

# Extreme species density of bees (Apiformes, Hymenoptera) in the warm deserts of North America

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## Abstract

Despite the long intertwined evolutionary histories of bees and plants, bee diversity peaks in the xeric areas of the eastern and western hemispheres and not the tropics, where plant diversity is greatest. Intensive sampling in the northeast Chihuahuan Desert of Mexico and the United States provide the first quantitative estimate of bee species richness where high diversity had been predicted in North America from museum records. We find that the density of bee species in a limited area of 16 km<sup>2</sup> far exceeds any other site in the world and amounts to approximately 14% of the bee species described from the United States. Long-term studies of bees and other pollinators from areas that are minimally impacted by humans provide much-needed baseline data for studies of bees where human impacts are more severe and as climate change accelerates.

## Keywords

Anthophila, bee-plant interactions, Biodiversity, Chihuahuan Desert, pollen specialization

## Introduction

The keystone role of bees in ecosystems has led to greater appreciation and a deeper understanding of some previously understudied aspects of their biology. These include the contribution of non-managed bee species to crop pollination (Kremen et al. 2002;

Winfree et al. 2008; Garibaldi et al. 2013), ecological and life history variables that predict vulnerability to environmental change among species (Winfree et al. 2009; Williams et al. 2010), and the environmental conditions that favor increases in bee populations and their species richness (Cane et al. 2006; Williams et al. 2010; Ollerton et al. 2014). Studies that have compared historical records from museums to more recent samples have concluded that bees along with other pollinators are in decline due to human activity (Biesmeijer et al. 2006; Leubhn et al. 2012; Burkle et al. 2013; Ollerton et al. 2014; Bartomeus et al. 2018; Mathiasson and Rehan 2019). Comparisons of bee faunas at sites where land-use histories differ have reached similar conclusions (reviewed in Winfree et al. 2011: but see Winfree et al. 2007; Minckley 2014). However, with some notable recent exceptions (Herrera 2019; Meiners et al. 2019 and references therein), most of this recent work has not extended beyond one or several years and has been focused on faunas in or near human-disturbed habitats. Needed are more long-term studies from habitats that are little disturbed by humans to provide baseline data to appropriately gauge how bee dynamics are influenced where there is anthropogenic disturbance (Winfree 2010; Archer et al. 2014; De Palma et al. 2016). Herrera (2019) has gone further to emphasize that studies are needed particularly where diversity is highest.

This study was done to thoroughly document the number of bee species (=species richness) in a bee biodiversity hotspot and serves to address the concern of Herrera (2019) mentioned above. We use repeat sampling to estimate the total number of bee species (observed as well as those not captured) from a defined area so both the number of species (species richness, an area free estimate) and number of species from a known area (species density) can be compared to data from other studies that are focused on elucidating biogeographic patterns of bees. The amount of area sampled strongly predicts species richness in all groups (Rozenzweig 1995) and allows species density to be evaluated separately from species richness (Gotelli and Colwell 2001). Global patterns of species richness remain one of the central questions to evolutionary ecology (Colwell and Lees 2000; Lomolino et al. 2017) and anomalous diversity patterns sometimes provide unusual insights into the mechanisms that generate diversity (Kindlmann et al. 2012). Bees are a species-rich group ( $N = 20,000$  species) and have very different and counterintuitive biogeographic patterns from their hosts, the flowering plants. Using species lists and museum records, Michener (1979) showed that the warm desert areas of North America and xeric regions around the Mediterranean Sea of the eastern hemisphere were unusually rich in bee species. Why bee diversity does not follow the temperate to tropic increase in species richness of their floral hosts remains poorly understood (Orr et al. 2020). One hypothesis is the persistently wet soils of tropical regions favor fungi and other pathogens of bees that nest in the soil (Michener 1979). This is consistent with the observation that many bee groups that occur in the tropics have their nests above-ground in trees and broken stems where moisture is reduced (Michener 2007). Bee diversity in the tropics may also be depressed because many tropical groups are highly eusocial with colonies that can be large. If floral resources are limiting, at least sometimes, social bees may successfully outcompete solitary bees. Also possible is that some feature of the ecosystems where warm xeric

climates occur favor bee diversification. In parts of the Chihuahuan and Sonoran Deserts of North America, and around the Mediterranean Sea in the eastern hemisphere rainfall and temperature patterns result in separate spring and summer blooms. Where this occurs, bee activity is also biseasonal and many of these bee species are active in only one season. The temporally separated but geographically co-occurring bee fauna may allow more species to occur in one area than could coexist otherwise (Michener 1979; Minckley 2008). Finally, topographical complexity and biogeography may also contribute to global patterns of bee diversity. Where bee species richness peaks are also areas with ongoing mountain building and associated tectonics (Casas-Sainz and de Vicente 2009; González-León et al 2011) that have been shown to favor diversification in other groups (Rahbek et al. 2019), and are where biomes converge (Spector 2002). Although it is possible that one factor is responsible for most variation in bee diversity, it is more likely that some combination of the factors listed above underlie where and how many bees occur worldwide.

We examined the hypothesis that bee richness peaks in the warm deserts of North America using intensive, standardized methods in one area of the Chihuahuan Desert along the international border between the United States and Mexico. Where this study was done had been cattle ranchland since the early 1800's, but has not been grazed for the past 20 years in Mexico and the past 50 years in the United States (Minckley 2013). This region is a biogeographical crossroads where the subtropical dry forest, Great Plains, Chihuahuan and Sonoran Desert intersect (Brown 1994). The pollinator fauna is largely native and strongly dominated by bees. The honey bee, *Apis mellifera*, is the sole introduced bee species representing 3.5% of all bee captures. The vast majority of collections in this study were within an area of approximately 16 km<sup>2</sup> on the floor of the San Bernardino Valley. Repeat sampling using the same protocol allowed us to use abundance data to make a quantitative estimate of bee species density including species not captured. We then compared estimates of bee species density from this 1-year intensive sampling to nine years of collecting using sampling by several methods from this same area. Combining sampling methods that vary in effort and efficacy violates some assumptions of the models used to estimate the richness of observed plus unsampled species (Gotelli and Colwell 2001). However, that bee communities, particularly those in deserts, vary dramatically across all spatial and temporal scales (Minckley et al. 1999; Williams et al. 2001; Russo et al. 2015; Herrera 2019) and in response to sampling effort, protocol, and technique (Toler et al. 2005; Roulston et al. 2007; Westphal et al. 2008; Droege et al. 2010; Cane et al. 2013; Prendergast et al. 2020), suggests that multiple approaches will yield more bee species, and more accurate estimates of the number of species. For an unusually well-studied, species-rich community of ants in Costa Rica, Longino et al. (2002) showed that the actual species richness was greatly underestimated with datasets from single sampling protocols; and only by combining different datasets was it possible to obtain an accurate estimate. In this study, bee species density estimates based on repeat samples with one protocol is compared to estimates based on a larger dataset from the same area that combined sampling protocols from more sites over nine years.

Our prediction was that intensive sampling using one technique (pan traps) over one year would underestimate the observed species richness obtained over more years using multiple sampling techniques from the same area. However, we also predicted this intensive pan trapping would provide a reasonable estimate of species richness using statistical methods that extrapolate from species observed to include species not captured but present (Gotelli and Colwell 2001).

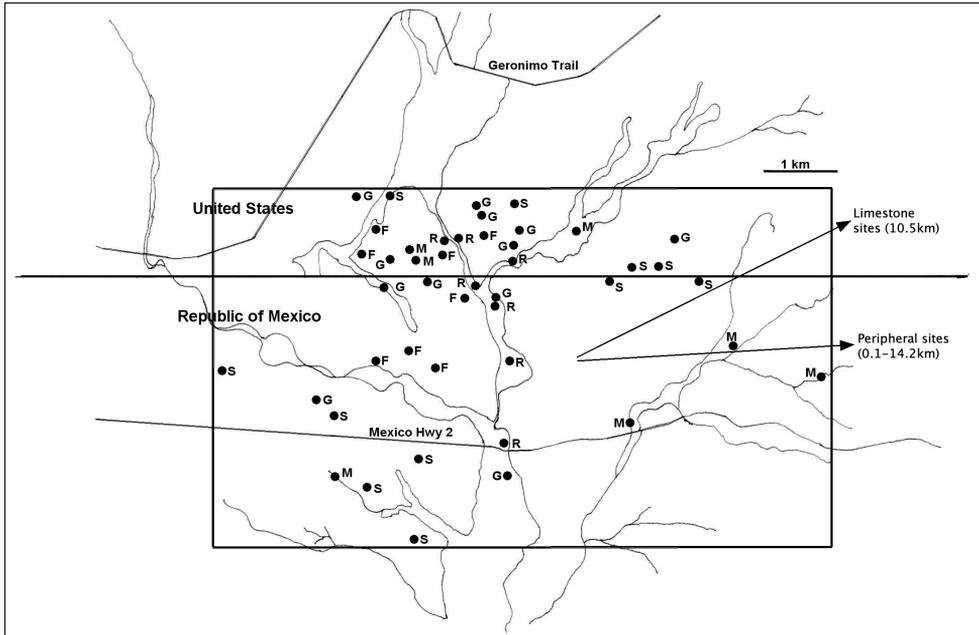
We also gauged how well our samples from the valley floor estimate the number of species in a broader area, by compiling a dataset from collections made in two nearby areas and making an assumption that this list of species from all collections combined was the best estimate for bee richness in this region. Extrapolation to the expected species richness from the multiyear samples made on the valley floor closely approximated the observed species richness of the larger regional dataset. In comparison to 21 other long-term studies of bees, the density of bee species in this part of the Chihuahuan Desert is greater than that reported from any other area.

## Methods

The study was done in the San Bernardino Valley in the northeastern Chihuahuan Desert of western North America near the confluence of Arizona and New Mexico, USA and Chihuahua and Sonora, Mexico. The San Bernardino Valley runs north-south across the Mexico-United States border in northeastern Sonora, Mexico and southeastern Arizona, USA. Elevation is approximately 1070 m and climate is xeric temperate with an annual average precipitation of 360 mm/ year. Approximately 50% of the annual precipitation occurs in July and August and the two driest months are April and May based on long-term weather records 30 kilometers west of the San Bernardino Valley at Douglas, Arizona. Minckley (2008, 2013) provides a detailed description of the climate, area and vegetation.

The main study area contains a number of habitats ranging from desert scrub to permanent springs that are the headwaters of the San Bernardino River. In 2000, seven to eleven permanently marked 1-ha sites were established in five different vegetation types (Fig. 1). Two vegetation types were in proximity to surface (riparian) or close subsurface (mesquite forest) water and were more mesic than other vegetation types. Two vegetation types were upland and were much drier (grassland, desert scrub) with cacti and shrubs characteristic of Chihuahuan Desert, such as *Acacia constricta* Benth. (cat claw), *Larrea tridentata* (DC.) Coville (creosote bush), and *Flourensia cernua* DC. (tarbush). One habitat was abandoned agricultural fields. All sites were within a 16 km<sup>2</sup> area and ranged from 1100 to 1220 m in elevation.

Collections of bees were made at all of the permanent sites by pan trap in 2001 and at approximately half of these sites from 2002 to 2008. Pan trap sampling was done using three yellow, three white and three blue 177 ml. pan traps placed out in alternating colors and spaced 3–4 m apart along a transect following the protocol of LeBuhn et al. (2007).



**Figure 1.** Map of the study area in the San Bernardino Valley (modified from Minckley 2014). Dots are the permanent sites where 2001 pan trap collections were made. Letters next to each permanent site indicate the habitat; F = field, G = grassland, M = mesquite, R = riparian, and S = scrub. The core area is delimited by the rectangle spanning the Mexico – United States border. The peripheral and limestone collection sites are not shown but the direction and distance from the center of the core area are indicated on the right side of the map.

All bee specimens were identified to species and sex by taxonomic experts and published keys (Suppl. material 1: Table S1). Most were identified to recognized species, except for 73 species that were recognized as morphospecies. These morphospecies are 1.43% of all individuals, and most are members of *Lasioglossum* (*Dialictus*), *Dufourea* and *Megachile*. All species and their abundance are listed in Table 1 and are held in the Minckley collection at the University of Rochester. Data are available from the Global Biodiversity Information Facility (GBIF) under the RL Minckley Insect and Plant Collection (<https://www.gbif.org/dataset/84b69033-f9de-40bc-8d5f-8ee41987d6cc>).

## Species density

Bee species density in the San Bernardino Valley was first estimated from the bee collections captured in pan traps at permanent sites in 2001 (Fig. 1). These samples were made at all 45 permanent sites on 10 to 14-day intervals from mid-April to mid-September, except for three weeks in June, the driest time of the year (Tables 2, 3).

A second estimate of bee species density was done from all samples in the same area circumscribed by the permanent sites described above (hereafter referred to as the

**Table 1.** List of bee species and their abundance found in the San Bernardino Valley, Sonora/Arizona. Columns refer to numbers of individuals from the four sets of samples: A is the 2001 pan trap samples made at permanent sites; B is the core area samples taken from 2000 to 2008 from the area circumscribed by the permanent sites less those samples in A; C is the samples taken from 2000 to 2008 in the area peripheral to the core area; D is samples taken from 2009–2014 from a limestone outcrop area of desert approximately 12 km north northeast of the valley floor area. The taxonomy follows that of Michener (2007) except for recent changes by Bossert et al. (2020).

	A	B	C	D
<b>Andrenidae</b>				
Andreninae				
<i>Ancylandrena rozeni</i> Zavortink, 1994	0	0	2	0
<i>Andrena</i> ( <i>Belandrena</i> ) <i>sphaeralceae</i> Linsley, 1939	0	0	2	0
<i>A.</i> ( <i>Diandrena</i> ) <i>olivacea</i> Viereck, 1917	0	1	0	0
<i>A.</i> ( <i>Euandrena</i> ) <i>auricomae</i> Smith, 1879	0	16	4	0
<i>A.</i> ( <i>Holandrena</i> ) <i>cressonii</i> Robertson, 1891	0	0	0	1
<i>A.</i> ( <i>Leucandrena</i> ) <i>monilicornis</i> Cockerell, 1896	0	1	3	1
<i>A.</i> ( <i>Melandrena</i> ) <i>cerasifolii</i> Cockerell, 1896	0	2	0	0
<i>A.</i> ( <i>Micrandrena</i> ) <i>piperi</i> Viereck, 1904	2	28	1	0
<i>A.</i> ( <i>Plastandrena</i> ) <i>fracta</i> Casad & Cockerell, 1896	4	111	34	19
<i>A.</i> ( <i>Plastandrena</i> ) <i>prunorum</i> Casad, 1896	0	1	0	59
<i>A.</i> ( <i>Rhaphandrena</i> ) <i>prima</i> Casad, 1896	0	3	1	2
<i>A.</i> ( <i>Scaphandrena</i> ) <i>capricornis</i> Casad & Cockerell, 1896	0	6	2	13
<i>A.</i> ( <i>Scaphandrena</i> ) <i>primulifrons</i> Casad, 1896	3	83	12	0
<i>A.</i> ( <i>Thysandrena</i> ) <i>w-scripta</i> Viereck, 1904	0	0	0	51
<i>A.</i> ( <i>Trachandrena</i> ) <i>semipunctata</i> Cockerell, 1902	0	9	2	0
<i>A.</i> ( <i>Tylandrena</i> ) <i>jessicae</i> Cockerell, 1896	0	1	0	0
<i>A.</i> sp. 4	0	0	0	3
<i>A.</i> sp. 10	3	8	1	0
<i>A.</i> sp. 11	0	1	2	0
<i>A.</i> sp. 19	0	1	12	0
<i>A.</i> sp. 23	0	1	3	0
<i>A.</i> sp. 27	0	10	1	0
<i>A.</i> sp. 30	0	6	0	0
<i>A.</i> sp. 36	1	5	0	0
Oxaeinae				
<i>Protoxea gloriosa</i> (Fox, 1893)	3	29	0	0
Panurginae				
Calliopsini				
<i>Calliopsis sonorana</i> (Timberlake, 1969)	10	1	0	0
<i>C.</i> ( <i>Calliopsima</i> ) <i>chlorops</i> Cockerell, 1899	0	1	0	0
<i>C.</i> ( <i>Calliopsima</i> ) <i>coloratipes</i> Cockerell, 1898	0	4	0	0
<i>C.</i> ( <i>Calliopsima</i> ) <i>crypta</i> Shinn, 1965	0	1	0	0
<i>C.</i> ( <i>Calliopsima</i> ) <i>pectidis</i> Shinn, 1965	0	1	0	0
<i>C.</i> ( <i>Calliopsima</i> ) <i>rozeni</i> Shinn, 1965	41	46	3	0
<i>C.</i> ( <i>Calliopsis</i> ) <i>empelia</i> Shinn, 1967	4	7	0	0
<i>C.</i> ( <i>Calliopsis</i> ) <i>sonora</i> Shinn, 1967	3	5	0	0
<i>C.</i> ( <i>Calliopsis</i> ) <i>squamifera</i> Timberlake, 1947	1	13	0	0
<i>C.</i> ( <i>Hypomacrotera</i> ) <i>callops</i> (Cockerell & Porter, 1899)	207	482	27	0
<i>C.</i> ( <i>Hypomacrotera</i> ) <i>persimilis</i> (Cockerell, 1899)	597	1071	11	0
<i>C.</i> ( <i>Hypomacrotera</i> ) <i>subalpina subalpina</i> Cockerell, 1894	23	257	32	0
<i>C.</i> ( <i>Nomadopsis</i> ) <i>australior</i> Cockerell, 1897	8	70	0	0
<i>C.</i> ( <i>Nomadopsis</i> ) <i>callosa</i> Timberlake, 1952	18	8	0	0
<i>C.</i> ( <i>Nomadopsis</i> ) <i>helianthi</i> Swenk & Cockerell, 1907	36	176	3	0
<i>C.</i> ( <i>Nomadopsis</i> ) <i>macswaini</i> (Rozen, 1958)	0	6	0	0
<i>C.</i> ( <i>Nomadopsis</i> ) <i>nigromaculata</i> Timberlake, 1952	3	4	0	0
<i>C.</i> ( <i>Nomadopsis</i> ) <i>obscurella</i> Cresson, 1879	0	1	4	0

	A	B	C	D
<i>C. (Nomadopsis) puellae</i> (Cockerell, 1933)	1019	752	61	2
<i>C. (Perissander) anomoptera</i> Michener, 1942	4	16	1	0
<i>C. (Perissander) gilva</i> Shinn, 1967	1	19	1	0
<i>C. (Perissander) limbus</i> Shinn, 1967	0	1	0	0
<i>C. (Perissander) rogeri</i> Shinn, 1967	2	2	1	0
<i>C. (Verbenapis) verbenae</i> Cockerell & Porter, 1899	4	2	0	0
<b>Perditini</b>				
<i>Macrotera (Cockerellula) parkeri</i> (Timberlake, 1980)	0	0	0	216
<i>M. (Cockerellula) rubida</i> (Timberlake, 1968)	1	0	0	0
<i>M. (Cockerellula) solitaria</i> (Cockerell, 1897)	2	1	0	0
<i>M. (Macrotera) texana</i> Cresson, 1878	0	1	0	0
<i>M. (Macroterella) mellea</i> Timberlake, 1954	2	16	0	0
<i>M. (Macroteropsis) latior</i> (Cockerell, 1896)	78	123	10	0
<i>M. (Macroteropsis) portalis</i> (Timberlake, 1959)	6	41	0	0
<i>Perdita (Cockerellia) albipennis</i> Cresson, 1868	0	1	0	0
<i>P. (Cockerellia) coreopsidis collaris</i> Cockerell, 1916	0	2	0	0
<i>P. (Cockerellia) verbesinae</i> Cockerell, 1896	0	1	0	0
<i>P. (Epimacrotera) biguttata</i> Timberlake, 1962	60	10	0	0
<i>P. (Epimacrotera) diversa</i> Timberlake, 1954	315	313	11	0
<i>P. (Glossoperdita) burdi</i> Timberlake, 1956	0	28	0	0
<i>P. (Heteroperdita) rhodogastra</i> Timberlake, 1954	35	68	0	0
<i>P. (Hexaperdita) asteris</i> Cockerell, 1986	3	0	0	0
<i>P. (Hexaperdita) callicerata</i> Cockerell, 1896	238	360	30	0
<i>P. (Hexaperdita) ignota</i> Cockerell, 1896	3	1	0	0
<i>P. (Pentaperdita) alboviittata</i> Cockerell, 1895	59	180	1	0
<i>P. (Pentaperdita) amoena</i> Timberlake, 1956	173	67	5	0
<i>P. (Pentaperdita) bradleyana</i> Timberlake, 1954	0	4	0	0
<i>P. (Pentaperdita) melanochlora</i> Cockerell, 1922	2	0	0	0
<i>P. (Perdita) affinis</i> Cresson, 1878	1	0	0	0
<i>P. (Perdita) ashmeadi</i> Cockerell, 1899	1	196	9	0
<i>P. (Perdita) chamaesarachae</i> Cockerell, 1896	3	31	16	0
<i>P. (Perdita) dasyliirii</i> Cockerell, 1907	0	0	46	0
<i>P. (Perdita) difficilis</i> Timberlake, 1964	0	3	0	0
<i>P. (Perdita) exclamans</i> Cockerell, 1895	8	301	30	0
<i>P. (Perdita) florisantella</i> Cockerell, 1906	47	148	38	0
<i>P. (Perdita) lenis</i> Timberlake, 1958	3	232	46	0
<i>P. (Perdita) luciae</i> Cockerell, 1899	0	50	0	0
<i>P. (Perdita) mimosae efferta</i> Timberlake, 1964	1	0	0	0
<i>P. (Perdita) munita</i> Timberlake, 1964	205	337	20	0
<i>P. (Perdita) pectidis</i> Cockerell, 1896	6	13	0	0
<i>P. (Perdita) punctifera</i> Cockerell, 1914	0	161	0	0
<i>P. (Perdita) punctosignata</i> Cockerell, 1895	5	112	1	0
<i>P. (Perdita) semicaerulea</i> Cockerell, 1896	1	467	21	0
<i>P. (Perdita) semicrocea</i> Cockerell, 1895	5	1	0	0
<i>P. (Perdita) sexmaculata</i> Cockerell, 1895	31	76	81	0
<i>P. (Perdita) stathamae</i> Timberlake, 1964	0	43	8	0
<i>P. (Perdita) triangulifera</i> Timberlake, 1964	2	59	16	0
<i>P. (Perditella) cladothricis</i> Cockerell, 1896	15	23	0	0
<i>P. (Perditella) larraeae</i> Cockerell, 1896	18	449	1	0
<i>P. (Perditella) minima</i> Cockerell, 1923	8	9	0	0
<i>P. (Pygoperdita) malacothricis</i> Timberlake, 1956	887	454	26	3
<i>Perdita</i> sp. 2	0	29	0	0
<b>Protandrenini</b>				
<i>Protandrena (Heterosarus) nanula</i> (Timberlake, 1964)	4	18	0	0
<i>P. (Heterosarus) townsendi</i> (Cockerell, 1897)	2	4	0	0
<i>P. (Protandrena) bancrofti</i> Dunning, 1897	1	3	0	0
<i>Pseudoanurgus fraterculus fraterculus</i> Cockerell, 1896	1	0	0	0

	A	B	C	D
<b>Apidae</b>				
Anthophorinae				
Anthophorini				
<i>Anthophora (Anthophoroides) californica</i> Cresson, 1869	4	41	31	1
<i>A. (Anthophoroides) vallorum</i> (Cockerell, 1896)	2	7	2	0
<i>A. (Lophanthophora) affabilis</i> Cresson, 1878	0	7	0	0
<i>A. (Lophanthophora) ursina</i> Cresson, 1869	1	1	0	0
<i>A. (Melea) bomboides</i> Kirby, 1838	0	1	0	0
<i>A. (Micranthophora) aff. estebana</i>	0	3	0	0
<i>A. (Micranthophora) curta</i> Provancher, 1895	4	73	4	0
<i>A. (Micranthophora) exigua</i> Cresson, 1878	0	0	1	0
<i>A. (Micranthophora) pachyodonta</i> Cockerell, 1923	0	1	0	0
<i>A. (Micranthophora) aff. estebana</i>	0	3	0	0
<i>A. (Heliophila) petrophila</i> Cockerell, 1905	0	21	5	0
<i>A. (Mystacanthophora) montana</i> Cresson, 1869	2	0	0	0
<i>A. (Mystacanthophora) urbana</i> Cresson, 1878	0	12	1	0
<i>A. (Paramegilla) centriformis</i> Cresson, 1879	1	1	8	0
<i>A. (Paramegilla) fulvicauda</i> Timberlake, 1937	0	1	0	0
<i>A. (Pyganthophora) lesquerellae</i> Cresson, 1878	0	0	0	4
<i>A. (Pyganthophora) vannigera</i> Timberlake, 1951	0	14	2	0
Apinae				
Apini				
<i>Apis (Apis) mellifera</i> Linnaeus, 1758	8	2508	43	5
Bombini				
<i>Bombus (Fervidobombus) pensylvanicus sonorus</i> Say, 1837	1	14	1	0
Centridini				
<i>Centris (Paracentris) angustifrons</i> Snelling, 1966	2	1	0	0
<i>C. (Paracentris) atripes</i> Mocsary, 1899	6	59	11	0
<i>C. (Paracentris) caesalpiniae</i> Cockerell, 1897	1	29	0	0
<i>C. (Paracentris) hoffmanseggeriae</i> Cockerell, 1897	1	98	0	0
<i>C. (Paracentris) rhodopus</i> Cockerell, 1897	1	2	0	0
<i>C. (Paracentris) apache</i> Vivallo, 2020	0	1	0	0
<i>C. (Paracentris) sp.</i>	1	0	0	0
Eucerinae				
Ancyloscelidini				
<i>Ancyloscelis melanostomus</i> Cockerell, 1923	44	76	0	0
Emphorini				
<i>Diadasia (Coquillettapis) afflictula</i> Cockerell, 1910	4	0	0	0
<i>D. (Coquillettapis) australis</i> (Cresson, 1878)	0	2	0	0
<i>D. (Coquillettapis) diminuta</i> (Cresson, 1878)	282	387	91	1
<i>D. (Coquillettapis) lutzii</i> Cockerell, 1924	3	5	24	0
<i>D. (Coquillettapis) martialis</i> Timberlake, 1940	3	1	6	0
<i>D. (Coquillettapis) megamorpha</i> Cockerell, 1898	1	1	0	0
<i>D. (Coquillettapis) opuntiae</i> Cockerell, 1901	26	293	208	2
<i>D. (Coquillettapis) rinconis</i> Cockerell, 1897	1316	898	72	2
<i>D. (Coquillettapis) sphaeralcearum</i> Cockerell, 1897	0	1	0	0
<i>D. (Dasiapis) ochracea</i> (Cockerell, 1903)	41	398	5	0
<i>D. (Dasiapis) tropicalis</i> (Cockerell, 1918)	2	2	0	0
<i>Prilothrix nr. sumichrasti</i> (Cresson, 1878)	69	57	0	0
Eucerini				
<i>Eucera (Synhalonia) actuosa</i> (Cresson, 1878)	107	410	5	36
<i>E. (Synhalonia) albescens</i> (Timberlake, 1969)	0	0	0	2
<i>E. (Synhalonia) aragalli</i> (Cockerell, 1904)	1	3	6	8
<i>E. (Synhalonia) conformis</i> (Timberlake, 1969)	1	5	7	2
<i>E. (Synhalonia) edwardsi</i> (Cresson, 1878)	0	0	1	0
<i>E. (Synhalonia) lepida</i> (Cresson, 1878)	0	4	0	0
<i>E. (Synhalonia) mohavensis</i> (Timberlake, 1969)	0	0	3	1
<i>E. (Synhalonia) nr. quadricincta</i> (Timberlake, 1969)	0	0	0	1

	A	B	C	D
<i>E. (Synhalonia) phaceliae</i> (Cockerell, 1911)	0	30	0	4
<i>E. (Synhalonia) quadricincta</i> (Timberlake, 1969)	2	1	0	0
<i>E. (Synhalonia)</i> sp. 1	0	0	1	0
<i>E. (Synhalonia)</i> sp. 2	0	1	0	0
<i>Martinapis (Martinapis) luteicornis</i> (Cockerell, 1896)	0	1	0	0
<i>Melissodes (Eumelissodes) agilis</i> Cresson, 1878	13	11	0	0
<i>M. (Eumelissodes) limbus</i> LaBerge, 1961	5	37	0	0
<i>M. (Eumelissodes) lutulentus</i> LaBerge, 1961	0	1	0	0
<i>M. (Eumelissodes) subagilis</i> Cockerell, 1905	2	81	0	0
<i>M. (Eumelissodes) tristis</i> Cockerell, 1894	373	455	9	0
<i>M. (Eumelissodes) verbesinarum</i> Cockerell, 1905	0	6	0	0
<i>M. (Melissodes) communis</i> Cresson, 1878	56	3	0	0
<i>M. (Melissodes) comptoides</i> Robertson, 1878	15	78	2	0
<i>M. (Melissodes) gilensis</i> Cockerell, 1896	1	0	0	0
<i>M. (Melissodes) paroselae</i> Cockerell, 1905	845	3134	62	25
<i>M. (Tachymelissodes) opuntiellus</i> Cockerell, 1911	3	3	0	0
<i>M. (Tachymelissodes) sonorensis</i> LaBerge, 1963	1	0	0	0
<i>M.</i> sp. 22	0	6	0	0
<i>Peponapis (Peponapis) pruinosa</i> (Say, 1837)	0	31	0	0
<i>P. (Xeropeponapis) timberlakei</i> Hurd & Linsley, 1964	0	7	0	0
<i>Svastra (Epimelissodes) helianthelli</i> (Cockerell, 1905)	0	11	0	0
<i>S. (Epimelissodes) machaerantherae</i> (Cockerell, 1904)	2	3	0	0
<i>S. (Epimelissodes) obliqua expurgata</i> (Cockerell, 1925)	1	0	0	0
<i>S. (Epimelissodes) sabinensis</i> (Cockerell, 1924)	118	31	1	0
<i>S. (Epimelissodes) sila</i> (LaBerge, 1956)	2	23	2	0
<i>S. (Epimelissodes)</i> sp. 4	1	0	0	0
<i>Syntrichalonia exquisita</i> (Cresson, 1878)	1	1	0	0
<i>Tetraloniella (Tetraloniella) eriocarpi</i> (Cockerell, 1898)	0	11	0	0
<i>T. (Tetraloniella) imitatrix</i> (Cockerell & Porter, 1899)	0	0	2	0
<i>T. (Tetraloniella) lippiae</i> (Cockerell, 1904)	0	1	0	0
<i>T. (Tetraloniella) sphaeralceae</i> LaBerge, 2001	1	2	0	0
<i>T. (Tetraloniella) vandyckei</i> LaBerge, 2001	803	251	4	0
<i>Xenoglossa (Eoxenoglossa) strenua</i> (Cresson, 1878)	0	1	0	0
<i>X. (Xenoglossa) angustior</i> Cockerell, 1900	0	1	0	0
<i>X. (Xenoglossa) patricia</i> Cockerell, 1896	0	27	0	0
Exomalopsini				
<i>Anthophorula (Anthophorisca) asteris</i> (Mitchell, 1962)	3	1	0	0
<i>A. (Anthophorisca) consobrina</i> (Timberlake, 1980)	34	14	0	0
<i>A. (Anthophorisca) exilis</i> (Timberlake, 1980)	7	5	1	0
<i>A. (Anthophorisca) ignota</i> (Timberlake, 1980)	0	2	0	0
<i>A. (Anthophorisca) parva</i> (Timberlake, 1980)	0	13	0	0
<i>A. (Anthophorisca) pygmaea</i> (Cresson, 1872)	56	1	0	0
<i>A. (Anthophorisca) sonorensis</i> (Timberlake, 1980)	2	0	0	0
<i>A. (Anthophorula) albata</i> (Timberlake, 1947)	0	1	0	0
<i>A. (Anthophorula) compactula</i> (Cockerell, 1897)	1030	564	13	0
<i>A. (Anthophorula) completa</i> (Cockerell, 1935)	46	80	2	0
<i>A. (Anthophorula) crenulata</i> (Timberlake, 1980)	0	1	0	0
<i>A. (Anthophorula) euphorbiae</i> (Timberlake, 1947)	0	4	1	0
<i>A. (Anthophorula) gutierreziae</i> (Timberlake, 1947)	0	1	0	0
<i>A. (Anthophorula) palmarum</i> (Timberlake, 1947)	0	0	1	0
<i>A. (Anthophorula) rozeni</i> (Timberlake, 1980)	26	77	1	0
<i>A. (Anthophorula) rufiventris</i> (Timberlake, 1947)	7	34	3	0
<i>A. (Anthophorula) scapalis</i> (Timberlake, 1980)	2	1	0	0
<i>A. (Anthophorula) torticornis</i> (Timberlake, 1980)	0	1	0	0
<i>A. (Anthophorula) tricinctula</i> (Timberlake, 1980)	3	0	0	0
<i>A. (Anthophorula) varleyi</i> (Timberlake, 1980)	0	5	0	0
<i>Exomalopsis (Stilbomalopsis) dimidiata</i> Timberlake, 1980	9	9	1	0
<i>E. (Stilomalopsis) solani</i> Cockerell, 1896	30	184	0	0

	A	B	C	D
<i>E. (Stilomalopsis) solidaginis</i> Cockerell, 1898	0	6	0	0
Nomadinae				
Ammobatini				
<i>Oreopasites (Oreopasites) arizonica</i> Linsley, 1941	4	1	0	0
<i>O. (Perditopasites) favreauae</i> Rozen, 1992	0	1	0	0
<i>O. (Perditopasites) linsleyi</i> Rozen, 1992	1	3	0	0
Ammobatoidini				
<i>Holcopasites apacheorum</i> (Hurd & Linsley, 1972)	3	3	0	0
<i>H. illinoiensis minimus</i> (Linsley, 1943)	6	14	1	0
<i>H. insoletus</i> (Linsley, 1942)	1	4	0	0
<i>H. stevensi</i> Crawford, 1915	2	11	0	0
<i>H. tegularis</i> Hurd & Linsley, 1972	2	0	0	0
Brachynomadini				
<i>Brachynomada (Melanomada) margaretae</i> (Rozen, 1994)	1	2	0	0
<i>Paranomada velutina</i> Linsley, 1939	0	1	0	0
<i>Triopasites penniger</i> (Cockerell, 1894)	0	5	0	0
Epeolini				
<i>Epeolus chamaesarachae</i> Onuferko, 2018	0	1	0	0
<i>E. compactus</i> Cresson, 1878	7	5	2	0
<i>E. mesillae</i> (Cockerell, 1895)	20	92	1	0
<i>Epeolus</i> sp. 1	1	1	0	0
<i>Epeolus</i> sp. 3	0	1	0	0
<i>Triepeolus circumculus</i> Rightmyer, 2008	0	1	1	0
<i>T. concavus</i> (Cresson, 1878)	0	2	0	0
<i>T. grandis</i> (Friese, 1917)	0	5	1	0
<i>T. helianthi</i> (Robertson, 1897)	0	3	0	0
<i>T. kathrynae</i> Rozen, 1989	1	9	0	0
<i>T. loomisorum</i> Rozen, 1989	0	2	0	0
<i>T. lunatus</i> (Say, 1824)	0	28	1	0
<i>T. norae</i> Cockerell, 1907	0	1	0	0
<i>T. penicilliferus</i> (Brues, 1903)	0	1	0	0
<i>T. remigatus</i> (Fabricius, 1804)	1	9	0	0
<i>Triepeolus</i> sp. 4	1	2	0	0
<i>T. townsendi</i> Cockerell, 1907	0	3	0	0
<i>T. verbesinae</i> Cockerell, 1897	3	329	4	0
Ericrocidini				
<i>Ericrocis lata</i> (Cresson, 1878)	0	7	1	0
<i>E. pintada</i> Snelling & Zavortink, 1984	1	9	0	0
Melectini				
<i>Melecta (Melecta) bobartorum</i> Linsley, 1939	0	1	0	1
Neolarrini				
<i>Neopasites (Micropasites) cressoni</i> Crawford, 1916	2	30	37	0
<i>Neolarra (Neolarra) batrae</i> Shanks, 1977	1	2	0	0
<i>N. (Neolarra) californica</i> Michener, 1939	9	73	0	0
<i>N. (Neolarra) cockerelli</i> (Crawford, 1916)	2	11	0	0
<i>N. (Phileremulus) rozeni</i> Shanks, 1977	27	156	0	0
<i>N. (Phileremulus) vigilans</i> (Cockerell, 1895)	23	25	2	0
<i>Townsendiella pulchra</i> Crawford, 1916	1	6	0	0
Nomadini				
<i>Nomada cf. gutierreziae</i> Cockerell, 1896	0	25	0	0
<i>Nomada cf. vegana</i> Cockerell, 1903	0	25	1	0
<i>Nomada</i> sp. 1	1	24	2	0
<i>Nomada</i> sp. 1a	0	18	0	0
<i>Nomada</i> sp. 2	0	1	1	0
<i>Nomada</i> sp. 3	0	1	0	0
<i>Nomada</i> sp. 4	0	1	0	0
<i>Nomada</i> sp. 5	0	1	0	0
<i>Nomada</i> sp. 6	0	2	0	0

	A	B	C	D
<i>Nomada</i> sp. 7	0	3	1	1
<i>Nomada</i> sp. 8	0	1	0	0
<i>Nomada</i> sp. 9	0	0	0	1
<i>Nomada</i> sp. 10	0	0	0	3
<i>Nomada</i> sp. 11	0	3	1	0
Xylocopinae				
Ceratinini				
<i>Ceratina</i> ( <i>Zadontomerus</i> ) <i>apacheorum</i> Daly, 1973	2324	2849	11	2
<i>C.</i> ( <i>Zadontomerus</i> ) <i>arizonensis</i> Cockerell, 1898	8	188	4	1
<i>C.</i> ( <i>Zadontomerus</i> ) <i>melanoptera</i> Cockerell, 1924	34	5	3	15
<i>C.</i> ( <i>Zadontomerus</i> ) <i>nanula</i> Cockerell, 1897	0	1	0	0
Xylocopini				
<i>Xylocopa</i> ( <i>Xylocopoides</i> ) <i>californica arizonensis</i> Cresson, 1879	0	8	2	2
<i>X.</i> ( <i>Neoxylocopa</i> ) <i>sonorina</i> Smith, 1874	0	2	0	0
<b>Colletidae</b>				
Colletinae				
Colletini				
<i>Colletes</i> <i>bryanti</i> Timberlake, 1951	0	2	0	0
<i>C.</i> <i>chyeonitens</i> Swenk, 1906	2	3	0	0
<i>C.</i> <i>eulophi</i> Robertson, 1891	0	2	0	0
<i>C.</i> <i>intermixtus</i> Swenk, 1905	0	1	0	0
<i>C.</i> <i>kincaidii</i> Cockerell, 1898	0	1	0	0
<i>C.</i> <i>louisae</i> Cockerell, 1897	0	12	1	0
<i>C.</i> <i>lutzi</i> Timberlake, 1943	0	1	0	0
<i>C.</i> <i>perileucus</i> Cockerell, 1924	0	18	0	0
<i>C.</i> <i>prosopidis</i> Cockerell, 1897	0	2	0	0
<i>C.</i> <i>simulans simulans</i> Cresson, 1868	0	2	0	0
<i>C.</i> <i>salicicola</i> Cockerell, 1897	1	141	17	0
<i>C.</i> <i>scopiventer</i> Swenk, 1908	0	57	17	0
<i>C.</i> <i>sphaeralceae</i> Timberlake, 1951	0	1	1	0
<i>C.</i> <i>wootoni</i> Cockerell, 1897	0	74	18	0
Diphaglossinae				
Caupolicanini				
<i>Caupolicana</i> ( <i>Caupolicana</i> ) <i>yarrowi</i> (Cresson, 1875)	0	3	0	0
<i>C.</i> ( <i>Zikanapis</i> ) <i>elegans</i> Timberlake, 1965	0	0	1	0
Hylaeinae				
<i>Hylaeus</i> ( <i>Hylaeus</i> ) <i>mesillae</i> (Cockerell, 1896)	18	469	5	0
<i>H.</i> ( <i>Paraprosopis</i> ) <i>asininus</i> (Cockerell & Casad, 1895)	2	90	11	0
<i>H.</i> ( <i>Prosopis</i> ) <i>episcopalis</i> (Cockerell, 1896)	0	340	4	0
<i>H.</i> ( <i>Prosopis</i> ) <i>insolitus</i> Snelling, 1966	0	1	2	0
<b>Halictidae</b>				
Halictinae				
Augochlorini				
<i>Augochlorella</i> ( <i>Augochlorella</i> ) <i>neglectula</i> (Cockerell, 1897)	4	21	27	6
<i>A.</i> ( <i>Augochlorella</i> ) <i>pomoniella</i> (Cockerell, 1915)	2	4	2	4
Halictini				
<i>Agapostemon</i> ( <i>Agapostemon</i> ) <i>angelicus</i> Cockerell, 1924	200	684	67	51
<i>A.</i> ( <i>Agapostemon</i> ) <i>melliventris</i> Cresson, 1874	32	75	0	11
<i>A.</i> ( <i>Agapostemon</i> ) <i>obliquus</i> (Provancher, 1888)	402	3	11	78
<i>A.</i> ( <i>Agapostemon</i> ) <i>texasus</i> Cresson, 1872		0	0	0
<i>A.</i> ( <i>Agapostemon</i> ) <i>tyleri</i> Cockerell, 1917	18	153	7	12
<i>A.</i> ( <i>Notagapostemon</i> ) <i>nasutus</i> Smith, 1853	0	1	0	0
<i>Augochloropsis</i> <i>metallica</i> (Fabricius, 1793)	0	12	2	0
<i>Halictus</i> ( <i>Odontalictus</i> ) <i>ligatus</i> Say, 1837	31	578	31	0
<i>H.</i> ( <i>Seladonia</i> ) <i>tripartitus</i> Cockerell, 1895	1296	1042	63	5
<i>Lasioglossum</i> ( <i>Dialictus</i> ) <i>arcantum</i> (Sandhouse, 1924)	0	1	0	0
<i>L.</i> ( <i>Dialictus</i> ) <i>clematisellum</i> (Cockerell, 1904)	8	252	3	0
<i>L.</i> ( <i>Dialictus</i> ) <i>comulum</i> Michener, 1951	401	768	81	675

	A	B	C	D
<i>L. (Dialictus) eophilus</i> (Ellis, 1914)	1	6	0	0
<i>L. (Dialictus) hudsoniellum</i> (Cockerell, 1919)	0	31	0	0
<i>L. (Dialictus) impavidum</i> (Sandhouse, 1924)	50	216	7	67
<i>L. (Dialictus) lilianae</i>	0	22	1	0
<i>L. (Dialictus) mesillense</i>	5	94	1	0
<i>L. (Dialictus) microlepoides</i> (Ellis, 1914)	1894	1772	72	542
<i>L. (Dialictus) minckleyi</i> Gardner & Gibbs, 2020	0	95	1	0
<i>L. (Dialictus) obnubilum</i> (Sandhouse, 1924)	0	2	0	0
<i>L. (Dialictus) occidentale</i> (Crawford, 1902)	10	88	1	0
<i>L. (Dialictus) perparvum</i> (Ellis, 1914)	0	4	0	0
<i>L. (Dialictus) pruinosum</i> (Robertson, 1892)	1	1	0	0
<i>L. (Dialictus) semibrunneum</i> (Cockerell, 1895)	97	207	4	0
<i>L. (Dialictus) semicaeruleum</i> (Cockerell, 1895)	14	326	34	0
<i>L. (Dialictus) aff. macroprosopum</i> Gibbs, 2010	0	1	0	0
<i>L. (Dialictus) aff. occidentale</i> (Crawford, 1902)	3	44	0	0
<i>L. (Dialictus) aff. perparvum</i> (Ellis, 1914)	1980	6170	308	288
<i>L. (Dialictus) cf. albuquerquense</i> (Michener, 1937)	3	25	6	0
<i>L. (Dialictus) cf. brunneri</i> (Crawford, 1902)	0	1	0	0
<i>L. (Dialictus) cf. comulum</i> (Michener, 1937)	0	2	0	0
<i>L. (Dialictus) cf. impavidum</i> (Sandhouse, 1924)	8	100	15	0
<i>L. (Dialictus) cf. lionotum</i> (Sandhouse, 1923)	0	1	0	0
<i>L. (Dialictus) cf. nevadense</i> (Crawford, 1907)	10	21	0	0
<i>L. (Dialictus) cf. obnubilum</i> (Sandhouse, 1924)	0	4	0	0
<i>L. (Dialictus) cf. perdifficile</i> (Cockerell, 1895)	0	2	0	0
<i>L. (Dialictus) sp. 1</i>	2	1	0	0
<i>L. (Evyllaes) amicum</i> (Cockerell, 1897)	4	154	6	0
<i>L. (Evyllaes) pectoraloides</i> (Cockerell, 1895)	76	337	8	0
<i>L. (Evyllaes) sp. 1</i>	0	1	0	0
<i>L. (Evyllaes) sp. 4</i>	0	2	0	0
<i>L. (Hemibalictus) angustius</i> (Cockerell, 1897)	0	7	0	0
<i>L. (Lasioglossum) acarophilum</i> McGinley, 1986	1	32	4	2
<i>L. (Lasioglossum) desertum</i> (Smith, 1879)	0	2	0	5
<i>L. (Lasioglossum) morrilli</i> (Cockerell, 1919)	1	1	1	36
<i>L. (Lasioglossum) jubatum</i> (Vachal, 1904)	0	2	0	0
<i>L. (Lasioglossum) sisymbrii</i> (Cockerell, 1897)	1	86	13	9
<i>Spbecodes fortior</i> Cockerell, 1898	0	15	0	0
<i>S. minor</i> Robertson, 1898	0	35	0	0
<i>S. aff. mandibularis</i> Cresson, 1872	10	132	3	0
<i>Spbecodes sp. 1</i>		0	0	1
Nomiinae				
<i>Dieunomia (Epinomia) boharti</i> (Cross, 1958)	0	1	0	0
<i>D. (Epinomia) nevadensis</i> (Cresson, 1874)	1	92	0	0
<i>Nomia (Acunomia) angustitibialis</i> Ribble, 1965	0	1	0	0
<i>N. (Acunomia) foxii</i> Dalla Torre, 1896	4	89	0	0
<i>N. (Acunomia) tetrazonata</i> (Cresson, 1874)	1	7	2	0
Rhopitinae				
<i>Conanthalictus (Phaceliapis) sp. 1</i>	27	42	17	0
<i>Dufourea malacothebis</i> Timberlake, 1939	324	266	213	0
<i>D. mulleri</i> (Cockerell, 1898)	50	152	189	0
<i>D. pulchricornis</i> (Cockerell, 1916)	28	29	38	0
<i>Dufourea sp. 1</i>	14	1	0	0
<i>Dufourea sp. 2</i>	0	1	4	0
<i>Dufourea sp. 3</i>	5	17	30	0
<i>Dufourea sp. 4</i>	23	12	0	0
<i>Dufourea sp. 5</i>	10	31	17	0
<i>Dufourea sp. 6</i>	23	0	0	1
<i>Dufourea sp. 10</i>	0	9	0	0
<i>Dufourea sp. 11</i>	0	1	0	0

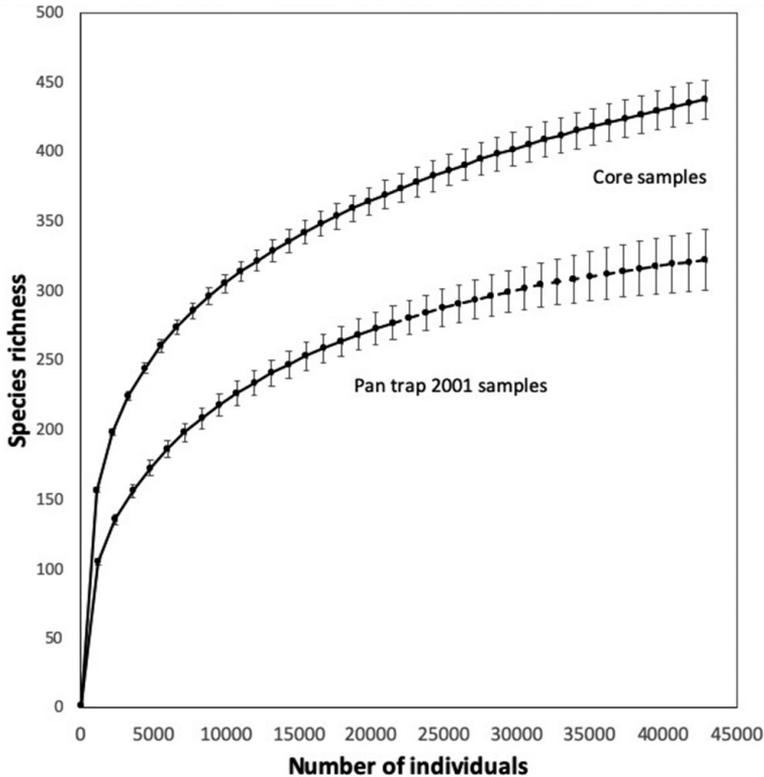
	A	B	C	D
<i>Dufourea</i> sp. 12	0	4	2	0
<i>Dufourea</i> sp. 13	0	2	1	0
<i>Protodufourea eickworti</i> Bohart & Griswold, 1997	5	2	0	0
<i>Sphecodosoma (Sphecodosoma) dicksoni</i> (Timberlake, 1961)	2	19	0	0
<i>S. (Sphecodosoma) pratti</i> Crawford, 1907	0	2	0	0
<b>Megachilidae</b>				
Megachilinae				
Anthidiini				
<i>Anthidium (Anthidium) cochimi</i> Snelling, 1992	6	10	1	0
<i>A. (Anthidium) cockerelli</i> Schwarz, 1928	8	106	4	0
<i>A. (Anthidium) jocosum</i> Cresson, 1878	471	390	11	7
<i>A. (Anthidium) labergei</i> Gonzalez & Griswold, 2013	1	13	6	0
<i>A. (Anthidium) maculifrons</i> Smith, 1854	3	3	0	0
<i>A. (Anthidium) maculosum</i> Cresson, 1878	6	13	1	0
<i>A. (Anthidium) palmarum</i> Cockerell, 1904	34	50	2	1
<i>A. (Anthidium) paroselae</i> Cockerell, 1898	4	0	1	0
<i>A. (Anthidium) quetzalcoatl</i> Schwarz, 1933	0	1	0	0
<i>A. (Anthidium) utahense</i> Swenk, 1914	3	13	2	0
<i>A. (Anthidium)</i> sp. 4	3	1	1	0
<i>Dianthidium (Dianthidium) curvatum</i> (Smith, 1854)	0	1	1	0
<i>D. (Dianthidium) discors</i> Timberlake, 1948	0	3	0	1
<i>D. (Dianthidium) heterulkei</i> Schwarz, 1940	0	2	1	0
<i>D. (Dianthidium) implicatum</i> Timberlake, 1948	1	3	0	0
<i>D. (Dianthidium) parkeri</i> Grigarick & Stange, 1964	0	4	0	0
<i>D. (Dianthidium) parvum</i> (Cresson, 1878)	6	16	0	0
<i>D. (Dianthidium) platyurum</i> Cockerell, 1923	0	3	0	0
<i>D. (Dianthidium) pudicum</i> (Cresson, 1879)	3	1	2	0
<i>D. (Dianthidium) ulkei</i> (Cresson, 1878)	0	2	0	0
<i>Stelis (Dolichostelis) perpulchra</i> Crawford, 1916	0	136	4	0
<i>S. (Stelis) elongativentris</i> Parker, 1987	105	599	6	12
<i>Stelis</i> sp. 2	0	2	0	0
<i>Stelis</i> sp. 3	0	2	0	0
<i>Stelis</i> sp. 4	1	31	1	0
<i>Stelis</i> sp. 5	2	9	1	0
<i>Stelis</i> sp. 6	0	16	0	0
<i>Stelis</i> sp. 7	0	4	1	0
<i>Stelis</i> sp. 8	0	3	0	0
<i>Stelis</i> sp. 9	1	2	0	0
<i>Stelis</i> sp. 10	0	1	0	0
<i>Trachusa (Heteranthidium) larreae</i> (Cockerell, 1897)	3	137	6	0
Dioxyini				
<i>Dioxya pomonae</i> Cockerell, 1910	0	0	0	1
<i>D. producta subrubra</i> (Cresson, 1879)	0	3	0	0
Lithurgini				
<i>Lithurgopsis (Lithurgopsis) apicalis</i> (Cresson, 1875)	11	39	24	0
<i>L. (Lithurgopsis) echinocacti</i> Cockerell, 1898	4	19	0	0
<i>L. (Lithurgopsis) planifrons</i> (Friese, 1908)	0	3	0	0
Megachiliini				
<i>Coelioxys (Boreocoelioxys) novomexicanus</i> Say, 1824	2	4	1	0
<i>Coelioxys (Boreocoelioxys) octodentatus</i> Say, 1824	0	24	1	0
<i>C. (Coelioxys) hirsutissimus</i> Cockerell, 1912	1	5	3	0
<i>C. (Syncoelioxys) apacheorum</i> Cockerell, 1900	0	2	0	0
<i>C. (Syncoelioxys) hunteri</i> Crawford, 1914	0	1	0	0
<i>C. (Syncoelioxys) texanus</i> Cresson, 1872	0	22	1	0
<i>C. (Xerocoelioxys) edita</i> Cresson, 1872	1	6	0	0
<i>Megachile (Argyropile) parallela</i> Smith, 1853	0	2	0	0
<i>M. (Chelostomoides) adelphodonta</i> Cockerell, 1924	0	5	3	0
<i>M. (Chelostomoides) chilopsidis</i> Cockerell, 1900	0	31	0	0

	A	B	C	D
<i>M. (Chelostomoides) discorbina</i> Cockerell, 1924	2	115	7	0
<i>M. (Chelostomoides) exilis</i> Cresson, 1872	1	0	0	0
<i>M. (Chelostomoides) lobatifrons</i> Cockerell, 1924	1	14	0	0
<i>M. (Chelostomoides) manni</i> Mitchell, 1934	0	1	0	0
<i>M. (Chelostomoides) odontostoma</i> Cockerell, 1924	4	53	3	1
<i>M. (Chelostomoides) prosopidis</i> Cockerell, 1900	0	5	1	0
<i>M. (Chelostomoides) reflexa</i> (Snelling, 1990)	0	1	0	0
<i>M. (Chelostomoides) spinotulata</i> Mitchell, 1934	2	18	0	0
<i>M. (Leptorachis) petulans</i> Cresson, 1878	0	2	0	0
<i>M. (Litomegachile) brevis</i> Say, 1837	2	8	2	0
<i>M. (Litomegachile) coquilletti</i> Cockerell, 1915	1	2	1	0
<i>M. (Litomegachile) gentilis</i> Cresson, 1872	14	59	3	0
<i>M. (Litomegachile) lippiae</i> Cockerell, 1900	1	5	0	0
<i>M. (Litomegachile) mendica</i> Cresson, 1878	2	4	0	0
<i>M. (Litomegachile) pankus</i> Bzdyk, 2012	2	0	0	0
<i>M. (Litomegachile) texana</i> Cresson, 1878	0	2	0	0
<i>M. (Megachile) sp 1</i>	1	2	0	0
<i>M. (Megachiloidea) alata</i> Mitchell, 1934	1	0	0	0
<i>M. (Megachiloidea) anograe</i> Mitchell, 1938	2	0	0	0
<i>M. (Megachiloidea) bradleyi</i> Mitchell, 1934	2	0	0	0
<i>M. (Megachiloidea) fucata</i> Mitchell, 1934	17	68	12	0
<i>M. (Megachiloidea) integra</i> Cresson, 1878	1	0	0	0
<i>M. (Megachiloidea) legalis</i> Cresson, 1879	0	0	1	0
<i>M. (Megachiloidea) maurata</i> Mitchell, 1936	1	2	1	0
<i>M. (Megachiloidea) sublaurita</i> Mitchell, 1927	99	47	16	1
<i>M. (Megachiloidea) xerophila</i> Cockerell, 1933	74	24	6	1
<i>M. (Megachiloidea) sp. 1</i>	19	20	2	0
<i>M. (Megachiloidea) sp. 2</i>	13	10	1	0
<i>M. (Megachiloidea) sp. 3</i>	1	1	0	0
<i>M. (Pseudocentron) sidalceae</i> Cockerell, 1897	27	20	3	0
<i>M. (Sayapis) inimica sayi</i> (Cresson, 1878)	0	4	1	0
<i>M. (Sayapis) newberryae</i> Cockerell, 1900	1	82	9	0
<i>M. (Sayapis) polycaris</i> Say, 1831	0	88	1	0
<i>M. (Sayapis) pugnata</i> Say, 1837	0	1	0	0
Osmiini				
<i>Ashmeadiella (Arogochila) breviceps</i> Michener, 1939	57	157	3	0
<i>A. (Arogochila) cazieri</i> Michener, 1939	3	7	10	5
<i>A. (Arogochila) clypeodentata</i> Michener, 1936	434	577	17	3
<i>A. (Arogochila) sp. 1</i>	0	1	0	0
<i>A. (Ashmeadiella) bigeloviae</i> (Cockerell, 1897)	46	149	0	0
<i>A. (Ashmeadiella) buconis</i> (Say, 1837)	2	48	2	0
<i>A. (Ashmeadiella) cactorum</i> (Cockerell, 1897)	23	220	4	10
<i>A. (Ashmeadiella) foveata</i> Michener, 1939	1	23	0	2
<i>A. (Ashmeadiella) gillettei</i> Titus, 1904	20	48	6	3
<i>A. (Ashmeadiella) leucozona</i> Cockerell, 1924	157	262	4	1
<i>A. (Ashmeadiella) maxima</i> Michener, 1936	0	0	0	3
<i>A. (Ashmeadiella) meliloti</i> (Cockerell, 1897)	55	324	34	13
<i>A. (Ashmeadiella) occipitalis</i> Michener, 1939	20	966	5	3
<i>A. (Ashmeadiella) opuntiae</i> (Cockerell, 1897)	18	121	30	6
<i>A. (Ashmeadiella) prosopidis</i> (Cockerell, 1897)	152	388	7	0
<i>A. (Ashmeadiella) sonora</i> Michener, 1939	0	3	0	0
<i>A. (Ashmeadiella) vandykiella</i> Michener, 1949	1	16	1	0
<i>A. (Ashmeadiella) sp. 2</i>	0	2	0	0
<i>A. (Chilosmia) rhodognatha</i> Cockerell, 1924	140	1716	31	8
<i>A. (Isosmia) hurdiana</i> (Michener, 1954)	13	13	1	3
<i>A. (Isosmia) rubrella</i> (Michener, 1943)	0	2	0	5
<i>Atoposmia (Atoposmia) anthodyta</i> (Michener, 1943)	0	3	1	0

	A	B	C	D
<i>A. (Atoposmia) arizonensis</i> (Michener, 1954)	2	2	1	0
<i>A. (Eremosmia) beameri</i> (Michener, 1951)	1	4	1	0
<i>A. (Eremosmia) hypostomalis</i> (Michener, 1954)	0	1	1	1
<i>Atoposmia</i> sp. 1	2	4	1	0
<i>A. (Hexosmia) copelandica arefacta</i> (Cockerell, 1935)	4	19	48	0
<i>Heriades (Neotrypetes) crucifera</i> Cockerell, 1897	0	4	0	0
<i>H. (Neotrypetes) micheneri</i> Timberlake, 1947	0	8	0	0
<i>H. (Neotrypetes) microthalma</i> Michener, 1954	0	5	0	0
<i>H. (Neotrypetes) texana</i> Michener, 1938	0	1	0	0
<i>H. (Neotrypetes) timberlakei</i> Michener, 1938	0	2	0	0
<i>Hoplitis (Alcidamea) grinnelli</i> (Cockerell, 1910)	0	8	4	0
<i>H. (Alcidamea) biscutellae</i> (Cockerell, 1897)	18	241	13	4
<i>H. (Alcidamea) producta interior</i> Michener, 1947	0	1	2	0
<i>H. (Proteriades) remotula</i> (Cockerell, 1910)	0	1	0	0
<i>Osmia (Diceratomia) subfasciata</i> Cresson, 1872	291	539	68	4
<i>O. (Melanosmia) cerasi</i> Cockerell, 1897	0	0	1	0
<i>O. (Melanosmia) clarescens</i> Cockerell, 1911	2	69	8	0
<i>O. (Melanosmia) liogastra</i> Cockerell, 1933	3	46	16	34
<i>O. (Melanosmia) marginata</i> Michener, 1936	1	10	0	0
<i>O. (Melanosmia) phenax</i> Michener, 1936	0	4	0	0
<i>O. (Melanosmia) prunorum</i> Cockerell, 1897	7	165	10	9
<i>O. (Melanosmia) unca</i> Michener, 1937	0	8	15	0
<i>Osmia</i> sp. 2.	1	9	0	0
<b>Mellitidae</b>				
Dasypodinae				
Dasypodaini				
<i>Hesperapis (Amblyapis) larreae</i> Cockerell, 1907	0	32	0	0
<i>Hesperapis (Disparapis) sp. 1</i>	27	40	0	0
<i>Hesperapis (Panurgomia) fuschi</i> (Viereck, 1909)	1	144	1	0

“core area”) made from 2000 to 2008 (Fig. 1). Not included were the samples made by pan traps at permanent sites in 2001. In this dataset, samples were included regardless of sampling technique (pan trap, aerial netting at flowering plants) or duration, and included collections made at the permanent sites and intervening sites (Tables 2, 3).

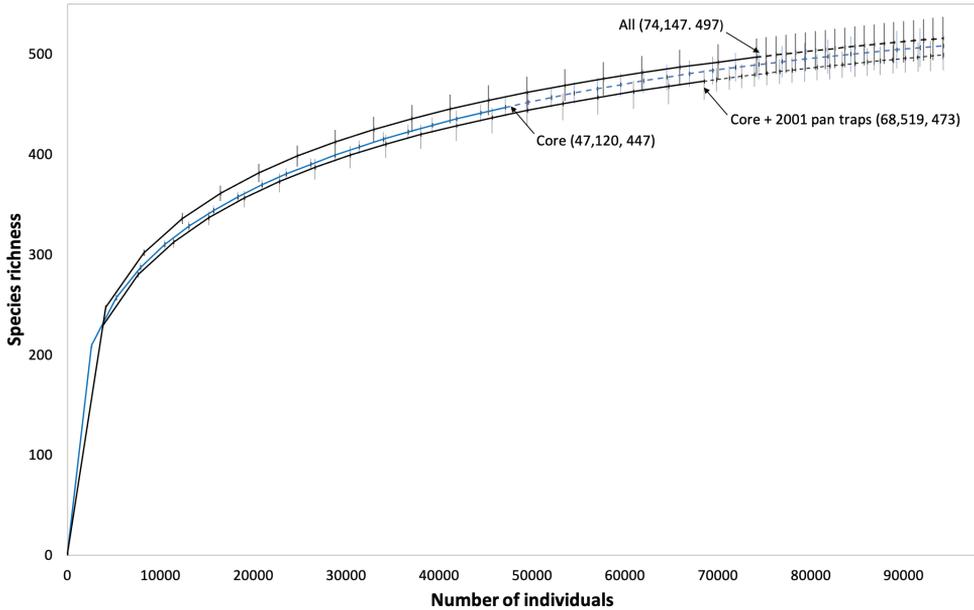
We tested if results from the 2001 intensive pan trap study differed from the results from the same “core area” sampled from 2000–2008 by comparing the accumulation curves from both datasets after they were standardized for equal sample size and coverage following the approach by Chao et al. (2014). Predicted species richness was estimated after the two samples were extrapolated to 42,798 individuals, twice the abundance of the smaller sample (pan traps from 2001 at the permanent sites,  $N_{\text{observed}} = 21,399$  individuals) as recommended by Chao et al. (2014) and implemented in the program iNext ([http://chao.stat.nthu.edu.tw/wordpress/software\\_download/inext-online/](http://chao.stat.nthu.edu.tw/wordpress/software_download/inext-online/)). Confidence intervals and standard errors were calculated from 50 bootstrap replicates. Curves were significantly different if confidence intervals did not overlap. The contribution of vegetation types to bee species richness is not considered in this study. An earlier study found that there was little difference among vegetation types in bee species richness and composition, most likely because of the close proximity of the habitats and sites sampled (Minckley 2014).



**Figure 2.** Species estimates differ among single year and multi-year bee sampling. Comparison of sample-sized-based rarefaction (solid lines) and extrapolation (dashed line) from the pan traps samples at permanent sites in 2001 and the samples made by netting and pan traps throughout the same area encompassed by the permanent sites over 9 years (the “core” area). Calculations here are for Hill numbers of order  $q=0$ ; orders  $q = 1$  and  $q = 2$  are in Suppl. material 1: Figures S1–S3. Bee species richness at the base sample size of 42,798 individuals (i.e., double the smaller reference size) is 406.0 for samples from the core area and 321.8 from the 2001 pan traps. Although bees were sampled from the same area, differences in sampling and years sampled gave different species richness estimates.

## Species richness

To examine if the samples from the valley floor approximated the species richness of the fauna in a larger regional area, we compared species composition and estimated species richness to our complete dataset of bees from the San Bernardino Valley that includes all bee samples including two from nearby areas. One area extended 18 km east from the valley floor area up to desert grassland habitat. We refer to the collections from this area as from “peripheral” sites (Fig. 1). These samples were made during the months when samples were made in the valley floor and used pan traps and aerial netting. A second set of samples was made from 2009–2014, as part of a study of cactus reproductive biology by W. Radke, at a limestone outcrop dominated by desert vegetation approximately 10.5 km north-northeast of the valley floor area (Fig. 1). Most, but



**Figure 3.** Estimates from all sampling regimes predict approximately 500 bee species in the San Bernardino Valley. Comparison of sample-sized-based rarefaction (solid lines) and extrapolation (dashed line) from samples made in the core area, core area combined with the 2001 pan trap sampling at permanent sites, and all samples made in the San Bernardino Valley. Numbers in parentheses are the number of individuals in each dataset and the number of species. Calculations here are for Hill numbers of order  $q=0$ ; order  $q = 2$  is in Suppl. material 1: Figure S4. Estimated bee species richness at the base sample size of 94,240 individuals (i.e., double the smaller reference size of the smallest dataset) is 499.3 species, 508.4 and 516.1 species for the Core, Core + 2001 pan trap and All datasets respectively.

**Table 2.** Sampling effort for bees among four areas in the San Bernardino Valley. Pan trap sampling followed the protocol of LeBuhn et al. (2007).

	Sampling years	Sampling months	Collections (date x site)	Floral host sp.	
				pans	net
2001 pan	1	Apr–Sep	848	848	n.a.
Core area	9	Apr–Sep	1370	788	590
Perimeter	9	Apr–Sep	131	109	22
Limestone	5	Mar–Apr	44	29	15

not all, of these samples were made in the spring months and included sampling by pan traps and nets. Tables 2, 3 show details on the number of collections and sampling protocols used for these two areas.

Here, and as described above, the standardized curves of species interpolation and extrapolation and sample coverage were generated by the program iNEXT ([http://chao.stat.nthu.edu.tw/wordpress/software\\_download/inext-online/](http://chao.stat.nthu.edu.tw/wordpress/software_download/inext-online/)), and comparisons of datasets and estimates of species richness were done as recommended by Chao et al. (2014). Predicted species richness from samples made in the core area, core area plus

**Table 3.** Specimen collections of bees from four areas in the San Bernardino Valley.

	# individuals	# species	# unique species
2001 pan	21403	277	23 (8.3%)
Core area	47120	447	132 (29.5%)
Perimeter	3253	221	12 (5.4%)
Limestone	2375	77	12 (15.6%)

2001 pan traps, and samples from all sites made in the region was estimated after the samples were extrapolated to 92,240 individuals, or twice the abundance of the smallest sample (core area collections,  $N_{\text{observed}} = 47,120$  individuals). Confidence intervals and standard errors were calculated from 50 bootstrap replicates, and accumulation curves were considered significantly different if confidence intervals did not overlap.

### Comparison to other studies

Meiners et al. (2019) recognized that comparisons among long-term bee studies would be more informative if differences in the area sampled were considered. To standardize species-area relationships, they generated the species-area curve from 22 long-term bee studies in the United States and then ranked each study based on the percent difference between observed and predicted species density. Meiners et al. (2019) included the San Bernardino Valley study in their analysis but calculated species density using the area of the San Bernardino National Wildlife Refuge (1088 km<sup>2</sup>), instead of the area among permanent sampling sites (16 km<sup>2</sup>), and an earlier estimate of bee species richness ( $N = 383$ ) reported in Minckley (2008) than known at present ( $N = 473$ ). We used the same data and study sites included in the Meiners et al. (2019) study to compare new results on species density from the San Bernardino Valley to the other studies. Table 4 in Meiners et al. (2019) with changes updated to reflect the findings in this study are in Suppl. materials 1: Table S2.

### Results

Samples limited only to pan traps at permanent sites in 2001 yielded a total of 21,399 specimens representing 277 bee species (Table 1) from 848 samples (day x site). Samples over nine years and more collections ( $N = 1370$ ) with both pan traps and netting at flowers (Table 2), and from the same area defined by the permanent sites, yielded more than twice the specimens and 447 species (Table 3), including 58 species not collected in the 2001 pan trap dataset. Of the total specimens represented when the two datasets are combined, 31% were from the intensive pan trap sampling in 2001 and 69% were from sampling using nets and pan traps across multiple years. The species accumulation curves from these two sets of samples differ significantly after 200 individuals, as judged by non-overlapping confidence intervals (Fig. 2), despite having been collected from the same area (Fig. 1) and representing robust samples based on

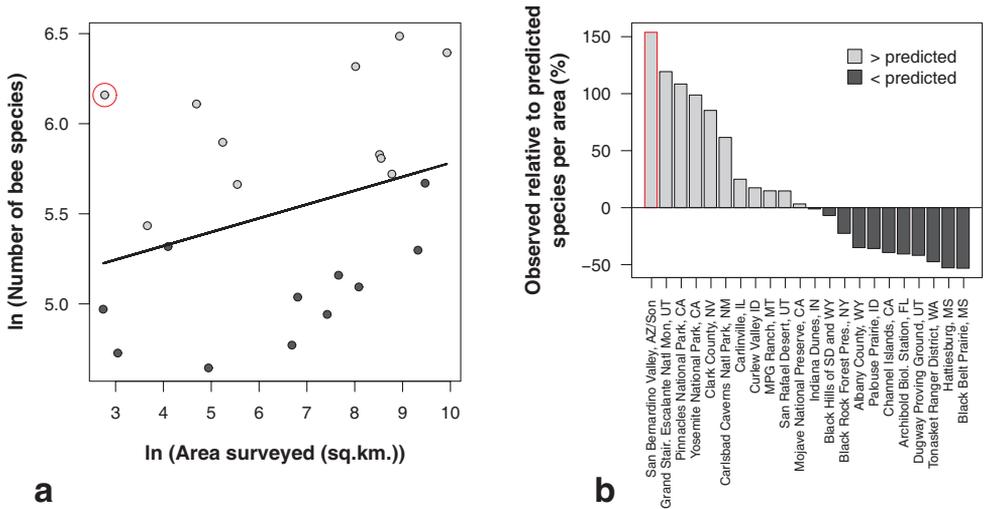
estimators that include sample coverage (Suppl. material 1: Figures S1–S4). The core area samples rarefied to the number of individuals captured in the 2001 pan trap samples ( $N = 42,798$ ) yielded significantly more species ( $N = 437.6$ ) than the 321.8 species predicted from the 2001 pan trap samples (Fig. 2). Overall, the observed species richness from the intensive 2001 pan trap sampling yielded 62% of the species collected from the core area over all 9 years.

Far fewer collections of bees were made from sites outside the core area and these amounted to fewer individuals and species of bees (Tables 2, 3). Nevertheless, the 221 species from the peripheral and limestone samples are a large fraction (79%) of the 277 species captured by pan traps in 2001 and about half the number of species represented in the core area dataset (Table 3). Twelve species were unique to the peripheral site samples. The limestone outcrop samples were the smallest in terms of specimens collected and species (Tables 2, 3), however, 12 of the species were unique even though sampling was focused primarily on pan traps and bees were recorded from only two floral hosts (Table 2).

Including all samples at all sites in the area defined by the permanent sites (2001 pan traps and core area) yielded 473 bee species (Table 1). With the additional sampling made at the peripheral sites and the limestone outcrop there are 497 bee species known from the San Bernardino Valley (Table 1). Overall, the two datasets from the area defined by the permanent sites (2001 pan traps and core area) captured most of the bee species richness in the desert areas of the San Bernardino Valley; samples for sites peripheral to the core area increased the total number of bee species by only 12 species.

Pooled across all sites in the region the collections total to 74,147 individuals and 497 bee species (Table 1). Although the core plus 2001 pan trap dataset has many more individuals ( $N = 68,519$ ) than the core dataset ( $N = 42,120$ ), it results in a species accumulation curve that is significantly lower than the curve based on all datasets combined (Fig. 3). Up to approximately 42,000 individuals, the species accumulation curve from the core dataset is significantly lower than the curve based on all datasets combined. However, at greater numbers of individuals the curves are statistically indistinguishable based on overlapping confidence intervals (Fig. 3). Extrapolations of species richness to 94,240 individuals predicted 508.4 species for the core area dataset and 498.3 species for the 2001 pan trap combined with the core area dataset and closely approximate the estimate of 516.1 bee species based on all samples made in the San Bernardino Valley (Fig. 3). The increasingly flattened accumulation curves as more individuals are sampled indicate these estimates of bee species richness are unusually robust (see Williams et al. 2001), and biologically reasonable, given that they closely approximate the number of bee species ( $N = 497$ ) from all samples combined made by us in the San Bernardino Valley.

Among the 22 long-term bee studies that Meiners et al. (2019) listed, three (Yosemite National Park, Clark County, Nevada and Grand Staircase Escalante National Monument) reported more bee species and only one (Black Rock Forest Reserve, New York) was from a smaller area than the core area sampled in the San Bernardino Valley (Suppl. material 1: Table S2). The updated information from the San Bernardino Valley



**Figure 4.** Higher bee species density in the San Bernardino Valley than that reported from other long-term studies. Species density of bees for large-scale studies in North America determined by species-richness relationships following Meiners et al (2019) with updated information from this study. a) the trend-line indicates expected change in species richness with area sampled based on 22 studies (listed in Table 4 of Meiners et al [2019]) plus the San Bernardino Valley (black dot circled in red). b) is the difference in bee species observed relative to the prediction from the trend line in a). Updated information from the San Bernardino Valley alters the rank of species density from that shown in Fig. 5 of Meiners et al (2019).

changed the species area curve and the rank order of species density for the 22 long-term bee studies as judged by the percentage change between observed and predicted species per area (Fig. 4a, b). Meiners et al (2019, see their fig. 5a, b) concluded that the six sites with the greatest percentage increase over that predicted from the species-area curve was Pinnacles National Park, California followed in descending order by Grand Staircase Escalante National Monument, Utah, Yosemite National Park, California, Carlsbad Caverns National Park, New Mexico, Clark County, Nevada and the San Bernardino Valley, Arizona/ Sonora. In our study with the new information reported herein, the San Bernardino Valley, Arizona/ Sonora is the highest ranked study followed in descending order by Grand Staircase Escalante National Monument, Utah, Pinnacles National Park, California, Yosemite National Park, California, Clark County, Nevada, and Carlsbad Caverns National Park, New Mexico. With these changes, bee species density from the valley floor samples in the San Bernardino Valley is greater than any other area in North America surveyed to date (Fig. 4b).

**Discussion**

The San Bernardino Valley of the Chihuahuan Desert is extremely rich for bees. An area of 16 km<sup>2</sup> that varies in elevation by less than 120 m yielded 277 species in

one year of sampling and 473 species over nine years. The four bee surveys in North America that have reported more bee species than are known from the San Bernardino Valley (N = 656 species, Great Staircase Escalante National Monument Utah; N = 598 species, Clark County Nevada; N = 554 species, Yosemite National Park California; N = 450 species, Pinnacles National Monument California) are much greater in area and topographic complexity (Suppl. material 1: Table S2, Meiners et al. 2019). When the effect of area alone is standardized, the density of bee species in the San Bernardino Valley, is the highest reported from any long-term study of bees in North America.

For questions that rely on accurate estimates of species composition and richness, this study highlights the importance of using a variety of sampling protocols and long-term sampling. Our dataset based on samples from one passive sampling protocol (pan traps) in 2001 that recovered more than 21,000 specimens yielded 93 fewer species than we found from samples made over nine years that included pan traps and aerial netting at flowers (Table 3). If we assume that the collections from 2001 pan traps and core area are complete measures of species richness, pan traps underestimated species richness by 38%. The significantly lower species accumulation curve from the 2001 pan trap samples than the long-term dataset from the same area (Fig. 2) is further evidence that surveys based only on pan traps underestimate bee species richness. Biases of pan trap sampling for bees have been well documented (reviewed in Packer and Darla-West 2021) but not from a long-term study in a bee diversity hotspot.

There are numbers of reasons why species richness estimates for desert bees are sensitive to sampling duration that broadly apply to biodiversity studies of most desert insects and bees in general. For one, many species, especially those bees that are specialists of one or several host plants, emerge as adults for a brief period per year, are small-bodied with limited dispersal capabilities and occur patchily (Minckley et al. 1999; Kazenel et al. 2020). Many species are rare: singleton (represented by one specimen) and doubleton (represented by two specimens) species represent 83 (16.7%) and 52 (10.5%) of all species in our full dataset, respectively. Finally, bee populations vary dramatically between years in response to changes in floral resources (Crone 2013) and propensity to remain in diapause (Minckley et al. 2013). Variation of species abundance taken at the same location across years is often marked (Stubblefield et al. 1993; Meiners et al. 2019). An extreme case occurred in spring 2006 when a drought resulted in the complete absence of 11 of 46 bee species that had been abundant in the San Bernardino Valley in the near-normal rainfall years before and after (Minckley et al. 2013). Of the absent species, seven were pollen specialists of plants that require rainfall to trigger growth and flower (annual species and creosotebush [*Larrea tridentata*]), and four were pollen generalists. In contrast, the five pollen specialist bee species of mesquite (*Prosopis velutina*), a deep-rooted perennial that blooms regardless of winter rainfall, were active during the drought.

The ability to undergo facultative diapause is common among desert bee species (Hurd, 1957; Rust et al. 1988; Danforth et al. 2019) and suggests a bet-hedging life history strategy is a common adaptation for persisting in these areas (Minckley et al. 2013). Danforth (1999) showed in a laboratory experiment that some *Macrotera portalis*

(Timberlake, 1954), a specialist of mallows (*Sphaeralcea* spp), emerged in response to moisture in the late-summer (when it is active) but others remained in diapause for one or two years. Desert plant species vary tremendously in their propensity to emerge and bloom (Bowers and Dimmitt 1994; Bowers 2005), even in common gardens (Gremer and Venable 2014; Gremer et al. 2016), which suggests that activity of the specialist bees that depend on different hosts will differ in their activity between years and across habitats. Sampling that is only occasional through the season or widely-spaced across an area may not detect many resident bee species. In the San Bernardino Valley, there is 80% turnover of pollen specialist species every two weeks in the spring (Minckley 2008), suggesting that samples for these and other short-lived solitary bees should be more than bimonthly. The samples in this study made over 9 years and using pan traps and nets minimize these biases and account for the higher estimates of bee species richness than from very intensive pan trapping in one year even when both datasets are from the same location.

The species richness estimates using extrapolation methods from the samples on the valley floor suggest approximately 500 bee species occur in the San Bernardino Valley, of which we captured 497 when all samples in the region were combined (Fig. 3, Table 1). Extrapolations of all samples suggests species richness is 516.1, not substantially more than the number of species observed, and approximately 14% of the 3562 species known for all of North America north of the United States-Mexico border (Ascher and Pickering 2020). The number of bee species from the San Bernardino Valley and their relative abundance sets a reasonable expectation for communities in other undisturbed desertscrub/ desert grassland habitats of the Chihuahuan Desert and can be usefully compared to areas with more severe human impacts. For example, a compilation limited to described bee species from southeast Arizona in the American Museum entomology collection and from the San Bernardino Valley yielded 540 bee species when desert scrub, mid-elevation grassland and high montane ecosystems were included (Minckley and Ascher 2013). Considered individually, the three desert areas north of the San Bernardino Valley had between 150–180 species but did not include some genera that had yet to be curated in the American Museum of Natural History collection. Thus, further taxonomic and curatorial work should substantially increase the bee species richness from these well-collected sites. Similarly, a 12-year study of bees on the extreme northern edge of the Chihuahuan Desert in New Mexico (approximately 510 km NNW of the San Bernardino Valley) captured 308 bee species using a modified pan trap design (Kazenel et al. 2020). Because bee species richness is often underestimated by pan traps, the reported number of species suggest this bee fauna is much richer and may be comparable to that in the San Bernardino Valley.

Museum records, taxonomic revisions, and surveys have long suggested that bee diversity runs counter to that of the plants they pollinate in that bees have peak diversity in the western hemisphere in the Chihuahuan, Mojave and Sonoran deserts and in the eastern hemisphere around the Mediterranean Sea (Michener 1979, 2007). The repeat sampling from a defined area in the Chihuahuan Desert provides empirical data that supports this counterintuitive biogeographical pattern. However, more sampling of bees is needed in tropical and subtropical areas, as well as a more complete picture

of herbaceous plant biogeography. Plant biogeography still rests largely on what we know about tree species, and when short-lived plant species are better documented (Massante et al. 2019) their distribution may more closely mirror the distribution of their primary pollinators, the bees.

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## Supplementary material I

### Tables S1, S2, Figures S1–S4

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Data type: tables and figures

Explanation note: **Table S1.** List of identification keys used for each of the genera sampled in the San Bernardino Valley. **Table S2.** Table 4 from Meiners et al (2019) of bee species density for native bee inventories with at least 100 species in natural or semi-natural areas across the United States. Information here is updated for the San Bernardino Valley (this study). **Figure S1.** Comparison of sample-sized-based rarefaction (solid lines) and extrapolation (dashed line) from the pan trap samples at permanent sites in 2001 and the samples made by netting and pan traps throughout the same area encompassed by the permanent sites over 9 years (the “core” area) following the approach of Chao et al (34). Bee species richness at the base sample size of 42,798 individuals (i.e., double the smaller reference size) is 406.0 for samples from the core area and 321.8 from the 2001 pan traps. The two top graphs are sample-size-based rarefaction and extrapolation curves for the pan trap samples from 2001 and the samples made in the core area from 2000–2008. The bottom three graphs are comparisons of samples from the pan trap samples from 2001 and the core area for each order of  $q$ . Although bees were sampled from the same area, differences in sampling and years sampled gave different species richness estimates for each order of  $q$ . The first graph in lower row is the same as Fig. 1 in the paper and presented here for completeness. **Figure S2.** Plot of sample coverage for rarified samples (solid line) and extrapolated samples (dashed line) as a function of sample size for the pan trap samples at permanent sites in 2001 and the samples made by netting and pan traps throughout the same area encompassed by the permanent

sites over 9 years (the “core” area). 95% confidence intervals calculated from 50 bootstrap replications are not prominent because of their small size. Both samples have greater than 95% coverage and broadly overlap up to their reference sizes (21,403 individuals for 2001 pan trap samples, 47,120 for core area samples) and when extrapolated to twice the reference sample size. **Figure S3.** Comparison of the coverage-based rarefaction (solid line) and extrapolation (dashed line), for the pan trap samples at permanent sites in 2001 and the samples made by netting and pan traps throughout the same area encompassed by the permanent sites over 9 years (the “core” area) for all three orders of  $q$ . In each of the three graphs the lower line is the 2001 pan trap samples and the upper line is the samples from the core area. Note that the lines do not intersect at any sample coverage. **Figure S4.** Comparison of the coverage-based rarefaction (solid line) and extrapolation (dashed line), for the samples made in the core area (middle line), core area combined with the pan trap sampling at permanent sites (blue line on bottom), and all samples made in the San Bernardino Valley (top line) at  $q=0$ . The confidence intervals are very small they do not show on the graph. Sample coverage is above 95% for diversity values below 200 species for the datasets and the extrapolations overlap broadly at higher sampling coverage indicating all three datasets predict very similar bee species richness in the San Bernardino Valley. Note that the analyses at other orders of  $q$  are not shown because the results match that shown here.

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