Bee diversity in naturalizing patches of Carolinian grasslands in southern Ontario, Canada

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Abstract—The bee fauna (Hymenoptera: Apoidea) of the Niagara Peninsula, at the eastern end of the Carolinian Zone in Ontario, Canada, is poorly known. From April to October 2003, we studied bee abundance and diversity in set-aside grasslands at Brock University and the Glenridge Quarry Naturalization Site in southern St. Catharines, Ontario. Using three sampling methods (pan traps, sweep nets, and aerial nets), we collected and identified 15 733 specimens of 124 species and morphospecies representing all bee families, except Melittidae, found in North America. Abundance-based diversity estimators suggested bee species richness to be as high as 148 species. There were three seasonal peaks in bee abundance (early spring, late spring, and mid-summer) with a lull in activity shortly after the summer solstice. Several indicators suggested substantial impacts of disturbance on the Niagara bee community, including evidence of high dominance by the most abundant species. Comparison of the sampling methods indicated considerable catch variation among taxa; Halictidae and Apidae were dominant in pan trap samples and in sweep–aerial net samples, respectively. However, bee abundances in pan traps and sweep nets were highly correlated, suggesting that both methods fairly sample local bee abundances.

Resume—La faune d'abeilles (Hymenoptera : Apoidea) de la péninsule de Niagara, à la bordure est de la zone carolinienne en Ontario, Canada, est mal connue. D'avril à octobre 2003, nous avons étudié l'abondance et la diversité des abeilles dans des prairies réservées à l'université Brock et le site de naturalisation Glenridge Quarry dans le sud de St. Catherines, Ontario. Nous avons récolté à l'aide de trois méthodes d'échantillonnage (pièges à cuvette, filets fauchoirs, filets aériens) et identifié 15 733 spécimens appartenant à 124 espèces et morpho-espèces, représentant toutes les familles d'abeilles retrouvées en Amérique du Nord, à l'exception des Melittidae. Des estimateurs de la diversité basés sur l'abondance font penser que la richesse spécifique des abeilles pourrait atteindre 148 espèces. Il y a trois pics saisonniers d'abondance (début du printemps, fin du printemps et milieu de l'été) avec une accalmie dans l'activité après le solstice d'été. Plusieurs indicateurs laissent croire à des impacts sérieux des perturbations sur la communauté d'abeilles de Niagara, en particulier la forte dominance des espèces les plus abondantes. Une comparaison des méthodes d'échantillonnage indique une variation considérable des récoltes en fonction des taxons; les Halictidae et les Apidae dominent respectivement dans les récoltes dans les pièges à cuvette et aux filets fauchoirs–aériens. Il existe cependant une forte corrélation entre les abondances d'abeilles dans les cuvettes et les filets fauchoirs, ce qui indique que les deux méthodes échantillonnent adéquatement les abondances locales d'abeilles.

[Traduit par la Rédaction]

Introduction

The Carolinian Zone in Canada is found only in the extreme south west corner of Ontario, where it represents the northernmost edge of the Eastern Deciduous Forest of eastern North America. The Carolinian Zone has long been regarded as a unique ecological region in Canada in which species normally associated with more southerly areas mix with more northerly species to create a region of relatively high biotic diversity (Riverie and Lawrence 1999). The Ontario Carolinian Zone includes both woodland and tallgrass prairie

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communities. The latter once covered approximately 1000 km^2, but less than 3% remains. Most of this habitat was lost 150–200 years ago during European settlement (Reid and Symmes 1997); although a few significant remnant tallgrass communities remain.

In the Niagara Peninsula, at the eastern end of Ontario's Carolinian Zone, no large relatively intact grasslands or meadow ecosystems remain due to intense human impacts, especially urbanization and intensive agriculture. However, many insect species can persist in relatively small patches of natural or naturalized habitat, and pollinators such as bees (Hymenoptera: Apoidea) can be quite successful in some urban environments (Tommasi *et al.* 2004; Cane *et al.* 2006; Matteson *et al.* 2008). Small pockets of relatively undisturbed habitat, especially woodland edges, grasslands, and meadows, likely have provided refugia for many insect species and supply colonists for new areas of habitat that become available as land use patterns change, especially when people attempt to restore patches of habitat to a more natural Carolinian state.

A major survey and description of the Niagara Peninsula bee fauna is a prerequisite to further studies of bee diversity and population biology. Bee diversity is a good correlate of community biodiversity (Duelli and Obrist 1998; Tscharntke *et al.* 1998), and patterns of bee diversity could be used as a baseline to measure bee community responses to landscape changes resulting from efforts to restore Carolinian flora. Despite the importance of bees as pollinators in natural and agricultural landscapes, their diversity in the Niagara Peninsula is poorly known. Located in southern St. Catharines on the southern crest of the Niagara Escarpment (a UNESCO-designated World Biosphere Reserve), Brock University and the Glenridge Quarry Naturalization Site contain areas of naturalized habitat of various ages. Surrounding habitat includes woodland, suburban gardens, highway corridors with grassy verges, and agricultural areas devoted mainly to cattle feedlots and crops such as corn. Natural areas, including old fields that have been fallow and rarely mowed for as long as 40 years, have been set aside on the Brock University campus. The Glenridge Quarry Naturalization Site was farmed intensively until about 1960 when it became a limestone quarry and then it was a major landfill site from 1976 to 2001. The landfill operation was closed at the end of 2001 and restoration of the site as a park with Carolinian vegetation was completed by 2003, creating a pollinator habitat where none had existed for at least 50 years.

Our first objective was to provide a detailed survey of bee diversity in the Niagara region, focusing on naturalized areas of the Brock University campus and the Glenridge Quarry Naturalization Site. We carried out weekly surveys using three sampling methods: pan trapping, sweep netting from vegetation, and aerial netting from flowers. Although the total geographic area surveyed was relatively small and undoubtedly contains only a portion of the total species pool of the Niagara Region, our study serves as a starting point for an ongoing assessment of the impact of ecological restoration activities on bee diversity, a study of bee population dynamics, and the monitoring of the introduction and possible spread of non-native species (Sheffield *et al.* 2010). Our second objective was to compare the sampling results to look for different taxonomic patterns in abundance between the sampling methods (Cane *et al.* 2000).

Methods

Field sites

Eight 1 ha collecting sites, encompassing a range of disturbance levels from undisturbed meadow to newly seeded ground, were established at Brock University campus (43.119°N, 79.249°W) and the Glenridge Quarry Naturalization Site (43.122°N, 79.237°W). Sampling began in seven of these sites (BrockS, BrockE, BrockN, and PhysEd on the Brock University campus and at Escarpment, Residences, and Pond at the Quarry Site) during the week of 20 April 2003 (week 1). At the eighth site (St. David's) sampling began in week 3 because of considerable construction traffic. A ninth field site (406) was added in week nine. The BrockN site was unexpectedly paved in mid-summer; we immediately replaced it with a very similar contiguous site (BrockW) and the two sites

were analysed as a single site. The PhysEd site was difficult to work in and was abandoned in May 2003; the small number of specimens collected there were included in the study.

Except as noted, sites were sampled approximately once a week from 21 April 2003 (week 1) to 1 October 2003 (week 23), using pan trapping, sweep netting of vegetation, and aerial netting from flowers ("flower collections"). Pan trapping began in week 1, sweep netting in week 5 (when vegetation was tall enough for sweeping), and flower collections in week 7. When sampling was interrupted by rain, collections were usually repeated later in the week. Even so, the weekly series of collections at each site were incomplete due to various interruptions. Therefore, for analyses that required equivalent catch effort among one time period, we used a biweekly series of specimens collected in odd-numbered weeks, filling in gaps in the series when necessary with samples collected the week before (if available) or the week after.

Pan trapping

Pan traps (170 gm plastic bowls, SOLO PS6-0099) were laid out in X-shaped patterns when field sites were approximately square (Brock sites), and in H-shapes where field sites were irregularly shaped (Glenridge Quarry sites). In each field site, 10 traps of each of three colours (fluorescent blue Krylon paint #3109, fluorescent yellow #3104, and white; $n = 30$) were filled with soapy water and placed along transects at 10 m intervals, alternating colours. Traps were put out before 0900 and collected after 1500. Trap contents were poured through a small sieve and the specimens were placed in plastic yoghurt containers labelled with the date and location. Samples were brought back to the laboratory where bees were removed and placed in vials containing 70% ethanol. The vials were labelled with site, date, and collection method.

Sweep netting

Beginning in week 5, bees were collected by two people using sweep nets (BioQuip 7625HS: sail cloth, 38.1 cm diameter, 61 cm wooden handles) in each field site for 30 min between 0900 and 1200 and again between 1300 and 1500. Weekly pan-trap and sweep-net sampling at a field site were often done on different days. The collectors walked beside each other, approximately 3 m apart, following a predetermined route so that the sweeping effort was spread over the entire plot. Each net was continuously swung in a figure-eight pattern from side to side to prevent escape of captured insects. No effort was made to visually locate bees before capture; insects were collected from all vegetation, ground, and air space covered by the sweep path. At the end of the sampling period, the contents of both nets were emptied into a small, clear plastic bag that was labelled with the date and location; it was transported to the laboratory and frozen at $-20\,^{\circ}$C to kill the insects. Bees were then removed and stored in 70% ethanol. Morning and afternoon collections were kept separate.

Flower collections

Beginning in week 7, bees were collected from blooms of flowering plants by two people using collapsible aerial nets (Bioquip 7112CP: 30.5 cm diameter, 12.7 cm aluminum handles). At each field site, sampling proceeded for 5 min in patches of the most abundant flowers (sufficiently abundant that no flowers were repeatedly sampled). This was conducted on the same day as sweep netting. Unlike sweep netting, bees were visually located on flowers and then netted. Flower collections usually took place in the morning and occasionally in the afternoon. Representatives of sampled flowering plant species were collected, pressed, and identified using field guides (Peterson and McKenny 1968; Booth and Zimmerman 1972; Dickinson *et al.* 2004). The number of collections on each flowering plant species was used as an approximate index of flower abundance, and the average number of bee specimens collected per 5 min sample was used as an index of flower attractiveness. Bee species turnover on flowers was estimated as the average number of bee species collected per 5 min sample.

Identification of bee specimens

Specimens were pinned and labelled according to location, date, collection method, and

floral host, when relevant. Most specimens were identified to genus using Michener *et al.* (1994) and to species using appropriate taxonomic literature (*e.g.*, Mitchell 1960, 1962; Laverty and Harder 1988; Romankova 2004*a*, 2004*b*). Voucher specimens were deposited in the Laurence Packer Collection at York University, Toronto, Ontario, and in M. Richards' collection at Brock University.

Biodiversity estimation and statistical analyses

All identified specimens, pooled across collection methods and collection sites, were used to assess total species diversity to provide the widest possible representative sample. We assumed that we did not catch specimens of all bee species present at our sites. To estimate the underlying ''true'' species richness of the bee community at our sites, we calculated the Abundance-based Coverage Estimator (ACE) and classical Chao1 estimators and chose the higher of the two estimators for the complete data set (Chao 1984; Chao and Lee 1992). We also calculated rarefaction curves using the Mao Tau estimator. All three estimators were calculated using EstimateS, version 8.2.0 (Colwell 2009) based on the total data set and the three subsets partitioned by collection method.

Analyses of phenology were based on pantrap and sweep-net samples caught in odd-numbered weeks, in order to equalize catch effort across weeks and sites.

Results

Bee diversity

We collected 15 733 specimens of 124 species and morphospecies representing five (Halictidae, Colletidae, Andrenidae, Apidae, and Megachilidae) of the six bee families found in North America (Table 1). Halictidae had the highest species richness (44 species) and was the most abundant family, comprising 45% of specimens collected. Colletidae had the lowest species richness (9 species), comprising 11% of specimens. The least common bees were Andrenidae (2%), comprising 17 species that were mostly early season fliers. New species records were added to the list as late as September. The overall distribution of species abundances differed significantly from log-normal

(Kolmogorov–Smirnov $D = 0.143$, $P < 0.001$; Anderson Darling $A^2 = 3.090$, $P < 0.001$).

The rank abundance of bees was assessed using specimens collected in biweekly pan-trap and sweep samples at sites sampled from spring through autumn ($n = 10\,789$; Fig. 1). The 10 most common species and morphospecies (in order of abundance) were the halictid *Augochlorella aurata* (Smith), the apid *Ceratina calcarata* Smith, the megachilid *Osmia conjuncta* (Cresson), the halictid *Halictus ligatus* Say, the apid *Ceratina dupla* L., the halictid *Halictus confusus* Smith, the colletid *Hylaeus affinis* (Smith), the apid *Apis mellifera* L., the halictid *Lasioglossum (D.) versatum*, and the colletid *Hylaeus modestus* Say. These 10 species comprised about 80% of all individuals, and the most abundant species, *A. aurata*, accounted for about 27% of all individuals.

Bees were collected from flowers of 29 plant species (Table 1). The relative abundance of each flowering species (estimated by the number of collections for each species) was correlated with bee abundance (Spearman rank $r = 0.77$, $P < 0.0001$) and species richness ($r = 0.77$, $P < 0.0001$) (Fig. 2). Flower attractiveness was not correlated with flower abundance ($r = 0.19$, n.s.), but bee species turnover on flowers was negatively correlated with flower abundance ($r = -0.52$, $P = 0.0049$). Flower attractiveness was correlated with the total number of bees ($r = 0.72$, $P < 0.0001$) and the total number of species ($r = 0.37$, $P = 0.056$) collected on each plant species.

Bee phenology

During 2003, three peaks in the abundance of bees collected by sweep netting and pan trapping occurred: in week 1 (late April), in weeks 5–9 (mid-May to early June), and in weeks 13–15 (mid- to late July) (Fig. 3). Relatively large numbers of bees continued to be captured until the end of September when the study ended.

Members of the five bee families exhibited distinct phenologies. Most andrenids represented spring species that overwinter as adults, and the majority of individuals were caught in week 1. However, two relatively common andrenid species appeared in midsummer, *Andrena wilkella* (Kirby) in week 7

Table 1. Complete list of specimens captured and identified from pan trap, sweep net, and flower collections at sites at Brock University and the Glenridge Quarry Naturalization Site in St. Catharines, Ontario, 2003. Acronyms for plant names are noted at the bottom of the table.

Family and genus	Subgenus and species	Social habit	Nesting habit	Pans	Sweeps	Flowers	Total	Flower associations
Andrenidae								
Andrena	*arabis* Robertson	Solitary	Ground	3			3	
	carlini Cockerell	Solitary	Ground	32		1	33	Ee
	cressonii Robertson	Solitary	Ground	108	12	2	122	Ee, Moy
	dunningi Cockerell	Solitary	Ground	26	2	1	29	Lv
	erigeniae Robertson	Solitary	Ground	2			2	
	erythronii Robertson	Solitary	Ground	8			8	
	forbesii Robertson	Solitary	Ground	2	2		4	
	hippotes Robertson	Solitary	Ground	3			3	
	mandibularis Robertson	Solitary	Ground	1			1	
	miserabilis Cresson	Solitary	Ground	4			4	
	nasonii Robertson	Solitary	Ground	19	5	4	28	Bv, Ee, Lc, To
	nigrihirta (Ashmead)	Solitary	Ground	1			1	
	thaspii Graenicher	Solitary	Ground	1			1	
	wheeleri Graenicher	Solitary	Ground	1			1	
	wilkella (Kirby)	Solitary	Ground	13	55	45	113	Hp, Lv, Lvu, Mow, Moy, Sv, Tp
Calliopsis	*andreniformis* Smith	Solitary	Ground	5	3		8	
Protandrena	*andrenoides* (Smith)	Solitary	Ground	1			1	
	Andrenidae TOTAL			230	79	53	362	
Apidae								
Anthophora	*terminalis* Cresson	Sol	Stems	1			1	
Apis	*mellifera* L.	Eusocial	Cavities	25	471	789	1285	An, Cir, Cn, Dc, Df, Hp, Mow, Moy, Pp, Sf, Sp, Sv, To, Tp
Bombus*	*bimaculatus* Cresson	Eusocial	Underground	2	2	23	27	Cn, Hp, Ll, Sv, Tp
	citrinus (Smith)	Parasitic	Likely host is *B. impatiens*	1	2		3	
	fervidus (F.)	Eusocial	Ground surface	2	1		3	
	griseocollis (DeGeer)	Eusocial	Ground surface	1	1	3	5	Hp, Moy, Sv

Table 1 (*continued*).

Family and genus	Subgenus and species	Social habit	Nesting habit	Pans	Sweeps	Flowers	Total	Flower associations
	impatiens Cresson	Eusocial	Underground	4	36	133	173	An, Cn, Dc, Df, Mow, Moy, Pp, Sf, Sl, Sp, Sv, Tp
	rufocinctus Cresson	Eusocial	Ground surface or underground	1	1	1	3	Pp
	ternarius Say	Eusocial					2	2	Mow
	vagans Smith	Eusocial					2	2	Am, Df
Ceratina	*calcarata* Smith	Solitary	Stems	422	1265	305	1992	Am, Bv, Ca, Ci, Cn, Ee, Ep, Fv, Hc, Hp, Lc, Ll, Lv, Mow, Moy, Sl, Sp, Sv, Tp
	dupla L.	Solitary	Stems	482	314	83	879	As, Bv, Cn, Ee, Ep, Fv, Hc, Lc, Ll, Lv, Mow, Moy, Sl, Sp, Sv, Tp
	strenua Cresson	Solitary	Stems	2	2	2	6	Hc, Sp
Melissodes	*apicata* Lovell and Cockerell	Solitary	Ground				4	4	Cn, Hp, Moy
	desponsa Smith	Solitary	Ground	4	2	5	11	Cn, Sf
	druriella (Kirby)	Solitary	Ground		8	13	21	An, Sf, Sp
Nomada	*articulata* Smith	Parasitic		2			2	
	bethunei Cockerell	Parasitic		1		1	2	Bv
	denticulata Robertson	Parasitic		3	7		10	
	pygmaea Cresson	Parasitic		3		1	4	Lc
	sayi/illinoensis Robertson	Parasitic			2		2	
	Form D	Parasitic		1			1	
	Form H	Parasitic		11	3		14	
	Form N	Parasitic		2			2	
	Form O	Parasitic		2			2	
	unknown	Parasitic		1		1	2	Fv
Xylocopa	*virginica* (L.)	Social	Wood	1	14	25	40	An, Cn, Hc, Mow, Moy, Pp, Sf

Table 1 (*continued*).

Family and genus	Subgenus and species	Social habit	Nesting habit	Pans	Sweeps	Flowers	Total	Flower associations
	Apidae TOTAL			974	2131	1393	4498	
Colletidae								
Colletes	*americanus* Cresson	Solitary	Ground			1	1	Sp
	compactus Swenk	Solitary	Ground			1	1	Sp
	simulans Swenk	Solitary	Ground	1	1	1	3	Dc
Hylaeus	*affinis* (Smith)	Solitary	Stems/cavities	288	460	135	883	Am, An, Ca, Dc, Ee, Fv, Hc, Hp, Lc, Lv, Sf, Sp, Mow, Moy, Tp
	affinis (Smith)/*modestus* Say (females)	Solitary	Stems/cavities	77	107	39	223	
	annulatus (L.)	Solitary	Stems/cavities	6	26	1	33	Dc
	hyalinatus Smith	Solitary	Stems			2	2	Dc
	illinoisensis (Robertson)	Solitary	Stems		8	1	9	Hp
	mesillae (Cockerell)	Solitary	Stems/cavities	16	206	80	302	Am, An, Cn, Dc, Ee, Fv, Hc, Hp, Lc, Lv, Moy, Sp, Sf, Tp
	modestus Say	Solitary	Stems/cavities	18	185	65	268	Ca, Cn, Dc, Ee, Hp, Lc, Lv, Moy, Sp, Sv
	Colletidae TOTAL			406	993	326	1725	
Halictidae								
Agapostemon	*virescens* (F.)	Communal	Ground	63	11	3	77	Ci, Ll
Augochlora	*pura* (Say)	Solitary	Wood	9	44	18	71	An, Cn, Df, Hc, Hp, Sf, Sp, Tp
Augochlorella	*aurata* (Smith)	Eusocial	Ground	2373	1157	211	3741	Am, An, Bv, Ca, Ci, Cn, Dc, Df, Ee, Fv, Hc, Hp, Lc, Ll, Lv, Mow, Moy, Sf, Sp, Sv, Ta, To, Tp
Augochloropsis	*metallica* (Smith)	Semisocial?	Ground		3	9	12	Lc, Lv
Dufourea	*monardae* (Cresson)	Solitary	Ground			1	1	

Table 1 (*continued*).

Family and genus	Subgenus and species	Social habit	Nesting habit	Pans	Sweeps	Flowers	Total	Flower associations
Halictus	*confusus* Smith	Solitary/ eusocial	Ground	265	319	65	649	Am, An, Bv, Ci, Dc, Ee, Fv, Hc, Hp, Ll, Lv, Mow, Moy, Sp, Ta, Tp
	ligatus Say	eusocial	Ground	374	284	261	919	Am, An, Bv, Ci, Cn, Cir, Dc, Df, Hc, Ll, Lv, Pp, Mow, Moy, Sf, Sp, Tp
	rubicundus (Christ)	Solitary/ eusocial	Ground	54	36	9	99	Cn, Dc, Hp, Mow, Moy, Tp
Lasioglossum	(*Dialictus*) *admirandum* (Sandhouse)	Eusocial?	Ground	128	32	5	165	Am, Dc, Ee, Ep
	(*Dialictus*) *albipenne* (Robertson)	Eusocial?	Ground			1	1	Sv
	(*Dialictus*) *asteris* (Mitchell)	Parasitic	Host is *L. imitatum*		1		1	
	(*Dialictus*) *atwoodi* Gibbs	Eusocial?	Ground	27	22	4	53	Am, Dc, Ep, Hc
	(*Dialictus*) *coeruleum* (Robertson)	Eusocial	Wood		1		1	
	(*Dialictus*) *cressonii* (Robertson)	Eusocial?	Wood	9	3	4	16	Am, Cn, Fv, Hc,
	(*Dialictus*) *dreisbachi* (*Mitchell*)				1		1	
	(*Dialictus*) *ellisiae* (Sandhouse)	Eusocial?	Ground	46	45	9	100	Bv, Dc, Lc
	(*Dialictus*) *ephialtum* Gibbs	Eusocial?	Ground	36	38	7	81	Dc, Hp, Lc, Mow, Sl
	(*Dialictus*) *divergens* (Lovell)	Solitary	Ground	1			1	
	(*Dialictus*) *fattigi* (Mitchell)	Eusocial?	Ground	84	26	4	114	Dc, Ee, Lc
	(*Dialictus*) *foxii* (Robertson)	Solitary	Ground	1	7	1	8	Mow

Table 1 (*continued*).

Family and genus	Subgenus and species	Social habit	Nesting habit	Pans	Sweeps	Flowers	Total	Flower associations
	(*Dialictus*) *imitatum* (Smith)	Eusocial	Ground	26	81	45	152	An, Cn, Dc, Ee, Hp, Lc, Lv, Sp, Tp
	(*Dialictus*) *laevissimum* (Smith)	Eusocial	Ground	5	8	5	18	Cn, Dc
	(*Dialictus*) *leucocomum* (Lovell)	Eusocial?	Ground	2			2	
	(*Dialictus*) *lineatulum* (Crawford)	Eusocial	Ground	2	21	2	25	Dc, Lc
	(*Dialictus*) *michiganense* (Mitchell)	Parasitic			1		1	
	(*Dialictus*) *mitchelli* Gibbs	Eusocial?	Ground	130	42	17	189	Ca, Cn, Sv, Dc, Lc, Lv, Lvu, Sf, Sp, Tp
	(*Dialictus*) *nigroviride* (Graenicher)	Eusocial?	Ground		4		4	
	(*Dialictus*) *oceanicum* (Cockerell)	Eusocial?	Ground	18	2		20	
	(*Dialictus*) *paradmirandum* (Knerer and Atwood)	Eusocial?	Ground	4			4	
	(*Dialictus*) *perpunctatum* (Ellis)	Eusocial?	Ground	2	2		4	
	(*Dialictus*) *planatum* (Lovell)	Eusocial?	Ground?	1	1		2	
	(*Dialictus*) *rufitarse* (Zetterstedt)	Solitary	Ground	6	18	1	25	Bv
	(*Dialictus*) *sagax* (Sandhouse)	Eusocial?	Ground	3			3	
	(*Dialictus*) *versatum* (Robertson)	Eusocial	Ground	170	33	20	223	Dc, Df, Ep, Hp, Sl, Sp
	(*Dialictus*) *viridatum* (Lovell)	Eusocial	Ground	13	59	9	81	Am, Cn, Dc, Hp, Sf, Sp
	(*Dialictus*) *zephyrum* (Smith)	Eusocial	Ground	2			2	
	(*Dialictus*) *zophops* (Ellis)	Eusocial?	Ground	1			1	
	(*Evylaeus*) *cinctipes* (Robertson)	Eusocial	Ground	7	3		10	
	(*Lasioglossum*) *coriaceum* (Robertson)	Solitary	Ground	20	3		23	
	(*Lasioglossum*) *leucozonium* (Schrank)	Solitary	Ground	53	20	5	78	Bv, Hc, Ll
	(*Lasioglossum*) *zonulum* (Smith)	Solitary	Ground	58	5	1	64	Hp

Table 1 (*continued*).

Family and genus	Subgenus and species	Social habit	Nesting habit	Pans	Sweeps	Flowers	Total	Flower associations
Sphecodes	*dichrous* Smith	Parasitic			1	2	3	Ee, Pp
	heraclei Robertson	Parasitic			5	3	8	Dc, Lc
	ranunculi Robertson	Parasitic			2		2	
	Halictidae TOTAL			3993	2342	721	7056	
Megachilidae								
Anthidiellum	*notatum* (Latreille)	Solitary	Makes nests on surfaces	4	6		10	
Anthidium	*manicatum* (L.)	Solitary	Cavities	30	1	3	34	Ep, Sv
Chelostoma	*rapunculi* (Lepeletier)	Solitary	Cavities	1	2		3	
Coelioxys	*octodentata* Say	Parasitic		3	2		5	
	rufitarsis Smith	Parasitic		1		1	2	Cn
Heriades	*carinatus* Cresson	Solitary	Cavities		6	2	8	Ca, Cn
	leavitti Crawford	Solitary	Cavities	1	48	7	56	An, Cn, Dc, Mow, Sp
	variolosus (Cresson)	Solitary	Cavities		8	2	10	Ci, Sl
Hoplitis	*pilosifrons* (Cresson)	Solitary	Cavities	48	11	7	66	Ca, Hc, Lv, Mow
	producta (Cresson)	Solitary	Cavities	19	10	8	37	Cn, Hc, Lv, Mow
	spoliata (Provancher)	Solitary	Cavities	7			7	
Megachile	*brevis* Say	Solitary	Cavities/ground	36	7	5	48	Ci, Mow, Sv
	campanulae (Robertson)	Solitary	Cavities		1		1	
	centuncularis (L.)	Solitary	Cavities	1			1	
	ericetorum Lepeletier	Solitary	Cavities	1			1	
	latimanus Say	Solitary	Ground	5	2	1	8	Df
	mendica Cresson	Solitary	Cavities/ground	3			3	
	pugnata Say	Solitary	Cavities			1	1	Df
	relativa Cresson	Solitary	Cavities		2	4	6	Ep, Lv, Sp, Sl
	rotundata (F.)	Solitary	Cavities	46	32	12	90	Ep, Hc, Hp, Lv, Moy
	texana Cresson	Solitary	Ground	4	3	4	11	Cn, Df, Sp, Sv
Osmia	*atriventris* Cresson	Solitary	Cavities	33	5	3	41	Bv, Hp, Mow
	conjuncta (Cresson)	Solitary	Snail shells	1387	97	17	1501	Bv, Ep, Cn, Fv, Hc, Lc, Ll, Lv, Mow, Moy, Tp
	lignaria Say	Solitary	Cavities	1			1	

Table 1 (*concluded*).

Family and genus	Subgenus and species	Nesting habit	Social habit	Pans	Sweeps	Flowers	Total	Flower associations
	pumila Cresson	Stems/cavities	Solitary	99	16	1	116	Moy
	simillima Smith	Wood	Solitary	1			1	
Stelis	*lateralis* Cresson		Parasitic	10	11	3	24	Ep, Lv
	Megachilidae TOTAL			1741	270	81	2092	
	Grand TOTAL			7344	5815	2574	15733	

Note: *Achillea millefolium* L. (Am); *Arenaria serpyllifolia* L. (As); *Symphyotrichum novae-angliae* (L.) G.L. Nesom (An); *Barbarea vulgaris* W.T. Aiton (Bv); *Convolvulus arvensis* L.(Ca); *Cichorium intybus* L. (Ci); *Cirsium* Mill. sp. (Cir); *Centaurea nigra* L. (Cn); *Daucus carota* L. (Dc); *Dipsacus fullonum* L. (Df); *Erigeron philadelphicus* L. (Ep); *Euphorbia esula* L. (Ee); *Fragaria virginiana* Duchesne (Fv); *Hieracium canadense* Michx. (Hc); *Hypericum perforatum* L. (Hp); *Lepidium campestre* (L.) W.T. Aiton (Lc); *Leucanthemum vulgare* Lam. (Lv); *Linaria vulgaris* Mill. (Lvu); *Linum lewisii* Pursh (Ll); *Melilotus officinalis* (L.) Lam. (yellow) (Moy); *Melilotus officinalis* (L.) Lam. (white) (Mow); *Polygonum pensylvanicum* L. (Pp); Flat-top *Solidago* L. sp. (Sf); *Symphyotrichum lateriflorum* (L.) A. Löve & D. Löve (Sl); Plume-top *Solidago* sp. (Sp); *Securigera varia* (L.) Lassen (Sv,); *Thlaspi arvense* L. (Ta); *Taraxacum officinale* F.H. Wigg. (To); *Trifolium pratense* L. (Tp). Eleven damaged specimens (1 *Andrena*, 9 *Hylaeus*, and 1 *Osmia*) that could not be identified to species were excluded from the list.

*Ecological and taxonomic information from Laverty and Harder, 1988.

and *Calliopsis andreniformis* Smith in week 11 (the latter species overwinters as mature larvae). Megachilid phenology also showed a single peak in abundance with the majority of individuals (species of *Osmia* Panzer) being caught in week 1; >85% of these were males of *O. conjuncta*. Apid phenology showed three peaks in abundance at weeks 1, 7, and 15. Captured apids were predominantly males of *Ceratina dupla* in week 1 (about 70%), males of *Ceratina calcarata* in week 7 (about 60%), and females of *Apis mellifera* (52%) and *C. calcarata* (30%) in week 15. Halictids exhibited three peaks of abundance in spring (week 5) and summer (weeks 13–15) with a smaller peak in autumn (week 23). Females of *Augochlorella aurata* comprised 82% of halictids collected in week 5, but only 26% of those collected in week 15. Colletidae exhibited the shortest flight season, the earliest individuals were caught in week 5. Their peak abundance was in week 15, with 55%–60% of individuals being *Hylaeus affinis*.

Methodological comparisons

Proportional representation of each bee family varied significantly according to collection method during weeks 7–23, when all three collection methods were being used at all sites (Fig. 4; $\chi^2 = 2206$, df = 8, $P < 0.0001$). The differences in distribution remained even when the comparison was limited to the set of paired pan-trap and sweep-net samples (flower collections were not evenly distributed among weeks or sites; $\chi^2 = 1352$, df = 4, $P < 0.0001$). Halictids and megachilids were caught more often in pan traps, whereas andrenids, apids, and colletids were caught more often in sweep nets. In general, these family-level differences were reflected at the genus level as well (Fig. 5).

Similar numbers of bees were caught in morning and afternoon sweep samples from the same day (paired *t* test, $t = 1.288$, df = 66, n.s.). When sites were sampled with pan traps and sweep nets on the same day, similar numbers of bees were caught with each method ($t = 0.611$, df = 36, n.s.), but daily species richness was higher in the sweep samples than in the pan traps ($t = 1.94$, df = 37, $P < 0.05$). Over the course of the summer, however, more species were caught by pan traps than by the other methods (Table 2). Although the proportions of single-

Fig. 1. Species abundance (black diamonds) and cumulative abundance (grey circles) for biweekly pan-trap and sweep-net samples at seven sites (all except PhysEd and 406, $n = 10\ 789$ specimens from 113 species and morphospecies) at Brock University and the Glenridge Quarry Naturalization Site in St. Catharines, Ontario.
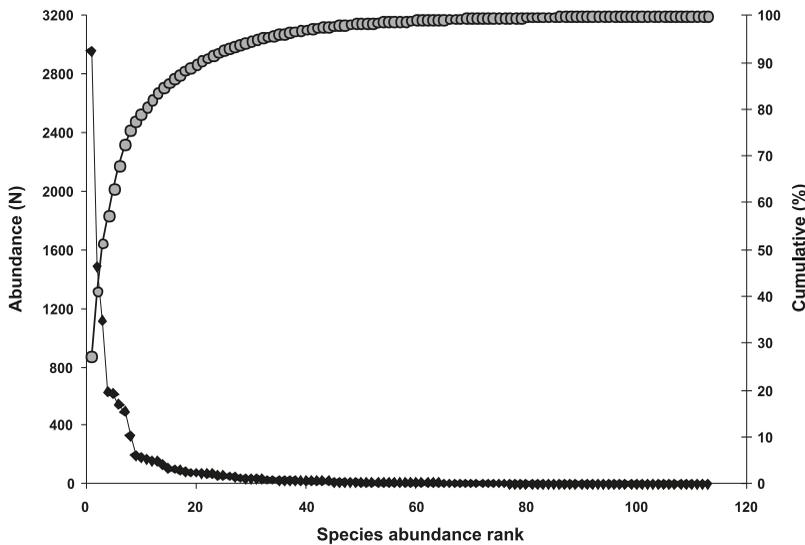
ton species did not vary significantly among the three methods, the proportion of exclusive species (those caught only by a single method) was considerably higher in pan traps than in the other methods. However, this higher diversity in pan traps was partly because this was the only method used in weeks 1–4. When the comparison of methods was limited to weeks 7–23, the number of species was greatest in sweep samples, followed by pan traps, and then by flower collections. There were no differences between sampling methods in the proportions of either singletons or exclusive species.

The higher of the two species richness estimators (ACE) calculated using the complete data set (Colwell 2009) suggests that the total number of bee species at our sites was about 148 (Table 3), indicating that as many as 24 additional species were not captured. The ACE and Chao1 estimators for the various data subsets allow further comparison of the efficacy of the various collection methods (Table 3). Total species richness was estimated at 140 species by ACE and Chao1 for the combination of pan and sweep samples. Pan samples alone generated a Chao1 estimate of 135 species, with a confidence interval from about 114 to 188 species (including the observed species richness

(124) based on all three methods). In contrast, the species richness estimates based on the sweeps only and flowers only subsets were markedly lower and the upper limits of the 95% confidence intervals for both subsets were well below 124.

These patterns are reflected in rarefaction curves calculated for each method and for the total collection (Fig. 6). Flower collections yielded the highest species diversity per specimen caught, but total diversity was low because relatively few specimens were caught using this method. Conversely, sweep-net samples yielded the lowest diversity per specimen samples, but total diversity was higher because more specimens were caught. Although partly because the total sample included the pan-trap sample, ollinearity between curves for pan traps and all methods combined suggests that, over time, pan traps would eventually catch as many different species as all methods combined.

Discussion

Niagara Escarpment bee assemblage in 2003

In this survey, we collected 124 bee species and morphospecies that likely represent the majority of bee species in our study sites and perhaps in that part of southern Ontario. As

Fig. 2. Average rates of capture of bee species and individuals in 5-min flower collections at Brock University and the Glenridge Quarry Naturalization Site in St. Catharines, Ontario. Native flower species names are followed by an asterisk (*).
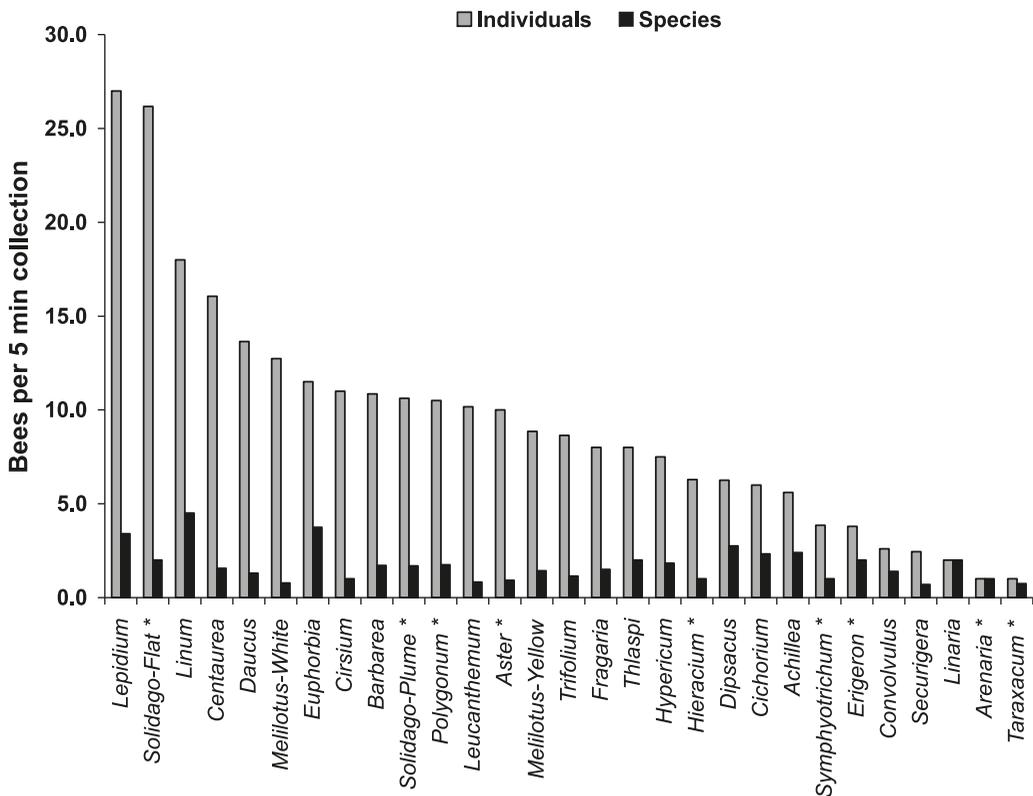
predicted by the ACE and Chao1 estimators, the number of species would certainly have risen if more bees were collected. There are several reasons for this. First, some of the abundant species may represent species complexes of cryptic or currently unrecognizable species. For example, the abundant species, *Ceratina dupla*, has been shown to comprise two genetically and behaviourally distinct species in the Niagara Region (Vickruck *et al.* 2011). Second, new species are probably being introduced into the Niagara Region at an undetermined rate. For example, our capture of a single specimen of the megachilid *Megachile ericetorum* Lepeletier (Table 1) is the first New World record of this European species (Sheffield *et al.* 2010). Another example is *Megachile sculpturalis* Smith, an Asian species first reported in Canada in 2002 (Paiero and Buck 2003), that we have observed nesting in abandoned nests of *Xylocopa virginica* (L.) at Brock University

(M. Peso and M. Richards, unpublished data). Third, the large number of singletons we collected indicates that the local bee community includes many rare species that have a low likelihood of being captured and suggests that a resampling of this community in subsequent years may add further names to the species list. Fourth, long-term studies of bee communities indicate that there may be considerable turnover in species composition from year to year (Minckley *et al.* 1999; Grixti and Packer 2006), suggesting that a single year of sampling cannot provide a complete picture of bee-community composition even in very large surveys. The third and fourth points are especially relevant because the number of species captured in our study represents only about one-third of the bee species recorded in Ontario (C.S. Sheffield and L. Packer, unpublished data).

The majority of species collected in our study were ground-nesters, including the most

Fig. 3. Biweekly phenology of bees collected in pan traps (black bars) and sweep nets (white bars) at Brock University and the Glenridge Quarry Naturalization Site in St. Catharines, Ontario in 2003. Week 1 began on 20 April, week 11 began 29 June, and week 21 began 7 September. Note the dearth of bees collected around week 11 (29 June–5 July).
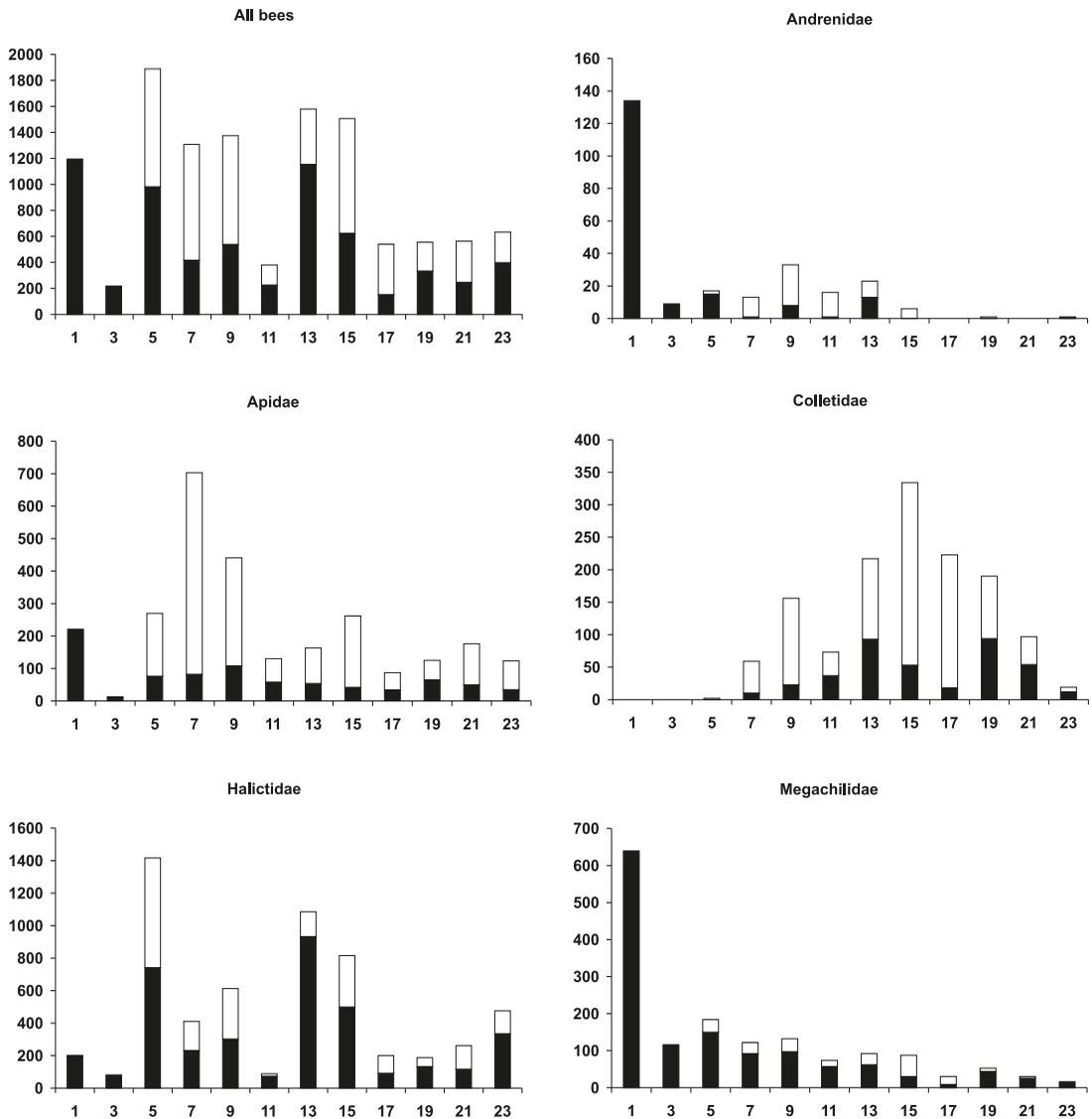

abundant species (*Augochlorella aurata*) and the most speciose group (29 species of *Dialictus* Robertson, a subgenus of *Lasioglossum* Curtis) (Table 1). Perhaps cavity nesters were less common because our sites were mostly newly restored grasslands that contained little woody habitat with pre-existing cavities suitable for those species. An interesting exception was *Osmia conjuncta*, one of the more abundant species in our study, and not previously recorded in Canada. It nests in empty snail shells (Cane *et al.* 2007) and its abundance is probably related to the high density of introduced land snails (*Cepaea* Held) in several of our study sites.

Although little information is available regarding foraging and flower preferences for bees found in the Niagara Region, it appears that most of the pollen collectors are generalists (the only bee species associated

Fig. 4. Differences in catchability by capture method for the five bee families caught at sites at Brock University and the Glenridge Quarry Naturalization Site in St. Catharines, Ontario.

Fig. 5. Differences in catchability by capture method for common bee genera caught at sites at Brock University and the Glenridge Quarry Naturalization Site in St. Catharines, Ontario.
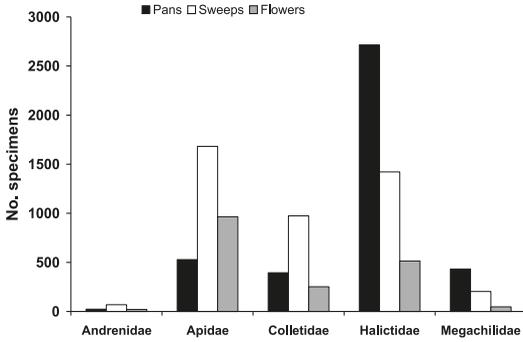
with a single flowering plant species were collected as singletons or doubletons). Most of the common, abundant species in our study were collected on flowers of a variety of different plant species. Many of these plants are non-native but are well-established in southern Ontario and are probably important components of Niagara bee habitat. For instance in the Niagara Region, teasel (*Dipsacus fullonum* L. (Dipsacaceae)) is used as a food plant by several species of *Bombus* Latreille and as nesting substrate by *Ceratina dupla*, *C. calcarata*, and, occasionally, species of *Hylaeus* F. (Vickruck 2010), while Queen Anne's lace (*Daucus carota* L. (Apiaceae)) is an important pollen source for *Hylaeus* and *Lasioglossum* (*Dialictus*).

Bees were collected from flowers of 29 common plant species. Because the number of collections per flowering species was more or less proportional to the relative abundance at each site, we used the number of collections as a measure of flower abundance. We found that flower abundance and attractiveness were associated with a greater abundance and diversity of bees. In both cases, the higher bee diversity is likely to be largely a sampling effect of greater abundance, *i.e.*, an ecological sampling effect related to flower visitations by the bees and a statistical sampling effect related to collecting the bees (Richardson and Richards 2008). A positive correlation between floral resources and bee abundance and diversity can be interpreted as evidence that the bee

community is structured by inter-specific competition (Tepedino and Stanton 1981). However, our approximate, relative measure of floral abundance cannot be used as strong support for such a conclusion (Tepedino and Stanton 1982).

At least 17 of the 29 common plant species that we sampled represent non-native introductions to North America. (In addition to *Daucus carota* and *Dipsacus fullonum* these were *Achillea millefolium* L., *Centaurea nigra* L., *Cichorium intybus* L., and *Leucanthemum vulgare* Lam. (Asteraceae); *Barbarea vulgaris* W.T. Aiton, *Lepidium campestre* (L.) W.T. Aiton, and *Thlaspi arvense* L. (Brassicaceae); *Convolvulus arvensis* L. (Convolvulaceae); *Melilotus officinalis* (L.) Lam., *Securigera varia* L., and *Trifolium pratense* L. (Fabaceae); *Euphorbia esula* L. (Euphorbiaceae); *Hypericum perforatum* L. (Clusiaceae); and *Linaria vulgaris* Mill. (Scrophulariaceae) as well as an unidentified species of *Cirsium* Mill. (Asteraceae) which may be non-native). One other species, *Linum lewisii* Pursh (Linaceae), was introduced from western North America. The impact of this diverse array of invasive herbaceous plants on the local bee community is difficult to assess. Before European settlement, the natural vegetation of the Niagara Escarpment was dominated by deciduous forest (Muller and Middleton 1994) that probably would have supported a lower diversity and abundance

Table 2. Comparison of abundance and diversity of bees caught in pan trap, sweep net, and flower collections at sites at Brock University and the Glenridge Quarry Naturalization Site in south St. Catharines, Ontario.

Sample	Method	Total specimens	Total species	Singletons	Exclusive species
All specimens	Pans	7344	96	16	29
	Sweeps	5815	85	8	10
	Flowers	2574	66	4	7
	Total	15 733	124	28	46
				$\chi^2 = 4.85$, n.s.	$\chi^2 = 13.94$, $P < 0.001$
Only weeks 7–23	Pans	4092	75	8	13
	Sweeps	4346	82	7	12
	Flowers	1799	67	6	9
	Total	10 237	105	21	34
				$\chi^2 = 0.23$, n.s.	$\chi^2 = 0.45$, n.s.

Note: Samples are from the entire 2003 collecting season and the period (weeks 7–23) when all three methods were in regular use. Exclusive species are those caught by a single method (including singletons). For all χ^2 tests, df = 2.

Table 3. Estimates of species richness of bees collected at sites at Brock University and Glenridge Quarry Naturalization Site in south St. Catharines, Ontario, based on the Abundance-based Coverage Estimator (ACE) and the Chao1 Estimator.

Data subset	Observed species (n)	ACE	Chao1 Mean $\pm$ SD	95% C.I.
Pans, sweeps, flowers	124	148.1	145.0 $\pm$ 9.6	133.7–175.0
Pans, sweeps	113	140.0	139.6 $\pm$ 11.0	126.1–174.0
Pans	96	128.6	135.1 $\pm$ 17.2	114.7–188.3
Sweeps	85	95.8	92.0 $\pm$ 4.45	87.6–108.0
Flowers	66	88.5	91.2 $\pm$ 10.0	80.3–116.6

Note: Estimators were calculated in EstimateS based on 50 runs of each data subset.

of native bees (Taki *et al.* 2007) than open meadow habitats would have. Conversely, the subsequent disappearance of native plants from woodlands and meadows of the area is likely associated with the disappearance of their specialist pollinators. Moreover, bee species that nest in substrates associated with woodlands (*e.g.*, *Augochlora pura* (Say) (Halictidae), which nests in rotting logs and tree trunks) have likely also declined as woodland areas have decreased. However, most of the bee species at our research sites appear to be floral generalists and favour nesting areas that are abundant in open meadows. Generalists likely take advantage of available, plentiful, and reliable sources of pollen and nectar regardless of biogeographic origin. Thus, the change from forest to open habitats with abundant floral

resources may have resulted in overall increases in bee abundance and diversity, despite the possible loss of species better adapted to Carolinian forests.

Phenology

Three distinct bee flight seasons, comprising distinct sets of species, were observed in 2003 and this was a pattern reminiscent of other bee assemblages (Griswold *et al.* 1997; Oertli *et al.* 2005). The early spring bees, which winter as adults (Stephen *et al* 1969), included species of *Osmia* and *Ceratina* Latreille and most of the species of *Andrena* F. It is likely that these bees forage on willows (*Salix* L. (Salicaceae)) and early-flowering fruit trees (Rosaceae) including hawthorn (*Crataegus* L.), apple (*Malus* L.), pear (*Pyrus* L.), and wild cherry (*Prunus*

Fig. 6. Rarefaction curves based on Mao's Tau, comparing numbers of species collected by pan trapping, sweep netting, and 5 min flower collections at Brock University and the Glenridge Quarry Naturalization Site in St. Catharines, Ontario. For this analysis, each collection site was treated as a sample (total of eight samples or sites).
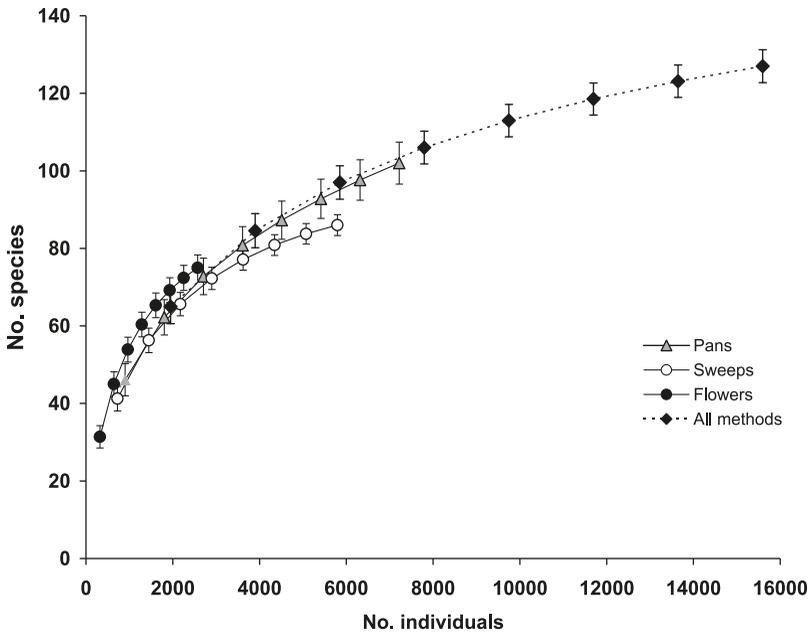
L.). The late spring peak was also composed of species that overwinter as adults. This peak was dominated by overwintered foundresses of *Augochlorella aurata*, a primitively eusocial ground-nester (the most common bee in our survey) and early emerging species of typical summer-flying genera, notably *Megachile* Latreille and *Hoplitis* Klug (Megachilidae). A notable late spring andrenid was *Andrena wilkella*, a European species with no other representatives of its subgenus (*Taeniandrena* Hedicke) in North America. The third abundance peak (July) was composed mainly of two distinct sets of bees: the spring (worker) generation of abundant, eusocial halictids such as *A. aurata*, *Halictus ligatus*, and *H. confusus*; and the newly emerged adults of species that overwinter as larvae and pupate in spring, including species in other families from common genera such as *Hylaeus* and *Megachile*. A distinctive feature of the whole bee community was the lack of flight activity around week 11, shortly after the summer solstice. This quiescent period partly reflected the gap between provisioning and emergence of the first and second broods of

the primitively eusocial and bivoltine species, but also occurred in univoltine, solitary species such as *Hylaeus mesillae* (Cockerell). The bee species caught in relatively high numbers during week 11 included the univoltine, communal halictid *Agapostemon virescens* (F.).

Comparison to another southern Ontario bee assemblage

Species richness and the proportion of singletons are two characteristics conducive to comparisons among bee biodiversity surveys (Cane and Tepedino 2001). A preliminary survey of symphytan and aculeate Hymenoptera in an Ontario oak savannah found only 40 bee species, although this was from only one day of malaise trap sampling (Sugar *et al.* 1998). A more interesting comparison is with two bee diversity surveys carried out in the Caledon Hills, near the eastern boundary of the Carolinian Zone in Ontario. Sampling there found 105 bees, including 14 singletons, in 1968–1969 (MacKay 1970; MacKay and Knerer 1979); subsequently 150 species, including 25 singletons, were found in 2002–2003 (Grixti and

Packer 2006). Species richness was underestimated in both studies because large Apidae (such as species of *Bombus* Latreille and probably *Xylocopa* Latreille) were excluded. This suggests that the Caledon bee fauna is richer than that in the Niagara Region. Some differences between the two bee communities may reflect natural regional variation. For example, some common Niagara megachilids such as *Osmia conjuncta*, *O. atriventris* Cresson, and *Megachile brevis* Say were rare or absent at Caledon, suggesting differences in the availability of suitable nesting substrate between the two areas. However, the considerably lower species richness in our study suggests that the bee fauna at the Glenridge Quarry (especially) and the various Brock University sites is highly depauperate, likely because of the severe anthropogenic disturbance with little time for recovery at those sites.

One way of comparing the diversity patterns of two different communities or assemblages is to use the proportions of singletons (Magurran 2004); these did not vary significantly among the two Caledon Hills studies and our Niagara study ($\chi^2 = 0.513$, df = 2, n.s.). Another method is to compare the slopes of regression lines drawn through rank-abundance plots (Magurran 2004). Comparison of slopes from the Niagara and 2002–2003 Caledon Hills studies suggests greater evenness in the Caledon bee community and greater dominance in the Niagara community (Fig. 7). Kevan *et al.* (1997) suggested that disturbed bee communities deviate significantly from a log-normal abundance distribution, as we observed in our samples. Re-examination of the Caledon Hills data shows that its bee community also exhibited significant departure from lognormality (Kolmogorov–Smirnov: D = 0.109, $P < 0.001$ (2002–2003 data) and D = 0.093, $P < 0.01$ (1968–1969 data)) despite being in a habitat that likely is less disturbed than the Niagara habitat. Lack of log-normality in the Caledon and Niagara communities may be a result of high species turnover resulting from high frequencies of transient species. At Caledon there was evidence of considerable change in the bee fauna at annual and decadal scales (Grixti and Packer 2006; Richardson and Richards 2008), and there were introduced species in both bee communities that may or

may not become permanently established (Paiero and Buck 2003; Sheffield *et al.* 2010). In future monitoring of species abundance at our Niagara sites, it may be useful to separate transient species from permanent residents in order to assess the "true" shape of the local species abundance distributions (Magurran 2004).

Methodological considerations

The use of all three sampling methods (pan trapping, sweep netting, and flower collections) in this study clearly improved our ability to determine the species representation of the local bee community. However, we could only equalize catch effort over time, among sites, and among collectors for two of these methods (pan trapping and sweep netting) because they do not require specialized skill in spotting, identifying, or catching specimens. Although we could not assume that catch effort was equalized among collectors doing flower collections, this method had the advantage of yielding floral association data that could be useful for evaluating and guiding further efforts to restore vegetation at our study sites and similar areas. Pan trapping has the advantages of effective early-season sampling (when effective sweep netting and flower sampling are relatively difficult), 24-h sampling, and requires less time input by collectors. As a result, despite lower daily species richness, we collected more kinds of bees in pan traps than other methods over our 23-week season. Bee abundance in pan traps was significantly correlated with abundance in sweep collections, suggesting that both methods sampled bee populations consistently and could be used to assess population variability. However, efficacy of sampling of different bee species clearly varies between sampling methods. The ease of pan trap use and the possibility for consistent sampling among years and among investigators makes pan traps an attractive option for long-term monitoring of bee communities. However, the differential susceptibility of male and female bees, of foraging and non-foraging bees, and of different species to being caught in pan traps (Cane *et al.* 2000) should be taken into account. Differential susceptibility to trapping by any method can potentially influence comparisons and interpretations of relative abundance among bee species within

Fig. 7. Comparison of southern Ontario bee communities studied in 2003 in the Niagara Region (this study) and the Caledon Hills (Grixti and Packer 2006). The species abundance distribution in both communities approximates a geometric series, although the fit is better for the Forks of the Credit community (Niagara: $R^2 = 0.93$, slope $= -0.055$; Caledon Hills: $R^2 = 0.97$, slope $= -0.043$). The slopes of the two lines are significantly different (ANCOVA, $F = 1746$, df $= 3270$, $P < 0.0001$).
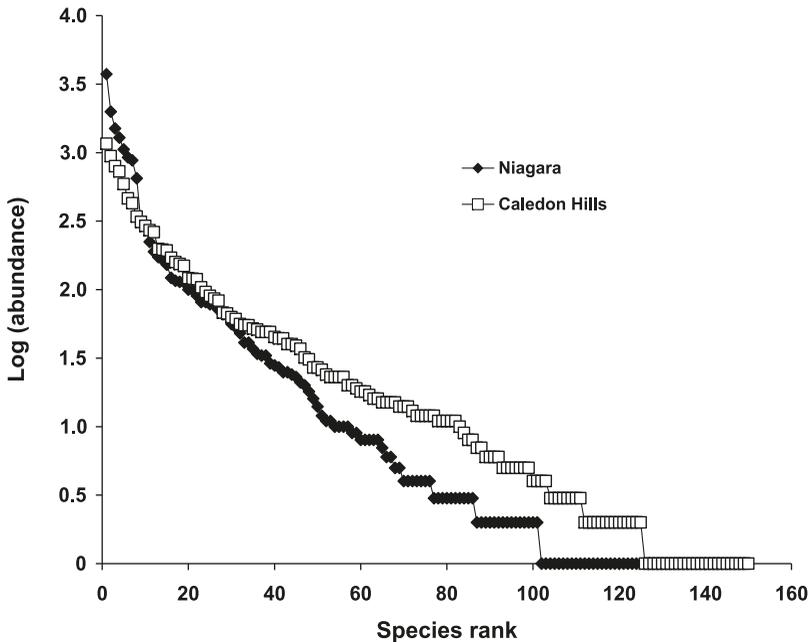
years, but should be less critical in comparisons of population and community dynamics across years. Pan-trap sampling in conjunction with nest collections has been successfully used to investigate seasonal phenology (Packer *et al.* 2007; Rehan and Richards 2010; Richards *et al.* 2010).

The primary objective of this study was to provide a preliminary assessment of bee diversity in the Niagara Peninsula in Ontario, Canada. The information presented here provides baseline information for long-term monitoring of Niagara bee community dynamics and can also be used for comparisons with other bee communities in the region and in similar habitats. Future studies should focus on how the Glenridge Quarry bee community adjusts to ongoing successional changes in vegetationas well as year-to-year variation in the population dynamics of abundant species.

Acknowledgments

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