Harvesting effects on wild bee communities in bioenergy grasslands depend on nesting guild

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Abstract.   Conversion of annual crops to native perennial grasslands for bioenergy production may help conserve wild bees by enhancing nest and food resources. However, bee response to the disturbance of biomass harvesting may depend on their nesting location, thus their vulnerability to nest destruction, and the response of the forb community on which they forage. Moreover, because bees have long foraging ranges, effects of local harvesting may depend on the amount of natural habitat in the surrounding landscape. We performed a large-scale one- and two-year experiment in Michigan and Wisconsin, USA, respectively, to examine how grassland harvesting, landscape context, and study year affect the forb community, above- and belowground-nesting bee species richness, community composition, trap nest emergence, and visitation rate. In Wisconsin, harvesting increased forb richness, cover, and evenness compared to unharvested control sites. Harvesting negatively affected aboveground-nesting bee richness and emergence from trap nests, possibly because of nest destruction during the previous harvest. By contrast, harvesting positively affected belowground-nesting bee richness, possibly because of the greater food resource availability and reduced thatch allowing greater access to nesting sites in the soil. Harvesting also affected bee community composition, reflecting the increase in belowground-nesting species at harvested sites. Despite harvesting effects on forb and bee communities, there was no effect on flower visitation rate, indicating little effect on pollination function. We did not find a harvest by landscape context interaction, which, in combination with the negative harvesting effect on trap nest emergence, suggests that harvesting can affect local population growth rather than simply affecting forager aggregation in different resource environments. For bees, there was no harvest by study year interaction, indicating a consistent response over a short timescale. Similarly, in Michigan, belowground-nesting species also responded positively to harvesting, which was more pronounced in sandier soils that are preferred for nesting. However, other components of the Michigan bee and forb communities were not significantly affected by biomass harvesting. Overall, our study demonstrates that harvesting grasslands can positively affect the ~80% of bee species that nest belowground by enhancing nest and/or forage resources, but that conserving aboveground nesters may require leaving some area unharvested.

Key words: agriculture; bees; biofuel; community; disturbance; diversity; fire; grassland; harvesting; management; pollination.

Introduction

In the midwestern United States, low-diversity annual crop production has expanded greatly in recent decades, reducing natural habitat area and homogenizing landscapes. For example, corn and soybean land area in Wisconsin has increased by 237% between 1964 and 2012 at the expense of other crop types and natural areas (USDA National Agriculture Statistics Service 2016). The associated loss of food resources and nesting habitat is a principal cause of the decline of many taxa, including bees (Hymenoptera: Apiformes; Winfree et al. 2009, Potts et al. 2010, Goulson et al. 2015). Renewable energy mandates are a major contributor to the recent expansion of these annual crops onto marginal agricultural lands (Foley et al. 2005, Wright and Wimberly 2013, Lark et al.

2015). To meet renewable energy standards while also helping to preserve biodiversity, it has been suggested that less-productive areas could be converted to perennial grassland for biofuel production (Tilman et al. 2006, Robertson et al. 2008, Gelfand et al. 2013, Werling et al. 2014). Such land-use transitions would likely support a greater diversity of bees and enhance pollination services (Bennett and Isaacs 2014, Werling et al. 2014). However, it is not yet clear how harvesting these grasslands would affect bee communities.

Harvesting grassland biomass may negatively affect wild bees through removal of the vegetation on which they rely for food and nesting resources. Increasing the frequency and advancing the timing of grassland mowing can lower floral diversity and abundance, reducing pollinator diversity and visitation rate (Knop et al. 2006, Fitzpatrick et al. 2007, Weiner et al. 2011, Buri et al. 2014). There is also potential for positive effects of grassland harvesting on bees if biomass removal mimics some of the beneficial effects of fire or grazing on plant communities (Ne'eman et al. 2000, Potts

et al. 2003, Vulliamy et al. 2006). For instance, plant biomass removal may promote the growth and diversity of plants that provide food resources for bees (Williams et al. 2007, but see Jungers et al. 2015) and expose areas of soil that are required for belowground-nesting species (Michener 2007). However, to our knowledge, studies on the effects of vegetation harvesting on bees are either observational or do not include an unharvested experimental control, which complicates the assessment of treatment effects.

Given the variable life-history traits of bees, it is likely that harvesting would have different effects on above- and belowground-nesting bee guilds. Most bee species nest below ground in preexisting cavities or in holes they excavate. But many species also nest aboveground in, for example, the hollow stems of vegetation (Michener 2007). These different nesting strategies can be important for determining how a species responds to disturbance. For example, Williams et al. (2010) found that aboveground-nesting species were more vulnerable to agricultural intensification and recent fire than belowground-nesters, likely because of the destruction of nesting habitat and direct mortality. The removal of plant biomass during a harvest should be a similar source of mortality for aboveground-nesting species. On the other hand, belowground-nesters may benefit from a reduction in the thatch layer after harvesting if the reduction provides greater access to nesting sites the following year (Potts et al. 2005), however, we are unaware of studies that address these potentially different responses to grassland harvesting.

Because many bees forage and disperse over a wide area, the diversity of local bee communities often varies with the surrounding landscape (Kremen et al. 2002, Steffan-Dewenter 2003, Carré et al. 2009, Kennedy et al. 2013, Spiesman and Inouye 2013). Potential effects of grassland harvesting on local bee communities may therefore depend on landscape context. For example, if harvesting increases local forb species richness or abundance, a coincident increase in local bee species richness may require that the surrounding landscape support a high diversity of bees to colonize or forage in the harvested areas. If so, it would suggest that harvesting merely provides a larger local pool of resources to which bees can aggregate instead of directly enhancing local bee reproduction. Therefore, to assess the potential conservation value of bioenergy grasslands, we also examined the extent to which harvesting effects are landscape dependent and how harvesting can affect local reproduction.

We conducted an experiment to examine the effects of biomass harvesting on bee biodiversity in grassland fields at a spatial scale relevant to cellulosic biofuel production (i.e., tens of hectares). We asked (1) How does grassland harvesting affect forb communities on which bees rely? (2) How does harvesting affect bee communities and do below- and aboveground-nesting bees have different responses? (3) Do harvesting effects depend on the surrounding landscape context? We assessed the response of bee communities by examining variation in bee species richness, composition, and flower visitation rate. In addition, since direct assessments of factors affecting population growth are uncommon in large-scale studies of bees (Steffan-Dewenter 2003, Williams and Kremen 2007), we used trap nests to examine the effect of harvesting on the reproduction of aboveground-nesting species that nest in the vegetation stems.

METHODS

Our study took place in southern Wisconsin and Michigan, USA (see Appendix S1: Fig. S1). The study region is dominated by annual agriculture (mainly corn [*Zea mays* L.] and soybean [*Glycine max* (L.) Merr.]) with areas of deciduous forest, wetlands, and grassland habitat. Grassland in the study region is characterized by native warm-season grasses including switchgrass (*Panicum virgatum* L.) and big bluestem (*Andropogon gerardii* Vitman), along with many native prairie forbs including blackeyed Susan (*Rudbeckia hirta* L.), eastern purple coneflower (*Echinacea purpurea* (L.) Moench), pinnate prairie coneflower (*Ratibida pinnata* (Vent.) Barnhart), and common milkweed (*Asclepias syriaca* L.), which were common at our study sites.

Study sites were selected in 18 grassland fields in Wisconsin and 12 fields in Michigan in 2012, which ranged in size from 5 to 25 ha. Sites within the two regions were separated by at least 2.5 km and the two nearest sites between regions were 227 km apart. None of the sites had been burned or harvested for at least 3 years prior to the start of the experiment. Because bee communities often respond to habitat variability in the surrounding landscape (e.g., Kennedy et al. 2013), sites were selected to span a gradient of surrounding natural and seminatural habitat that reflects the range of variability in the study regions. We quantified natural area, or landscape context, as the total amount of grassland, forest, and wetland cover types within a 2-km radius using the 2011 USDA Cropland Data Layer (CDL; USDA National Agriculture Statistics Service 2011). Natural area surrounding our Wisconsin and Michigan sites ranged from 18–64% and 21–88%, respectively. Each site was randomly assigned a harvest or control treatment while ensuring that both treatments spanned similar ranges of the gradient in landscape context. Thus, we had nine harvest and nine control sites in Wisconsin and six harvest and six control fields in Michigan. The regions share a similar climate with mean annual high temperatures of 13.5°C and 14.4°C, and mean annual rainfall of 909 and 909 mm in Wisconsin and Michigan, respectively (Thornton et al. 2017).

Harvesting was performed by cooperating farmers by cutting, bailing, and removing the plant biomass from entire grassland fields. In Wisconsin, sites were first harvested during September 2012, prior to the first year of sampling in 2013. After first-year sampling was complete, sites were harvested again in September 2013 before a second year of sampling in 2014. Two additional sites, one harvest and one control, were added in 2014. The Michigan harvest treatment sites were first harvested in September 2013 and were sampled the following summer of 2014. Thus, Wisconsin sites were sampled one (18 sites in 2013) and two (20 sites in 2014) years post-harvest, and Michigan sites were sampled one year (12 sites in 2014) post-harvest.

Sampling was conducted within a 50 × 100 m area within each grassland field, at least 50 m from the field boundary, on three occasions each year in June, July, and August. During each round of sampling, bee communities were sampled using five pan trap arrays (Lebuhn et al. 2013) spaced equally along a 100-m transect running the length of the sampling area. Each array consisted of three 350-mL colored bowls (blue, yellow, and white) half filled with soapy

water. Thus, the sampling area and effort were identical across sites. Pan traps accumulated bees for two rain-free days, and then all collected bees were returned to the lab for species-level identification using the online key to Bees of Eastern North America in addition to species-level keys (Gibbs 2011, Rehan and Sheffield 2011; keys *available online*).[8] Each bee species was classified as either nesting above- or belowground, regardless of the particular type of nest (Williams et al. 2010). For example, stem-nesting species and species that nest in dead wood were all classified as aboveground-nesters since they are more likely to be affected in similar ways by the harvesting of aboveground biomass than species that nest belowground. Similarly, species that generally nest belowground were classified as belowground-nesters, regardless of whether they excavate their own nest or utilize a preexisting cavity. For the analyses described below, we estimated bee species richness and abundance using the observed number of species and the number of captured individuals, respectively, at each equal-effort site.

Flower visitation by bees was observed at a subset of five control and five harvest sites in Wisconsin and five control and six harvest sites in Michigan each year on three occasions corresponding with pan trap sampling. During each round of sampling, three 10–12 min observations were made of each forb species in flower (~8–15 species in flower at each site per round). For an observation, flowering individuals of a target species were randomly selected and a 1-m^2 quadrat was placed around the target species. All visitors to flowers of the target species within the quadrat were collected using small hand-held vacuums (BioQuip, Rancho Dominguez, California, USA). Most specimens were returned to the lab for identification of bee visitors but easily identifiable specimens (e.g., honey bees, *Apis mellifera*) were recorded and released. The species-specific visitation rates (number of bee visits per minute of observation) to each forb species were weighted by their site-level estimate of relative cover to calculate site-level visitation rates. Site-level visitation rates are an estimate of the mean visitation rate to each individual forb in flower across the three sampling rounds.

Bees have large foraging ranges, which can make it difficult to differentiate a treatment effect on local population growth from a treatment effect on aggregation (Williams et al. 2015). We therefore used trap nests, which serve as artificial aboveground nesting sites, to assess the effect of harvesting on the local, or within-field reproduction of stem-nesting bees and wasps. Counting the number of individuals that emerged the following spring allowed us to quantify relative reproductive output, which directly contributes to population growth (Williams and Kremen 2007). Trap nests were made from white rectangular 11.4-L plastic boxes and filled with ~1-cm diameter bamboo sticks cut to 25-cm lengths, with the node at the back end of each stick. Trap nests contained a mean of 275.9 ± 23.8 sticks (mean ± SD). In Wisconsin in 2013 and Michigan in 2014, two boxes per site were horizontally mounted to fence posts in mid-May and then collected in the first week of September. Boxes were wrapped in fine mesh and stored in an unheated barn for the winter. Insects that emerged the following spring were collected, enumerated, and identified to species as described above.

[8] www.discoverlife.org

The flowering plant community was sampled along two 2 × 100-m belt transects at each site on three occasions each year corresponding with pan trap sampling and flower observations. During each round of sampling in Wisconsin, the belt transects were divided into 0.5-m^2-cell grids and the relative floral cover of each species in flower was estimated as the count of grid cells in which flowers of each species were present. In Michigan, the relative floral cover of each species in flower was estimated as the count of individual stems within the belt transects. Within a region, we pooled data across sample periods to calculate season-long forb species richness (the count of different plant species in flower), total relative forb cover (the sum of cover estimates of each species), and forb species evenness (Pielou 1975).

The fraction of sand, silt, and clay in soils at each site was assessed using standard techniques (Cane 1991). Ten 25-cm soil cores were taken at each site in 2014, spaced evenly along a 100-m transect running the length of the sites. The contents of each soil core were homogenized, suspended in a water and soap solution, then allowed to settle for 48 h. The thickness of sand, silt, and clay layers were measured to the nearest mm, and percent sand was used in analyses of bee responses to grassland harvesting.

Landscape context was quantified as the percent area of natural habitat within a 2-km radius of each site center. We used land cover data from the 2013 and 2014 CDL (USDA National Agriculture Statistics Service 2014) to quantify natural habitat for our analyses as described above.

Statistical analysis

We analyzed the effects of harvesting on different components of grassland bee and flowering plant communities using general linear models, separately for each state, using R v3.4.1 (R Development Core Team 2017). Specifically, we examined the responses of forb species richness, forb cover, forb species evenness, total bee species richness, aboveground-nesting richness, and site-level flower visitation rate. For each analysis, main effects were harvest treatment and landscape context (i.e., the proportion of natural habitat within a 2-km radius). For Wisconsin analyses, year was included as a main effect and as an interaction with the harvest treatment. We also examined the interaction between harvest treatment and landscape context to determine if harvesting effects depended on the habitat in the surrounding landscape. For these and other analyses, nonsignificant interactions (i.e., $P > 0.05$) were removed to simplify the analysis. We performed separate analyses for each state to account for plant sampling differences and because we initiated the Michigan component of the experiment one year after the Wisconsin component.

Grassland harvesting reduced the volume of accumulated plant litter at our research sites (Kim et al. 2017), which may benefit belowground-nesting species by exposing soil and increasing access to nest sites. Therefore, to examined how harvesting mediated the effects of nesting substrate quality (i.e., percent sand in soils) on belowground-nesting bee species richness. We used general linear models to test for an interaction between the harvest treatment and the percent sand in soils.

The response of bee species composition to grassland harvesting was analyzed using distance-based redundancy

analysis (dbRDA; Legendre and Anderson 1999). We applied a Hellinger standardization to the cumulative abundances of bee species captured over the course of a season and used Bray-Curtis dissimilarities. As above, separate analyses were performed for each state, which included year (for the Wisconsin analysis), harvest treatment, landscape context, and their interactions. We specified 9,999 permutations with P values based on type-II tests. dbRDA was conducted using the R package vegan v2.4-4 (Oksanen et al. 2017).

If a dbRDA analysis showed a significant harvest treatment effect on community composition, we examined which bee species responded to the harvest treatment, and thus contributed to differences in composition. Because our data sets contain counts of individuals and many zeros (i.e., unobserved species), we used zero-inflated negative binomial models to examine how bee species' abundances varied with the harvest treatment (R package pscl v1.5.2; Zeileis et al. 2008). Treatment was the only predictor in the model of abundance performed on each species. For bee species where $P < 0.10$, we calculated 95% confidence intervals around harvest treatment coefficients using the confint function in R.

The effects of grassland harvesting on the number of individual bees and other Hymenoptera emerging from trap nests were analyzed using linear mixed-effects models. In each analysis, the number of individuals that emerged was included as the response variable and harvest treatment, landscape context, and their interaction were included as fixed factors. Two trap nests were placed at each site, so site was included as a random factor. We performed separate analyses for total emergence and for select numerically dominant species. Analyses were performed in R using the lme4 package v1.1-12 (Bates et al. 2015) and significance levels were assessed with Wald chi-square tests using the car package v2.1-3 (Fox and Weisberg 2010).

RESULTS

Forb communities were composed of 81 species in Wisconsin and 78 species in Michigan, ranging from 12 to 33 species and 14 to 27 species per site, respectively. Grassland harvesting in Wisconsin resulted in an increase in forb species richness (Fig. 1A, $t_{1,34} = 2.56$, $P = 0.015$; see Appendix S2: Table S1 for full results of harvesting effects on forb communities) and evenness (Fig. 1C, $t_{1,34} = 2.71$, $P = 0.010$). Harvest and year had interacting effects on forb cover in Wisconsin, with greater cover at harvested sites in 2014 but not 2013 (Fig. 1B, $t_{1,33} = 2.78$, $P = 0.009$). There was no significant effect of harvesting on Michigan forb communities (Fig. 1). Because there was no significant interaction between the effects of harvest treatment and landscape context on forb or bee communities in any analysis, the interaction term was removed from all analyses. In these and subsequent analyses, Mantel tests revealed no significant spatial autocorrelation and examination of variance inflation factors indicated low multicollinearity.

Over the course of the study, we sampled a total of 94 bee species in Wisconsin and 65 in Michigan, ranging from 10–34 and 11–24 species per site, respectively. In Wisconsin and Michigan, 21% and 18% were classified as aboveground nesters, respectively. The remaining 79% and 82% were classified as belowground nesters in Wisconsin and Michigan,
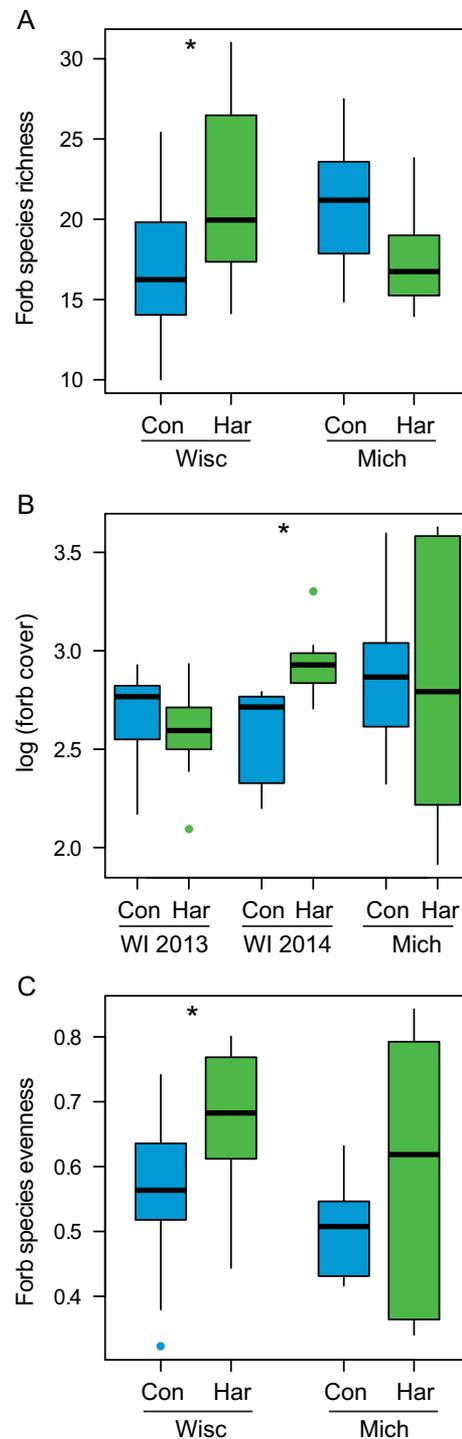

FIG. 1. Effects of grassland harvesting on forb (A) species richness, (B) cover, and (C) evenness in Wisconsin (Wisc) and Michigan (Mich). Boxes indicate the first and third quartiles, black bars the median, and whiskers extend above or below boxes to 1.5× the interquartile range. Asterisks indicate a significant difference ($P < 0.05$) between harvested (Har) and unharvested control (Con) treatments within states and years.

respectively (a species list with nesting classifications is shown in Appendix S3). The harvest treatment did not have a significant effect on total bee species richness in Wisconsin ($t_{1,34} = 0.28$, $P = 0.784$) or Michigan ($t_{1,9} = 0.34$, $P = 0.742$;

see Appendix S2: Table S2). There was, however, a positive effect of more natural habitat in the landscape on total bee richness in Wisconsin ($t_{1,34} = 3.05$, $P = 0.005$), but not Michigan ($t_{1,9} = 1.42$, $P = 0.189$). There was a marginal year effect in Wisconsin ($t_{1,34} = -1.89$, $P = 0.067$), with more bee species observed in 2013 compared to 2014.

Harvest treatment effects on bee species richness only emerged when above- and belowground-nesting species were analyzed separately. For aboveground-nesting bee species, harvesting had a negative effect on richness in Wisconsin (Fig. 2A; $t_{1,34} = -2.66$, $P = 0.012$; see Appendix S2: Table S3). There was no effect of year or landscape context on Wisconsin aboveground-nesting bee richness. There was no significant effect of harvesting on aboveground-nesting bee richness in Michigan (Fig. 2A; $t_{1,9} = -0.27$, $P = 0.795$).

Belowground-nesting species richness, on the other hand, benefited from harvesting and greater sand content of soils (Figs 2B and C). In Wisconsin, belowground-nesting richness was greater at harvested sites ($t_{1,33} = 2.21$, $P = 0.034$; see Appendix S2: Table S4) and increased with greater sand content ($t_{1,33} = 2.12$, $P = 0.042$). Belowground-nesting richness in Wisconsin was also greater the first year after harvesting ($t_{1,33} = -2.15$, $P = 0.039$) and increased with greater natural habitat in the surrounding landscape ($t_{1,33} = 2.39$, $P = 0.023$). In Michigan, there was an interaction between harvesting and soil sand content such that belowground-nesting bee richness was greater at harvested sites but only in sandier soils ($F_{2,9} = 6.69$, $P = 0.017$; Fig. 2C).

The site-level rate of flower visitation by bees did not vary with the harvesting treatment in Wisconsin ($t_{1,16} = 1.42$, $P = 0.175$) or Michigan ($t_{1,8} = 0.34$, $P = 0.741$). In Wisconsin, visitation rates were positively correlated with forb species richness ($r = 0.51$, $P = 0.022$) and evenness ($r = 0.61$, $P = 0.005$). Visitation rate as marginally correlated with forb cover in Michigan in 2014 ($r = 0.595$, $P = 0.053$).

The dbRDA results indicated that Wisconsin bee species composition was affected by the harvesting treatment (Fig. 3; $F_{1,34} = 1.58$, $P = 0.021$; see Appendix S2: Table S5). Study year ($F_{1,34} = 3.53$, $P < 0.001$) and landscape context ($F_{1,34} = 2.85$, $P < 0.001$) significantly affected composition, however, neither effect interacted with the harvest treatment. The 11 Wisconsin bee species whose abundances were most affected by the harvest treatment ($P < 0.10$) are shown in Appendix S1: Fig. S2. Of these species, most belowground-nesting species' abundances increased at harvested sites, whereas the abundances of aboveground-nesting species were lower at harvested sites. This suggests that the different harvest responses of the two nesting guilds contribute to the differences in community composition. Michigan bee species composition was not affected by the harvest treatment ($F_{1,9} = 1.20$, $P = 0.281$), but there was a marginal effect of landscape context ($F_{1,9} = 1.51$, $P = 0.089$).

Trap nests were primarily occupied by two species in Wisconsin: a bee (*Megachile pugnata*, pugnacious leaf-cutter bee) and a wasp (*Isodontia mexicana*, grass-carrying wasp), which made up 57% and 42% of the total number of individuals emerged, respectively. Michigan trap nests also had relatively high percent emergence of *M. pugnata* (27%) and *I. mexicana* (20%), but *Euodynerus foraminatus* (mason wasp; 21%), and *Hylaeus leptocephalus* (slender-faced bee; 12%) were also relatively abundant. On average, total emergence was 66% lower
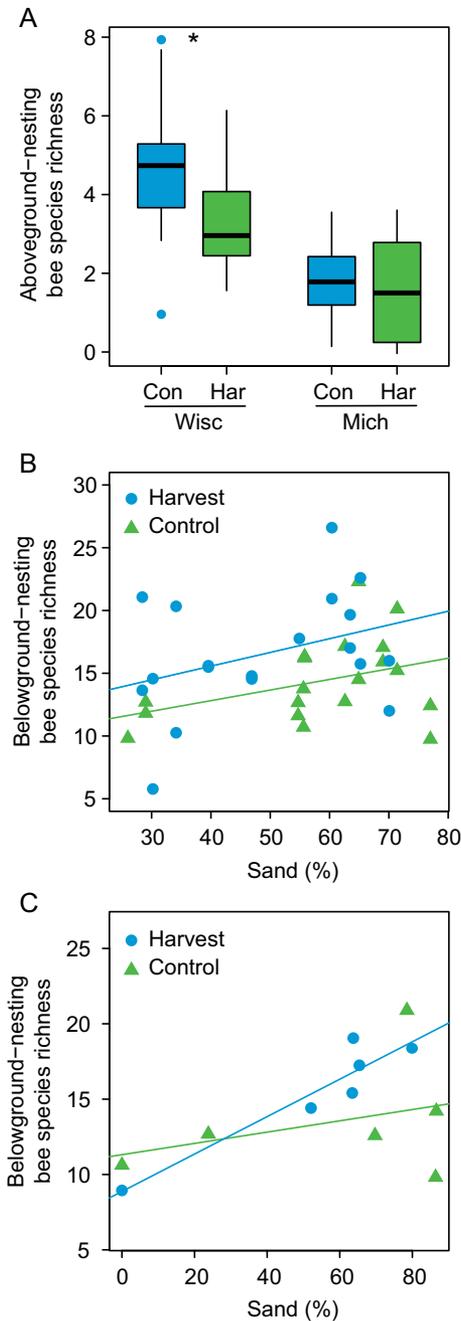

Fig. 2. Harvesting effect on the species richness of (A) aboveground-nesting bees and belowground-nesting bees in (B) Wisconsin and (C) Michigan. Asterisks indicate significant differences ($P < 0.05$) between harvested (Har) and unharvested control (Con) treatments.

in Wisconsin harvested compared to control sites (Fig. 4; $\chi^2_1 = 5.08$, $P = 0.024$; see Appendix S2: Table S6), but there was no emergence difference between harvest and control sites in Michigan (Fig. 4, see Appendix S2: Table S6). In Wisconsin, *M. pugnata* ($\chi^2_1 = 3.54$, $P = 0.060$) and *I. mexicana* ($\chi^2_1 = 3.40$, $P = 0.065$) both had a marginally lower number of individuals emerge in harvested sites (12.9 ± 7.7 [mean ± SE] and 20.6 ± 4.2, respectively) compared to control sites (62.4 ± 36.0 and 35.0 ± 6.5, respectively; see Appendix S2: Table S6).

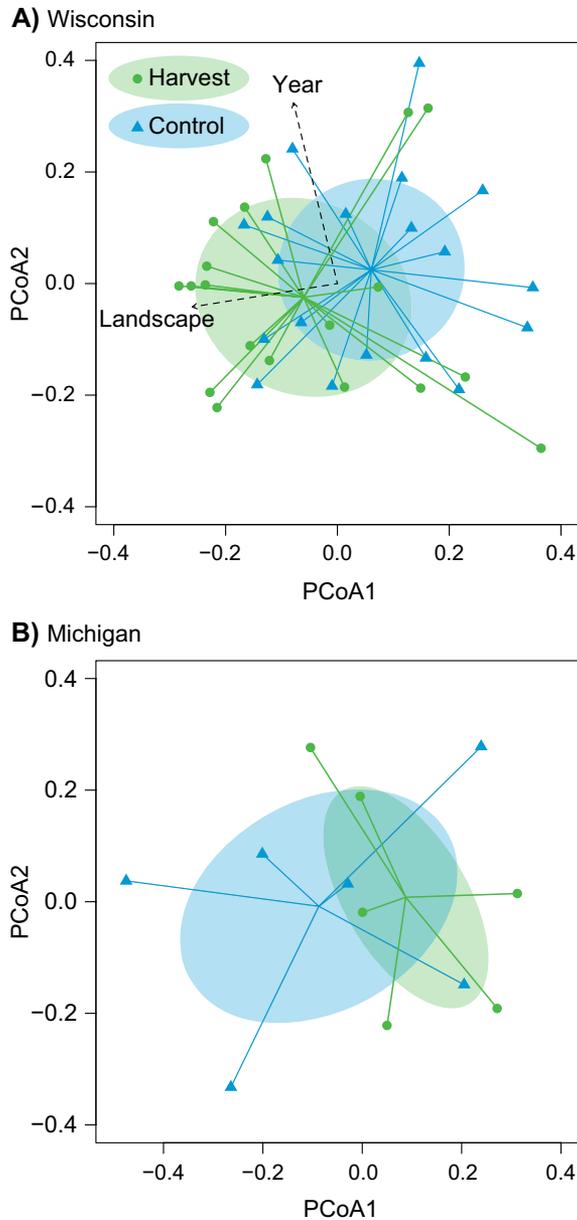## A) Wisconsin

B) Michigan

Fig. 3. Principal coordinates analysis (PCoA) visualization of the Bray-Curtis dissimilarity among bee communities at harvested (Har) and unharvested control (Con) sites in (A) Wisconsin and (B) Michigan. Solid black and gray lines indicate the relative distance of each community to the centroid of its respective group: harvest or control. Ellipses indicate the 95% confidence limits of the SE of group centroids. Dashed arrows indicate significant correlations ($P < 0.05$) between PCoA axes and year or landscape context.
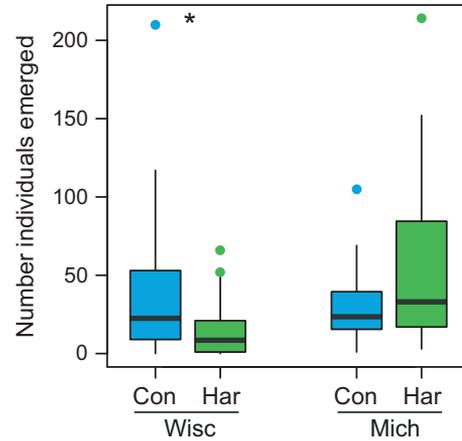

Fig. 4. Harvesting effect on the total number of bee and wasp individuals that emerged from trap nests in Wisconsin (Wisc) and Michigan (Mich). Asterisks indicate significant differences ($P < 0.05$) between harvested (Har) and unharvested control (Con) treatments.

depended on the sand content of the soil in which they nest. However, harvesting had little effect on other components of the bee and forb communities in Michigan. It is possible that a smaller sample size and broader spatial distribution of sites, which could introduce greater variation in disturbance responses and soil types, may have contributed to the difficulty of detecting a harvesting effect in Michigan. Overall, our results suggest forb and belowground-nesting bee communities generally benefit from (i.e., a positive effect), or are robust to (i.e., no effect), the disturbance caused by late-season grassland harvesting, but that aboveground nesters are negatively affected.

Disturbance plays a key role in grassland ecology and ecosystem dynamics (Hobbs and Huenneke 1992). Fire, for example, can reduce litter accumulation, open bare ground, allow soil to warm faster, and suppress competitively dominant plant species that may otherwise reduce the productivity and diversity of grassland plant communities (Howe 2011). Moderate grazing can have similar effects (Hartnett et al. 1996). Although region dependent, our study showed that grassland harvesting can mimic some of these beneficial effects of fire and grazing on grassland forb communities and allow increased forb richness, cover, and evenness (see also Williams et al. 2007, Jungers et al. 2015). Moreover, harvesting reduced the volume of the thatch layer at our study sites (Kim et al. 2017). These biotic and abiotic effects on grasslands likely mediated the positive and negative harvesting effects we found on below- and aboveground-nesting species, respectively.

Whether bees establish nests above or below ground is important for how they respond to disturbance (Williams et al. 2010). When analyzing nesting guilds together, harvesting had no effect on total bee species richness. But examining above- and belowground-nesting bee species separately revealed differential responses. Aboveground-nesting species in Wisconsin responded negatively to harvesting, highlighting the vulnerability to direct mortality of larvae and pupae when vegetation is removed. Furthermore, reduced emergence from trap nests suggests that harvest-induced mortality can negatively affect reproduction and lower population

DISCUSSION

We found that grassland harvesting had taxon- and region-dependent effects on bee and forb communities. At Wisconsin sites, harvesting enhanced forb communities (richness, cover, and evenness) and the species richness of belowground-nesting bees. On the other hand, aboveground-nesting species had lower richness and trap nest emergence at harvested sites. At Michigan sites, belowground-nesting species richness had a similar positive response to harvesting, but the benefit

sizes of aboveground-nesting species. That is, mortality of nests established in the natural vegetation that was harvested in 2012 could have reduced local population sizes so that fewer individuals were present to colonize (and eventually emerge from) the trap nests that were set out in 2013. Because some bee and wasp species have large foraging ranges, this effect on emergence is evidence that harvesting can affect local population dynamics and that observed differences among bee communities are not simply a result of movement to and from different resource environments.

Many ecologically important pollinators construct nests in the stems of vegetation. For example, bees in the genus *Megachile*, such as *M. pugnata*, are frequent pollinators in native grassland systems and are important pollinators of some agricultural crops (Pitts-Singer and Cane 2011). The wasp *Isodontia mexicana* is a frequent flower visitor and pollinator, but it is also a predator of herbivorous insects as it provisions its nest with Tettigoniidae and Gryllidae (Medler 1965). Thus, the potentially negative effect of harvesting on aboveground-nesting insects should be considered in conservation plans.

Nests established belowground, on the other hand, are less likely to be affected by aboveground disturbance (Williams et al. 2010). Accordingly, we found positive effects of harvesting on belowground-nesting species in both Wisconsin and Michigan, but this was evident only when soil texture was also considered. It is possible that the reduced thatch layer at harvested sites allowed for greater access to belowground nesting locations, thus resulting in higher bee species richness. However, in Michigan the strength of this effect increased with sandier soils, which are generally favored by ground-nesting bees over soils with high silt or clay content (Cane 1991). Because harvesting can also enhance the forb community, it is possible that greater nest site accessibility and food resource availability at harvested sites act in concert with nesting substrate to affect belowground-nesting bees. Additional experiments are required to explore these potential mechanisms.

Harvesting shifted bee species composition in Wisconsin, which was associated with the different nesting guild responses to harvesting. Belowground-nesting bee abundance was more likely to increase at harvested sites, whereas aboveground-nesting bee abundance was more likely to decrease at harvested sites. These compositional changes further indicate that harvesting effects can be dependent on nesting guild (sensu Williams et al. 2010).

The frequency of grassland harvesting can affect interactions between plants and their pollinators (Weiner et al. 2011). However, in our study, the rate of bee visitation to flowers did not vary between harvested and unharvested sites, even though harvesting affected bee richness and composition. The lack of an effect on visitation rate indicates that pollination, a key ecological function of bees in grasslands, may not be significantly impacted by harvesting over the short term. However, because we found that visitation rates can be correlated with forb richness, cover, and evenness, the cumulative effects of harvesting on the forb community over multiple years of management for biofuel production may eventually affect visitation.

Landscape context can have significant effects on local bee communities (Steffan-Dewenter 2003, Kennedy et al. 2013, Spiesman and Inouye 2013). Although the amount of natural habitat in the landscape affected bee communities in our study, there was no interaction with our harvesting treatment, suggesting that harvesting effects on bees do not depend on the quality of the surrounding landscape. This provides additional evidence that harvesting influenced local population growth and persistence, rather than attracting foraging bees nesting elsewhere in the landscape.

Caveats and implications for management

Two important caveats of our study should be considered. First, this was a two-year study. Long-term harvesting in the absence of fire can deplete grassland diversity (Rooney and Leach 2010), so there may be different dynamics seen if harvesting continues for many years. This may, for example, reduce fire-dependent germination of native plants or contribute to the depletion of key nutrients important for plant productivity. Longer-term studies are therefore necessary to understand how best to manage grasslands for bioenergy production in ways that maintain biodiversity and ecosystem services. It is also not clear how the particular years in which our study was conducted influenced our results. A significant year effect on belowground-nesting bees and composition in Wisconsin may be related to interannual variation in precipitation. However, the lack of a year by harvest treatment interaction suggests that, on a short timescale, the effects of harvesting are consistent.

A second caveat is that our annual harvest treatment was applied once in the fall after bee foraging activity had begun to subside. If management intensity of grasslands for biomass production included more frequent and/or earlier harvests it is unclear how bee communities would respond. Differences in the timing and frequency of harvesting, and also the use of fertilizers to increase biomass production, can affect bee communities (Knop et al. 2006, Fitzpatrick et al. 2007, Buri et al. 2014). However, considering these limitations, our results have several implications for the management of perennial grassland systems for bioenergy production, and for grassland conservation in general.

Grasslands are maintained by fire (Bond and Keeley 2005). However, prescribed fire can be costly and its application is dependent on a restrictive set of environmental conditions, which often prevent land managers from burning as much land as is optimal (Rave et al. 2013; USFWS, *personal communication*). Harvesting grassland plant biomass (e.g., for bioenergy or hay) is an alternative to prescribed fire because costs can be lower and scheduling more flexible. Our results indicate that, from a forb and bee community perspective, harvesting of grasslands in the study region can be a viable temporary alternative to prescribed fire for the maintenance of grassland ecosystems.

Previous research has shown that conversion of marginal agricultural lands to perennial grasslands enhances biodiversity and ecosystem services (Werling et al. 2014). Our experiment suggests that these biodiversity gains for bees and forbs would not be undone by the harvesting necessary for bioenergy production, at least in the short-term. However, there is a trade-off. Belowground-nesting bees, comprising most bee species, seem to benefit from greater access to nesting sites and/or floral resources at harvested sites. Aboveground-nesting

species, on the other hand, can be negatively affected by mortality associated with nest destruction. Therefore, to mitigate these negative effects, it may be important to set aside unharvested sections of fields to maintain robust stem-nesting pollinator populations. Set-aside programs such as wildflower plantings can benefit bee diversity by creating persistent food (Carvell et al. 2007, Blaauw and Isaacs 2014) and nesting resources (May 2015), but their ability to also provide a haven for aboveground-nesting bees and wasp remains, to our knowledge, untested.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1828/full

Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.s7d4g4t