

POLLINATOR RESPONSES TO FARMLAND HABITAT FEATURES: ONE-SIZE DOES NOT FIT ALL

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Abstract—Globally, pollinating insects face significant pressure, largely due to intensively managed agricultural systems. There has been considerable focus on the provision of resources for pollinators in agricultural landscapes, but without understanding how existing farmland habitats affect pollinators there is a risk these conservation actions could fail.

The aim of this study was to explore the relationships between the quantity, diversity, and quality of on-farm habitats with pollinator communities. To meet this aim, pollinator, floral and habitat features were assessed at twenty-nine sites, encompassing both livestock and crop systems, at a range of farming intensities, in two regions of Ireland.

Results showed that the three main taxonomic pollinator groups (hoverflies, social bees, and solitary bees) were inconsistent in their responses to habitat and environmental variables. Hoverflies were negatively associated with farms with increasing amounts of linear feature and fewer drainage ditches, whereas bumblebees were positively associated with crop farms and the number of grassy margins, drainage ditches and hedgerows at a site. Solitary bees were negatively associated with crop farms and positively associated with high floral species richness. At a species level, community analysis showed that within taxonomic groups, individual species responded differently to environmental variables.

This study demonstrates that different farm types and habitat features impact pollinator groups differently. One-size does not fit all, thus on-farm conservation actions should be designed with knowledge of taxon-specific responses to maximise benefits. The quantity and diversity of essential habitats are important along with the quality of those features in terms of their capacity to provide sufficient resources for pollinators.

Keywords—Pollinators, habitat quality, farmland ecology, abundance, species richness, flowers

Journal of Pollination Ecology,
36(3), 2024, pp 29-46

DOI: [10.26786/1920-7603\(2024\)753](https://doi.org/10.26786/1920-7603(2024)753)

Received 23 March 2023,
accepted 22 January 2024

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INTRODUCTION

Identified as a crucial group, pollinating insects (hereafter referred to as pollinators) deliver a range of ecosystem services, most notably pollination (Ollerton et al. 2011; Rader et al. 2020), culminating in approximately three-quarters of the world’s main crop and nearly 90% of wild plant species

benefiting from insect pollination for reproduction and yield (Klein et al. 2007; Ollerton et al. 2011). However, this group is currently facing significant environmental pressures due to global anthropogenic change (Potts et al. 2010; González-Varo et al. 2013; Zattara & Aizen 2021). Agriculture is a key anthropogenic activity influencing pollinators (Kremen et al. 2002; González-Varo et

al. 2013; Kennedy et al. 2013), which is of particular importance considering that 38% of global land area is farmed (FAO 2020). Changes in agricultural practices, such as use of agrochemicals and destruction of natural habitats have been heavily implicated in global pollinator declines (Goulson et al. 2015; IPBES 2016).

Bees (*Anthophila*) and hoverflies (*Syrphidae*) are important pollinating insects, and species diversity within these groups is vital for sustaining delivery of multiple ecosystem services, including crop production, in agricultural contexts (Dainese et al. 2019; Woodcock et al. 2019). Beyond direct pollination services, bees and hoverflies also contribute directly and indirectly to a range of ecosystem services including pest control (Rodríguez-Gasol 2020) and soil functioning (Christmann 2022). A diverse assemblage of pollinator species on farmland enhances crop yield stability and resilience against environmental changes, thereby helping to support food security (Garibaldi et al. 2013). Moreover, diverse pollinator communities can help buffer against the decline of individual species and ensure the continuity of pollination services in changing environments (Winfrey et al. 2018). However, these insects face multiple abiotic and biotic threats and stressors which have already led to losses in species richness, diversity (Biesmeijer et al. 2006; Zattara & Aizen 2021) and local extinctions (Ollerton et al. 2014). Serious declines in some bumblebee species have also been found (Graves et al. 2020; Guzman et al. 2021). Across Europe, at least 9% of bee species are considered threatened, whereas in Ireland almost one third of bee species are already placed in this category (Fitzpatrick et al. 2006; Nieto-Romero et al. 2014). For many locations worldwide the presence and scale of any potential declines are difficult to quantify due to a lack of long-term monitoring data (Zattara & Aizen 2021).

Bees and hoverflies are biologically and ecologically diverse groups of insects that vary significantly in their fundamental requirements for food, nest sites and non-floral resources (Alarcón et al. 2008; Kubo et al. 2009; Requier & Leonhardt 2020). Furthermore, these groups exhibit a wide variety of functional traits, which have been shown to respond differently to environmental drivers in agricultural systems (Williams et al. 2010; Le Féon

et al. 2016; Coutinho et al. 2018). For example, a meta-analysis by Coutinho et al. (2018) found that in agricultural landscapes, the abundance of ground nesting bees responded negatively to increasing structural complexity of crops, whereas social bee species richness responded positively to this change. These differences can be particularly apparent when spatial scale is considered, as functional traits such as sociality and nesting location influence how differences in agricultural environments affect the richness and abundance of pollinators at both the local (Williams et al. 2010; Coutinho et al. 2018) and landscape scale (Kleijn & van Langevelde 2006; Raderschall et al. 2021). In this context, diverse landscapes with a variety of habitat types and features are considered optimal for supporting rich communities of pollinators and biodiversity in general (Tschamntke et al. 2005; Mallinger et al. 2016; Coutinho et al. 2021). Nevertheless, knowledge gaps still remain in terms of clarifying how different pollinator groups respond to farmland habitat variability.

Although the quantity and configuration of pollinator-friendly habitats within a landscape are undoubtedly important, concerns have been raised about how the quality of different habitats can be measured in terms of the benefits they provide (Cole et al. 2019). Several recent studies have indicated the importance of habitat quality, where 'quality' refers to the ability of a habitat feature (e.g. hedgerows, heathland, field margins) to provide resources for pollinating insects through time, both within and between seasons, so that high species diversity is maintained (Kennedy et al. 2013; Ahmed et al. 2021; Bottero et al. 2021). In this study, quality specifically refers to the floral metrics measured on the habitat features and the capacity of features to provide nesting opportunities for pollinators. To date, European agri-environmental policy has often focused on the provision or protection of particular types or classes of habitats, and increasing the area or quantity of these desired habitat types or features, while no relationship has been found between habitat quantity and habitat quality (Rotchés-Ribalta et al. 2021). Less attention has been paid to establishing the quality of these resources, and actions that maintain or improve quality, so that benefits are provided to a greater range of pollinator species and across a fuller range of seasons (Wood et al. 2015). Within pollinator

research, habitat quality is often linked to floral metrics such as floral abundance, richness, and diversity, which have frequently been shown to have positive effects on bee abundance, bee diversity, and pollinator diversity (Holzschuh et al. 2007; Widhiono et al. 2016; Wu et al. 2021). At the local scale in agricultural contexts, the provision of floral resources is frequently linked with on-farm linear features such as hedgerows (Byrne & delBarco-Trillo 2019) and field margins (Zamorano et al. 2020), and the central importance of linear habitat quality in providing floral resources for pollinators has been demonstrated empirically (Garratt et al. 2017; Ahmed et al. 2021; Zamorano et al. 2020).

In this study we build on previous research by examining four linear habitat types simultaneously (hedgerows, drainage ditches, stone walls and field margins), along with the fields themselves. Drainage ditches, field margins, and fields potentially serve as invaluable foraging grounds for pollinators, offering a variety of floral resources essential for their nutrition and energy needs (Potts et al. 2010; Wood et al. 2015). In contrast, features like stone walls and hedgerows offer structural complexity and a variety of microhabitats, fostering an environment conducive for nesting (Kremen et al. 2007; Xie et al. 2020). These elements provide shelter, nesting materials, and suitable substrates for egg-laying for a multitude of pollinator species (Williams & Kremen 2007). Field margins may support a rich floral community for foraging while simultaneously offering refuge and nesting sites (Marshall et al. 2006). The integration of these diverse habitat features within agricultural landscapes can significantly contribute to the conservation of pollinator communities (Wratten et al. 2012). We consider the effects of the quality, quantity and diversity of these habitat features on the abundance and richness of bee and hoverfly species, across livestock and crop farms.

Due to its high percentage ($\approx 64\%$) of land cover under agriculture (DAFM 2018) and high proportion ($\approx 30\%$) of bee species threatened with extinction (Fitzpatrick et al. 2006), the Republic of Ireland (hereafter referred to as Ireland) represents a useful case study to establish the status and resource requirements of bees and hoverflies in agricultural landscapes. While previous studies

have examined and compared different farming systems in specific regions in Ireland e.g. bioenergy crops (Stanley & Stout 2013); organic dairy farming (Power & Stout 2011), this is the first study to take a more generalised view and investigate the correspondence of bee and hoverfly pollinators and their habitats across different farm types and geographical regions. In Ireland, as across other nations, the capacity of farmland to support biodiversity is highly variable from high intensity crops with large fields and little on-farm habitat diversity, to low intensity livestock farming with small fields that have retained many semi-natural features. In Ireland, 92% of agricultural land is classified as grassland and rough grazing, primarily livestock farms used for grazing purposes, with the remainder being dedicated to crop production (Central Statistics Office 2016).

The principal research hypotheses of this study were:

1. Responses to farm type and linear feature (length, type and diversity) will differ between the three pollinator groups (social bees, solitary bees and hoverflies):
 - a. Social bees will show no response to farm type but will be positively associated with sites with lots of hedgerow due to the importance of this feature in providing forage and nesting resources for this group.
 - b. Hoverflies will be positively associated with crop farms due to the abundance of larval food for aphidophagous species at these sites, and sites with drainage ditches due to the larval associations with watercourses of some common species.
 - c. Solitary bees will be positively associated with linear feature length and diversity due to their short flight ranges and requirement to have all necessary resources in proximity. Stone walls will be particularly important due to their capacity to act as nest sites for ground and cavity nesting bees.
2. The abundance and species richness of all pollinator groups will correlate positively with floral abundance and floral species richness.

The final goal of this work was to develop informed recommendations of how agri-

environment policy may be improved for bees and hoverflies.

MATERIALS AND METHODS

STUDY SITES

Two study regions in climatically-contrasting areas of Ireland were selected: County Sligo in the north west (mean temperature 9.6°C; average rainfall 1260.1 mm), and County Wexford in the south east (mean temperature 9.8°C; average rainfall 840.2 mm). Thirty farms were selected (15 in each region) which represented a range of stocking rates, field sizes and enterprise (permanent pastures for livestock versus crop dominated farmland) (Fig. 1). To promote statistical independence, specific sites within each farm were selected to increase the likelihood of spatial independence of pollinator data. Sampling locations for pollinators were a minimum of 1 km apart. The floral and habitat data were measured within a 100 m radius of the centre point of each site. Sites were chosen to be representative of the whole farm make up. In Sligo, all selected sites

were dedicated to livestock production, and consisted of managed grasslands and semi-natural pastures. In Wexford, in addition to livestock production, five sites had areas used for cereals and other crops (e.g. barley, radish). One site in Wexford, was excluded from the analysis after data collection, as the fields surveyed were not farmed in the year of the data collection, and thus it was not considered to be representative of farming in the area. Digital habitat maps following Fossitt's (2000) level 2 classification were developed for each site (Ruas et al. 2022), and these were used to guide the placement of pollinator traps and floral survey transects (see details below).

POLLINATOR SAMPLING

Insect samples were collected at approximately three-weekly intervals, from May to August 2019 (five sampling rounds in total). Samples were collected using sets of coloured pan traps, which have been shown to be suitable for determining overall bee species richness across habitats and regions (Westphal et al. 2008).

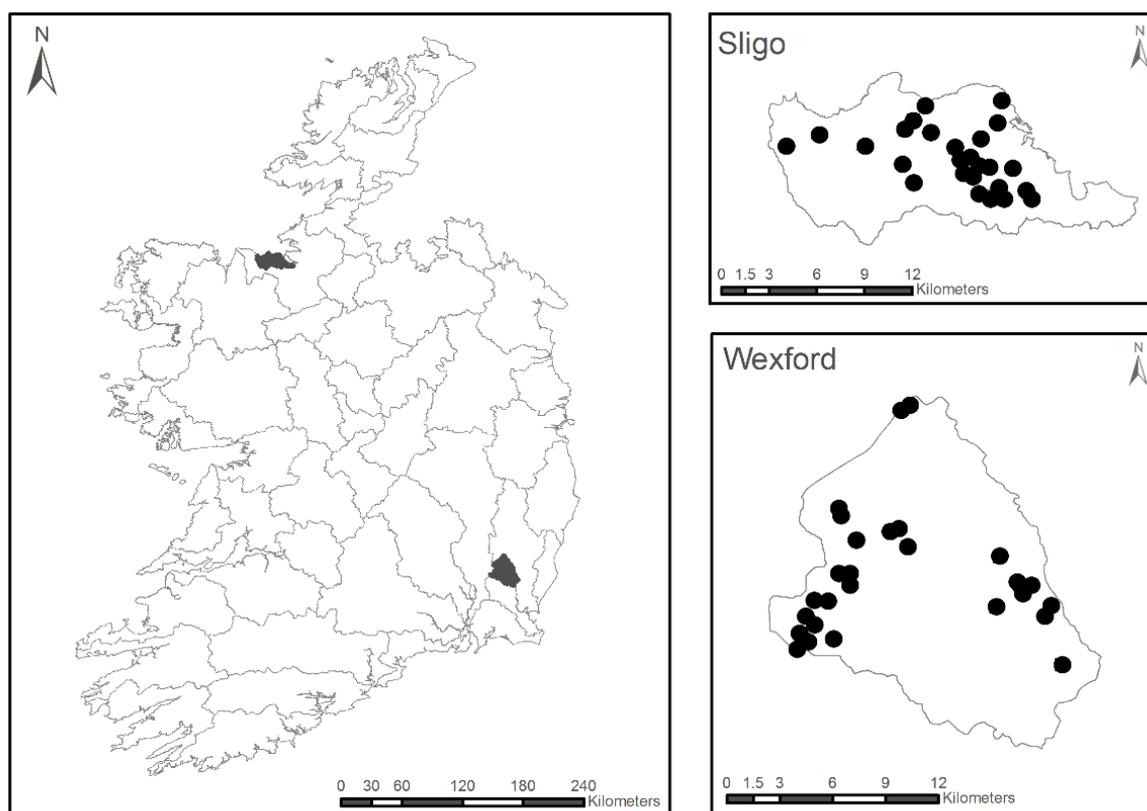


Figure 1: Map of Ireland showing the 29 farms included in the study

Although pan traps have some noted biases, particularly with regard to sampling bumblebees (O'Connor et al. 2019), they were the most appropriate sampling method for this study as a number of constraints prevented us from employing transect methods. These included issues with time and variable local weather conditions. Additionally, the geographical distance between the regions made standardising transects across regions infeasible. Each trap set consisted of three plastic bowls (375 ml capacity, 135 mm diameter), painted one of three colours (blue, white, and yellow to imitate floral visual signalling; Moreira et al. 2016). At each site, three sets of pan traps were installed (nine bowls in total) along a linear feature. Each set of traps was positioned 15 m apart and at least 10 m away from the end of the linear feature.

On each sampling date, the pan traps were partially filled with water, with a drop of detergent added to break surface tension. Traps were emptied after 48 h in the field and all captured specimens (per linear feature) pooled and stored in 70% ethanol for later identification (Stanley et al. 2013). Pollinators were identified to species level using Stubbs and Falk (2002), Ball and Morris (2015), Else and Edwards (2018), and Falk (2015). Specimens were subsequently used to develop reference collections to be housed at the Natural History Museum Ireland, Trinity College Dublin and Teagasc. The abundance of each pollinator species per site was calculated as the sum of the individuals found in the traps at each site at each sampling round. Species richness was calculated as the number of unique species recorded at each site at each sampling round.

FLORAL SAMPLING

The floral sampling protocol was specifically designed to comprehensively assess floral resource availability for pollinators over a season and in a variety of habitat types (see Supp. 1) and built on the protocol developed by Hodge et al (2022). At each site, flowering plants were assessed in four linear features and in two randomly selected fields. Using the habitat maps, the four most common linear feature types across all farms were identified. These were hedgerows, stone walls, drainage ditches and grassy margins. At sites where all four habitat types were present, one of each type was randomly selected for survey.

Where a feature type was not present, features were selected on the basis of their wider representation within the farm e.g. in a farm with 400 m hedgerow, 100 m stone wall and 100 m drainage ditch there would be two hedgerows, one stone wall and one drainage ditch surveyed.

Floral surveys were conducted during the same five sampling rounds used for the pollinator sampling (see above). Only plants that were in flower were recorded, as these were taken to represent the food resources available to pollinating insects at the time of surveying. Stone walls, drainage ditches and grassy margins were surveyed using two 1 m x 1 m ground quadrats, 20 m apart and at least 10 m from the ends of the feature. Fields were surveyed using two randomly placed 1 m x 1 m quadrats. Within each quadrat, all herbaceous species in flower (excluding graminoids) were recorded and the percentage cover of the flowering portion of each species was estimated. Floral ground cover in fields (i.e. not associated with linear features) was similarly low across all sites (median cover = 0.5%) and was therefore not included in further analysis. Due to their more complex vertical structure, hedgerows were surveyed using two methods. Firstly, two quadrats were used to assess ground flora in the same fashion as for the other linear features described above. Additionally, a 30 m transect was performed to assess percentage floral cover of the hedgerow for each tree and shrub species in flower and for the number of flowering species of trees and shrubs.

In order to reduce the number of variables included in further analysis, three summary floral variables were calculated per sampling location and visit to represent; a) the diversity of available floral resources at each site, b) the mean % cover of ground floral resources associated with linear features within 100 m of pan trap, and c) the mean proportion of shrub and tree floral resources per m hedgerow length within 100 m of the pan trap. The diversity of the floral resource was calculated as the number of unique species in flower across all sampled habitat features at a site for each survey visit. To calculate the mean cover (m²) of the ground floral resource associated with linear features within 100 m of the pan trap, the length of linear features of each type within 100m of the pan-trap was first calculated using ArcGIS habitat

maps (Ruas et al. 2022, 2021). The mean ground cover per m² associated with linear features, was then calculated by multiplying the % cover per m² per linear feature type by the length of each linear feature type, summing these, and then dividing by the total length of all linear features within 100 m of the trap. Mean cover of shrub and tree floral abundance per site visit was calculated as the mean percentage cover per m² (vertical quadrats) multiplied by the mean height of the hedgerow, to account for the impact of the vertical height on the amount of floral resource available. Mean rainfall and mean maximum temperature for each survey period were derived using data obtained from Met Éireann (www.met.ie) for weather stations at Johnstown Castle (Co. Wexford) and Sligo Airport.

DATA ANALYSIS

The lengths of each of the four linear feature types at each site were analysed using Principle Components Analysis (PCA). The purpose of this analysis was twofold: firstly, it enabled us to identify the key axes of variation in the sites in terms of the linear features present (Fig. S1); and secondly, as the first and second PC axes explained most of the variation between feature types (87.4%) these axes scores were used as explanatory variables in the subsequent GLMM analyses to represent linear feature diversity. Prior to PCA analysis, length variables were transformed using a Hellinger transformation for normality (Borcard et al., 2011). The first axis represented 62.7% of variation in feature types and can be interpreted as a continuum from sites with a relatively higher proportion of drainage ditches to those with a higher proportion of stone walls (referred to as 'Feature PCA1' hereafter), and the second axis represents 24.7% of variation and a continuum from sites with more ditches and stone walls to those with more hedgerows (referred to as 'Feature PCA2' hereafter). Further information on the PCA analysis can be found in Supp. 2.

Associations between pollinators and descriptors of landscape features and floral resources were investigated using a GLMM framework. Pollinators were divided into three groups prior to analysis, hoverflies (*Syrphidae*), social bees (*Apis mellifera* and *Bombus* spp) and solitary bees (*Colletidae*, *Andrenidae*, *Halictidae*, *Megachilidae* and *Nomada* spp). For each insect group, total abundance and species richness were

calculated, and a separate GLMM fitted for each response variable.

A multi-model inference framework was used to ascertain the best model fitting GLMM for each response variable based on the lowest Akaike Information Criterion value adjusted for small sample size (AICc) (Burnham & Anderson 2002). The model selection procedure was as follows: an initial global model was fitted for each response variable (see details below), then all possible subsets of the explanatory variables in the global model were tested using the R package MuMIn (Bartoń 2022) and the optimal model selected as the model with the lowest AICc value. Floral data could not be collected at four site visits due to adverse weather conditions, therefore initial models were fitted without these site visits (n = 141). Where floral data variables were not included in the final best fitting model, the model was refitted with full dataset (n = 145) to make best use of the available dataset. All GLMMs were fitted using the R package 'glmmTMB' (Brooks et al., 2022).

For each response variable, an initial global model was fitted containing the explanatory variables: farm type (a two level factor – Crop/Animal), mean rainfall, mean maximum temperature, floral species richness, average floral cover of ground flora per m² along linear features (%), average floral cover of tree and shrub species per m² along hedgerows (%), total length of linear features within 100m of the pan trap, feature PCA1 and PCA2 axes, county (a two level factor representing the two study regions – Sligo/Wexford) and survey period (1-5). The 'Farm ID' was fitted as a random factor (29 levels) to account for autocorrelation of measurements between sampling dates within sites. Continuous predictor variables (other than the PC axes) were rescaled to units of standard deviation prior in analyses. Models for abundance of each pollinator group (hoverflies, social bees, and solitary bees) were fitted with a negative binomial response distribution with a log link function. Species richness models were fitted with a Poisson response distribution. Overdispersion was tested for using the function 'overdispersion_check' in the R package 'performance' (Lüdtke et al. 2020) and was not detected for any taxonomic group.

Differences in pollinator community composition were analyzed using partial Redundancy Analysis (pRDA) using the R package ‘vegan’ (Oksanen et al. 2022). Environmental variables used to describe the species community were the same as those included in the GLMM analyses, while county and survey period were fitted as conditional (‘partial’) variables. Continuous predictor variables (other than the PC axes) were rescaled to units of standard deviation prior in analyses. Species which were present but were recorded on fewer than five site visits were grouped by taxa into two categories ‘Other Syrphidae’ and ‘Other bees’, to account for broader patterns in rarer species in the study area (See Supp. 3).

RESULTS

SUMMARY OF LINEAR FEATURE, FLORAL AND POLLINATOR DATA

One hundred and sixty seven species of plant were recorded in flower across sites and survey periods (129 in Wexford and 92 in Sligo) (Supp. 4). The number of flowering species per site visit ranged from 1 to 26 (median = 10), and was marginally higher in crop (median = 13) than grassland sites (median = 9). Average ground floral cover associated with linear features within 100 m ranged from 0 to 29.8% across sites and survey periods, while hedgerow floral abundance ranged from 0 to 2.2 m² per horizontal m of hedgerow (this can be > 1, because the amount per m² quadrat is multiplied by hedgerow height in m).

A total of 1266 bees were collected belonging to 43 species (43% of Irish bee fauna) (Supp. 5). Of these, 908 specimens were solitary bees representing 33 species and 358 specimens were social bees representing ten species. In Sligo, 482

specimens were recorded belonging to 27 species, and in Wexford, 784 specimens representing 38 species. Twenty-two species were common to both counties, with eleven of the remaining species recorded only as singletons. In Sligo, the most abundant species were *Lasioglossum calceatum* (152 specimens), *Bombus lucorum* agg (78), *Andrena haemmorhoa* (47), *Lasioglossum fratellum* (44) and *Lasioglossum albipes* (41). In Wexford, the most abundant species were *Halictus rubicundus* (272), *Andrena coitana* (117), *Andrena haemmorhoa* (58), *Apis mellifera* (58), and *Bombus lucorum* agg (53). *Bombus lucorum* agg was the most widespread species, occurring at 27 of the 29 sites, followed by *Lasioglossum calceatum* (24 sites) and *Bombus hortorum* (19 sites).

A total of 1159 syrphids were collected, belonging to 53 species (approximately 29% of Irish hoverfly fauna; Table 1). In Sligo, 462 specimens were recorded belonging to 45 species, and in Wexford, 697 specimens representing 34 species. Twenty-six species were common to both counties, with ten of the remaining species recorded only as singletons. In Sligo, the most abundant species were *Syrphus ribesii* (60 specimens), *Helophilus pendulus* (48), *Rhinga campestris* (45), and *Melanogaster hirtella* (41). In Wexford, the catch was highly dominated by *Episyrphus balteatus* (477 specimens), followed by *Platycheirus peltatus* (47), which we did not record in Sligo, and *S. ribesii* (30). *Platycheirus albimanus* and *S. ribesii* were the most widespread species, occurring at 21 of the 29 sites, followed by *E. balteatus* (18 sites) and *Eristalis tenax* (16 sites).

In total, 23,274 m of linear feature were recorded across all sites (Table 1). Many field boundaries consisted of more than one type of linear feature e.g. hedgerow over stone wall, and

Table 1: Mean length (m) and minimum and maximum lengths of each linear feature type within 100m of pollinator trapping locations in both sub-catchments on animal

	Wexford		Sligo
	Animal	Crop	Animal
Hedgerow	536 (194 - 912)	313 (68 - 581)	346 (54 - 836)
Stone wall	345 (116 - 528)	45 (0 - 187)	336 (0 - 874)
Drainage ditch	26 (0 - 132)	87 (0 - 363)	127 (0 - 607)
Grassy margin	0 (0 - 0)	66 (0 - 291)	55 (0 - 567)
Total linear features	907 (301 - 1426)	511 (185 - 1319)	864 (518 - 2088)

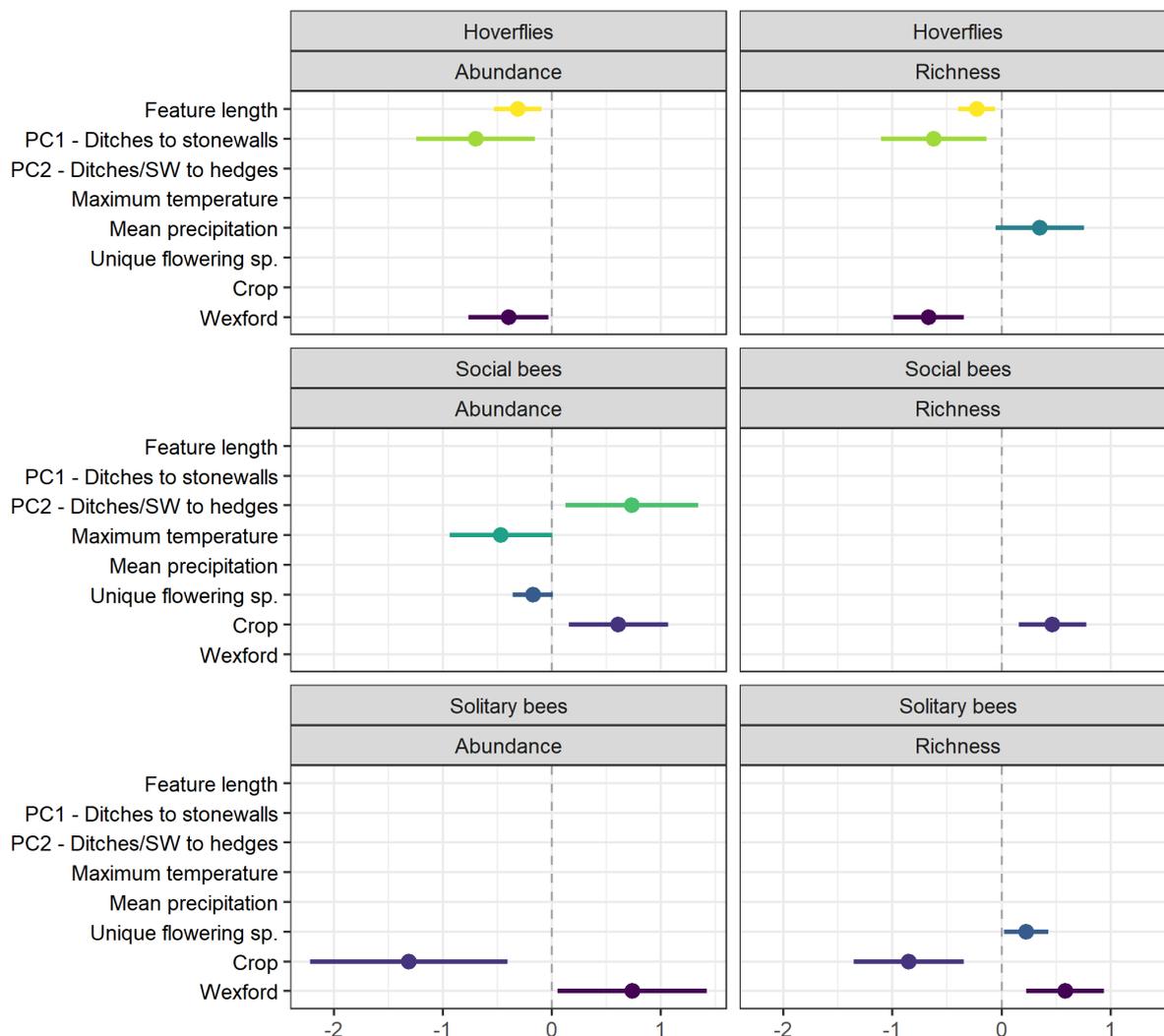


Figure 2: Association between abundance and richness of insect taxa and predictor variables. Circles show coefficient values of predictor variables in best fitting models. Lines indicate 95% confidence intervals on coefficient estimates. For categorical variables, 'Crop' and 'Wexford', the coefficients represent the difference from the reference condition 'Animal farming' and 'County Sligo' respectively. Differences between weeks were included in all final models, but are not shown here for simplicity (see Supp. 7, for full coefficient tables)

so these figures are representative of the total amount of habitat and not a measure of the length of field boundary. The amount of each type of linear feature varied across farm type and county with hedgerow being the most prevalent feature. Stone walls were common on grassland sites in both Wexford and Sligo but were uncommon in crop systems.

POLLINATOR ABUNDANCE AND SPECIES RICHNESS

Six GLMM analyses were performed to investigate how abundance and species richness responses (of the three pollinator groups) responded to the explanatory variables. In all six analyses, survey period was a significant factor, reflecting the temporal variation of hoverfly, social

bee, and solitary bee populations over the four-month collecting period (Supp. 6). Hoverfly abundance was found to have significant negative associations with total length of linear features within 100 m of the pan traps ($P = 0.01$) and PCA1, indicating a negative relationship with sites with fewer drainage ditches ($P = 0.005$) (Fig. 2; Supp. 7). Hoverfly abundance was also lower in Wexford than in Sligo. Hoverfly species richness exhibited the same relationships with these two variables. Social bee abundance was positively associated with crop farms ($P = 0.008$) and PCA2, indicating a positive association with sites containing more hedgerows. Social bee species richness was also positively associated with crop farms ($P = 0.003$)

(Fig. 2; Supp. 7). Solitary bees were more abundant in Wexford than Sligo ($P = 0.03$) and exhibited a negative relationship with crop farms ($P = 0.004$). Solitary bee species richness had the same relationships with these two variables but was also significantly positively associated with floral species richness ($P = 0.03$) (Fig. 2; Supp. 7).

COMMUNITY COMPOSITION

In terms of community composition, explanatory factors accounted for 28.22% of the variance ($P < 0.001$), with 19.62% accounted for by differences between survey periods and counties, and 8.6% attributable to the other environmental and habitat variables. Permutation tests indicated that average maximum temperatures ($P = 0.01$), farm type ($P < 0.001$) and average floral cover of tree and shrub species per m² ($P = 0.041$) explained significant proportions of variation in the overall pollinator community (Table 2). The variance explained by environmental variables depended on the focal pollinator species and ranged from 1.0% to 27.0% depending on the species (Supp. 8; Fig. 3). The species with the highest proportion of variance explained by environmental variables was the hoverfly *Platycheirus peltatus* (27%). Excluding the ‘other bees’ category, the four bee species that had the highest proportion of their variation explained by habitat and environmental variables were all small-bodied solitary species; *Andrena coitana*, *Lasioglossum albipes*, *Hylaeus communis* and *Halictus rubicundus*.

DISCUSSION

This study recorded 43 (43%) of the 99 bee species present in Ireland at the time of survey and 53 (29%) of the approximately 180 hoverfly species,

representing significant proportions of these taxonomic groups. The study revealed divergent responses among the three main pollinator groups to the habitat and environmental variables. Hoverflies showed a negative association with farms having more linear features and fewer drainage ditches, while bumblebees exhibited a positive correlation with crop farms and sites rich in hedgerows (PCA2). Additionally, solitary bees had a negative association with crop farms but were positively related to areas with high floral species richness.

POLLINATOR GROUPS EXHIBIT DIVERSE RESPONSES TO ENVIRONMENTAL CHARACTERISTICS

Both social bee abundance and species richness were higher on crop farms while abundance was higher on sites dominated by hedgerow. Hedgerows can offer significant amounts of forage due to the presence of mass flowering species such as *Rubus fruticosus* agg. and *Ulex europaeus* and can also offer suitable nesting sites for bumblebee species, which frequently nest in long grass and cavities (Kells & Goulson 2003). In Ireland, all but one of the true bumblebee species (*Bombus hypnorum* L.) nest in these conditions, and, therefore, farms dominated by hedgerow features have the capacity to offer bumblebees multiple ecological resources. Contrary to our hypothesis, floral abundance and species richness were not found to be good predictors of social bee metrics. This seems counterintuitive as differences in bee abundance, richness and diversity, in agricultural contexts, have frequently been linked to floristic variables (Potts et al. 2009; Blaauw & Isaacs 2014; Eeraerts et al. 2019). In this case, it is possible that social bee metrics were not correlated with floral

Table 2: Summary of variance in pollinator community composition explained by habitat and environmental variables

	Df	Variance	F	Pr(>F)
Average rainfall	1	0.00646	1.45	0.9725
Average max temp	1	0.01370	3.07	0.0099 **
Floral species richness	1	0.00508	1.14	0.2558
Total feature length (m)	1	0.00336	0.75	0.7694
Farm type	1	0.01200	2.69	0.0003 ***
Average floral cover ground species (m ²)	1	0.00341	0.77	0.7226
Average floral cover tree and shrub species (m ²)	1	0.00986	2.21	0.0409 *
PC1 (Drainage ditches to stone walls)	1	0.00432	0.97	0.3951
PC2 (Drainage ditches/stone walls to hedges)	1	0.00362	0.81	0.6792
Residual	126	0.56127		

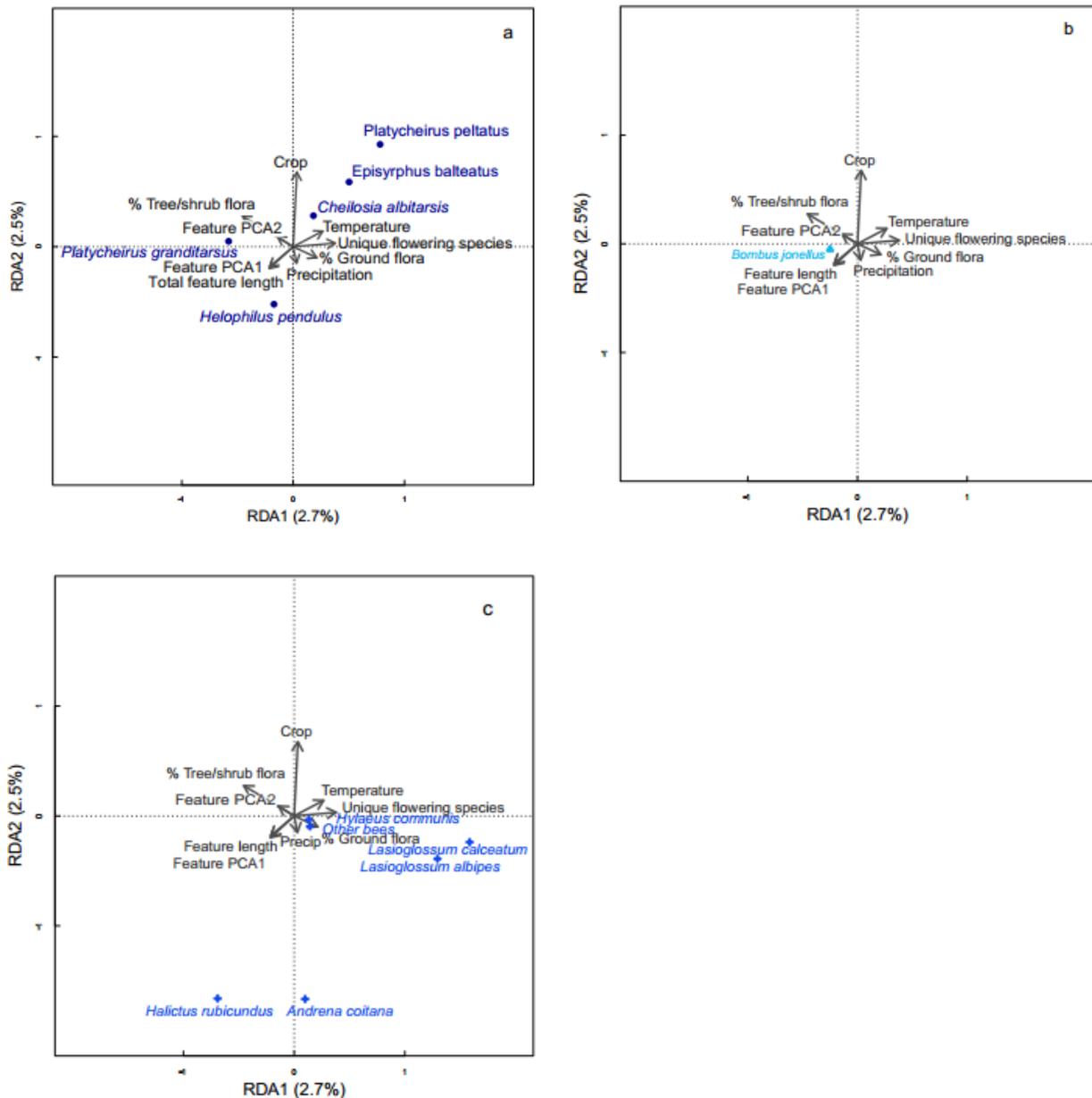


Figure 3: Redundancy Analysis (pRDA) plots showing relationship between environmental variables and a) hoverflies, b) social bees, c) solitary bees, after accounting for differences between survey periods and counties by partial RDA. Only species for which environmental variables explained more than 10% of their variation are plotted (see Supp. 8).

variables because of sampling limitations and potential biases associated with using pan traps. Previous studies have found that pan traps may not accurately estimate bumblebee abundance, particularly in habitats with high floral density where pans are not as attractive as in areas with low floral density (Portman et al. 2020); but see Wood et al. 2015). Only 9/21 Irish bumblebee species were recorded on our sites. In Ireland, the rarest bumblebee species are found in the West of Ireland which is the last refuge of the semi-natural grassland habitat preferred by the rarer species

(Fitzpatrick et al. 2007), which none of our sites offered. These limitations may also explain why the variance accounted for by the explanatory variables in the community analysis of the *Bombus* species was so low. The general lack of relationships between the bumblebees and measurements of floral availability, may also have transpired because the study did not measure floral resources and habitat features over a large enough area to reflect the scale at which bumblebees use the landscape. Social bees have been shown to respond to landscape level

characteristics, in large part due to their long flight ranges up to several km from the nest (Goulson & Stout 2001; Beekman & Oldroyd 2018). This enables them to exploit resources from across a diverse range of habitats and negates the need for all of their required resources, throughout the full life cycle of the colony, to be in very close proximity. This is in strong contrast to solitary bee species, which, with much shorter flight ranges (hundreds of metres) and without the benefits of task specialisation that exists in social species, require all of their necessary resources to be within much closer geographical distance (Kendall et al. 2022).

Solitary bee abundance and richness were higher in Wexford than Sligo and were both negatively associated with crop farms. The higher abundance and richness of solitary bees in Wexford is likely attributable to a combination of more favourable climatic and weather conditions in this region (National Biodiversity Data Centre 2011). The availability of suitable nesting sites is an important factor in terms of solitary bee health and community structure (Potts et al. 2005; Harmon-Threatt 2020), and during the course of field surveys solitary bees were observed nesting in the bare soil banks of drainage ditches, gaps in dry stone walls and in small patches of bare earth adjacent to some hedgerows. These features are more likely to be present in grassland systems (due to farm animal behaviour), which may partly explain the negative association with crop farms. We observed one ground-nesting species, *Halictus rubicundus*, nesting in stone walls, and our analysis confirmed that this species was strongly associated with sites with more of this feature. These results reaffirm that, even when just considering solitary bees, the provision of a diverse range of microhabitats would support more nest site specialists and, as a consequence, a more diverse pollinator assemblage.

Solitary bee species richness was positively associated with floral species richness within 100m, and this was the only taxonomic group/pollinator metric to respond to a floral metric. The short flight ranges of many solitary bee species means they can be responsive to local conditions and require both nesting and foraging resources to be present within a small area (Zurbuchen et al. 2010; Xie et al. 2020). The four bee

species that responded most to habitat and environmental variation were all small-bodied, solitary species, which further supports the suggestion that solitary species are more reliant on all necessary ecological resources being present at the local scale. Increasing floral richness and abundance could, therefore, have a significant effect on solitary bee diversity, and abundance, particularly as the RDA revealed that some species (e.g. *Lasioglossum albipes* and *L. calceatum*) were strongly responsive to floral species richness and ground flora.

Syrphids were more species rich and abundant at sites with fewer linear features and an abundance of drainage ditches. As hypothesised, this association with drainage ditches is likely because many syrphid species rely on waterbodies for larval development (Speight 2008). Adult hoverflies utilise nectar and pollen for nutrition (Ball & Morris. 2015) but no strong association with any floral metric was identified in this study. While some studies have shown that floral abundance and floral density are positively associated with syrphid abundance and diversity (Gabel 2021; Sutherland et al. 2001) and that additional floral resources are beneficial for hoverfly abundance and richness in agricultural landscapes (Tschumi et al. 2016), at least one other study has found that local floral resources are poor predictors of hoverfly species richness and abundance in agricultural contexts (Schirmel et al. 2018). This may be because highly modified agricultural landscapes are more likely to have assemblages of common, generalist species that are highly mobile and more responsive to landscape-level factors (Speight 2015; Schirmel et al. 2018). Almost 70% of catches in Wexford consisted of *E. balteatus*, a finding consistent with other European studies of hoverflies in agricultural landscapes (Meyer et al. 2009; Trzciński & Piekarska-Boniecka 2013; Schirmel et al. 2018). This highly mobile, aphidophagous, generalist species is less vulnerable to landscape simplification than other hoverfly species and is strongly associated with the availability of aphids for larval food (Rodríguez-Gasol 2020). This association was borne out in the community analysis where *E. balteatus* was strongly associated with crop farms. As a group, hoverflies are highly diverse in terms of functional traits and therefore, analysis at the level of functional groups can be more

illuminating (Schweiger et al. 2007; Moquet et al. 2018). Functional trait analysis of the hoverfly data in this study can be found in Ahmed (2021).

In terms of community composition, farm type, maximum temperature and floral cover of tree and shrub species were the factors that explained the most variation in pollinator community. The effects of temperature may be an artefact of the fact that some species, particularly small bodied species, may not be on the wing in cooler temperatures (Kenna et al. 2021). The observed floral effect was associated with shrub and tree flora i.e. the hedgerows themselves, as opposed to the ground flora at the sites. In general, floral resources were more abundant in the hedgerows but the ground flora was more diverse. This effect appears to be driven by the response of the solitary bees to the diverse ground flora (Fig. 3c), which supports recent work showing that diverse floral resources in agricultural landscapes promote solitary bee reproduction (Klaus et al. 2021). This is further supported by the results from the solitary bee GLMMs which showed that species richness in this group is correlated with floral species richness (Fig. 1). We also found that social bees are associated with sites with hedgerow so this community level effect is likely being reinforced by this social bee response. Although we did not find an effect of farm type for syrphid abundance or richness, three hoverfly species (*P. peltatus*, *E. balteatus* and *Cheilosia. albitarsis*) exhibited strong associations with crop farms in the community analysis.

ONE SIZE DOES NOT FIT ALL: RECOMMENDATIONS FOR POLLINATING INSECTS AGRI-ENVIRONMENT SCHEMES

This study demonstrates the need for targeted conservation measures, specific to pollinator communities across various farm systems (Benton et al. 2003; Tscharrntke et al. 2005).

Our findings indicate that while crop-dominated farms may present challenges for supporting diverse solitary bee communities, they are nonetheless capable of providing sufficient resources for both social bees and hoverflies. To this end, crop farmers are encouraged to incorporate diverse linear features such as hedgerows (Wood et al. 2015) as the protection, enhancement, or incorporation of key environmental features is essential (Wratten et al. 2012). Furthermore, conservation policies could be

adapted to the unique characteristics of different farms that attract or maintain specific pollinator taxonomic groups (Kremen et al. 2007). Hedgerows, enriched with mass flowering species like *R. fruticosus* agg. and *U. europaeus*, and diverse ground flora, should be managed for sequential flowering and increased floral abundance (Williams & Kremen 2007). In the case of livestock farms, enriching the diversity and quantity of ground flora is pivotal for attracting and supporting solitary bees (Potts et al. 2010). Recent work examining the plant-pollinator networks in Ireland found that, unlike in many other contexts, the networks in Irish agricultural landscapes are highly asymmetrical, with more plant species than pollinators (Russo et al. 2022). However, the many non-native plant hosts present on agricultural land were shown not to be attractive to pollinators. The findings from this study suggest that the optimal floral mix for pollinators on farms constitutes native species that attract both a high abundance of pollinators (e.g. *R. fruticosus* agg. and *Ranunculus repens*) and high diversity (e.g. *Cirsium arvense* and *C. nigra*). While systematic pollinator transects were not possible during this study, they were performed at the linear features of the Wexford sites when weather conditions were favourable (dry, temperature >13°C) (Supp. 8). Thirty surveys were completed in this way and while the results were not robust enough for statistical analysis, they did support the findings of Russo et al. (2022) in that *R. fruticosus* agg. was most frequently interacted with (209 interactions). Protecting these floral resources from grazing animals is also important, particularly on farms with cattle. Fencing off some of these areas would give plants an opportunity to flower, while continuing to allow animals to access some other areas (particularly hedgerow over earthen banks) can help encourage the creation of bare ground for nest sites. Like bare sloped ground, dry stone walls can also offer important opportunities for nesting (Xie et al. 2020) and should be valued as such.

This study demonstrates that with regard to conservation of pollinating insects one size does not fit all, and conclusions regarding habitat quality can be highly subjective and dependent on which pollinator taxon is considered (Bottero et al. 2021; Larkin & Stanley 2021). For social bees, the highest quality habitat was related to abundant hedgerows, for solitary bees it was animal farms

with diverse floral communities, while hoverflies preferred sites with a prevalence of drainage ditches. Agri-environment policy which aims to support and protect pollinating insects must, therefore, consider these differences and operate in a manner that is appropriate for each taxon and for each conservation intervention. In light of the multiple pressures facing pollinators, this study shows how Irish farmland can be managed to provide suitable resources for different pollinator groups, and thus increase the likelihood of sustaining highly biodiverse pollinator communities within these highly productive agricultural landscapes.

ACKNOWLEDGEMENTS

This project received funding from the Dept. of Agriculture, Food and the Marine. The authors wish to extend their deepest gratitude to the farmers who allowed us to access their land, this study would not have been possible without their willing cooperation and warm welcomes. We also thank two anonymous reviewers who gave their time to improve this manuscript.

AUTHOR CONTRIBUTION

Stephanie Maher, Sara Ruas, Ruth Kelly, Jane Stout, Roser Rotchés-Ribalta, James Moran and Daire Ó hUallacháin conceived the ideas and designed methodology; Stephanie Maher, Ruth Kelly, Sara Ruas, Karzan D. Ahmed and Ellen O'Hora collected the data; Ruth Kelly, Stephanie Maher and Simon Hodge analysed the data; Stephanie Maher, Ruth Kelly, Simon Hodge and Jane Stout led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors. Author JS is an Associate Editor of the Journal of Pollination Ecology. Thus, the peer-review process for this article was handled independently by another member of the editorial board.

DATA AVAILABILITY STATEMENT

Please contact the corresponding author for data requests.

APPENDICES

Additional supporting information may be found in the online version of this article:

Fig S1. PCA of the four linear feature types

Fig S2. Mean abundance of social bees, solitary bees and hoverflies per site across the five survey periods

Table S4. Floral species recorded throughout the study

Table S5. Combined list of hoverfly and bee species recorded throughout the study.

Table S7. Summary of the results of the generalized linear mixed models for the response variables, hoverfly, social bee and solitary bee abundance and species richness.

Table S8. Variance in species abundances explained by environmental variables and temporal/spatial variables (survey period and county) in pRDA analyses.

Table S9. Pollinator survey data

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ISSN 1920-7603