

Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado

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Abstract Insects provide essential ecological services in both the natural environment and in human-dominated habitats. Because pollinator declines associated with land use change have been reported across the globe, there is great concern that pollinators and the ecosystem services they provide will be negatively affected. This study examines the diversity and abundance of bee pollinators in grasslands in Boulder County, Colorado, USA. Over five years, 5,200 bees were collected in grassland plots with different levels of urbanization. Most of the difference in species composition among three levels of urbanization was due to rare species that may not have been discovered in all plots. Neither the number of species nor their abundance differed significantly among the plot types, although the trend indicated increasing diversity with increasing distance from urbanization. Most notably, measures of urbanization, such as the amount of pavement and development, were not correlated with diversity. The most important factor affecting bee abundance, particularly for ground-nesting bees, was grazing regime. Bee abundance also was positively related to the number of flowering plant species. Other studies of different insects (grasshoppers and butterflies) in these plots showed results similar to ours. In contrast, previous studies on song-birds, raptors, and rodents showed significant differences between urban edge and remote plots in terms of organism abundance and diversity. Together, these results suggest that factors other

than the degree of urbanization are important in determining insect abundance and diversity.

Keywords Insects · Pollinators · Grasslands · Bee diversity · Bee abundance · Urbanization · Grazing

Introduction

Reports of pollinator declines around the globe have focused attention on the important roles that these organisms perform in natural biological communities and for humans (Buchmann and Nabhan 1996; Allen-Wardell et al. 1998; Kearns et al. 1998). Pollinators are responsible for fruit and seed production for 60–70% of flowering plants (Richards 1986). Seeds represent future generations of plants, and seeds and fruits provide food for numerous organisms. A major disruption in pollination services therefore could disrupt numerous communities. In addition, estimates suggest that pollinators are involved in the production of one-third of human food plants (Buchmann and Nabhan 1996). One cause of pollinator declines is the changing landscape caused by urban sprawl (Turner et al. 2004; Cane 2005a; Johnson and Klemens 2005a). Development of cities and suburbs results in habitat loss or habitat degradation (Johnson and Klemens 2005b). The loss or degradation of the landscape can eliminate or reduce the availability of resources necessary for pollinators to survive; thus, the new habitat can no longer support the original organisms (Johnson and Klemens 2005b). Urbanization also changes vegetation patterns such that previously unfragmented landscapes become a mosaic of pavement, buildings, parks, gardens, and small remnants of native habitat (French et al. 2005; Johnson and Klemens 2005b). For pollinators, urbanization means a change in the

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availability of nesting sites as well as the quality and accessibility of food plants, resources that must generally be located within close proximity to nest sites. Remnant fragments of natural habitat surrounded by development may be unable to support the original diversity of native pollinators or plants upon which they depend.

Studies have shown that community composition of varying arthropods can differ in response to urban land use (Bańkowska 1980, 1981; Kakutani et al. 1990; McIntyre et al. 2001). Recent studies have specifically addressed the bee fauna of urban habitats (Tomassi et al. 2004; Cane 2005b; Frankie et al. 2005; Zanette et al. 2005; Cane et al. 2006; McFrederick and LeBuhn 2006; Hinners 2008; Matteson et al. 2008). An analysis of data from several urban studies indicates that more than 90% of the individual bees collected belonged to only 12 common genera (Cane 2005b). It appears that some elements of the natural bee fauna disappear from urban habitats. Generalist bee species with broad tolerances are favored in urban areas (Cane 2005b), while specialists suffer from the absence of their host plants and decrease in number. These studies also indicate that cities can support diverse bee faunas, although the composition of plantings and the proximity to natural landscapes strongly affect that diversity. While some garden flowers are cultivated for showiness at the expense of nectar and pollen, others may be very attractive to pollinators. Plantings of native flowers often concentrate bee resources in a small area and can be a magnet for native pollinators (Frankie et al. 2002). Because bees are central foragers, bee diversity in urban areas may depend on the proximity of nesting sites and floral resources within their limited flight ranges (150–750 m for most solitary bees; Gathmann and Tscharntke 2002; Steffan-Dewenter et al. 2002; Cane 2005b). In addition, suitable patches of habitat must not be isolated from similar patches, or normal colonization and extinction may be disrupted, and small populations may ultimately collapse (Cane 2005b). There is evidence that rural open space, hedgerows, and undeveloped fields surrounding urban centers will help to maintain floral diversity and thereby augment bee diversity in urban habitats (Osborne et al. 1991; O'Toole 1993; Osborne and Corbet 1994; Steffan-Dewenter et al. 2002).

Boulder, Colorado, USA (latitude: 39°55'–40°5' N, longitude: 105°10'–105°17' W; elevation: 1,655 m), where this research was conducted, is a city of 102,000 residents plus an additional 30,000 university students. The population of Boulder has increased by about 75,000 people in the last half century (Collinge et al. 2003), and human activities have dramatically changed the environment. The bee fauna may have changed as well. But unlike many cities, Boulder is surrounded by extensive public lands. Since 1868, when the

first public land purchase was made by the residents of Boulder (City of Boulder Open Space and Mountain Parks 2006), undeveloped public lands have continued to expand and currently the City of Boulder Open Space and Mountain Parks manages over 43,000 acres of open space. Outside the city proper, Boulder County Open Space manages an additional 70,000 acres (Stewart 2005–2006) and the Boulder Ranger District manages 160,000 acres of National Forest (USDA 2007).

Changes in community composition related to urbanization in Boulder are known for many species of organisms. In 1994, Bock and Bock (1994) established a set of grassland biodiversity plots that have been used by various researchers to look for patterns of species composition associated with urbanization. Researchers using these plots have examined raptor (Berry et al. 1998), grasshopper (Craig et al. 1999), songbird (Haire et al. 2000), rodent (Bock et al. 2002), and butterfly (Collinge et al. 2003) communities. The vegetation of these plots has also been catalogued and plant species have been assigned importance indices based on percentage cover in the plots (Bennett 1997). The plots have been characterized as “urban” or “remote” and evaluated for multiple habitat characteristics (Haire et al. 2000). Urban plots bordered on areas of human activity (within 100 m) and remote plots were surrounded by more natural habitat (750 m and greater from development; Bock et al. 2002). Our study used a subset of these biodiversity plots plus four additional grassland plots to assess how native bees respond to different levels of urbanization, habitat fragmentation, vegetation changes, and other land use parameters. A future paper will evaluate dipteran pollinators in these plots.

Insect populations can be difficult to sample because of large spatial and temporal variability (Herrera 1988; Minckley et al. 1999; Cane and Tepedino 2001; Roubik 2001; Williams et al. 2001) but several researchers have had success in making comparisons of insect surveys among habitats sampled with the same techniques (Bańkowska 1980, 1981; Inoue et al. 1990; Kakutani et al. 1990; Kato et al. 1990; Hughes et al. 2000). This study uses the comparative approach and supplements comparisons among habitats with historical information.

It is often difficult to produce a complete species list of insects in a particular area. Compared to short sampling periods, longer sampling periods are likely to produce additional species that are uncommon, more difficult to collect, or have migrated into the area since sampling began (Magurran 2006). This study uses the program EstimateS (Colwell 2005) which calculates multiple measures of species richness and species diversity based on the pattern of species accumulation over multiple samples.

Hypotheses

Our main hypothesis was that bee species richness and abundance would differ between urban and remote plots. In addition, we hypothesized that features of each plot, such as the extent of development and whether or not the plot was grazed, would also affect bee diversity. Urban and remote plots were expected to show differences in the proportions of ground-nesting and cavity-nesting bees, with ground-nesting bees dominating the remote sites.

Methods

Flower-visiting bees and flies were collected in 20 grassland biodiversity plots over the course of five summers from 2001 to 2005. In 2001, pollinator sampling was conducted in 16 Boulder Open Space biodiversity plots (Bock and Bock 1994). All plots were designated as remote or urban based on their proximity to urban development, roadways and urban parks. In addition, we recorded whether grazing by cattle was occurring in each plot. Each plot was marked with a central stake and GPS coordinates were recorded. Circular transects with a radius of 35 m from the central stake were marked with pin flags that remained in place for the field season. Sampling involved collecting all flower-visiting bees and flies in the circular transect with sweep nets within a standardized time frame. One researcher walked the perimeter and collected insects on flowers within an arm's length of either side of the circular transect. A second researcher sampled the interior of the plot. Each insect collected was given an accession number, field identification, and the flower species on which it was collected was recorded. Sampling was conducted during periods of peak bee activity from 10:00 am until 3:30 pm on sunny days with temperatures between 75 and 95°C. Sampling took place in each plot once a week from mid-June to mid-August.

In 2002, four additional “Hayes” plots (named for the landowner) were added to the study. These additional plots were located on private property and used through a landowner agreement with Boulder Open Space. They were chosen because they were more isolated from development than the other remote plots, and the landowner had tried to maintain the habitat in a natural condition. None of these plots had been grazed by livestock within at least 20 years. In 2002 and 2003, all 20 plots were sampled as described above.

In 2004, plots were sampled with pan traps every 2 weeks in order to determine whether additional pollinator species were present that were not being collected on flowers. Three different colored pan traps [3.5-oz. Solo brand soufflé cups painted Bee Blue, Bee Yellow (Risk Reactor Paints), or left the original white] were set out in each plot for each

sampling period (modified protocol from LeBuhn et al. 2003). Pans were filled 1/3 full with a weak solution of soapy water. Bees and flies collected in pans were rinsed, blow-dried, pinned, and given accession numbers. In 2005, plots were sampled by hand-netting in May and early June, since early-season samples were under-represented in previous years. In addition, eight gardens were sampled by hand-netting and pan trapping as described above.

Bees were identified to genus when possible and sent to Robert Minckley at the University of Rochester for species (or morphospecies) identifications. Solitary bees were classified as ground nesting, cavity nesting or cleptoparasites. The percentages of ground-nesting and cavity-nesting bees were compared among plot types. Voucher specimens were placed in the University of Colorado Museum's entomology collection.

Habitat surrounding the 20 plots was characterized for two qualitative variables (urban or remote character and grazing regime) and seven quantitative environmental variables. Quantitative variables were measured for the 20 ha surrounding the central plot marker using Boulder Open Space vegetation maps and aerial photographs and tables (City of Boulder Open Space and Mountain Parks 2004), aerial photographs (USGS 1999) and ArcGIS (ESRI software 2004) mapping programs. The seven quantitative variables consisted of the number of square meters that were cultivated, developed, paved roads, grassland, urban park, water, and wetland. Additionally, the total number of plant species flowering in each plot, the mean number of species flowering over sampling periods for each plot, and the number of flowering species in that plot as determined by Bennett (1997) were recorded. Primarily wind-pollinated plants were not included in these measures.

Data analysis

For each plot, the number of species and number of hand-netted bees were tallied by year for 2001–2003 and totaled over years. Pan trap data and data from early season samples in 2005 were used to add any potential pollinating species to the species list. Data analysis on those hand-trapped bees identified to the species/morphospecies level was conducted using EstimateS 7.52 (Colwell 2005) and SAS 9.1 (SAS Institute Inc. 2002–2003). EstimateS is a statistical program that determines the true species richness in an area. Two species richness predictors were calculated: ACE and CHAO2. These statistics are based on abundance data rather than incidence data and as such are more appropriate for determining species richness of mobile organisms such as insects (Hellman and Fowler 1999; Brose and Martinez 2004). In addition, both Shannon and Simpson species diversity indices were calculated using

SAS 9.1 for the following: each plot per year, each plot over the years 2001–2003 (full summers of hand-netting), all remote plots, all urban plots, all Hayes plots, all grazed plots, and all non-grazed plots.

Comparisons of abundance, species richness, and species diversity were made using SAS general linear models (Proc GLM). ACE and CHAO2 and abundance of non-*Apis* bees were log transformed to meet the assumptions of normality. Correlations between abundance, species richness, species diversity and environmental variables were made using Spearman's correlation coefficients (SAS Proc CORR). Raw abundance and relative proportions of ground and cavity-nesting solitary bees were analyzed for differences related to urbanization (SAS Proc GLM) and for correlations with environmental variables (SAS Proc CORR). Indices of similarity were calculated for urban, remote and Hayes plots.

Results

Over 2,100 bees were collected by hand-netting and 3,000 by pan-trapping in plots (5,207 specimens) in 450 samples. Eighty-eight species were collected by hand-netting in the remote, urban and Hayes plots. Only two of these species were exclusive to the Hayes plots. Using EstimateS to predict the actual species richness, we arrived at predictors of 100.84 (ACE) and 98.98 (CHAO2; 91.94–118.58; 95% confidence interval; Fig. 1). Sixteen additional species were collected in pan traps for a total of 104 grassland species. Five hundred and twenty bees were collected in gardens, adding four new species (“Appendix”).

The index of similarity was 0.56 between the remote and urban plots, 0.41 between the remote and Hayes plots, and 0.44 between the urban and Hayes plots. Although it

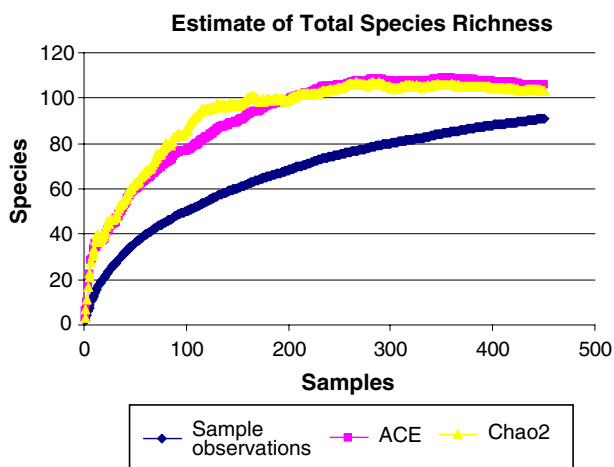


Fig. 1 Species richness of entire sample area including all plots, and based on hand-netted specimens

appeared that each of the three types of plots have different community composition, most of the difference was due to species that existed in low abundance and may have been rare enough not to find in all plots. For example, of the 49 species that only occur in one plot type, the mean abundance was 1.48 individuals. Those species that were abundant in one plot type were also abundant in the other plot types. The most abundant species were generalists found in all plot types: *Apis mellifera*, *Augochlorella striata*, and *Halictus ligatus*. *Halictus tripartitus* and *Lasioglossum (Dialictus) morphospecies 1* were abundant in remote and urban plots, and present in smaller numbers in Hayes plots. All of these species are eusocial bees. Some species of *Lasioglossum (Dialictus)* are eusocial as well.

Hand netting bees produced a total of 64 species of bees in the eight original remote plots, 62 species in urban plots, and 42 in the Hayes plots (Table 1). The number of species collected per plot did not differ among remote, urban and Hayes plots (SAS Proc GLM, $P = 0.67$), nor did the abundance of bees (SAS Proc GLM, $P = 0.74$). Estimates for true species richness and for species diversity did not differ significantly among urban, remote and Hayes plots (Table 1; ACE (log transformed for normality) $P = 0.59$; Chao2 (log transformed for normality) $P = 0.96$; Shannon index $P = 0.82$; Simpson index $P = 0.90$). The abundance of non-*Apis* bees did not differ among remote, urban, and Hayes plots (Proc GLM, $P = 0.74$), nor did the abundance of *Apis* (SAS Proc GLM, $P = 0.78$).

Environmental variables measured in the 20 ha surrounding each plot marker differed among remote, urban and Hayes plots (Table 2). In general, there was no correlation between measures of species richness, species diversity, bee abundance and these environmental variables. The correlation between the number of species in a plot and the amount of development was not significant (Spearman's correlation coefficient -0.05 , $P = 0.80$), nor was the correlation between abundance of non-*Apis* bees and development (Spearman's correlation coefficient -0.20 , $P = 0.39$). There was, however, a significant negative correlation between the number of bee species and the amount of grassland in the 20 ha surrounding the central plot marker (Spearman correlation coefficient -0.45 , $P = 0.05$). In addition, bee diversity in plots was correlated with the mean number of species flowering in the plot over the course of sampling (Simpson index of bee diversity and flowers: Spearman correlation coefficient 0.45, $P = 0.04$; Shannon index of bee diversity and flowers: Spearman correlation coefficient 0.52, $P = 0.01$), as well as Bennett's value for the number of flowering species in the plot (Simpson index of bee diversity and Bennett value: Spearman correlation coefficient 0.57, $P = 0.02$; Shannon index of bee diversity and Bennett value: Spearman correlation coefficient 0.53, $P = 0.04$).

Table 1 Comparison of hand-netted bee data from urban, remote and Hayes plots

	Urban plots	Remote plots	Hayes plots	Sum of all plots
Number of species	62	64	42	91
ACE	83.16	91.64	52.78	100.84
CHAO2 ^a	74.59 (66.29–98.97)	90.86 (74.43–133.15)	69.11 (50.05–128.30)	98.98 (91.94–118.58)
Shannon index	2.68	2.77	2.8	2.87
Simpson Index	5.98	6	8.96	6.67

Estimators calculated with EstimateS (Colwell 2005)

^a 95% Confidence interval

Table 2 Plot variables

Plot	Plot type	Grazing regime	Cultivated (sqm)	Developed (sqm)	Highway (sqm)	Grass (sqm)	Park (sqm)	Water (sqm)	Wetland (sqm)	Bennett flowers	Recorded flowers	Mean flowers
1	Urban	Not	0	156701.5	0	918,747	0	0	0	81	71	10.81
2	Urban	Notgrz	0	6720.984	0	1,068,728	0	0	0	74	52	8.46
4	Remote	Notgrz	0	0	0	1,023,642	0	0	51804.8	78	53	9.07
5	Remote	Notgrz	28849.52	0	0	1,046,597	0	0	0	76	52	9.22
12	Remote	1 Year	0	0	0	1,027,225	0	0	48219.1	72	66	10.27
13	Remote	1 Year	0	0	0	1,015,450	0	0	59993.9	80	76	12.4
14	Urban	1 Year	0	143543.5	0	166,468	429,763	335,669	0	73	63	9.11
15	Urban	1 Year	0	315596.4	0	660,606	41650.9	0	57591.7	81	63	9.92
28	Urban	Grazed	0	247,237	0	806,886	21339.5	0	0	75	59	8.61
29	Urban	Grazed	0	208953.8	0	750,737	107,928	0	7844.81	74	60	9.58
46	Remote	Notgrz	0	0	21797.4	998,952	0	0	54711.4	41	51	9.27
47	Remote	Notgrz	0	0	0	957,823	0	0	117,638	18	42	6.38
58	Urban	Notgrz	639114.2	179163.7	0	257,187	0	0	0	39	41	7.76
59	Urban	Notgrz	960394.4	2064.764	0	113,005	0	0	0	32	47	6.92
60	Remote	Grazed	0	0	0	1,075,495	0	0	0	58	48	8.42
61	Remote	Grazed	0	0	0	1,075,499	0	0	0	62	57	10.13
67	Hayes	Never	0	0	0	932,866	0	0	142,601	–	47	8.47
68	Hayes	Never	0	0	0	709,102	0	0	366,366	–	37	7.16
69	Hayes	Never	0	0	0	1,075,499	0	0	0	–	51	10.74
70	Hayes	Never	0	4779.153	0	1,056,893	0	0	13796.7	–	47	11.05

Sqm refers the number of square meters of that environmental variable found within the 20 ha surrounding the central plot marker

Bennett flowers refers to the number of species of animal pollinated plants recorded in the plot by Bennett (1997)

Recorded flowers refers to the number of species of animal pollinated plants recorded over the course of our study

Mean flowers refers to the average number of species flowering within the plot on a sampling date

Two significant differences were detectable among plots under the four different grazing regimes [four grazing regimes: (1) Hayes plots not grazed for 20+ years; (2) plots not grazed during study; (3) plots grazed during 1 year of the study; (4) plots grazed throughout the study]. First, overall, the abundance of native bees was significantly different among the four different regimes (Proc GLM, $P = 0.005$ on log transformed abundance variable). Abundance decreased with increased grazing. The mean number of bees collected per year was highest in plots that were not grazed (Hayes plots 27.13^a, plots not grazed during the study 27.53^{ab}). The number of bees decreased in plots with more grazing (means

for plots grazed 1 year 15.25^{bc}, plots grazed over course of study 13.83^c) Superscripts represent Duncan groupings of the log transformed variables. Although bee abundance differed among grazing regimes, there were no significant differences in species richness.

The second difference among the four grazing regimes was in the number of plant species that were flowering (Proc GLM, $P = 0.003$). Those plots that were grazed only 1 year during the course of the study had significantly more species flowering in that year of grazing (mean number of species flowering in plots grazed 1 year 67^a) compared to other grazing regimes (mean number of species flowering

in Hayes plots 45.5^b; in plots not grazed during the study 51.13^b; in plots grazed throughout the study 56^b. Supercripts represent Duncan groupings.

We examined the relative abundance of ground-nesting and cavity-nesting solitary bee species in our plots. The percentage of ground-nesting bees was positively correlated with the amount of grassland within the 20 ha surrounding each central plot marker (Spearman correlation coefficient 0.55, $P = 0.011$). The abundance of ground-nesting bees differed among remote, urban and Hayes plots ($P = 0.06$), with Hayes plots having the highest mean abundance of bee species (32.0), followed by remote plots (26.8) and then urban plots (17.0). The abundance of ground-nesting bees also differed among grazing regimens ($P = 0.02$). Plots grazed for 1 year had the highest mean abundance of ground-nesting bees (36.50) followed by the Hayes plots that had not been grazed in over 20 years (23.00). Routinely grazed plots had a mean abundance of 18.5 ground-nesting bees, and plots that had not been grazed during our study had a mean abundance of 16.25 bees. The abundance of cavity nesting bees was low at all sites, and the percentage of cavity nesting bees (arcsin transformed) was not significantly different among the remote, urban and Hayes plots, nor among different grazing regimes.

Discussion

The 108 bee species collected in this study compare favorably with the 116 species found in similar Boulder County habitats in 1907 (Cockerell 1907; analysis in Kearns and Oliveras, in preparation). Thus, Boulder County does not appear to have suffered significant losses in bee diversity despite the environmental and human population changes that have occurred in the past century. Although urban, remote, and Hayes plots differed in respect to environmental variables, all plot types were species-rich. Comparable measures of ACE and CHAO2 within plot types increase our confidence in these values. EstimateS indicated that all plot types were likely to contain additional species, especially the remote and Hayes plots. Both Shannon and Simpson species diversity indices suggest that diversity increased from urban plots to remote plots to Hayes plots as we anticipated, but differences in overall abundance and species richness were not dramatic and did not follow predicted patterns.

In some of the earlier studies conducted in the Bock biodiversity plots, species composition changed dramatically between urban edges and remote plots. For example, Haire et al. (2000) found that grassland nesting songbirds decreased in abundance in more urban habitats. In contrast, robins, starlings, grackles, house finches and house sparrows were almost five times as abundant in urban edge plots as remote (interior) plots (Bock et al. 1995, 1999).

Another study of diurnal raptors in these plots demonstrated that 5–7% urbanization was a critical threshold value that limited bald eagles, ferruginous hawks, rough-legged hawks and prairie falcons (Berry et al. 1998). In contrast, red-tailed hawks, Swainson's hawks and American kestrels were not sensitive to the amount of urbanization in the urban plots (Berry et al. 1998). For the most part, rodent studies in the biodiversity plots also showed that species composition differed between remote, interior areas and urban edges. Bock et al. (2002) showed that three species of native rodents were most abundant in remote plots; however, the non-native house mouse was found equally in both urban and remote plots.

Two studies of insects on these biodiversity plots showed results more consistent with our bee study. Craig et al. (1999) found that grasshopper populations were not seriously affected by urban development. Collinge et al. (2003) found that urbanization did not have a predictable effect on butterfly abundance or species richness. Perhaps because of their size and mobility, insects are responding to habitat changes at a different scale. Insects are influenced by habitat fragmentation associated with human land use, such that smaller fragments support fewer species (McGeoch and Chown 1997; Bolger et al. 2000; Collinge 2001; Hinners 2008). It is possible that small fragments are less likely to contain the resources that bees require, such as appropriate nesting sites, food, water, etc. Thus, bees, grasshoppers and butterflies might be more affected by the presence or absence of specific habitat features rather than direct effects of urbanization.

Surprisingly, there were few correlations between bee richness and the seven quantitative environmental variables for the area surrounding each plot. We had predicted that an increase in development would result in a decrease in species richness. Instead, we found no relationship between urban development and species richness. Our failure to find a correlation between development and species richness may be due to the differences in scale with which humans and insects perceive the environment. We were sampling in Open Space at the edge of development, and the area of developed land was measured for the 20 ha surrounding the center of the plot. However, bees typically fly short distances. They may have had all the resources they needed at the urban edge and may not have flown into the developed area. Alternatively, it is possible that the high prevalence of generalist species (*A. mellifera*, *A. striata*, and *H. ligatus*) in each of our plots weakened any effect that the environmental variables might have had. These species are not limited by a narrow range of suitable ecological factors; the plots may have contained a variety of resources that they could use, despite the varying levels of development as measured by our plot variables.

Grazing by cattle had effects on both bee abundance and on flowering. Plots that were routinely grazed had the lowest

abundance of bees. Our Hayes plots (grazing regime 1), which had not been grazed in over 20 years, had the highest abundance of bees. The Hayes plots differed significantly from the plots that were grazed (grazing regimes 3 and 4). Thus, grazing alone may not have been the cause for this difference, since other aspects of the habitat were likely to be different in these more natural Hayes plots. Nonetheless, the plots that were not grazed during the course of this study (grazing regime 2) still had a higher abundance of bees than those plots that were grazed during the study. These results are similar to those of Kruess and Tschardtke (2002) who found that decreased grazing resulted in increased abundance of bees in grasslands in Germany. As in our study, species richness was not affected.

Flowering was also affected by grazing. The number of species flowering under the different grazing regimes was similar with one exception. Those plots that were grazed only 1 year of the study (grazing regime 3) had a greater number of species flowering each sampling period during that year of grazing. We believe that this is due to intermediate disturbance effects. A moderate disturbance by cattle during that 1 year of grazing may have reduced the dominant forms of vegetation and allowed other plant species to grow and flower. In comparison, there was no grazing in the Hayes plots or in the eight plots of grazing regime 2; the lower levels of disturbance in these plots may have precluded the establishment, growth, and flowering of new plant species that are more attractive to bees. Similarly, the decreased number of flowers in the plots that were grazed routinely (grazing regime 4) may be due to their consumption by cows.

The abundance of solitary ground-nesting bees differed among plot types as well as grazing regimes. The abundance of ground-nesting bees was positively correlated with the amount of grassland in the plot, as might be expected. In addition, the abundance of ground-nesting bees was highest in grazing regime 3 plots during the 1 year when those plots were grazed and had record numbers of species flowering. This finding is in agreement with other studies that found that floral abundance was the best predictor of pollinator abundance in pastures (Carvell 2002; Sjödin 2007). The results of our study suggest that grazing indirectly affected bee diversity by influencing the number of flowering species present at any time. That bee diversity increases with the number of flowering species seems natural, as different sizes and colors of flowers are likely to attract different bee species.

Other investigators examining grazing and the status of ground-nesting bees have obtained differing results. For example, Vulliamy et al. (2006) found that in Mediterranean habitats, intensive grazing increased bee abundance by increasing nesting sites and maintaining a diverse flora. In contrast, Gess and Gess (1993) and Sugden (1985) both

found that grazing decreased bee abundance in their studies. Gess and Gess (1993) and Sugden (1985) measured the effects of grazing in semi-arid habitats in southern Africa and in California, respectively. Their results indicated that grazing animals trampled bees and compressed the ground making it less suitable for nest sites. In addition, the foraging done by grazing animals in these two studies increased the abundance of plants that were not attractive to bees. These three factors may have contributed to the decrease in bee abundance in these studies. Another variable that may influence bee numbers is the amount of moisture present in the habitat. In our study, the plots that were routinely grazed were often dry and lacked the abundance of flowers found in other plots. It is possible that the amount of moisture in the habitat may mediate the effects of grazing.

Other studies have documented higher numbers of cavity-nesting bees in small urban areas compared to larger, more natural habitats (Cane et al. 2006; Hinners 2008). We also expected to find that cavity-nesting bees would be more prevalent in the urban plots, but our study revealed no differences in the abundance of cavity-nesting bees in remote, urban or the Hayes plots. This finding may be due to the fact that cavity-nesting species made up a small percentage of all the bees collected.

Overall, our results indicate that the bee community in Boulder County grasslands is doing well and is comparable to the community that existed 100 years ago. While urban development was not a good predictor of insect abundance, the diversity indices indicated a trend of increased species diversity from urban, to remote, to the Hayes plots. Other environmental variables (e.g. square meters in the plot that were cultivated, grass, park, water, or wetland) were also not useful in predicting pollinator abundance. In contrast, the number of flowers in the plot and the grazing regimen were both correlated with bee numbers; bee diversity was highest in plots with many flowers and in plots that were grazed for 1 year. It appears that, similar to the findings of Sjödin (2007) and Carvell (2002), floral abundance is the best predictor of bee abundance.

Human population growth in Boulder County has increased greatly in the past century. Similar urban growth has been seen in many areas of the United States. In fact, urban development in the United States covers a land area greater than the combined area of all the state and national parks (McKinney 2002). Urban areas are characterized by sealed surfaces (pavement and buildings) and managed vegetation. Since urban areas continue to grow, the opportunity exists to plan developments that attract and encourage pollinators, native plants, and wildlife in general. Urban planning can incorporate native vegetation in such a way as to create corridors that connect urban parks with extensive plantings attractive to pollinators and other wildlife. Development of parks, office complexes,

campuses, and home gardens with pollinators in mind can produce esthetically pleasing urban environments while preserving the diversity of flora and fauna. For example, several recent studies indicate that gardens and parks in urban areas can maintain diverse bee assemblages (McFrederick and LeBuhn 2006; Matteson et al. 2008), especially when native flowering species are planted (Frankie et al. 2002, 2005; Cane et al. 2006). As we gain an understanding of the resources needed by pollinators, we can actively try to incorporate them in the development of our urban areas to ensure that urban and suburban areas do not suffer losses in overall biodiversity.

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Appendix

See, Table 3.

Table 3 Bee species collected

<i>Agapostemon</i>	<i>virescens</i>
<i>Agapostemon</i>	<i>angelicus/texanus</i>
<i>Andrena</i>	<i>claytonim</i> ^a
<i>Andrena</i>	<i>crataegi</i>
<i>Andrena</i>	<i>cressonii</i> (?)
<i>Andrena</i>	<i>gardineri</i> (?)
<i>Andrena</i>	sp 1
<i>Andrena</i>	sp 3
<i>Andrena</i>	sp 4
<i>Andrena</i>	sp 5
<i>Andrena</i>	sp 6

Table 3 continued

<i>Andrena</i>	sp 7
<i>Andrena</i>	sp 8
<i>Andrena</i>	sp 9
<i>Anthidium</i>	<i>mormonum</i>
<i>Anthidium</i>	<i>porterae</i>
<i>Anthidium</i>	sp 1
<i>Anthophora</i>	<i>montana</i>
<i>Anthophora</i>	<i>smithii</i>
<i>Anthophora</i>	sp 2 ^a
<i>Anthophora</i>	sp 3
<i>Apis</i>	<i>mellifera</i>
<i>Augochlorella</i>	<i>striata</i>
<i>Augochloropsis</i>	<i>metallica</i>
<i>Augochloropsis</i>	<i>sumptuosa</i> ^a
<i>Bombus</i>	<i>appositus</i>
<i>Bombus</i>	<i>bifarius</i>
<i>Bombus</i>	<i>centralis</i> ^{a, b}
<i>Bombus</i>	<i>fervidus</i>
<i>Bombus</i>	<i>flavifrons</i>
<i>Bombus</i>	<i>fraternus</i>
<i>Bombus</i>	<i>griseocollis</i>
<i>Bombus</i>	<i>huntii</i>
<i>Bombus</i>	<i>morrisonii</i>
<i>Bombus</i>	<i>nevadensis</i>
<i>Bombus</i>	<i>pennsylvanicus</i>
<i>Bombus</i>	<i>rufocinctus</i> ^b
<i>Ceratina</i>	<i>nannula</i>
<i>Ceratina</i>	<i>neomexicana</i>
<i>Coelioxys</i>	<i>sayi</i>
<i>Ceratina</i>	sp 1
<i>Colletes</i>	<i>phaceliae</i>
<i>Diadasia</i>	<i>australis</i>
<i>Diadasia</i>	<i>diminuta</i> ^a
<i>Dianthidium</i>	<i>curvatum</i>
<i>Dianthidium</i>	<i>pudicum, pudicum consimile</i>
<i>Doerengiella (Triepeolus)</i>	<i>grandis</i> ^a
<i>Doerengiella (Triepeolus)</i>	<i>helanthe</i>
<i>Doerengiella (Triepeolus)</i>	sp 1
<i>Epeolus</i>	sp 1
<i>Halictus</i>	<i>confusus</i>
<i>Halictus</i>	<i>ligatus</i>
<i>Halictus</i>	<i>rubicundus</i>
<i>Halictus</i>	<i>tripartitus</i>
<i>Heriades</i>	<i>carinata</i> ^a
<i>Hoplitis</i>	<i>pilosifrons</i>
<i>Hoplitis</i>	<i>producta</i>
<i>Hoplitis</i>	<i>spoliata</i> ^a
<i>Hylaeus</i>	<i>affinis</i>
<i>Hylaeus</i>	<i>cressonii</i>

Table 3 continued

<i>Hylaeus</i>	<i>episcopalis</i>
<i>Hylaeus</i>	<i>mesillae</i>
<i>Lasioglossum (Evylaeus)</i>	<i>cooleyi</i> ^a
<i>Lasioglossum (Lasioglossum)</i>	<i>paraforbesii</i> ^a
<i>Lasioglossum (Dialictus)</i>	<i>sisymbrii</i>
<i>Lasioglossum</i>	sp.2
<i>Lasioglossum (Dialictus)</i>	<i>aberrans?</i>
<i>Lasioglossum (Dialictus)</i>	<i>anomalus</i>
<i>Lasioglossum (Dialictus)</i>	<i>imatatum</i>
<i>Lasioglossum (Dialictus)</i>	<i>laevissimus</i>
<i>Lasioglossum (Dialictus)</i>	<i>pruinosa</i>
<i>Lasioglossum (Dialictus)</i>	<i>pruinosisiformis</i>
<i>Lasioglossum (Dialictus)</i>	sp 1
<i>Lasioglossum (Dialictus)</i>	sp 2
<i>Lasioglossum (Dialictus)</i>	sp 3
<i>Lasioglossum (Dialictus)</i>	sp 4
<i>Lasioglossum (Dialictus)</i>	sp 5
<i>Lasioglossum (Evylaeus)</i>	sp 1 ^a
<i>Lasioglossum (Evylaeus)</i>	sp 2 ^a
<i>Lithurge</i>	<i>apicalis</i>
<i>Megachile</i>	<i>brevis</i>
<i>Megachile</i>	<i>fortis</i>
<i>Megachile</i>	<i>latimanus</i>
<i>Megachile</i>	<i>manifesta</i> ^a
<i>Megachile</i>	<i>montivaga</i>
<i>Megachile</i>	<i>parallela</i>
<i>Megachile</i>	<i>sexdunata</i> ^a
<i>Megachile</i>	sp 1
<i>Megachile</i>	sp 2 ^a
<i>Megachile</i>	sp 3
<i>Megachile</i>	sp 4 ^a
<i>Megachile</i>	<i>subexilis</i>
<i>Megachile</i>	<i>wootoni</i>
<i>Melissodes</i>	<i>tristis</i>
<i>Melissodes</i>	<i>agilis</i>
<i>Melissodes</i>	<i>bimaculatus</i> ^b
<i>Melissodes</i>	<i>coreopsis</i>
<i>Melissodes</i>	<i>grindelia?</i>
<i>Melissodes</i>	<i>menuachus</i>
<i>Nomada</i>	sp 1 ^a
<i>Osmia</i>	<i>atrocyanea</i>
<i>Osmia</i>	<i>bruneri</i>
<i>Osmia</i>	<i>cordata</i>
<i>Osmia</i>	<i>nanula</i> ^a
<i>Perdita</i>	<i>rectangulata</i>
<i>Perdita</i>	sp 1
<i>Sphecodes</i>	<i>eustictus</i>
<i>Sphecodes</i>	sp 1
<i>Sphecodes</i>	sp 2 ^{a, b}

Table 3 continued

<i>Sphecodes</i>	sp 3
<i>Stelis</i>	<i>monticola</i>
<i>Svastra</i>	<i>obliqua</i>

^a Pan trapped only

^b Gardens only

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