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The following is the established format for referencing this article:

Williams, N. M., R. L. Minckley, and F. A. Silveira. 2001. Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology* 5(1): 7. [online] URL: <http://www.consecol.org/vol5/iss1/art7/>

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Synthesis, part of Special Feature on [Pollinator Decline](#)

Variation in Native Bee Faunas and its Implications for Detecting Community Changes

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ABSTRACT

Changes in flower-visiting insect populations or communities that result from human impacts can be documented by measuring spatial or temporal trends, or by comparing abundance or species composition before and after disturbance. The level of naturally occurring variation in populations and communities over space and time will dictate the sampling effort required to detect human-induced changes. We compiled a set of existing surveys of the bee faunas of natural communities from around the world to examine patterns of abundance and richness. We focused on a subset of these studies to illustrate variation in bee communities among different sites and within sites over different spatial and temporal scales. We used examples from our compilation and other published studies to illustrate sampling approaches that maximize the value of future sampling efforts. Existing studies suggest that bee faunas are locally diverse, highly variable in space and time, and often rich in rare species. All of these attributes indicate that intense sampling among sites and years will be required to differentiate changes due to specific impacts from the natural dynamics of populations and communities. Given the limits on

time and funding for studying bees, approaches that maximize information for effort must be sought for future studies. Reliable information on population and community changes may be gleaned from examining "functional groups" rather than entire faunas. Regardless of the purpose of the study, standardized sampling protocols using replicated designs will increase the value of data. Standardization permits statistical testing of changes in bee populations and communities, and allows for rigorous comparison between studies.

KEY WORDS: Apiformes, Apoidea, faunal surveys, flower-visiting insects, functional groups, monitoring long-term changes, sampling protocol, solitary bees, species composition, species richness, worldwide bee faunas.

Published: April 5, 2001

INTRODUCTION

The increased attention to the role of mutualistic relationships in ecosystem function has led to questions of how floral visitors respond to habitat modifications resulting from human activity (Bronstein et al. 1990, Banaszak 1995, Allen-Wardell et al. 1998, Kremen and Ricketts 2000) and the introduction of exotic species (Thorp et al. 1992). Many biologists believe the impact of human activities on native pollinators to be unrelentingly negative (Vinson et al. 1993, Buchmann and Nabhan 1996; but see Bohart 1972). Few empirical data exist that demonstrate such effects on either pollination services or pollinator populations (Aizen and Feinsinger 1994, Washitani 1996, Frankie et al. 1997, [Thomson 2001](#)). Estimates suggest that 60-70% of plant species rely on insects for pollination (Axelrod 1969, Richards 1986). Although Lepidoptera and certain Diptera are important pollinators for some plant species (e.g., Kearns and Inouye 1994, Hodges 1995, Johnson et al. 1998, [Kearns 2001](#)), and in certain biomes (e.g., alpine; Kearns 1992), bees, with 20,000-30,000 species worldwide, stand out as the dominant pollinating group in nearly all geographic regions. If human activity negatively affects native bee faunas, taxa rich with behavioral and morphological diversity may be lost, as may be the principal pollinators of many plant species.

Detection of changes in bee communities is made difficult by two factors. First, bee communities exhibit substantial variation over space and time. For example, only one-third of the bee species visiting flowers of *Lavandula latifolia* in Spain occurred in every year of a 5-yr study (Herrera 1988). The same study found similarly high variation in the occurrence of species among repeat samples made 7 d apart along the same transect and among transects spaced at 300 m intervals. In a separate study, samples collected at creosote bush (*Larrea tridentata*) in the southwestern United States shared 18% of the bee species when collected at sites > 1100 km apart, and still shared only 39% when collected from sites 1-5 km apart (Minckley et al. 1999). Although both surveys focused on a single host plant species, high turnover was also reported from surveys of entire floras and over other spatial and temporal scales (reviewed in Minckley et al. 1999).

Second, bee faunas even of local areas appear diverse and contain large proportions of rare species (Michener 1979: Table 2). Mesic temperate and tropical areas are not considered particularly speciose for bees, yet 85-150 species were found at sites as small as 1 ha in the west-central USA, Brazil, and Japan (Sakagami and Fukuda 1973, Tepedino and Stanton 1981, Silveira et al. 1993, Carvalho and Bego 1996). In eastern North America, a population of the bee wolf, *Philanthus sanbornii*, captured 78 bee species in 3138 prey items examined at one nesting site (Stubblefield et al. 1993). In areas of peak bee species richness, the number of species may reach more than 700 (Timberlake, cited in Michener 1979). In these same studies, despite intensive sampling, 16-42% of species were represented by a single specimen.

In this review, we examine the levels of variation in bee populations and communities across spatial and temporal scales, working with a compilation of all known published studies that report bee diversity and relative abundance of species for different sites in North America and other continents. We consider the effect that this variability has on our ability to detect changes in bee species composition and population abundance. Knowledge of existing diversity and variation may help to target the most effective approaches and the effort required for assessing possible faunal changes. Using a set of studies, we explore whether samples from a subset of flower hosts can provide an accurate picture of relative abundance, richness, and variation in these metrics for the bee fauna of a particular community. Finally, we suggest several ways to standardize samples, so that collections made at different sites or at different times can be compared more effectively.

We note at the outset that identifying changes in bee communities is not synonymous with demonstrating effects on pollination, because insect visitors vary in quality as pollinators of individual plant species (e.g., Tepedino 1981, Stanton et al. 1991, Wilson and Thomson 1991), and vary depending on the composition of pollinators in the community (Thompson and Pellmyr 1992, Thomson et al. 2000). However, identifying changes in pollinators is a necessary step in any study of pollination deficit.

METHODS

We compiled surveys of bee faunas primarily from the published literature. The compilation included any study that reported specimens identified to species or morphospecies, and the number of individuals of each species. Data restricted to select taxa (e.g., *Anthophora*, *Osmia*) or to select life histories (e.g., twig-nesting species) are used only during our discussion of variation. Surveys were included regardless of sampling protocol, area surveyed, number of replicate samples, and number of collectors. The list builds on one compiled by Michener (1979), and is not exhaustive of potential data sets, many of which remain unpublished, or are old or obscure enough not to be indexed by searching methods available in libraries.

For each study, we recorded the number of individuals, number of species, sampling locality, collecting protocol (e.g., haphazard, transect, pan traps, sweeping with nets), number of collectors, collecting duration (e.g., total hours, days, and months), and the number of plant hosts sampled. If numbers of host plant species sampled were not given, then we considered the study to have included all flowering species available. We also calculated the ratio of species to individuals (a measure of evenness in the community) and the proportion of species represented by single specimens (singletons, IC) for each sample. IC has been proposed as one measure of sample completeness; this ratio approaches zero as more species are resampled (Coddington et al. 1996). Detailed discussion of the general issues and techniques involved in species richness estimation and sampling can be found elsewhere (Colwell and Coddington 1994, Brown and Feener 1995, Coddington et al. 1996, DeVries et al. 1999).

Comparing studies

We compared species accumulation patterns and richness from the compiled studies to illustrate diversity among regions, and the sampling effort required to characterize the diversity of an area. Most studies reported the number of species and individuals collected during the entire study and not per collection effort (e.g., sampling hours, trap units, etc.); therefore, species accumulation through time could not be examined. Instead, we used the estimated asymptotic richness (S_a) based on lognormal abundance distributions (Fagen and Karieva 1997) to compare species richness between studies. We illustrated species accumulation using rarefaction curves (Colwell and Coddington 1994; J. Seger, University of Utah, randomization program). We are aware that such rarefaction curves do not provide estimates of S_a , but the shapes of these randomization curves do illustrate whether the amount of sampling effort was adequate to capture most species within the community.

We compared IC values for studies that sampled bees from single plant species vs. those that sampled from all blooming plant species. Values might differ between samples made at single plant species and those from entire floras if rare species are not evenly distributed among floral hosts. In addition, the persistence of singletons despite increasing sampling effort reflects the pervasiveness of rare species within the community. We used ANCOVA, with number of specimens collected as the covariate, to account for sampling effort (SAS-GLM, SAS Institute 1998). We could not include area sampled as a covariate in this analysis because we lacked data on area for many studies involving single plants.

Levels of spatial and temporal variation

We discuss the spatial variation in species composition reported by three studies that sampled bees at sites within 60 km of each other, at similar elevation, over the same time period, and in similar environments (Tepedino and Stanton 1981, Minckley et al. 1999; F. A. Silveira, *unpublished data*). We reasoned that climatic features that directly influence the flowering of plants would be similar among sites in close proximity, so that most differences in the bee fauna would be due to intrinsic site differences (e.g., plant species composition and historical colonization effects).

We discuss general levels of temporal variation from different published monitoring studies. We then focus on temporal variation using data from one study (F. C. Evans, *unpublished data*, University of Michigan). Evans sampled bees from the E. S. George Reserve, Michigan, USA, during a 40-yr period (1957-1998). The sampling effort varied widely between years and times of the season, limiting the range of questions that we could address and suggesting some caution when interpreting results. To minimize noise due to strikingly undersampled years, we included years during which collecting effort was most equal and data were collected on at least two days during each of four consecutive months. For two years, we accepted a single sampling day in one of the months. We limited data to bees collected from May through August, when collecting effort was most equal among years. We compared community composition between samples made during three decades, 1950s, 1970s, and 1980s, using the Morisita-Horn Index (EstimateS, Colwell 1997). Data were pooled for three years in each decade. To investigate the sensitivity of such comparisons to sampling intensity, we also calculated similarity between each set of years and 1972-1973. Five times more specimens were collected during each of these two years than during any other year.

In addition to community composition, we explored the variation in population abundances of different bees in the community during the 40-yr period. We calculated the coefficient of variation among years for each species, using the mean square error from a multiple regression of species abundance on number of days sampled within the flight period of that species and on years. We used MS errors to adjust for the effect of sampling effort and to remove long-term trends in population abundance. Trends themselves could also be explored; however, our focus was to illustrate population variation that might obscure detection of trends. This analysis used data from 1957, 1958, 1959, 1964, 1972, 1973, 1975, 1978, 1979, 1981, 1984, 1986, and 1989. All calculations were made using SAS-REG (SAS Institute 1998).

Effects of sampling effort and area

Despite the variety of ecosystems and geographic areas covered by the compiled surveys, we were interested to know whether increased sampling effort and area sampled would still lead to a greater number of species discovered. We regressed the number of species discovered on the number of days during which specimens were collected, and on the area sampled for surveys that collected bees at all flowering plants (SAS-REG, SAS Institute 1998). The number of sampling days incorporates aspects of sampling duration and sampling effort. The initial model included the number of specimens collected, another measure of effort. This variable was strongly correlated with days ($r = 0.94$), and the model was over parameterized for the number of data ($n = 12$ studies), so we removed "number of specimens" for final analyses. All variables were log-transformed prior to analysis. We avoided months as a metric of effort because the number of days sampled within months varied greatly among studies; thus, months would more likely reflect the range of seasons incorporated. In addition, studies lasting 12 months probably differed in their actual sampling period among tropical, subtropical, and temperate regions.

Predictability of subsampling

Limited samples underestimate the total diversity of an area. In some cases, however, specific types of subsamples may still provide a reliable metric of variation or changes in bee communities. Subsamples might be limited to a portion of the day or season, a few floral hosts, or a subset of the bee fauna (e.g., cavity-nesting species in trap-nests). We used data from North America and Eastern Europe to evaluate how samples from subsets of host plants approximated total bee diversity in an area. We calculated the similarities of bee communities collected from two dominant flowering plants (creosote bush *Larrea tridentata* and sunflower *Helianthus annuus*) growing at three sites in southeastern Arizona and southwestern New Mexico, USA (Hurd and Linsley 1975, Hurd et al. 1980). We also used data of Osychnyuk (1967), who collected bees from all flowering plants in the Carpathian Mountains, Ukraine, over two years, and reported the species-abundance data for bees collected from each plant family. We calculated the similarity of the entire bee fauna collected from all plants to bee species collected from plants in the Asteraceae. Both analyses used Jaccard's similarity index.

RESULTS

Overview of all studies

Published studies vary considerably in duration, collecting intensity, and protocol (Table 1). Differences stem, in part, from the intent of the study. Some were carried out specifically to evaluate total bee diversity in an area, whereas others were designed to test hypotheses concerned with plant-pollinator coevolution, pollination biology, or bee population dynamics. The area sampled varied from about 1 ha to > 290 ha. The number of plant species included in the studies ranged from all plant species in flower to one species, usually the dominant flowering plant in the area. Two studies that included more than one plant host indicated that they had excluded some plants visited by bees (Kratowil 1988, Marlin and LaBerge 2001). In general, whole-flora samples lasted longer (one or two flight seasons), covered a broader area, and included a greater number of microhabitats than did samples restricted to one host plant. Studies that collected at all plant species in a given area over the flight season recovered more bee species and individuals (106.6 ± 13.1 species, mean ± 1 SE, range 11-201 species; 2382.5 ± 451.3 individuals, range 149-8114 individuals) than did studies that sampled bees from one plant species (19.6 ± 2.5 species, range 8-54 species; 534.0 ± 109.4 individuals, range 44-1959 individuals). However, samples at single floral hosts collected individuals and new species faster than did samples from the whole flora (Mann-Whitney U -test, $n = 12$, $n = 21$, respectively, both $P < 0.005$). The means for single hosts were 44.0 ± 10.1 individuals and 1.42 ± 0.2 species per collector-hour; for entire flora, they were 13.1 ± 2.3 individuals and 0.86 ± 0.12 species per collector-hour. This difference probably exists because researchers chose plants that were heavily visited by bees for single-plant surveys. Rate of discovery and number of specimens collected are not completely independent, but the relationships can differ depending on the distribution of species' abundances within the community. In all except one study included in Table 1, researchers used nets to collect bees, although in several studies that assessed population trends for subsets of species, workers used other standardized techniques (e.g., Wolda and Roubik 1986, Frankie et al. 1993, Roubik 2001).

Table 1. Surveys of bees from different parts of the world that included data on abundance of all species collected.

No. specimens	No. species	No. specimens/	No. singletons	Proportion of	Sampling duration	Area (ha)	Flower data	Location	Reference
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		species		singletons ^a	Months	Days	Hours ^b		List	No. spp.		
-	333	-	-	-	-	182	-	-	Y	-	USA, UT, San Rafael Desert (scattered years, 1966-1993)	Griswold et al. (1998) ^c
15000	214	-	-	-	-	-	-	81,300	Y/N	all	USA, IL, Carlinville and surrounding areas	Robertson (1928)
8114	212	38.27	52	0.25	12	52	468.0	100.0	Y	all	Brazil, Ribeirão Preto SP (gardens, abandoned area, University campus, w/o Meliponines)	Camargo and Mazucato (1984)
1904	169	11.27	68	0.40	12	52	408.0	2.1	N	all	Brazil, Viçosa	Cure et al. (1993)
4642	169	27.47	35	0.21	-	-	-	-	-	-	Ukraine, Carpathian Mts.	Osychnyuk (1967)
5241	168	31.20	26	0.15	12	-	-	>10,000	Y/N	all	USA, IL, Chicago area	Pearson (1933)
1906	167	11.41	49	0.29	12	43	150.0	107.0	N	all	Brazil, S.J. dos Pinhais PR (secondary grassland)	Bortoli and Laroça (1990)
4217	167	25.25	53	0.32	12	36	144.0	21.0	N	all	Brazil, S.J. dos Pinhais, PR (secondary grassland)	Sakagami et al. (1967)
2361	158	14.94	43	0.27	12	36	216.0	15.0	N	all	Brazil, Lapa, PR (field impacted by cattle grazing)	Barbosa and Laroça (1993)
-	151	-	-	-	8	30	120.0	1.0	Y/N	all	USA, WY (shortgrass prairie)	Tepedino and Stanton (1981)
-	144	-	-	-	8	30	120.0	1.6	Y/N	all	USA, WY (shortgrass prairie)	Tepedino and Stanton (1981)
2996	145	20.66	23	0.16	12	90	-	7.7	Y/N	all	USA, MI, E.S. George Reserve (1972-1973)	Evans database, U. Michigan
1226	128	9.58	54	0.42	12	24	195.0	1.0	Y	all	Brazil, Uberlândia, MG (cerrado)	Carvalho and Bego (1996)

874	119	7.34	46	0.39	12	18	82.0	1.0	Y	all	Brazil, Ponte Nova (abandoned pasture near small forest)	Silveira et al. (1993)
712	98	7.27	33	0.34	6	26	75.0	1.4		all	Brazil, Viçosa	Cure et al. (1992)
634	90	7.04	28	0.31	-	-	-	-	Y	all	USA, MS, Hattiesburg	Michener (1947)
2430	89	27.30	16	0.18	6	24	96.0	-	Y	all (76)	Japan, eastern Hokkaido	Usui et al. (1976)
3744	85	44.05	14	0.16	6	25	92	9	-	all	Japan, Hokkaido Botanical Garden	Sakagami and Fukuda (1973)
2789	78	40.23	19	0.24	-	-	-	-	N	all	USA, MA, near Cambridge	Stubblefield et al. (1993)
3099	77	40.25	13	0.17	6	25	89	150	-	all	Japan, Hokkaido University	Sakagami and Fukuda (1973)
1045	55	19.00	11	0.20	5	18	56.5	35	N	all	Japan, eastern Hokkaido	Fukuda et al. (1973)
950	45	21.11	20	0.44	12	24	195.0	-	N	all	Brazil, S. Joao do Cariri, PB caatinga	Aguiar and Martins (1997)
848	24	35.33	3	0.13	-	-	115.0	-	N	all	Japan, eastern Hokkaido	Uehira et al. (1979)
417	22	18.95	6	0.27	4	-	-	290.0	Y/N	all	USA, CA, Anacapa Is.	Rust (1985)
211	13	16.23	3	0.23	-	-	-	-	-	-	Germany	Kratochwil (1988)
149	11	13.55	1	0.09	-	-	-	-	-	-	Japan, Ogasawara Is.	Kato (1992)
361	37	9.76	7	0.19	2	5	40.0	-	Y	1	USA, WY, Grand Tetons National Park	Tepedino and Stackhouse (1987)
560	25	22.40	6	0.24	4	6	72.0	1.0	Y	1	USA, AZ, Tucson (undisturbed <i>Larrea</i> stand, one plant)	Minckley and Cane (<i>unpublished</i>)
757	25	30.28	8	0.32	-	-	-	-	Y	1	Germany	Kratochwil (1988)
250	13	19.23	4	0.31	4	4	12.0	1.0	Y	1	USA, AZ, Tucson (undisturbed <i>Larrea</i> stand, one plant)	Minckley et al. (1999)
115	13	8.85	4	0.31	1	4	8.0	0.5	Y	1	USA, NE, Cherry Co. (<i>Penstemon</i>)	Lawson et al. (1989)

105	8	13.13	4	0.50	1	2	4.0	1.0	Y	1	USA, NE, Morrill Co. (<i>Penstemon</i>)	Lawson et al. (1989)
1959	54	36.28	12	0.22	1	2	37.5	-	Y	1	USA, NM, Hidalgo Co., near Rodeo	Hurd et al. (1980)
1095	41	26.71	12	0.29	1	2	25.0	-	Y	1	USA, NM, Hidalgo Co., near Animas	Hurd et al. (1980)
174	26	6.69	8	0.31	1	2	11.0	-	Y	1	USA, NM, Grant Co., near Silver City	Hurd et al. (1980)
211	23	9.17	8	0.35	1	1	6.0	-	Y	1	USA, AZ, Cochise Co., Benson	Hurd et al. (1980)
734	16	45.88	2	0.13	1	1	42.0	-	Y	1	USA, CA, Madera Co., Madera	Hurd et al. (1980)
1404	14	100.29	5	0.36	1	1	12.5	-	Y	1	USA, CA, San Joaquin Co., Escalon	Hurd et al. (1980)
677	12	56.42	4	0.33	1	1	7.0	-	Y	1	USA, CA, Kings Canyon, Corcoran	Hurd et al. (1980)
502	10	50.20	5	0.50	1	1	7.5	-	Y	1	USA, CA, Riverside Co., Indio	Hurd et al. (1980)
264	10	26.40	4	0.40	1	1	7.5	-	Y	1	USA, CA, Inyo Co., Bishop	Hurd et al. (1980)
1293	9	143.67	0	0.00	1	1	11.0	-	Y	1	USA, CA, Madera Co., Madera	Hurd et al. (1980)
703	9	78.11	1	0.11	1	1	9.0	-	Y	1	USA, CA, Madera Co., Madera	Hurd et al. (1980)
338	9	37.56	0	0.00	1	1	8.0	-	Y	1	USA, CA, Merced Co., Merced	Hurd et al. (1980)
82	24	3.42	13	0.54	1	3	0.5		N	1	USA, NY, Finger Lakes (cultivated site-CF)	MacKenzie and Eickwort (1996)
68	19	3.58	8	0.42	1	3	0.5		N	1	USA, NY, Finger Lakes (cultivated site-CP)	MacKenzie and Eickwort (1996)
51	17	3.00	6	0.35	1	3	0.5		N	1	USA, NY, Finger Lakes (natural site-NF)	MacKenzie and Eickwort (1996)
44	18	2.44	9	0.50	1	3	0.5		N	1	USA, NY, Finger Lakes (natural site-NS)	MacKenzie and Eickwort (1996)

^a Proportion of singletons = IC.

^b Hours represents the total collector hours.

^c This study is included despite the lack of species abundances, which are available from the authors.

The high proportion of singletons and doubletons in nearly all surveys results in very high estimated richness compared to the number collected. This pattern is evident from rarefaction curves (Fig. 1), few of which appear to reach an asymptote for the given number of specimens collected during the survey. Interestingly, the proportion of all species represented by single specimens (IC) did not differ between samples made at entire floras and those made at one host plant (Fig. 2, Table 2), suggesting that rare bee species are homogeneously distributed among plant species. The number of singletons also did not decline significantly with sampling effort (number of bee specimens collected; Fig. 2). The continued presence of many singletons in larger surveys indicates that (1) even these surveys were undersampled; (2) a real, and unacknowledged, pattern of persistent and widespread rarity exists in many communities; or (3) many communities contain a sizeable number of transient species that are unlikely to be successful there, and that may be more abundant elsewhere. These possibilities carry very different implications for population and community stability as well as bee conservation.

Fig. 1. Species accumulation (rarefaction) curves for all studies (Table 1). Curves are generated as the mean number of species for a given number of specimens sampled. Means are from 100 iterations of sampling without replacement (J. Seger, Discover program).

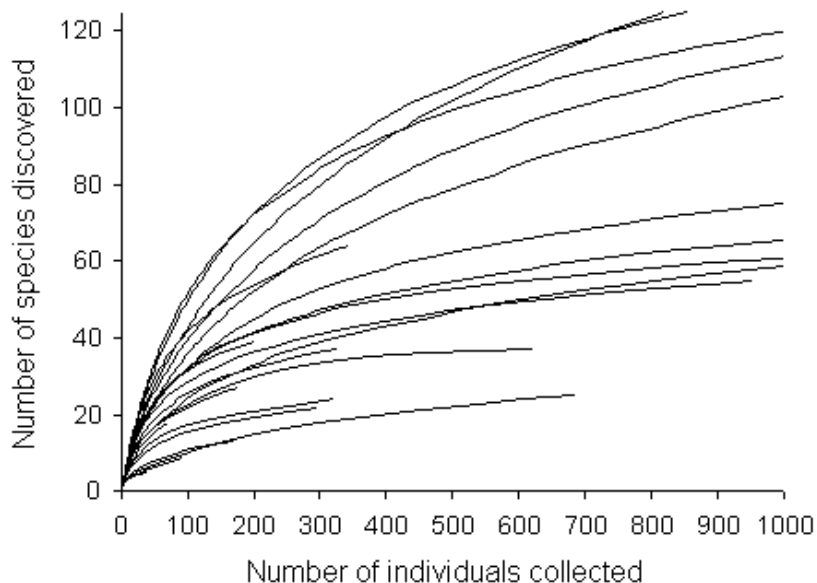
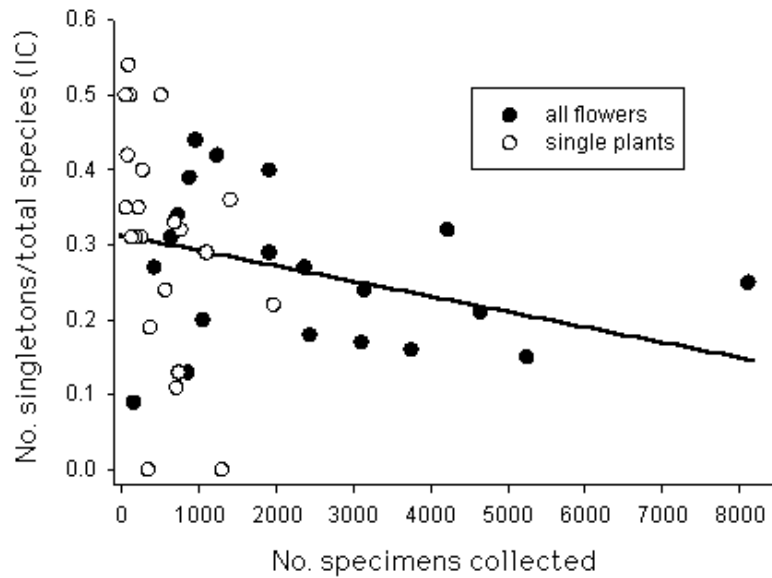


Table 2. Results from ANCOVA of the proportion of singletons (species represented by one individual in the sample) collected in studies that collected at single plant species vs. all flowering species. The number of specimens collected was used as a covariate. Significance was tested using type III SS to account for "specimens collected" as a covariate.

Source	df	MS	F	P
Plants sampled	1	0.0003	0.02	0.8942
Specimens	1	0.0311	1.88	0.1785
Error	39	0.0165		

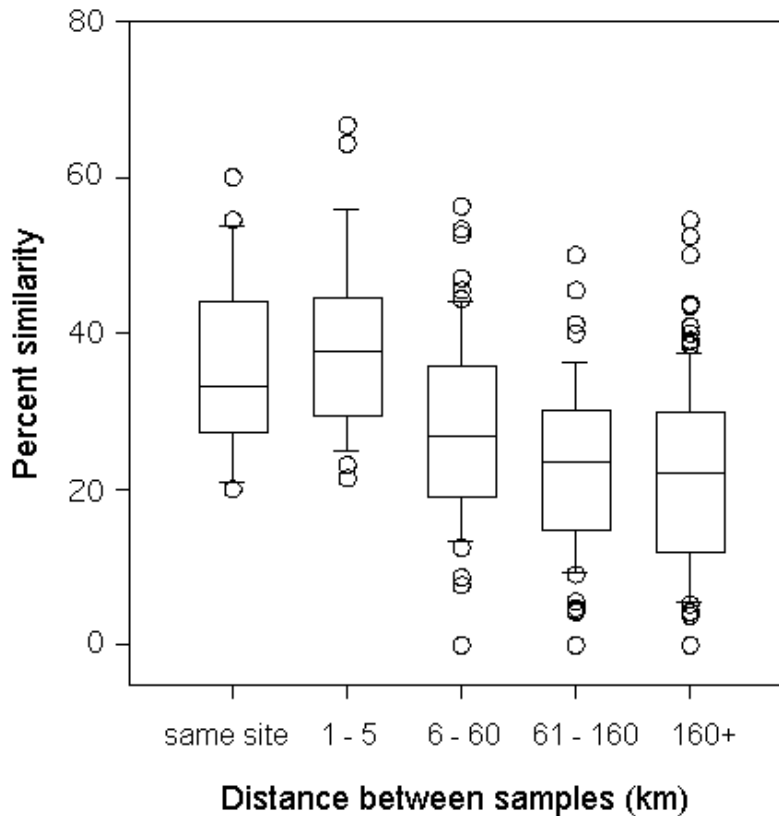
Fig. 2. Relation between the proportion of species represented by single specimens (IC) and the number of specimens collected during a survey. Solid circles indicate studies that collected bees from all plants within an area; open circles indicate studies that collected bees at a single flowering plant species within an area. The line is the pooled least-squares regression from ANCOVA, $Y = 0.312 + (-2.038 (10)^{-5})X$.



Spatial and temporal variability of bee samples

Bee communities display marked turnover even between nearby sites. In a study of bees visiting creosote bush, Minckley and colleagues (1999) found that communities separated from each other by 6-60 km shared only 27% of species, and even those within 5 km of each other shared < 40% of their species, on average (Fig. 3). Silveira and collaborators (F. A. Silveira and J. Damasceno, *unpublished manuscript*) found similar spatial variability in surveys of several reserve areas in and around the city of Belo Horizonte, Minas Gerais, Brazil. There, no single area yielded > 40% of the total number of species collected in all areas together. In Wyoming grassland, bee communities appear more homogeneous. The distribution of species among families did not differ significantly between sites in either of two years ($G = 6.90$, $P > 0.1$, $df = 5$; $G = 3.94$, $P > 0.1$, $df = 5$; based on data from Tepedino and Stanton 1981). Similarity of species compositions could not be calculated from available data.

Fig. 3. Summary of faunal similarity (Jaccard's index) of bees collected from *L. tridentata* between sites separated by different distances and from the same sites sampled multiple times during the flowering season (modified from Minckley et al. 1999). The midline of the box indicates the median. The box indicates 25% and 75% confidence intervals and bars extend from 10% to 90% limits.



Temporal variation in abundance and species composition rivals variation between sites. Although published monitoring studies were limited to taxonomic subsamples of the total bee fauna and report different statistics, all show the same general pattern. The relative abundances of individual species within communities vary greatly and exhibit unique trends among years (Wolda and Roubik 1986, Roubik and Ackerman 1987, Frankie et al. 1993, 1998, Stubblefield et al. 1993). The abundance of the sampled community as a whole appears stable in comparison to that of individual species (Wolda and Roubik 1986, Frankie et al. 1993). Species composition and abundance also fluctuate widely within years. The composition of species visiting *Larrea tridentata* over its 5-wk flowering season differed more than the composition between neighboring sites sampled during the same time period (Fig. 3; Minckley et al. 1999). Studies from various biomes report similarly dramatic fluctuations in populations (e.g., Tepedino and Stanton 1981, Wolda and Roubik 1986, Roubik and Ackerman 1987; S. Droege, F. Parker, and V. Tepedino, unpublished data).

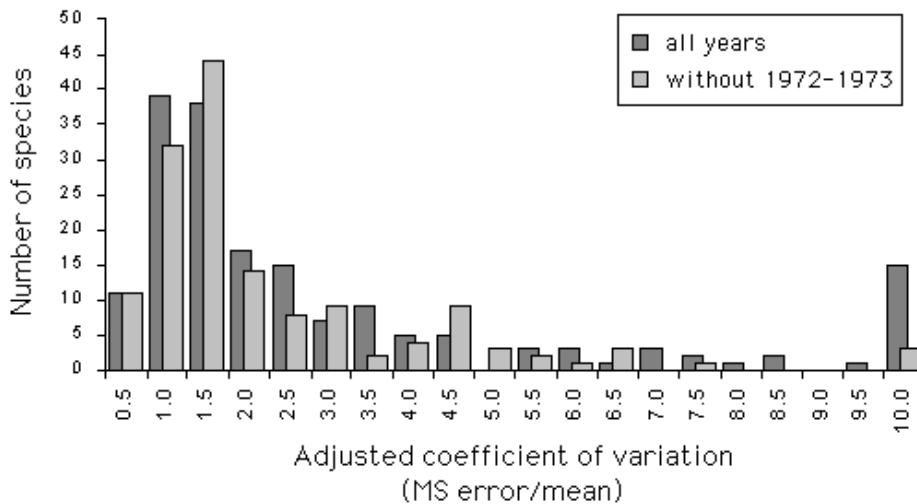
Repeat samples from the same site collected at greater intervals also suggest considerable variation in some aspects of the bee fauna. In cases in which a site experienced no known impact, such comparisons might provide reasonable measures of expected variation over time. We provide three examples. Species composition shifted substantially among decades at the E. S. George Reserve (Table 3). Relative abundance of different species also varied widely. The coefficient of variation for population abundance varied greatly among species (Fig. 4) and, on average, exceeded 200%. This variation changed little whether or not we included 1972 and 1973, which involved five times greater collecting effort. Estimates of population trends are unreliable when coefficients of variation exceed 50% (S. Droege, USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA, personal communication). Some remaining variation in the Evan's data no doubt results from poor sampling, which reiterates the importance of consistent, standardized methods. At a secondary grassland, São José dos Pinhais, Brazil, sampled species richness increased slightly from 161 to 167, between the 1960s and 1980s ($S_a = 322$ and 334, respectively). However, only 11 of the dominant species from 1962-1963 were found among the 28 dominant species from 1981-1982 (these 28 represented 75% of all individuals collected; Sakagami et al. 1967, Bortoli and Laroca 1990). In a mixed chaparral/woodland site in California, total richness remained constant between 1950 and 1990 (24 species $S_{obs} = S_a$); however, the survey from each period contained seven unique species, and all but one of the five dominant species in each survey differed. The five dominant species represent 74.1% and 67.6% of the individuals collected, respectively (Barthell et al. 1997).

Table 3. Similarity (Morisita-Horn index) of species composition for bees sampled at the E. S. George Reserve from June through August during different time periods over a 40-yr study.

Sampling period ^a	No. species (no. specimens)	Sampling period		
		1970	1980	Early 1970
1950	70 (297)	0.54	0.27	0.44
1970	86 (647)	-	0.69	0.90
1980	82 (553)	-	-	0.66
Early 1970s	138 (2729)	-	-	-

^a1950 = 1957, 1958, 1959; 1970 = 1975, 1978, 1979; 1980 = 1984, 1986, 1989. We included early 1970s (1972, 1973), during which very intensive sampling was carried out, to illustrate the effect of different sampling effort on similarity measures.

Fig. 4. Distribution of adjusted coefficients of variation (CV) of population abundance for bee species collected at the E. S. George Reserve. CVs were calculated using MS error from multiple regression, with independent variables being number of days sampled per year and year.



Effects of sampling effort and area sampled

Strong conclusions about the effects of sampling effort and area are difficult, based on surveys made at such diverse areas (e.g., North American prairies, tropical forests). Nevertheless, some trends are evident. Overall, significantly more species were discovered in larger areas and with more days sampled; however, neither effect was significant by itself (Fig. 5, Table 4). The initial analysis showed a negative trend in number of species collected with increasing area, but the effect was due to a single study that sampled a relatively large area over a short period of time (Fukuda et al. 1973; Table 4B). Lack of significance is very likely due to a limited sample size ($n = 14$ studies). Interpretation of an effect of species area warrants some caution because few compiled studies report the area of suitable bee habitat surrounding the sampled plot. The area effect stems, in part, from an increase in the diversity of habitats covered during the survey. Comparison of two years of sampling by Pearson (1933) in the Chicago, Illinois, USA, region (>10,000 ha) with two years of sampling at the George Reserve, Michigan, USA (7.7 ha; Evans 1986) illustrates this point (see Table 1). The Chicago survey included many habitats and plant communities, whereas the E. S. George reserve represented a single old-field habitat. A more controlled comparison between samples made from 140 ha for 106 h and samples from six transects (total area = 0.4 ha, inside the first area) for 118 h illustrates the magnitude of the effect (Silveira et al. 1993). The former yielded 790 specimens (4.94/ha) and 151 species (0.94/ha), the latter 188 (1.59/ha) specimens and 66 species (0.56/ha). The increase in species and specimens collected per hectare suggests an effect of area independent of habitat diversity.

Fig. 5. Log of number of species discovered during surveys as a function of the number of collector-days (log of days) in the survey and the area sampled (log of area sampled). The circled data point represents the outlying survey removed in the reanalysis. See Table 4 for multiple regression results.

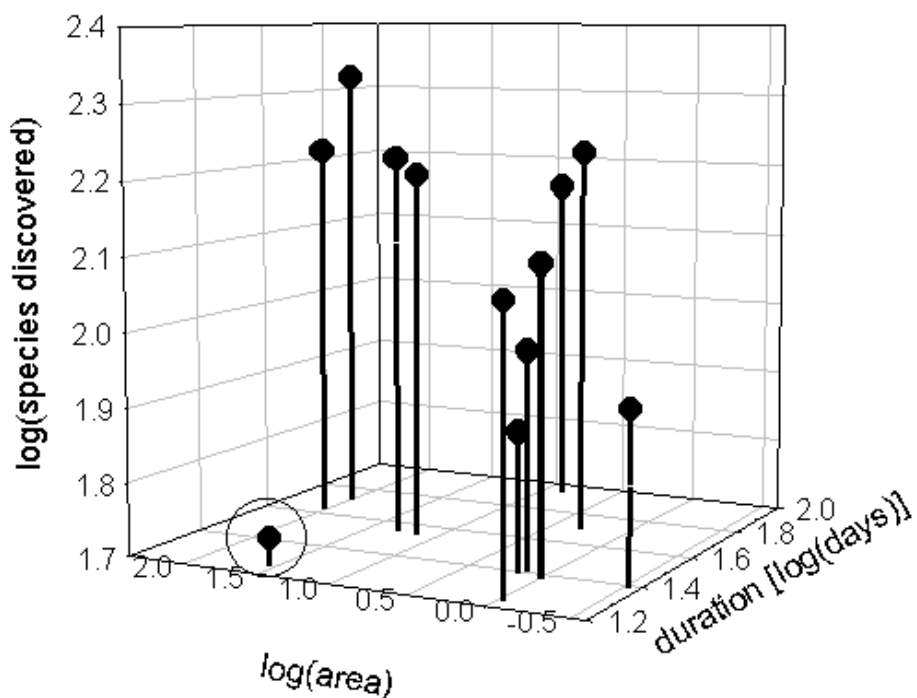


Table 4. Results from two multiple regression analyses of bee species discovered as a function of study duration (days) and area sampled. (A) The first analysis included all surveys that collected bees from all flowering plants ($n = 14$). (B) The second analysis removed a single outlying datum ($n = 13$). The table combines regression results with the partial regression coefficients for each parameter in the model.

Parameter	Partial reg. coeff. b'	MS	df	p^a	R^2 , overall model
A) Model with all data					
Model		0.337	3	0.034	0.565
Error		0.078	10		
Intercept	4.271				
log(days)	0.137	0.015	1	0.673	
log(area)	-0.701	0.191	1	0.149	
log(days) x log(area)	0.206	0.199	1	0.141	
B) Model with outlier removed					
Model		0.202	3	0.042	0.581
Error		0.049	9		
Intercept	3.743				
log(days)	0.303	0.068	1	0.268	
log(area)	0.463	0.033	1	0.433	

log(days) x log(area)	-0.103	0.022	1	0.521	
Error					

^aSignificance testing was based on type III SS. The response variable was log(species collected). The second model removed a single outlying datum (see text and Table 1 for details).

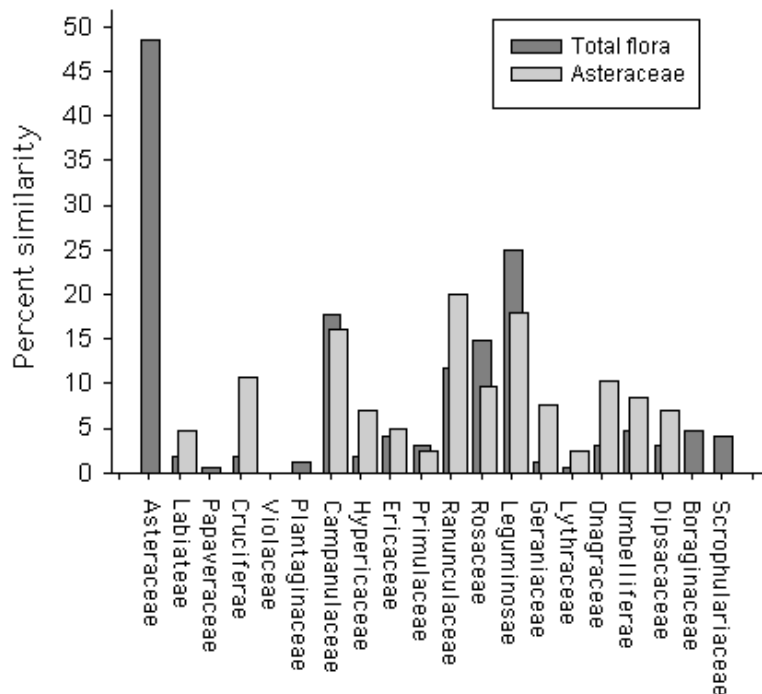
Samples from subsets of host plants (similarity indices)

Samples of bees collected from subsets of flower species varied in how well they represented the bee fauna as a whole. Sunflower and creosote bush sampled in three sites in the southwestern United States yielded very different bee faunas and different average numbers of species (Hurd and Linsley 1975, Hurd et al. 1980). During the two studies, 100 species were collected at the three sites. Species overlap was low between samples from sunflower and creosote bush relative to samples from the same plants made at different sites (Table 5). Such high species richness and low overlap of bee species between host plants indicate that bee faunas visiting single plant species may not represent the entire bee fauna. Comparisons of bees "sampled" at individual plant families vs. the entire flora in the Carpathian Mountains (Osychnyuk 1967) suggest that, although no single plant family could be considered a typical exemplar of the bees for this area, the Asteraceae may provide a reasonable estimate of patterns of bee diversity and abundance. Plant families varied tremendously in the percentage of the entire bee fauna that visit their flowers (Fig. 6). However, more than 58% of the individuals and 68% of the bee species collected in the entire fauna were taken from Asteraceae (for North America, see Graenicher 1911). Violaceae, Papavaraceae, Plantaginaceae, and Lythraceae yielded very few bees. Similarities of bee faunas on each plant family vs. the total bee fauna and on each plant family vs. the Asteraceae follow the same general pattern (Fig. 6). For example, bee faunas of the Campanulaceae, Ranunculaceae, and Leguminosae are well represented by the bee fauna of the Asteraceae. However, there are exceptions. No bee species collected on Asteraceae were also collected on flowers of Scrophulariaceae, Boraginaceae, or Plantaginaceae.

Table 5. Similarity (Jaccard's index) of species composition for bees sampled from sunflower *Helianthus annuus* and creosote bush *Larrea tridentata* at three areas in New Mexico and Arizona (USA).

	Sunflower			Creosote bush		
	Hidalgo Co. 1	Hidalgo Co. 2	Cochise Co.	Hidalgo Co. 1	Hidalgo Co. 2	Cochise Co.
Sunflower						
HC1	-	0.3231	0.3208	0.0816	0.0638	0.1250
HC2		-	0.3333	0.0727	0.0566	0.1321
CC			-	0.0351	0.0526	0.1282
Creosote						
HC1				-	0.4375	0.2857
HC2					-	0.4118

Fig. 6. Overlap of the bee species collected from the whole flora vs. individual plant families and from the Asteraceae vs. other individual plant families in the Carpathian Mountains (Osychnyuk 1967), measured using Jaccard's similarity index.



DISCUSSION

Data from existing surveys of bee faunas suggest that detecting changes in bee populations and communities due to habitat loss or invasion by exotic bees or plants may be formidable. Bee populations and local diversity are highly dynamic. Dramatic changes in the abundance of generalist and specialist species at single locations introduce temporal variation over the season and between years (Ginsberg 1983, Stubblefield et al. 1993, Minckley et al. 1994). Very different faunas can occur at adjacent sites (Herrera 1988, Minckley et al. 1999; F. A. Silveira and J. Damaceno, *unpublished manuscript*). Local extinction and recolonization, for which we have virtually no data, presumably add to the dynamic of local bee biota. The pervasiveness of rare species in all surveys, regardless of duration or sampling intensity, suggests that undersampling very likely will aggravate variation among samples. Rare species account for much of the difference among samples made at similar sites. For example, samples made by two collectors of bees at creosote bush flowers shared 90% of the abundant species, but only 20% of the rare species (Minckley et al. 1999). Future studies will face the substantial challenge of how to control or account for such variation. High replication and intense sampling for more than one season will almost certainly be required in order to differentiate putative human impacts from the "noise" of natural variation. Where high spatial variation occurs, multiple sampling locations may also be required. The levels of temporal and spatial variation and the goals of the investigation will dictate whether it is most effective to maximize resampling or sampling locations. At the same time, concerns for the sufficiency of samples must be weighed against the possibility that the system may be altered through intensive survey efforts. Such alterations may not only damage the community of interest, but also bias our assessment of changes in the bee fauna.

Detection of population trends for individual bee species may be particularly difficult, except where the impacts have been dramatic (e.g., Frankie et al. 1997). Theoretical investigations suggest that trends are difficult to detect statistically, even in cases in which changes appear substantial, and data seem to bear this out (Pechmann and Wilbur 1994, Reed and Blaustein 1995, Thomas 1997). Trends may only be detected for common, widespread species, which are easily sampled with standardized methods. Rare species potentially could be identified a priori, and sampling could be adjusted so that sufficient numbers of these species would be obtained. This latter option will be successful only to the extent that rare species are rare because they are not readily detected by the sampling protocol used or the sampling effort employed. If such species naturally persist in low populations, quantification of population trends may not be practical. Adjusting protocol to detect trends in particular species will also reduce the utility of such studies for identifying changes in community composition. Thus, the appropriate sampling techniques may depend on the focus of the study. Unfortunately, in some cases, adopting a particular protocol may limit the utility of the study for certain comparisons. In all cases, detailed records of sampling protocols including sampling duration, effort, and area will probably increase the value of a study for future comparison.

Failure of many studies to report sampling duration, effort, and area, combined with lack of standardized sampling, seriously limits the value of most historical data sets for addressing the effect of species introductions or habitat changes on native bee faunas. In cases in which the historical survey encompassed a single season or area, it is difficult to attribute differences between past and current data to a particular impact, such as loss of habitat, because we lack an estimate of the natural variation among years. Increasing the duration and intensity of sampling can mitigate temporal and spatial variation. If the interest is in comparisons over larger regions or longer time periods, then pooling data from replicate sites or across seasons within each period reduces the variation due to smaller scale fluctuation. Where data are pooled without indication of the effort devoted to subsamples within the whole, statistical testing of trends becomes impossible. Major impact may still be detected.

Two studies have demonstrated changes in bee communities associated with human-induced changes in natural vegetation. Archer (1989) resampled bees from Allerthorpe common, UK, following reforestation. The complete change in dominant vegetation resulted in a decline of species richness (before, $S_a = 128$; after, $S_a = 57$) and changes in the composition of the bee community (Archer 1989). We cannot test the significance of this change, but because of its magnitude and the number of years sampled prior to and following the impact, it appears unmistakable. Increase in plant diversity can have the opposite effect. Sakagami and Fukuda (1973) sampled two sites at the University of Hokkaido, Japan. The Botanical Garden was 9 ha and contained mixture of natural and exotic plant species. The University site was 150 ha and contained primarily native vegetation. Both were isolated from continuous tracts of natural vegetation by the city. Despite its smaller size, the Botanical Garden yielded one-third more species ($S = 85$, $S_a = 144$ species at the Botanical Garden; $S = 77$, $S_a = 108$ species at the University), perhaps as a response to increased floral diversity. Again, statistical testing of these data is prohibited, but the proximity of the two sites rules out climatic effects, and the sampling effort (months, days, hours, and specimens collected) was nearly identical for both sites.

The value of subsamples

Samples from specific floral hosts

Whether bees collected from subsamples of the flora reflect the bee fauna as a whole will probably depend on the plant sampled and the rest of the floral community available to the bees. Samples from single species are less likely to reflect the entire bee community where multiple abundant flowering species grow. In communities in which one or a few dominant flower species are hosts for the majority of the bee species, subsampling may be a reasonable approach. Our comparison of bees sampled from Asteraceae in the Carpathian Mountains (Osychnyuk 1967) probably underestimates the similarity to bees from the whole flora because the sampling duration for the whole flora greatly exceeded that on the Asteraceae. More accurate comparisons require data on sampling duration so that differences in effort can be equalized among studies. A. G. Damasceno and F. A. Silveira (*unpublished manuscript*) surveyed the bees visiting flowers of *Pterodon emarginatus* (bees' main nectar source in the area during that period) during the four weeks of this plant's flowering season. Their survey yielded 83 species, 2.5 times more species than another survey obtained from all 14 other plants blooming concurrently at the same area. All but two species collected at the surrounding vegetation were collected at *P. emarginatus*. The bee species collected at the flowers of *P. emarginatus* represent about 80% of all species known to occur in the area, based on data from 12 months of the bee flying season (A. A. Azevedo and F. A. Silveira, *unpublished manuscript*). Such data are encouraging, given the effort required to sample bees from an entire plant community. Even if the bees visiting a single plant species do not fully represent the entire fauna, subsampling from particular plants may capture the essence of the variation or changes in the bee community over space and time resulting from specific human or natural impacts (Frankie et al. 1997, *in press*, Minckley et al. 1999; R. L. Minckley and J. Cane, *unpublished data*).

Functional groups

Limitations on time and funding may make sampling an entire fauna unmanageable for some situations. An alternate approach for studying changes in bee faunas is to compare the dynamics and diversity of groups of species that differ biologically in variables such as dispersal capability, nesting habit, or degree of floral specialization (Frankie et al. 1993, Minckley et al. 1999, 2000; J. H. Cane, R. L. Minckley, L. Kervin, and T. H. Roulston, *unpublished data*). Because species are pooled when functional groups are used, one faces the danger of obscuring trends among single species. This potential weakness is also the method's strength. Use of functional groups incorporates high local diversity and avoids the extreme dynamics shown by single species of bees (Herrera 1988, Stubblefield et al. 1993). Comparisons between such groups may provide information on the nature of impacts or susceptibility of bee communities to different types of human disturbance. Loss of a rare floral host might more strongly affect bee species that specialize on that plant than generalists, whereas loss of dominant plant species in an ecosystem might adversely affect generalists and specialists (Frankie et al. 1997; R. L. Minckley and J. Cane, *unpublished data*). Ground- vs. twig-nesting species may differ in vulnerability to ecological impacts such as fire (Frankie et al. 1993) or reforestation (Archer 1989). Concordant changes among functional groups reveal key ecological variables. Such variables, combined with information on the biology of these species, could be used to infer responses of species that have not been studied because they are rare, occur in other habitats, or otherwise have not been examined (Wahlberg et al. 1996, Nieminen and Hanski 1998).

Recommendations for future sampling

Our review of natural variability and diversity of bee faunas and our attempts to collate and compare studies of different researchers from different time periods have clarified the impediments for assessing changes in bee faunas raised by lack of data on effort and area sampled, and lack of repeatable standardized sampling protocols. We reiterate the need for standardized collecting procedures and summarize recommendations previously suggested by Silveira and Godínez (1996) for systematic surveys of bees (see also Sakagami et al. 1967). Simply standardizing is not sufficient. Standardization will not correct for unknown bias or imprecise techniques, and should not lead to complacency about the quality of the data collected. This hazard calls for comparative investigations of the sampling and survey methods themselves, so that inherent biases and limitations of the methods can be identified and adjusted during summary and analysis.

Sampling protocol

Any sampling protocol will bias collection toward particular species. Time constraints, terrain and habitat type of the study area, and the particular question of interest affect which techniques are feasible. Unfortunately, we are not aware of any studies that have compared protocols for repeatability or bias. Where possible, multiple collecting methods should be employed. We mention three techniques, each conducive to standardized protocols: sweep sampling at flower hosts, pan-trapping, and trap-nesting. Although there are few data comparing these protocols (J. Cane, USDA Bee Biology Lab, Logan, Utah, *unpublished data*), different sexes of the same species (Leong and Thorp 1999) and probably different species (T. Griswold, USDA Bee Biology Lab, Logan Utah, *personal communication*) turn up in pan traps of different colors.

Netting bees at flowers provides data on relative frequencies of each bee species at the flowers that they visit. This association is crucial if the ultimate goal of the study is to assess pollinator declines. Silveira and Godínez (1996) provide detailed suggestions for sweep sampling along transects and in standard areas. Variations of this protocol have been used profitably by other researchers (Herrera 1988, Minckley et al. 1999).

Recently, more attention has been paid to pan-trapping (Leong and Thorp 1999) and trap-nesting (Frankie et al. 1993, 1998). Neither method provides association of bee species with flower hosts, and traps are known to capture only a portion of the size range of bee species. Traps have the advantage that collecting effort is substantially reduced and collector bias is removed. Pan-traps also capture species that are not easily detected by netting (T. Griswold, R. Minckley, and N. Williams, *personal observation*). In trapping as in sweeping, it is critical to report effort, in particular the numbers of traps used, the spatial arrangement, and the subsites sampled within areas. In the case of pans, colors must be reported; for trap-nests, the sizes of tunnels used must be reported (see Frankie et al. 1993).

Sampling effort and area

Regardless of the protocols adopted, we suggest that all studies should report sampling time per collector in days and hours. These are relatively simple data to record and they greatly facilitate comparisons across studies, because unequal sampling times can be standardized by unit time for specimens and species collected. Such data indicate how complete samples are for a particular area, and they can be used to decide where to focus further sampling efforts (Fagen and Karieva 1997). Data on the collection effort (time spent collecting, number of pans, etc.) add power to comparisons of the relative abundance of bees. These data, combined with a list of the species including respective numbers of specimens collected, allow for comparisons of relative abundance of specific taxa and more objective comparisons of relative richness, expected richness, and shapes of species accumulation curves (Hurlbert 1971, Soberón and Llorente 1993, Silveira and Campos 1995, Fagen and Kareiva 1997). In our current review, we have often had to forge ahead without specific data on effort, even though differences in effort are likely to bias comparisons that are sensitive to curve shape. Indeed, most historical data sets are useless for addressing population changes and changes in communities because they provide no estimate of the collecting effort involved. Even data sets that provide measures of effort have limitations; for example, collections started at different times of the season are likely to produce different patterns of species accumulation with effort.

Our results show that the size of the surveyed area can influence the number of species collected, especially when the landscape contains heterogeneous habitats (see also MacArthur and Wilson 1967, Freemark and Merriam 1986, Silveira and Godínez 1996). In large surveys, data should be collected from small, standard sampling plots that can be replicated across larger areas. Using this method, one can also assess variation among local areas and can use subsets of samples from larger areas to compare different-sized areas. Although this approach cannot control for the higher habitat diversity of larger areas, it is superior to ignoring area differences among surveys. As suggested by prior surveys, smaller sampling areas will exacerbate variation among sites. If the interest is in reporting species diversity, such samples can always be pooled, but if collections are made haphazardly across a large area, then the effect of area cannot be controlled in comparisons with other sites, nor can spatial variation among sites be assessed.

Replication of sites and seasons

High variation in the composition of species among sites demands that multiple "undisturbed" sites be used as controls so that natural variation can be separated from that due to the impact of interest. Sites should also be sampled for more than one flight season to account for variation between years. Statistical tests of changes in bee populations or communities are only possible with sufficient replication.

Periodicity

Seasonal variation in species abundance necessitates collecting throughout the active season so that different components of the local fauna and population dynamics can be represented in the sample. Intervals between sampling should be short enough to reduce the influence of yearly variation in the start of spring/summer, wet/dry seasons, or short periods of rain and droughts. Of course, different conditions will impose constraints on the periodicity that will be possible to achieve. We suggest

sampling at weekly or biweekly intervals. If longer intervals (months) are required between sampling, then collection on multiple consecutive days will mitigate fluctuations due to daily weather pattern.

Bee activity varies through the day, and different species may concentrate their activities at different times (e.g., Linsley and Cazier 1970, 1972, Tepedino 1981, Neff and Simpson 1990). If collecting from flowers, samples made during different blocks of the day should be included within the lowest unit of replication (e.g., day, week; Herrera 1988, Minckley et al. 1999). It is essential, however, to include in the sample the hours of peak activity for most of the bee species (mid-morning to mid-afternoon).

CONCLUSION

The widespread sense that there is a pollination crisis (Allen-Wardell et al. 1998, Kearns et al. 1998) requires that as much information as possible be obtained on the community and population parameters necessary to evaluate the conservation status of pollinators. This information is crucial for deciding management actions. The value of past studies for assessing pollinator declines appears to be uniformly restricted by a lack of standardized sampling techniques. Current and future studies must adopt a minimum standardization of methods to allow comparisons across regions, time, and independent studies.

RESPONSES TO THIS ARTICLE

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Acknowledgments:

We thank the National Center for Ecological Analysis and Synthesis for logistical support during the conference on Pollinator Declines in North America, and are grateful to J. H. Cane, V. J. Tepedino, and J. D. Thomson for invitation to participate. J. Seger, University of Utah, provided a program for calculating rarefaction curves and W. Fagen, one for estimating species richness (S_d). Statistical analyses benefited greatly from the insights of L. D. Harder and E. E. Crone. Peter Serdiukov kindly provided some Russian translation. E. E. Crone, S. Droege, and V. J. Tepedino provided many useful suggestions on different drafts of the manuscript. Publication costs were defrayed by a grant from the National Science Foundation through NCEAS. N. M. Williams was funded by an I. W. Killam Foundation Postdoctoral Fellowship, R. L. Minckley by NFS #DEB-0084295, and F. A. Silveira by CNPq (Brazilian council for development of science and technology) and FAPEMIG (Minas Gerais State fund for research support).

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