

Response of Wild Bees (Hymenoptera: Apoidea: Anthophila) to Surrounding Land Cover in Wisconsin Pickling Cucumber

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ABSTRACT Cucumber (*Cucumis sativus* L.) is among the plants highly dependent on insect-mediated pollination, but little is known about its unmanaged pollinators. Both domestic and wild bee populations in central Wisconsin pickling cucumber fields were assessed using a combination of pan trapping and floral observations before and during bloom. Together with land cover analyses extending 2,000 m from field centers, the relationship of land cover components and bee abundance and diversity were examined. Over a 2-yr sample interval distributed among 18 experimental sites, 3,185 wild bees were collected representing >60 species. A positive association was found between both noncrop and herbaceous areas with bee abundance and diversity only during bloom. Response of bee abundance and diversity to land cover was strongest at larger buffers presumably because of the heterogeneous nature of the landscape and connectivity between crop and noncrop areas. These results are consistent with previous research that has found a weak response of wild bees to surrounding vegetation in moderately fragmented areas. A diverse community of wild bees is present within the fields of a commercial cucumber system, and there is evidence of floral visitation by unmanaged bees. This evidence emphasizes the importance of wild pollinators in fragmented landscapes and the need for additional research to investigate the effectiveness of individual species in pollen deposition.

KEY WORDS wild bees, cucumber, Wisconsin, pan trapping

A decline in the richness and abundance of pollinators is concerning, especially because crops dependent upon pollinators have doubled in acreage from 1961 to 2008 (Garibaldi et al. 2011a). Many crops may continue to face even greater yield deficits with future pollinator declines and shortages. An estimated 78% of temperate plant communities are dependent upon animal pollinators (Ollerton et al. 2011), and bees are the main pollinators for many of these wild, noncrop plants as well as managed crops. Even though a diverse group of bees often has been observed in cucurbit (Kremen et al. 2004, Winfree et al. 2008) as well as other Upper Midwest cropping systems (Tuell et al. 2009, Watson et al. 2011), honey bees have been relied upon as the dominant pollinator in most agricultural systems to satisfy an increasing demand. Although the number of honey bee hives has increased globally over the last 50 yr (vanEngelsdorp and Meixner 2010), there have been steep, regional declines of up to 50% in North America (FAO 2009). Remaining hives are at further risk because of the recently characterized Colony Collapse Disorder. Wild pollinators, an alternative to the domestic pollination provided by honey bees, are threatened by several issues, including introduced pathogens (Singh et al. 2010, Cameron et al. 2011); nontarget impacts of pest management practices

(Desneux et al. 2007); and habitat loss (Ricketts et al. 2008). This dual loss of wild and managed pollinators, resulting from a combination of pathogens and environmental influences, increases the risk posed to cultivated crops that are highly dependent on insect pollination.

Natural area (Winfree et al. 2008), forested area (Julier and Roulston 2009), and grassland habitats (Hines and Hendrix 2005) have been investigated for their descriptive value of bee communities associated with cropping systems and undisturbed areas. These plant communities often contain stable supplies of floral resources and are believed to impart an overall positive effect on bee abundance and diversity, although the extent of the response can vary. Notably, some wild bees thrive in disturbed areas dominated by agriculture (Westphal et al. 2003, Winfree et al. 2007). Previous work has demonstrated that the flowers of watermelons [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] in Pennsylvania and New Jersey and pumpkins in Virginia received more visits from wild bees than *Apis mellifera* L. (Winfree et al. 2008, Julier and Roulston 2009). It is not unusual for wild bees to contribute significantly to the pollination of crops, although this contribution ranges from one quarter of visits in California sunflower (*Helianthus californicus* DC.) (Greenleaf and Kremen 2006) to >50% of pollination in the cultivated tropical fruit Longan (*Dimocarpus*

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longan Lour.) in Australia (Blanche et al. 2006). Reportedly, the remnants of natural habitat surrounding these fields on a regional level supplemented the managed crop by acting as corridors of resources to support wild bees. Diverse landscapes can provide connectivity between crop and wild flowers and offer a greater potential for temporal continuity of resources throughout growing seasons. These natural and seminatural areas vary in their resources and nesting opportunities (Roulston and Goodell 2011), but the presence of unmanaged areas in the regional landscape can lead to greater stability of wild bee populations.

Diversity in wild bee feeding habits and ecology can benefit the pollination output in a cultivated crop such as cucumber (*Cucumis sativus* L.). There are >400 species of wild bees in Wisconsin (Wolf and Ascher 2009) with pollen specialization ranging from oligolectic (pollen specialist) squash bees (family Apidae) to polylectic (pollen generalist) sweat bees (family Halictidae). Inadequate resources threaten pollination by native bees in managed crops, and the effects of resource limitation are magnified in fields isolated from natural area (Kremen et al. 2002, Ricketts et al. 2008, Winfree et al. 2009). The dominance of individual taxa visiting cucurbits at specific periods of the growing season (Tepedino 1981, Julier and Roulston 2009) can provide a source of unmanaged pollination services, but these species ultimately require a stable source of alternative resources.

The wild bee community within cucumber fields remains largely undescribed, and an understanding of alternative pollinators and potential conservation regimes remain relevant goals to growers and the scientific community (Mayer et al. 2011). Previous studies have mentioned native bee visits in cucumber, but most have neglected to consider species other than bumble bees and honey bees (Kauffeld and Williams 1972, Gingras et al. 1999). Presumably, cucumber was pollinated by insects other than honey bees, because it is not indigenous to regions where the honey bee is the common pollinator. It is precarious to rely on a single bee species, namely *A. mellifera*, for pollination when it is not the most efficient pollinator (Stanghellini et al. 2002) and at risk of further population decline. Because wild bees contribute to the pollination services of many crops and exhibit varying response to landscape, it is reasonable to sample the potential pollinators of cucumber to determine if future opportunities exist for utilization of unmanaged bees as a source of crop pollination.

Shifting land use has resulted in conversion of land to agricultural and other uses and necessitates further work to determine if the remaining natural and seminatural area in a pickling cucumber agroecosystem influences wild bees. Land cover analysis associated with cucumber has been scarce, and it is unclear if bees respond to landscape surrounding cucumber in a manner similar to other cucurbits. As a monoecious crop, cucumber has separate male and female flowers on the same plant. Cucumber is highly dependent on insect-mediated pollination because of its large and sticky pollen grains that travel poorly in wind, and

self-pollination is inefficient at producing unblemished, complete fruits (Gingras et al. 1999). In this study, pollinators were sampled in fields with a gradient of surrounding natural area to investigate if landscape is a useful predictor of bee abundance and diversity. This study will provide a comprehensive sampling of bees in commercial cucumber fields and evaluate the scale at which the wild bee community is impacted by surrounding vegetation. We hypothesize that the abundance and diversity of wild bees will increase as the proportion of natural and seminatural unmanaged areas surrounding pickling cucumber increases. By completion of these objectives, we will provide an improved understanding of the spatial scale and population dynamics of wild bees in relation to landscape around cucumber.

Materials and Methods

Study Area. Cucumber fields in this study were located in the Central Sands, an area of central Wisconsin characterized by well-drained sandy loam soils. Historically, tall grass prairie and oak savannah were the primary land cover types. However, waves of human settlement have resulted in a more fragmented landscape with forested stands, including oak-hickory (*Quercus* spp.), maple-basswood, and white-red-jack pine (*Pinus* spp.), accounting for $\approx 28\%$ of the total land cover (DNR Ecological Landscapes of Wisconsin), an increase from previous timber use. The understory in noncrop areas is minimally diverse with huckleberry (Family Ericaceae), bracken fern (*Pteridium aquilinum*), and Pennsylvania Sedge (*Carex pensylvanica*) as the dominant perennials. Agriculture remains the dominant land class in this region with significant grassland and wetland areas contributing to the remainder of regional land composition. The central Wisconsin climate is continental with a growing season of ≈ 130 – 140 d between first and last frost. In this and other continental climates, cucumber is planted in late spring or summer when the soil temperature has reached 55°F .

Data Collection. Our sampling efforts were designed to determine which bees were present before and during bloom and included sites planted at varying periods of the growing season in Portage and Waushara Counties (Fig. 1). In 2009, we sampled four fields during bloom in July and August, and in 2010 we sampled 15 fields before and during bloom between June and August. A prebloom sampling with pan traps was added in 2010 after seedling emergence and during the vegetative stages of plant development when the plants possessed no flowers. A second in-bloom sampling occurred in most fields 1 wk after the initial bloom sampling, except when poor weather conditions or repeat fungicide applications prevented a balanced resampling. Cucumber fields ranged in size from 15 to 57 ha, with an average field size of 36 ha, and all were overhead irrigated. All fields received supplemental managed honey bee hives that were present at field borders from the first week of flowering until harvest. No sites were located closer than 1 km, a distance greater than the foraging range of most bees

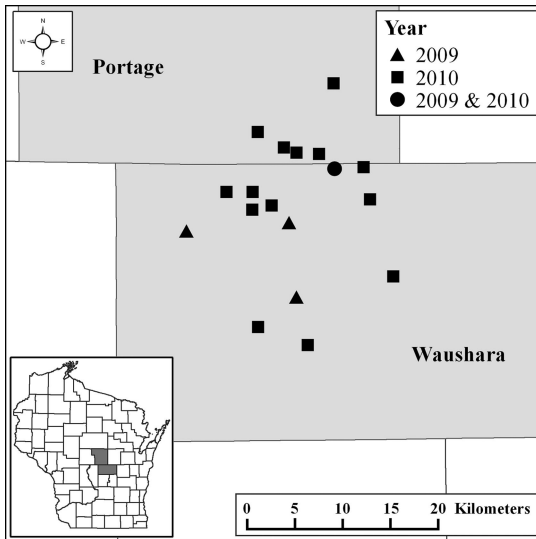


Fig. 1. Location of cucumber field sites in central Wisconsin in 2009–2010.

(Gathmann and Tschamtko 2002, Zurbuchen et al. 2010) with a separation of 3–28 km between most fields. The presence of spatial autocorrelation among sites for wild bee abundance and diversity was tested using Moran's I (Paradis et al. 2004) but none was detected ($P > 0.05$).

Bees were sampled in each field by using 6 oz (148-ml) plastic bowls (Chinet Company, De Soto, KS) referred to as pan traps, filled with water and a small amount of liquid soap (Dawn: blue dishwashing soap, Cincinnati, OH). All pan traps were placed at flower level and collected 24 h after initial placement. An equal number of white, fluorescent yellow, and fluorescent blue bowls were used to minimize bias in pan trap visitation (Leong and Thorp 1999). In 2009, we set eight transects of pan traps (white, blue, and yellow) perpendicular to the field borders at the field edge and at 10-, 20-, and 30-m increments. Our original intent was to measure the effects of distance from field edge on bees. However, no significant difference ($F_{3,12} = 0.24$, $P = 0.87$, analysis of variance in bee abundance was observed between any of these four distances values in 2009 at any of the four field sites. To provide a more accurate assessment of the in-field bee community, we changed the transect placement in 2010. Instead, six transects (50 m) were placed parallel to field edges at a distance of 25 m within each field ($N = 15$). Along the length of each transect, twelve bowls of alternating colors were spaced ≈ 3 –5 m apart. Nearly all data collection occurred on sunny to partly cloudy days, with average wind speeds below 2.5 m/s at the time of collection. Temperatures at the time of pan trap placement were recorded from a local weather monitoring station. All collected bees were stored in 75% ethanol until identification to species or the lowest taxonomic level.

Pan traps have been used to document regional bee communities, sample bees over a longer period of the

day than sweep netting, and to limit observer bias. However, pan traps, alone, often provide an incomplete survey of pollinator fauna (Cane et al. 2000, Wilson et al. 2008) and cannot distinguish between pollinators and bees passing through fields (Russell et al. 2005). Instead, complementary floral observations are more suitable for recording large bodied pollinators that are less likely to land in pan traps and can confirm if the species collected in pan traps were visiting cucumber flowers. Visual observations of flowers were performed twice at all fields when cucumber was in bloom. While walking along two randomly selected transects per field where pan traps had been placed, all encountered bee visits lasting for at least 1 second on open cucumber flowers were recorded for a total of 10 min per transect. To minimize disruption to pollination, we netted specimens, identified them to genus or to the lowest taxonomic level possible, and released them. Several unidentified specimens on flowers were kept and preserved for further identification. Voucher specimens were deposited at the University of Wisconsin-Madison Insect Research Collection.

Land Cover Analysis. We analyzed the proportion habitat types around fields to examine the response of the wild bee community to land cover around cucumber. Land use classifications were obtained through digitized-aerial photographs with a 1-m resolution generated by the National Agriculture Imagery Program in ArcGIS 9.3.1 (ESRI 2009, NAIP 2010, Redlands, CA). From these land use polygons, buffers were created at 250-m increments up to 2,000 m surrounding field centers. The study extent of 2,000 m was selected as the maximum landscape scale in this study, because few larger and medium-sized pollinators are reported to forage from the nest at greater distances (Zurbuchen et al. 2010). Field buffers included biologically relevant land categories that were categorized into a general grouping of 1) natural or semi-natural landscape, which included permanent pasture, herbaceous scrub, forested areas, as well as roadsides and adjacent weedy areas; or 2) agricultural or disturbed landscape, which encompassed field and vegetable crops as well as impermeable surfaces and developed areas. Calculated acreages of field buffers were transformed into the proportion of habitat relative to total area surrounding fields. Percent natural area around fields ranged from 10 to 90% within a 500-m radius and 14–82% within a 2,000-m radius of field centers.

Statistical Analysis. Differences in mean honey bee and wild bee abundance as well as the bee community before bloom and during bloom were compared by paired Student's t -tests. We used the average wild bee abundance at sites with two in-bloom sampling dates. Wild bee populations were analyzed separately for pan trap and visual observations, except in regression models as described below. Within each site, we characterized species richness, the raw number of species, and the Shannon Diversity Index:

$$H' = - \sum p_i \times \ln p_i,$$

Table 1. List of bees recorded through visual observations of cucumber flowers during bloom from 2009 and 2010

Family	Genus	Species	Total	
Apidae	<i>Apis</i>	<i>mellifera</i> L.	379	
	<i>Bombus</i>	spp.	17	
	<i>Bombus</i>	<i>griseocollis</i> (DeGeer)	1	
	<i>Bombus</i>	<i>impatiens</i> Cresson	5	
	<i>Bombus</i>	<i>rufocinctus</i> Cresson	1	
	<i>Bombus</i>	<i>ternarius</i> Say	1	
	<i>Eucera</i>	<i>hamata</i> (Bradley)	3	
	<i>Nomada</i>	spp.	1	
	<i>Peponapis</i>	<i>pruinosa</i> (Say)	8	
	<i>Melissodes</i>	spp.	2	
	<i>Melissodes</i>	<i>bimaculata</i> Lepeletier	2	
	Unknown		2	
	Halictidae	<i>Agapostemon</i>	spp.	1
		<i>Lasioglossum</i>	spp.	13
<i>Lasioglossum</i>		<i>leucozonium</i> (Schrank)	2	
Unknown			19	
Megachilidae	<i>Megachile</i>	spp.	4	
Unknown			8	
Total			468	

where p_i = proportion of individuals of species “i” within community of N species), using combined pan trap and visual observation data as measures for wild bee diversity. To analyze the importance of surrounding land cover on bee abundance and diversity, we performed simple linear regression by using proportion natural area, forested area, herbaceous scrub, and crop areas as predictor variables. Similarly, linear models were created substituting Shannon diversity, number of taxa per field, and species evenness (natural $\log_{10}^{\text{Shannon diversity/number of species}}$) as response variables. In addition, we computed a multiple stepwise forward regression by combining all of the land cover predictor variables listed above and added temperature at sampling as an independent variable to determine if a combination of variables would best predict bee abundance and diversity. Model comparisons were performed using the Akaike Information Criterion values. Count data initially were transformed to a logarithmic scale [$\log_{10}(x + 1)$] when assumptions of normality were not met. All of the above statistical tests were completed using the R software (R Development Core Team 2010), unless

noted otherwise, and include combined data from 2009 and 2010.

Results

In total, 3,185 wild bees were collected and identified from among 68 species in pan traps and visual observations during 2009 and 2010 (Supp. Table S1). Two species of cucurbit pollen specialists, *Peponapis pruinosa* (Say) and *Xenoglossa kansensis* Cockerell, were collected in limited abundance from multiple fields. However, the most frequently sampled species were generalist pollinators including *Lasioglossum leucozonium* (Schrank), *L. pilosum* (Smith), *L. oceanicum* (Cockerell), and *Agapostemon texanus* Cresson. These four species comprised an average of 25% of the total sampled bees at each field during bloom and 56% of the total sampled bees before bloom. The two sites with the greatest recorded bee abundance were dominated by *L. leucozonium* and *L. pilosum*, which represented one half to two thirds the total bee community. *Lasioglossum* was the genus with the greatest number of species collected ($N = 27$), followed by *Bombus* ($N = 8$) and *Melissodes* ($N = 7$). Sampling efforts discovered the presence of several undocumented species present in the Central Sands as well as four species, *Melissodes communis* Cresson, *M. coreopsis* Robertson, *X. kansensis*, and *Lasioglossum zophops* (Ellis), which are new records for Wisconsin. Most wild bees foraging in cucumber are described as soil-nesting species with the exception of several cavity nesters from the genera *Osmia* and *Megachile*.

Visual observations were a beneficial tool for noting which bees were active within fields and, indeed visited cucumber flowers. We observed 468 visits to flowers from wild bees and honey bees (Table 1). The honey bee was an overwhelmingly dominant visitor to open flowers of cucumber ($t_{37} = 7.46$, $P < 0.0001$). This trend was less pronounced in pan traps, where mean wild bee and honey bee abundance were not significantly different ($t_{14} = 0.91$, $P = 0.38$; Fig. 2). Several species visiting cucumber, such as *Bombus ternarius* Say, were only identified through visual ob-

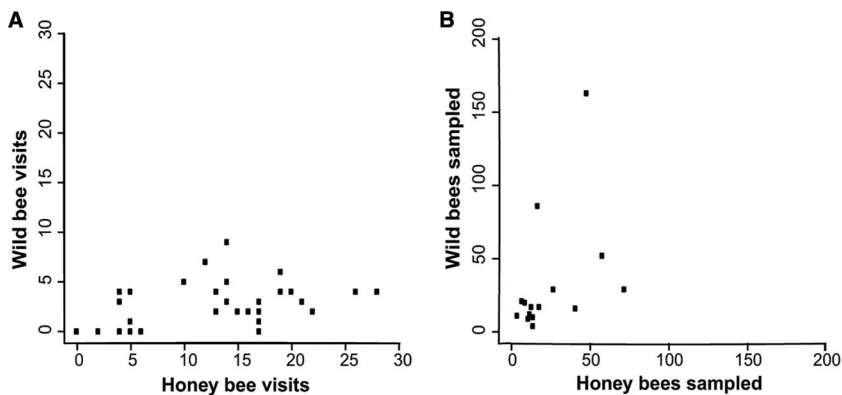


Fig. 2. Ratio of wild bees to honey bees observed in: A) visual observations and B) pan traps, during bloom among sites sampled in 2010. Each point represents the ratio of total bee abundance per sample site.

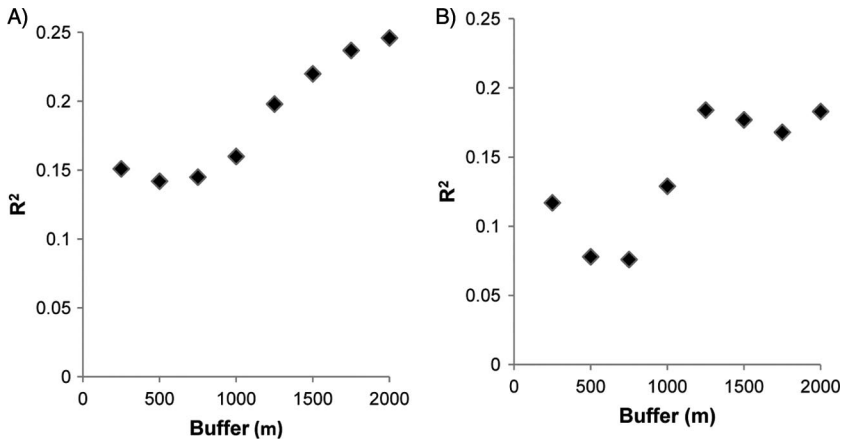


Fig. 3. Goodness-of-fit (R^2 values) estimates generated from models measuring the association of: A) natural area, and B) forested area to wild bee abundance during bloom at 250-m increments of surrounding land cover from field centers.

servations. Other pollinators more common in floral observations included larger bees in the family Apidae, such as *P. pruinosa*, and several species of bumble bees. To a lesser extent, we observed small bees in the family Halictidae, including *Lasioglossum (Dialictus)* spp., visiting open flowers. The low number of wild bees recorded from visual observations limited the scope of analysis for these data.

Relationship of Bee Abundance and Richness to Land Cover. Land cover had minimal association with the wild bee community before bloom and a weak, but positive association during bloom. The scale of surrounding land cover was influential in determining the strength of the association between wild bee abundance and natural area (Fig. 3), as the most significant positive associations were observed when including the greatest buffer distances (up to 2,000 m). Individual types of land cover produced associations with bee abundance that were weaker compared with overall natural area (Table 2). All natural area variables had positive associations with bee abundance or richness. More immediate or local spatial scales (250–750 m) around fields were not significant in predicting bee abundance based on pan trap data. To the contrary, there was a significant association between the number of floral visits by wild bees and surrounding proportion of natural area only at small spatial scales (≤ 500 m, $R^2 = 0.17$, $P = 0.03$).

Species richness exhibited a similar positive response to percent natural area surrounding fields. At the local scale (≤ 500 m), there was no significant association between species richness and natural area ($R^2 = 0.05$, $P = 0.39$). However, increasing the scale of surrounding land cover to 1,500 m ($R^2 = 0.25$, $P = 0.03$) or greater led to significant associations between number of species and natural area (Table 2). Although bee richness was associated with natural and seminatural areas, there was no significant relationship between Shannon diversity and surrounding natural area before ($R^2 = 0.14$, $P = 0.18$) or during ($R^2 = 0.08$, $P = 0.22$) bloom. Similarly, species evenness and natural area around fields were unassociated before bloom. Greater species diversity generally was correlated with greater bee abundance before bloom and during bloom (Spearman's $r = 0.86$) at all periods of the growing season. Considering the 2009 experimental sites separately ($N = 4$), there was a very strong association between number of species and percent natural area at 1,000 m and 2,000 m radii around fields ($R^2 = 0.93$, $P = 0.03$). All four fields sampled in 2009 had higher species richness, with an especially diverse bumble bee assemblage, compared with sites sampled in 2010.

Stepwise multiple regression confirmed the importance of natural area in predicting bee response but indicated that the combined effect of land cover vari-

Table 2. Simple linear regression model estimates for response of bee community to individual land cover variables and sum of total natural area at 2,000-m field buffer (*, $P \leq 0.05$; **, $P \leq 0.01$)

Land cover classification	Data set	Model R^2	Model P	Slope	\pm SE
Herbaceous	Abundance	0.19	0.06	0.002	0.001
Forest	Abundance	0.21	0.05*	0.001	0.0005
Crop	Abundance	0.14	0.11	-0.0002	0.0001
Total natural	Abundance	0.26	0.03*	0.03	0.01
Herbaceous	Richness	0.34	0.009**	0.002	0.0005
Forest	Richness	0.49	0.0009**	0.0008	0.0002
Crop	Richness	0.10	0.20	-8.2×10^{-5}	$6.1 \text{ by } 10^{-5}$
Total natural	Richness	0.27	0.02*	0.013	0.005

ables provided the most explanatory, minimal model in explaining wild bee response. Proportion forested area and herbaceous area around fields were significant predictors of species richness during bloom ($Y = -0.79 + 0.006\text{Forest} + 0.013\text{Herbaceous}$, $F = 7.92$, $R^2_a = 0.43$, $P = 0.004$). Proportion total natural area around fields and temperature were significant predictors of log transformed bee abundance ($Y = 9.12 - 0.10\text{Temperature} + 0.03\text{Natural area}$, $F = 7.77$, $R^2_a = 0.43$, $P = 0.004$). Temperature by itself had an inverse association with species richness ($Y = 48.89 - 0.54\text{Temperature}$, $F = 7.57$, $R^2 = 0.31$, $P = 0.01$) and bee abundance ($Y = 12.36 - 0.13X$, $F = 9.39$, $R^2 = 0.36$, $P = 0.007$) in pan traps. Once again, significant associations between land cover variables and bee community only were detected during bloom.

Landscape Level Influence on Individual Taxa. Wild bees with different floral preferences may demonstrate population level fluctuations that are unique and perhaps independent from land cover. Because several taxa, namely the genus *Lasioglossum*, the green bees (genera of *Agapostemon* spp., *Augochlora* spp., and *Augochlorella* spp.), and the family Apidae, were the dominant bees present in pan traps during bloom, we examined taxa level response to changes in land cover. Beginning at the smallest buffer distance, there were no significant associations between natural area and *Lasioglossum* ($R^2 = 0.17$, $P = 0.08$), Apidae ($R^2 = 0.01$, $P = 0.68$), or green bees ($R^2 = 0.14$, $P = 0.11$). Only *Lasioglossum*, the most commonly collected genus, had a significant positive association with proportion of surrounding natural area at buffer distances $\leq 1,500$ m ($R^2 = 0.29$, $P = 0.02$). Bumble bee abundance had no association with natural or forested areas. Species and genera level associations were slightly stronger than the associations with total bee abundance and surrounding natural area. Similar to overall abundance comparisons, there were no significant associations between any taxa and land cover in prebloom sampling.

Wild Bee Dynamics in Bloom. Wild bee abundance in pan traps was significantly reduced during bloom compared with prebloom samples ($t_{21} = -2.92$, $P = 0.008$). A similar trend was observed with bee richness also being lower during bloom ($t_{14} = 3.34$, $P = 0.005$). This reduction coincided with a decrease in dominance of wild bees relative to managed honey bees when cucumber was flowering. The number of species observed in fields during bloom ranged from three in a field surrounded by a low proportion natural area to 26 in a field surrounded by a high proportion natural area. As a whole, there was greater bee diversity in prebloom sampling with the exception of two fields where the number of species remained static and another field where it increased. The highest number of species was collected before bloom at several fields in areas of high agricultural use. Comparing the abundance of the most common species revealed that mean abundance was significantly higher before bloom for dominant species including *A. texanus* ($t_{15} = 2.82$, $P = 0.01$), *L. leucozonium* ($t_{14} = 3.49$, $P = 0.004$), and *Agapostemon virescens* (Fabricius) ($t_{15} = 3.52$, $P =$

0.003). Within bloom, some species were present more frequently and at discrete time intervals. As an example, *Bombus* spp. and *Melissodes bimaculata* (Lepeletier) were most abundant from July to the latter portion of August.

Discussion

Bees foraging in cucumber represented a wide range of feeding habits, body sizes, and life history characteristics. This diverse bee population exhibited a positive response to natural area at spatial scales of 1,500–2,000 m around fields. Specifically, herbaceous and forested areas, the dominant subclasses of natural area within the Central Sands, had a combined positive linear relationship with wild bee diversity measured from pan traps and floral observations. Pan-trap collected bees had a more general association with overall natural area. This response of bee abundance to natural area was similar to previous work comparing the relationship of flower visiting bees and natural area (Steffan-Dewenter et al. 2002, Kremen et al. 2004) as well as the relationship of pan-trap collected bees and forested area (Watson et al. 2011). Median bee abundance was three times higher when natural and semi-natural area composed $>75\%$ of the total area surrounding fields. A single site from 2009, where bee abundance was five to 20 times greater than all remaining sites, could have been influential in strengthening the positive association with landscape. Simple linear regression without the 2009 site produced a slightly lower association with natural area but was, nonetheless, significant at the two highest buffers. Overall, increasing the spatial scale around cucumber fields to include buffers of 1.5–2 km provided a more positive response of bee abundance and diversity and has been described as an optimal scale related to crop pollination (Kremen et al. 2004).

An immediate question that emerges is why models analyzing land cover at local buffer distances (250–750 m) had the weakest predictive value for bee abundance and richness in pan traps during bloom? Firstly, all sites had accessible floral resources through wild flowers or forested areas at one more field borders. The availability of suitable forage at field margins ensures the opportunity for alternate resources over longer periods and enhances bumble bee abundance (Pywell et al. 2005). Including greater amounts of land in buffers is likely to encompass a more complex landscape containing a diversity of crops and plants beneficial for insect biodiversity (Tscharntke et al. 2005). These plant communities can contain nesting sites and potential noncrop resources that benefit a wide range of bees (Westrich 1996), thus offering pollinators an incentive to remain within foraging distance of cucumber. Despite the potential for including a more diverse plant assemblage, the presence of additional floral resources may not be suitable for species with restricted floral preferences, such as *P. pruinosa* (Julier and Roulston 2009). Even though diverse floral resources may only support a fraction of the pollinator community, the availability of alternate pollen sources

near field edges would be expected to facilitate the resilience of bees when a managed crop is not flowering.

The heterogeneous composition of the Central Sands, which includes small gardens, pastures, and wild flowers, offers evidence of bee resilience in spite of habitat fragmentation. A meta-analysis by Winfree et al. (2009) determined that only extreme habitat loss (i.e., <10% remaining natural area) was a significant predictor for a decrease in bee richness and abundance. In this scenario, no cucumber field was truly isolated from alternate floral resources. In fact, most fields in this study would be classified as situated within a heterogeneous agricultural landscape according to Tscharntke et al. (2005), because the complexity in land cover may compensate for a loss in biodiversity. This connectivity between crop and noncrop habitats also benefits natural enemies (Tscharntke et al. 2007) by creating patchiness for migration and host location. The similar abundance of wild bees and honey bees in pan traps suggests that the floral requirements of numerous species are satisfied within the framework of a fragmented agroecosystem. Moderately fragmented areas can stabilize pollinator abundance across fields not isolated from natural area (Garibaldi et al. 2011b), and wild bees can even provide a majority of floral visits in these landscapes (Winfree et al. 2008). Although few wild bees were recorded visiting cucumber flowers, the positive association between floral observations and natural area at a smaller buffer lends support to the importance of local, albeit patchy, resources. Studies including fields in regions of extreme land simplification have been implicated for providing more significant landscape effects on wild bees (Winfree et al. 2009), and wild bee communities may remain suitable pollinators in areas of moderate habitat loss.

Environmental stress and preferred floral hosts may be more indicative of a bee's success as a pollinator, because some species are present in fields irrespective of the distance from natural habitat (Greenleaf and Kremen 2006). In this study, only *Lasioglossum* spp. in pan traps responded significantly to increasing natural area at buffers >1,500 m. This appears counterintuitive, as sweat bees have limited foraging ranges. However, natural area outside of fields may not be the dominant predictor for some species of ground-nesting bees in the genera *Lasioglossum* and *Melissodes*, which nest within field borders (Kim 2004). The proximity of natural area has a varying effect on bees based on their degree of specialization and body size (Williams et al. 2010) and may explain the lack of a landscape effect with bumble bees. An improved understanding of the effects of nesting habits of individual species and other farm management practices may explain this result and the lack of a uniform, positive response to natural area across fragmented systems (Winfree and Kremen 2009). When considering the activity of individual bee species, a loss of preferred plant families rather than the entirety of local land cover would have a greater impact.

Factors including increased herbicide use (Gabriel and Tscharntke 2007), exposure to weather extremes, or changes in soil composition (Dormann et al. 2008) confound the association between natural area and wild bee community. The above variables not directly related to landscape may fluctuate over time and drive poorer resource quality. One of these, the negative influence of temperature on bee abundance associated with pan trap captures, was a surprise, because temperatures recorded were above minimum foraging thresholds for social species (Corbet et al. 1993) and within the range for bee activity. It is possible that this relationship was influenced by bumble bees, which are active in cooler weather (Heinrich 2004). The response to temperature was reversed in floral observations with a positive, but not statistically significant, association with bee abundance. Flower opening often responds to temperatures, and flowers that require a longer period to open in cool, dark conditions (van Doorn and van Meeteren 2003) might result in a temperature dependent attraction to pan traps.

The dramatic decrease in pan-trap collected wild bees during bloom demonstrates the shortcomings of passive sampling and a lack of floral visits by unmanaged pollinators. The bare, flowerless nature of fields before bloom combined with the presence of colored pan traps may have attracted bees that otherwise would not forage in cucumber fields. Bees may be drawn to cucumber as a secondary host, but pan traps cannot provide conclusive information regarding this and potential pollen transfer. It is further assumed that a high number of generalist species, such as *L. leucozonium*, were collected because of the large, ephemeral source of nectar and pollen in fields. The smaller size of this and other bees could necessitate a greater number of floral visits for pollen deposition compared with pollination provided by bumble bees (Stanghellini et al. 1997). Furthermore, the high density of cucumber flowers could have competed with pan traps for bee visits and prevented bees from flying into pan traps. The conclusion that honey bees account for the majority of visits in cucumber would be strengthened by collecting pollen from the most abundant bees in pan traps. This will determine if similarities in honey bee and wild bee capture rates were because of a sampling of foraging bees flying through fields or if wild bees indeed visit flowers but were not accounted for with the level of observations from this study.

Employing strategies that protect natural areas near cropping systems ensures a pollinator community that better withstands disturbance, because the level of noncrop habitats surrounding fields affects wild bee communities in fragmented areas (Steffan-Dewenter et al. 2002, Williams and Kremen 2007). This option would require management tools that minimize harm against bees during bloom and for the duration of the growing season such as limiting tilling that threatens squash bees within fields (Shuler et al. 2005). Ultimately, the unpredictable nature of wild bee populations as well as large field sizes (Isaacs and Kirk 2010) are major reasons that honey bees are used as the preferred pollinator of pickling cucumber. Our results

suggest that unmanaged solitary bees are visiting cucumber and should be further examined for their role in cucumber pollination. The diverse bee community foraging within fields and visiting flowers is a positive signal that present levels of natural area in a fragmented agroecosystem can sustain wild bees that may complement the pollination services of honey bees.

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