Preliminary Survey of Bee (Hymenoptera: Anthophila) Richness in the Northwestern Chihuahuan Desert

Robert L. Minckley
Department of Biology, University of Rochester, Rochester, New York

John S. Ascher
Department of Entomology, American Museum of Natural History, New York, New York

Abstract—*Museum records indicate that the peak number of bee species occurs around the Mediterranean Sea and in the warm desert areas of North America, whereas flowering plants are most diverse in the tropics. We examine this biogeographic pattern for the bee species known from a limited area of northeastern Chihuahuan Desert, Mexico/United States. This topographically complex area has been studied for more than 50 years for bees, which allows us to compare faunas in nearby areas that vary from low elevation desert scrub to high elevation montane forest. Our analysis indicates that bee diversity in this area is unusually high, and also that there is a poorly documented unique montane fauna.*

Introduction

Bees (Hymenoptera, Anthophila) are a group of ca. 20,000 species worldwide (Ascher and Pickering 2012; Michener 2007), and the predominant pollinators in most terrestrial ecosystems. Yet, paradoxically, given their reliance on flowering plants, the literature and museum records suggest that bee species richness peaks in xeric, Mediterranean-climate areas far from the wet tropical areas where most groups, including flowering plants, reach their highest known species richness. Worldwide diversity of bee species is thought to be highest in xeric warm-temperate areas of the Western Hemisphere and around the eastern Mediterranean Sea in the Eastern Hemisphere (Grace, 2010), and to decrease in mesic environments and towards the tropics (Michener 1979, 2007). Local bee faunas in North America can be extremely diverse but appear to be particularly so in deserts of the southwestern United States and northwest Mexico (Ayala and others 1993; Michener 1979 table 1; Moldenke 1976). Of the roughly 3500 described bee species in North America north of Mexico, about 75% occur in the topographically diverse western United States. The most diverse bee faunas are reported for seasonally dry areas, including chaparral (and adjacent vegetation types) in Riverside California (439 species, Timberlake *in* Linsley 1958), sparse Sonoran Desert scrub in and around Palm Springs, California (more than 500 species, Timberlake, in Michener 1979), chaparral and other habitats in the inner Coast Ranges of central California (393 species, Messinger & Griswold 2002) and Great Basin Desert in Utah (334 species, Griswold and others 1997). The bee fauna in lowland subtropical deciduous forest in Chamela, Jalisco in western Mexico has intermediate diversity (228 species, Ayala 1988). In contrast, numbers of bee species reported from mesic areas of eastern and central United States are 64 species in Miami, Florida (Graenicher 1930), 103 in Hattiesburg, Mississippi (Michener 1947), 169 in the Chicago, Illinois, area (Pearson 1933), 297 in Carlinville, Illinois (Robertson 1929), and 552 in the large and topographically extreme Boulder County, Colorado (Scott and others 2011).

Although the bee studies listed above suggest that there is high bee diversity in the xeric areas of western North America, these studies differ tremendously in the area sampled and duration over which collections were made. Large or topographically complex areas can have increased species richness due to greater numbers of habitats, greater area, or both (Rosenzweig 1995). Sampling that is limited temporally, for example from one part of the activity season or from only a few years, can greatly underestimate local bee diversity (Williams and others 2001). The purpose of this study is to examine known bee species richness for an unusually well-sampled area of the northwestern Chihuahuan Desert. This is a region of North America where bee diversity has been thought to be unusually high. One set of specimen records is associated with activity associated with the Southwestern Research Station of the American Museum of Natural History (AMNH). Numerous researchers, including J. G. Rozen, Jr. and others based at this station have collected and studied bees most years since the station was founded in 1955. For the past 13 years, massive collections from individuals based there have been made in association with the Bee Course on bee identification and biology that has been held at the Southwestern Research Station. A second set of specimens is from an ecological study of bee diversity that has been underway since 2000 south of the Southwestern Research Station along the United States-Mexico border in the San Bernardino Valley (Minckley 2008). Collections in this area were started initially to estimate bee species richness in this area using standardized methods, but have broadened in association with other projects (Minckley and Roulston 2006).

Lists of bee species from the two efforts described above are still increasing as additional species are collected and identified (or recognized as new). Despite the preliminary status of the data, a compilation

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Table 1—Number of bee species, number (and proportion) of species and collection phenology recorded from six Chihuahuan Desert localities. Also shown is the year each locality was first sampled and the numbers of years and days bees were made.

	Number species	Number and proportion unique species	First year sampled	Total years sampled	Total days sampled
San Bernardino Valley	435	223 (0.51)	2000	11	516
Douglas	141	3 (0.02)	1943	41	116
Apache to Rodeo	144	12 (0.08)	1956	39	111
Willcox	155	15 (0.09)	1952	46	150
Apache southwest	129	6 (0.05)	1956	37	134
Upper montane	104	15 (0.14)	1950	43	116

of records assembled to date is useful because sampling from the region is now unusually large in scope (duration and intensity) and very large numbers of specimens have been identified to species and databased. Furthermore, many bee species reach the extreme limits of their distribution in this area (Burquez 1997; Minckley and Reyes 1996). Here we compile and compare lists of known species from six well-sampled localities to gain some insight into (1) the number of species in this area, (2) the differences in the faunas in desert, mid elevation and upper montane areas, and (3) the future work needed for a fuller understanding of bee species richness in this region and its implications for assessing larger-scale patterns.

Methods

A total of 65,485 bee specimens were included in this study; all from Cochise County in southeastern Arizona, United States and extreme northeastern Sonora, Mexico. We limited the species included to specimens from six localities (five in Cochise County well represented in the AMNH database and the San Bernardino Valley that have been unusually well-sampled. Thus, other bee species known from this area (i.e. Cochise County, Arizona, and adjacent northernmost Mexico) are not considered in this study because they either do not occur or have yet to be recorded from these localities. These localities demarcate an area approximately 5700 km^2 that is topographically complex, ranging in elevation from 1100 to 2895 m. Vegetation is mainly Chihuahuan Desert scrub at the lowest elevations and shifts through desert grassland, oak woodland, pine-oak, and coniferous forest at progressively higher elevations (Brown 1994). Collections were also made at unusual, more localized habitats including limestone outcrops in the San Bernardino Valley and sand dunes near Willcox, Arizona.

For brevity, hereafter we refer to those specimen records that are being assembled as part of a larger collaborative effort to document information from specimens housed in a number of North American museums as the AMNH specimens or database (see acknowledgements)

Localities

Following is a brief description of each of the six localities.

San Bernardino Valley, Arizona/Sonora (31° 20' N, 109° 15' W, 1134m)—This is the headwaters of the Rio Yaqui in southeastern Arizona, United States that runs south across the Mexico-United States border into northeastern Sonora, Mexico (31° 20' N, 109° 15' W). Most collections in the United States were made in the San Bernardino National Wildlife Refuge, a 900-hectare preserve in southeastern Cochise County, Arizona. In Mexico, most collections were made at Rancho San Bernardino, 30 km east of Agua Prieta, Municipio of Agua Prieta, Sonora, Mexico. Elevation ranges from 1100 to 1340 m. Minckley (2008) provides a detailed description of the climate and area. Vegetation is a mix of creosote bush (*Larrea tridentata* (Sessé & Moc. ex DC.), Coville and velvet mesquite (*Prosopis velutina* Wooton) dominated Chihuahuan Desert scrub in the lowest elevations, and Chihuahuan Desert grasslands (*sensu* Brown 1994) at the higher elevations (see also Minckley, *Trajectory and Rate of Desert Vegetation Response Following Cattle Removal*, this volume).

Unlike all other localities, the San Bernardino Valley study extensively used pan traps in addition to net sampling, the method used to obtain the vast majority of collections at other localities.

Douglas, Cochise County, Arizona (31° 21' N, 109° 27' W, 1220m)—Most collections in this area are from "1 mile east of Douglas" at 1300 m elevation. Specimens with label data from within 6 km of Douglas in any direction were included in this study because vegetation in this area is desert scrub similar to that described above for the lower elevations of the San Bernardino Valley. Although only 25 km due west of the San Bernardino Valley, this area is in the Sulfur Springs Valley and separated from the San Bernardino Valley by the southern end of the Pedregosa Mountains.

Cazier and Linsley (1963) provide a description of the site "1 mile east of Douglas" and the late-summer vegetation. Since that description, some of this area has been developed. Collections span from 1943 to the present.

Apache, Cochise County, Arizona (31° 41' N, 109° 08' W, 1336 m)—Collections included in the area are along Highway 80 that runs along the north-flowing San Simon River in the San Simon Valley. Specimens were included if label data indicated they were between 2 km south of Apache to 2 km south of Rodeo, Hidalgo County, New Mexico (23 km in total). This area is primarily desert scrub similar to that described for the lower elevations of the San Bernardino Valley (see above). Apache, Arizona, is 60 km north of the San Bernardino Valley. They are separated by grasslands on the San Bernardino volcanic field.

This locality along Highway 80 is a primary corridor between the Southwestern Research Station and Douglas, the nearest city, and numerous biological studies of bees describe this area (Danforth 1989, 1991, 1999; Hurdand and Linsley 1975; Hurd, LaBerge and Linsley 1980. Collections span 1956-2011.

Willcox, Cochise County, Arizona (32° 11' N, 109° 44' W, 1290 m)—This area is along the northeast boundary of the Willcox playa, a closed basin (i.e. lacking external drainage) and remnant of the Pluvial Lake Cochise that had been a much larger and deeper lake at its maximum

13,750-13,400 yr B.P (Waters 1989). The area has typical vegetation of the desert scrub community in addition to other, less common plant species associated with the sand dunes (*Oenothera* spp., *Psorothamnus scoparius* (A. Gray) Rydb., *Euphorbia* spp., *Nama demissum* A. Gray, and *Wislizenia refracta* Engelm.), and many notable bees (Rozen 1987, 1992; Rozen and Rozen 1986).

The most common locality on labels from this area references "4 mi east of Willcox." For the species list included here we also included sites in the vicinity of Willcox that are bounded by Interstate 10 on the north and by the Willcox Playa on the south. This locality is the furthest north of any other in this study. It is ca. 110 km NNW of the San Bernardino Valley on the opposite side of the Chiricahua Mountains.

Southwest of Apache, Cochise County, Arizona: (31° 34' N, 109° 15' W, 1400m)—This locality is also along Hwy 80 and was included because it is the best-collected area in the Chihuahuan Desert grassland (i.e. at lower elevations than oak and pine woodland) and because it has a rich and distinctive fauna (Rozen 1989, 1992). Most labels refer to "[13, 13.5, or] 14 miles southwest of Apache," a roadside site along a railway line among cinder cones. It is just north of a riparian area along Silver Creek, a stream that drains a large area of the southern Chiricahua Mountains. Higher water availability and cold air drainage in habitats such as these enables some plant species to occur at lower elevations than they do normally (Shreve 1922), which may influence where bees occur.

Upper Chiricahua Mountains, Cochise County, Arizona (31° 51' N, 109° 17' W, 2700m)—Several roads climb to the oak-pine and pine forest found on the upper elevations of the Chiricahua Mountains. We included any bee species in this mountain range that had been collected over 1580 m, where oak, oak-pine, or coniferous are the dominant vegetation type. By using this elevation as a cutoff we excluded a very large set of specimens collected at the Southwestern Research Station where disturbance associated with building construction has created an unusually open and more xeric habitat allowing bees typical of desert scrub to occur above their usual range.

Bee Species Lists

Lists were limited to specimens that were identified to genus and species. This excluded a number of species from the San Bernardino Valley study that are now designated as morphospecies.

A complete list of the bee species at each of the six localities will be published in the journal Checklist (www.checklist.org.br/) and made available as a Research Species list in Madrean Archipelago Biodiversity Assessment (MABA)/Southwest Environmental Information Network (SEINet) online database (Madrean.org). All specimens records in the AMNH Bee Database and associated databases are available at Discover Life (Schuh and others 2010).

We compared the similarities of bee species lists rather than using statistical approaches based on incidence that species were collected or species abundance (Gotelli and Colwell 2001) because of the differences in how species lists were assembled at the AMNH and in the San Bernardino Valley study. Records of species from five sites (Douglas, Willcox, Apache-Rodeo, 14 miles southwest of Apache, and Upper Chiricahua Mountains) represented in the AMNH database is ongoing and does not presently include comprehensive records of all individuals of each species, or the number of times they were collected at each site. Also, retrospective data capture from information on specimen labels is from identified material, mostly housed in the AMNH and is in progress. In contrast, all material from every collection made in the San Bernardino Valley is recorded in a database but species-level identifications of some specimens remain to be verified.

Results

Localities

The number of bee species at the six localities differed from 435 in the San Bernardino Valley to 104 species in the high elevations of the Chiricahua Mountains (table 1, fig. 1). The five localities in the AMNH database have much closer numbers of species among themselves than any have to the San Bernardino Valley.

Approximately 55% of all species (300 of 540 species), were recorded at one locality and very few were extremely widespread (fig. 2), consistent with high bee richness in our study area. The proportion of unique bee species reported only from the San Bernardino Valley (52%) was far greater than found in the other localities (fig. 1). In

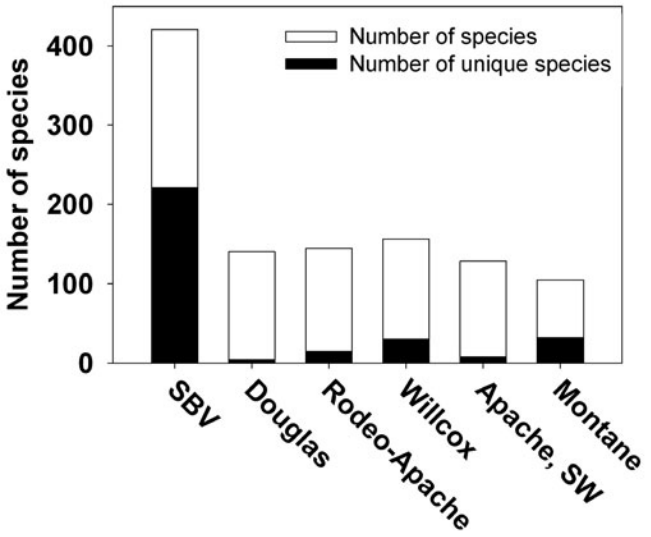

Figure 1—Bee species recorded from six localities in the northwestern Chihuahuan Desert. Locality designations used here are the same as in the text except for SBV = San Bernardino Valley. Numbers of species that are found only at the locality are indicated on the bar in black.

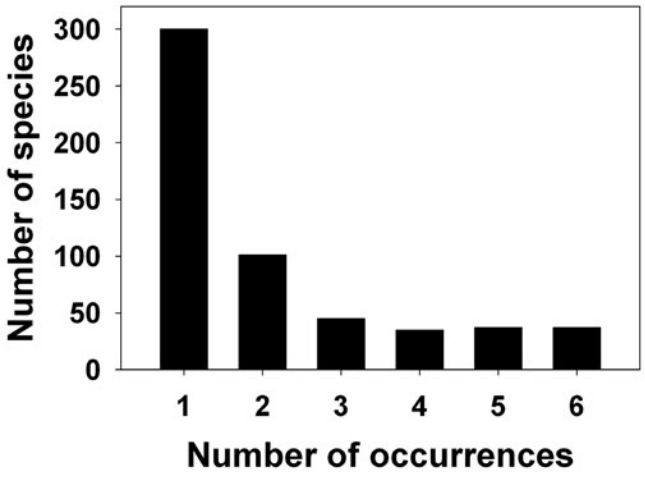

Figure 2—Number of localities where bee species were recorded. Most species occur at one locality and very few are extremely widespread.

descending order, the proportion of unique species at the other localities were montane (30%, 32 of 105 species); Willcox (19%, 30 of 156 species); between Rodeo, New Mexico, and Apache, Arizona, on Highway 80 (8%, 15 of 144 species); southwest of Apache, Arizona (6%, 8 of 128 species); and Douglas, Arizona (3%, 4 of 120 species).

Vegetation Associations

The three major vegetation types represented in the localities were desert scrub, oak-grassland, and oak pine or coniferous forest. By far, most bee species were found in one vegetation type (N = 386), none were reported from two, and few were found in all three (N = 44).

The number of unique species recorded from the desert scrub localities was far greater (N = 390) than reported from grassland (N = 34) or upper montane (N = 57) (fig. 3). However, the proportion of unique species was high and similar in the desert (78%) and the upper montane (72%) habitats, and was intermediate in the transition zone of Chihuahuan grassland and oak (41%).

Collecting Effort

Collections in the San Bernardino Valley span the fewest years of any locality but amount to four to five times more collection days than at other localities (table 1). The other five localities range from 111 to 150 collection days (table 1). The proportion of all collections represented by the AMNH specimens included in this study and the San Bernardino Valley are shown in figure 4. AMNH collections are biased towards August (particularly mid-late August), when the Bee Course is offered (see Introduction) and fewer collections are in early summer and spring. In contrast, San Bernardino Valley collections were made in most months, except for a deficit towards the end of the bee activity season (late September and October).

Discussion

In total, 540 species are represented in this study. In the western United States, a four-year study reported 656 bee species and morphospecies in Grand Staircase National Monument, Utah (Griswold and others 1997). The Utah study included collections made throughout the monument. The similar number of bee species in that study to just six localities included here from the northeastern Chihuahuan Desert hints at high bee diversity. The San Bernardino Valley, where the greatest number of bee species was recorded from the six localities, was where the most collections were made across a wider date range and where pan traps were used extensively in addition to nets. Pan traps are known to sample a different portion of the bee fauna than other methods (Droege and others 2009; Rouston and others 2007). Thus, more data are needed to establish if the bee diversity in the San Bernardino Valley is unusual or collecting bias.

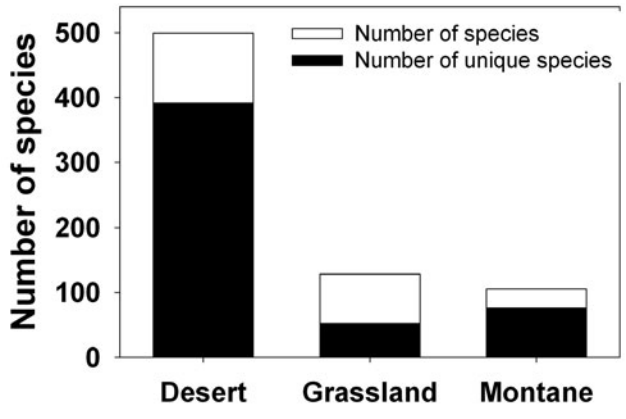

Figure 3—Bee species recorded from three primary vegetation habitats in the northwestern Chihuahuan Desert. Locality designations used here are the same as in the text except for Montane = Upper Montane. Numbers of unique species (recorded from one locality) are indicated on the bar in black.

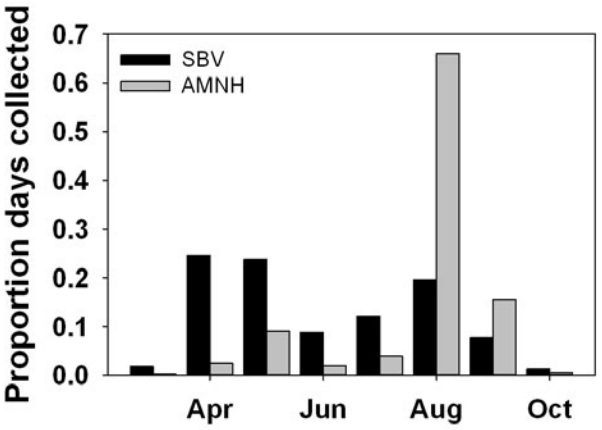

Figure 4—The phenology of collections made at San Bernardino Valley (SBV) and the other five localities (AMNH specimens) expressed as a proportion. Of note, is the difference in collection effort in March and April.

Few bee species are widespread and many are localized (N = 44 in three vegetation types, none in two, and 386 in one). The variation in species number among localities reflects both statistical issues with these data and underlying biological pattern. Statistical biases arise from the way the species lists are being assembled at the AMNH. First, database information on AMNH specimens is ongoing making statistical estimates of species richness or species turnover not possible. Second, some differences can be attributed to where taxonomic expertise of specific bee groups has been focused. *Triepeolus*, *Lasioglossum* (*Dialictus*), and *Osmia* have been curated more thoroughly from the San Bernardino Valley than in the AMNH specimens whereas *Andrena*, *Pseudopanurgus*, and *Protandrenini* were more thoroughly curated at the AMNH than those same taxa from the San Bernardino Valley. Finally, biases in the timing of collections also confound these types of analyses. The proportion of spring collections is far greater in the San Bernardino Valley than in collections made at the other localities (fig. 4). Most bee species in the warm deserts of North America have short flight seasons and are solitary, particularly those oligolectic species that visit one or a few host plants for pollen. Approximately 35% of pollen-collecting bee species (excluding *cleptoparasitic* species) are oligolectic (Minckley 2008). In solitary bee faunas, the effect of sampling effort should be pronounced, as will be the presence of host plants required by those species that are oligolectic. Many of the spring-active bee species found in the San Bernardino Valley samples are not represented in the AMNH database.

There are many biological reasons why bee species composition differed among sites. First, rarity in desert bees is pervasive; collections

that differ in distance and time have all found the proportion of rare (i.e. rarely-detected) species in deserts is high (Minckley and others 1994; Williams and others 2001). Second, in some cases, rare bees or those with limited local distributions only occur where their host plant is found. Two pollen specialist bee species, *Calliopsis macswaini* (Rozen 1958) and *Perdita wislizeniae* (Timberlake 1964), were found only at the locality their host plant, *Wislenzia refracta*, occurs in the sand dunes near Willcox, and the former is absent from recent samples. The extremely rare bee, *Macrotera parkeri* (Timberlake 1980), is a cactus specialist species known previously only from Austin, Texas, (two individuals) and Puebla, Mexico (one specimen) (Danforth 1996). In the San Bernardino Valley it visits the cactus, *Coryphantha robbisorum* (W. Earle) A.D. Zimmerman, a limestone soil endemic. Finally, beta-diversity is expected to be exceptional given that this study is focused at an intersection of major North American biomes where many bee species reach their range limits (Minckley and Reyes 1996). Two notable examples of species in this dataset at the northernmost point of collection are *Eulonchopria punctatissima* Michener, the northernmost-occurring species of Neopasiphaeinae (formerly included in Paracolletinae or Colletinae sensu lato) that visits species of *Acacia* with white flowers (*Acacia angustissima* (Mill.) Kuntze and *A. millefolia* S. Watson) and was found in the past but not in recent years along Highway 80 in Cochise County, and what is likely to be a transient individual of *Agapostemon nasutus* Smith, 1853, a widespread Neotropical species known in the San Bernardino Valley from only a single female (Mexico: Sonora, 30 km E. Agua Prieta, 29 May 2007, on *Sphaeralcea angustifolia*, RL Minckley [coll.]).

Identifying why most bee species in this study are geographically limited or rare is not easily explained. Many species are similar to the pollen specialist bee *Lasioglossum lusorium* (Cresson 1872) that has been recorded in this study only near Willcox, Arizona, but has a much broader distribution (southern Canada, California, central Mexico Kansas) (McGinley 2003).

The most notable findings of this preliminary study are the low species overlap in the desert and upper montane habitats in this limited area, and the high proportion of unique bee species found in these same habitats. The Sky Island region above 2300 m elevation are the northernmost known localities for the Neotropical genus (*Mexalictus*) (Eickwort 1978), known in the Chiricahua Mountains only from a recent collection by JSA (new information) and the southernmost known localities of two species with Holarctic affinities; *Lasioglossum boreale* (Svensson and others 1977) and *L. dasiphorae* (Cockerell 1907) (Packer and Taylor 1997). In Mexico, in the northern Sierra Madre Occidental at Yécora, one specimen of a stingless bee (*Partamona bilineata*) (Say 1837) was collected in pine-oak forest, which represents the most northern record of the tribe Meliponini in North America (Minckley and Reyes 1996). Ten tropical bee species have been rarely collected from this area and all but one of these occurred in oak woodlands or pine-oak forests of Sky Islands along the Arizona-Mexico border (Minckley and Reyes 1996). Recent collections from the oak woodland in the Sierra San Luis, just 3 km south of the United States-Mexico border (31° 17' N, 108° 47' W), have yielded two new species of spring-active species of *Osmia* (Rightmyer and Griswold 2010). A new species of *Lasioglossum* (*L. viridipetrellum* Gibbs 2009) is known only from Sky Islands above 2200 m in southeast Arizona (Gibbs 2009), as is an undescribed species allied to *L. (D.) ruidosense* (J. Gibbs, pers. comm.). These recent descriptions, in addition to the study reported here, suggest there is greater bee endemism in the upper montane habitats of these areas than has been appreciated. Given the distinctiveness of this bee fauna, the predicted increasing frequency of fires (Westerling and others 2007), and effects of climate change (International Panel on Climate Change 2007) on these upper elevation habitats, further documentation and sustained monitoring of this bee fauna is of particular and pressing interest.

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