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Original article

Faunal composition and species richness differences of bees (Hymenoptera: Apiformes) from two north American regions*

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Abstract – Host breadth and global bee species diversity are thought to be linked. Areas where bee species richness is greatest have a greater proportion of oligolectic species and fewer social species. I compared the bee faunas of two North American regions (one mesic, one xeric) and two nearby habitats (riparian and desert scrub). Species richness is greater in the xeric than in the mesic North American region. Despite strongly bimodal bloom in the xeric region and continuous bloom in the mesic region, their bee faunas were similar in the proportion of solitary oligolectic and polylectic bees. Oligolectic species of both areas have short lifespans. Social and cleptoparasitic species made up a greater percentage of the fauna in the mesic North American region. Nearby mesic and xeric habitat both had social species but xeric habitats were richer in oligolectic species. Phylogeny and historical biogeography in combination with ecology of bees and plants will be needed to understand differences of bee faunas.

biodiversity / host specialization / species gradient / pollinator / oligolecty

1. INTRODUCTION

Recent changes in our understanding of the evolutionary relations among bees indicate that pollen host specialization (i.e., oligolecty) occurred early in the evolutionary history of bees, that shifts among pollen host generalization (i.e., polylecty) and specialization have occurred repeatedly (Danforth et al., 2006), and that the loss of specialization may be as common as its gain (Müller, 1996; Larkin et al., 2006). These findings indicate host breadth in bees can respond quickly to ecological variability, and opens the tantalizing possibility that narrow host specificity originated in the sphecid ancestors of bees and in the context of hunting insects rather than in the context of harvesting pollen. Further work on relationships among bees and sister groups in the Spheciformes (*sensu* Michener, 2007) will be needed to support or refute this latter hypothesis. Nevertheless, this points out how a solid understanding of apoid phylogeny provides insights into our understanding of host breadth ecology and evolution among bees.

Pollen host breadth and worldwide bee diversity are thought to be linked. Where bee diversity reaches its maximum in xeric temperate areas (Michener, 1954, 1979, 2000), the proportion of the solitary bee species that are pollen specialists is greatest (Moldenke, 1976). Furthermore, the proportion of the bee fauna that are social species is low. Multiple, often interrelated, hypotheses have been suggested to explain these patterns. Michener (1954, 1979) proposed that competition among bee species for floral resources may generate the diversity gradient. Social bee species are pollen generalists that require floral resources throughout the spring and summer as their colonies develop. Therefore, social bees may be rare in xeric areas because

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floral resource availability can be seasonally scarce. This lack of social species in deserts may result in less competition for available floral resources and, in turn, allow greater diversification of solitary bees. In addition, the high numbers of solitary bee species in xeric areas may allow more species to co-occur because available floral resources are divided more finely.

Hypotheses unrelated to competition have also been proposed to explain bee species diversity gradients. First, specialist bee species may be more common in xeric areas because they are able to predict more accurately when bloom on their host plant occurs than can pollen generalist bee species (Minckley et al., 2000). Deserts are characterized as having low overall annual precipitation and periods lasting months to years of little or no precipitation. Minckley et al. (2000) showed that species richness and abundance of pollen specialist bees that use *Larrea tridentata* was greatest where the host plant bloomed least frequently, and suggested that the cues pollen specialist species use that signal if they should either remain in diapause or emerge enables these species to persist in deserts. For bees that specialize on one or several closely-related plant species, the likelihood of evolving cues that seasonally synchronize emergence activity with host plant flowering should increase and selection for this match of emergence/diapause cues and host plant bloom should be strongest where rainfall/bloom is least predictable, a pattern with what Minckley et al. (2000) found. Generalist bees do not experience the same level of selection to synchronize with bloom because they use multiple hosts. Similarly, under these same conditions of unpredictable bloom, social species tend to be excluded because floral resources are not available throughout the entire season during which colonies develop.

A second hypothesis proposed by Rozen (in Michener, 2007) suggests that ground-nesting solitary species are excluded from tropical areas because fungi and other pathogens that attack nest provisions are more common in water-saturated tropical soils. Finally, Michener (1979) noted that bee communities in xeric areas are dominated by short-lived species that are active either in the spring or late summer. Such low overlap of two faunas per year could further contribute to greater species richness.

In this study, I compare the bee faunas of a mesic region and a xeric region in North America to examine if these predictions are supported. The mesic region is Carlinville, Illinois, a temperate area with continuous flowering throughout the spring, summer and fall months. The xeric region is the San Bernardino Valley Sonora, Mexico and Arizona, USA (hereafter referred to as San Bernardino), an area with one spring bloom, an intervening dry period, and a second late-summer bloom. Bee collections from Carlinville and San Bernardino were made from limited areas that are not topographically complex and have been continued for multiple years so are unusually well-studied for bees.

In addition to the comparison of two geographically distant regions in North America, I compare bee samples made from a mesic riparian habitat and from a nearby xeric desert scrub habitat at San Bernardino, to evaluate if patterns found between Carlinville and San Bernardino are repeated at local spatial scales. Because these plots share a common pool of bee species, differences in the bee faunas should be primarily due to local ecological conditions. The specific predictions I examine with these comparisons are as follows. One, are social species less common in xeric areas? Support for this hypothesis will be if the proportion of social species is significantly greater in Carlinville than in San Bernardino and in the riparian habitat more than desert scrub habitat at San Bernardino. Two, are short-lived species favored in xeric areas with a short, discrete bloom period? This hypothesis predicts that a greater proportion of bee species are long-lived in the Carlinville fauna than the San Bernardino bee fauna, and more long-lived species occur in mesic plots than in xeric plots in the San Bernardino. Finally, are pollen specialist bee species more diverse in xeric habitats? This prediction will be supported if the proportion of specialist species is greater at San Bernardino than at Carlinville, and greater in xeric desert scrub habitat than in mesic riparian habitat at San Bernardino.

2. MATERIALS AND METHODS

2.1. Study sites and bee faunal data

2.1.1. Carlinville, Illinois, USA

Charles Robertson collected floral visitors within a 16 km radius of Carlinville, Illinois between 1884 and 1916 and self-published his observations (Robertson, 1929). Based on climate data taken at Carlinville between 1971 and 2000, the area is mesic temperate. Average total precipitation/year is 98 cm. and when bees are active (April–October) rain averages nearly 10 cm/month, with slightly more in the spring (April = 10 cm, May = 10.1 cm, June = 9.9 cm) than in the late-summer months (July = 9.3 cm, August = 8.5 cm, September = 5.8 cm).

2.1.2. Carlinville bee fauna

I entered all animal-plant records Robertson reported (Robertson, 1929) into a database. Bee names were checked for their current taxonomic status following Michener (2007). Plant names were updated to current status as recognized by the Integrated Taxonomic Information System (www.itis.gov).

Robertson observed bees visit 436 of the 458 plant species he studied. Bees totaled 288 species in 51 genera. For each plant species, he reported the first and last date in any year flowers were open. I therefore estimated seasonal phenology of bloom by scoring the number of plant species in flower each two weeks of the year. Robertson did not report total abundance of floral visitors, but did note if they were rare, common, or abundant and if their visits to a plant were to collect nectar, pollen or were exploratory. Also not reported by Robertson were the dates when bees were active. I therefore estimated the activity period for each bee species by using the earliest and latest date their recorded floral hosts were in flower. Although not ideal as a measure of seasonal phenology for bees, the discrepancy invariably overestimates the actual activity period and provides a conservative test for the pattern I seek to characterize (bee species turnover). Robertson sampled at most plant species on multiple days and years (Marlin and LaBerge, 2001), thus undersampling (Williams et al., 2001) should not overly bias bee-plant visitation patterns. Marlin and LaBerge (2001) determined that Robertson generally focused on one or a few plant species per day and kept a detailed voucher collection. Plants that bloomed only briefly were transplanted to his residence and observed, so insect records include visits to plants in native and cultivated habitats.

2.1.3. San Bernardino Valley, Sonora Mexico and Arizona, USA

The San Bernardino Valley runs north-south at 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 36 cm/year. Based on data from 1928–1982 taken at the nearest weather station (Stephens Ranch, Arizona), rain averages 4.1 cm/month when bees are active (April–October), with spring months much drier (April = 0.5 cm, May = 0.7 cm, June = 1.3 cm) than late-summer months (July = 9.6 cm, August = 8.1 cm, September = 3.9 cm).

In 2000, 52 permanent 100 × 100 m plots were established in San Bernardino to sample bees and flowering plants, and to understand how habitat heterogeneity contributes to local bee species richness in a semi-pristine ecosystem. Habitats where plots were established represent a mesic-xeric gradient that include desert marsh, riparian, mesquite forest, upland desert wash, grassland and desert scrub. Data from plots used in this study are from eight of the permanent plots, four in riparian habitat and four in desert scrub habitat. Riparian plots are dominated by cottonwood (*Populus fremontii*), mesquite (*Prosopis juliflora*) and emergent aquatic vegetation, whereas desert scrub sites are dominated by creosote bush (*Larrea tridentata*). All plots in both habitats are within a four square kilometer area.

The complete list of bee species for San Bernardino is based on over 24 000 specimens collected by net and pan traps from all 52 plots between 2000 and 2007. In total, 383 species in 69 genera are represented with ** identified as morphospecies and four still undescribed (Appendix 1 online). All bee species were collected for later identification in the laboratory except *Apis mellifera* which often could be identified on the wing. This present species list underestimates actual bee species richness. Less than 40% of the specimens that have been collected are identified and species determination of some species-rich genera (e.g., *Lasioglossum*, *Melissodes*, *Nomada*, *Eucera*, and *Habropoda*) has not been adequate. Therefore the comparisons of total bee fauna made here with the better-known fauna of Carlinville are preliminary in the sense that results may change as more species are identified.

2.1.4. San Bernardino riparian and desert scrub habitats

Comparisons of bees in riparian and desert scrub habitats in San Bernardino are based on data from samples taken with pan traps at each plot once every 10–14 days in most months of 2001 throughout the bee active season. Three yellow, three white and three fluorescent blue traps filled with soapy water were placed along a transect at each site for three to five hours beginning between 0830–1000 h. Colored pan traps have several known biases in the bees they attract. They are effectively avoided by large-bodied, strong-flying bee species, and sample fewer species than netting in standardized manner (Roulston et al., 2007 and references therein). However, they have the advantages of capturing bees when flowers are not in the plot and of avoiding disparities that arise among collectors with different collecting abilities. All specimens from these plots collected in 2001 were identified to species level.

On each day the plots were sampled, the plant species in flower on the plot were recorded. Seasonal bloom phenology was then estimated by averaging the number of flowering plant species per plot.

2.1.5. Categorization of Carlinville and San Bernardino bee species

Bee species from Carlinville and San Bernardino were placed into the following functional ecological groups: social or solitary, oligolectic or polylectic, and pollen-collecting or cleptoparasitic. Information on host breadth for bees from Carlinville came primarily from Linsley (1958) and Krombein et al. (1979), and for bees from San Bernardino from Krombein et al. (1979). Species which lacked information on social status or host breadth were still scored if all other species in the taxonomic group shared the same biological characteristic. For example, I categorized all species in the subgenus *L.* (*Dialictus*) as social because no temperate species are known to be solitary, and all species of *Perdita* and *Calliopsis* as oligolectic because a majority, of species in these genera are oligolectic. I scored species of *Ceratina* and *Xylocopa* as solitary because most or all females of the species in these two areas nest as solitary individuals (Gerling and Hermann, 1978; Michener, 1988). All social species were considered polylectic because they are active longer than any single floral host, so eventually shift to other various hosts through the season. Species were not used in the analyses if their social status or host breadth were not known, or if they were in groups that have both social and solitary or oligolectic and polylectic species.

2.2. Seasonal species turnover at Carlinville and San Bernardino

To examine the rate and extent that the bee fauna changed through the activity season (species turnover) at Carlinville, I recorded the bee species active every two weeks from April to the end of September and compared these lists to the list of bees active during the first two weeks of April. One analysis was done for all pollen-collecting bee species. I then examined the same pattern separately for groups of pollen-collecting bee species that were social and polylectic, solitary and polylectic, and solitary and oligolectic. The same comparisons were made for bees from San Bernardino. For this analysis, I combined the pan trap samples from the riparian and desert scrub habitats to make the San Bernardino fauna as representative of the entire fauna as possible. I expected that high similarity of bee faunas active later in the season to bee faunas active early in the season would indicate many bee species were long-lived or had multiple generations per year. In contrast, if bee communities in these same two periods were very dissimilar a fauna dominated by short-lived species would be indicated. Faunal similarity was measured using Jaccard's similarity index.

2.3. San Bernardino mesic and xeric sites

The bee fauna from the desert scrub and riparian habitats at San Bernardino was categorized as described above (social, solitary, oligolectic, polylectic, pollen-collecting, cleptoparasitic). Comparisons of bee species composition and abundance from mesic and xeric sites were done using contingency tests.

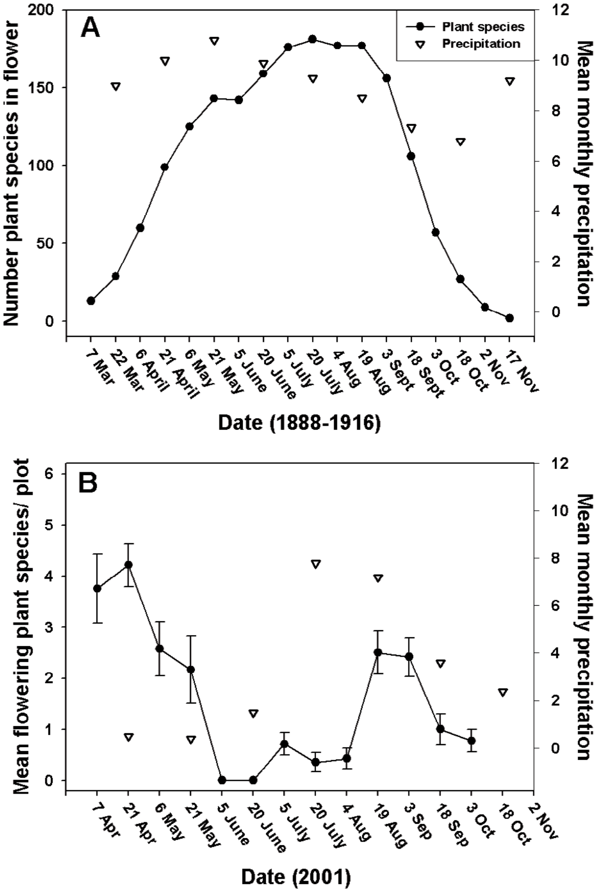

Figure 1. Phenology of flowering plants (mean number of flowering plant species/plot) and precipitation (mean cm/year) during the activity period for bees in (A) Carlinville, Illinois (March to November) and (B) San Bernardino Valley, USA/Mexico (April to September).

3. RESULTS

3.1. Carlinville bee fauna

Flowering phenology of plant species at Carlinville is unimodal with a peak of more than 150 species in July (Fig. 1A). Precipitation averages more than 6 cm in all months when bees are active.

Of the 288 bee species collected in Carlinville (Appendix 1 online), 71 (25%) species were cleptoparasites, 30 (10%) were eusocial, 180 (63%) were solitary. Social status of six species was scored a uncertain. Of the social species, nine are in the genus *Bombus*, 17 in *Lasioglossum* (*Dialictus*), and three in *Lasioglossum* (*Evylaeus*). Sixty nine species (24%) in 20 genera were oligolectic at the level of plant family, tribe, genus or species. Most oligolectic species were in the genus *Andrena* or *Melissodes*.

The social bee fauna at Carlinville remains stable through the season, while the solitary bee fauna changes markedly (Fig. 2A). Faunal similarity of social bee species remained above 80% throughout the year. In contrast, by early July approximately half of the solitary polylectic species and most of the oligolectic species are not the same from those active in early April. Less difference through the season among solitary polylectic bee species than among solitary oligolectic species indicates

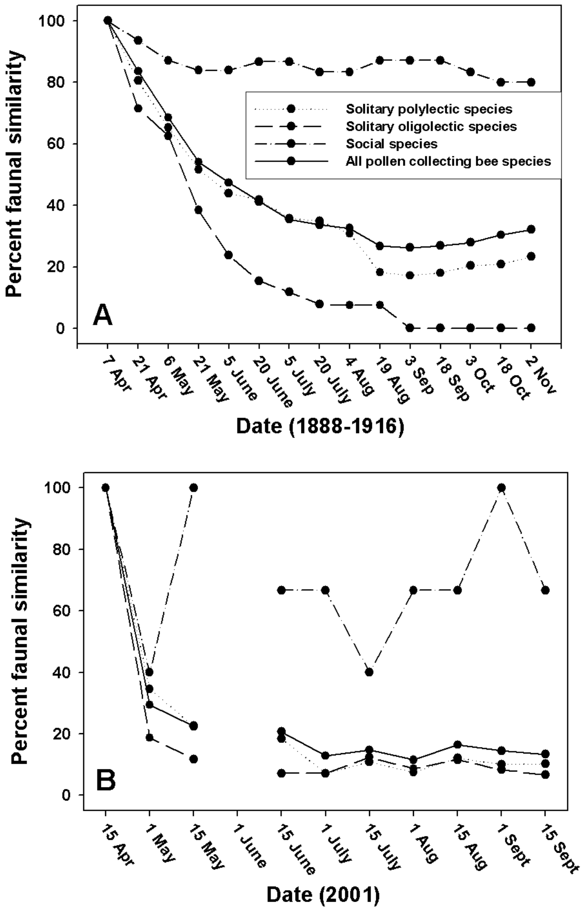

Figure 2. Bee fauna turnover through the season for all pollen-collecting species, social species, solitary polylectic species and solitary oligolectic species for (A) Carlinville, Illinois, and (B) San Bernardino Valley.

that some solitary polylectic bee species are long-lived or multivoltine. However, many solitary polylectic and most oligolectic bee species are univoltine and short-lived.

3.2. San Bernardino bee fauna

San Bernardino receives little or no precipitation between March and June, however, many plants flower in the spring in response to rains the previous winter (Fig. 1B). By late-May and June, higher temperatures and lack of precipitation results in progressively less flowering until after rains begin again in July. Biseasonal rainfall generates a bimodal seasonal flowering pattern (Fig. 1B).

Of the 383 bee species at San Bernardino, 65 (17%) species are cleptoparasites, 13 (3%) are social, and 304 (79%) are solitary. Only one species of social bee is in the genus *Bombus*, ten are in *Lasioglossum* (*Dialictus*), and two are in *Halictus*. Oligolectic species comprise 30% of the bee fauna (114 species), with almost half (51 species) in the genus *Perdita*. The second largest group of oligolectic species is in the genus *Calliopsis* (N = 16).

Species turnover in San Bernardino followed the same general pattern as observed in the Carlinville fauna with little turnover of social species and rapid turnover of solitary species (Fig. 2B). The oligolectic bee species of San Bernardino changed by more than 80%

Table I. Species number and abundance of solitary, social and cleptoparasitic bees collected by pan traps in 2001 in the San Bernardino Valley, USA/Mexico at desert scrub and riparian sites.

	Desert scrub sites		Riparian sites	
	Species	Abundance	Species	Abundance
Solitary sp.	76	583	85	1762
Social sp.				
H. tripartitus		21		158
H. ligatus		1		5
B. pensylvanicus		0		1
L. (*Dialictus*) spp.		486		403
Total social sp.	5	508	8	567
Cleptoparasitic sp.	10	18	9	23
Total	93	1119	102	2352

in samples taken two weeks apart in April. Visual comparison of the species turnover curves suggests solitary species at San Bernardino may turnover more rapidly than in Carlinville. Unfortunately, there is no way to discern if this pattern is due to true differences in the biology of bees from these two areas or a result of differences in how data were collected and reported.

Only one native (*Halictus ligatus*) and one introduced (*Apis mellifera*) bee species occur at both Carlinville and San Bernardino. The bee fauna of San Bernardino is richer in species and genera, and composed of a greater proportion of solitary species than the Carlinville fauna (Appendix 1). The Carlinville fauna may have a greater proportion of social species and clearly has a greater proportion of cleptoparasitic bee species than the San Bernardino fauna. Both faunas are composed of many oligolectic species. Patterns of turnover among solitary species in Carlinville and San Bernardino were similar and may be largely the same. Based on patterns of species turnover, the fauna of oligolectic bee species and of solitary polylectic bee species was short-lived in both geographic areas.

3.3. Riparian and desert scrub habitats in San Bernardino

Table I shows the species richness and abundance of solitary, social and cleptoparasitic bee species from the riparian and desert scrub sites in 2001. Overall fewer species and individuals were collected at the xeric desert scrub plots (N = 1119) than at the mesic riparian plots (N = 2352). Counter to the prediction that social bees would be excluded from xeric areas, the proportion of solitary, social and cleptoparasitic bee species did not differ statistically in riparian and desert scrub habitats (Chi-square = 0.37, d.f. = 1, P = 0.83). However, there was a statistical difference in the abundance of solitary, social and cleptoparasitic bees among riparian and desert scrub habitats (Chi-square = 172.44, d.f. = 1, P = 0), due primarily to species of *Lasioglossum* (*Dialictus*) and *Ceratina*. (*L. Dialictus*) was proportionally more common in the desert scrub habitat than in the riparian habitat. Absent or rare in desert scrub were several larger social bee species *Halictus tripartitus*, *H. ligatus*, and *Bombus pensylvanicus sonorus*. *Ceratina* spp. were much less abundant in the desert scrub habitat than in the riparian habitat (Tab. II). *Ceratina* species are long-lived bees that nest aboveground in twigs and grass stems. To examine if longevity might explain local changes in the bee fauna, I combined *Ceratina* species with social species, which are also long-lived. This analysis showed that species composition in desert scrub and riparian habitats was not different (Chi-square = 1.68, P = 0.2) but the abundance of long-lived species was significantly greater in riparian habitats (Chi-square = 107.9, P = 0.0). I repeated this analysis with and without species of *Agapostemon* included because these species are multivoltine, but it is not clear if they are

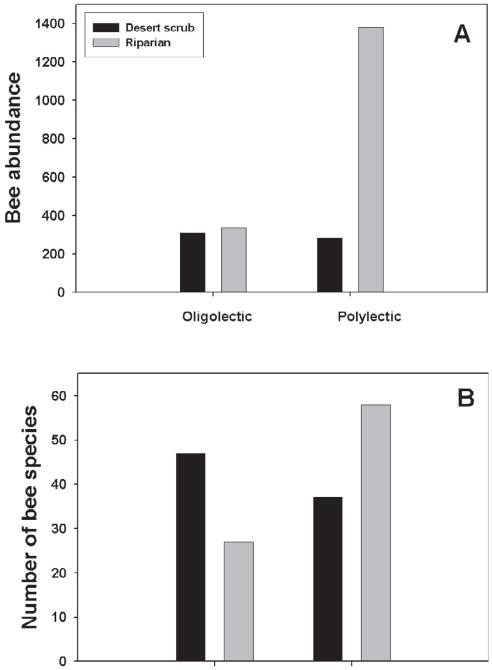

Figure 3. Differences in the number of oligolectic and polylectic (A) bee species, and (B) individuals in desert scrub and riparian sites in San Bernardino Valley, USA/Mexico.

short- or long-lived. The pattern of species composition and abundance remained significant if these *Agapostemon* species were placed in the long- or short-lived category. Overall, more bee species occurred in the riparian than in the desert scrub plots and the proportion of oligolectic and polylectic species differed in species richness (Chi-square = 10.04, P = 0.0015, d.f. = 1) and abundance (Chi-square = 229, P = 0.0, d.f. = 1). More species of oligolectic bees occurred in desert scrub habitat and more species of polylectic bees occurred in riparian habitats (Fig. 3A, B).

4. DISCUSSION

4.1. Comparisons of Carlinville and San Bernardino bee faunas

More bee species and genera occur in San Bernardino than in Carlinville. This difference should only grow larger as more specimens are identified and collections are made at San Bernardino. However, comparison of species richness from Carlinville to San Bernardino will always be limited because sampling effort by Robertson cannot be evaluated statistically. For example, Marlin and LaBerge (2001) in their re-study of the Carlinville bee fauna added 14 bee species from collections made on only 24 of the 458 plant species sampled by Robertson 75 years earlier. These 14 species could have been present yet undetected by Robertson or be recent colonists. I did not include these 14 species in this study because the time elapsed between samples and the difference in plant species sampled.

Bee species of San Bernardino and Carlinville are predominately solitary pollen-collecting species, with a greater proportion at San Bernardino (80%) than at Carlinville (65%). The Carlinville bee fauna had a higher proportion of social (10%) and cleptoparasitic bee species (25%) than San Bernardino (3% social, 17% cleptoparasitic). Part of this pattern for cleptoparasitic bee species relates to the distribution of *Nomada*, which is particularly species rich in Carlinville (20 species vs. 11 species at San Bernardino), and its most common host, *Andrena* (49 species at Carlinville, 12 species at San Bernardino). Nevertheless, cleptoparasitic species from 11 genera occurred in Carlinville and from 15 genera in San Bernardino suggesting the entire pattern cannot be explained by the diversification of one or a few lineages. Wcislo (1987) proposed that bee cleptoparasitism was favored when seasonality drives hosts to synchronize, a hypothesis that predicts more cleptoparasitic species in the fauna of San Bernardino than of Carlinville. As presently known, the bee fauna for San Bernardino does not support the seasonality hypothesis given that this area is much more seasonal than Carlinville. Petanidou et al. (1995) also found that bee faunas from xeric temperate areas were more depauperate in cleptoparasitic bees than mesic temperate areas, which Michener (2007) has interpreted as a pattern stemming largely from the absence of *Nomada* and parasitic species of *Bombus* (*Psithyrus*) in these xeric areas. Clearly, reanalysis of

Table II. Species number and abundance of short-lived solitary bees and long-lived social and solitary bees collected by pan traps in 2001 in the San Bernardino Valley, USA/Mexico, in desert scrub and riparian sites. Numbers of total long-lived species differ because longevity of *Agapostemon* spp. is uncertain. Abundance data are totals for all traps.

	Desert scrub sites		Riparian sites	
	Species	Abundance	Species	Abundance
Short-lived sp.	74 (80)	576	79	794
Long-lived sp.				
Ceratina	1	10	3	924
Agapostemon	1	7	3	23
Social	5	508	8	611
Total long-lived sp.	6/7	518/525	11/14	1535/1558

the seasonality hypothesis by considering phylogenetic history are needed to establish what underlies changes in cleptoparasitic bee diversity.

The similarities among the two geographically-distant bee faunas are as notable as their differences. Species richness of social, solitary and cleptoparasitic bees did not differ greatly even though the taxonomic composition of these ecological groups was very different. Most species are solitary and short-lived despite continuous flowering throughout the bee-active season at Carlinville and pulsed and bimodal flowering in San Bernardino. Both areas have rich faunas of oligolectic bees, which the species turnover curves suggest are more short-lived than other species (Fig. 2A, B), as observed by Robertson (Robertson, 1914).

4.2. Hypotheses of species richness

I examined three predictions that may account for why bee species richness is greater in xeric areas than mesic areas: (1) that social species are excluded from xeric areas; (2) that short-lived species are favored in xeric areas with a short, discrete bloom period, and (3) that oligolectic species are more common in xeric habitats.

4.2.1. Social species

The San Bernardino bee fauna shows that social bee species do occur in desert areas and can be common. In addition, many social species at San Bernardino occur in both xeric desert scrub and mesic riparian habitats. However, two patterns from San Bernardino suggest that many social bee species are excluded or do poorly in xeric areas, and that further study on this matter is warranted. First, the proportion – and probably the actual numbers – of social species in the bee fauna, is less than at Carlinville. More taxonomic study is needed on the *Lasioglossum* (*Dialictus*) species of San Bernardino before the actual numbers of species are known, however, sampling to date has been sufficient to conclude that few other social species in other subgenera/ genera remain to be discovered. Second, abundance of the social bee species, *H. tripartitus*, *H. ligatus* and *B. pensylvanicus*, was significantly less in desert scrub habitat than in the riparian habitat. For *H. tripartitus*, the difference in abundance was five-fold. *L. (Evylaeus) pectoraloides*, another species that was absent from the desert scrub and common (43 individuals) in the riparian habitats, may further support this pattern. The biology of this species has yet to be studied but many *L.* (*Evylaeus*) species are social (Danforth, 2001). Interestingly, all three of these social species (four, if *L.* (*Evylaeus*) *pectoraloides* is included) are larger-bodied than any of the other social species at San Bernardino. Large body size may require more resources than are available in desert scrub habitat in the midsummer dry period, a constraint species with small body size do not suffer.

Conspicuously absent from San Bernardino and present in the social bee fauna of

Carlinville are bumblebees (*Bombus* spp.). Nine species occur in Carlinville and only *B. pensylvanicus sonorus* occurs in San Bernardino, where it is rare. Absence of a single monophyletic group may be due to phylogeny, an ecological, physiological or behavioral trait these species share, or a combination of these factors. Nest site limitation in xeric areas seems unlikely to account for the absence of this group. Temperate *Bombus* species often nest in abandoned rodent burrows which are common in both xeric and mesic temperate areas. Lack of floral resources or water over the dry season (discussed above) may also account for the absence of *Bombus* in xeric areas.

4.2.2. Are short-lived species favored?

Comparisons of bee faunas in the riparian and desert scrub habitats suggested that long-lived species occur in both habitats, but are much more abundant in riparian than in desert scrub habitats (Tab. II). This analysis was confounded by social species which are all long-lived. However, most of the difference in bee abundance between riparian and desert scrub habitat was due to the greater numbers in the riparian areas of solitary bee species in the genus *Ceratina* and analyses done when bees are divided in solitary and social groups showed no difference in bee species richness and abundance among the riparian and desert scrub habitats (Tab. I). *Ceratina* are long-lived, but differ from most bee species at San Bernardino by nesting in twigs and grass stems. Two large perennial grass species, Sorghum (*Sorghum halepense*) and Sacaton (*Sporobolus wrightii*), that are used by *Ceratina* for nest sites (pers. obs.), occur in riparian habitats but not desert scrub habitats at San Bernardino. Both grass species are used as nest sites by *Ceratina* (unpubl. data) and probably account for differences in bee abundance between the desert scrub and riparian habitats. A similar response by cavity-nesting bees was found 150 km northwest of San Bernardino in desert fragments created by urbanization (Cane et al., 2006). There cavity-nesting bees were much more abundant and species-rich in the city than nearby desert outside the city, a result interpreted as a response to greater nest availability. Cavity-nesting species also responded positively to nest availability in areas with different fire history in Israel (Potts et al., 2005). Further field observations and experiments are needed to separate the contribution of nest site availability, sociality and longevity to differences in species richness and composition between xeric and mesic areas.

4.2.3. Oligolectic species

The finding that the proportions of polylectic and oligolectic solitary bees in the desert scrub and riparian habitats differed was surprising given that these plots were less than 4 km apart. Local distribution of host plant species probably accounts for some of the differences among oligolectic species. Most plant species that occur in desert scrub habitats also occur in the sand deposits and persistently dry microsites in the riparian area, albeit at lower abundance levels. Polylectic bee species may be favored in the riparian areas because bloom duration is longer due to water availability. Nearly all introduced plant species at San Bernardino occur only in the riparian habitat (unpubl. data) which also might favor the persistence of polylectic species more than oligolectic species.

This study shows that social species can be diverse in desert environments, that oligolectic species broadly co-occur with social species, and that both can be abundant in sympatry. In addition, this study shows that solitary generalist and specialist bee species are short-lived in desert areas. An important contribution to bee diversity in the San Bernardino Valley may be that different bee species are active during the spring and late-summer bloom. This pattern was very similar in Carlinville, but the species turnover curves for that region suggest that at least some solitary species there are active through long periods of the year. The midsummer dearth of bloom in the San Bernardino Valley has a strong effect on the bee species that are able to occur in this area. Comparison of this bee fauna with nearby bee faunas in higher elevations where bloom is more constant through the year may be help clarify if the effect of the floral dearth period in deserts excludes long-lived and multivoltine bee species or favors diversification of short-lived seasonal bee specialists.

5. CONCLUSION

Largely separate biogeographic histories of the Carlinville and San Bernardino regions are reflected in distinctiveness of their bee faunas. Only one native bee species (*Halictus ligatus*) are shared between these two areas. Ten of the 51 genera represented at Carlinville are not found at San Bernardino while 28 of the 69 genera at San Bernardino do not have representative species at Carlinville. The Carlinville fauna is composed of some groups that are most diverse in western North America (*Perdita*, *Calliopsis* and *Ashmeadiella*) and a number of groups with peak species richness in the Holarctic (*Andrena*, *Colletes* and *Osmia*). The San Bernardino bee fauna consists of elements with tropical affinities (*Ancylosceli*, *Peponapis*, *Xenoglossa*), north temperate/ Holarctic affinities (*Osmia*, *Andrena)* and many North American desert endemics (*Macrotera*, *Anthophorula*, *Diadasia*, *Sphecodosoma*, *Atoposmia* and others). Genera found in San Bernardino and not Carlinville include nine composed of all oligolectic species, seven composed of only polylectic species, two composed of both generalist and specialist species, and seven that are entirely cleptoparasitic species (Appendix 1 online). This even distribution of unique specialist, generalist and cleptoparasitic genera indicate functional groups based on ecological traits do not easily explain differences in the bee faunas of these two regions. Other differences in the bee faunas of Carlinville and San Bernardino are due to groups of closely related species, suggesting diversification also contributes to faunal diversity. Many oligolectic bee species in Carlinville were *Salix* or composite specialists in the genus *Andrena* and in San Bernardino almost half the oligolectic species are in the genus *Perdita*. Thus, although *Andrena* and *Perdita* are in the same family (Andrenidae), different subfamilies in this family contribute substantially to the oligolectic bee fauna of these two areas. Similar patterns can be seen in cleptoparasitic species. As discussed earlier, the genus *Nomada* was represented by 20 species and the genus *Bombus* was represented by 9 species in the Carlinville fauna. Taken together, these patterns suggest that an understanding of bee phylogeny and historical biogeography for these areas must be combined with ecological information on host plant distribution, etc. before we will fully understand why regions differ in their bee diversity patterns.

Bees are biogeographically unusual compared to many groups because their species richness appears to be greater in xeric temperate areas than in mesic tropical and temperate areas (Michener, 1979, 2007). This pattern is particularly curious because it is so discordant with global patterns of plant diversity. Tropical diversity of tree species far exceeds that found in temperate areas north and south of the equator (Gentry, 1988) yet the diversity of bees, which are the primary pollinators of plants in most terrestrial ecosystems, is quite different from that of their hosts. In studies of effects of landscape-level anthropogenic change on bees it has been shown that plant diversity is correlated with bee diversity at local scales (Banaszak, 1996; Steffan-Dewenter and Tscharntke, 2001; Potts et al., 2003) and that bee diversity is greater when the sizes and shapes of flowers in the community increases (Bosch et al., 1997; Potts et al., 2003). This points to the possibility that bees are preferentially attracted to non-trees (shrubs, sub-shrubs and annual plants), which do not follow the species richness pattern for trees. However, I know of no global studies of richness for these kinds of plants that would provide a basis for a comparison of plant community diversity and bee species richness over biogeographically relevant scales.

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Composition de la faune et différences dans la richesse en espèces chez les abeilles (Hymenoptera : Apiformes) de deux régions d'Amérique du Nord.

Biodiversité / spécialisation / gradient d'espèces / pollinisateur /oligolectie

Zusammenfassung – Faunenzusammensetzung und Unterschiede im Artenreichtum bei Bienen (Hymenoptera: Apiformes) in zwei nordamerikanischen Regionen. Die meisten Tiergruppen haben ihre höchste Artendiversität in den Tropen. Bienen sind in diesem Zusammenhang ungewöhnlich, da sie ihren größten Artenreichtum in trocken gemäßigten Regionen haben. Etliche Hypothesen wurden aufgestellt, um diese nicht eingängige Verteilung zu erklären. Eine besagt, dass mehr spezialisierte Arten in Wüstenklimaten gefunden werden, wodurch mehr Arten miteinander koexistieren können. Eine andere geht davon aus, dass durch das Fehlen von sozialen Bienenarten Solitärbienen bessere Möglichkeiten zur Diversifizierung haben. Und schließlich könnten zwei Blühperioden es ermöglichen, dass auch zwei verschiedene Bienenfaunen ein und dasselbe Wüstenhabitat besiedeln.

Ich habe einige Voraussagen dieser Hypothesen geprüft, indem ich die Bienenfauna zweier gut untersuchter Regionen in Nordamerika untersuchte (eine Region mit mittlerer Feuchtigkeit, eine trockene Region) und zwei Habitate innerhalb der trockenen Region (eine Uferzone mit mittlerem Feuchtigkeitsgrad und ein trockenes Wüstenbuschland-Habitat). Der Artenreichtum ist in den trockenen Gebieten höher als in der feuchten Region Nordamerikas und lediglich zwei Arten kommen in beiden Regionen vor. Trotz der ausgeprägten bimodalen Blüte in der Trockenregion und der kontinuierlichen Blüte in der feuchten Region zeigten die Bienenfaunen in beiden Regionen ähnliche Zusammensetzungen in Bezug auf Pollenspezialisten und Pollengeneralisten. Die Pollenspezialisten in beiden Gebieten haben eine kürzere Lebensdauer als die meisten anderen Bienenarten. Soziale und kleptoparasitische Arten waren stärker in der feuchteren nordamerikanischen Region vertreten. Ein Vergleich der Bienenfaunen in Parzellen mit aneinandergrenzenden mittelfeuchten und trockenen Flächen ergab für Pollenspezialisten einen höheren Artenreichtum in dem trockenen Buschland-Habitat.

Ich schließe daraus, dass Daten zur Bienenphylogenie und historische Befunde zur Biogeographie in Verbindung mit Aspekten der Bienenökologie sowie die Verteilung der Wirtspflanzen zusammen beurteilt werden müssen, um globale und lokale Unterschiede der Bienenfaunen zu verstehen.

Biodiversität / Wirtsspezifität / Artgradienten / Bestäuber / Oligolektie

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Online Material

Appendix I. List of bee genera and number of species collected in the San Bernardino Valley USA/ Mexico (SBV) and Carlinville, Illinois. Numbers in parentheses indicate numbers of pollen specialist species, an E in parentheses indicates an introduced species, and a P in parentheses indicates a cleptoparasitic species. Two genera have both pollen-collecting and cleptoparasitic taxa, *Bombus* and *Lasioglossum*.

		SBV	Carlinville
ANDRENIDAE			
Andreninae	*Ancylandrena*	1 (1)	
	Andrena	12 (2)	49 (22)
Oxaeinae	*Protoxea*	1 (0)	
Panurginae			
Calliopsini	*Calliopsis*	16 (16)	3 (3)
Perditini	*Macrotera*	3 (3)	
	Perdita	51 (51)	3 (3)
Protandrenini	*Anthemurgus*		1 (1)
	Protandrena	5 (0)	1 (0)
	Pseudopanurgus	1 (0)	8 (8)
APIDAE			
Apinae			
Anthophorini	*Anthophora*	7 (0)	4 (1)
	Habropoda	1 (0)	1 (0)
Apini	*Apis*	1 (E)	1 (E)
Bombini	*Bombus*	1 (0)	9 (0)
Centridini	*Centris*	7 (0)	
Emphorini	*Ancyloscelis*	1 (1)	
	Diadasia	10 (10)	
	Melitoma		1 (1)
	Ptilothrix	1 (0)	1 (1)
Ericrocidini	*Ericrocis*	2 (P)	
Eucerini	*Cemolobus*		1 (1)
	Eucera	6 (0)	6 (0)
	Florilegus	1 (0)	
	Melissodes	13 (0)	16 (8)
	Peponapis	3 (3)	1 (1)
	Syntrichalonia	1 (0)	
	Svastra	4 (0)	4 (3)
	Tetralonia	1 (0)	1 (1)
	Tetraloniella	1 (0)	
	Xenoglossa	2 (2)	1 (1)
	Tetraloniella	1 (0)	1 (0)
Exomalopsini	*Anthophorula*	13 (2)	
	Exomalopsis	3 (0)	
Melectini	*Melecta*		1 (P)
Nomadinae			
Ammobatini	*Oreopasites*		2 (P)
Ammobatoidini	*Holcopasites*	4 (P)	2 (P)
Biastini	*Neopasites*	1 (P)	
Brachynomadini	*Triopasites*	1 (P)	
	Paranomada	1 (P)	
Epeolini	*Epeolus*	4 (P)	7 (P)
	Triepeolus	17 (P)	11 (P)
Neolarrini	*Neolarra*	6 (P)	

Appendix I. Continued.

Nomadini	*Nomada*	5 (P)	22 (P)
Townsendiellini	*Townsendiella*	1 (P)	
Xylocopinae			
Ceratini	*Ceratina*	5 (0)	2 (0)
Xylocopini	*Xylocopa*	3 (0)	1 (0)
COLLETIDAE			
Colletinae			
Colletini	*Colletes*	8 (2)	15 (9)
Diphaglossinae			
Caupolicanini	*Caupolicana*	1 (0)	
Hylaeinae			
	Hylaeus	6 (0)	9 (0)
HALICTIDAE			
Halictinae			
Augochlorini	*Augochlora*		2 (0)
	Augochlorella	2 (0)	2 (0)
	Augochloropsis	1 (0)	1 (0)
Halictini	*Agapostemon*	4 (0)	4 (0)
	Halictus	2 (0)	4 (0)
	Lasioglossum	22 (0)	30 (0)
	Sphecodes	6 (P)	12 (P)
Nomiinae	*Dieunomia*	1 (0)	
	Nomia	1 (0)	1 (0)
Rhophitinae	*Conanthalictus*	1 (0)	
	Dufourea	7 (5)	1 (1)
	Sphecodosoma	1 (1)	
MEGACHILIDAE			
Lithurginae			
Lithurgini	*Lithurgus*	3 (3)	
Megachilinae			
Anthidiini	*Anthidiellum*	2 (0)	1 (0)
	Anthidium	11 (0)	2 (1)
	Dianthidium	5 (0)	
	Dolichostelis	1 (P)	
	Stelis	5 (P)	3 (P)
	Trachusa	1 (1)	
Dioxyini	*Dioxys*	1 (P)	
Megachiliini	*Megachile*	22 (2)	16 (7)
	Coelioxys	7 (P)	6 (P)
Osmiini	*Ashmeadiella*	22 (2)	1 (1)
	Atoposmia	3 (0)	
	Chelostoma		1 (0)
	Heriades	4 (0)	2 (0)
	Hoplitis	4 (1)	2 (0)
	Osmia	9 (0)	12 (1)
MELITTIDAE			
Melittinae			
Melittini	*Macropis*		1 (1)
Dasypodinae			
Dasypodaini	*Hesperapis*	2 (1)	