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Response of bee and hoverfly populations to a land-use gradient in a Quebec floodplain

Olivier Slupik [1,*], Frédéric McCune [1], Chris Watson [2], Raphaël Proulx [2], Valérie Fournier [1]

[1] Centre de recherche et d'innovation sur les végétaux (CRIV), Département de phytologie, Faculté des sciences de l'agriculture et de l'alimentation, Université Laval, QC, Québec, Canada

[2] Centre de recherche sur les interactions bassins versants écosystèmes aquatiques (RIVE), Département des sciences de l'environnement, Université du Québec à Trois-Rivières, QC, Trois-Rivières, Canada

[*] *Author for correspondence (e-mail: olivier.slupik.1@ulaval.ca)*

ORCID
Frédéric McCune: 0000-0002-2710-6580
Chris Watson: 0000-0003-3320-431X
Raphaël Proulx: 0000-0002-9188-9225

Abstract

The main objective of this study was to inventory the abundance and species richness of wild bees and hoverflies in the Lac Saint-Pierre floodplain according to a land-use gradient. In 2019 and 2020, pollinators were sampled using pan-traps in three landscape types: Crop field margins, Perennial hayfields, and Natural habitats. Bee and hoverfly populations were dominated by a few species throughout the study area. Crop field margins contained greater floral availability and attracted more individuals and species of bees than other landscape types. Although hoverflies were not affected by either land-use type or flooding, the abundance and species richness of bees appeared to be reduced when spring flooding lasted longer, suggesting a mortality effect of flooding on their populations.

Implications for insect conservation:

Our results make a case for the key role of field margins in the conservation of pollinating insects in agricultural landscapes, especially in a floodplain context.

Keyword

Flower Flies, Flower Strips, Natural Habitat, Agriculture Intensification, Inundation, Fluvial Lake

Statements and Declarations

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial or non-financial interest in the subject matter or materials discussed in this manuscript.

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Author contributions

Raphaël Proulx and Valérie Fournier contributed to the study conception and design. Material preparation, data collection and analyses were performed by Olivier Slupik, Frédéric McCune, and Chris Watson. The first draft of the manuscript was written by Olivier Slupik and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Introduction

Insect pollination plays an essential role in the functioning of terrestrial ecosystems, particularly agro-ecosystems (Ollerton 2017; Grab et al. 2019). More than 85% of angiosperms (Ollerton et al. 2011), and approximately 70% of the world's important crops (Klein et al. 2007; Häussler et al. 2017) benefit from entomophile pollination. It is estimated that one-third of the food produced results from entomophile pollination and that this is responsible for $235 to $577 billion per year in farm income (Potts et al. 2016). While an abundance of pollinators is important to maximise the number of flowers pollinated, there is a clear relationship between their diversity and the number of fruits produced per plant (Vergara et al. 2009; Garibaldi et al. 2013; Winfree et al. 2019). According to Kleijn et al. (2015), no less than 25 species of pollinating insects contribute a value greater than $100/ha annually, and 93 species contribute up to $100/ha on average annually. Moreover, this diversity ensures stability in the pollination system, since each species responds differently to environmental disturbances (Grab et al. 2019).

Bees (Hymenoptera: Apoidea) and hoverflies (Diptera: Syrphidae) are respectively the first and second most important groups of pollinating insects (Ssymank 2008). Most species of bees possess characteristics that make them successful pollinators, such as hairy bodies (Goulson, 2010) and sonication behaviour (Venturini et al. 2017), an efficient way of harvesting viable pollen from anthers of certain plant groups used by some bees, including species of bumble bees (*Bombus* spp.) and *Andrena* spp. (Orford et al. 2015). The approximately 730 different bee species in Canada (Packer et al. 2007) occupy many ecological niches and harbour diversified functional traits, ranging from specialist to generalist (Forup and Memmott 2005; Kennedy et al. 2013), from soil to cavity nesters (Cane 1991), and from solitary to eusocial (Wilson and Carril 2016). Almost all of the 413 known hoverfly species in eastern North America (Skevington et al. 2019) feed on pollen and nectar as adults. They are found in almost all terrestrial habitats, since larvae feed on a wide range of ecological niches, ranging from aphidophagous, to phytophagous, and including many others (Skevington et al. 2019). Hoverflies require less energy for pollinating than bees, which can make them more efficient, depending on environmental conditions (Ssymank 2008). In addition, their frequency of interaction with flowers is high (Rader et al. 2016), and their population can outnumber bees under certain conditions (Öckinger and Smith 2007; Haenke et al. 2009; Garibaldi et al. 2013). Finally, they are known to be more resilient than bees to intensive agriculture and urbanization, with many species able to find resources in highly transformed habitats (Winfree et al. 2011; Orford et al. 2015; Rader et al. 2016).

According to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2016), the decline in pollinating insects is one of the greatest environmental concerns of the 21st century. Recently, Zattara and Aizen (2021) found that 25% fewer bee species were detected between 2006 and 2015 than before 1990, suggesting an accelerated decline over the last three decades. Moreover, 16.5% of the world's pollinating species may be threatened with extinction (IPBES 2016). A major cause of this decline is agricultural intensification (Potts et al. 2010; Kennedy et al. 2013; Breeze et al. 2016; Grab et al. 2019), which leads to the degradation, fragmentation, and conversion of natural habitats to agricultural land (Haenke et al., 2009; Kremen et al., 2007; Morrison et al., 2017; Öckinger and Smith, 2007; Sánchez-Bayo and Wyckhuys, 2019). Common conventional agricultural practices involve the use of large areas of land under low-nectar-producing and often monocultures such as corn and soybeans (Ahrent and Caviness, 1994), increased use of pesticides (Krupke et al. 2012; Van der Sluijs et al. 2013) and weeding in nearby areas that lead to the depletion of floral resources throughout the area (Goulson et al. 2008; Scheper et al. 2014).

Natural habitats and semi-natural grasslands are known to represent particularly suitable habitats for native pollinators in agricultural contexts. Less disturbed by human activity than cultivated areas, these habitats encompass a greater diversity of resources and nesting sites at the landscape level (Knop et al. 2006; Holzschuh et al. 2010b; Ponisio et al. 2016). This greater diversity of resources encourages a more complex network of interactions between the species present (Knop et al. 2006), and promotes pollinator diversity and abundance (Kremen et al. 2007; Rader et al. 2014, 2016; Zou et al. 2017). In addition, these environments include floral species that are essential for some bees but absent from environments altered by agriculture (Kremen et al. 2007), and therefore support a wider range of pollinator species than more disturbed environments (Öckinger and Smith 2007). When such habitats are scarce in the agricultural landscape, field margins may play a similar keystone role in pollinator conservation. Since field margins are mowed less for weed control and subject to less pesticide treatment than crops (Hass et al. 2018), they offer floral resources and nesting sites for pollinating insects (Kells et al. 2001; Van Geert et al. 2010; Morrison et al. 2017). According to Zou et al. (2017), the abundance of pollinators in agricultural areas is more influenced by the floral resources present on site than by the contribution of adjacent natural environments. The literature on this topic suggests that patches of floral resources (e.g., field margins) become increasingly important for supporting pollinators in landscapes that are more heavily transformed by agriculture (Haenke et al. 2009; Holzschuh et al. 2016; Morrison et al. 2017).

Although wetlands have long been highly disturbed by agriculture in North America (King et al. 2006; Dahl 2011), pollinator populations have been little studied in this context (Stephenson et al. 2017). According to Stephenson et al. (2017), wetland-specific interactions between pollinating insects and flowers are affected by agricultural intensification, since many bee species are specialists of wetland-related flowers. Spring floods, often linked with wetlands, also alter the long-term functioning of terrestrial ecosystems (Harris et al. 2018). Flooding can be lethal to bees by depriving soil nesting larvae of oxygen, as observed by Fellendorf et al. (2004) for a population of *Andrena vaga* (Hymenoptera: Andrenidae), and by Batra (1966) for a population of *Lasioglossum zephyrum* (Hymenoptera: Halictidae). However, pollinating insects' degree of resistance to severe flooding events has been little studied (Fellendorf et al. 2004). Since spring floods can affect species differently, there is a need to better understand the consequences on pollinating insects and the dynamics involved.

The objective of this project was to compare the response of bee and hoverfly populations to a land-use gradient of agriculture intensification in the Lac Saint-Pierre (Quebec, Canada) floodplain. This region represents a vast set of natural and semi-natural habitats subject to a dynamic of recurrent, severe spring flooding and agricultural intensification since the 1990s (MDDEFP 2013). We conducted a two-year inventory of bees and hoverflies in three types of landscapes: field margins in conventional farming crops, semi-natural grasslands, and natural habitats. We hypothesised 1) that the assemblage of species of bees and hoverflies will be dominated by a few generalist/common species in crop field margins sites, more so than in other land-use types; 2) that a greater abundance and species richness of bees and hoverflies will be found in semi-natural grassland and natural habitat sites than in crop field margins sites; and 3) that the flooding regime will have a variable impact on pollinator species.

Materials and Methods

Study area

The study was conducted in the Lac Saint-Pierre region, Quebec, Canada (46° 12′ 15″ N, 72° 49′ 58″ W). This lake is an important widening of the St. Lawrence River extending from Sorel-Tracy to Trois-Rivières. It is the core convergence point where many tributaries, including twelve important Quebec rivers (MDDEFP 2013), meet. Seasonal flooding is common in the littoral zone of the lake, occurs on average every other year due to snowmelt in April, and lasts from less than a week to up to eight weeks. The water level of Lac Saint-Pierre then increases so dramatically that, based on data published in 2013, up to approximately 28,000 ha of riparian and terrestrial areas around the lake are flooded, making it the largest expanse of freshwater flooded land in Quebec (MDDEFP 2013). During the flooding period, flood waters inundate natural areas, perennial hayfields and annual croplands alike, and there are no regional controls within the study areas to redirect these waters. In the littoral zone, natural habitats extend over an area that in 2013 covered more than 22,500 ha, of which 21,559 ha were wetlands, 637 ha shrublands, and 322 ha forests. Cultivated areas totalled 5,264 ha, of which perennial crops and annual crops represented 3% and 20% of the littoral zone, respectively (MDDEFP 2013). Dominant annual crops then included corn, soybean, and small-grain cereals. Due to its natural flooding dynamics, Lac Saint-Pierre encompasses multiple types of natural landscapes that support an exceptional animal diversity, including 72% and 70% of Quebec bird and freshwater fish species, respectively, in 2013. Lac Saint-Pierre was declared a UNESCO Biosphere Reserve in 2001 (MDDEFP 2013).

Experimental sites in this study were strips of herbaceous vegetation located either at the margin between two agricultural fields, or within a larger patch of natural habitat. Sites were co-located at the same elevation, as determined by lidar-based land surface modelling. The lack of regional flood controls and relatively flat gradient of the floodplain meant that all sites were subject to the same natural flooding regime in a given year. Each site was assigned a category according to the predominant land-use type in a 300m radius, which we refer to as the land-use treatment (Fig. 1), representing an agricultural intensification gradient. Eight sites in forests or natural meadows were pooled as "Natural habitats", five sites in permanent or temporary meadows were pooled as "Perennial hayfields", and seven sites located in field margins of annual corn and soybean crops in conventional agriculture were pooled as "Crop field margins" (Table S1). Crop fields in this region are typically long and narrow (approximately 50m wide), separated by vegetated field margins approximately 10m in width. Accordingly, the sampling transects were established within the field margin vegetation, parallel to the crop fields. The eight sites that were pooled as Natural habitats occurred in areas comprising a mosaic of natural wetland vegetation types, including closed swamp forests (often dominated by silver maple; *Acer saccharinum* Linnaeus, 1753), wet meadows comprising a complex mix of grasses, sedges and semi-aquatic species, and shrubby forest margins dominated by *Salix* and *Cornus* species. The five sites in forage crops or pastures that were pooled as Perennial hayfields were mowed between two to four times per year, according to growing conditions. Pollinator sampling was not conducted within five days of harvesting operations. The sites were located in four municipalities: Pierreville (four sites) and Baie-du-Febvre (five sites) on the south shore of Lac Saint-Pierre, and Saint-Barthélémy (five sites) and île-Dupas (six sites) on the north shore. One site in the Perennial hayfields land-use treatment at île-Dupas was used only in 2019 and removed from the 2020 sampling season at the owner's request. Two new sites in Perennial hayfields at île-Dupas and Saint-Barthélémy (one site each) were added in 2020, for a total of 18 sites in 2019 and 19 sites in 2020. Because the municipalities are geographically close, the temperate climate, topographic height of the land, and duration of flooding are very similar. All sites were seasonally flooded in the spring of both years. The severity of flooding was similar between sites (height and duration) for each year of the project. At the peak of flooding the water depth above the sites reached over 1.5m in 2019 and over 0.5 m in 2020. Each site was separated from any other by at least 500 m, except for two pairs, which were 400 m apart. Those pairs may be within foraging range of bumblebees, some large solitary bees, and hoverflies moving from one site to the other, and thus are likely to not be totally independent (Gathmann and Tscharntke 2002).

Survey of pollinators and plants

At each site, we set up a linear transect of 15 pan-traps placed above canopy levels and deployed 1 m apart. The same locations were used for all sampling events. Pan-traps consisted of plastic bowls 15 cm in diameter, and were placed in alternating colour order of yellow, blue, and white (five traps per colour per site). These colours were selected because they are known to attract the widest array of pollinator species (Campbell and Hanula 2007). We added a drawing inside the pan-traps with a black marker pen to act as a flower nectar guide, in order to improve their attractiveness (Russell et al. 2005). Pans were filled up to three-quarters full of soapy water and deployed for periods of 48 hours without rain. Sampling events were separated from each other by two to four weeks, depending on weather conditions. In 2019, a total of five sampling events were taken on eighteen sites between June and September. In 2020, we were able to perform six sampling events on nineteen sites from May to September. The intensity and duration of spring flooding was considerably higher in 2019 than in 2020, lasting from April 16 to June 8 (54 days) in 2019 and from March 30 to April 17 (18 days) in 2020. Sampling thus started one month earlier in 2020 than in 2019.

Specimens were collected from pan-traps with a mesh-net, put in Whirl-Pack bags (Nasco, Wisconsin, USA) containing 70% ethanol and stored in a freezer until further investigations could be performed. All bee and hoverfly specimens were later sorted from Whirl-Pack bags, rinsed, pinned, and dried following FAO protocol (LeBuhn et al., 2016) for monitoring pollinator communities. Furthermore, they were identified to species level when possible, with only a few specimens left at the genus level, using Gibbs (2010), Ascher and Pickering (2014), and Packer et al. (2007) keys for bees, and Miranda et al. (2013) and Skevington et al. (2019) for hoverflies. Vouchers are stored in Dr. Fournier's laboratory at Laval University (Quebec, Canada). Identifications were performed by O. Slupik and validated by A. Gervais.

To check for correlation between land-use type and floral presence, we assigned a floral score (1-4) to each of our sites, in a radius of 100 m in Perennial hayfields and Natural habitat sites and in a transect of 100 m in field margins in the Crop field margins treatment, during four of the six sampling events in 2020. The score corresponded to a visual estimate of the coverage in flowers of nectar-producing plants at each site: 1 (trace, <1%), 2 (low, 1-5%), 3 (average, 5-20%), and 4 (high, more than 20%). Finally, we conducted an inventory of the main floral species encountered at each sampling event in 2020 and at each of the nineteen sites within this radius, by collecting specimens for laboratory identification, to species level when possible, using Marie-Victorin's (1964) key. Plants were not vouchered.

Statistical approach

Bees and hoverflies were analysed separately due to their different biologies. Honey bees (*Apis mellifera*) were not considered in our analyses because they most likely came from commercial apiaries (IPBES 2016). As the pan-trap method may underperform in detecting certain types of species (Hudson et al. 2020), we used the nonparametric Chao1 estimator to estimate the total number of species of bees and hoverflies for each land-use treatment and year. This estimator works on the basis of the captured singletons and doubletons and the observed richness, and assumes that rare species carry the most information about the number of undetected species (Gotelli and Chao 2013). Floral scores were modeled with a Pearson Chi-square test for association with the land-use treatment.

Since our sampling revealed a strong dominance of certain species for both bees and hoverflies, the Berger-Parker index (Berger et Parker, 1970) was calculated at each site for each year as the ratio between the abundance of the most dominant species over the total abundance. This index is effective in transformed or disturbed habitats (Caruso et al. 2007). We used it to compare the relative dominance of the most abundant species between land-use treatments and between sampling years with one-way ANOVAs.

Species richness and abundance for bees and hoverflies were modeled separately for each year using generalised linear mixed models (GLMMs). The negative binomial distribution was used because it provided the best fit according to the AIC criterion and residuals were normally and homogeneously distributed. Land-use treatment (Natural habitats, Perennial hayfields, Crop field margins) and Year (2019, 2020) were fixed effects in the models. Sampling dates (day of the year) and regions (Pierreville, Baie-du-Febvre, Saint-Barthélémy, île-Dupas) were considered as random effects. The interaction between land-use treatment and year did not improve the statistical fit and was removed from final models.

All statistical analyses were performed using R Studio software (RStudio v1.2.5019). GLMMs were fitted using effects (Fox, 2003) and lme4 (Bates et al., 2013) packages in the R environment (RStudio v1.2.5019).

Results

A total of 2,099 bee specimens from 85 species (Table 1) and 2,373 hoverfly specimens from 41 species (Table 2) were collected during 2019 and 2020. The most abundant bee species were *Lasioglossum novascotiae* (Mitchell) and *L. zonulum* (Smith), together accounting for 38% of all bee specimens collected. For hoverflies, *Toxomerus marginatus* (Say) and *T. geminatus* (Say) together accounted for 66% of the specimens collected, and this total rises to 81% when *Tropidia quadrata* (Say) and *Helophilus latifrons* (Loew) are included. Rare bees and hoverflies ($N<10$) accounted for a significant portion of the number of species recorded, 75% and 65% respectively. The singletons represented, respectively, 25% and 20% of the species of bees and hoverflies found. The results of the Chao1 estimator suggest that we underestimated the diversity of bees and hoverflies in all land-use treatments and years, especially in the Natural habitats treatment (Table 3). The number of potential additional species to be discovered ranged from 2 (15%) to 11 (32%) in the Perennial hayfields treatment, from 13 (52%) to 21 (55%) in the Crop field margins treatment, and from 11 (39%) to 75 (155%) in the Natural habitats treatment.

For the average abundance and species richness of bees per unit effort, the GLMMs showed an overlap in the confidence intervals of the Crop field margins and Perennial hayfields treatments, and of the Perennial hayfields and Natural habitats treatments (Fig. 2). However, confidence intervals of the Crop field margins and Natural habitats treatments do not overlap, indicating significantly lower abundance and species richness in natural habitats than crop field margins (Table 6). In terms of the average abundance and species richness of hoverflies, we found an overlap in the confidence intervals of all habitat treatments. No statistical differences were found between the three types of land-use. Twenty-seven bee species were collected only in the Crop field margins (41% of the species collected in the Crop field margins and 31% of all bee species), while Perennial hayfields had no species only caught in this land-use type and the natural areas only six of 56 (11%). Hoverflies were more evenly distributed and the Natural habitats had the highest proportion of species only caught in one land-use type (five of 31 vs three of 33 for the field margins).

Pearson's Chi-squared test on floral scores showed a correlation (χ-squared = 17.007, $p=0.009$) between the land-use treatment and floral presence (Table 4). The presence of flowers appeared to be higher in the Crop field margins treatment, followed by the Perennial hayfields treatment, and the Natural habitats treatment. Moreover, we consistently observed that flowers were less diversified but highly concentrated in field margins in the Crop field margins treatment (Table S2). In contrast, flowers were more diversified, but generally lower in number and more dispersed over the area, in the Perennial hayfields and the Natural habitats treatments.

Analysis of variance of the Berger-Parker index revealed no differences between land-use treatments regardless of the pollinator group or the year (Table 5). No difference was found for bees between the two years (Table 5; $F_{1,33}$=1.975; p=0.169), site averages showed a higher proportion of dominant species for hoverflies in 2019 than in 2020 (Table 5; $F_{1,35}$=5.831; p=0.0211).

Comparing data from the two years, 366 bee specimens from 44 species and 951 hoverfly specimens from 26 species were collected in 2019, while 1,733 bee specimens from 75 species and 1,422 hoverfly specimens from 35 species were collected in 2020. In fact, the last sampling in 2020 harvested 59% (N=838) of the season's hoverflies, without which hoverflies would have been present in slightly lower abundance in 2020 than in 2019. GLMMs showed a significant increase and non-overlapping confidence intervals of the predicted values of abundance and species richness for bees from 2019 to 2020, but no significant difference for hoverflies (Table 6).

Discussion

We found that the assemblages of bees and hoverflies were similarly dominated by a few species in all land-use treatments. We also found that bees were more abundant and species rich in the Crop field margins sites compared to other land-uses, which could be explained by an attractive effect of floral resources concentrated in field margins. Finally, we observed that bee populations increased in terms of abundance and species richness in the second year, suggesting a negative impact of the prolonged flooding that occurred during the first year of the study, but only on bees.

Bee and hoverfly inventory

Pollinator populations have been studied less in wet environments than in dry, warm ones (Moroń et al. 2008). Our total bee species richness is similar to that observed in other wetland studies (Moroń et al. 2008; Stephenson et al. 2017), and our assemblages were dominated by a few generalist species. The studies cited above used more than one capture method (net, van-trap), which may enable capturing more individuals of certain groups less attracted to pan-traps (Wilson et al. 2008; Gonzalez et al. 2020). Moreover, we found a very high number of singleton species, and the results suggest that we underestimated the diversity of bees and hoverflies (Table 3). In particular, the number of bee species obtained with the Chao1 estimator from natural habitats is more than 2.5x the number of species we actually observed in 2020 (124 vs 49 species). For hoverflies, we found a species richness similar to that observed in previous studies conducted in cranberry crops (Gervais 2015) and blueberry crops (Moisan-DeSerres et al. 2015), with similar dominant species (*Toxomerus* spp.).

The pollinator populations of Lac Saint-Pierre appear to be dominated by a few generalist species, as suggested by Berger-Parker indices of 39% for bees and 57% for hoverflies, and no differences across land-use types. Only two species of the generalist genus *Lasioglossum* spp. accounted for 38% of the bee specimens. In total, 70% of the total bee population belonged to the genus *Lasioglossum* spp., while 69% of the bumblebees belonged to the species *Bombus impatiens*, two taxa that are thought to be tolerant to anthropogenic disturbances (Grab et al. 2019). For hoverflies, only four species accounted for 81% of the specimens collected, which is consistent with the results for bees. A bias in our sampling method might contribute to this result as pan-traps favor the catch of Halictidae among other bee families. Indeed, many studies that employ pan-traps find that Halictidae make up most specimens collected (Portman et al. 2020). Droege et al. (2010), as a notable example, found that Halictidae made up from 40.1 to 99.4% of specimens captured at nine sites across North America with the pan-traps method. Despite knowing this, we can't ignore another hypothesis to explain the predominance of so few species of both bees and hoverflies, which is that habitat degradation and high pesticide exposure reduce populations to a few tolerant generalist species (Dormann et al. 2007). Although it is normal that generalist species dominate biological inventories, natural environments are expected to have less dominance than transformed ones (Caruso et al. 2007; Dormann et al. 2007). Normally, natural environments and agricultural landscapes share different assemblages of species, the latter often being dominated by generalist species such as *Lasioglossum* spp., like we observed. The former has normally more brood parasites and wood, stem, and cavity-nesting species because of the presence of trees (Harrison, 2017), but that is not the case in our study. Furthermore, in Perennial hayfields and Natural habitat sites, the Berger-Parker indices showed the same degree of assemblage simplification and domination by Halictidae as in the Crop field margin sites. Thus, the entire landscape of the Lac Saint-Pierre shoreline shows assemblages equally dominated by a few generalist species even in habitats thought to be the most natural, which is characteristic of agriculturally disturbed and degraded environments (Dormann et al. 2007; Grab et al. 2019).

Land-use type effect

Contrary to our hypothesis, bee abundance and species richness were higher in Crop field margins sites. We found a correlation between the availability of floral resources and land-use treatment, which matches the pattern of bee species richness and abundance. These results suggest that field margins were associated with a higher floral resource that may act as refuge habitat for pollinators (O'Connor et al., 2019). It may attract and concentrate pollinators over a wider radius as well (Zou et al., 2017), especially since the surrounding crops were non-nectar-producing. Several studies have shown that flower strips attract and support locally higher densities and species richness of bees and hoverflies (Jönsson et al. 2015; Scheper et al. 2015; Ramseier et al. 2016; Buhk et al. 2018) compared to agricultural control areas, and support bee abundance not only locally but across the entire landscape (Jönsson et al. 2015). The greater number of bee species only caught in Crop field margins compared with other land-use types also highlight that more flowers bring more bees.

Similarly, a wider scattering of bees may explain their lower numbers in Natural habitat sites. Other studies suggested that a lower flower abundance may also increase the attractiveness of pan-traps (Wilson et al. 2008; O'Connor et al. 2019). It is unclear whether this effect could compensate for bee scattering in natural habitats in our experiment. Nevertheless, bees' relative species richness and abundance among sites should reflect the probability of floral resource use at these locations. Thus, the lower catches in natural environments are consistent with a lower floral presence (O'Connor et al. 2019). Our results allowed us to identify field margins as a key habitat for pollinators in the Lac Saint-Pierre landscape, and even more so for bees than hoverflies. This observation, along with our Berger-Parker indices, aligns with findings by Holzschuh et al. (2016) and Zou et al. (2017). It demonstrates that conservation of pollinating insects relies on floral resources, especially in highly disturbed agricultural landscapes.

Our results suggest that field margins are an important resource for a diversity of bees in the Lac Saint-Pierre floodplain. In contrast, previous studies in agricultural landscapes found that natural habitats and perennial hayfields support a higher richness of pollinator species, including bees (Kremen et al. 2007; Rader et al. 2016). One explanation is that our Natural habitat and Perennial hayfield sites support bees for other reasons than alimentation, such as the availability of nesting grounds (Knop et al. 2006; Kennedy et al. 2013). For instance, it has been shown that bee communities shrink as they move closer to the center of non-nectar-producing crops, and expand as they move closer to field margins and nearby natural environments (Holzschuh et al. 2010; Kratschmer et al. 2019; Venturini et al. 2017).

Hoverflies showed little response to the type of land-use, with a wide overlap between the three land-use treatments, for both abundance and species richness. These results are consistent with those of Verboven et al. (2014), who found no greater hoverfly presence in a rural-natural gradient, and Schirmel et al. (2018), who found that floral resources were a poor predictor of hoverfly abundance and species richness. Because hoverflies do not have nests, they can move more freely across the landscape (Rader et al. 2016). In addition, hoverfly larvae do not consume pollen or nectar, which may explain the presence of adults in areas with fewer flowers but with other resources possibly used by larvae (Jauker et Wolters, 2008; Rader et al., 2014). Still, within agricultural areas, adult hoverflies concentrate on the most rewarding resources, such as field margins (Haenke et al. 2009), as the crops around them are not nectar-producing. Therefore, the fact that field margins attracted as many hoverflies as the other two environment types is sufficient to consider field margins important for supporting hoverfly foraging in this agricultural floodplain.

Year effect

From 2019 to 2020, the abundance of bees per unit effort more than quadrupled, while species richness nearly doubled. An environmental factor that changed drastically from one year to the other was the duration of flooding, which was longer in 2019 (54 days), and shorter in 2020 (18 days). Since we do not have replicate of this effect, flooding duration and intensity remains only a possible explanation for our results and should be taken as conjecture. We initially thought that cavity-nesting bees could be less impacted by flooding than soil-nesting bees, as they might find shelter above ground for wintering (Wilson et al. 2016). Several bee species are known to avoid the consequences of flooding to some extent (Cane 1991; Visscher et al. 1994), such as *Perdita floridensis* (Hymenoptera: Andrenidae), whose prepupae, once flooded, can move themselves to better oxygenated areas in which the oxygen is provided by algae (Norden et al. 2004). Other soil-nesting bee species can resist humidity by building nests with hydrophobic lipid cell linings (Roubik 1989; Cane 1991), just as bumble bees secrete a hydrophobic wax to waterproof their nests (Roubik 1989), and bees of the tribe Meliponini make the outer walls of their nest impermeable to water by building thin batumen layers made of resin (Wille

1966). However, the proportion of soil-nesting bee specimens found each year was similar at approximately 89%. In fact, the water level during flooding in both years may have remained high long enough to impact the two nester guilds equally. Thus, low bee abundance observed in 2019 may be due to excessive mortality of adults and larvae in the soil and vegetation due to prolonged flooding in spring (Batra, 1966; Fellendorf et al., 2004). In addition, since vegetation growth and flowering were delayed in May and June 2019, a lack of floral resources may have deprived early active bees of food for their offspring. In contrast, no effect of the year was found on hoverflies. Among our hoverflies, only the genera *Eristalis* spp., *Helophilus* spp. and *Parhelophilus* spp. are aquatic or semi-aquatic (Skevington et al. 2019) and they accounted for 7% of total abundance in 2019 and 23% in 2020. Flooding in 2019 did not appear to have impacted terrestrial larval hoverflies as their proportion was not heavily reduced. The marked responses of bees between years contrasts with the weak response of hoverflies, which suggests that the two groups had divergent responses and adaptations to spring flooding conditions.

However, we would need further investigation over more years to test the effect of flooding on pollinators communities. While the variation in population we observed between 2019 and 2020 is remarkable, both generalist and specialist bee species are known to exhibit high interannual variation in abundance and diversity (Williams et al. 2001; Bruninga-Socolar et al. 2022). For instance, Herrera (1988) found that only one-third of the bee species visiting flowers of *Lavandula latifolia* were captured any given year of a five-year study. Minckley et al. (1999) also reported high variations in abundance and species occurrence from surveys. Transect surveys along the elevation gradient of the floodplain would allow disentangling the effect of flood duration, irrespective of land-use or inter-annual variability. Nonetheless, prolonged flooding can induce high bee mortality (e.g., Fellendorf et al., 2004).

Conclusion

Field margins can act as flower strips and provide alternative floral resources for pollinators (Ramseier et al. 2016). Thus, agricultural practices should emphasise their protection and enhancement. A recognised formula for optimizing the effectiveness of flowers strips is to cover about 10% of the targeted agricultural area with them (Buhk et al. 2018).

Encouraging greater pollinator species richness by planting flower strips in agricultural fields is also influenced by landscape heterogeneity at a broader scale. In fact, establishing flower strips with host plants for pollinators does not directly increase species diversity in a given agricultural landscape, but supports species already present (Rundlöf et al. 2018). They offer refuge, serve as a food source and improve connectivity between natural environments for pollinators (Buhk et al. 2018). However, they can locally increase bee diversity if source populations are present in the landscape. Host plants can have a bigger impact on the populations of pollinators for which a standard array of weeds is not sufficient. The conservation of natural and semi-natural environments goes hand in hand with the enhancement of flower strips in agriculture.

Our study demonstrates the key role of field margins in the conservation of pollinating insects in a landscape transformed by agricultural activity. Furthermore, to our knowledge, this study is the first to document an apparently severe reduction in overall bee populations that might be due to spring flooding, which indicates that field margins may be even more important when the landscape is impacted by flooding events. However, we do not have replicates over many years or elevation zones to confirm this finding. Nevertheless, we believe that our results will be echoed in future studies investigating this effect with replicates of dry and flooded years or transect surveys along an elevation gradient, controlling for other environmental factors or population dynamic effects of pollinating insects. A better understanding of flooding impact on pollinators will help establish more effective measures for their conservation in floodplain systems.

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Figure captions

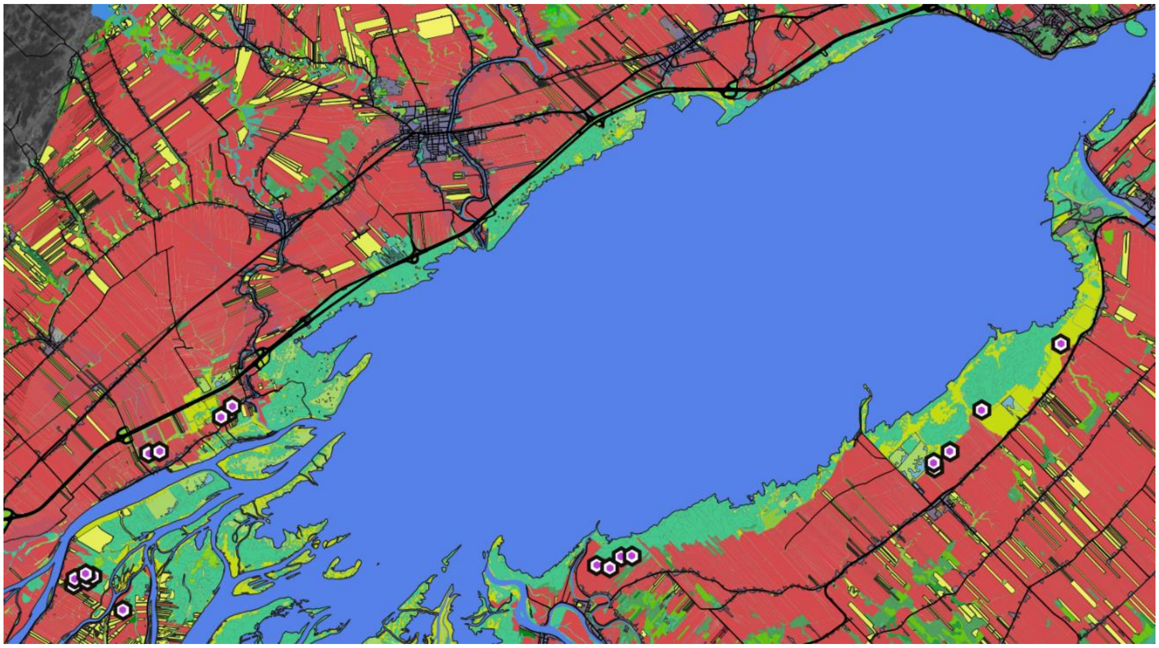

Fig. 1 Distribution of sites along the Lac Saint-Pierre shoreline. Red represents agricultural areas, yellow represents Perennial hayfields and green represents natural habitats

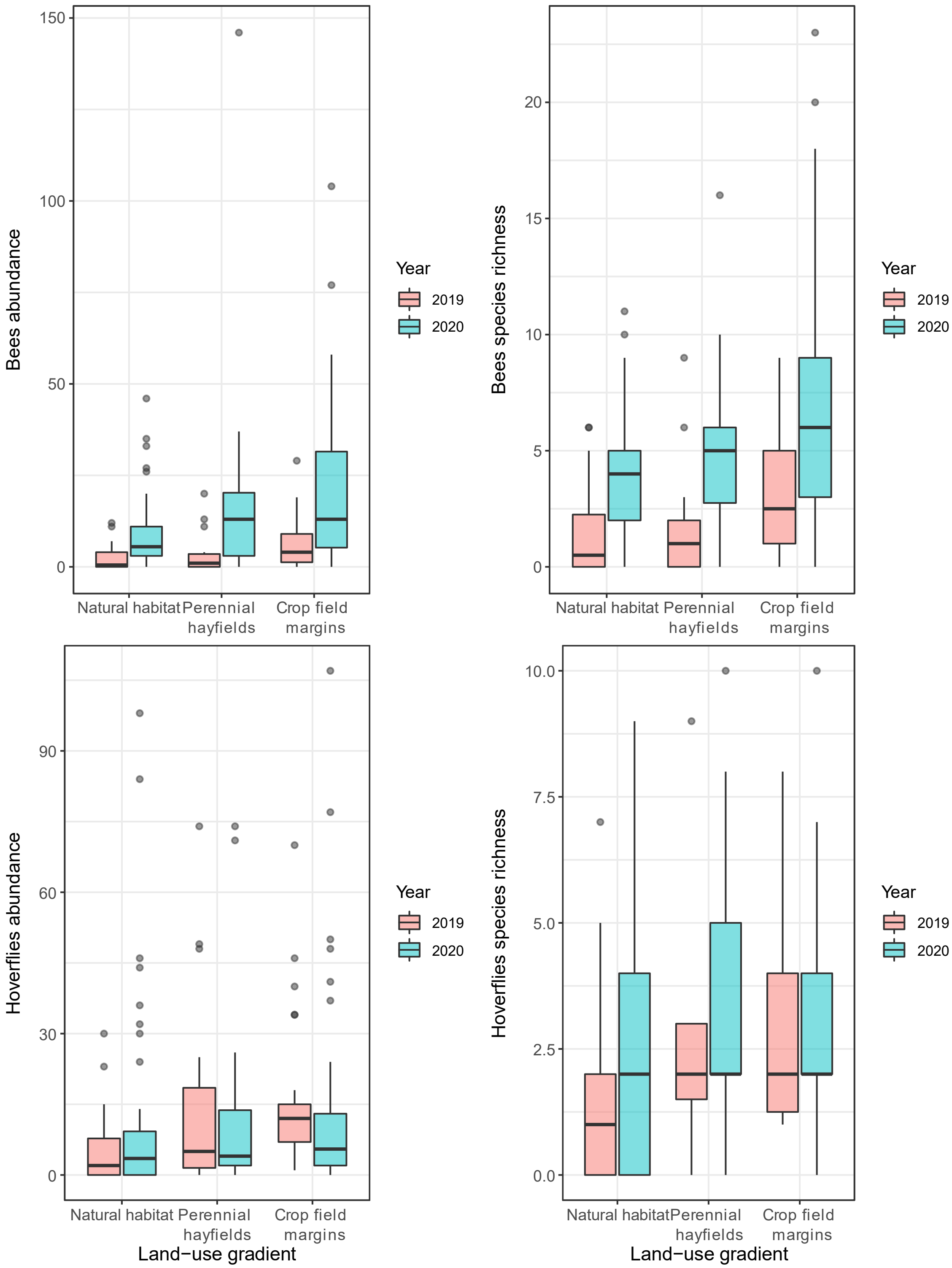

Fig. 2 Boxplot of bee and hoverfly abundance and species richness per land-use type and year. Horizontal lines inside the box represent the median, box limits represent 25th and 75th percentiles, vertical lines represent lower and upper 25th and 75th percent

Tables

Table 1 Total number of specimens caught per bee species per land-use type for 2019 and 2020. Species are sorted by family, then alphabetically

Taxon	Crop field margins	Perennial hayfields	Natural habitats
Andrena barbilabris (Kirby, 1802)	1	0	1
Andrena bradleyi Viereck, 1907	1	1	1
Andrena cressonii Robertson, 1891	1	0	2
Andrena nivalis Smith, 1853	2	0	0
Andrena persimulata Viereck, 1917	1	0	0
Andrena rugosa Robertson, 1891	4	2	4
Andrena vicina Smith, 1853	2	0	0
Andrena wilkella (Kirby, 1802)	1	0	0
Andrena w-scripta Viereck, 1904	2	0	0
Andrena ziziae Robertson, 1891	2	3	0
Perdita octomaculata (Say, 1824)	1	0	0
Anthophora terminalis (Cresson, 1869)	1	2	2
Bombus bimaculatus Cresson, 1863	1	0	0
Bombus borealis Kirby, 1837	8	1	3
Bombus citrinus (Smith, 1854)	2	0	0
Bombus griseocollis (De Geer, 1773)	20	3	4
Bombus impatiens Cresson, 1863	69	21	34
Bombus rufocinctus Cresson, 1863	2	0	0
Bombus sandersoni Franklin, 1913	1	0	0
Bombus ternarius Say, 1837	2	0	3
Bombus terricola Kirby, 1837	0	0	4
Ceratina mikmaqi Rehan and Sheffield, 2011	2	0	2
Melissodes denticulatus Smith, 1854	1	0	0
Melissodes desponsus Smith, 1854	3	0	0
Melissodes druriellus (Kirby, 1802)	10	0	1
Peponapis pruinosa (Say, 1837)	1	2	3
Colletes kincaidii Cockerell, 1898	1	0	0
Hylaeus affinis (Smith, 1853)	1	0	4
Hylaeus annulatus (Linnaeus, 1758)	9	3	12
Hylaeus floridanus (Robertson, 1893)	1	0	0
Hylaeus illinoisensis (Robertson, 1896)	5	6	4
Hylaeus mesillae (Cockerell, 1896)	1	0	1
Hylaeus modestus (Say, 1837)	38	15	29
Hylaeus nelumbonis (Robertson, 1890)	3	1	1
Hylaeus rudbeckiae (Cockerell & Casad, 1895)	0	0	1
Hylaeus saniculae (Robertson, 1896)	0	0	3
Hylaeus schwarzii (Cockerell, 1896)	0	0	1
Hylaeus spp.	4	0	1
Agapostemon texanus Cresson, 1872	8	0	0
Agapostemon virescens (Fabricius, 1775)	49	1	1
Augochlora pura (Say, 1837)	14	4	54

Augochlorella aurata (Smith, 1853)	0	3	1
Halictus confusus Smith, 1853	8	0	1
Halictus ligatus Say, 1837	17	2	3
Halictus rubicundus (Christ, 1791)	26	1	12
Lasioglossum admirandum (Sandhouse, 1924)	0	1	0
Lasioglossum athabascense (Sandhouse, 1933)	2	0	0
Lasioglossum atwoodi Gibbs, 2010	0	0	1
Lasioglossum coeruleum (Robertson, 1893)	0	1	1
Lasioglossum ephialtum Gibbs, 2010	11	7	4
Lasioglossum foveolatum (Robertson, 1902)	1	0	0
Lasioglossum heterognathum (Mitchell, 1960)	1	0	0
Lasioglossum hyalinum (Crawford, 1907)	0	2	2
Lasioglossum imitatum (Smith, 1853)	1	0	0
Lasioglossum leucozonium (Schrank, 1781)	31	18	16
Lasioglossum lineatulum (Crawford, 1906)	23	22	7
Lasioglossum novascotiae (Mitchell, 1960)	211	191	58
Lasioglossum oblongum (Lovell, 1905)	58	37	52
Lasioglossum pectorale (Smith, 1853)	5	0	5
Lasioglossum perpunctatum (Ellis, 1913)	35	6	1
Lasioglossum pilosum (Smith, 1853)	4	1	1
Lasioglossum planatum (Lovell, 1905)	4	1	0
Lasioglossum sagax (Sandhouse, 1924)	26	20	16
Lasioglossum sheffieldi Gibbs, 2010	5	0	0
Lasioglossum subversans (Mitchell, 1960)	1	0	1
Lasioglossum tenax (Sandhouse, 1924)	93	5	8
Lasioglossum versans (Lovell, 1906)	1	0	0
Lasioglossum versatum (Robertson, 1902)	52	33	10
Lasioglossum vierecki (Crawford, 1904)	2	0	0
Lasioglossum zephyrum (Smith, 1853)	2	2	1
Lasioglossum zonulum (Smith, 1948)	169	65	139
Lasioglossum spp.	0	1	1
Sphecodes banksii Lovell, 1909	1	0	0
Coelioxys sp.	1	0	0
Heriades variolosa (Cresson, 1872)	2	0	1
Hoplitis pilosifrons (Cresson, 1864)	0	0	1
Hoplitis producta (Cresson, 1824)	1	0	1
Hoplitis truncata (Cresson, 1878)	0	0	1
Megachile brevis Say, 1837	3	0	1
Megachile inermis Provancher, 1888	5	2	0
Megachile latimanus Say, 1823	2	1	1
Megachile lapponica Thomson, 1872	1	0	1
Megachile mendica Cresson, 1878	3	0	0
Megachile perihirta Cockerell, 1898	3	0	0
Osmia albiventris Cresson, 1864	0	1	1
Total	1,086	488	525
Mean specimens per trap	0.940	0.651	0.461

Table 2 Total number of specimens caught per hoverfly species per land-use type for 2019 and 2020. Species are sorted by subfamily, then alphabetically

Taxon	Crop field margins	Perennial hayfields	Natural habitats
Anasimyia anausis (Meigen 1822)	1	0	1
Chalcosyrphus nemorum (Fabricius, 1805)	1	2	3
Eristalis anthophorina (Fallen, 1817)	4	3	3
Eristalis arbustorum (Linnaeus, 1758)	17	2	1
Eristalis dimidiata (Wiedemann, 1830)	1	1	0
Eristalis flavipes Walker, 1849	3	0	0
Eristalis stipator Osten Sacken, 1877	1	1	1
Eristalis tenax (Linnaeus, 1758)	61	17	19
Eumerus strigatus (Fallen, 1817)	3	0	0
Eurimyia stipata (Walker, 1849)	7	3	13
Helophilus fasciatus Walker, 1849	20	2	15
Helophilus hybridus Loew, 1846	14	2	8
Helophilus latifrons Loew, 1863	119	8	37
Neoascia spp.	1	0	2
Parhelophilus laetus (Loew, 1963)	12	6	15
Parhelophilus rex Curran and Fluke, 1922	2	0	1
Sericomyia chrysotoxoides (Macquart, 1842)	3	6	13
Sericomyia militaris Walker, 1849	1	0	2
Syritta pipiens (Linnaeus, 1758)	1	1	1
Tropidia quadrata (Say, 1824)	120	37	44
Xylota confusa Shannon, 1926	0	0	1
Xylota subfasciata Loew, 1866	0	1	0
Xylota tuberculata (Curran, 1941)	0	0	1
Heringia calcarata Loew	3	5	0
Heringia canadensis Curran, 1921	1	0	0
Heringia elongata (Curran, 1921)	1	0	0
Heringia salax (Loew, 1866)	5	2	0
Allograpta obliqua (Say, 1823)	2	2	0
Eupeodes americanus (Wiedemann, 1830)	25	34	9
Eupeodes latifasciatus (Macquart, 1829)	4	2	1
Melanostoma mellinum (Linnaeus, 1758)	0	1	4
Meliscaeva cinctella (Zetterstedt, 1843)	0	0	1
Platycheirus quadratus (Say, 1823)	1	1	1
Platycheirus sp.	0	0	1
Sphaerophoria brevipilosa Knutson, 1973	8	6	0
Sphaerophoria philanthus (Meigen, 1822)	7	3	3
Syrphus knabi Shannon, 1916	0	0	1
Syrphus rectus Osten Sacken, 1875	0	2	2
Syrphus ribesii (Linnaeus, 1758)	2	1	1
Toxomerus geminatus (Say, 1923)	199	140	406
Toxomerus marginatus (Say, 1823)	456	240	125
Total	1,106	531	736

Table 3 Number of bee and hoverfly species observed (S.obs), predicted number of species (S.chao1) and standard error of predicted number of species (Se.chao1), per land-use type and year

Land-use type	Year	Bee S.obs	Bee S.chao1	Bee Se.chao1	Hoverfly S.obs	Hoverfly S.chao1	Hoverfly Se.chao1
Crop field margins	2019	38	59	13.14	25	38	11.15
Crop field margins	2020	63	77	8.09	27	45	15.05
Perennial hayfields	2019	15	20	5.51	13	15	3.15
Perennial hayfields	2020	34	45	8.47	24	28	3.89
Natural habitats	2019	22	44	19.25	12	40	21.3
Natural habitats	2020	49	124	45.43	28	39	8.87

Table 4 Contingency table. Frequency of flowers score given for nineteen sites during four of the six samplings in 2020 and grouped per land-use type. Pearson's Chi-squared test: χ-squared = 17.007, df = 6, p-value = 0.009258

		Floral score (coverage in flowers of nectar-producing plants)			
		High (>20%)	Average (5-20%)	Low (1-5%)	Trace (<1%)
Land-use	Crop field margins	3	10	8	7
	Perennial hayfields	0	4	6	6
	Natural habitats	1	3	5	23

Table 5 One-way ANOVA of Berger-Parker index per land-use type per year, and per year

		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Bees 2019	Land-Use	2	0.1608	0.08041	2.333	0.136
	Residuals	13	0.4481	0.03447		
Bees 2020	Land-Use	2	0.00765	0.003825	0.217	0.808
	Residuals	16	0.28245	0.017653		
Hoverflies 2019	Land-Use	2	0.0324	0.01621	0.362	0.702
	Residuals	15	0.6717	0.04478		
Hoverflies 2020	Land-Use	2	0.1380	0.06902	3.023	0.077
	Residuals	16	0.3654	0.02283		
Bees 2019-2020	Years	1	0.0538	0.05381	1.975	0.169
	Residuals	31	0.8990	0.02724		
Hoverflies 2019-2020	Years	1	0.2012	0.2012	5.831	0.0211
	Residuals	35	1.2075	0.0345		

Table 6 Predictor effect GLMMs, bee and hoverfly abundance & species richness ~ 1 + Land-use + Year + (1 | Date) + (1 | Region). Family: Negative binomial. AIC = 1325.5

Response variable	Explanatory variable	Predicted values	Standard error	Lower confidence limit	Upper confidence limit
Bees species richness	Natural habitats	2.37	0.33	1.80	3.12
	Perennial hayfields	3.12	0.51	2.26	4.32
	Crop field margins	4.67	0.64	3.57	6.11
	2019	1.91	0.34	1.34	2.72
	2020	4.85	0.75	3.58	6.57
Bees abundance	Natural habitats	4.41	0.86	3.01	6.48
	Perennial hayfields	8.49	2.03	5.3	13.61
	Crop field margins	10.86	2.16	7.34	16.07
	2019	3.25	0.81	1.99	5.31
	2020	12.79	2.83	8.27	19.77
Hoverflies species richness	Natural habitats	5.29	1.35	3.19	8.76
	Perennial hayfields	9.92	2.85	5.63	17.49
	Crop field margins	11.05	2.87	6.62	18.46
	2019	8.55	2.98	4.30	17
	2020	7.37	2.37	3.91	13.89
Hoverflies abundance	Natural habitats	1.82	0.34	1.25	2.63
	Perennial hayfields	2.34	0.47	1.58	3.47
	Crop field margins	2.70	0.50	1.87	3.89
	2019	2.02	0.49	1.25	3.26
	2020	2.37	0.53	1.53	3.69