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Influence of bioenergy crops on pollinator activity varies with crop type and distance

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Abstract

Compared to traditional arable crops, second-generation perennial energy crops (PECs) are generally associated with increased biodiversity and ecosystem services, but robust experimental studies on this subject are few. Consequently, the potential for PEC cultivation to contribute to enhanced pollination processes in adjacent farmland remains unclear. In a 4-year field study across multiple sites and two PECs (*Miscanthus x giganteus* and willow short-rotation coppice), we examine whether pollinator visits to crop margin wildflowers were augmented by PEC cultivation. Each field was paired with two cereal fields, one adjacent to the PEC and one distant, and we recorded wildflower visits to crop margins by three pollinator groups: hoverflies, bumblebees and butterflies/moths. We also quantified floral resources, since crop-specific management seemed a likely means of influencing margin wildflowers and thus pollinator activity. Our results add quantitative support to the suggestion that PECs should enhance ecosystem processes in agri-landscapes. However, benefits were highly context-dependent. Consistent enhancement of pollinator activity in margins of PEC fields was only apparent for willow where the relative frequency of flower visitation was higher for all three pollinator groups compared to adjacent or distant cereals. This distribution was most likely positively associated with the increased availability of preferred food plants in willow margins. In *Miscanthus*, by contrast, opposing trends arose for different pollinator taxa: Lepidoptera were the only pollinator group more frequently associated with PEC margins; bumblebees showed no variation while hoverflies were comparatively more abundant in distant cereal margins than in other crop types. Future land-use practices should consider how PEC identity affects both target species and ecosystem processes. Tackling anthropogenic climate change through cultivation of willow, in particular, may yield local conservation benefits for both wildflowers and pollinators, although strategic cultivation of PECs to enhance pollination processes in the wider agri-environment may not be achievable.

KEYWORDS

agriculture, biodiversity, bioenergy, biofuel, conservation, *Miscanthus*, pollination, willow short-rotation coppice

1 | INTRODUCTION

A global decline in insect pollinator abundance and diversity is well established and associated ramifications for crop and wildflower pollination widely debated (De Palma et al., 2016; Hallmann et al., 2017; Potts et al., 2010; Vanbergen & Insect Pollinator Initiative, 2013; but see Ghazoul, 2005). The impact of agricultural intensification on insect pollinators like bees has received particular attention, driving major declines in both wild and managed species (Biesmeijer et al., 2006; Goulson, Hanley, Darvill, Ellis, & Knight, 2005; Vanbergen & Insect Pollinators Initiative, 2013). Other pollinators are also faring poorly; European hoverfly communities are represented by fewer species (Biesmeijer et al., 2006) while European Lepidoptera have declined in abundance and distribution (Fox et al., 2013, 2015; van Dyck, Strien, Maes, & Swaay, 2009; van Swaay, Nowicki, Settele, & Strien, 2008). Conservation actions to halt and reverse these declines are necessary, both to retain biodiversity and the key ecosystem service (ES) pollinators provide (Gallai, Salles, Settele, & Vaissierre, 2009; Goulson, Rayner, Dawson, & Darvill, 2011).

Counter to historic trends, future land-use changes could help reverse pollinator decline. Although the success of “pollinator-friendly” agri-environment schemes (e.g., wildflower strips) are debated (Batáry, Dicks, Kleijn, & Sutherland, 2015), and further research necessary (Wood, Holland, & Goulson, 2016), effects on pollinator communities and associated ES provision appear largely positive (McCracken et al., 2015). Organic farming has similarly been associated with benefits to pollinator communities (Holzschuh, Steffan-Dewenter, Kleijn, & Tscharntke, 2007; Tuck et al., 2014), but the likely contribution of organic farms to the global food supply remains doubtful (Seufert, Ramankutty, & Foley, 2012). Changes in conventional cropping systems may also contribute to pollinator conservation. The cultivation of mass-flowering crops (MFCs) such as oilseed rape (*Brassica napus* L.) and field bean (*Vicia faba* L.) has, for example, been linked to increased bumblebee abundance at the landscape-scale and more visits to wildflowers in the margins adjacent to the crop (Hanley et al., 2011; Holzschuh et al., 2007).

As part of a global commitment to reduce greenhouse gas emissions, the cultivation of bioenergy crops (BECs) is now widely practised. In particular, so-called second-generation lignocellulosic BECs such as the fast-growing perennial grass, *Miscanthus*, and short-rotation coppice (SRC)

species (principally willow and poplar) are widely grown throughout Europe and North America (Somerville, Youngs, Taylor, Davis, & Long, 2010). Although there is concern that perennial energy crops (PECs) may displace traditional food crops (Gelfand et al., 2013), it is widely held that PECs are locally beneficial for farmland biodiversity, due to the relatively low chemical inputs and disturbance regimes they require (Bourke et al., 2014; Dauber, Jones, & Stout, 2010; Rowe et al., 2011; Wiens, Fargione, & Hill, 2011). In addition, key ecosystem processes such as decomposition and predation are enhanced within the PEC compared to adjacent cereal crops (Rowe et al., 2013). Taken together, these findings have led to the suggestion that the strategic location of PECs could boost local pollinator abundances and thus benefit ecosystem service provision. This in turn would enhance ecosystem processes such as flower visitation to margin wildflowers, both within the field and in the local arable landscape (Manning, Taylor, & Hanley, 2015; see also Holland et al., 2015; Milner et al., 2016).

As an important ES in the agri-environment, any benefits accruing to pollinators and pollination from the strategic cultivation of PECs are of considerable importance, not least because of widespread concerns about global pollinator declines. Consequently, there is a pressing need to understand how pollinator communities respond to PEC cultivation (Manning et al., 2015; Rowe et al., 2013). Local pollinator spillover from MFCs to adjacent field margin wildflowers (Hanley et al., 2011) offers a precedent to investigate whether PECs may similarly enhance pollination processes to margin flowers, both within the field and surrounding landscape. This hypothesis remains largely untested, however. In this study, we investigated the influence that *Miscanthus* and willow SRC cultivation had upon guild-specific pollinator visits to native plants in margins adjacent to the crop, and compared this to margins of traditional annual cereals in a replicated, paired design. Visitation within the PEC field is principally management driven rather than “spillover” of pollinators from the crops themselves, as the crops are either sterile (*Miscanthus*) or do not provide floral resources during the study period (willow). In addition, we investigated the potential for locally enhanced flower visitation in the surrounding landscape by comparing frequency of pollinator visits along the margins of adjacent and distant conventional cereal fields. All surveys were undertaken in England, United Kingdom.

2 | MATERIALS AND METHODS

2.1 | Study crops and sites

Miscanthus x giganteus Greef et Deu. is a perennial grass of Asian origin, a sterile hybrid of *M. sinensis* Anderss. and *M. sacchariflorus* (Maxim.) Hack. Despite its C_4 physiology, *Miscanthus* produces good yields in temperate climates averaging between 12 and 16 ODT (oven-dried tonnes) ha^{-1} in England and growth rates in excess of 2.5 m per year (DEFRA, 2007). The rhizome remains viable in the soil for 15–20 years, reducing tillage and soil disturbance. Moreover, unlike conventional arable crops, *Miscanthus* has a low requirement for agrochemical inputs; high nitrogen-use efficiency enables nutrient recycling back to the rhizome or soil (as leaf-litter) prior to winter/spring harvest. Willow (typically *Salix viminalis* L.) SRC regrows rapidly from stools over a typical 3- to 4-year coppice cycle (DEFRA, 2004). Willow is densely planted with ~15,000 trees/ha; an erect growth habit produces high yields (up to 12 ODT ha^{-1} year $^{-1}$) for up to 30 years (DEFRA, 2004).

Surveys of crop margin visits by pollinators for *Miscanthus* centred on six locations in southwest England, and for willow SRC, five locations in central England, that is, Nottinghamshire and Lincolnshire (Table 1). Each site comprised three fields (Figure 1), a focal PEC, an adjacent cereal and a distant cereal situated a minimum of 920 m from the focal PEC or any other BEC or MFC (based on field centres); this distance is thought to minimize non-independence of mobile bumblebee pollinators (Knight et al., 2005). As far as possible, cereal fields in each “triplicate” were matched with the focal PEC for margin characteristics, field area, slope, altitude and aspect and for the most part were represented by wheat (*Triticum* spp. L.) with barley (*Hordeum vulgare* L.) as the alternative where wheat was unavailable. Both crops are principally wind-pollinated, hence not themselves key floral resources, and represent the two most commonly cultivated crops in the UK (DEFRA, 2015). Investigation of *Miscanthus* and cereal controls involved fieldwork in 24 fields across 3 years (2012, 2014 and 2015), while 22 fields were studied across 2 years (2013 and 2015) for comparison of willow and controls. During data collection, it was established that treatments did not differ significantly in terms of relative land cover classes in the landscape (1 km radius), wind speed, cloud cover or temperature.

2.2 | Pollinator surveys

Investigation of pollinator activity along crop margins followed the methods outlined by Hanley et al. (2011) and Hanley and Wilkins (2015). For *Miscanthus*, we set out 50 m \times 2 m transects along the centre part of opposing

margins in each field, with equivalent margin aspect between the three crop fields comprising each site; in SRC, we used 100 m \times 2 m transects. Differences in transect length were purely for logistical reasons, and the length of transects was consistent across all sites for each PEC and their respective cereal control fields. Differences in transect length therefore do not bias the trends investigated for either PEC when compared to paired cereal controls as the length is identical between treatments; thus, relative trends are comparable between PECs. In southwest England (*Miscanthus*), field boundaries were comprised of established hedgerows dominated by native woody plants, for example, hawthorn (*Crataegus monogyna* Jacq.), English oak (*Quercus robur* L.), blackthorn (*Prunus spinosa* L.), dog rose (*Rosa canina* L.), blackberry (*Rubus fruticosus* L. agg.) and gorse (*Ulex europaeus* L.). A naturally colonizing, diverse basal flora included cock's-foot (*Dactylis glomerata* L.), foxglove (*Digitalis purpurea* L.), cleavers (*Galium aparine* L.), herb robert (*Geranium robertianum* L.), hogweed (*Heracleum sphondylium* L.), creeping buttercup (*Ranunculus repens* L.), red campion (*Silene dioica* (L.) Clairv.), hedge woundwort (*Stachys sylvatica* L.), and common nettle (*Urtica dioica* L.). Current UK agricultural policy requires a 1-m border between the field boundary and crop edge; for our fields, this border was comprised of perennial herb and grass species typical of hedgerow margins. This border, plus an additional 1 m extending into a point about half way into the hedgerow, formed the 2 m width of our transects in southwest England. In Nottinghamshire and Lincolnshire (SRC), field margins were dominated by *C. monogyna*. Species composition was similar to southwest England although thistles were a dominant component (e.g., spear thistle (*Cirsium vulgare* Savi (Ten.)) and meadow thistle (*C. dissectum* (L.) Hill)). Fields at Gainsborough did not contain hedgerows; uncultivated field margins were therefore compared using 2-m-wide transects from the crop edge, delimited by ditches. This did not influence results because hedgerows were absent in all treatments at Gainsborough and field margins were therefore comparable between willow and controls.

Miscanthus transects were walked between the hours of 09:00 and 16:00 on each of three or four separate occasions beginning late June, through July and August, on days favourable to pollinator activity (Goulson & Darvill, 2004). The longer willow transects were walked once per day between 10:00 and 18:00. Surveys encompassed transects undertaken across both the morning and afternoon. Due to separation between sites, it was impossible to survey all fields in a single day, but it was ensured that fields within each triplicate were surveyed during the same day, with the relative order randomly assigned.

We identified and recorded actively foraging insects (i.e., observed visiting an inflorescence) belonging to three

TABLE 1 Locations (approximate field centres) and characteristics of study sites in southwest and central England. Coordinates: WGS 1984. Information obtained using Google Earth (Google Earth, 2017). N, S, E and W are representative of cardinal directions

Year	Location	Crop	Lat. Lon.	Field Area (ha)	Altitude (m)	Aspect
2012	Buckfastleigh, Devon	Miscanthus	50° 28.330'N, 3° 47.621'W	12.6	95	SE
		Adjacent Cereal	50° 28.532'N, 3° 47.487'W	20	101	SE
		Distant Cereal	50° 26.144'N, 3° 47.016'W	5	133	SE
	Pelynt, Cornwall	Miscanthus	50° 21.886'N, 4° 31.222'W	4.8	142	S
		Adjacent Cereal	50° 21.916'N, 4° 31.118'W	4.4	145	S
		Distant Cereal	50° 22.925'N, 4° 31.239'W	4.2	121	NW
	St Minver, Cornwall	Miscanthus	50° 33.124'N, 4° 51.373'W	3.8	44	SW
		Adjacent Cereal	50° 33.240'N, 4° 51.334'W	5.6	53	SW
		Distant Cereal	50° 32.434'N, 4° 51.050'W	5.5	17	NW
	Wadebridge, Cornwall	Miscanthus	50° 31.518'N, 4° 46.450'W	2.2	106	NW
		Adjacent Cereal	50° 31.551'N, 4° 46.288'W	4.3	103	N
		Distant Cereal	50° 31.529'N, 4° 44.517'W	6.1	100	SW
2014	Eglosayle, Cornwall	Miscanthus	50° 31.560'N, 4° 48.191'W	7.1	76	W
		Adjacent Cereal	50° 31.560'N, 4° 48.024'W	7.9	75	SE
		Distant Cereal	50° 31.021'N, 4° 49.055'W	7.8	42	SW
	Pelynt, Cornwall	Miscanthus	50° 21.886'N, 4° 31.222'W	4.8	142	S
		Adjacent Cereal	50° 21.916'N, 4° 31.118'W	4.4	145	S
		Distant Cereal	50° 21.831'N, 4° 29.760'W	4.7	102	SE
	St Minver, Cornwall	Miscanthus	50° 33.124'N, 4° 51.373'W	3.8	44	SW
		Adjacent Cereal	50° 33.240'N, 4° 51.334'W	5.6	53	SW
		Distant Cereal	50° 33.226'N, 4° 50.177'W	2.9	18	NE
	Wadebridge, Cornwall	Miscanthus	50° 31.518'N, 4° 46.450'W	2.2	106	NW
		Adjacent Cereal	50° 31.551'N, 4° 46.288'W	4.3	103	N
		Distant Cereal	50° 31.380'N, 4° 44.462'W	4.3	100	W
2015	Lostwithiel, Cornwall	Miscanthus	50° 25.704'N, 4° 37.887'W	5.6	113	SW
		Adjacent Cereal	50° 25.857'N, 4° 37.483'W	7.1	134	NE
		Distant Cereal	50° 25.811'N, 4° 35.418'W	2.6	163	NW
	Pelynt, Cornwall	Miscanthus	50° 21.886'N, 4° 31.222'W	4.8	142	S
		Adjacent Cereal	50° 21.916'N, 4° 31.118'W	4.4	145	S
		Distant Cereal	50° 21.901'N, 4° 29.433'W	5.9	84	NE
	St Minver, Cornwall	Miscanthus	50° 33.076'N, 4° 51.233'W	5.4	47	SW
		Adjacent Cereal	50° 33.100'N, 4° 50.914'W	9.3	55	SE
		Distant Cereal	50° 33.226'N, 4° 50.177'W	2.9	18	NE
	Wadebridge, Cornwall	Miscanthus	50° 31.518'N, 4° 46.450'W	2.2	106	NW
		Adjacent Cereal	50° 31.551'N, 4° 46.288'W	4.3	103	N
		Distant Cereal	50° 31.380'N, 4° 44.462'W	4.3	100	W
2013	Newark, Nottinghamshire	Willow	53° 15.122'N, 0° 49.430'W	8.18	17	SW
		Adjacent Cereal	53° 15.089'N, 0° 49.257'W	7.35	21	S
		Distant Cereal	53° 14.835'N, 0° 48.686'W	10.96	10	SE
	Gainsborough, Lincolnshire	Willow	53° 26.036'N, 0° 48.150'W	5.49	2	E
		Adjacent Cereal	53° 25.898'N, 0° 48.098'W	8.93	2	E
		Distant Cereal	53° 27.172'N, 0° 47.815'W	7.8	5	SE

(Continues)

TABLE 1 (Continued)

Year	Location	Crop	Lat. Lon.	Field Area (ha)	Altitude (m)	Aspect
2015	Stapleford, Nottinghamshire	Willow	53° 6.590'N, 0° 43.029'W	11.01	17	E
		Adjacent Cereal	53° 6.557'N, 0° 42.898'W	7.82	18	S
		Distant Cereal	53° 6.703'N, 0° 42.037'W	9.36	16	SE
	Retford, Nottinghamshire	Willow	53° 16.490'N, 0° 59.394'W	7.49	40	SW
		Adjacent Cereal	53° 16.490'N, 0° 59.669'W	6.19	36	SW
		Distant Cereal	53° 16.951'N, 0° 59.071'W	8.84	37	NE
	Newark, Nottinghamshire	Willow	53° 14.758'N, 0° 49.295'W	13.1	15	SW
		Adjacent Cereal	53° 14.820'N, 0° 49.130'W	11.8	15	SE
		Distant Cereal	53° 12.814'N, 0° 49.838'W	5.1	27	E
	Gainsborough, Lincolnshire	Willow	53° 26.036'N, 0° 48.076'W	8.8	2	E
		Adjacent Cereal	53° 26.044'N, 0° 48.252'W	2.1	2	W
		Distant Cereal	53° 27.172'N, 0° 47.815'W	2	5	SE
	Stapleford, Nottinghamshire	Willow	53° 6.590'N, 0° 43.029'W	11.1	17	E
		Adjacent Cereal	53° 6.557'N, 0° 42.898'W	7.7	18	S
		Distant Cereal	53° 6.015'N, 0° 42.597'W	13	14	SW
	Whatton, Nottinghamshire	Willow	52° 55.840'N, 0° 54.436'W	4.6	30	NW
		Adjacent Cereal	52° 55.946'N, 0° 54.436'W	6.2	30	NW
		Distant Cereal	52° 56.489'N, 0° 54.342'W	14.2	26	NW

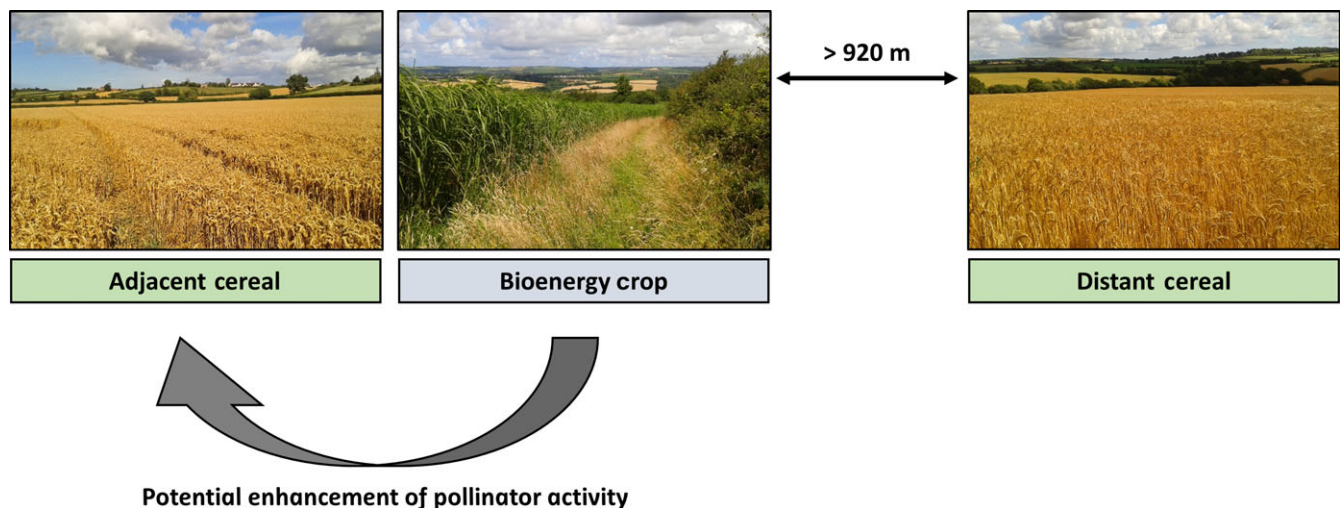


FIGURE 1 Triplicate experimental design. Figure shows field arrangement used at each site in both southwest England and central England in order to determine potential local enhancement of flower visitor activity in the margins of cereal fields neighbouring bioenergy crops

major pollinators groups, hoverflies, bumblebees and Lepidoptera, together with the plants upon which they foraged. Generally, individuals were identified to species level. However, due to the difficulty of separating workers of the subgenus *Bombus* s. str. (i.e., buff-tailed bumblebee (*Bombus terrestris* (L.)), white-tailed bumblebee (*B. lucorum* (L.)), northern white-tailed bumblebee (*B. magnus* Vogt.) and the cryptic white-tailed bumblebee (*B. cryptarum* (Fabricius))) in the field (Williams et al., 2012), we made no attempt to distinguish between these species and

throughout refer to this group collectively as *B. terrestris* agg. We did not capture foraging insects, but because transects were linear and completed relatively rapidly, it is extremely unlikely that the same individual was recorded more than once during each transect walk. A total of 564 pollinator transects were undertaken.

Immediately after completing insect surveys, we estimated the number of flowers of every plant species likely to be visited by pollinators along each transect to determine variation in floral resource availability. Estimates for total

flower number were achieved by counting the number of flowers on 10 separate inflorescences of a given plant species and then to multiply this mean value by the estimated total number of inflorescences observed along the transect. For Apiaceae and Asteraceae, an umbel and a capitulum were each considered to be a single “flowering unit.”

2.3 | Statistical analysis

Following graphical and statistical consideration of normality (Shapiro–Wilk) and homogeneity of variance (Levene's test), one-way ANOVA or Kruskal–Wallis tests were conducted to investigate “crop type” effects. Where appropriate, non-normal data were $\log_{10} + 1$ transformed in preference to non-parametric analyses; Welch's ANOVAs were run for normal but heteroskedastic data. It was not possible to use repeated-measures analysis because the crops present at some field sites differed between years (i.e., PECs were removed at certain sites or became unusable when cereal controls were rotated to alternative crops); sites with data across multiple years were therefore averaged across years for each site-crop combination, with either the mean proportion of flower visits, species richness, diversity or flower number acting as the replicate in the analyses. The proportion of flower visits was favoured in the analysis over raw count data as proportions prevented trends being influenced by any difference in the absolute number of transects undertaken in a given year. This was necessary as low visitation frequencies at the transect level meant that site counts were pooled transect totals rather than transect means. Without correction, greater survey effort in a particular year would have resulted in trends for that year contributing disproportionately to overall trends as counts would have been of a greater magnitude in more frequently surveyed years. Tukey's HSD and pairwise comparisons were used, respectively, for parametric and non-parametric post hoc analyses. Shannon–Wiener diversity indices were used as a measure of diversity for species-level identifications only. Species richness data encompassed all unique taxa including those at higher resolution than species when no overlap occurred with species-level identifications. Analyses were carried out using SPSS (version 22, IBM Inc.).

3 | RESULTS

In total, 7,747 insects belonging to the three target taxa (hoverflies, bumblebees, Lepidoptera) were observed visiting flowers in the margins of the three crop types studied. Across treatments, there were 52 and 55 insect “species” (unique taxa) described in central and southwest England, respectively. For bumblebee and Lepidoptera pollinator guilds, species richness was significantly higher next to

willow than along adjacent and distant cereal controls, respectively. Shannon–Wiener indices also revealed that Lepidoptera diversity was significantly higher in the margins of willow than distant cereals (Table 2). *Miscanthus* exhibited significantly higher Lepidoptera richness than distant cereals. However, no differences in species richness or diversity were apparent between *Miscanthus* and cereal controls for any other taxa.

Of the three target insect taxa, the majority of individuals observed in southwest England ($n = 2,531$ total flower-visiting insects) were hoverflies (76%), followed by bumblebees (17%) and Lepidoptera (7%). In central England ($n = 5,216$ total flower-visiting insects), hoverflies (49%) and bumblebees (35%) dominated, with Lepidoptera much less common (16%). Bumblebees represented the vast majority (88%) of bees for both regions and PECs, and all analyses of bees focus on this group only. The marmalade hoverfly (*Episyrphus balteatus* De Geer) was by far the most common of the hoverflies (62% of all observations), but the relative abundance of hoverflies in general (and this species in particular) varied considerably with respect to PEC type.

The top five most visited plant species accounted for at least 50% of visitations, often exceeding 80% of flower visits for some taxa in certain treatments (Supporting Information Appendix S1: Table S1–S6). In southwest England, most visits were to *Heracleum sphondylium* (27%), while in central England, most visits were to *Cirsium vulgare* (20%). The most visited plants were not the most regionally abundant however; hedge bedstraw (*Galium mollugo* L.) dominated in southwest England with 65% of flowers and *H. sphondylium* had greatest floral abundance in central England accounting for 15% of flowers.

When all three pollinator taxa were considered together, cumulative margin flower visits did not differ between *Miscanthus* and cereal controls ($F_{2,15} = 3.262$; $p = 0.067$; Supporting Information Appendix S1: Figure S1). This was not the case between willow and cereals however ($F_{2,12} = 20.256$; $p = <0.001$), with multiple comparisons demonstrating significantly higher pollinator flower visitation in willow when compared to both adjacent ($p = 0.001$) and distant ($p = <0.001$) cereals, with no difference between controls ($p = 0.903$; Supporting Information Appendix S1: Figure S1). In order to determine whether all three taxa exhibited a similar lack of response to *Miscanthus*, and to establish which taxa were driving the elevated flower visits in willow, further taxonomic breakdown of flower visitation was conducted.

3.1 | Hoverflies

A significant “crop type” effect was found for flower-visiting hoverflies in *Miscanthus* field triplicates ($F_{2,15} = 9.2$;

TABLE 2 Mean species richness and Shannon–Wiener diversity indices for transects undertaken in the margins of two perennial energy crops, *Miscanthus x giganteus* and willow short-rotation coppice, and their respective cereal control fields. Standard error of the mean (SE) and output of statistical analysis are given for each pollinator guild that was recorded visiting flowers, as well as the respective floral composition

	Hoverfly			Bumblebee			Lepidoptera			Margin wildflowers		
	Mean	SE	Test Output	P	Mean	SE	Test Output	P	Mean	SE	Test Output	P
Species richness												
Willow	8	0.88	$F_{2,12} = 3.053$	0.085	5.1 ^a	0.29	$F_{2,12} = 4.657$	0.032	9.4 ^a	0.98	$H_{2,12} = 10.231$	0.006
Adjacent cereal	5.3	0.97			3.7 ^b	0.3			4.9 ^{a,b}	0.87		
Distant cereal	5.9	0.51			4.1 ^{a,b}	0.4			3.8 ^b	0.46		
Miscanthus	6.6	1.13	$F_{2,15} = 0.544$	0.591	3.6	0.6	$F_{2,15} = 0.147$	0.865	3.7 ^a	0.92	$F_{2,15} = 5.857$	0.013
Adjacent cereal	6.2	0.84			3.5	0.59			2.3 ^{a,b}	0.38		
Distant cereal	7.8	1.38			3.2	0.34			1.1 ^b	0.48		
Species diversity												
Willow	0.92	0.08	$F_{2,12} = 0.486$	0.627	1.11	0.05	$H_{2,12} = 4.16$	0.125	1.73 ^a	0.17	$F_{2,12} = 5.288$	0.023
Adjacent cereal	0.78	0.1			0.86	0.11			1.22 ^{a,b}	0.16		
Distant cereal	0.85	0.12			0.83	0.21			1.07 ^b	0.12		
Miscanthus	1.33	0.2	$F_{2,15} = 0.728$	0.499	1	0.17	$F_{2,15} = 0.105$	0.901	0.87	0.22	$F_{2,15} = 2.228$	0.142
Adjacent cereal	1.11	0.11			0.92	0.2			0.57	0.16		
Distant cereal	1.11	0.11			0.91	0.1			0.31	0.18		

Note. $\alpha = 0.05$, different letters indicate significant difference between treatment means following Tukey's HSD or paired comparisons.

$p = 0.002$). Multiple comparisons revealed significantly greater flower visits in the field margins of distant cereals than those of *Miscanthus* and cereals adjacent to *Miscanthus* (Figure 2a); there was no significant variation between *Miscanthus* and adjacent cereal margins. For willow, multiple comparisons revealed that a significant “crop type” effect ($F_{2,12} = 7.216$; $p = 0.009$) arose due to greater hoverfly visitation in the PEC margins compared to both distant cereal controls and adjacent cereal controls, with no difference between the two controls (Figure 3a).

3.2 | Bumblebees

Abundances of bumblebees actively visiting flowers were significantly different among willow and cereal controls (Figure 3b, $F_{2,12} = 27.653$; $p < 0.001$), but varied remarkably little between *Miscanthus* and cereals (Figure 2b, $F_{2,9.507} = 0.832$; $p = 0.465$). Pairwise testing across willow triplicates highlighted a more than threefold significant increase in bumblebee visitation along SRC margins, compared to both adjacent and distant cereals (Figure 3b). *B. terrestris* agg. dominated bumblebee visits in all treatments (with 54% of visits). Red-tailed bumblebees (*B. lapidarius*, with 15% of visits) and common carder bees (*B. pascuorum*, with 12% of visits) were relatively common, but patchily distributed.

3.3 | Lepidoptera

Lepidoptera were more responsive to PEC cultivation than the other two guilds. We found a significant “crop type” effect in *Miscanthus* (Figure 2c, $F_{2,15} = 10.508$; $p = 0.001$) and in willow (Figure 3c, $F_{2,12} = 108.387$; $p < 0.001$). For both willow and *Miscanthus*, Lepidoptera were significantly more abundant floral visitors along PEC margins than along margins of distant cereals. In willow, a significant difference additionally emerged between margins of willow and adjacent cereal fields. Overall Lepidoptera abundances among nectaring insects were far higher in central England than the southwest. In central England, three species represented >45% of visits with meadow brown (*Maniola jurtina* (L.)) comprising 17%, small white (*Pieris rapae* (L.)) 15% and small tortoiseshell (*Aglais urticae* (L.)) 14% of Lepidoptera floral visits. Gatekeeper (*Pyronia tithonus* (L.)) had highest overall abundance in the southwest, accounting for 20% of flower visits.

3.4 | Floral resources

A total of 93 flowering plant species were present along transects in southwest England and 59 in central England. There was, however, no evidence for variation in floral

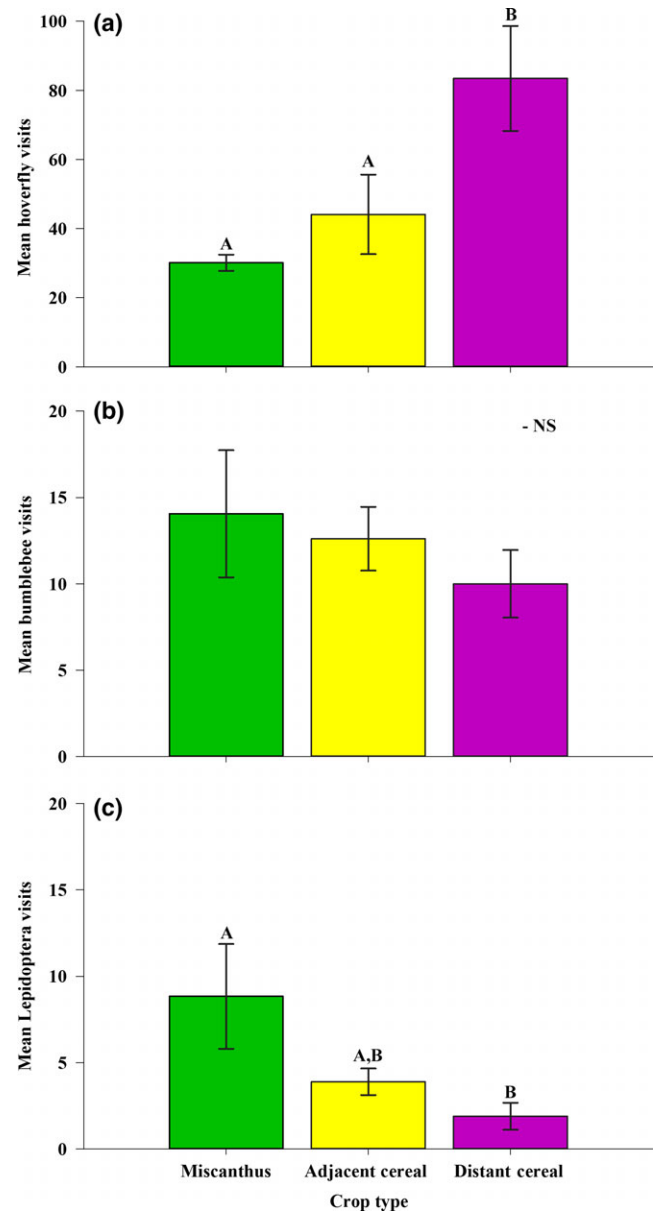


FIGURE 2 Mean (\pm SE) margin wildflower visits by target insect guilds across triplicate fields, *Miscanthus*, adjacent and distant cereals, at sites in southwest England. Different letters indicate significant differences between treatment means following Tukey's HSD ($p < 0.05$)

species richness and diversity between each PEC and their cereal controls (Table 2). Floral availability (i.e., total flower counts along floral transects) did not vary between *Miscanthus* and cereal controls ($H_{2,15} = 0.082$; $p = 0.96$), but did differ significantly between willow and cereal controls ($F_{2,9} = 9.001$; $p = 0.007$); post hoc comparisons showed more flowers in willow than both adjacent ($p = 0.016$) and distant cereals ($p = 0.01$). Flowers of species important to pollinator guilds (i.e., the 2–8 plant species accounting for 80% of visits) were more abundant in willow margins for flowers visited by bumblebees ($F_{2,9} = 11.259$; $p = 0.004$) and Lepidoptera ($F_{2,9} = 11.401$; $p = 0.003$), compared to

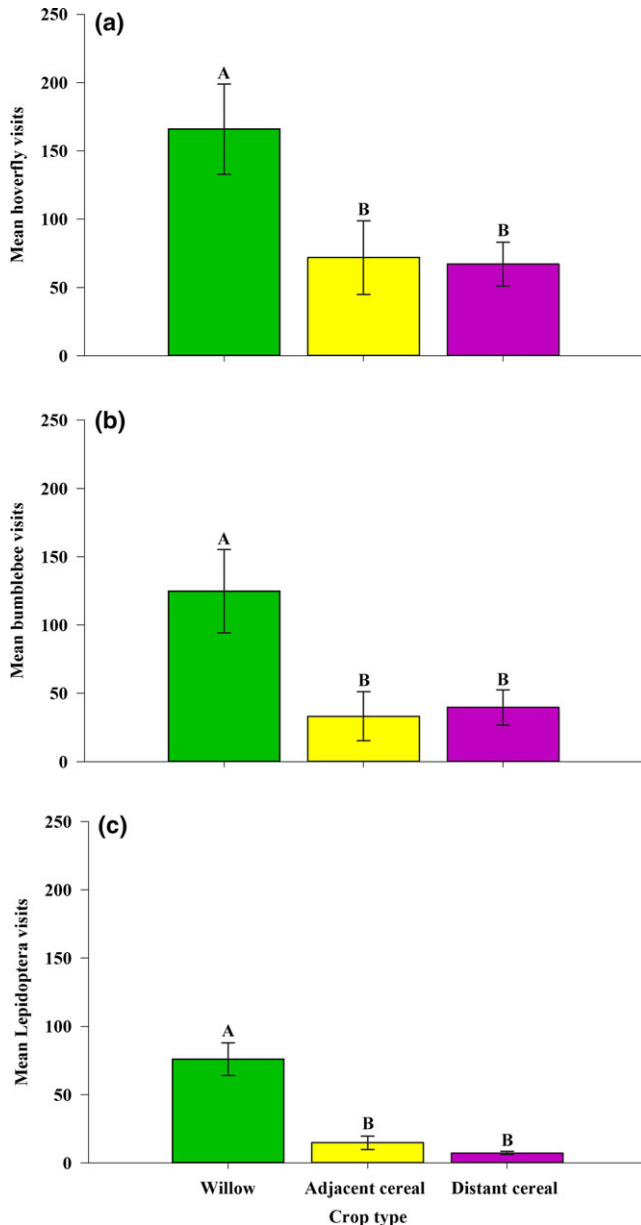


FIGURE 3 Mean (\pm SE) margin wildflower visits by target insect guilds across triplicate fields, willow short-rotation coppice and adjacent and distant cereals, at sites in Nottinghamshire and Lincolnshire, central England. Different letters indicate significant differences between treatment means following Tukey's HSD ($p < 0.05$)

adjacent ($p = 0.025$) and distant controls ($p = 0.003$) (Supporting Information Appendix S1: Table S9). Although non-significant, flower counts of plant species receiving 80% of hoverfly visits were three- and fourfold higher in willow than adjacent and distant cereals, respectively. Trends are similar for each pollinator group as similar subsets of plants were preferred across pollinator guilds. The dominant individual pollinator species for bumblebees (*B. terrestris* agg.) and for butterflies (*M. jurtina*) similarly had access to significantly higher abundances of their preferred flowers

(*C. vulgare*; *R. fruticosus*; *H. sphondylium*; *C. dissectum*; and white clover (*Trifolium repens* L.)) in willow compared to adjacent and distant cereals ($p = <0.05$; Supporting Information Appendix S1: Table S12).

4 | DISCUSSION

Cultivation of second-generation BECs has been widely observed to have positive implications for biodiversity compared to conventional arable cropping systems (Milner et al., 2016; Rowe et al., 2013, 2011); our results generally corroborate this pattern. When taken together, we found evidence that PEC willow cultivation significantly increased pollinator margin flower visitation for all pollinator guilds (hoverflies, bumblebees and Lepidoptera), while *Miscanthus* had a positive effect only for Lepidoptera. However, these effects attenuated quickly with distance from the PEC and we found no evidence to support the (largely untested) hypothesis that the increases in biodiversity associated with PEC cultivation would have a concomitant benefit to the provisioning of an ecosystem process in the surrounding landscape (Manning et al., 2015); that is, there was no instance where pollinator numbers along adjacent cereal margins were significantly higher than distant cereals. The nearly threefold decline in the numbers of flower-visiting hoverflies when going from the edge of the distant cereals to *Miscanthus* margins was particularly unexpected. Furthermore, hoverfly activity in distant cereals was significantly higher than in cereals adjacent to *Miscanthus*, suggesting that *Miscanthus* cultivation is also likely to negatively affect hoverfly–wildflower interactions in fields surrounding the PEC. Our results contrast markedly with the neutral effect observed by Bourke et al. (2014) working on *Miscanthus* in Ireland. While regional differences in community composition may be important, that is, in the study by Bourke et al. (2014), the sun fly (*Helophilus pendulus*) was dominant rather than *Episyrphus balteatus*, there were also differences in methodology. Bourke et al. (2014) used pan traps (perhaps attractive to *H. pendulus* given its aquatic larvae), while we quantify abundance of insects actively visiting wildflowers (an ecosystem process rather than a biodiversity metric).

As floral resource availability varied little between *Miscanthus* and cereal margins in our study, other factors likely explain the differences in Lepidoptera and hoverfly activity we observed in southwest England. One possibility for hoverflies is that there are few major *Miscanthus* pests in Britain (DEFRA, 2007); aphid abundance has been shown to be particularly low (Semere & Slater, 2007). It is possible that female hoverflies in particular foraged in areas (i.e., cereal crops and margins) where aphid populations, and thus larval brood sites, were more abundant (Almo-hamad, Verheggen, Francis, & Haubruge, 2007).

Regardless of the underlying mechanism, lower hoverfly activity in *Miscanthus* and surrounding cereals implies not only a reduction in pollination services to margin plants, but perhaps diminished aphid biocontrol by aphidophagous hoverfly larvae (Tenhumberg & Poehling, 1995).

Lepidoptera visitation, in contrast, was enhanced along *Miscanthus* margins, although the relatively low overall frequency of visits, even within the PEC margins, might suggest limited ES benefit, particularly as Lepidoptera often visit only a small number of preferred nectar plants (Jennersten, 1984). Since floral resource availability was unlikely to account for crop-specific variation in imago numbers, the variation in larval food plant abundance (e.g., uncut cock's-foot *Dactylis glomerata* L. used by large skipper *Ochlodes sylvanus* (Esper)) may explain our observations. Nonetheless, for a group of species suffering widespread decline in the agri-environment (Fox et al., 2015, 2013), our findings corroborate other studies showing benefits of *Miscanthus* to Lepidoptera (Semere & Slater, 2007).

Generally thought to be widely involved in pollinator service provision (Garratt et al., 2014), the limited response of bumblebees to *Miscanthus* cultivation observed here suggests that local enhancement of pollinator visitation in the agri-environment (Manning et al., 2015), or indeed wider conservation value of this crop to bumblebees, is unlikely (see also Stanley & Stout, 2013). In contrast to *Miscanthus*, bumblebee activity (in addition to Lepidoptera) was higher along willow SRC margins than either adjacent or distant cereals, although again, this did not enhance visitation in adjacent cereal fields. Given that we observed consistently more preferred (and total) flowers in willow SRC margins than cereal margins, the most parsimonious explanation for increased pollinator visitation (and increased Lepidoptera diversity) in willow is that insects were responding to higher floral resource availability (Hanley & Wilkins, 2015; Pywell et al., 2011; Sutherland, Sullivan, & Poppy, 2001). Several authors (Cunningham, Bishop, McKay, & Sage, 2004; Rowe et al., 2011) have noted how the low chemical input and low disturbance regimes applied to woody PECs have a positive effect on associated plant communities. Remarkably, however, aside from butterflies, to our knowledge, no previous study has attempted to examine how cultivation of woody SRCs (e.g., willow or poplar) affects the flower visitation of other pollinator taxa compared with conventional arable crops. Our data are the first, therefore, to underscore the importance of willow cultivation for hoverflies and bumblebees which likely benefit from elevated floral resource provision. However, without further investigation it is not possible to make unequivocal statements about the specific factors driving pollinator trends; it may be that differences in weed flora within the crop influence pollinator activity, for

example, and suggestions made here regarding increased larval food plant abundance remain qualitative rather than quantitative. Nonetheless, the evidence we present makes it clear that, when compared to cereals, agronomic and/or management practices associated with the two PECs alter trends in pollinator flower visitation.

Although we found little evidence for the enhancement of pollinator activity over long distances as a result of *Miscanthus* or willow PEC cultivation (Manning et al., 2015), willow offered considerable local benefits to the pollinator community. However, we acknowledge that our study focuses on a single ecosystem process (flower visitation) and the consequences for plant reproduction (i.e., fruit/seed set) require further attention. Although the dominant flower visitors in this study are understood to be effective pollinators in many systems, future investigation of pollinator effectiveness (King, Ballantyne, & Willmer, 2013) would also expand on our findings. In addition, to determine whether elevated bumblebee visitation seen in willow is a consequence of increased colony size or increased nest number, genetic analysis is necessary. Furthermore, while we explicitly set out to investigate whether PECs enhance pollinator flower visitation in adjacent cereal crops, we did not consider how the presence of the PEC at the landscape-scale might influence overall pollinator numbers and thus pollinator service provision. In MFCs for example, a putative "dilution" effect has been evidenced at the landscape-scale, as wild bee pollinators are widely dispersed over the large quantity of MFC floral resources (Holzschuh et al., 2016; Holzschuh, Dormann, Tscharntke, & Steffan-Dewenter, 2011). Should PECs differ to MFCs in this regard, they may play a particularly important role in insect conservation when grown as an alternative to mass-flowering biofuel crops, even when cultivated at high densities in the landscape. Nonetheless, from a conservation perspective, our findings suggest that willow crops, in particular, offer the potential to enhance farm-scale biodiversity, with positive effects evident for at least three threatened pollinator groups. Incorporation of willow SRC into conventional mixed farming systems may yet help to support pollination services to wild margin plants.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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