Bee (Apoidea) community response to perennial grass treatments managed for livestock production and conservation

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ABSTRACT

Most grasslands world-wide have been converted into various row crops for agriculture and pasture for livestock foraging. This conversion has likely disrupted arthropod communities, including pollinating bee communities. Pollinating native bees have been in decline in recent decades and much of this decline has been attributed to intensive agricultural practices. Native warm-season grasses have been promoted as alternatives to non-native grasses [e.g., bermudagrass (*Cynodon dactylon*)] in beef production systems. Reestablishing native grasses may provide an opportunity for land-sharing where agricultural production can enable conservation practices that potentially enhance bee biodiversity. Therefore, agricultural practices such as growing native perennial grasses for livestock forage that may minimize pollinating bee community disruption should be considered. We used colored pan traps to collect bees in four treatments of perennial grass plantings associated with operational livestock pastures during 2011−2012. The four treatments were: (1) mix of Bermuda and tall fescue (*Schedonorus arundinaceus*) grass grazed with cattle; (2) monocultures of Indiangrass (*Sorghastrum nutans*) grazed with cattle; (3) native grass polyculture [(Indiangrass, little bluestem (*Schizachyrium scoparium*), and big bluestem (*Andropogon gerardii*)] grazed with cattle; and (4) native grass polyculture without cattle. We generally documented greater abundances and richness of bees in native grass treatments compared to exotic grass treatments; however, treatment-level differences were bee genera- or species-dependent. Lack of grazing in the native grass mixture treatment did result in higher bee abundance and taxa richness compared to the native grass mixture treatment with cattle. Our results support the conception that perennial native grasses have the potential to attract numerous, beneficial bee species and may provide some pollen rewards and suitable nesting substrate for bees. Therefore, using native perennial grasses as livestock forage may be a more ecologically friendly surrogate to non-native forage used for livestock production to promote pollination services and native bee diversity in agricultural lands.

1. Introduction

Conversion of natural environments to agricultural land causes biodiversity loss and may be deleterious to conservation efforts (Donald, 2004; Wright et al., 2012). To simultaneously alleviate biodiversity loss and utilize land for agricultural practices, many land managers use land-sparing or land-sharing practices (also known as wildlife-friendly farming). Land-sparing practices are designed to maximize agriculture in one area in order to avoid further conversion of natural habitat in other areas, whereas land-sharing attempts to maintain biodiversity within agricultural landscapes by employing farming techniques that are less intensive compared to standard agricultural practices (Phalan et al., 2011). Although both practices employ different philosophies for conservation measures, they both are based on trade-offs between agriculture and conservation (Phalan et al., 2011). However, whether these techniques are truly effective for alleviating biodiversity loss is debatable (Kleijn et al., 2011) and may also cause loss of agricultural productivity (Kaphengst et al., 2011). Concerns over land-sharing and

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land-sparing techniques also exist for temperate grassland ecosystems (Egan and Mortensen, 2012; Wright and Wimberly, 2013).

Temperate grasslands are considered one of the most endangered biomes globally (Hoekstra et al., 2005). For example, much of the Great Plains region of the United States has been converted to cropland (Olimb et al., 2017). Similar habitat destruction and land conversion are occurring in grasslands and savannas worldwide in order to provide food and fuel for the increasing human population (Henwood, 1998; Murphy et al., 2016). The Black Belt region of the southeastern United States, originally named for the color of its fertile soil, is a crescent shaped area running from southern Tennessee through the eastern portion of Mississippi into middle Alabama (Washington, 1901; Webster and Sampson, 1992). Historically, the open prairie of the Black Belt was dominated by native prairie grasses that also are found within the Great Plains but, like the Great Plains, most of this region has been converted to agriculture and pasture for livestock production (Barone, 2005). Additionally, exotic grasses and other non-native plants have invaded many of these degraded prairie habitats creating drastically different successional habitat compared to intact native prairie (Kulmatiski, 2006; Tognetti and Chaneton, 2012)

Utilizing native perennial grasses in agricultural operations has several ecological benefits, such as the following: (1) limited soil erosion (Liebig et al., 2006); (2) decreased water usage (Mclaughlin and Kszos, 2005); (3) reduced greenhouse gas emissions (Hudiburg et al., 2016); (3) decreased usage of pesticides and herbicides (Tilman et al., 2006); and (4) maintained and potentially improved wildlife habitat (Robertson et al., 2012). Additionally, utilizing native perennial grasses instead of exotic grasses [e.g., bermudagrass (*Cynodon dactylon*)] can also provide some positive ecological and economic benefits (Monroe et al., 2016, 2017a).

The vast majority of angiosperms are dependent on insect pollination services (Ollerton et al., 2011). Further, approximately 75 % of the main global food crops depend on insects for pollination services (Klein et al., 2007). Unfortunately, pollinators are in decline for numerous reasons, including increased pesticide use, deleterious agricultural practices (e. g., tilling, native habitat conversion), habitat fragmentation, invasive species colonization, spread of pathogens, urbanization, and climate change (Potts et al., 2010; Abbate et al., 2019). Koh et al. (2016) modeled wild bee abundance across the United States and found an average decline of 23 % in wild bee abundance between 2008 and 2013; the majority of this decline was attributed to habitat conversion to row crops. Many intensive agricultural practices (e.g., plowing, planting monocultures, etc.) are considered harmful to pollinator communities because they destroy native bee nesting sites and provide few pollen/-nectar rewards. For example, monocultures of corn have been shown to harbor lower abundances and richness of bees compared to other grasses (Gardiner et al., 2010). Large-scale agricultural monocultures usually involve removing surrounding native vegetation, thus limiting plant and pollinator diversity in field borders. Compared to annual plants like corn, planting native perennial grasses limits disruption of soil communities by eliminating the need to plow before every growing season. Perennial native grasses require less fertilizer than exotic grasses, such as bermudagrass and fescue, and also provide far more benefits to wildlife than exotic grasses (Lewandowski et al., 2003; Fulbright et al., 2013).

Despite negative effects caused by some intensive agricultural practices, sound agricultural practices can minimize and potentially eliminate the disruption of pollinator communities. Although several staple crops (e.g., corn, rice, wheat) are wind pollinated and may provide few resources for pollinators, other wind-pollinated crops (e.g., perennial grasses) may provide nesting habitat and other structure for native bees and other beneficial insects. Indeed, bees are known to visit wind-pollinated grasses. For example, honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.) visited millet in Georgia, United States (Leuck and Burton, 1966); solitary bees transferred grass pollen in Australia (Clifford, 1964); stingless bees visited bambusoid grasses in

rain forests (Soderstrom and Calderón, 1971); honey bees gathered pollen from sugarcane and corn in South Africa (Anderson et al., 1983). Wind-pollinated grasses can augment native bee populations which, in turn, could provide pollination services for nearby crops that require insects for pollination. Morandin et al. (2007) found that canola fields with adjacent pasturelands had more foraging bumble bees than canola fields with minimal adjacent pasturelands. Native bees have been shown to be fully capable of providing necessary crop pollination services (Winfree et al., 2007), despite many farmers relying solely on the honey bee for commercial pollination services (Kennedy et al., 2013). Garibaldi et al. (2013) also noted that for many crop systems, honey bees are inefficient pollinators and that native bee visits resulted in more seed/fruit production than visits from honey bees. Due to regional honey bee population declines in many areas of the world (Potts et al., 2010), finding crops and land management practices that do not disrupt biological communities, especially native pollinators, should be a priority for conservationists, land managers, and farmers alike.

The main objective of this research was to determine if native perennial grass treatments used for grazing had relative positive or negative effects on bees compared to exotic bermudagrass and tall fescue. We hypothesized native bees would be more apt to forage within native grasses compared to non-native grasses because native grass mixtures could provide groundcover heterogeneity that might allow more sites for ground-nesting bees than in native monocultures or exotic pastures (Hopwood, 2008; Moroń et al., 2009).

2. Materials and methods

2.1. Site location and description

Our study was conducted at Mississippi State Prairie Research Unit (hereafter "Prairie site") located in the Black Belt Prairie region, Monroe County, Mississippi, USA during 2011−2012. The Black Belt is a subdivision of the East Gulf Coastal Plain physiographic province underlain by Cretaceous age Selma Chalk, which created a mosaic of soil types supporting a diversity of vegetation types, including open prairie and forested habitats (Logan, 1904; Hill et al., 2009).

For our study, three blocks (∼40 ha each) of operational cattle grazing land were broken into ∼10 ha plots in which one of the following four treatments were assigned: (1) native warm-season grass mixture with cattle (hereafter "NG-C"); (2) native warm-season grass mixture without cattle (hereafter "NG-NC"); (3) monoculture of Indiangrass with cattle (hereafter "IG-C"); and (4) exotic bermudagrass and tall fescue with cattle (hereafter "BG-C"). Native warm-season grass mixtures were composed of Indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), and big bluestem (*Andropogon gerardii* Vitman). Native grass mixtures and Indiangrass plots were established in 2008 once bermudagrass and other non-native grasses were removed with herbicide and fire. Bermudagrass plots contained bermudagrass and tall fescue (*Schedonorus arundinaceus* Schreb). Each grazed plot contained an average of 2.7 cattle per ha (2.5 ac) and was grazed from mid-May to early September in 2011 and late August in 2012. Plots were within the normal range for cattle production in the southeastern United States (United States Department of Agriculture National Agricultural Statistics Service USDA NASS, 2014). During each spring, we managed native pastures with prescribed fire (grazed and non-grazed) as recommended for native warm season grasses (Harper et al., 2015). We applied fertilizer to exotic grass pastures at twice the rate as native grass treatments (67.3 kg/ha vs. 33.6 kg/ha) following results from soil tests and best management practices for each treatment. We applied 2,4-D herbicide to all pastures (grazed and non-grazed) in early June 2012 to control for forbs and maintain consistent plot conditions. The native grass non-grazed treatment (NG-NC) served as a land-sparing treatment, whereas the bermudagrass/tall fescue treatment (BG-C) served as an intensive agricultural treatment; thus, these two treatments serve as bounds on the end of a

management intensity gradient. Therefore, the two remaining treatments (NG-C and IG-C) act as examples of land-sharing.

2.2. Bee sampling

We captured bees using yellow, blue, and white pan traps (18-ounce Solo™ bowls). Pan traps have also been used to collect bees within switchgrass monocultures and in other wind-pollinated crops (Gardiner et al., 2010; Lee et al., 2018). Within a plot, we established three sampling stations that were spaced at least >50 m from stand edges to avoid edge effects and ≥ 50 m from the nearest sampling station to ensure independence between individual sampling stations. At each sampling station, we set one of each bowl color placed on a "rack system" that enabled pan height to be adjusted as the grasses grew (Campbell et al., 2016). To limit interference from cattle, a cattle guard (i.e., fencing with large openings so as to not hinder bee movement) was built around each pan set within the treatments containing cattle. Beginning May 2011 and June 2012, we collected pan trap samples approximately twice a month (minimum of 10-day intervals). We concluded bee sampling in October of each year. During each trapping period, pan traps were active for 72 -h intervals. A total of 20 sampling periods (8 sampling periods in 2011 and 12 in 2012) were conducted during the 2-year study. We preserved collected insect samples in a 70 % ethanol solution for future identification. All insects were identified to the lowest taxonomic level possible by JW Campbell and representative samples were also sent to S Droege (USGS Patuxent Wildlife Research Center) for confirmation of identifications.

2.3. Statistical framework and analysis

We plotted counts of all captured bee taxa and visually binned them into one of the following three abundance levels: 1) superabundant; 2) abundant; and 3) rare. We set the cutoff for inclusion of individual bee taxon in analyses at the break between abundant and rare bee groups, thereby excluding all rare bees with relatively low counts from analyses (*see* Grodsky et al., 2018a, b). For example, the cutoff between abundant and rare bees in treatments was $n = 37$ because counts of bee captures dropped from $n = 37$ to $n \leq 12$ at that point on the plot of bee counts.

We conducted Poisson generalized linear mixed models (GLMMs) with number of captured individuals for each bee taxon, each bee nesting guild, and bee taxa richness pooled across sampling periods in each plot in each pasture (e.g., treatment) and year as the dependent variable and pasture as a random effect to test response of bees to grass cover treatments [function glmer in R package lme4 (Bates et al., 2014); *see also* Campbell et al., 2019]. We first included a year × treatment interaction term, treatment, and year as explanatory variables, the log of sampling effort (i.e., number of visits) per year as an offset. If we detected a significant year × treatment interaction, we developed a model for each year separately and included treatment as an explanatory variables and pasture as a random effect. We performed likelihood ratio tests on all GLMMs to determine significant treatment effects. We conducted *post hoc* Tukey's pairwise comparisons of treatment means using general linear hypothesis testing (glht function; single-step method) in the R package multcomp (Hothorn et al., 2013). We set α = 0.05 to determine statistical significance.

3. Results

3.1. Bee abundance and richness

We captured 5454 bees composed of 22 genera and at least 44 species within our experimental treatments (Table 1). *Lasioglossum* was the most common genera, comprising 74.5 % of collected bees, followed by *Melissodes* (8.3 %) and *Augochlorella* (5.2 %). Overall bee taxa richness was higher in the NG-NC treatments compared to the NG-C and BG-C treatments (Fig. 1). IG-C treatments showed variable responses with

Table 1

List of all bees captured from four grass cover treatments from Mississippi State Research Unit ("Prairie site") during 2011-2012. NG-C = native warm-season grass mixture with cattle, NG-NC = native warm-season grass mixture without cattle, IG-C = monoculture of Indiangrass with cattle, BG-C = exotic bermudagrass and tall fescue with cattle.

		BG-C	IG-C	NG-C	NG-NC
Andrenidae	*Andrena macra*	0	1	0	1
	Perdita octomaculata	0	0	1	0
	Perdita sp.	0	6	0	0
Apidae	*Apis mellifera*	71	25	20	36
	Bombus bimaculatus	0	1	1	0
	Bombus impatiens	1	0	0	0
	Bombus griseocollis	1	0	0	1
	Bombus pensylvanicus	8	8	5	11
	Ceratina calcarata	0	2	0	0
	Ceratina dupla	6	18	2	13
	Ceratina strenua	1	8	2	5
	Melissodes bimaculata	15	31	29	90
	Melissodes boltoniae	0	0	3	1
	Melissodes comptoides	47	30	43	57
	Melissodes communis/triodis	2	0	0	0
	Melissodes tepaneca	13	10	24	22
	Melissodes wheeleri	0	1	0	0
	Melissodes spp.	6	4	9	15
	Melitoma taurea	0	1	0	1
	Svastra atripes	30	18	33	39
	Svastra obliqua	5	6	1	3
	Xylocopa virginica	1	0	3	1
Colletidae	*Hylaeus affinis*	1	0	0	0
	Hylaeus mesillae	0	1	0	0
	Hylaeus sp.	1	1	1	0
Halictidae	*Agapostemon virescens*	1	0	0	1
	Augochlora pura	17	12	6	6
	Augochlorella spp.	38	129	47	71
	Augochloropsis metallica	2	2	5	2
	Dieunomia nevadensis	0	0	0	1
	Halictus poeyi	18	34	69	46
	Halictus sp.	0	0	0	1
	Lasioglossum spp.–*including L. bruneri, L. callidum, L. mitchelli, L. pruninosum*	725	952	985	1401
	Nomia melanderi	1	1	4	1
	Sphecodes sp.	1	0	0	0
Megachilidae	*Heriades* sp.	0	0	0	1
	Megachile spp.	2	5	4	4
	Megachile albitarsis	1	0	0	0
	Megachile campanulae	0	0	0	1
	Megachile sculpturalis	1	1	0	0
	Osmia georgica	1	0	0	0
	Total Bees	1017	1308	1297	1832

generally higher abundances of bees compared to BG-C but did not differ in bee taxa richness compared to the other treatments (Fig. 1, Table 2).

Abundance of bee genera and species showed some variable treatment effects but native bees generally preferred the native grasses over exotic bermudagrass and tall fescue mix in most cases (Table 2). In 2011, overall bee abundance was different among all treatments with NG-NC harboring the most bees followed by NG-C, IG-C, and BG-C, respectively. Similarly, in 2012, NG-NC contained the highest abundance of bees with the other treatments showing variable response (Table 2). *Apis mellifera* L. (a non-native species) was the only bee species that we determined to have greater numbers within the BG-C treatments compared to some of the other treatments during the two-year experiment. We detected *Augochlorella* in higher abundances in the IG-C and NG-NC treatments compared to NG-C and BG-C treatments in 2011; in 2012, they showed greater abundances in the IG-C treatments compared to all other treatments (Table 2). *Ceratina* had greater abundances in the NG-NC and IG-C treatments compared to other NG-C treatments. *Lasioglossum* was more abundant in the NG-NC treatments compared to all other treatments for 2011 and in 2012 were more abundant in the NG-NC and IG-C treatments compared to NG-C and BG-C. Collectively,
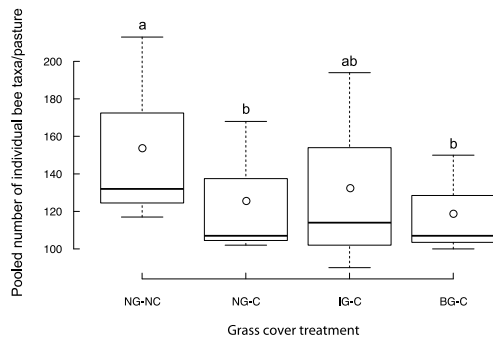
Fig. 1. Bee taxa richness pooled across plots and sampling periods in four grass cover treatments within pastures (3 replicates of 4 treatments, n = 12 pastures), Mississippi State Prairie Research Unit, 2011 and 2012. Different letters indicate significant difference of treatment means (plus signs) at α = 0.05. Box plots show medians (thick black lines), means (open circles), interquartile ranges (boxes), and minimum and maximum counts (whiskers). NG-C = native warm-season grass mixture with cattle, NG-NC = native warm-season grass mixture without cattle, IG-C = monoculture of Indiangrass with cattle, BG-C = exotic bermudagrass and tall fescue with cattle.

Melissodes was found in greater abundances in the NG-NC treatments compared to all other treatments. However, individual *Melissodes* species showed variable responses. For example, in 2012, *Melissodes bimaculata* Lepeletier was found in greater abundances in the NG-NC treatments compared to all other treatments and in the NG-C treatments compared to the BG-C and IG-C treatments, although no differences were detected in 2011. Other relatively common genera (e.g., *Bombus*) abundances did not differ for the duration of this study.

3.2. Bee guilds

Most of the bees we captured were ground-nesting bees (94.8 %), compared to wood/cavity nesting bees (2.4 %). Honey bees (2.8 %) were not included in the guild analysis. Overall, ground-nesting bee abundance was greater in the NG-NC treatments compared to the all other treatments in 2011 and both the BG-C and NG-C treatments for 2012 (Fig. 2). Wood/cavity nesting bees were more abundant in the IG-C treatments compared to the NG-C treatments but not the other treatments (Fig. 3).

4. Discussion

We compared bee communities among four treatments that represented a gradient from land sparing to a common, relatively intensive grazing system in a grassland biome. We found that sparing land for wildlife, bees in this case, generally leads to more wildlife abundance. However, the land sharing treatments generally offered greater abundances of pollinators than the more intensive beef production system. Our results, coupled with those of Monroe et al. (2016, 2017a) provide strong evidence that grazed native grass can offer an economically and ecologically sound alternative to exotic grasses.

Overall, our results are congruent with Gardiner et al. (2010) that found increased bee abundances and richness in switchgrass and mixed prairie grasses compared to corn. Additionally, moth diversity and overall insect diversity have also been found to be higher in native perennial grasses compared to non-native grasses and corn (Robertson et al., 2012; Harrison and Berenbaum, 2013). Monroe et al. (2017b) documented changes in Hemiptera and Orthoptera assemblages that were correlated with bermudagrass and fescue cover. Indeed, we chose not to use corn or any other row crop as one of our treatments due to the numerous studies showing that corn and other row crop monocultures can limit arthropod diversity compared to native grasses (e.g., Landis et al., 2008; Gardiner et al., 2010) and the inability of corn monocultures

Table 2
Mean (± SE) number of bees captured in four grass cover treatments within pastures (3 replicates of 4 treatments, n = 12 pastures), Mississippi State Prairie Research Unit, pooled across all sampling periods in 2011 and 2012, respectively. Different letters indicate significantly different pair-wise comparisons of treatment means. §Indicates significant treatment × year interaction. †Indicates significant year effect after correcting for sampling effort. We set $\alpha \leq 0.05$. [a,b]Indicates statistical difference.
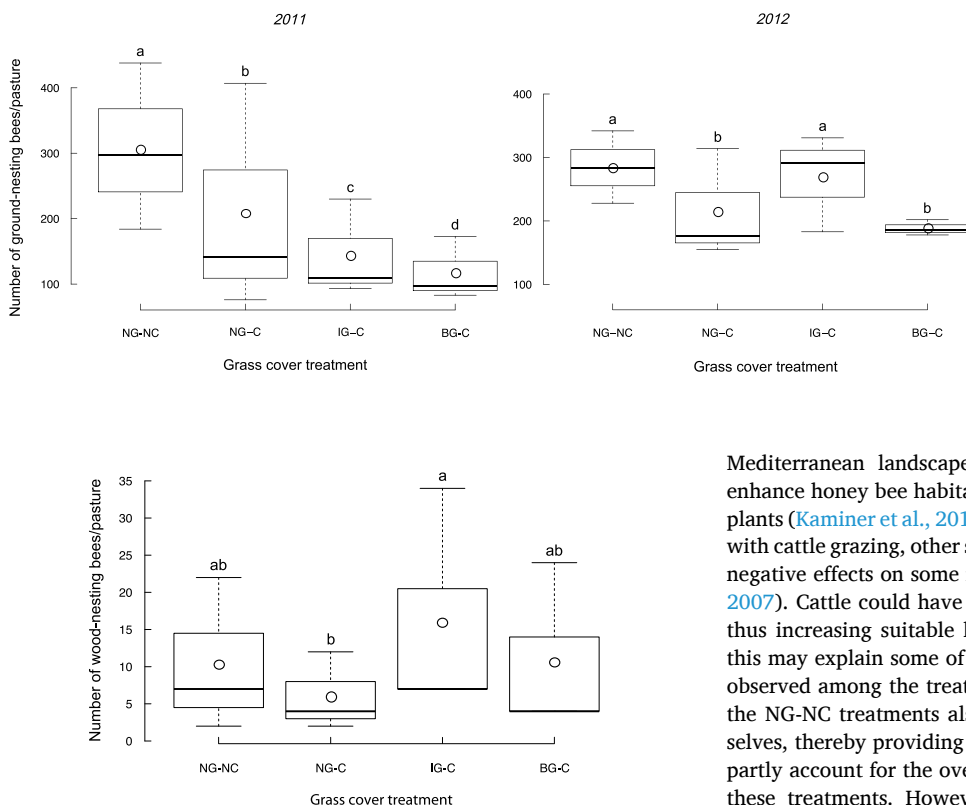
Bee taxa	LRT_TRT	PR (Chi)_TRT	NG-NC	NG-C	IG-C	BG-C
All bees§						
2011	249.03	<0.001	325.3[a] (71.0)	222.7[b] (100.9)	162.7[c] (48.7)	136.3[d] (31.1)
2012	107.85	<0.001	357.0[a] (50.3)	249.0[c] (55.7)	311.3[b] (51.3)	236.0[c] (22.5)
Apis mellifera§						
2011	18.01	<0.001	2.3[b] (1.2)	4.0[b] (3.0)	3.7[b] (0.9)	9.3[a] (3.2)
2012	33.05	<0.001	9.7[ab] (2.0)	2.7[c] (1.7)	4.7[bc] (1.2)	14.3[a] (9.8)
Augochlorella§						
2011	45.06	<0.001	14.7[a] (4.2)	7.7[b] (4.8)	21.0[a] (12.2)	4.7[b] (1.8)
2012	31.33	<0.001	9.0[b] (8.0)	8.0[b] (6.6)	22.0[a] (20.0)	8.0[b] (4.5)
Bombus	2.23	0.53	4.0 (2.1)	2.0 (0.6)	3.0 (0.6)	3.3 (0.3)
Ceratina	26.74	<0.001	6.0[ab] (5.0)	1.3[c] (0.9)	9.3[a] (6.0)	2.3[bc] (2.3)
Halictus poeyi†	32.71	<0.001	15.3[ab] (11.5)	23.0[a] (18.2)	11.3[bc] (7.8)	6.0[c] (1.0)
Lasioglossum§						
2011	267.86	<0.001	266.7[a] (64.7)	172.7[b] (83.1)	109.3[bc] (24.4)	102.3[bc] (24.8)
2012	61.87	<0.001	200.3[a] (12.8)	155.7[b] (34.5)	208.0[a] (38.6)	139.3[b] (16.8)
Melissodes	58.99	<0.001	61.7[a] (21.4)	36.0[b] (7.5)	25.7[b] (8.0)	27.7[b] (9.8)
Melissodes bimaculata§						
2011	8.68	0.03	7.3 (4.5)	2.7 (0.7)	3.3 (2.4)	2.7 (1.8)
2012	68.27	<0.001	22.7[a] (13.8)	7.0[b] (2.7)	7.0[c] (2.5)	2.3[c] (1.9)
Melissodes comptoides§						
2012	14.63	0.002	19.0[a] (8.5)	13.3[ab] (6.9)	8.0[b] (3.2)	15.0[ab] (10.5)
Melissodes tepaneca†	7.48	0.06	7.3 (3.3)	8.0 (3.1)	3.3 (1.5)	4.3 (1.5)
Svastra atripes†	8.84	0.03	13.0[a] (1.5)	11.0[ab] (6.6)	6.0[b] (1.0)	10.0[ab] (4.0)

NG-C = native warm-season grass mixture with cattle, NG-NC = native warm-season grass mixture without cattle, IG-C = monoculture of Indiangrass with cattle, BG-C = exotic bermudagrass and tall fescue with cattle; LRT_TRT= likelihood-ratio test, PR(Chi)_TRT= chi-squared test.

to support agricultural co-benefits like livestock grazing. Although we only seeded treatments with various native grasses, some forbs and other plants did colonize the plots, which allowed for some non-grass floral resources to establish themselves. However, overall forb coverage in plots was similar between years in all treatments (Monroe et al., 2017b). Despite all of the planted grasses being wind pollinated, bees will use perennial grass fields (Bennett and Isaacs, 2014). During periods of pollen production by grass species, bees may gather and use grass pollen. Indeed, native bees and honey bees have been documented gathering wind-pollinated grass pollen (Erickson and Atmowidjojo, 1997; Immelmann and Eardley, 2000).

Additionally, bees may also use livestock grass plantings for a nesting resource. Most of the bees we captured were ground-nesting bees (e.g., *Lasioglossum*, *Melissodes*). The native grass treatments provided bare ground (Monroe et al., 2017b), presumably allowing for suitable nesting structure for ground-nesting bees to develop. However, we caution that we did not quantify ground nests as our methods only allowed for the collection of foraging bees. Despite this, the majority of bees that were

Fig. 2. Number of ground-nesting bees pooled across plots and sampling periods in four grass cover treatments within pastures (3 replicates of 4 treatments, $n = 12$ pastures), Mississippi State Prairie Research Unit, in 2011 and 2012, respectively. Different letters indicate significant difference of treatment means (plus signs) at $\alpha = 0.05$. Box plots show medians (thick black lines), means (open circles), interquartile ranges (boxes), and minimum and maximum counts (whiskers). NG-C = native warm-season grass mixture with cattle, NG-NC = native warm-season grass mixture without cattle, IG-C = monoculture of Indiangrass with cattle, BG-C = exotic bermudagrass and tall fescue with cattle.

Fig. 3. Number of wood-nesting bees pooled across plots and sampling periods in four grass cover treatments within pastures (3 replicates of 4 treatments, $n = 12$ pastures), Mississippi State Prairie Research Unit, in 2011 and 2012. Different letters indicate significant difference of treatment means (plus signs) at $\alpha = 0.05$. Box plots show medians (thick black lines), means (open circles), interquartile ranges (boxes), and minimum and maximum counts (whiskers). NG-C = native warm-season grass mixture with cattle, NG-NC = native warm-season grass mixture without cattle, IG-C = monoculture of Indiangrass with cattle, BG-C = exotic bermudagrass and tall fescue with cattle.

collected (e.g., *Lasioglossum*) had relatively small body sizes and smaller bees generally have small foraging ranges (Greenleaf et al., 2007; Zurbuchen et al., 2010). Thus, it is likely that many of these bees were nesting within our treatments. One of our treatments (grazed exotic bermudagrass and fescue) is typical of many pasturelands in the southeast and is considered the most intensive treatment with regards to agricultural inputs. Bermudagrass has indeterminate rhizomes producing thick mats (i.e., stoloniferous mats) compared to the short, determinate rhizomes produced by the native grasses used in this study. The dense mats produced by bermudagrass may limit the availability of bare ground to ground-nesting bees compared to the native grasses, which tended to produce interspaces between their bunched growth form. Additionally, tilling is not necessary once perennial grasses are established. Tilling has been shown to negatively affect ground-nesting bees, and research indicates that any decrease in tilling of agricultural land could enhance local ground-nesting bee populations (Williams et al., 2010). Wood- and cavity-nesting bees were not frequently collected, probably due to limited suitable nesting material within the grass treatments. We surmise that the wood- and cavity-nesting bees we captured were probably nesting within wooded hedge rows adjacent to the pastures, and the wood- and cavity-nesting bees we collected in the study were foraging within the pastures.

Although the native grass mixtures without cattle (NG-NC treatments) generally had higher abundances of native bees compared to the native grass mixtures with cattle, these differences were not always statistically significant. Vulliamy et al. (2006) found that cattle grazing enhanced floral resources and nesting habitat for Halictidae in

Mediterranean landscapes. Cattle grazing has also been shown to enhance honey bee habitat by increasing abundance of some flowering plants (Kaminer et al., 2010). Despite these positive attributes associated with cattle grazing, other studies have found that cattle grazing can have negative effects on some native bee abundances (Hatfield and LeBuhn, 2007). Cattle could have created small bare spots and compacted soil, thus increasing suitable habitat for some ground-nesting bee species; this may explain some of the significant differences in bee abundances observed among the treatments containing cattle. The lack of cattle in the NG-NC treatments also allowed for some forbs to establish themselves, thereby providing some foraging resources for bees, which may partly account for the overall increased bee abundance and richness in these treatments. However, forbs were not common in the NG-NC treatments, and the increased bee taxa richness in the NG-NC treatments compared to the NG-C treatments was not expected. Thus, our results suggest that cattle grazing may have some negative impacts on bee diversity. However, in the second year of the study, some bermudagrass did invade the NG-C pastures (Monroe et al., 2017b) potentially explaining some of the negative responses by bees. This also highlights the difficulty of limiting the spread of non-native grasses like bermudagrass and fescue. Some genera such as *Bombus* showed no selection for a particular treatment. While solitary bees are known to generally have a small foraging range, large bodied bees like *Bombus* have much larger foraging areas (Greenleaf et al., 2007). Therefore, *Bombus* probably foraged within entire experimental blocks, thus allowing for equal chances of capture within all treatments.

Interestingly, both bermudagrass and the honey bee (Eurasia) are native to Asia (USDA-NRCS, 2000), suggesting a possible evolutionary linkage; thus potentially explaining why *Apis mellifera* was found more often in our bermudagrass treatments. Erickson and Atmowidjojo (1997) found that honey bees do not prefer to feed on bermudagrass pollen but will use it when other acceptable pollen sources are unavailable. However, our data supports the notion that honey bees prefer bermudagrass and fescue grass over other types of wind-pollinated grasses. Almost all of the other bee species we captured were native species and would be expected to prefer feeding on native plant pollen from plants that they share evolutionary history within the study region. Indeed, native bees have been shown to prefer native flowering plants over non-native species (Williams et al., 2011; Morandin and Kremen, 2013).

Although intensive agriculture is often at odds with biodiversity conservation, using perennial native grasses for cattle feedstock may help increase overall biodiversity in intensively managed agricultural areas. For example, Robertson et al. (2010) compared arthropod abundance between corn fields and switchgrass fields and found a significant increase in arthropod family diversity and biomass, including higher pollinator biomass within switchgrass fields. Increases in pollinator biomass may not only benefit nearby crops but arthropod biomass increases in general also benefit insectivorous birds and mammals (Landis and Werling, 2010) and can bolster the overall food web (Polis et al.,

1997). During the first year, our data suggested that using perennial native grasses can increase pollinating bee abundance compared to non-native grasses (e.g., bermudagrass and tall fescue) and, as other researchers have noted, are more ecologically friendly than other wind pollinated crops (e.g., corn). Once established, perennial grasses require little to no cultivation, allowing for nesting structure to develop and subsist for ground-nesting bees. Simply having grasslands adjacent to crops requiring insect pollination services has been shown to increase wild bee abundance and richness around crop fields (Morandin et al., 2007; Bennett and Isaacs, 2014). Perennial grasses also require less agrochemical usage compared to corn and soybean (Tilman et al., 2006), which also could lead to less disruption of pollinating bee and other beneficial insect communities. Additionally, prescribed fire is recommended for managing perennial grass fields (Harper et al., 2015) and numerous studies have shown positive impacts of prescribed fire on bee abundance and richness (Venturini et al., 2017; Campbell et al., 2018). Additionally, many native grasses provide food for larval butterflies that may also act as pollinators as adults. However, these trends for bees did not hold true during the second year of the study with BG-C being comparable for many species and genera of bees as some of the native grass treatments. Although we do not explicitly know why this occurred, it does show the complexity of grassland ecosystems and that bee responses to restoration efforts may be variable.

Overall, despite native perennial grasses being wind pollinated, bee abundance and richness can be enhanced by using perennial native grasses within an agricultural landscape. Land-sparing or land-sharing with native perennial grasses for cattle production not only has the potential to augment native bee abundance but also provides platforms for habitat restoration of imperiled grasslands.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgments

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