

NEGATIVE EFFECTS OF EARLY SPRING MOWING ON A BEE COMMUNITY: A CASE STUDY IN THE NIAGARA REGION

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Abstract

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Mowing of bee habitats can change the availability of nesting habitat both above and below ground. Disturbances such as mowing with heavy equipment (“bush-hogging”) that remove all woody vegetation, may affect bees by killing them outright or by altering the availability of nesting and foraging resources. In this case study, we studied the effects of three years (2017 to 2019) of early spring mowing with heavy equipment that removed both herbaceous and woody vegetation from a previously undisturbed, 3 ha meadow (Brock South) in St. Catharines, Ontario, Canada. We predicted that mowing would decrease the abundance of bees that require woody vegetation as their nesting substrate and increase the abundance of below-ground nesters that build nests in exposed soil. We used two approaches to address these predictions. First, using paired, biweekly pan trap collections in 2018 and 2019, we compared bee abundance and diversity from the mowed site (Brock South) to that in an adjacent site of similar size that was unmowed but otherwise very similar (Brock Southwest). Bee abundance and diversity were lower in absolute terms in mowed Brock South than in unmowed Brock Southwest. In mowed Brock South, the carpenter and cavity-nesting bee guilds were lower in relative abundance, while below-ground nesters were higher in relative abundance. Second, we hypothesized that in the absence of mowing, temporal patterns in bee abundance in mowed Brock South should have been like those at undisturbed control sites nearby. Based on pan trap samples collected at three control sites within 1 km of the mowed Brock South site, bee abundance in the absence of disturbance was higher in 2018 and 2019 than in previous years (2008–2017). In contrast, bee abundance in mowed Brock South was not higher in 2018 and 2019 than previous years. Thus, both approaches suggest that even relatively mild disturbances, like mowing once per year, may result in alterations to local bee communities, detectable at small spatial scales of tens to hundreds of metres.

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Introduction

Two kinds of critical resources, floral resources (pollen and nectar) and nesting substrate, directly affect bee abundance. While there is considerable evidence that greater floral abundance leads to greater bee abundance (Roulston and Goodell 2011), how the availability of nesting resources influences bee abundance is not as well understood, at least partly because availability of nesting resource is difficult to measure. Bees exhibit a wide variety of nesting habits. Some construct burrows underground in soil or above ground in substrates like twigs, lumber, or rotting wood. Some construct new cavities, whereas others modify existing holes and crevices.

One way to investigate how the availability of a resource influences the abundance of its consumers is by augmenting or removing it and subsequently observing the effect on local populations. Many landscape management techniques such as plowing, grazing, mowing, and periodic burning, remove or adjust vegetation or soil that bees use as foraging and nesting resources (Buckles and Harmon-Threatt 2019). An immediate effect of mowing is that bees may be killed directly, in their hibernacula, nests, or even on flowers; indirect effects include removal or alteration of nesting and foraging resources (Buri *et al.* 2014; Johansen *et al.* 2019; del Toro and Ribbos 2020). However, in the longer term, mowing can also encourage woody plant growth and floral production of pollen and nectar, increasing both nesting and foraging resources, resulting in increased bee abundance (Lerman *et al.* 2018; Johansen *et al.* 2019). Bee responses to localized disturbances like mowing may vary, depending on the timing and magnitude of the disturbance, but also in ways that reflect the particular traits of the bees themselves (Rutgers-Kelly and Richards 2013; van Klink *et al.* 2019). For instance, when mowing removes above-ground vegetation, above-ground nesters are more likely to be negatively affected than those nesting below-ground, because of the destruction of their nesting substrate (Spiesman *et al.* 2019). Mowing or burning may also adjust the distance between nest sites and foraging sites. Since small-bodied species tend to fly short distances to forage, they may be more severely affected by removal of nesting resources than are large-bodied species that can fly longer distances (Greenleaf *et al.* 2007; Bommarco *et al.* 2010). Similarly, when plowing disturbs the soil, ground-nesting bees with very deep burrows are likely to survive, whereas those in shallow burrows are likely to be killed (Ullmann *et al.* 2016).

The bee fauna of the Niagara Peninsula of southern Ontario, Canada, comprises at least 160 species from five families (Richards *et al.* 2011; Onuferko *et al.* 2015). Most Niagara bees are foraging generalists, gathering pollen and nectar from an array of floral species that are abundant in open habitats across the region (Richards *et al.* 2011). In contrast to their generalist foraging habits, Niagara's bee assemblage includes multiple specialized nesting guilds that use different nesting substrates, materials, and locations. The most abundant group in the region are the sweat bees (Halictidae), almost all of which are ground-nesters (Richards *et al.* 2011). Also very abundant in Niagara are the small carpenter bees (*Ceratina* Latreille, Apidae), which construct nests in woody stems and twigs of shrubs such as raspberry (*Rubus* L.), teasel (*Dipsacus fullonum* L.), and sumac (*Rhus typhina* L.) (Rehan and Richards 2010, Vickruck and Richards 2012). Masked bees (*Hylaeus* Fabricius, Colletidae), mason bees (*Osmia* Panzer, Megachilidae) and leafcutter bees (*Megachile* Latreille, Megachilidae) are also very abundant. These do not construct their own burrows,

but seek out holes and crevices, including burrows abandoned by other species, such as *Ceratina*. Another common megachilid is the mason bee *Osmia conjuncta* Cresson, which nests in the empty shells of land snails (Richards *et al.* 2011).

The diversity of nesting habits among Niagara bees suggests that the consequences of landscape alterations should differ among bee species. In this study, we investigated this hypothesis by taking advantage of an acute anthropogenic disturbance conducted by landscape managers at one of our research sites on the campus of Brock University in St. Catharines, Ontario. In the early spring of 2017, an undisturbed meadow site, Brock South, was ‘bush-hogged’, mowed with heavy machinery, removing all vegetation to a height of a few centimetres above ground level. The purpose of the mowing was to remove tall, woody perennials, shrubs and small trees in preparation for a site survey presaging future construction of a stadium in 2020. The mowing was repeated in the springs of 2018 and 2019. After the mowing, flowering plants were left to grow throughout the spring, summer, and fall. We predicted that the main effect of mowing was the removal of nesting substrate rather than nutritional resources, which in turn should lead to a significant decline in the abundance of bees that use woody stems and twigs as nesting substrates, especially the carpenter (e.g. *Ceratina*) and cavity-nesting guilds (e.g. *Hylaeus* and *Megachile*). We also predicted that the use of heavy machinery for mowing would increase the amount of bare soil surface in the field, thus increasing nesting resources for ground-nesting bee species (e.g. *Lasioglossum* Curtis and *Halictus* Latreille).

We used two approaches to examine the effects of mowing on the bee assemblage at the Brock South site. Ideally, to assess the effects of mowing on bee abundance and diversity, we would compare replicated mowed and unmowed sites, before and after mowing. However, this was not possible, given that the mowing of our research site was not discovered until after the fact. We elected to treat this as an opportunity for a case study of the consequences for the local bee community, of a relatively small, localized disturbance that clearly had removed above-ground nesting habitat in the form of woody shrubs and herbaceous stems. We devised two approaches to address the limitations imposed by this unplanned, “natural” experiment. First, in 2018 and 2019, we carried out biweekly pan trap sampling of the bee assemblages of the mowed site, Brock South, and an adjacent, unmowed site, Brock Southwest. These comparisons demonstrated that both bee abundance and diversity were lower in mowed Brock South than in unmowed Brock Southwest. Second, we used comparisons with nearby control sites to assess the likelihood that bee abundance in Brock South was lower after mowing than before, based on the premise that in the absence of mowing, overall bee abundance trends should have been similar across sites.

Materials and methods

Field sites and pan-trapping methods

The focal sites for this study were two adjacent meadows on the southern edge of the Brock University campus in St. Catharines, Ontario (43°6′45” N 79°14′46” W, Figs. 1, 2). At least from 2003 to 2017, neither meadow had been mowed. From 2003–2013, the easternmost of the two sites, Brock South, was monitored as part of a long-term study

(Richards *et al.* 2011, Onuferko *et al.* 2018). From 2014 to 2016, Brock South was used for studying the nesting biology of small carpenter bees, *Ceratina*, as the abundance of woody shrubs in this site provided a reliable source of nesting material. On an unknown date in April 2017, the Brock South site was mowed to a grass height of 15 cm and “bush-hogged” to remove woody shrubs and small trees. The site was mowed again on 23 March 2018 (Fig. 2) and on 27 March 2019. After the initial mowing in each year, vegetation was left undisturbed and allowed to regrow.

The Brock Southwest site was directly west of and adjacent to Brock South but was not mowed, and no heavy machinery has been used there in recent years. Brock Southwest contained woody vegetation similar to that in Brock South before the mowing. It was separated from Brock South and protected by a dense hedgerow of trees and shrubs about 14 m wide (Fig. 1). The edges of both sites consisted of dense treeline with forest and a small lake to the south and west and playing fields and parking lots to the north and east. Using the surrounding hedgerows for measurements, the dimensions of Brock South were 233 m × 145 m (3.1 ha) and of Brock Southwest were 271 m × 92 m (2.3 ha) (measured using <https://maps.niagararegion.ca/Navigator/>, accessed December 2020).



FIGURE 1: Satellite images of the unmowed Brock Southwest (BrSW) and mowed Brock South (BrS) sites on the campus of Brock University in St. Catharines in July 2019. The arrow points north. The effects of mowing on BrS are clear in the greater extent of open grassy areas. Using the surrounding hedgerows for measurements, the dimensions of BrS were 233 m × 145 m (3.1 ha) and of BrSW were 271 m × 92 m (2.3 ha). The BrS site had been mowed three times prior to when this photo was taken. Photo was obtained from Google Maps (<https://www.google.ca/maps/@43.1122643,-79.2481538,911m/data=!3m1!1e3!5m1!1e4>).

Pan trapping was used to assess bee population abundance and diversity in both Brock South and Brock Southwest. Pan trapping was carried out simultaneously in both sites using the methods outlined in Richards *et al.* (2013). To summarize, pan traps were 170 g Solo brand PS6- 0099 plastic bowls (Solo Cup Company, Lake Forest, IL, USA) filled with water and a small amount of soap to act as a surfactant. Thirty traps were placed on the ground every 3 m in alternating colours (white, yellow, and blue) along a straight transect, 87 metres long. Transects were placed in different areas of each site to get a better representation of the bee assemblage within each field. Traps were placed before 0900 h and collected between 1600 and 1700 h. Trapping was done only on days without rain to ensure bees were actively foraging. Simultaneous pan trapping was carried out approximately biweekly (depending on weather) in both sites from May to September on sunny days without rain. Sampling began in spring with dry, sunny weather, and daily temperatures that reached about 15 °C or more. In late summer, sampling ended when no bees were captured in the traps.

Additional field sites

Since neither Brock South nor Brock Southwest was surveyed prior to the mowing events, we could not examine bee abundance before and after mowing in these two sites. Instead, we compared the Brock South and Brock Southwest sites to three undisturbed sites (Esc, Pon, and Summit) at the Glenridge Quarry Naturalization Site (GQNS), about 900 m away (straight-line distance), based on the premise that environmental conditions at GQNS



FIGURE 2: Ground-level photos of Brock South (BrS) and Brock Southwest (BrSW) in April 2018. All shrubs and woody vegetation had been removed from BrS and the grass was cut short.

should be very similar to those south of the Brock campus. All three GQNS sites were grassy meadows, and Esc and Pon were described previously (Rutgers-Kelly and Richards 2013, Onuferko *et al.* 2018). The Summit site (43°7'19" N 79°14'10" W) was first used in 2015 and is located at the top of the central hill in the middle of the GQNS. Pan trapping methods at the GQNS were essentially identical to those used at Brock South and Brock Southwest, with approximately biweekly surveys, usually from May to September (Table 1; Rutgers-Kelly and Richards 2013, Onuferko *et al.* 2018).

Bee identification

Bees trapped in 2018 and 2019 were stored in 70% ethanol, then pinned and labelled with the site location, date, and trapping method. Bees were identified to species using the following taxonomic keys: Mitchell 1960, Packer *et al.* 2007, Rehan and Richards 2008, Gibbs 2010, Gibbs 2011, Gibbs *et al.* 2013, Sheffield *et al.* 2011a, Sheffield *et al.* 2011b, and online, multi-chotomous keys at discoverlife.org (Ascher and Pickering 2020). *Andrena* Fabricius were identified only to genus due to difficulties with identification. *Hylaeus affinis* (Smith) and *H. modestus* Say, *Ceratina mikmaqi* Rehan and Sheffield and *C. dupla* Say, and bidentate species of *Nomada* Scopoli were combined into three morphospecies, respectively. Nine specimens were damaged and identified only to genus; these were not included in counts of morphospecies richness. Initial specimen sorting to morphospecies was carried out by the first author (TA) and all specimens were identified to species by the second author (NR), with confirmations for a subset of difficult groups such as *Lasioglossum* subgenus *Dialictus* Robertson by Dr. Thomas Onuferko. All specimens are currently stored in the collection of the Brock Bee Lab at Brock University in St. Catharines. Nesting guild information was obtained from Cane *et al.* (2007) and Onuferko *et al.* (2015).

Data analysis

Week numbers were assigned using the WEEKNUM function in Excel, setting the last week of April to week 1. Statistical analyses were carried out in R, version 3.6.3, running under the R-Studio shell, version 1.0.143 (RStudio Team 2020).

In week 3 of 2019, we could not collect bees from the Brock South site due to construction activity, so we excluded week 3 from all analyses. All remaining collections in Brock South (BrS) and Brock Southwest (BrSW) in 2018 and 2019 were done simultaneously, allowing direct comparisons of bee abundance, measured as the number of bees caught per biweekly collection (a collection is the entire set of bees caught in 30 traps over the course of one day). We used a general linear model of the form Abundance = Site + Week * Year (where * denotes an interaction term) to compare Brock South and Brock Southwest, because bee abundance and community composition are known to change significantly from week to week due to differences in phenology among local families and guilds (Onuferko *et al.* 2018). Because sample size is itself a cause of apparent differences in the species richness of two samples (Richardson and Richards 2008), we used rarefaction curves as implemented in the R *vegan* package, *rarecast* function, to compare species richness in 2018, 2019, and both years pooled. Rarefaction methods generate different-sized, random subsamples of a dataset, and count the number of species or morphospecies in each sample. Guild composition of the bee assemblages in Brock South and Brock Southwest was compared in terms of the relative proportions of bees in each guild category, using χ^2 tests of homogeneity.

TABLE 1. Numbers of pan trapping collections that captured at least one specimen at all research sites used in this study, 2008–2019. There was no trapping at these sites in 2014 or 2016. BrS was mowed in 2017, 2018, and 2019 while all other sites were undisturbed (indicated by *M*). Esc, Pon, and Summit are three long-term monitoring sites undisturbed since 2003. All sites were pan trapped with identical methods and schedules. Within a year, the numbers of collections varied slightly due to inclement weather or because construction schedules prevented trapping.

Year	Sampling dates	Site				
		BrS (mowed)	BrSW (unmowed)	Esc (control)	Pon (control)	Summit (control)
2008	22 Apr. – 24 Sep.	22			18	
2009	5 May – 29 Sep.	18		18	16	
2010	21 Apr. – 30 Aug.			8		
2011	25 May – 8 Oct.	10		10	10	
2012	22 Mar. – 20 Sep.	12		10	11	
2013	1 May – 2 Oct.	12		13	11	
2015	18 May – 4 Sep.			9	9	9
2017	10 May – 26 Sep.	(<i>M</i>)		10		10
2018	8 May – 28 Sep.	11 (<i>M</i>)	11	10		
2019	6 May – 13 Sep.	8 (<i>M</i>)	9		8	8

To assess temporal change in bee abundance at the control sites near Brock South, we analysed pan trap abundance at the three control sites during two time phases, “Before” (2008 to 2017) and “After” (2018 to 2019). Demographic patterns may vary among bee families and since collecting effort varied among sites and years (Table 1), we calculated the average annual number of bees of each family per collection (total number of bees collected at a site each year / number of collections in that same site each year). This generated a matrix of estimated bee abundance for each family (5 columns) for each of 18 site-by-year combinations (18 rows). This matrix was then analysed using permutational multivariate analysis of variance (permanova), as implemented in the R *vegan* package (version 2.5-6), employing a model of the form [Abundance matrix] = Phase, with Site as a random factor.

Results

Effects of mowing, 2018 and 2019

Table 2 presents the complete list of bee species collected via pan traps in the mowed Brock South and unmowed Brock Southwest sites in 2018 and 2019. Most species collected had been previously identified in the region (Onuferko *et al.* 2015), but the megachilid, *Osmia bucephala*, represents a new record for Niagara.

TABLE 2. Complete list of bee species and morphospecies collected in the mowed BrS and unmowed BrSW sites in 2018 and 2019 (excluding week 3 of 2019). The three *Lasioglossum* subgenera are *Lasioglossum* (*La.*), *Leuchalictus* (*Le.*), and *Dialictus* (*D.*). Species marked with an asterisk (*) were unidentifiable due to damage. SR = morphospecies richness. Nesting guilds are as follows: Ground = digs underground burrows, Cavity = nests in pre-existing cavities, Carpenter = excavates nests from pith within stems or in wood (or in oak-apple galls, as is the case with *O. simillima*), Parasite = lays eggs in nests of other bee species, Rotting wood = nests under the bark or inside of rotting stumps, Snail shell = nests in the empty shells of land snails.

Family and species	BrS (mowed)		BrSW (unmowed)		Nesting guild
	2018	2019	2018	2019	
Andrenidae					
<i>Andrena cressonii</i> Robertson	1	0	1	0	Ground
<i>Andrena</i> sp.	2	0	6	2	Ground
Family abundance (SR)	3 (2)	0 (0)	7 (2)	2 (1)	
Apidae					
<i>Apis mellifera</i> Linnaeus	0	5	0	12	Cavity
<i>Bombus borealis</i> Kirby	0	0	1	0	Ground
<i>Bombus griseocollis</i> (DeGeer)	1	0	0	0	Ground
<i>Bombus impatiens</i> Cresson	1	0	2	0	Ground
<i>Bombus rufocinctus</i> Cresson	3	1	4	0	Ground
<i>Ceratina calcarata</i> Robertson	17	9	46	42	Carpenter
<i>Ceratina dupla/mikmaqi</i>	27	30	54	68	Carpenter
<i>Melissodes druriella</i> (Kirby)	0	0	1	2	Ground
<i>Nomada denticulata</i> Robertson	0	0	0	1	Parasite
<i>Xylocopa virginica</i> (Linnaeus)	0	0	1	0	Carpenter
Family abundance (SR)	50 (5)	45 (4)	111 (7)	125 (5)	
Colletidae					
<i>Hylaeus affinis/modestus</i>	16	14	20	20	Cavity
<i>Hylaeus annulatus</i> (Linnaeus)	2	0	1	7	Cavity
<i>Hylaeus hyalinatus</i> Smith	0	0	1	0	Cavity
<i>Hylaeus illinoisensis</i> (Robertson)	1	0	0	6	Cavity
<i>Hylaeus</i> sp.*	0	0	0	1	Cavity
Family abundance (SR)	19 (3)	14 (1)	22 (3)	34 (4)	
Halictidae					
<i>Agapostemon virescens</i> (Fabricius)	2	0	5	1	Ground
<i>Augochlora pura</i> (Say)	0	0	1	1	Rotting wood
<i>Augochlora aurata</i> (Smith)	58	60	76	36	Ground
<i>Halictus confusus</i> Smith	8	11	19	32	Ground
<i>Halictus ligatus</i> Say	50	50	111	79	Ground
<i>Halictus rubicundus</i> (Christ)	2	1	4	0	Ground
<i>Lasioglossum</i> (<i>La.</i>) <i>coriaceum</i> (Smith)	0	0	0	1	Ground
<i>Lasioglossum</i> (<i>D.</i>) <i>cressonii</i> (Robertson)	0	0	0	1	Ground
<i>Lasioglossum</i> (<i>Le.</i>) <i>leucozonium</i> (Schrank)	4	3	2	4	Ground
<i>Lasioglossum</i> (<i>D.</i>) <i>admirandum</i> (Sandhouse)	7	4	0	0	Ground

TABLE 2 continued...

<i>Lasioglossum (D.) atwoodi</i> Gibbs	4	3	5	3	Ground
<i>Lasioglossum (D.) hitchensi</i> Gibbs	56	9	11	14	Ground
<i>Lasioglossum (D.) lineatulum</i> Crawford	0	0	0	1	Ground
<i>Lasioglossum (D.) nymphaearum</i> (Robertson)	2	9	1	2	Ground
<i>Lasioglossum (D.) oblongum</i> (Lovell)	0	0	0	1	Ground
<i>Lasioglossum (D.) versatum</i> (Robertson)	9	13	11	25	Ground
<i>Lasioglossum (Le.) zonulum</i> (Smith)	1	0	0	0	Ground
<i>Lasioglossum (D.)</i> sp.*	4	0	4	0	Ground
Family abundance (SR)	207 (12)	163 (10)	250 (11)	201 (14)	
Megachilidae					
<i>Anthidium manicatum</i> (Linnaeus)	0	1	3	2	Cavity
<i>Anthidium oblongatum</i> (Illiger)	0	0	12	3	Cavity
<i>Hoplitis pilosifrons</i> (Cresson)	1	2	1	3	Cavity
<i>Hoplitis producta</i> (Cresson)	0	3	1	5	Cavity
<i>Hoplitis spoliata</i> (Provancher)	1	1	1	1	Cavity
<i>Megachile brevis</i> Say	3	5	5	0	Cavity
<i>Megachile campanulae</i> Robertson	0	0	0	2	Cavity
<i>Megachile centuncularis</i> (Linnaeus)	0	1	0	0	Cavity
<i>Megachile ericetorum</i> Lepeletier	1	0	1	0	Cavity
<i>Megachile gemula</i> Cresson	0	0	1	0	Ground
<i>Megachile latimanus</i> Say	1	0	0	0	Ground
<i>Megachile relativa</i> Cresson	1	0	4	2	Cavity
<i>Megachile rotundata</i> (Fabricius)	0	1	1	0	Cavity
<i>Osmia atriventris</i> Cresson	1	2	6	2	Cavity
<i>Osmia bucephala</i> Cresson	4	0	11	0	Cavity
<i>Osmia conjuncta</i> Cresson	68	5	49	6	Snail Shell
<i>Osmia pumila</i> Cresson	3	1	15	3	Cavity
<i>Osmia simillima</i> Smith	1	0	0	0	Carpenter
<i>Stelis lateralis</i> Cresson	0	0	0	1	Parasite
Family abundance (SR)	85 (11)	22 (10)	111 (14)	30 (11)	
Total abundance (SR)	364 (33)	244 (25)	501 (37)	390 (34)	

Overall, biweekly bee abundance was lower in mowed Brock South than in unmowed Brock Southwest, particularly in the latter half of the summer (Fig. 3), and the difference between sites was highly significant and consistent between years (Table 3). Not only was bee abundance lower in mowed Brock South, but bee diversity, measured as morphospecies richness, was also lower. In 2018, mowed Brock South yielded 33 species, while unmowed Brock Southwest had 37. In 2019, mowed Brock South had 25 species, while unmowed Brock Southwest had 34. Thus, the divergence in species richness between mowed and unmowed sites seems to have increased over time. This is further illustrated in the rarefaction curves (Fig. 4), which show that the lower morphospecies richness in mowed Brock South was not simply due to lower bee abundance there. These comparisons suggest that spring mowing led to a decrease in both abundance and diversity of the bee assemblage in Brock South.

Comparisons between mowed Brock South and unmowed Brock Southwest also

revealed differences in community composition (Table 4). Most noticeable was the lower relative abundance in Brock South of carpenters and cavity-nesters, contrasting with the higher abundance of ground-nesters, changes that were predicted due to changes in nesting substrate availability for these two guilds. Also of note, snail shell-nesters, represented by the very abundant species, *Osmia conjuncta*, were proportionately twice as abundant in mowed Brock South as in unmowed Brock Southwest in 2018 (the omission of week 3 from 2019, prevented comparison in 2019, since most *O. conjuncta* are found in early May).

Abundance trends before and after 2018

Average annual abundance of each of the five bee families before (2008 to 2017) and after mowing (2018 to 2019) is compared in Fig. 5. In the undisturbed control sites, bee abundance was significantly higher in 2018 and 2019 than in the preceding years (permanova, $R^2 = 0.247$, $F_{1,16} = 5.253$, $P = 0.006$). This suggests that in the absence of disturbance, bee abundance in mowed Brock South should also have been higher in 2018 and 2019 than in previous years, but the abundance of bees in each of the five families was not significantly different in 2018 and 2019 than in previous sampling years (Permanova, $R^2 = 0.061$, $F_{1,5} = 0.327$, $P = 0.86$). That bee abundance in the mowed Brock South site failed to increase in 2018 and 2019, is consistent with the hypothesis that bee abundance was lower after mowing than it would have been without mowing.

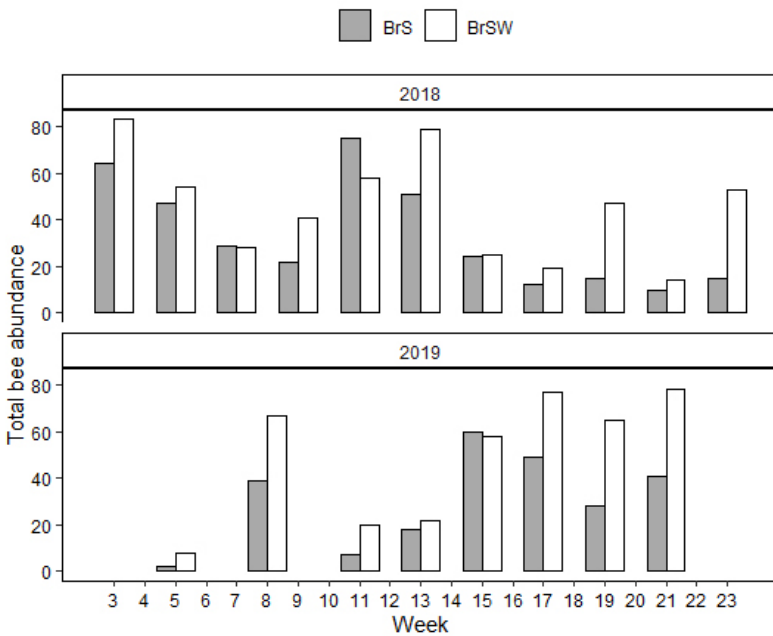


FIGURE 3: Comparison of bee abundance in paired pan trap collections at BrS and BrSW in 2018 and 2019. Note that in week 3 of 2019, only the BrSW site was sampled, so these data were omitted from the comparison.

TABLE 3. Results for general linear model analysing variation in bee abundance (total number of bees per collection) in BrS and BrSW in 2018 and 2019. The Site term indicates significantly higher bee abundance in BrSW than in BrS. Differences among weeks are due to differences in bee phenology over time. There was no significant effect of Year (2018 vs. 2019), although there was a significant interaction between Week and Year (see Fig. 3).

Source	Degrees of freedom	F value	P (>F)
Site	1	21.86	0.0002
Week	11	4.09	0.0042
Year	1	1.57	0.226
Week * Year interaction	6	24.53	<0.0001
Residuals	18		

This case study suggests that even limited disturbance, mowing a single field once per year in early spring, was enough to influence the abundance and composition of the bee assemblage foraging and nesting in that field. Overall, the mowed site (Brock South) had lower bee abundance and diversity than the unmowed site, suggesting that mowing exerted a negative impact through loss of nesting substrate or food resources (or both). In fact, the observed differences between the mowed and unmowed sites may underestimate the differences between them. The two sites were adjacent fields about three hectares in area, which suggests that the bee assemblages in these two fields were spatially differentiated on a scale of only ten to hundreds of metres. This in turn implies that the bees foraging and nesting in these fields might be responding to nesting and nutritional resources at quite a small spatial scale. This seems especially likely for small-bodied bees like *Ceratina* or *Lasioglossum (Dialictus)*, which likely have short, breeding dispersal distances from their natal nests and short commutes from their nests to foraging sites (Greenleaf *et al.* 2007). Moreover, the unmowed and mowed sites were separated by a thick hedgerow, which remained undisturbed by mowing and could have provided considerable bee nesting habitat, especially for carpenters and cavity-nesters. These bees could have foraged in either the mowed or unmowed fields, which would have obscured differences in bee abundance between fields. One reason for moving the pan trap transects around the sites was to avoid systematic spatial errors that might be associated with over-collecting bees with very short foraging distances (Greenleaf *et al.* 2007). Taken together, these considerations suggest that the significant differences detected here likely underestimate the differences in bee assemblages between the two sites.

Differences between the mowed and unmowed sites in the proportional representation of the different nesting guilds suggest trait-specific responses of bees to disturbance (Klink *et al.* 2019). Mowing certainly reduced the availability of nesting substrate for the carpenter and cavity-nester guilds and likely also altered access to nesting substrate for ground nesters and possibly snail shell nesters. At the same time, the mowed site had proportionately more ground-nesters than the unmowed site. If mowing had directly increased the availability of open soil surface for ground-nesters, attracting more ground-

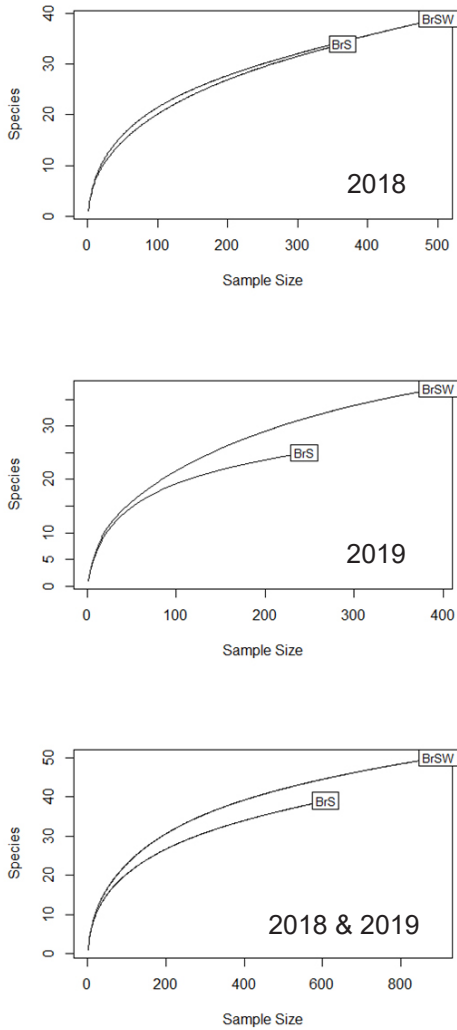


FIGURE 4: Rarefaction curves comparing the number of species expected in subsamples of pan trap collections from mowed BrS versus unmowed BrSW, in 2018, 2019, and in both years pooled.

nesters like *Lasioglossum* into the Brock South area, then we would have expected an increase in their absolute numbers, not just an increase in relative abundance. It seems most likely that removal of above-ground nesting substrate was the main reason for the decline in the carpenter and cavity-nesting guilds, creating an apparent increase in the proportion of ground nesters. One difference not predicted between mowed and unmowed sites was the higher proportion of snail-shell nesters (*Osmia conjuncta*) in the mowed site in 2018. It is possible that mowing reduced the vegetational cover for snails, exposing them to higher mortality risk due to high temperature exposure and desiccation risk, and thus increasing the availability of shells for *O. conjuncta* to nest in.

The higher bee abundance in the control sites in 2018 and 2019 suggests that in the absence of disturbance, local bee populations were generally on the increase. However, these increases at nearby sites were not matched by an increase in bee abundance at the mowed site, Brock South. This provides additional evidence that after mowing, bee abundance was lower in Brock South than it would have been if the site had not been mowed. Exactly why abundance declined is unclear, but either mortality or migration could have played a part. Many carpenter and cavity-nesting bees that were in nests or hibernacula during the early spring mowing of 2017 likely died as a direct result of being crushed during mowing operations. Survivors could have moved to nearby fields and meadows with appropriate nesting substrate, including Brock Southwest, since the maximum distance from Brock South to neighbouring areas was just a

TABLE 4. Nesting guild abundance in BrS (mowed) and BrSW (unmowed) sites in 2018 and 2019. For each guild, numbers represent the number of specimens collected, and percentages represent proportional representation at each site. The data for the parasite and rotting wood guilds were excluded from the chi-square tests because of small sample sizes.

Nesting guild	2018		2019	
	BrS	BrSW	BrS	BrSW
Carpenter	45 (12.4%)	101 (20.3%)	39 (16.0%)	110 (28.1%)
Cavity	34 (9.4%)	83 (16.7%)	36 (14.8%)	69 (17.6%)
Ground	216 (59.5%)	265 (53.2%)	164 (67.2%)	207 (52.8%)
Snail shells	68 (18.7%)	49 (9.8%)	5 (2.0%)	6 (1.5%)
χ^2 test, df = 3	29.639, $P < 0.0001$		15.688, $P = 0.0013$	

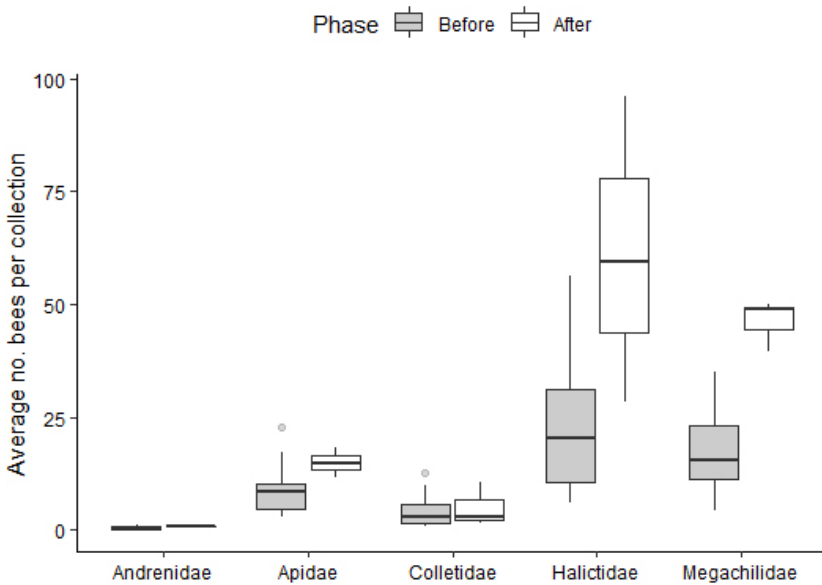


FIGURE 5: Changes in the average abundance of each bee family at three control sites during the two time phases before (2008 to 2017, grey) and after (2018 and 2019, white) mowing at the BrS site. See Table 1 for annual pan trapping schedules at the control sites.

little more than 233 m. Moreover, after mowing, the Brock South site would probably not have attracted as many carpenters or cavity-nesters, given the lack of nesting substrate. The lower absolute abundance of this guild in mowed Brock South compared to unmowed Brock Southwest, was therefore most likely due to a combination of mortality due to mowing and lack of nesting resources to attract immigrants. If mowing also decreased floral abundance in Brock South, then this is another reason that fewer foragers would have been attracted to the site.

The lower absolute abundance of ground nesters in Brock South is harder to explain than the lower abundance of carpenters and cavity-nesters. It is possible that mowing did not improve access to bare soil patches, or that the movement of heavy equipment may have compacted the soil, making it less suitable for sweat bees and other ground nesters (Buckles and Harmon-Threatt 2019). If as suggested above, mowing actually decreased floral abundance, then there would have been fewer foragers in the mowed site and thus fewer bees caught in pan traps.

Conclusion

Whether mowing killed bees directly or induced them to move elsewhere, this case study demonstrates that bee populations may respond negatively to relatively low levels of disturbance, and that this response is detectable at a small spatial scale. Conversely, previous studies of bee abundance and diversity in Niagara have demonstrated positive responses of bee populations to habitat restoration; after extremely severe disturbances that eradicated local bee populations for decades, habitat restoration at the Glenridge Quarry Naturalization Site resulted in rapid and sustained recovery of bee abundance and diversity within only three to five years (Rutgers-Kelly and Richards 2013; Onuferko *et al.* 2018). It appears that bee populations respond rapidly to changes in the availability of critical resources (Tscharntke *et al.* 1998; Winfree *et al.* 2009; Spiesman *et al.* 2019), suggesting considerable variability in bee abundance and diversity at spatial and temporal scales both small and large.

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