Open-canopy ponds benefit diurnal pollinator communities in an agricultural landscape: implications for farmland pond management

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Running Title: Open-canopy ponds benefit pollinators

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ABSTRACT

1. Declines in pollinating invertebrates across intensively-cultivated landscapes linked to reductions in flower-rich habitats constitute a key threat to biodiversity conservation and the provision of ecosystem services. Over recent decades, many ponds in agricultural landscapes have become overgrown with woody vegetation, resulting in heavily-shaded, flower-poor pond basins and margins. Restoration of farmland ponds through removal of sediment and encroaching woody vegetation (canopy management) from pond margins greatly enhances freshwater biodiversity. However, the consequences of pond management for pond-margin plants and pollinating insects remains poorly understood. Here, we studied these effects for ponds in Norfolk, eastern England.

2. We compared richness, abundance, and composition of pollinating insects (hymenopterans and syrphids) and insect-pollinated plant communities between open-canopy pond systems subjected to either (i) long-term regular management of woody vegetation or (ii) recent restoration by woody vegetation and sediment removal with those communities at (iii) ponds dominated by woody vegetation.

3. Canopy management increased the richness and abundance of pollinators and insect-pollinated plants. Pollinator richness and abundance was best explained by improvements in flower resources at open-canopy ponds. Management most strongly influenced hymenopteran communities.

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4. Ponds represent important semi-natural habitats for insect-pollinated plant and pollinator communities in farmland. To enhance food resources, diversity, and abundance of diurnal pollinators, conservation management at ponds should aim for mosaics of ponds at different successional stages with a high proportion of early-successional open-canopy ponds. Agricultural ponds are emerging as important habitats not only for aquatic biodiversity, but also for terrestrial species, thus warranting their prioritisation in future agri-environment schemes.

Keywords: biodiversity conservation, farmland ponds, habitat heterogeneity, pollinator community, pollinator diversity, semi-natural habitats.

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1. INTRODUCTION

In recent decades, agricultural industrialisation has focused strongly on increased crop yields, resulting in largely homogenised agricultural landscapes. Agricultural landscapes have thus been progressively transformed into 'ecological deserts', with associated major declines in farmland biodiversity (Carvell *et al.*, 2006; Conrad *et al.*, 2006; Carré *et al.*, 2009; Ollerton *et al.*, 2014). These declines include key diurnal pollinator groups such as bees and hoverflies (Steffan-Dewenter *et al*., 2002; Goulson *et al.*, 2005; Biesmeijer *et al.*, 2006; Popov *et al.*, 2017), with reductions in habitat quality and losses of nectar- and pollen-providing plant species key drivers of observed declines (Goulson *et al.*, 2005; Carvell *et al.*, 2006; Pywell *et al.*, 2006; Botham *et al.*, 2015; Wood *et al.*, 2015a). With agricultural intensification, plant species richness has declined not only in agricultural fields, but also in increasingly fragmented adjacent semi-natural habitats (Steffan-Dewenter *et al.*, 2002; Pywell *et al.*, 2005; Clough *et al.*, 2014). Pollinator communities generally benefit from improved habitat heterogeneity, as provided by variations in habitat-types and microhabitats within the wider landscape, because such heterogeneity increases ecological niche space that promotes plant diversity (Harrison *et al.*, 2018; Hall *et al.*, 2019). Improvements in habitat heterogeneity therefore benefit **a range of** pollinating insect groups chiefly due to enhancements of their adult (Steffan-Dewenter *et al*., 2002; Pywell *et al.*, 2006) or larval (Meyer *et al.*, 2009) food supplies or nesting requirements (Ekroos *et al.*, 2013; Fabian *et al.*, 2013). Research in temperate zones has indicated that semi-natural habitat (i.e. hedgerows, grasslands and woodland fragments) enhancement through restoration or careful management increases flowering plant diversity and associated resources (Ekroos *et al.*, 2008; Cole *et al.*, 2017; Lucas *et al.*, 2017; Kremen *et al.*, 2018; Paterson *et al*., 2019). These habitats have consequently been a major focus of pollinator conservation initiatives (Pollinator Health Task Force, 2015; Underwood *et al.*, 2017). However, one type of semi-natural habitat still ubiquitous in many temperate agricultural landscapes has been largely overlooked in this context; namely farmland ponds and their associated margins.

Within a wider landscape context, freshwater ecosystems are recognised as important habitat components that provide key resources for a wide range of aquatic and semi-aquatic taxa (Williams *et al.*, 2004; Dudgeon *et al*., 2006; Davies *et al*., 2008). Ponds in particular are known to provide suitable environmental conditions for a broad variety of these species, with high inter-pond environmental heterogeneity known to elevate species diversity in pondscapes (Biggs *et al.*, 1994, 2005; Ruggiero *et al.*, 2008; Hassall *et al.*, 2011; Vad *et al.*, 2017). Farmland ponds, however, are more than just aquatic ecosystems. These small habitats are embedded within agro-ecosystems in field-edge or centre-field positions – dependent on their various former and current uses, for example as livestock watering holes or for clay and marl extraction (Boothby & Hull, 1997; Upex, 2004). Such ponds commonly include a margin characterised by a complex topography that routinely represent aquatic – terrestrial and semi-natural – arable crop ecotones. Pond margins are furthermore characterised by steep

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soil moisture gradients, promoting the development of diverse marginal vegetation that often forms an important potential food source for pollinators. Despite their great potential benefits to wildlife, farmland ponds have experienced steep declines over recent decades in both numbers and biological quality (Beja & Alcazar, 2003; Wood *et al.*, 2003; Angélibert *et al.*, 2004; Declerck *et al.*, 2006; Williams *et al.*, 2010; Sayer *et al.*, 2012).

Research **of** UK farmland ponds shows that terrestrialisation of ponds results in a sharp decrease in pond biodiversity at the landscape scale (Sayer *et al*., 2012, 2013). Terrestrialisation, or overgrowing, is a natural process whereby ponds succeed from an open state with abundant aquatic macrophytes to often macrophyte-free water bodies shaded by dense, encroaching woody vegetation rapidly establishing on pond margins. Overgrowth, in turn, promotes pond infilling through increased detrital inputs. Farmland ponds in UK lowlands are now widely overgrown due to a cessation of management activities since the 1960s-1970s (Sayer *et al.*, 2013). Management cessation is believed to have occurred as ponds were increasingly regarded as non-beneficial components of modern agricultural landscapes when **many** farms were converted to arable dominance (Prince, 1962) and ponds were no longer needed for livestock. Encouragingly, both restoring late-successional agricultural ponds to an early successional state through removal of accumulated pond sediment and large areas of woody vegetation and long-term canopy management to open up ponds to sunlight and prevent major terrestrialisation increase the richness and abundance of a wide variety of aquatic species (Sayer *et al*., 2012, 2013), as well as benefiting local farmland bird communities (Davies *et al*., 2016; Lewis-Phillips *et al.*, 2019). Much less is known, however, regarding the impacts of pond management and restoration on terrestrial invertebrate communities, including insect pollinators, which may occupy pond margins.

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Stewart *et al.* (2017) showed that the presence of farmland ponds next to cropland significantly improved bumblebee and hoverfly abundance and crop-set of strawberries, suggesting that ponds may be of importance for insect pollinators **resulting in** pollination services. This study did not, however, provide insights into overall pollinator richness at ponds, or the potential impacts of pond restoration and management on pollinator assemblages. With many ponds within pond-rich agricultural landscapes having been left in a state of 'benign neglect' that has resulted in decreased plant diversity (Boothby & Hull, 1997; Hassall *et al.*, 2012; Sayer *et al.*, 2012), conservation strategies encouraging canopy management at ponds to improve aquatic and avian communities (Sayer *et al.*, 2012, 2013; Davies *et al.*, 2016; Lewis-Phillips *et al.*, 2019) may also have beneficial effects for pollinator communities. Management-related disturbance activities have previously reported such benefits within other semi-natural habitats (Gardiner & Vaughan, 2008; Lucas *et al.*, 2017; Paterson *et al.*, 2019), with these activities providing additional habitat for pollinator communities. Consequently, open-canopy and overgrown farmland ponds need urgent research to establish their role as habitats for pollinating insects to better inform farmland conservation practices and policy.

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In this study, we aim to establish the role of small agricultural ponds in general, and of canopy management at these ponds in particular, in enhancing pollinating insect assemblages of agricultural landscapes. We test the hypothesis that open pond margins **benefit** a greater diversity and abundance of classically-studied hymenopteran (social bees, solitary bees, and wasps) and syrphid (hoverflies) pollinator communities when compared to overgrown pond margins, hypothesizing that open ponds support a richer, more abundant flowering plant community than highly shaded overgrown ponds. We furthermore hypothesize that on-going management of encroaching woody vegetation at pond margins leads to the establishment of distinct pollinator assemblages representing species with a wide array of habitat and flower feeding preferences, in comparison to assemblages encountered at either formerly overgrown, recently restored ponds, or highly overgrown ponds.

2. METHODS

The study focuses on nine farmland ponds in Norfolk, eastern England, occurring on the edge or in the centre of **intensively managed arable** fields (with wheat, sugar beet, and beans being commonly grown crops) in a predominantly agricultural landscape also containing fragmented woodland, hedgerows, and pasture. The ponds represented three distinct treatments: i) heavily shaded overgrown ponds that have not been managed for several decades (n = 3), ii) formerly overgrown ponds that underwent 'restoration' in 2011 or 2014 consisting of major scrub and sediment removal (n = 3) resulting in open-canopy, macrophyte-dominated ponds (Sayer, unpublished data) surrounded by a herbaceous plant-dominated margin with some remnant woody vegetation, and iii) long-term managed ponds that have been maintained in an open, macrophyte-dominated state for several decades due to periodic, light-to-moderate management of woody vegetation and emergent aquatic plants, as well as occasional sediment removal (n = 3). All observed plant communities arose from natural dispersal and local seedbanks. Assemblages of insect-pollinated plants and pollinating invertebrates at the nine ponds were surveyed once-monthly during the growing seasons (March-October) of 2016 and 2017 with a total of 12 survey intervals per pond.

2.1 Study Area

All study ponds were located in North Norfolk. In this region, chalk bedrock is overlain by glacial deposits of sand, silt, gravel, and marl. The region contains a large number of farmland ponds arising from marl extraction activities especially during the 18th and 19th

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centuries (Prince, 1964; Sayer *et al.*, 2013). The study ponds are distributed across two areas: Bodham-Baconsthorpe and Briston (Figure 1). The Briston ponds were situated at Manor Farm that harbours some 40 ponds subject to regular woody vegetation and occasional sediment management over the last 40-50 years, resulting in a mosaic of ponds at different successional stages (Sayer *et al*., 2012, 2013; Lewis-Phillips *et al.*, 2019). All three long-term managed ponds used for this study were open, early successional ponds (Figure 2a). The three formerly overgrown, recently restored farmland ponds and the three unmanaged, overgrown ponds were located in similar intensively-managed farmland settings in the villages of Bodham and Baconsthorpe, some 14 km to the northeast of Manor Farm (Figure 2b-c). Despite differences in pond location that may introduce spatial correlations in the data, we were limited by the availability of ponds subjected to long-term management, a rare scenario at present. Care was taken, however, to select ponds that were located in near-identical landscape matrices in terms of environmental conditions and similar intensities of surrounding cultivation practices. This increased our confidence that reported trends could capably depict the major trends in plant and pollinator assemblages, allowing a direct evaluation of the impact of pond management, restoration and terrestrialisation on these communities.

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There was a mean distance of 1.5 km between the ponds in Bodham-Baconsthorpe and a mean distance of 1.6 km between the ponds in Briston. While social bee foraging ranges regularly exceed these distances (Knight *et al.*, 2005; Osborne *et al*., 2008), solitary bees, wasps, and hoverflies are known to have forage ranges of less than 1 km (Gathmann & Tscharntke, 2002; Kleijn & van Langevelde, 2006). This indicates that differences in richness and abundance between ponds can be credibly attributed to management category.

All ponds in this study were small (< 475 m^2; range: 121-455 m^2) and shallow (≤ 1.3 m depth). Each pond was surrounded by non-cropped margins composed of rough grassland, hedgerow shrubs (dominated by *Crataegus monogyna* Jacq. or *Prunus spinosa* L.) and trees (shrubs and trees dominated the overgrown ponds) with widths of between 5 and 17.2 m (mean: 8.7 m), resulting in a total mean footprint area of 2694 m^2 ± 464 m^2 (Lewis-Phillips *et al.*, 2019). Other pond characteristics that could have potential impacts on flowering plant and pollinator communities, including water area (open water area and total water area), area covered by trees or shrubs, area covered by bramble (*Rubus* spp.), and margin area within the total pond footprint were calculated and determined by Lewis-Phillips *et al.* (2019) using aerial photographs obtained during summer 2017. Surveying was undertaken from the shallow pond edges to the beginning of surrounding cropland or hedgerow habitats.

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2.2 Flowering plant surveys

Since pollinator richness and activity is strongly linked to the presence of insect-pollinated plant communities in a landscape (Biesmeijer *et al.*, 2006; Popov *et al.*, 2017), the abundance of all plants in flower that were potential nectar- or pollen-resources for adult pollinating insects (including terrestrial, semi-aquatic, and aquatic plant species) was recorded during each monthly pond visit with the aid of Rose (2006). Flower abundance for each plant species during each monthly survey was estimated on the DAFOR scale based on relative abundance estimates for the combined pond and pond margin (Bullock, 2006; Sayer *et al.*, 2012). Plant communities at each pond were surveyed during the first week of each survey month during both 2016 and 2017. As the DAFOR scale is categorical, the maximum value reached by each plant species over the 12 surveys was used to rank the species at the end of the study. DAFOR scores were converted into percentages for each species found at an individual pond following Sutherland (1996) (no observation: 0%, rare: 1%; occasional:

11%; frequent: 26%; abundant: 51%; dominant: 75%). To standardise the data for wild flower coverage at each pond, the percentages of all plant species were used to calculate mean coverage for the pond. Plants were subsequently categorised based on life form and soil moisture tolerance (Rose, 2006) into 5 categories: aquatic, wetland emergent, herbaceous damp arable weeds, herbaceous arable weeds and woody vegetation.

2.3 Pollinator surveys

Insect pollinator surveys were undertaken on the same day as the plant surveys. We focused on taxa considered to represent economically important pollinators of both herbaceous and woody plants in agricultural landscapes, where they provide crucial ecosystem services (Klein *et al.*, 2007; Rader *et al.*, 2011, 2016). These included social bees (family Apidae, subfamily Apinae), solitary bees (families Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), flower-visiting wasps (families Chrysididae, Crabronidae, Cynipidae, Eurytomidae, Ichneumonidae, Sapygidae, Sphecidae, and Vespidae) and hoverflies (family Syrphidae). Three methods were used to survey pollinator communities through an entire day during each monthly visit to obtain a standardised, comprehensive overview of the target assemblages: pan trap sampling, time-lapse photography, and visual observation. Environmental conditions during surveys were standardised by restricting allowable ambient air temperature (≥ 8°C) and wind speeds (< 25 km/h). **Surveys were undertaken regardless of the presence of any precipitation during each respective day. While the environmental conditions (especially the temperature range) set for this study therefore departs from those more commonly used (see Pollard & Yates, 1993; Wood *et al.*, 2015b), this allowed us to effectively sample all ponds throughout the entire study period (March-October), therefore accounting also for species active in cooler spring**

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and late autumn months (Corbet *et al.*, 1993; Stubbs & Falk, 2002; Falk, 2015) that might otherwise have been discounted from the analysis.

Pan trap-based surveys are considered a good method for recording hoverfly and some bee species and represent a common approach to surveying daytime insect assemblages (Moericke, 1951; Leong & Thorp, 1999; Gollan *et al.*, 2011; Vrdoljak & Samways, 2012). In this study, standard-coloured white, yellow, and blue 355 mL plastic bowls (PMS® and Tesco® brands) were used for the pan traps, since these colours have wavelength associations with flowers preferred by bees and hoverflies (Cane *et al.*, 2000; Vrdoljak & Samways, 2012). Bowls were not painted with fluorescent paint as catches of hymenopterans are not significantly altered by such paint and flies have been shown to be caught more frequently in pan traps without fluorescent paint (Shrestha et al., 2019). At each pond, two trays capable of holding four pan traps were separately set near differing flower resources. Pan trap trays were adjusted to a height corresponding to the flowering plant patch they were placed in, since hoverfly and some bee species have been observed to forage within a narrow flower-height range (Gollan *et al*., 2011). Bowl colours were chosen based on the dominant colours of the respective flowering patch they were placed in, but all three colours were present in each tray during each survey. In addition, each flower patch was chosen to have different dominant colours to further reduce chances for bias due to consistent use of a single bowl colour over others. Bowls were filled with a 5% saline solution mixed with a small amount of liquid detergent to break surface tension (Moericke, 1951). The pan trap sets were left throughout a single day between 07:30 and 18:00 (Supplementary Information Figure S1), a time interval representing the major active period for diurnal pollinators (Campbell *et al.*, 2014). Specimens were collected at the end of the day and dried for subsequent identification.

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Time-lapse photography was used at all ponds during each survey. This approach can be a valuable way of surveying pollinating insect populations when used in conjunction with other methods (Edwards *et al.*, 2015; Georgian *et al.*, 2015), as direct flower-visiting observations can be made during the entire surveying event. Two Timelapse Cam 8.0 camera systems (© EBSCO Industries, Inc., Birmingham, AL) were placed within the pond margin and aimed at randomly-chosen patches of flowers not already occupied by pan traps. Cameras were set no more than 50 cm from flower patches to ease identification, with an average of 75 cm of viewing width and multiple flowers in view. The cameras were programmed to take photographs at 30 second intervals from 07:30 to 18:00 to target major activity periods for diurnal pollinators (Campbell *et al*., 2014). This approach conserved battery power but captured as many flower visits as possible. All images were visually assessed for the presence of target pollinator taxa, with only insect visitors that could be clearly identified to genus or species level based on morphological features included in the analysis.

Pan trapping and time-lapse photography are important tools for surveying pollinators, but limitations exist in their ability to detect abundances of some target groups, specifically bumblebee species (Wood *et al.*, 2015b; Carvell *et al.*, 2016), and observations may be influenced by floral abundance (Baum & Wallen, 2011). These limitations were surmounted by including a standardised visual observation period to document pollinator presence and activity at each pond. All insect-pollinated plants in the pond and its margin, including tree and shrub species, were intensively observed for thirty minutes during each monthly survey, with any sighting of hymenopterans or hoverflies with clearly identifiable morphological features recorded to the lowest taxonomic level possible, as well as activity mode (flying, foraging on flower, resting, nesting activity). Any specimens that proved difficult to identify

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directly in the field were photographed for further analysis before inclusion in the sampling data. Observational surveys occurred concurrently with pan trap and time-lapse surveys at each pond. Due to the small size of the habitat patches, instead of setting up transects, visual observation was undertaken by the same observer slowly circumnavigating each pond and its margin. One complete circumnavigation was completed for each pond during all visual surveys, and all micro-habitat patches encountered were observed to reduce observer bias. Although there are potential issues with overcounting, this was not seen to be problematic as pan trapping and time-lapse surveys likely undercounted the number of individuals observed.

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For every survey technique, all specimens observed were identified to the lowest taxonomic level possible. Bee species were identified using Owens & Richmond (2012) and Falk (2015). Wasps were identified using Archer (2014) and Yeo & Corbet (2015). Hoverfly species were identified using Stubbs & Falk (2002). Off-site identification of all pollinator species was additionally assisted by use of NatureSpot (2018).

2.4 Statistical analysis

Clear seasonal trends were observed in plant flowering patterns and in the appearance of pollinators. However, as our aim was to investigate the impact of canopy management at ponds on overall flowering plant and pollinator assemblages, seasonal patterns remain outside the scope of this study. In addition, the small sample sizes for pollinators during some sample months render such an analysis less robust. For this study, the total number of pollinating invertebrate species and individuals within hymenopteran and hoverfly groups were therefore pooled for each pond using the three survey methods to determine the impact of pond management on community richness and abundance.

Insect-pollinated plant richness was determined as the number of insect-pollinated flowering plant species observed by the end of all survey intervals at each pond. The alpha-diversity of each pollinator group was assessed using the bias-corrected form of the species diversity estimator Chao1, with rarefaction curves used to account for differences in sample sizes by combining all samples collected for the ponds within each management category. Differences in richness and abundance between ponds representing the 3 different management categories were calculated using Bonferroni-corrected pairwise t-tests (Rice, 1989; Cabin & Mitchell, 2000; Gotelli & Ellison, 2004).

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To determine the specific effects of landscape factors on pollinator richness and abundance, generalised linear mixed-effect models (GLMM) were used after the data were subjected to an overdispersion test to determine the necessary distribution model. Plant and pollinator sub-group (Apinae, non-Apinae hymenopterans, all hymenopterans, syrphids, and all communities combined) richness and abundance data were found to be overdispersed, therefore a GLMM with quasipoisson distribution setting (Bolker *et al*., 2009) was run. Models for insect pollinated-plant communities included monthly richness data as response variable, pond management category as a fixed factor, year (2016 or 2017) and pond name as random effects, and bramble area, tree coverage, and waterline perimeter as explanatory variables. GLMMs for pollinator sub-groups were calculated using monthly estimated species richness or abundance data as response variables, pond management category as a fixed factor, and year (2016 or 2017) and pond name as random effects. Bramble area, monthly insect-pollinated plant species richness and mean wild flower coverage area were used as explanatory variables. Margin area was included as an offset in the models to account for differences in habitat area surveyed. Models were checked for collinearity to determine if highly linear relationships existed between any of the explanatory variables, after which a model average was calculated for all models with Akaike's information criterion (AICc) < 2 to report conditional averages of the best predictive models (Burnham & Anderson, 2002; Grueber *et al.*, 2011).

Principal Components Analysis (PCA) performed on overall abundance data was used to determine plant and pollinator community responses (using the maximum DAFOR ranking for each plant species and the total number of individual pollinator specimens at each pond) to the different pond management regimes, with management category used as a passive variable (Gotelli & Ellison, 2004; Zuur *et al.*, 2007). Using PCA instead of Correspondence Analysis allowed greater stress to be placed on abundant taxa most likely representing the dominant species occupying a specific pond category (Gotelli & Ellison, 2004). Euclidean distance was used to display dissimilarity (Elmore & Richman, 2001) between individual pond sites affording a general overview of species turnover across the ponds, but without a full beta-diversity analysis.

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All numerical analyses were undertaken using R (Version 3.5.1 GUI El Capitan build, © 2016) and the vegan (Oksanen *et al.*, 2018), iNEXT (Hsieh *et al.*, 2018), and lme4 packages (Bates *et al.*, 2015). PCAs were performed in Canoco 5 (Braak & Šmilauer, 2012).

3. RESULTS

3.1 Insect-pollinated plant communities

A total of 88 species of zoophilic flowering plants were observed during the two growing seasons across all ponds. Of these, long-term managed ponds harboured the greatest species richness (mean = 49, SD = 8.08, Figure 3, Supplementary Information Table S1a, Table S2), being significantly richer than overgrown ponds (mean = 33, SD = 3.51, d.f. = 2, t = -3.03, P

= 0.02). Recently restored ponds had an observed mean species richness of 44 flowering plants (SD = 3), and hence occupied an intermediate position between the long-term managed and overgrown ponds. Overall abundance data indicated that individual insect-pollinated plant species flowering within the pond margins were often more abundant at long-term managed, followed by recently restored ponds, when compared to overgrown ponds (Supplementary Information Table S1a, Figure 3). Results from GLMM model averaging similarly indicated that pond management was a significant predictor of flowering plant richness, with management-type 'overgrown' having a negative effect on plant richness (Table 1). No other factor or explanatory variable had a significant link with plant richness.

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According to the PCA, all long-term managed and two recently restored ponds were characterised by strong associations with a specific, diverse assemblage of flowers available to pollinators. This assemblage included aquatic (e.g. *Alisma plantago-aquatica* L.) and emergent wetland (e.g. *Mentha aquatica* L., *Epilobium hirsutum* L.) plants, herbaceous damp arable (e.g. *Ranunculus repens* L.), and herbaceous arable weed species (e.g. *Hypericum perforatum* L., *Heracleum sphondylium* L.; Supplementary Information Table S3, Figure S2). In general, overgrown ponds had strong associations with shrubs such as *P. spinosa* and some herbaceous arable weeds like *Hieracium* agg. or *Taraxacum* agg., indicative of the reduced diversity of "within habitat" characteristics reflecting the occurrence of a widely homogenous community of insect-pollinated plants.

3.2 Pollinator communities

3.2.1 Hymenopterans

A total of 3,645 individual pollinating insects were recorded from a combination of all methods. These were divided into 2,362 hymenopterans (bee, bumblebee and wasp) and

1,284 syrphid (hoverfly) specimens. Of the 2,362 hymenopterans, 1,819 individuals belonged to 12 species within the subfamily Apinae, including *Apis mellifera* (L.) (honey bee), and 11 *Bombus* species. Remaining hymenopteran specimens accounted for a further 60 species, representing chiefly solitary bees and wasps (Supplementary Information Table S1b). The hoverfly community consisted of 61 species (Supplementary Information Table S1c). A summary of how many specimens were collected by each survey method and within each categorical group is provided in the Supplementary Information (Tables S4 & S5).

Apinae species richness was similar across the pond categories (Table 2, **Figure 5a**, Supplementary Information Table S2). The richness of non-Apinae hymenopterans (i.e. excluding those from the subfamily Apinae) was, however, significantly higher (d.f. = 2, t = -243.64, P = 0.003) at recently restored ponds in comparison to overgrown ponds, with long-term managed ponds also showing a significantly higher richness than overgrown ponds (d.f. = 2, t = -3.11, P = 0.03). Estimated species richness of all hymenopterans at recently restored ponds was significantly higher than at the overgrown ponds (d.f. = 2, t = -16.89, P = 0.002), as was hymenopteran richness at long-term managed ponds in comparison to overgrown ponds, although this pattern was less pronounced (d.f. = 2, t = -3.62, P = 0.03). Mean Apinae abundances were highest at long-term managed ponds, followed by recently restored and overgrown ponds (Table 2, Supplementary Information Figure S3). Similarly, mean abundance in non-Apinae hymenopterans was highest at long-term managed ponds, with recently restored ponds showing an intermediate mean abundance between long-term managed and overgrown ponds (Table 2, Supplementary Information Figure S3).

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Corresponding to these results, rarefaction curves (Figure 5b) for all hymenopteran subgroup showed that recently restored ponds were generally characterised by a greater overall species richness compared with long-term managed and overgrown ponds. Extrapolation of the curves indicated that recently restored ponds had the greatest species richness for all hymenopteran subgroups, followed by long-term managed ponds. No significant differences in abundances within Apinae, non-Apinae, or total hymenopteran communities were detected between management categories (Supplementary Information Figure S3). This reflects the high variability in pollinator observations at each individual pond within the management categories.

The GLMM model averaging (Tables 3 & 4) revealed flowering plant community richness to be a significant positive predictor of both richness and abundance of Apinae communities. The area covered by wild flowers in contrast was significantly negatively linked with Apinae richness. Abundance and richness of non-Apinae hymenopterans and total hymenopterans was significantly positively linked to flowering plant richness (Table 4). Management was not included as a significant parameter in the models with AICc < 2 for either richness or abundance of the hymenopteran community.

The PCA for all hymenopteran species based on overall abundance data (Figure 6a) indicated diverse and abundant assemblages at long-term managed and recently restored ponds, with some similarities in species composition between these two categories when compared to assemblages at the overgrown ponds. Hymenopteran communities positively associated with terrestrialised ponds consisted of a small selection of species representing ichneumonid wasps, sand wasps, sweat bees, and some members of the Apinae, chiefly *Bombus hypnorum* Linnaeus 1758 and *B. rupestris* Fabricius 1793. By contrast, most mining bee species (*Andrena* spp.), several vespid wasp species, *A. mellifera*, *Bombus hortorum* Linnaeus 1761, *B. lapidarius* Linnaeus 1758, *B. lucorum* Linnaeus 1761, *B. pascuorum* Scopoli 1763, *B.*

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sylvestris Le Peletier 1832, and *B. terrestris* Linnaeus 1758 were more strongly associated with long-term managed and recently restored ponds based on their abundance.

3.2.2 Syrphid and total pollinator communities

Species richness in syrphids showed a different pattern to hymenopterans, with overgrown ponds having the highest estimated species richness (Table 2, Supplementary Information Table S2), followed by recently restored ponds. Long-term managed ponds had the lowest estimated species richness of syrphids. Rarefaction curves for Syrphidae nonetheless indicated that species richness was similar across all pond categories (Figure 5b). The abundance of hoverflies was highest at recently restored ponds (Table 2), followed by long-term managed and overgrown ponds (Supplementary Information Figure S3). Flowering plant richness was a strong predictor of syrphid richness and abundance (Table 3 & 4), showing positive effects on both parameters. Management was again not included as a significant predictor of syrphid richness or abundance in **models within the set confidence limits**.

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While no significant differences were found for either Syrphidae richness or abundance between the three pond management categories, the richness for the combined Hymenoptera and Syrphidae communities (Supplementary Information Table S2) was significantly greater at recently restored ponds than at either long-term managed ponds (d.f. = 2, t = 4.27, P = 0.04) or overgrown ponds (d.f. = 2, t = -10.00, P = 0.01). Rarefaction curves for the combined pollinator community also indicated that recently restored ponds had the highest species richness, although this result was tempered by a high degree of overlap in the rarefaction curves. Model averaging results from GLMMs indicated that flowering plant richness again was the only significant predictor of richness and abundance of total pollinator communities (Table 3 & 4), with positive effects shown in the model.

Hoverfly assemblage structure (Figure 6b) showed some similarity between 2 of the 3 ponds within each of the categories, but one long-term managed pond (WADD17) and one recently restored pond (BECK) were strongly dissimilar from others in their respective categories. Several hoverfly species were positively associated with long-term managed and recently restored ponds due to higher abundances of individual species at these pond categories. It was also clear, however, that many hoverfly species were not associated with any specific management category, thus clouding any discernible trends.

4. DISCUSSION

Our study provides an important first insight into the influence of pond management and restoration on populations of bees, wasps, and hoverflies providing key pollination services in agricultural landscapes. To date, little consideration has been given to ponds and their margins as farmland conservation features for pollinators. While some interpretive caution is needed given the range of survey methods employed, as well as potential spatial effects at each studied pond, this study reveals a highly species-rich insect-pollinated plant community at open-canopy ponds. Moreover, the data indicate that this diverse vegetation is closely associated with diverse and abundant communities of bees, wasps and hoverflies that utilise the pond margins and ponds themselves. Comparisons of our results with existing literature indicate that, within comparable agricultural landscapes, small farmland ponds and their margins may sustain levels of richness of pollinator species that are similar to the diversity found in other, generally more extensive semi-natural habitats such as grassland (Meyer *et al.*, 2009; Lucas *et al.*, 2017) or hedgerows (Wood *et al.*, 2015a). As such, the prevalence of ponds in many European agricultural landscapes may make them uniquely suited to achieve

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landscape-scale goals of biodiversity conservation and enhancement of pollination ecosystem services. Directly comparative research of ponds and other semi-natural habitats is, however, urgently needed to further test this inference.

Although our results are in line with the hypothesis that open-canopy ponds generated by recent pond restorations or long-term canopy management attract more abundant and speciose pollinator communities than overgrown ponds, the combination of multiple survey methods and spatial clustering of study sites arguably limits the robustness of this outcome. The observed similarity in species richness of hoverfly communities across all pond types in this context may be indicative of hoverfly communities in the agro-ecosystem being dominated by generalist species (Stubbs & Falk, 2002; Schweiger *et al.*, 2007) that do not respond strongly to differences in habitat structure between open-canopy and overgrown ponds. It is furthermore clear from this research that, whilst long-term managed and recently restored ponds have somewhat similar overall pollinator communities, recently restored ponds harbour a more species-rich pollinator community in relation to non-Apinae hymenopterans when compared with long-term managed and overgrown ponds. Nonetheless, due to considerable variability in richness across ponds within each management category, a larger sample size is required to further examine the robustness of this observation.

4.1 Drivers of pollinator richness and abundance

Our results for ponds corroborate previous findings within intensive agricultural landscapes in other temperate zones that indicate the richness and abundance of hymenopteran and hoverfly communities can be directly **linked to the richness of flowering plant communities** (Blaauw & Isaacs, 2014; Cole *et al.*, 2017). Forage resources are generally regarded as a key driver of pollinator activity and richness (Potts *et al.*, 2003; Pywell *et al.*,

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2005; Carvell *et al.*, 2006; Jönsson *et al.*, 2015; Lucas *et al.*, 2017). Hence, as corroborated by our models, the significant improvement in diverse floral nectar and pollen resources at recently restored and long-term managed ponds is likely the key correlating link that explains elevated pollinator diversity and abundance. A probable major factor underlying this observation is the removal of extensive shading from pond margins at recently restored sites or long-term managed ponds, as well as the resulting richer plant communities, **potentially increasing the stability of forage resources throughout the growing season**. Such actions allow diverse flowering plant communities to develop along the pond margin soil moisture gradient, and in particular extensive beds of plants known to be important to pollinators such as *M. aquatica*, *Lycopus europaeus* L., *Cirsium arvense* (L.) Scop., and *Rubus fruticosus* agg. (Walton *et al.*, 2020). The negative effect of wild flower coverage area on Apinae species, as demonstrated by GLMM model averaging, could be a result of these species being highly selective in the plant species they target (Seeley *et al.*, 1991; Cnaani *et al.*, 2006; Ruedenauer *et al.*, 2016). As the most prolific sources of nectar and pollen are commonly chosen by their colonies, as shown by their elaborate dancing and communicating pheromones (von Frisch, 1967; Dornhaus & Chittka, 2001), the overall area of general food resources is likely less of an important driver than the actual quality of resources offered in pond margins (i.e. quality beats quantity).

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Although not measured directly in this study, the effects of management and restoration activities themselves presumably improved “within habitat” heterogeneity. Such improvements may result in higher insect-pollinated plant richness and abundance at ponds (Brose, 2001; Lindborg & Eriksson, 2004; Roschewitz *et al.*, 2005), through the creation of micro-habitats, enhanced soil moisture gradients, and increased availability of diverse nesting resources. Moreover, open, sun-filled habitats have been shown to have greater richness and abundance of bee populations (Harrison *et al.*, 2018; Hall *et al.*, 2019). In this context, open-canopy ponds with associated sun-exposed flowering herb-rich margins may provide important pollinator habitats, especially where restoration and management activities do not remove all woody vegetation, thus leaving a wide variety of microhabitats (Sayer *et al.*, 2013) and accommodating a variety of trees, shrubs, herbaceous perennials and annual flowering plants. **Additionally, wood debris and other detrital plant matter left within open-canopy pond margins in conjunction with marginal plant vegetation can provide suitable nesting habitat for many adult hymenopteran species** (Roulston & Goodell, 2010; Westerfelt *et al.*, 2015)**, as well as larval resources for saprophytic hoverfly species** (Hartley, 1963; Rotheray & Lyszkowski, 2015; Rotheray, 2019)**, thus further contributing to the diverse micro-habitat conditions characteristic for these ponds.**

Despite PCAs indicating some general affinities of individual pollinator species for particular pond categories, our results also suggest some distinct “within category” pond-specific associations. Previous research has shown pond habitats to be highly heterogeneous with regards to their aquatic plant (Brian *et al.*, 1987; Jeffries, 1998, 2008) and invertebrate communities (Angélibert *et al.*, 2004; Biggs *et al.*, 2005), and our study suggests that this heterogeneity extends to the invertebrate assemblages inhabiting pond margins, regardless of the presence or absence of management of encroaching woody vegetation. Inter-pond differences within the same category, in this respect, will likely relate to factors such as pond shape, slope, ecological history, local settings, seedbank variability, and specific management histories. As such, the links between flowering plant richness and abundance, pollinator communities, and pond structuring factors at individual ponds need further research.

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The presence of more abundant, and potentially rewarding food resources within their foraging ranges (Beekman & Ratnieks, 2000; Osborne *et al*., 2008), may also be linked to an increased density of the nests of these pollinator species near open-canopy ponds due to improved food resources (Darvill *et al.*, 2004; Knight *et al.*, 2005). Indeed, this may account for the higher observed abundances of Apinae species at open-canopy restored and managed ponds if nesting site suitability and availability is increased (see Potts *et al.*, 2005). Similarly, the strong associations between open-canopy ponds and many solitary bee species can be accounted for by their tendency to nest in sites with high flower availability (Osborne *et al.*, 2008) since their forage ranges are much smaller than for ranges in most social Apinae (Gathmann & Tscharntke, 2002; Rands & Whitney, 2011).

The heterogeneous habitat structure of restored ponds may be especially suited for a diverse array of nesting solitary bee species as some may make use of bare soil (Darvill *et al.*, 2004; Westerfelt *et al.*, 2015) that is often exposed by restoration activities, while other species would make use of the remaining patches of woody vegetation (Westerfelt *et al.*, 2015). This deliberation is strengthened by the anecdotal observation from our data that ground-nesting solitary bee species are more abundant at long-term managed ponds and cavity-nesting solitary bees are more abundant at recently restored ponds. Despite nesting density and resources not being directly measured in this study, these factors could be important drivers for distinct hymenopteran assemblages, but this is also likely directly influenced by available vegetation structures and suitable ground nesting media (Roulston & Goodell, 2010). Overall, enhanced floral resources through improved habitat heterogeneity therefore remains a likely key factor in the conservation of hymenopteran populations utilising farmland pond environments.

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The tendency for open ponds to be favoured habitats by more abundant hoverfly communities might be explained by a number of factors. Kleijn and van Langevelde (2006) showed that hoverfly species do not disperse widely across the landscape when searching for food. Adult syrphid flies instead tend to congregate in local patches with a great abundance of food resources (Kleijn & van Langevelde, 2006; Jönsson *et al.*, 2015; Power *et al.*, 2016; Lucas *et al.*, 2017; Moquet *et al.*, 2018). Results from our model averaging also partially align with those from previous studies (Kleijn & van Langevelde, 2006; Power *et al.*, 2016; Lucas *et al.*, 2017) where abundance of hoverfly individuals is tied specifically to flowering plant-richness and abundance. As such, our models indicate that improved floral richness at the long-term managed and recently restored ponds are key factors for the increased abundance of hoverflies within those management categories.

Recent research has shown hoverfly species with semi-aquatic larvae to be commonly associated with wet grassland and marsh habitats (Lucas *et al.*, 2017). Despite larvae not being specifically investigated in this study, the open-canopy ponds provided larger patches of wet grassland and marshy habitat than overgrown ponds. This was likely due to heavy shading of the wet pond margin at overgrown ponds that prevented this vegetation from thriving. **Hoverfly larvae of different species vary considerably in their habitat requirements. However, many species' larvae thrive in woody, stagnant aquatic habitats, while adults commonly favour warm, sun-filled environments** (Thompson & Rotheray, 1998)**. The observed lack of clear trends in hoverfly richness related to pond management may thus be related to the combined influences of larval and adult habitat requirements, indicating that all types of pond management are providing suitable larval and/or adult resources which in turn help maintain diverse hoverfly assemblages across the agricultural landscape.**

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It should be noted that, whilst long-term managed and recently restored ponds harboured a greater diversity of pollinator species, no rare or threatened species were observed at any of the ponds. In fact, generalist species were abundant across the ponds in all categories, with very few flower specialist species recorded. This finding is in line with trends found more generally within diurnal pollinator communities across the globe (Biesmeijer *et al.*, 2006; Ekroos *et al.*, 2010; Burkle *et al.*, 2013), as the less stringent dietary requirements of generalist species make them much better placed to deal with the significant and rapid habitat changes associated with modern agricultural practices (Goulson *et al.*, 2005; Blüthgen & Klein, 2011). While this points to wider issues for pollinators across agricultural landscapes, there are still some notable, beneficial changes to species richness in pollinator communities following pond restoration and subsequent pond margin management. For example, many of the charismatic and economically-important Apinae species (i.e. *A. mellifera*, *B. hortorum*, *B. lucorum*, *B. terrestris*, etc.), as well as many mining bee (i.e. *Andrena* spp.) and vespid wasp species (i.e. *Dolichovespula vulgaris* Scopoli 1763, *Symmorphus gracilis* Brullé 1832, *Vespula vulgaris* Linnaeus 1758, etc.), showed positive associations with the two open-canopy pond categories in our study (see Figure 6a, Supplementary Information Tables S1b & S5).

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4.2 *Pond management and pollinator conservation*

Our study has provided much-needed evidence for the importance of farmland pond habitats in supporting diurnal pollinator communities in agricultural landscapes through the provision of flower-rich vegetation. Three key pollinator taxa (bees, wasps, and hoverflies) are shown to frequently visit farmland pond margins throughout the growing season, and their community composition and abundance seems to be governed by the openness of the ponds and their margins. Beyond this, the results have shown that **restoring ponds** by the removal of encroaching woody vegetation and pond sediment, followed by periodic light-to-moderate management of woody vegetation, rapidly improves the richness and abundance of sections of the diurnal pollinator community. As with previous research on aquatic plant, invertebrate, and farmland bird communities (Williams *et al.*, 2004; Sayer *et al.*, 2013; Davies *et al.*, 2016; Lewis-Phillips *et al.*, 2019), it is apparent that not all pond systems need regular canopy management in order to support rich and abundant pollinator communities. Rather, we echo calls to introduce management of encroaching woody vegetation carefully to a proportion of existing ponds within the landscape each year, with a view to creating heterogeneous pond landscape mosaics composed of ponds at different successional stages (Hassall *et al.*, 2012; Sayer *et al.*, 2012, 2013; Davies *et al.*, 2016).

While additional research is needed on the impacts of canopy management on pollinator nesting resources **and larval requirements**, and to directly compare pond systems with other semi-natural habitats included in agri-environment measures for pollinator support (e.g. hedgerows, **species-rich grasslands**), it is clear from this research that pond and pollinator conservation have a shared interest, with open-canopy ponds providing sites of potentially high importance for hymenopterans and syrphids, and, hence pollination services. Our study suggests that farmland ponds may represent critical habitat patches for a wide range of pollinator taxa and, in turn, pollination services. Due to their frequent abundance in agricultural landscapes, farmland ponds warrant recognition and utilisation in agri-environmental schemes aimed at conserving pollinator communities.

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Competing Interests

The authors have no competing interests to declare.

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Literature Cited

Angélibert, S., Marty, P., Céréghino, R. & Giani, N. (2004) Seasonal variations in the physical and chemical characteristics of ponds: implications for biodiversity conservation. *Aquatic Conservation Marine and Freshwater Ecosystems*, **14**, 439–456. https://doi.org/10.1002/aqc.616.

Archer, M.E. (2014). *The Vespoid Wasps: (Tiphiidae, Mutillidae, Sapygidae, Scoliidae, and Vespidae) of the British Isles*. Royal Entomological Society, London, UK.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software,* **67**, 1–48. https://doi.org/10.18637/jss.v067.i01.

Baum, K.A. & Wallen, K.E. (2011) Potential bias in pan trapping as a function of floral abundance. *Journal of the Kansas Entomological Society,* **84**, 155-159. https://doi.org/10.2317/JKES100629.1.

Beja, P. & Alcazar, R. (2003) Conservation of Mediterranean temporary ponds under agricultural intensification: an evaluation using amphibians. *Biological Conservation*, **114**, 317–326. https://doi.org/10.1016/S0006-3207(03)00051-X.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science*, **313**, 351–354. https://doi.org/10.1126/science.1127863.

Biggs, J., Corfield, A., Walker, D., Whitfield, M. & Williams, P. (1994) New approaches to the management of ponds. *British Wildlife*, **5**, 273–287.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P. & Weatherby, A. (2005) 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 693-714. https://doi.org/10.1002/aqc.745.

Blaauw, B.R. & Isaacs, R. (2014) Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wild flowers. *Basic & Applied Ecology*, **15**, 701–711. https://doi.org/10.1016/j.baae.2014.10.001.

Blüthgen, N. & Klein, A.-M. (2011) Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic & Applied Ecology*, **12**, 282–291. https://doi.org/10.1016/j.baae.2010.11.001.

Boothby, J. & Hull, A.P. (1997) A census of ponds in Cheshire, North West England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **7**, 75–79.

Botham, M.S., Fernandez-Ploquin, E.C., Brereton, T., Harrower, C.A., Roy, D.B. & Heard, M.S. (2015) Lepidoptera communities across an agricultural gradient: how important are habitat area and habitat diversity in supporting high diversity? *Journal of Insect Conservation*, **19**, 403–420. https://doi.org/ 10.1007/s10841-015-9760-y.

Bolker, B.M, Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., & White, J-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, **24**, 127-135. https://doi.org/10.1016/j.tree.2008.10.008.

Brian, A., Price, P., Redwood, B. & Wheeler, E. (1987) The flora of the marl-pits (ponds) in one Cheshire parish. *Watsonia*, **16**, 417–426.

Brose, U. (2001) Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in east-German farmland. *Ecography*, **24**, 722–730. https://doi.org/10.1111/j.1600-0587.2001.tb00533.x.

Bullock, J.M. (2006) Plants, in: Sutherland, W.J. (Ed.), *Ecological Census Techniques: A Handbook*, 2nd Edition, pp. 186–213. Cambridge University Press, Cambridge, UK.

Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013) Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function. *Science*, **339**, 1611. https://doi.org/10.1126/science.1232728

Burnham, K. & Anderson, D. (2002) *Model Selection and Mulitmodel Inference*. 2nd Ed. Springer-Verlag, New York, NY.

Cabin, R.J. & Mitchell, R.J. (2000) To Bonferroni or Not to Bonferroni: When and How Are the Questions. *Bulletin of the Ecological Society of America*, **81**, 246–248.

Campbell, J.W., Starring, A.M. & Smith, G.L. (2014) Flower Visitors of *Hymenocallis coronaria* (Rocky Shoals Spider-lily) of Landsford Canal State Park - South Carolina, USA. *Natural Areas Journal*, **34**, 332–337. https://doi.org/10.3375/043.034.0316.

Cane, J.H., Minckley, R.L. & Kervin, L.J. (2000) Sampling bees (Hymenoptera : Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *Journal of the Kansas Entomological Society*, **73**, 225–231.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyorgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M. & Vaissiere, B.E. (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture, Ecosystems & Environment*, **133**, 40–47. https://doi.org/10.1016/j.agee.2009.05.001.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D. & Goulson, D. (2006) Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, **132**, 481–489. https://doi.org/10.1016/j.biocon.2006.05.008.

Carvell, C., Isaac, N., Jitlal, M., Peyton, J., Powney, G., Roy, D., Vanbergen, A., O'Connor, R., Jones, C., Kunin, B., Breeze, T., Garratt, M., Potts, S., Harvey, M., Ansine, J., Comont, R., Lee, P., Edwards, M., Roberts, S., Morris, R., Musgrove, A., Brereton, T., Hawes, C. & Roy, H. (2016) *Design and Testing of a National Pollinator and Pollination Monitoring Framework*. NERC/Centre for Ecology & Hydrology, Wallingford, UK.

Clough, Y., Ekroos, J., Baldi, A., Batary, P., Bommarco, R., Gross, N., Holzschuh, A., Hopfenmueller, S., Knop, E., Kuussaari, M., Lindborg, R., Marini, L., Ockinger, E., Potts, S.G., Poyry, J., Roberts, S.P.M., Steffan-Dewenter, I. & Smith, H.G. (2014) Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecology Letters*, **17**, 1168–1177. https://doi.org/10.1111/ele.12325.

For Review Only

Cnaani, J., Thomson, J.D., & Papaj, D.R. (2006) Flower choice and learning in foraging bumblebees: effects of variation in nectar volume and concentration. *Ethology*, **112**, 278-285. https://doi.org/10.1111/j.1439-0310.2006.01174.x.

Cole, L.J., Brocklehurst, S., Robertson, D., Harrison, W. & McCracken, D.I. (2017) Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment*, **246**, 157–167. https://doi.org/10.1016/j.agee.2017.05.007.

Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S. & Woiwod, I.P. (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, **132**, 279–291. https://doi.org/10.1016/j.biocon.2006.04.020.

Corbet, S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., Smith, K. (1993) Temperature and the pollinating activity of social bees. *Ecological Entomology*, **18**, 17-30. https://doi.org/10.1111/j.1365-2311.1993.tb01075.x

Darvill, B., Knight, M.E. & Goulson, D. (2004) Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos*, **107**, 471–478. https://doi.org/10.1111/j.0030-1299.2004.13510.x.

Davies, B., Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Sear, D., Bray, S. & Maund, S. (2008) Comparative biodiversity of aquatic habitats in the European agricultural landscape. *Agriculture, Ecosystems & Environment*, **125**, 1–8. https://doi.org/10.1016/j.agee.2007.10.006.

Davies, S.R., Sayer, C.D., Greaves, H., Siriwardena, G.M. & Axmacher, J.C. (2016) A new role for pond management in farmland bird conservation. *Agriculture, Ecosystems & Environment*, **233**, 179–191. https://doi.org/10.1016/j.agee.2016.09.005.

Declerck, S., De Bie, T., Ercken, D., Hampel, H., Schrijvers, S., Van Wichelen, J., Gillard, V., Mandiki, R., Losson, B., Bauwens, D., Keijers, S., Vyverman, W., Goddeeris, B., De Meester, L., Brendonck, L. & Martens, K. (2006) Ecological characteristic's of small farmland ponds: Associations with land use practices at multiple spatial scales. *Biological Conservation*, **131**, 523–532. https://doi.org/10.1016/j.biocon.2006.02.024.

Dornhaus, A., & Chittka, L. (2001) Food alert in bumblebees (*Bombus terrestris*): possible mechanisms and evolutionary implications. *Behavioral Ecology and Sociobiology,* **50**, 570-576. https://doi.org/10.1007/s002650100395.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Leveque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182. https://doi.org/10.1017/S1464793105006950.

Edwards, J., Smith, G.P. & McEntee, M.H.F. (2015) Long-term time-lapse video provides near complete records of floral visitation. *Journal of Pollination Ecology*, **16**, 91–100. http://dx.doi.org/10.26786/1920-7603%282015%2916

Ekroos, J., Piha, M. & Tiainen, J. (2008) Role of organic and conventional field boundaries on boreal bumblebees and butterflies. *Agriculture, Ecosystems & Environment*, **124**, 155–159. https://doi.org/10.1016/j.agee.2007.09.003.

Ekroos, J., Heliola, J. & Kuussaari, M. (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology*, **47**, 459–467. https://doi.org/10.1111/j.1365-2664.2009.01767.x.

Elmore, K.L. & Richman, M.B. (2001) Euclidean distance as a similarity metric for Principal Component Analysis. *Monthly Weather Review*, **129**, 540-549. https://doi.org/10.1175/1520-0493(2001)129<0540:EDAASM>2.0.CO;2.

Falk, S. (2015) *Field Guide to Bees of Great Britain and Ireland*. British Wildlife Publishing, Totnes, UK.

Gardiner, T. & Vaughan, A. (2008) Responses of ground flora and insect assemblages to tree felling and soil scraping as an initial step to heathland restoration at Norton Heath Common, Essex, England. *Conservation Evidence*, **5**, 95-100.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**, 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x.

For Review Only

Georgian, E., Fang, Z., Emshwiller, E. & Pidgeon, A. (2015) The pollination ecology of *Rhododendron floccigerum* Franchet (Ericaceae) in Weixi, Yunnan Province, China. *Journal of Pollination Ecology*, **16**, 72–81. http://dx.doi.org/10.26786/1920-7603%282015%2911

Gollan, J.R., Ashcroft, M.B. & Batley, M. (2011) Comparison of yellow and white pan traps in surveys of bee fauna in New South Wales, Australia (Hymenoptera: Apoidea: Anthophila). *Australian Journal of Entomology*, **50**, 174–178. https://doi.org/10.1111/j.1440-6055.2010.00797.x.

Gotelli, N.J. & Ellison, A.M. (2004) *A Primer of Ecological Statistics*. Sinauer Associates Publishers, Sunderland, MA, USA.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005) Causes of rarity in bumblebees. *Biological Conservation*, **122**, 1–8. http://doi.org/10.1016/j.biocon.2004.06.017.

Grueber, C.E., Nakagawa, S., Laws, R.J., & Jamieson, I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology,* **24**, 699-711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Hall, M. A., Nimmo, D. G., Cunningham, S. A., Walker, K., & Bennett, A. F. (2019) The response of wild bees to tree cover and rural land use is mediated by species' traits. *Biological Conservation*, **231**, 1–12. https://doi.org/10.1016/j.biocon.2018.12.032

Harrison, T., Gibbs, J., & Winfree, R. (2018) Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Global Change Biology,* **24**, 287–296. https://doi.org/10.1111/gcb.13921.

Hartley, J.C. (1963) The cephalopharyngeal apparatus of syrphid larvae and its relationship to other Diptera. *Proceedings of the Zoological Society of London*, **141**, 261-280. https://doi.org/10.1111/j.1469-7998.1963.tb01612.x

Hassall, C., Hollinshead, J. & Hull, A. (2011) Environmental correlates of plant and invertebrate species richness in ponds. *Biodiversity & Conservation*, **20**, 3189–3222. https://doi.org/10.1007/s10531-011-0142-9.

Hassall, C., Hollinshead, J. & Hull, A. (2012) Temporal dynamics of aquatic communities and implications for pond conservation. *Biodiversity & Conservation*, **21**, 829–852. https://doi.org/10.1007/s10531-011-0223-9.

Holland, J.M., Smith, B.M., Storkey, J., Lutman, P.J.W. & Aebischer, N.J. (2015) Managing habitats on English farmland for insect pollinator conservation. *Biological Conservation*, **182**, 215–222. https://doi.org/10.1016/j.biocon.2014.12.009.

Hsieh, T.C., Ma, K.H. & Chao, A. (2018) iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.15. http://chao.stat.nthu.edu.tw/blog/software-download/

Jeffries, M.J. (1998) Pond macrophyte assemblages, biodisparity and spatial distribution of ponds in the Northumberland coastal plain, UK. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **8**, 657–667. https://doi.org/10.1002/(SICI)1099-0755(199809/10)8:5<657::AID-AQC306>3.3.CO;2-3.

Jeffries, M. (2008) The spatial and temporal heterogeneity of macrophyte communities in thirty small, temporary ponds over a period of ten years. *Ecography*, **31**, 765–775. https://doi.org/10.1111/j.0906-7590.2008.05487.x.

Jönsson, A.M., Ekroos, J., Danhardt, J., Andersson, G.K.S., Olsson, O. & Smith, H.G. (2015) Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the wider landscape. *Biological Conservation*, **184**, 51–58. https://doi.org/10.1016/j.biocon.2014.12.027.

Kleijn, D. & van Langevelde, F. (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, **7**, 201–214. https://doi.org/10.1016/j.baae.2005.07.011.

Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 303–313. https://doi.org/10.1098/rspb.2006.3721.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, A. & Goulson, D. (2005) An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*)

For Review Only

species. *Molecular Ecology*, **14**, 1811–1820. https://doi.org/10.1111/j.1365-294X.2005.02540.x.

Kremen, C., M'Gonigle, L.K., Ponisio, L.C. (2018) Pollinator community assembly tracks changes in floral resources as restored hedgerows mature in agricultural landscapes. *Frontiers in Ecology and Evolution*, **6**, 170. https://doi.org/10.3389/fevo.2018.00170.

Leong, J.M. & Thorp, R.W. (1999) Colour-coded sampling: the pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. *Ecological Entomology*, **24**, 329–335. https://doi.org/10.1046/j.1365-2311.1999.00196.x.

Lewis-Phillips, J., Brooks, S., Sayer, C.D., McCrea, R., Siriwardena, G. & Axmacher, J.C. (2019) Pond management enhances the local abundance and species richness of farmland bird communities. *Agriculture, Ecosystems & Environment*, **273**, 130–140. https://doi.org/10.1016/j.agee.2018.12.015.

Lindborg, R., & Eriksson, O. (2004). Effects of restoration on plant species richness and composition in Scandinavian semi-natural grasslands. *Restoration Ecology*, **12**, 318–326. https://doi.org/10.1111/j.1061-2971.2004.00334.x.

Lucas, A., Bull, J.C., de Vere, N., Neyland, P.J. & Forman, D.W. (2017) Flower resource and land management drives hoverfly communities and bee abundance in seminatural and agricultural grasslands. *Ecology & Evolution*, **7**, 8073–8086. https://doi.org/10.1002/ece3.3303.

Meyer, B., Jauker, F. & Steffan-Dewenter, I. (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic & Applied Ecology*, **10**, 178–186. https://doi.org/10.1016/j.baae.2008.01.001.

Moericke, V. (1951) Eine Farbafalle zur Kontrolle des Fluges von Blattlausen, insbesondere der Pfirsichblattlaus, *Myzodes persicae* (Sulz.). *Nachrichtenblatt des Deutschen Pflanzenschutzdiensten*, **3**, 23-24.

Moquet, L., Laurent, E., Bacchetta, R. & Jacquemart, A.-L. (2018) Conservation of hoverflies (Diptera, Syrphidae) requires complementary resources at the landscape and local scales. *Insect Conservation & Diversity*, **11**, 72–87. https://doi.org/10.1111/icad.12245.

Morandin, L.A. & Kremen, C. (2013) Bee Preference for Native versus Exotic Plants in Restored Agricultural Hedgerows. *Restoration Ecology*, **21**, 26–32. https://doi.org/10.1111/j.1526-100X.2012.00876.x.

NatureSpot (2018) *NatureSpot: Recording the Wildlife of Leicestershire & Rutland*. www.naturespot.org.uk. 08 September 2017.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2018) vegan: Community Ecology Package. R package version 2.5-2. https://cran.R-project.org/package=vegan.

Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. (2014) Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, **346**, 1360–1362. https://doi.org/10.1126/science.1257259.

Osborne, J.L., Martin, A.P., Carreck, N.L., Swain, J.L., Knight, M.E., Goulson, D., Hale, R.J. & Sanderson, R.A. (2008) Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, **77**, 406–415. https://doi.org/10.1111/j.1365-2656.2007.01333.x.

Owens, N. & Richmond, D. (2012) *Bumblebees of Norfolk*. Norfolk & Norwich Naturalists' Society, Norwich, UK.

Paterson, C., Cottenie, K., & MacDougall, A.S. (2019) Restored native prairie supports abundant and species-rich native bee communities on conventional farms. *Restoration Ecology*, **27**, 1291-1299. https://doi.org/10.1111/rec.12987.

Pollard, E. & Yates, T.J. (1993) *Monitoring Butterflies for Ecology and Conservation: the British Butterfly Monitoring Scheme*. Conservation Biology Series No. 1. Chapman & Hall, London, UK.

Pollinator Health Task Force (2015) *National Strategy to Promote the Health of Honey Bees and Other Pollinators*. The White House, Washington, D.C. (https://obamawhitehouse.archives.gov/sites/default/files/microsites/ostp/Pollinator%20Health%20Strategy%202015.pdf).

For Peer Review Only

Popov, S., Milicic, M., Diti, I., Marko, O., Sommaggio, D., Markov, Z. & Vujic, A. (2017) Phytophagous hoverflies (Diptera: Syrphidae) as indicators of changing landscapes. *Community Ecology*, **18**, 287–294. https://doi.org/10.1556/168.2017.18.3.7.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P. (2003) Linking Bees and Flowers: How Do Floral Communities Structure Pollinator Communities? *Ecology*, **84**, 2628–2642. http://dx.doi.org/10.1890/02-0136.

Power, E.F., Jackson, Z. & Stout, J.C. (2016) Organic farming and landscape factors affect abundance and richness of hoverflies (Diptera, Syrphidae) in grasslands. *Insect Conservation & Diversity*, **9**, 244–253. https://doi.org/10.1111/icad.12163.

Prince, H.C. (1962) Pits and Ponds in Norfolk. *Erdkunde*, **16**, 10–31.

Prince, H.C. (1964) The origins of pits and depressions in Norfolk. *Journal of the Geographic Association*, **49**, 15–32.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R. & Sherwood, A. (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*, **121**, 479–494. https://doi.org/10.1016/j.biocon.2004.05.020.

Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R. & Sherwood, A. (2006) Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*, **129**, 192–206. https://doi.org/10.1016/j.biocon.2005.10.034.

Rader, R., Edwards, W., Westcott, D.A., Cunningham, S.A. & Howlett, B.G. (2011) Pollen transport differs among bees and flies in a human-modified landscape. *Diversity & Distributions*, **17**, 519–529. https://doi.org/10.1111/j.1472-4642.2011.00757.x.

Rader, R.A., Bartomeus, I.B., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R.G., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R.M., Brittain, C.N., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B.A., Freitas, B.M., Gemmill-Herren, B. u, Ghazoul, J.V., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipolito, J., Jaggar, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindstroem, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., Pereira, N. de, Pisanty, G., Potts, S.G., Reemerf, M., Rundloef, M., Sheffield, C.S., Scheper, J., Schueepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyoergyi, H., Taki, H., Vergara, C.H., Viana, B.F. & Woyciechowski, M. (2016) Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 146–151. https://doi.org/10.1073/pnas.1517092112.

Rands, S.A. & Whitney, H.M. (2011) Field Margins, Foraging Distances and Their Impacts on Nesting Pollinator Success. *PLoS One*, **6**, e25971. https://doi.org/10.1371/journal.pone.0025971.

Rice, W.R. (1989) Analyzing Tables of Statistical Tests. *Evolution*, **43**, 223–225.

Roschewitz, I., Gabriel, D., Tscharntke, T., & Thies, C. (2005) The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology*, **42**, 873–882. https://doi.org/10.1111/j.1365-2664.2005.01072.x.

Rose, F. (2006) *The Wild Flower Key: How to identify wild flowers, trees, and shrubs in Britain and Ireland* (2nd ed.). Penguin Group, London.

Rotheray, G.E. (2019) Saprophagy, Developing on Decay. in: Rotheray, G.E. (ed.) *Ecomorphology of Cyclorrhaphan Larvae (Diptera)*, pp. 141-173. Springer International, Cham, Switzerland.

Rotheray, G., & Lyszkowski, R. (2015) Diverse mechanisms of feeding and movement in Cyclorrhaphan larvae (Diptera). *Journal of Natural History*, **49**, 2139-2211. https://doi.org/10.1080/00222933.2015.1010314

Roulston, T.H., & Goodell, K. (2010) The Role of Resources and Risks in Regulating Wild Bee Populations. *Annual Review of Entomology*, **56**, 293–312. https://doi.org/10.1146/annurev-ento-120709-144802.

Ruedenauer, F.A., Spaethe, J., & Leonhardt, S.D. (2016) Hungry for quality – individual bumblebees forage flexibly to collect high-quality pollen. *Behavioral Ecology and Sociobiology*, **70**, 1209-1217. https://doi.org/10.1007/s00265-016-2129-8.

For Review Only

Ruggiero, A., Céréghino, R., Figuerola, J., Marty, P. & Angélibert, S. (2008) Farm ponds make a contribution to the biodiversity of aquatic insects in a French agricultural landscape. *Comptes Rendus – Biologies*, **331**, 298–308. https://doi.org/10.1016/j.crvi.2008.01.009.

Sayer, C., Andrews, K., Shilland, E., Edmonds, N., Edmonds-brown, R., Patmore, I., Emson, D. & Axmacher, J. (2012) The role of pond management for biodiversity conservation in an agricultural landscape. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22**, 626–638. https://doi.org/10.1002/aqc.2254.

Sayer, C., Shilland, E., Greaves, H., Dawson, B., Patmore, I., Emson, D., Alderton, E., Robinson, P., Andrews, K., Axmacher, J. & Wiik, E. (2013) Managing Britain's ponds - conservation lessons from a Norfolk farm. *British Wildlife*, **25**, 21–28.

Sayer, C.D. (2019) Presidential Address 2019: Talk to the person on the farm: the huge value to conservation of lived natural history knowledge. *Transactions of the Norfolk and Norwich Naturalists Society*, **52**, 2–16.

Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekoetter, T., Hendrickx, F., Herzog, F., Liira, J., Maelfait, J.-P., Speelmans, M. & Dziock, F. (2007) Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos*, **116**, 461–472. https://doi.org/10.1111/j.2007.0030-1299.15372.x

Seeley, T., Camazine, S.,& Sneyd, J. (1991) Collective decision-making in honey bees: how colonies choose among nectar sources. *Behavioral Ecology and Sociobiology* **28**, 277-290. https://doi.org/10.1007/BF00175101).

Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C., Dodson, C.-A., Evans, R.L., McKerchar, M., Morton, R.D., Moss, E.D., Roberts, S.P.M., Kunin, W.E. & Potts, S.G. (2015) The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society B-Biological Sciences*, **282**, 20150294. https://doi.org/10.1098/rspb.2015.0294.

Shrestha, M., Garcia, J.E., Chua, J.H.J., Howard, S.R., Tscheulin, T., Dorin, A., Nielsen, A. & Dyer, A.G. (2019) Fluorescent pan traps affect the capture rate of insect orders in different ways. *Insects*, **10**, 40. https://doi.org/10.3390/insects10020040.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2.

Stewart, R.I.A., Andersson, G.K.S., Brönmark, C., Klatt, B.K., Hansson, L.-A., Zülsdorff, V. & Smith, H.G. (2017) Ecosystem services across the aquatic-terrestrial boundary: linking ponds to pollination. *Basic & Applied Ecology*, **18**, 13–20. https://doi.org/10.1016/j.baae.2016.09.006.

Stubbs, A. & Falk, S. (2002) *British Hoverflies: An Illustrated Identification Guide*, 2nd ed. British Entomological & Natural History Society, Reading, UK.

Sutherland, W.J. (1996) *Ecological Census Techniques: A Handbook.* Cambridge University Press, Cambridge, UK.

ter Braak, C.J.F. & Šmilauer, P. (2012) *Canoco Reference Manual and User's Guide: Software for Ordination*, Version 5.0. Microcomputer Power, Ithaca, NY, USA.

Thompson, F. C., & Rotheray, G. E. (1998) Family Syrphidae. in: Papp, L. & Darvas, B. (eds.) *Manual of Palaearctic Diptera*, vol. 3, pp. 81-139. Science Herald, Budapest, Hungary.

Underwood, E., Darwin, G. & Gerritsen, E. (2017) *Pollinator Initiatives in EU Member States: Success Factors and Gaps*. Report ENV.B.2/SER/2016/0018. Institute for European Environmental Policy, Brussels, Belgium. (https://ec.europa.eu/environment/nature/conservation/species/pollinators/documents/ieep_2017_pollinator_initiatives_in_eu_member_states.pdf).

Vad, C.F., Pentek, A.L., Cozma, N.J., Foldi, A., Toth, A., Toth, B., Bode, N.A., Mora, A., Ptacnik, R., Acs, E., Zsuga, K. & Horvath, Z. (2017) Wartime scars or reservoirs of biodiversity? The value of bomb crater ponds in aquatic conservation. *Biological Conservation*, **209**, 253–262. https://doi.org/10.1016/j.biocon.2017.02.025.

von Frisch, K. (1967) *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge, MA, USA.

For Review Only

Vrdoljak, S.M. & Samways, M.J. (2012) Optimising coloured pan traps to survey flower visiting insects. *Journal of Insect Conservation*, **16**, 345–354. https://doi.org/10.1007/s10841-011-9420-9.

Walton, R.E., Sayer, C.D., Bennion, H., & Axmacher, J.C. (2020) Nocturnal pollinators strongly contribute to pollen transport of wild flowers in an agricultural landscape. *Biology Letters*, **16**, 20190877. https://doi.org/10.1098/rsbl.2019.0877.

Westerfelt, P., Widenfalk, O., Lindelöw, Å., Gustafsson, L. & Weslien, J. (2015) Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. *Insect Conservation & Diversity*, **8**, 493–504. https://doi.org/10.1111/icad.12128.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P. & Sear, D. (2004) Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation*, **115**, 329–341. https://doi.org/10.1016/S0006-3207(03)00153-8.

Williams, P., Biggs, J., Crowe, A., Murphy, J., Nicolet, P., Weatherby, A. & Dunbar, M. (2010) *Countryside Survey: Ponds Report from 2007*. Technical Report No. 7/07. (Technical Report No. 7/07). NERC/Centre for Ecology & Hydrology, Wallingford, UK.

Wood, P.J., Greenwood, M.T. & Agnew, M.D. (2003) Pond biodiversity and habitat loss in the UK. *Area*, **35**, 206–216. https://doi.org/10.1111/1475-4762.00249.

Wood, T.J., Holland, J.M. & Goulson, D. (2015a) A comparison of techniques for assessing farmland bumblebee populations. *Oecologia*, **177**, 1093–1102. https://doi.org/10.1007/s00442-015-3255-0.

Wood, T.J., Holland, J.M., Hughes, W.O.H. & Goulson, D. (2015b) Targeted agri-environment schemes significantly improve the population size of common farmland bumblebee species. *Molecular Ecology*, **24**, 1668–1680. https://doi.org/10.1111/mec.13144.

Wood, T.J., Holland, J.M. & Goulson, D. (2017) Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology*, **54**, 323–333. https://doi.org/10.1111/1365-2664.12718.

Yeo, P.F. & Corbet, S.A. (2015) *Solitary Wasps*. 2nd Ed. Pelagic Publishing, Exeter, UK.

Zuur, A.F., Ieno, E.N. & Smith, G.M. (2007) Canonical correspondence analysis of lowland pasture vegetation in the humid tropics of Mexico, in: *Analysing Ecological Data*, pp. 561-574. Springer, New York, NY, USA.

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Tables

Table 1. GLMM model averaging for richness of insect pollinated plants at nine farmland ponds. Component model term codes: 1) Bramble Area and 2) Management. Estimates for model averaging are based on conditional average parameters (AICc) < 2.

Component Models	df	Loglik	AICc	delta	Weight
2	7	-314.05	643.21	0	0.71
1.2	8	-313.79	645.04	1.83	0.29
Plant Richness	**Estimate**	**SE**	**Z**	**P**	**Significance**
(Intercept)	2.46	0.07	32.654	<0.001	***
Management – Recently Restored	-0.04	0.11	0.34	0.73	
Management – Overgrown	-0.43	0.11	3.83	<0.001	***
Bramble Area	-0.04	0.06	0.70	0.48	

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Table 2. Estimated richness of pollinating insect groups at farmland ponds under three management treatments between 2016-2017. Table depicts the mean estimated richness (Chao1) and number of individuals observed between the three ponds in each treatment with standard deviation given.

		Long-term Managed	**Recently Restored**	**Overgrown**
Apinae	Chao1	9.00 ± 1.00	9.50 ± 2.78	9.08 ± 1.88
	Individuals (Abundance)	288 ± 182.78	214 ± 22.72	117 ± 83.43
Non-Apinae Hymenopterans	Chao1	32.10 ± 6.57	39.55 ± 0.91	20.14 ± 0.77
	Individuals (Abundance)	351 ± 15.95	282 ± 13.87	170 ± 18.56
All Hymenopterans	Chao1	41.82 ± 5.61	50.83 ± 4.01	29.29 ± 2.35
	Individuals (Abundance)	638 ± 144.42	496 ± 9.00	287 ± 83.94
Syrphids	Chao1	28.42 ± 3.11	37.39 ± 14.02	39.25 ± 21.53
	Individuals (Abundance)	166 ± 73.60	200 ± 94.55	69 ± 65.68
Hymenoptera & Syrphidae	Chao1	68.36 ± 3.48	92.32 ± 12.07	60.51 ± 7.95
	Individuals (Abundance)	512 ± 206.59	476 ± 90.12	232 ± 85.50

Table 3. GLMM model averaging component models for richness and abundances of pollinator communities at nine farmland ponds. **Term codes: 1) Bramble Area, 2) Plant Richness, 3) Management, 4) Wild Flower Coverage**

		Component Models	df	loglik	AICc	delta	Weight
Apinae	Group Richness	2.4	7	-242.20	499.51	0	0.60
		1.2.4	8	-241.45	500.36	0.84	0.40
	Group Abundance	2	6	-372.86	758.54	0	0.72
		1.2	7	-372.65	760.42	1.88	0.28
Non-Apinae Hymenopterans	Group Richness	2	6	-274.67	562.18	0	0.56
		2.4	7	-274.46	564.04	1.86	0.22
		2.3	8	-273.32	564.10	1.92	0.22
	Group Abundance	2	6	-424.02	860.86	0	0.72
		1.2	7	-423.83	862.77	1.91	0.28
All Hymenopterans	Group Richness	2	6	-337.52	687.88	0	0.51
		2.4	7	-336.92	688.95	1.08	0.3
		1.2	7	-337.37	689.87	1.99	0.19
	Group Abundance	2	6	-474.09	961.02	0	0.72
		1.2	7	-473.91	962.94	1.93	0.28
Syrphids	Group Richness	2	6	-270.43	553.70	0	0.53
		2.4	7	-269.39	553.91	0.21	0.47
	Group Abundance	4	6	-325.02	662.88	0	0.38
		1.2.3.4	10	-320.73	663.72	0.84	0.25
		2.4	7	-324.51	664.14	1.26	0.20
		1.2	7	-324.77	664.66	1.78	0.16
Hymenopterans & Syrphids	Group Richness	2	6	-389.78	792.40	0	0.58
		2.4	7	-388.96	793.03	0.64	0.42
	Group Abundance	2	6	-499.45	1011.73	0	0.70
		1.2	7	-499.13	1013.38	1.65	0.30

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Table 4. GLMM model averaging for pollinator richness and abundance at nine farmland ponds. Estimates for model averaging are based on conditional average parameters (AICc) < 2. Explanatory variables with NA indicate that there were no instances of (AICc) < 2 for that variable and relevant model.

		Flowering Plant Richness		Wild Flower Coverage		Bramble Area		Management - Overgrown		Management - Recently Restored	
		Group Richness	Group Abundance	Group Richness	Group Abundance	Group Richness	Group Abundance	Group Richness	Group Abundance	Group Richness	Group Abundance
Apinae	**Estimate**	0.12	0.20	-0.21	NA	0.11	-0.09	NA	NA	NA	NA
	SE	0.02	0.03	0.10	NA	0.10	0.13	NA	NA	NA	NA
	Z	5.24	6.97	2.06	NA	1.20	0.64	NA	NA	NA	NA
	P	<0.001 ***	<0.001 ***	0.04 *	NA	0.23	0.52	NA	NA	NA	NA
Non-Apinae Hymenopterans	**Estimate**	0.11	0.12	-0.07	NA	NA	-0.07	0.26	NA	0.43	NA
	SE	0.02	0.02	0.11	NA	NA	0.11	0.28	NA	0.26	NA
	Z	4.32	5.46	0.64	NA	NA	0.61	0.91	NA	1.62	NA
	P	<0.001 ***	<0.001 ***	0.52	NA	NA	0.54	0.36	NA	0.10	NA
All Hymenopterans	**Estimate**	0.10	0.15	-0.11	NA	0.05	-0.07	NA	NA	NA	NA
	SE	0.02	0.02	0.11	NA	0.10	0.12	NA	NA	NA	NA
	Z	4.26	6.02	1.09	NA	0.54	0.60	NA	NA	NA	NA
	P	<0.001 ***	<0.001 ***	0.28	NA	0.59	0.55	NA	NA	NA	NA
Syrphids	**Esti-mate**	0.14	0.24	-0.20	-0.49	NA	-0.34	NA	-1.39	NA	0.31
	SE	0.03	0.03	0.14	0.37	NA	0.21	NA	0.79	NA	0.39
	Z	4.24	7.36	1.42	1.32	NA	1.62	NA	1.74	NA	0.78
	P	<0.001 ***	<0.001 ***	015	0.19	NA	0.10	NA	0.08 $^{+}$	NA	0.44
Hymenoptera & Syrphids	**Estimate**	0.10	0.16	-0.15	NA	NA	-0.10	NA	NA	NA	NA
	SE	0.02	0.02	0.12	NA	NA	0.12	NA	NA	NA	NA
	Z	4.16	6.59	1.27	NA	NA	0.80	NA	NA	NA	NA
	P	<0.001 ***	<0.001 ***	0.20	NA	NA	0.43	NA	NA	NA	NA

Figure Captions

Figure 1. Location of the nine studied farmland ponds used in North Norfolk, eastern England. Recently restored and overgrown (terrestrialised) ponds are in the left map and long-term managed ponds are on the right map. All field boundaries near ponds are hedges except at WADD10 which has a farm track running adjacent to the pond margin and a hedgerow to the left of the pond margin.

Figure 2. Photographs of ponds in North Norfolk, UK representing three treatment categories: (**a**) long-term managed pond (WADD10) near the village of Briston, (**b**) recently restored pond (BECK) near the village of Baconsthorpe, and (**c**) overgrown pond (NROAD) near the village of Baconsthorpe. All photos taken in July 2016 by R. Walton.

Figure 3. Boxplot analysis of total insect-pollinated plant species observed at farmland ponds between 2016-2017. Differences in richness with P-values = 0.01 - 0.05 are marked with a single asterisk (*). P-values from Bonferroni-corrected pairwise t-tests are given in Supplementary Information, Table S2.

Figure 4. Number of plant species in each DAFOR ranking based on pond management category (**a**) and boxplots of plant species found within each pond management category based on growth type: aquatic, wetland emergent, herbaceous damp arable, herbaceous arable, and woody vegetation (**b**).

Figure 5. Boxplot analysis (**a**) and rarefaction curves with confidence intervals (**b**) of Apinae, Non-Apinae Hymenopterans, All Hymenopterans, Syrphids, and Total Hymenopterans and Syrphids species at the studied farmland ponds. In Figure 5a, species richness differences with p-values < 0.01 are marked with double asterisk (**) and p-values = 0.01 - 0.05 are marked with a single asterisk (*), Bonferroni-corrected pairwise t-test p-values are given in Supplementary Information Table S2. Please note the difference in y-axis scales in Figure 5a.

Figure 6a. PCA of hymenopteran community associations (Apinae inclusive) with the farmland ponds. Species are coloured according to social status. **6b.** PCA plot of Syrphid community association with the farmland ponds.

For Review Only

Open-canopy ponds benefit diurnal pollinator communities in an agricultural landscape: implications for farmland management

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Supplementary Information

Figure S1. Pan trap assembly amidst a patch of insect-pollinated flowers within a pond margin.

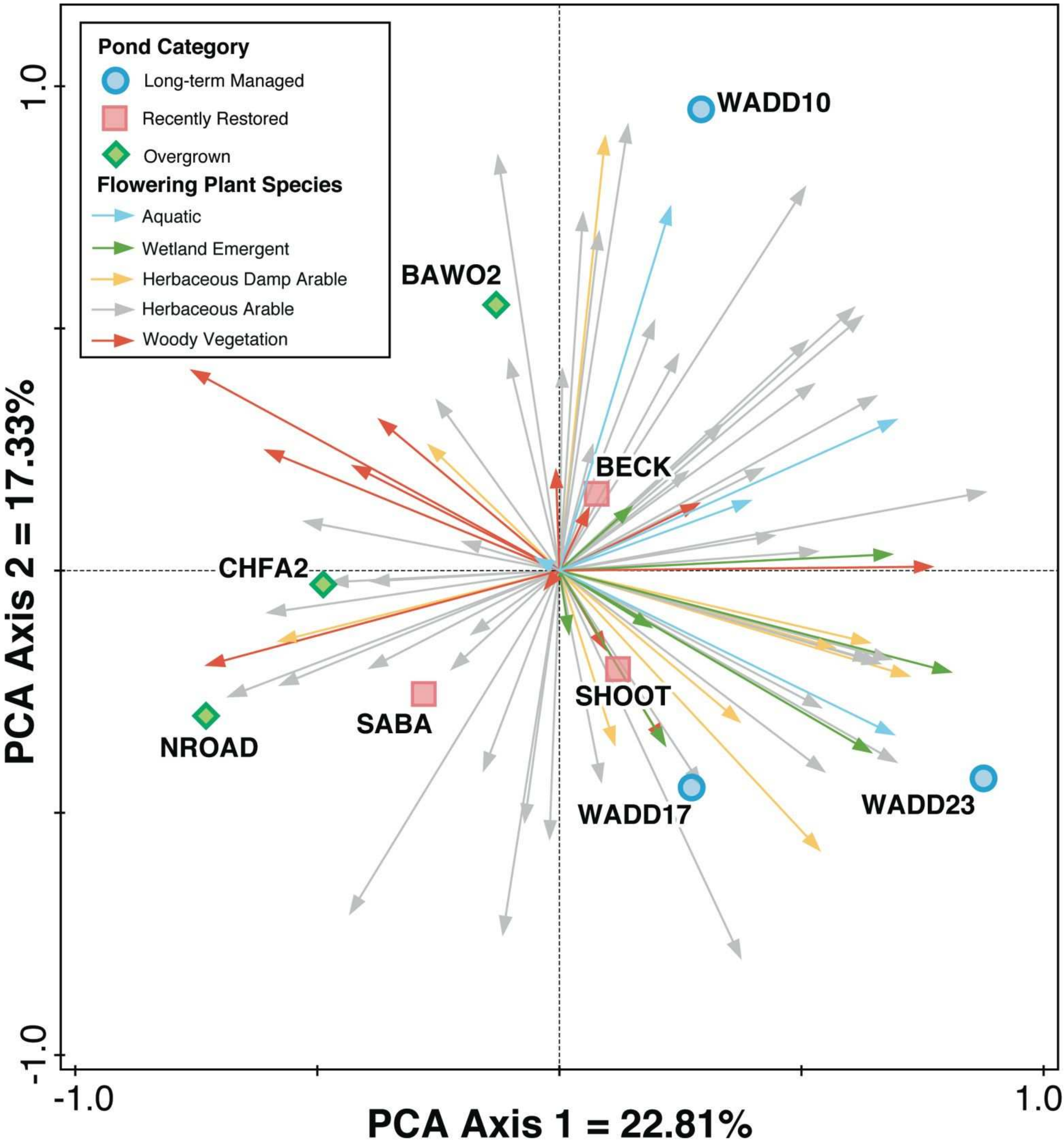

Figure S2. PCA plot of flowering plant community association with the farmland ponds. Species arrows are colourised according to habitat occupied (provided in Legend) within the pond or its margin.

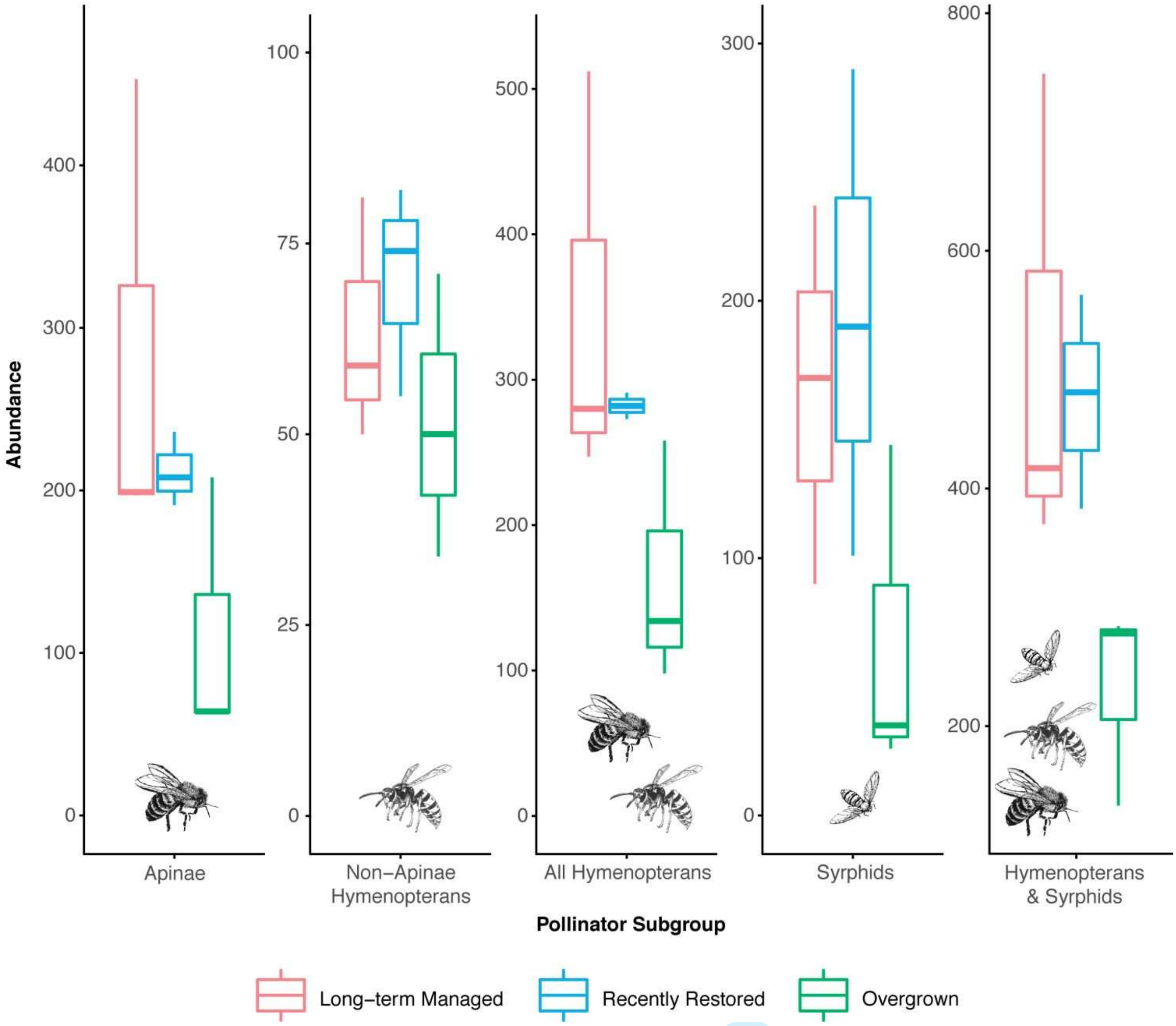

Figure S3. Abundance boxplots of pollinator sub-groups at three differing management treatments of farmland ponds 2016-2017 based on combination of three survey methods.

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