis rufipuncatatus	Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Woodlands, Lower Mogollon Transition, Montane Conifer Forests, Mogollon Transition Conifer Forests
	Trimorphodon biscutatus	Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands
	Trimorphodon lambda	Madrean Basin Grasslands, Madrean Lower Montane Woodlands, Lower Mogollon Transition
Elapidae	*Micruroides euryxanthus*	Madrean Lower Montane Woodlands, Lower Madrean Woodlands, Lower Mogollon Transition, Montane Conifer Forests
Leptotyphlopidae	*Rena dissecta*	Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands
	Rena humilis	Madrean Lower Montane Woodlands, Lower Mogollon Transition
Viperidae	*Crotalus atrox*	Madrean Lower Montane Woodlands, Lower Madrean Woodlands, Lower Mogollon Transition, Arizona Upland/Eastern Sonoran Basins, Arizona Upland/Eastern Sonoran Mountains, Low Mountains and Bajadas
	Crotalus cerberus	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Basin Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Woodlands, Lower Mogollon Transition, Arizona/New Mexico Subalpine Forests, Montane Conifer Forests, Mogollon Transition Conifer Forests, Low Mountains and Bajadas
	Crotalus lepidus	Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Montane Conifer Forests

Appendix 2.—Continued.

Family	Species	MHE Community Occurrence
	Crotalus molossus	Madrean Basin Grasslands, Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Madrean Woodlands, Lower Mogollon Transition, Montane Conifer Forests, Mogollon Transition Conifer Forests
	Crotalus ornatus	Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Montane Conifer Forests
	Crotalus pyrrhus	Madrean Lower Montane Woodlands, Lower Mogollon Transition, Arizona Upland/Eastern Sonoran Basins, Arizona Upland/Eastern Sonoran Mountains
	Crotalus scutulatus	Chino/Coconino Grasslands and Shrub-Steppe, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas, Lower Mogollon Transition, Low Mountains and Bajadas
	Crotalus tigris	Lower Mogollon Transition
	Crotalus viridis	Chihuahuan Desert Grasslands, Madrean Lower Montane Woodlands, Conifer Woodlands and Savannas
	Sistrurus tergeminus	Madrean Basin Grasslands