

Bee communities (Hymenoptera: Apoidea) of small Iowa hill prairies are as diverse and rich as those of large prairie preserves

Stephen D. Hendrix · Kyle S. Kwaiser · Stephen B. Heard

Received: 8 June 2009 / Accepted: 13 February 2010 / Published online: 27 February 2010
© Springer Science+Business Media B.V. 2010

Abstract Natural small, xeric hill prairies in forested landscapes throughout the Midwest United States often contain high diversity and unique species of some organisms because of their unusual landscape context and microclimate. We measured the diversity, richness, and abundance of the bee communities of five hill prairies located in northeastern Iowa and we compared these to values for large prairie preserves in northwestern Iowa, using a Monte Carlo resampling approach to standardize sampling effort between habitat types. We also measured the diversity and richness of the flowering forb communities at the hill prairies and we quantified percentage of the landscape at a 1 km radius in different landscape elements. Bee diversity at the five hill prairies spanned the range of diversity values for large prairie preserves, so although the hill prairies are small (<5 ha), their bee communities are not uniformly depauperate compared to larger western prairie preserves. Bee diversity was significantly related to flowering forb diversity, and may have been influenced by landscape features within 1 km—particularly the percentage of agricultural row crops and open water, which may negatively affect bee diversity at the sites. Iowa’s hill prairie bee communities were largely composed of widespread eastern species, although about 10% of the bee species have more northern or western ranges and appear to be taking advantage of the region’s unique habitat features. Given the dependence of the

Electronic supplementary material The online version of this article (doi:[10.1007/s10531-010-9797-x](https://doi.org/10.1007/s10531-010-9797-x)) contains supplementary material, which is available to authorized users.

S. D. Hendrix (✉) · K. S. Kwaiser
Department of Biological Sciences, The University of Iowa, 134 Biology Building, Iowa City,
IA 52242-1324, USA
e-mail: stephen-hendrix@uiowa.edu

Present Address:

K. S. Kwaiser
University of Michigan Biological Station, University of Michigan, Ann Arbor, MI 48109, USA

S. B. Heard
Department of Biology, University of New Brunswick, P.O. Box 4400, Fredericton, NB E3B 5A3,
USA

bee communities on the plant diversity of the sites, management of the plant community to maintain its diversity will also likely benefit bee diversity.

Keywords Bee community composition · Bee diversity · Iowa hill prairies · Iowa prairie preserves · Paleozoic Plateau · Plant diversity

Introduction

Hill prairies along the Missouri, Mississippi and Illinois River corridors (Hanson 1922; Robertson et al. 1996) as well as areas of the Ozarks and Appalachia (Lawless et al. 2006) are natural, usually small islands of xeric prairie vegetation located on steep, south- or west-oriented slopes within a forest matrix (Ugarte 1987). The isolation and inaccessibility of Iowa's hill prairies indicate they may be some of the best remaining examples of pre-settlement prairie vegetation in the eastern portion of the tallgrass prairie biome (Glenn-Lewin et al. 1984), although many are threatened by woody plant invasion resulting from fire suppression (Behnke and Ebinger 1989; Robertson et al. 1996). Iowa hill prairies generally have the same dominant grasses and forbs as tallgrass prairies of western one-half of Iowa (Hanson 1922; Kilburn and Warren 1963; Robertson et al. 1996; Owens and Cole 2003), which are currently and historically more extensive than hill prairies and which are considered representative of the wider tallgrass prairie biome that stretched from Manitoba to Oklahoma (Steinauer and Collins 1996). However, hill prairies and western prairies may differ in the relative abundances of plant species (Curtis 1959) and may not be exemplars of western prairies with respect to many components of their fauna because of their unique landscape context and microclimate (Reeves et al. 1978). Many of these Iowa hill prairie sites may contain high diversity and/or unique species of some specific groups (Theler 1997), as does the Paleozoic Plateau of northeast Iowa in general (Howe 1984).

The bee communities (Hymenoptera: Apoidea) of Iowa hill prairies are of particular interest because of their critical role in pollination of many prairie forb species (Cane 2006; Slagle and Hendrix 2009); more generally, bees pollinate the majority of the world's angiosperms (Fægri and van der Pijl 1979; Buchmann and Nabhan 1996; Michener 2000; Fenster et al. 2004). In Iowa, prairies dominated the landscape since the Holocene, but now represent less than 1% of it (Steinauer and Collins 1996). Despite prairie fragmentation, inventories of bees that visit prairie plant species indicate that many native plants support dozens of bee species (Robertson 1928; Reed 1995; Merlin and LaBerge 2001). These intensive surveys reveal a very rich prairie bee community and provide information on species abundance distributions of bee communities. They are of limited usefulness, however, for comparative purposes because intensive surveys have very high levels of sampling effort which strongly influences measures of species richness, diversity, and composition (Margurran 2004). In general, comparative studies of bee communities using systematic sampling are rare (but see Hemsley 2005; Davis et al. 2008; Kwaiser and Hendrix 2008).

We examined richness and species composition of the bee communities of Iowa hill prairies, making explicit comparisons to tall-grass prairies in western Iowa. Such comparisons are important for at least two reasons. First, it is not clear whether the richness or diversity of bee communities in Iowa hill prairie remnants is low compared to that of other, larger prairie preserves. On the one hand, bee communities of these small hill prairies may be less diverse than larger prairie preserves because floral resources are limited. Studies in European grasslands (Tscharrntke et al. 1998), tropical forests (Heithaus 1974; Powell and

Powell 1987), and Mediterranean habitat (Potts et al. 2003) all indicate that sites with lower floral abundance and richness often attract a lower abundance and/or richness of flower visitors because of their smaller size. On the other hand, positive relationships between bee community richness and floral characteristics are not universal (Tepedino and Stanton 1981; Becker et al. 1991, unpublished data reviewed by Cane 2001) and other factors such as abundant landscape-scale floral resources (Hines and Hendrix 2005) and close proximity to natural areas (Steffan-Dewenter and Tscharntke 1999; Kremen et al. 2004) may positively influence bee richness and abundance. Furthermore, in Iowa even very small, high quality remnants may act as “oases” for bees in landscapes dominated by agriculture such that the richness and diversity of bees at such sites is equivalent to that of larger nearby preserves (Davis et al. 2008).

Second, whether bee species composition of hill prairies is very different from that of tallgrass prairies is unclear. Many bee species and genera are widely distributed across much or all of North America (Mitchell 1960, 1962) and it is likely that much of the northeast Iowa bee fauna will consist of widespread species shared with other prairie sites and even non-prairie habitats. However, the Paleozoic Plateau in general has unique karst landforms, which result in habitat suitable for relict populations of plants in hill prairies (Smith 1984) and animals associated with forest and stream habitats such as land snails, amphipods, and crayfish (Howe 1984) at the edges of their distributions. Whether this is true for bees as well is unknown. The bee communities of Iowa hill prairies also may contain bees more often associated with western prairies which remained as “relict” species associated with prairie expansion and retraction. Baker et al. (1990) has suggested that following the expansion of prairie flora into eastern Iowa in the middle Holocene, it was subsequently replaced largely by forests about 4000 BP. Hill prairies are an exception to this reforestation history.

In this study, we test the null hypothesis that the diversity and abundance of the bee communities of five Iowa hill prairies located in northeastern Iowa is similar to that of large prairie preserves in northwestern Iowa. In addition, we analyze the geographic distributions of the bee species at these sites to determine if they harbor unique or rare species that represent relicts typically distributed either further north or west. Lastly, we test for an effect of local plant resources on bee abundance and diversity and examine the role of landscape features in shaping bee diversity at these sites.

Materials and methods

Study sites

All study sites were located in Allamakee County, Iowa, USA in the Paleozoic Plateau which crosses into the neighboring states of Illinois, Minnesota and Wisconsin, covering an area of approximately 74,000 km² (Prior 1991). This region is topographically diverse, consisting primarily of steep, forested carbonate and sandstone bluffs (Hallberg et al. 1984) and lowland floodplains that have been converted to agriculture. We sampled five geographically separate (≥ 2 km apart) hill prairies of at least 1 ha in size in Allamakee County, IA USA in the summer of 2005. The Iowa hill prairies in this study ranged in slope from 40° to 55° with aspects facing from southwest to southeast.

We summarized variation in landscape context by calculating the percent-landscape composition of five different land-cover classes around each sample site. Land cover classes were: water, forest, row-crop agriculture (corn and soybeans, which are rarely used

by bees), grassland/alfalfa and hill prairie. To quantify the land-cover classes within a 1 km radius around each site, we used high-resolution (1 m) color infrared orthophotos with a K-means ISODATA clustering algorithm in Erdas Imagine 9.0 (Erdas Inc, Atlanta, Ga, USA). The images were acquired on May 3, 2002 and are publicly available at www.igsb.uiowa.edu. Because the clustering algorithm grouped known hill prairies with row-crop agriculture, we reclassified all row-crop agriculture with slopes greater than 30° (i.e. too steep to accommodate row-crop agriculture) to the hill prairie class. We excluded the sample site itself from the percent landscape composition calculation to separate local and landscape scale effects.

Bee and plant community sampling

We sampled the bee and floral communities of each prairie in June, July and August of 2005. In each monthly sampling period, we completed sampling of all sites within 2 days in order to give an accurate snapshot of the communities at that time. We conducted bee sampling only in temperatures greater than 15.5°C with wind speeds less than 32 km/h.

To sample the bee community we used two techniques: sweep-net sampling and pan-trap sampling from 1 ha plot established at each prairie. No plot had more than 20% combined coverage of *Rhus* spp. and *Juniperus* spp. For sweep-net sampling, we split each plot into halves, each of which was sampled for 15 min by two different collectors for a total of 1 h in the morning (9 am–12 pm) and 1 h in the afternoon (1 pm–4 pm) each month. We patrolled plots and examined all forbs in bloom for the presence of bees. When bees were observed, we captured them using a sweep-net and recorded the species of the plant on which each was found. We did not include handling time with search time. For pan-trap sampling, we placed twelve 6 oz. plastic bowls, each filled with soapy water, 10 m apart along a transect within the 1 ha sample plot. Each transect consisted of 4 fluorescent yellow, 4 fluorescent blue, and 4 white bowls that were alternated regularly within the transect line. We determined the order of colors within transects randomly prior to placement. Bowls remained in place for 6 h.

We identified mounted bee specimens to genus using Michener et al. (1994) and Michener (2000) and to species using monographic keys and Mitchell (1960, 1962) except for *Lasioglossum* (*Dialictus*) specimens, which were identified by S. Droege of the United States Geological Survey Patuxent Wildlife Research Center. Specimens are deposited in the collection of S.D. Hendrix at The University of Iowa.

We conducted floral surveys in 5 × 100 m strip-subplots placed within the 1 ha sweep-sampling plots. We measured the abundance of floral resources as the total number of ramets of a species that had flowers containing nectar or pollen rewards.

Statistical analysis

We measured diversity and evenness of bee and plant communities using Shannon–Wiener indices (\log_2). We expressed similarity of bee communities among sites using the Morisita Index. We used linear regression analysis to test for relationships between bee species diversity and plant species diversity and between bee and plant community similarities. To compare the diversity and richness of bee communities at hill prairies of northeast Iowa to prairies in northwest Iowa, we used Monte Carlo simulations to assemble synthetic NW Iowa bee “communities” with the same intensity of sampling as we used for our hill prairies. We had data for seven state of Iowa prairie preserves (Anderson, Cayler, Doolittle, Kalsow, Kirchner, Mori, and Steele), with over 5,000 bees collected over a 3-year

period. These prairie preserves range in size from 11 to 67 ha. Sampling in these preserves was done using the same sweep and pan-trap procedures described above, in June, July, and August of 2002, 2003, and 2004. The Monte Carlo simulation assembled a bee “community” by drawing one sweep-net and one pan-trap sample for each month, from the set of 21 (7 prairies \times 3 years) available samples. The six samples (3 sweep-net and 3 pan-trap) were combined, and richness, diversity, and bee abundance calculated as for the hill prairie communities. We used 1,000 Monte Carlo “communities” to establish a distribution of expected diversities for NW Iowa prairie preserves, and we used the fraction of Monte Carlo values more extreme than a given hill prairie value for richness or diversity as a P value using a two-tailed test. Because multiple comparisons were made, we used the sequential Bonferonni correction (Rice 1989) to determine significance of the P values obtained. We used the Mann–Whitney U test to compare the plant species richness and abundance at the hill prairie sites with identical sampling of three northwestern prairies (Cayler, Steele, and Kalsow).

Results

In total, we collected 1,149 bees representing 73 species from 24 genera (Appendix 1). The pan-trap technique accounted for 69.3% of total abundance and represented 44 bee species, 21 species of which were unique to the pan-trap samples. Of the 352 bees caught with the sweep-net technique, we captured 67.3% during the morning collection periods.

Bee diversity indices at the five hill prairies (Table 2a) spanned the range of diversity values generated in the Monte Carlo simulation (Fig. 1), although four of the five Iowa hill prairies had diversity indices in the lower one-half of the simulation distribution. The diversity of Dock Prairie was significantly lower than northwestern Iowa prairies ($P = 0.004$) while diversity at Mullen was significantly higher ($P = 0.007$). Diversity values for Capoli, Reinke and Weymiller Prairies were not significantly different from northwest Iowa prairies. Only the species richness at Reinke Prairie (Table 2a) was significantly greater than expected ($P < 0.003$) compared to the Monte Carlo simulations.

Of the 73 species captured, 68 are distributed either throughout the eastern US or across the continent (Mitchell 1960, 1962; Hurd 1979; Discover Life 2009). Three species have ranges coinciding with the original extent of prairies in North America (*Colletes susanna*, *Lasioglossum (Dialectus) pictum*, and the eastern *pallidipennis* form of *Perdita albipennis*) (Stephen 1954; Hurd 1979; Discover Life 2009). Two species in the Iowa hill prairies may represent range extensions. *Lasioglossum (Dialectus) dreisbachi* was known previously

Fig. 1 Distribution of 1,000 Shannon–Wiener \log_2 diversity indices of bee communities generated by Monte Carlo simulation with location of the diversity indices for five Iowa hill prairies indicated. *DO* Dock, *CA* Capoli, *WE* Weymiller, *RE* Reinke, and *MU* Mullen

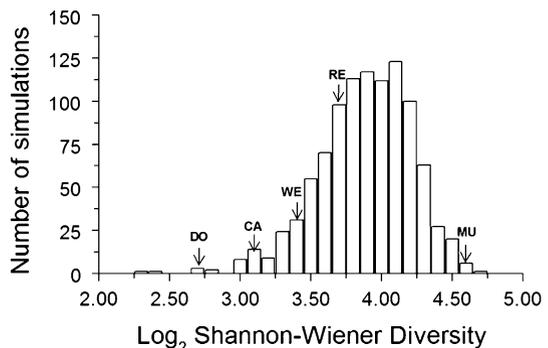
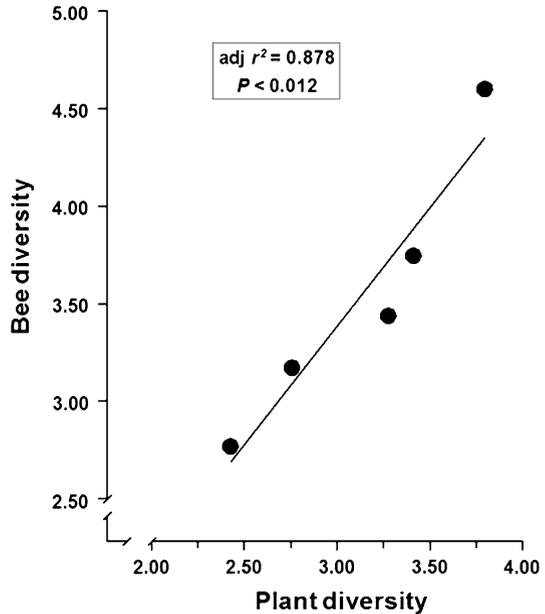


Fig. 2 Relationship between plant species diversity and bee species diversity at five Iowa hill prairies in northeast Iowa. Diversity values are \log_2 Shannon–Wiener indices. $Y = 1.21 X + 0.25$



only from New York, Maryland, Michigan and Minnesota (Hurd 1979) and *Dufourea monardae* was previously known only from Wisconsin, Michigan, Illinois and Tennessee (Hurd 1979), although it has also been reported recently in Colorado (Discover Life 2009).

We counted over 4,000 flowering ramets representing 51 plant species. Plant diversity, richness, and abundance of flowering ramets varied among sites (Table 2b). Mullen Prairie had the greatest plant diversity and species richness while Dock Prairie has the poorest. Capoli and Dock Prairies had the most similar plant community composition (Morisita Index = 0.925); Capoli and Reinke Prairies and Capoli and Mullen Prairies were most dissimilar in composition (Morisita Indices 0.113 and 0.126, respectively). There was a trend for plant similarity between two sites to predict the similarity of their bee communities (adjusted $r^2 = 0.285$, $P = 0.065$). Site size was unrelated to bee diversity ($r = -0.44$, $P = 0.45$) and floral diversity ($r = -0.26$, $P = 0.68$). Bee diversity of the Iowa hill prairies was positively and significantly correlated with plant diversity (Fig. 2). The dozen most-visited plant species regardless of abundance account for 81% of the bees and 90% of the species caught in sweep net samples (Table 3), but represent only 37.8% of the ramets sampled. Seven of these most-visited plant species are members of the Asteraceae. Native plants account for ten of these species; among introduced plants, only two *Cirsium* species received many bee visits. Overall, introduced species accounted for 12.5% of all ramets. Plant species richness at the hill prairies was significantly less than at northwest Iowa prairies ($U_{(3,5)} = 14.5$, $P < 0.05$), but there was no difference in ramet density ($U_{(3,5)} = 10$, $P > 0.10$).

Forests were a major component of landscape context for all sample sites, with at least 40% cover within the 1 km radius (Table 1). Mullen Prairie was unique among the five study sites because of its highly forested context (~65% forest) with a canopy approximately 50% closed by mature oak trees (based on visual estimation). Capoli Prairie and Dock Prairie are located immediately adjacent to the Mississippi River, which accounts for approximately 43 and 39% of the landscape within a 1 km radius of the site, respectively.

Table 1 Site size and percent composition of the landscape in land cover categories (excluding the site itself) in a 1 km radius around each sample site

	Capoli	Dock	Mullen	Reinke	Weymiller
Site size (ha)	5.60	2.70	1.20	5.40	4.60
Land cover					
Forest	40.12	40.3	65.98	43.68	46.95
Water	43.42	38.5	0.63	3.34	0.12
Agriculture	3.7	16.2	16.73	45.28	31.93
Grassland/alfalfa	11.05	4.25	15.88	7.07	19.41
Prairie	1.71	0.72	0.78	0.62	1.59

Reinke Prairie was distinguished by a landscape approximately 45% in row crop agriculture. Weymiller Prairie also was dominated by agriculture (~31%) and was the only site with a confirmed hill prairie within 1 km of the site. Capoli Prairie was the only study site with less than 15% row-crop agriculture (~3%). Prairies made up less than 2.0% of the landscape at all the sites examined.

Discussion

The bee communities of the hill prairies of northeast Iowa along the Mississippi River vary widely in diversity, but are by no means uniformly depauperate when compared to larger northwest Iowa prairie preserves (Fig. 1; Table 2a). The bee community of one hill prairie (Mullen Prairie) was significantly more diverse than those of northwestern prairies, while three (Capoli, Reinke and Weymiller) were similar, and one (Dock) was significantly less diverse, indicating that factors other than physical size strongly influence bee diversity at these sites. The species richness of the Iowa hill prairies showed a similar pattern. Four prairies were not significantly different in richness from prairies of northwest Iowa and one (Reinke) had significantly greater richness. Our results are similar to those of Hemsley (2005) and Davis et al. (2008), who found that bee diversity and richness at small remnants (1–5 ha) along active and abandoned railway lines in northwest Iowa were not significantly

Table 2 Diversity (Shannon–Wiener \log_2), evenness, species richness, and abundance of solitary bees (a) and flowering forb species (b) based on seasonal totals at hill prairies in northeastern Iowa

Characteristic	Capoli	Dock	Mullen	Reinke	Weymiller
(a) Bees					
Diversity	3.174	2.770	4.601	3.748	3.440
Evenness	0.623	0.597	0.890	0.700	0.694
Richness	33	25	36	41	31
Abundance	232	167	118	400	239
(b) Plants					
Diversity	2.754	2.423	3.793	3.409	3.273
Evenness	0.621	0.542	0.840	0.752	0.803
Richness	15	11	28	22	13
Abundance	607	783	1206	1541	521

Table 3 Numbers of individual bees and bee species (number of bumblebee species) caught in sweep net samples on the 12 most-visited hill prairie plant species

Plant species	Number of bees	Number of species
<i>Helianthus occidentalis</i> Riddell	71	13 (1)
<i>Dalea purpurea</i> Vent.	33	11 (1)
<i>Cirsium</i> spp. ^a	31	11 (3)
<i>Cirsium hilli</i> (Canby) Fern.	31	11 (3)
<i>Solidago gigantea</i> Aiton	23	9 (1)
<i>Erigeron strigosus</i> Muhl.ex Willd.	20	10 (0)
<i>Monarda fistulosa</i> L.	16	7 (3)
<i>Ratibida pinnata</i> (Vent.) Barnh.	16	5 (0)
<i>Campanula rotundifolia</i> L.	14	9 (0)
<i>Liatris cylindracea</i> Michx.	14	4 (3)
<i>Coreopsis palmata</i>	13	6 (0)

^a Introduced *C. vulgare* and *C. arvensis*

different from diversities of larger prairie preserves (the same ones used in the Monte Carlo simulations here). As with small remnants in northwestern Iowa (Davis et al. 2008), desert communities (Cane et al. 2006), shrublands (Donaldson et al. 2002), and tropical forest clearings (Brosi et al. 2008), the hill prairies of northeast Iowa act as “resource oases” for bees.

Local plant community characteristics (Table 2b) had a significant influence on the diversity of bee communities. The diversity and richness of hill prairie bee communities was significantly correlated with diversity of flowering forb resources at these sites (Fig. 2). The plant species visited by the greatest number of bee species (Table 3) temporally span most of the plant reproductive season (June–September) and some, such as *Dalea*, produce relatively large amounts of pollen (Cruden and Miller-Ward 1981) thereby providing a relatively stable food base throughout the lifespan of most bee species. Other studies show that more diverse plant communities generally attract a greater abundance and/or species diversity of flower visitors than less diverse ones (see introduction), although there are exceptions to this pattern (Tepedino and Stanton 1981; Becker et al. 1991, unpublished data reviewed by Cane 2001).

Landscape features surrounding these sites (Table 1) also likely affected the range of diversities found. For example, the sites with the two lowest diversity values (Dock and Capoli) had landscapes within 1 km dominated by the Mississippi River, which reduced potential foraging habitat by approximately 40%. The two sites (Reinke and Weymiller) with diversity most similar to larger Iowa prairies had landscapes similarly dominated by agriculture (45 and 32%, respectively), as most northwest Iowa preserves (Davis et al. 2007). Lastly, the site with the highest diversity (Mullen) had the greatest percentage of natural habitat (forest and grassland/alfalfa) of any site. While it would be interesting to make quantitative comparisons of the influences of these variables on bee diversity, our set of 5 sites is not large enough to provide sufficient replication for a multivariate statistical model. Sampling more hill prairies would allow testing of more complex models, but the labour-intensive nature of bee sampling and identification would make this an extremely ambitious undertaking. Other studies, however, have demonstrated that landscape features can influence bee diversity and abundance at farm sites (Kremen et al. 2002; Greenleaf and Kremen 2006).

The bee communities of Iowa hill prairies consist primarily of species that have wide ranges geographically and that use hill prairie plants opportunistically as part of a polylectic diet of pollen. Nevertheless, one bee species (*L. dreisbachii*) with a more northerly distribution may be taking advantage of abundant resources in xeric hill prairies located in the otherwise relatively cool, moist climate of the Paleozoic Plateau. The region supports other relict species of plants and animals (Glenn-Lewin et al. 1984; Smith 1984). The presence of few western and mid-western bee species indicates that even though prairies spread from the west into eastern Iowa during the middle Holocene (Baker et al. 1990), bee species associated with western prairies do not appear to have “followed” these incursions. If they did, they may have been eliminated from these sites when prairie habitat was largely replaced by forests in eastern Iowa about 4,000 years ago. There may also be some east–west differences in the bee communities of northeastern and northwestern Iowa prairies, possibly resulting from greater plant species richness in the northwest. However, the overall similarity in species composition and abundance of resources, indicate that east–west differences may be relatively minor. Furthermore, since most of our bee species were wide-ranging, we suspect that eastern/western Iowa regional variation is not a major confounder of local bee community structure.

Temporally or spatially intensive inventories of prairie bees and other insects (Robertson 1928; Reed 1995) have indicated far richer bee communities associated with particular prairie plant species than we find in this study. For example, Robertson (1928) found 55 species visiting *Dalea purpurea* and 28 bee species visiting *Monarda fistulosa*, while in our study we found 11 and 7 species, respectively. We believe these differences are largely the result of sampling effort. Robertson (1928) collected over many years and Reed (1995) collected intensively (up to 20 h on a single plant species) over a much greater total area (54 ha) than in this study (5 ha). We predict that additional sampling at Iowa hill prairies will reveal similar richness to that found by intensive inventory studies.

Our results indicate that the hill prairies are an important resource for bee communities of northeast Iowa, which have ranges of bee richness and diversity similar to much larger northwest Iowa preserves when sampling effort is standardized. Furthermore, about 6.8% of the bee species collected (five of 73 species) have more western or northern distributions and likely represent species taking advantage of the unique features of these sites. Given the dependence of the bee communities on the plant diversity of the sites, management of the plant community to maintain its diversity will also likely benefit bee diversity. The major threat today to hill prairies is invasion by woody species, which has been prevented in the past by a combination of a regular fire regime, high evapotranspiration rates, thin soils, and grazing (Hanson 1922; Robertson et al. 1996). However, fire suppression in recent years has reduced the size of hill prairies by permitting woody plant invasions (Behnke and Ebinger 1989; Robertson et al. 1996) and this is likely to have had a negative effect on their bee communities if flowering forb diversity is reduced as a result. On the other hand, decreased burn frequency may account for increased abundance of cavity nesting bees at small remnants compared to big preserves in northwestern Iowa (Davis et al. 2008). Further studies of hill prairie faunas and floras will likely hold valuable lessons for our efforts to conserve and manage other prairies because these naturally small sites may reveal potential long-term effects of small size and shifting landscapes on bee communities.

Acknowledgments We thank D. Mullen, J. and J. Dock, R. and J. Buckmaster, G. and D. Weymiller, and R. and S. Reinke for access to the study sites on private land. B. Johnson, C. Owens, D. Christensen, K. Robles, R. Kaye and J. Krippel assisted with data collection and cataloguing. M. Wendel and C. Hemsley

assisted in bee specimen identification. We thank two anonymous reviewers for comments on the manuscript. Our research was supported in part by grants to SDH from Iowa Living Roadway Trust Fund, to KSK from Prairie Biotic Research and the Avis Cone Fellowship Program at The University of Iowa, and by a Discovery Grant to SBH from the Natural Sciences and Engineering Research Council (Canada).

References

- Baker RG, Chumbley CA, Witinok PM et al (1990) Holocene vegetational changes in eastern Iowa. *J Iowa Acad Sci* 97(4):167–177
- Becker P, Moure JS, Peralta FJA (1991) More about euglossine bees in Amazonian forest fragments. *Biotropica* 23(4):586–591
- Behnke G, Ebinger JE (1989) Woody invasion of glacial drift hill prairies in east-central Illinois. *Trans Ill Acad Sci* 82(1):1–4
- Brosi BJ, Daily GC, Shih TM, Oviedo F, Duran G (2008) The effects of forest fragmentation on bee communities in tropical countryside. *J Appl Ecol* 45(3):773–783
- Buchmann SL, Nabhan GP (1996) *The forgotten pollinators*. Island Press, Washington, DC
- Cane JH (2001) Habitat fragmentation and native bees: a premature verdict? *Conserv Ecol* 5(1): [online] URL: <http://www.consecol.org/vol5/iss1/art3/>
- Cane JH (2006) An evaluation of pollination mechanisms for purple prairie-clover, *Dalea purpurea* (Fabaceae: Amorphaeae). *Am Midl Nat* 156:193–197
- Cane JH, Minckley RL, Kervin LJ, Roulston TH, Williams NM (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecol Appl* 16(2):632–644
- Cruden RW, Miller-Ward S (1981) Pollen-ovule ratio, pollen size, and the ratio of stigmatic area to the pollen-bearing area of the pollinator: a hypothesis. *Evolution* 35:964–974
- Curtis JT (1959) *The vegetation of Wisconsin an ordination of plant communities*. University of Wisconsin Press, Madison
- Davis JD, Debinski DM, Danielson BJ (2007) Local and landscape effects on the butterfly community in fragmented midwest USA prairie habitats. *Landscape Ecol* 22:1341–1354
- Davis JD, Hendrix SD, Debinski DM et al (2008) Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. *J Insect Conserv* 12:69–79. doi:10.1007/s10841-006-9063-4
- Discover Life (2009) <http://www.discoverlife.org/mp/20q?search=Apoidea>. Accessed 12 May 2009
- Donaldson J, Nänni I, Zachariades C, Kemper J (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. *Conserv Biol* 16(5):1267–1276
- Fægri K, van der Pijl L (1979) *The principles of pollination ecology*, 3rd edn. Pergamon Press, Oxford
- Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and floral specialization. *Ann Rev Ecol Syst* 35:397–403
- Glenn-Lewin DC, Laushman RH, Whitson PD (1984) The vegetation of the Paleozoic Plateau, northeastern Iowa. *Proc Iowa Acad Sci* 9(1):22–27
- Greenleaf SS, Kremen C (2006) Wild bee species increase tomato production and respond differently to surrounding land use in northern California. *Biol Conserv* 133(1):81–87. doi:10.1016/j.biocon.2006.05.025
- Hallberg GR, Bettis EA, Prior JC (1984) Geologic overview of the Paleozoic Plateau region of northeastern Iowa. *Proc Iowa Acad Sci* 91(1):5–11
- Hanson HC (1922) Prairie inclusions in the deciduous forest climax. *Am J Bot* 9(6):330–337
- Heithaus ER (1974) The role of plant-pollinator interactions in determining community structure. *Ann Mo Bot Gard* 61:675–691
- Hemsley CJ (2005) Diversity, abundance, and similarity of solitary bee communities in tall grass prairie fragments. Dissertation, University of Iowa
- Hines HM, Hendrix SD (2005) Bumblebee (Hymenoptera: Apoidea) diversity and abundance in tallgrass prairie patches: effects of local and landscape floral resources. *Environ Entomol* 34:1477–1484
- Howe RW (1984) Zoogeography of Iowa's Paleozoic Plateau. *Proc Iowa Acad Sci* 91(1):32–36
- Hurd PD Jr (1979) Superfamily Apoidea. In: Krombein KV, Hurd PDJ, Smith DR, Burks BD (eds) *Catalog of Hymenoptera in North America north of Mexico*, 1st edn. Smithsonian Institution Press, Washington, DC

- Kilburn PD, Warren DK (1963) Vegetation-soil relationships in hill prairies. *Trans Ill Acad Sci* 56(3):142–145
- Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. *Proc Natl Acad Sci USA* 99:16812–16816
- Kremen C, Williams NM, Bugg RL et al (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol Lett* 7:1109–1119. doi:10.1111/j.1461-0248.2004.00662.x
- Kwaiser KS, Hendrix SD (2008) Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. *Agric Ecosyst Environ* 124:200–204
- Lawless PJ, Baskin JM, Baskin CC (2006) Xeric limestone prairies of eastern United States: review and synthesis. *Bot Rev* 72(3):235–272. doi:10.1663/0006-8101(2006)72[235:XLPOEU]2.0.CO;2
- Margurran AE (2004) Measuring biological diversity. Blackwell, Oxford
- Merlin JC, LaBerge WE (2001) The native bee fauna of Carlinville, Illinois, revisited after 75 years: a case for persistence. *Conserv Ecol* 5(1):9. [online] URL:<http://www.consecol.org/vol5/iss1/art9>
- Michener CD (2000) The bees of the world. Johns Hopkins University Press, Baltimore
- Michener CD, McGinley RJ, Danforth BN (1994) The bee genera of North and Central America (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, DC
- Mitchell TB (1960) Bees of the eastern United States, vol 1. The North Carolina Agricultural Experimental Station, Raleigh
- Mitchell TB (1962) Bees of the eastern United States, vol 2. The North Carolina Agricultural Experiment Station, Raleigh
- Owens NL, Cole GN (2003) 25 Years of vegetational changes in a glacial drift hill prairie community in east-central Illinois. *Trans Ill Acad Sci* 96(4):265–269
- Potts SG, Vulliamy B, Dafni A et al (2003) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84:2628–2642
- Powell AH, Powell GVN (1987) Population dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica* 19:176–179
- Prior JC (1991) Landforms of Iowa. University of Iowa Press, Iowa City
- Reed CC (1995) Species richness of insects on prairie flowers in southeastern Minnesota. In: Hartnett DC (ed) Proceedings of the 14th annual North American prairie conference: prairie biodiversity. Kansas State University, Manhattan Kansas, July 1994, pp 103–115
- Reeves JT, Zimmerman UD, Ebinger JE (1978) Microclimatic and soil differences between hill prairies and adjacent forests in east-central Illinois. *Trans Ill Acad Sci* 71(2):156–164
- Rice W (1989) Analyzing tables of statistical tests. *Evolution* 43:223–225
- Robertson C (1928) Flowers and insects. Lists of visitors to four hundred and fifty-three flowers. Science Press, Lancaster
- Robertson KR, Schwartz MW, Olson JW et al (1996) 50 Years of change in Illinois hill prairies. *Ergenia: J Ill Nativ Plant Soc* 14:41–52
- Slagle MW, Hendrix SD (2009) Reproduction of *Amorpha canescens* (Fabaceae) and diversity of its bee community in a fragmented landscape. *Oecologia* 161:813–823
- Smith DD (1984) Iowa's driftless area: symposium. *Proc Iowa Acad Sci* 91(1):1–2
- Steffan-Dewenter I, Tschantke T (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121:432–440
- Steinauer EM, Collins SL (1996) Prairie ecology: the tallgrass prairie. In: Samson FB, Knopf FL (eds) Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Washington, DC, pp 39–52
- Stephen WP (1954) A revision of the bee genus *Colletes* in America north of Mexico. *Univ Kans Bull* 36:149–527
- Tepedino V, Stanton N (1981) Diversity and competition in bee-plant communities on short-grass prairie. *Oikos* 36:35–44
- Theler JL (1997) The modern terrestrial gastropod (land snail) fauna of western Wisconsin's hill prairies. *Nautilus* 110(4):111–121
- Tschantke T, Gathmann A, Steffan-Dewenter I (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *J Appl Ecol* 35:708–719
- Ugarte EA (1987) The hill prairies of northeast Iowa: vegetation and dynamics. Dissertation, Iowa State University