Ponds as insect chimneys: restoring overgrown farmland ponds benefits birds through elevated productivity of emerging aquatic insects

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Abstract

Farmland bird populations have experienced severe declines across Europe and elsewhere. Agricultural intensification is believed to be a main factor behind these declines, with losses of non-cropped features, such as farmland ponds, identified as a key driver. Since the 1950s, many European farmland ponds have been in-filled or, through lack of management, become terrestrialised. Restoring terrestrialised farmland ponds has been shown to significantly increase the abundance and

diversity of local farmland bird communities. It has been hypothesised that farmland birds are specifically attracted to open-canopy ponds due to increased emergent aquatic insect availability, but this link has hitherto been little explored.

This study investigates how farmland pond management influences emergent aquatic insects, and how emergent insect abundance and biomass is linked to local bird assemblages. Insect emergences showed an 18-fold higher abundance and a 25-fold higher biomass at managed open-canopy ponds in comparison to their unmanaged overgrown counterparts, with day-to-day fluctuations in pond water temperature a key predictor of insect emergences. Species richness and abundance of birds at farmland ponds were strongly positively linked to the abundance of emergent insects. Furthermore, insect emergence peaks occurred on different days in different restored ponds such that the pond landscape afforded extended feeding opportunities for birds. Our findings suggest that restoring networks of terrestrialised farmland ponds to open-canopy macrophyte-dominated conditions could be a highly effective way of increasing the availability of aquatic insect prey for birds. This study highlights an urgent need to re-evaluate pond restoration and management within agri-environmental schemes in Europe and beyond.

Keywords

Aquatic habitat restoration; Biodiversity conservation; Aquatic insect emergence; Trophic links; Wetland subsidies

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1. Introduction

Bird populations associated with agricultural land have experienced severe population declines in Europe (Inger *et al.* 2015) and North America (Mineau and Whiteside, 2013; Hill *et al.*, 2014). In both regions, agricultural intensification, including the widespread removal of economically non-productive terrestrial and aquatic habitats (Benton *et al.* 2002; Robinson & Sutherland 2002; Wood *et al.* 2003; Sayer *et al.* 2012; Reif 2013) and increased application of agro-chemicals (Aebischer, 1991; Newton, 2004; Bright, Morris and Winspear, 2008; Hallmann *et al.*, 2014), have been identified as key drivers of bird population declines (Butler *et al.* 2010; Reif 2013).

In Europe, despite the introduction of agri-environment schemes (AES) from the 1980s that are aimed to address biodiversity declines in agricultural landscapes (Natural England, 2009; Davey *et al.*, 2010), farmland bird populations have continued to fall, in part due to ongoing declines in available invertebrate prey (Aebischer 1991; Hallmann *et al.*, 2017). Farmland bird populations are strongly influenced by invertebrate availability as they form a key food source (Grice *et al.* 2004; Newton 2004; Aebischer *et al.* 2015) especially over the breeding season (Baker *et al.* 2012). During this time the majority of chicks, regardless of adult diet, rely on invertebrates to provide protein for growth (Holland *et al.*, 2006). The

negative impact of reductions in invertebrate availability have been shown for birds at both the community and species level. For example, Hallmann *et al.* (2014) found that reductions in invertebrate abundance were a plausible driver of local bird population trends, while Morris *et al.* (2005) showed that reduced invertebrate abundance impacted on yellowhammer *Emberiza citrinella* foraging intensity, and Potts (1986) found that the decline of grey partridge *Perdix perdix* in the UK was partly a consequence of reduced chick survival due to reductions in insect food supply. Further, recent research has highlighted the specific importance of aquatic invertebrate availability for breeding birds (Twining *et al.* 2018). Therefore, the provision of habitats such as ponds that foster high aquatic invertebrate abundances, but which are currently poorly represented in agri-environmental measures, might have potential to enhance local farmland bird populations through increased food provision across European agricultural landscapes and beyond.

In modern, intensively managed agricultural landscapes, the majority of remnant farmland ponds are in a highly terrestrialised state and commonly become encroached and overgrown by Willow *Salix* spp. and European Alder *Alnus glutinosa* trees (Sayer *et al.* 2013). Restoration of overgrown ponds to an open-canopy state by removal of scrub and pond sediment has been shown to rapidly increase aquatic plant and invertebrate diversity (Sayer *et al.* 2013; Sayer, 2014). Additionally, landscapes of ponds managed to maintain a mosaic of early and late successional stages support a substantially higher aquatic diversity than pond landscapes dominated by overgrown ponds (Sayer *et al.* 2012). More recent work has shown significant increases in local farmland bird abundance and species richness at early

successional restored and managed open-canopy ponds, suggesting important aquatic-terrestrial linkages (Davies *et al.* 2016; Lewis-Phillips *et al.* 2019).

The positive link between local bird communities and pond management is believed to be due to increased aquatic emergent invertebrate food availability, alongside suitable habitat for nesting (Davies *et al.*, 2016; Lewis-Phillips *et al.*, 2019), but the underlying drivers that link pond management with bird community changes have not been clearly identified. This paper aims to explore whether the productivity of emergent pond insects, namely species with aquatic larval stages that emerge as winged adults from ponds (chiefly Diptera, Ephemeroptera, Trichoptera and Odonata spp.), provide the missing link between pond management and the enhancement of local bird communities.

We specifically test the hypotheses that a) both abundance and biomass of aquatic emergent insects are significantly higher at managed open-canopy ponds compared to their unmanaged overgrown counterparts, that b) insect emergence patterns are strongly linked to day-to-day changes in pond water temperature, and finally that c) abundance and species richness of local bird assemblages are positively associated with increased emergent insect abundance and biomass.

2. Methods

2.1. Study site

This study was completed at a set of eight farmland ponds in North Norfolk, situated close to the village of Bodham (52.9146°N, 1.1614°E) in eastern England (Figure 1).

The ponds were situated across four farms, with ponds representing the same management type distributed across the different farms. As per Lewis-Phillips *et al.* (2019), study ponds were also situated within similar landscape settings, dominated by arable land alongside a combination of hedgerows, woodland patches and grazed meadows. The area is representative of UK lowland agricultural landscapes, especially in south-east England, with a landscape pond density comparable to many other agricultural regions in Europe (Alderton *et al.*, 2017). All study ponds were created prior to the early 19th century, likely due to marl extraction (Prince 1962) and would be managed by periodic scrub removal until the 1960s-70s, after which traditional pond management practices began to decline.

Figure 1. The farmland study ponds and surrounding landscape in North Norfolk, eastern England.

The study ponds consisted of four open-canopy (< 10% shaded water surface), macrophyte dominated ponds that had been subject to recent (within 5 years) restoration by major scrub removal, and of four overgrown ponds (> 85% shaded water surface) that had not been subject to any management within at least the last 30 years (Figure 2). Managed open-canopy pond sites all featured high aquatic (> 90%) and emergent plant cover comprising > 20 species, whereas aquatic macrophytes were largely absent from the unmanaged overgrown ponds, where the water area was widely overgrown by *Salix* spp. Both pond management types held water permanently over the study period.

Mean pond surface area was 248 m² (SD: 134 m²), with values ranging from 62 m² to 489 m², while mean water depth in all cases was < 1.5 m. The average total footprint of the ponds including their surrounding margins was 3057 m² (SD: 2231 m²), ranging from 708 m² to 6772 m². A minimum distance of 200 m between study ponds (mean distance = 1461 m, SD = 677 m) was maintained to reduce the strength of potential spatial autocorrelations (Ralph, Droege and Sauer, 1995).

Figure 2. Restored open-canopy pond (a) and unmanaged overgrown pond (b).

2.2. Insect monitoring

A single purpose-built floating emergence trap measuring 50 cm x 50 cm x 100 cm (w x l x h, Figure 3) featuring a collection bottle at the top was positioned and

secured at a central location on the surface of each pond. All trapped emergent insects were collected from each of the eight study ponds between 12:00 and 16:00 every day between May 2nd and May 31st 2017. Any individuals not contained within the collection bottle, but trapped within the mesh frame were manually collected using a HB-type aspirator with a 12 mm collection pipe.

For each daily pond sample, individuals were identified to order level using the Freshwater Biological Association key (FBA 2011). The number of individuals in each insect order were counted, with samples freeze-dried and subsequently weighed to the nearest mg.

Figure 3. Floating emergence traps in-situ at a restored open-canopy study pond (a) and an unmanaged overgrown study pond (b).

2.3. Bird monitoring

Bird monitoring was completed every day at each study pond between May 2nd and May 31st, 2017. Surveys were completed throughout by the first author on arrival at the pond sites between 12:00 and 16:00, prior to insect collection. The surveying time period was selected because mayfly emergence has been shown to peak

around midday (Harper *et al.* 2008). Furthermore, Lewis-Phillips *et al.* (2019) found that bird foraging continued throughout the day at farmland ponds over the bird breeding season, with afternoon surveys providing the best opportunity to incorporate hirundine foraging behaviour (Zielinski & Wojciechowski 1999) alongside a wide range of other bird species foraging on emerging insects.

A five minute point count survey (BTO 2011) was completed, recording all bird species with the exception of the aerial insectivores, Barn Swallow *Hirundo rustica*, Swift *Apus apus* and House Martin *Delichon urbicum*. This survey duration was selected to maximise bird detection and to minimise the duplication of individual recordings (Bibby *et al.* 1998). One minute after the point count survey was completed, a 'snapshot' survey was undertaken to specifically record the aforementioned aerial insectivore species at that moment. This survey was immediate, lasting <1 minute. Following Lewis-Phillips *et al.* (2019), in order to reduce potential detectability bias, bird individuals were recorded by both sound and sight from a set position that maximised the visibility of the pond and its margin (Bibby *et al.* 1992). Birds flushed on approach were also recorded (Voříšek *et al.*, 2008), and all birds detected within the pond or margin area, including those within 10 m above the water surface, were included.

2.4. Pond environmental variables

A single daily water temperature recording was taken at each study pond throughout May 2018 using a Milwaukee MS-PH55 thermometer. Temperature was measured

at a depth of 20 cm in the immediate vicinity of the emergence trap after the insect samples were collected, and within 15 minutes of completion of the bird survey.

Further environmental data was collated for each pond in summer 2017 (Appendix A). Total water area (m^2), non-shaded and shaded water area (m^2), aquatic macrophyte surface area (m^2), herbaceous margin area (m^2), understory area (m^2) (defined as dense vegetation < 3 m tall, mainly comprising of bramble *Rubus* spp., hawthorn *Crataegus monogyna* and blackthorn *Prunus spinosa*), tree area (m^2) (defined as tree species > 3 m tall) within the margin, and distance to the nearest hedgerow or woodland patch (m) (hereafter referred to as connectivity), were all recorded. Aerial photographs were taken of each pond using a DJI Mavic Pro unmanned aerial vehicle, with a scale marker placed at each pond, and habitat areas were then calculated using the scale tool in Photoshop Creative Cloud 2017. Habitat areas around each study pond were subsequently verified by field surveying. At overgrown sites, shaded water area was calculated during field surveys.

2.5. Data analysis

2.5.1. Emerging insect abundance

Daily insect abundance (number of all sampled insects per pond and day/ m^2) and daily insect biomass (biomass of all sampled insects per pond and day/ m^2) were measured throughout the survey period. The results were combined over the sampling period to provide total insect abundance (the total combined number of all sampled insects per pond over the entire survey period/ m^2) and total insect biomass (the total combined biomass of all sampled insects per pond over the entire survey

period/ m²). Alongside these measures, insect order abundance and the mean biomass of the orders that dominated the samples (Diptera and Ephemeroptera) were also calculated.

T-tests were used to compare total insect abundance, total insect biomass and mean biomass of Diptera and Ephemeroptera between pond management types, using the *t.test* function in R software 3.5.2 (R Core Team, 2017). Insect order abundance (all orders) was compared using Mann Whitney tests, using the *wilcox.test* function. All further analyses was also completed using R software version 3.5.2.

2.5.2. Bird abundance, species richness and diversity

Following Lewis-Phillips et al. (2019), bird abundance, estimated as the total number of individual bird detections of all species combined over all surveys, was calculated for each pond over the month of survey. As individual birds do not behave independently, bird flocks or family groups were treated as a single detection and therefore our results provide a conservative measure of bird abundance at pond sites. Bird species richness was calculated as the number of species recorded at each pond over the survey period. Diversity was represented by Shannon's exponential diversity index (Crist *et al.*, 2003; Jost, 2006), calculated using the 'vegan' package (Oksanen *et al.* 2013). T-tests were used to compare bird abundance and species richness between the two pond management groups.

2.5.3. Environmental influences on insect abundance and biomass

We estimated the relative strength of links between environmental predictor variables and insect abundance and insect biomass using Generalised Linear Mixed Models (GLMMs). We modelled effects using a Poisson distribution and by applying a log link function with models computed using the lme4 package (Bates & Maechler 2010). Pond ID was included as a random effect in the models in order to control for potential temporal autocorrelation associated with ponds being surveyed repeatedly throughout the survey period. To select predictor environmental variables for inclusion in GLMM models, Pearson correlations between potential predictors of insect abundance and biomass were calculated, and individual variables from pairs with correlation coefficients > 0.7 were removed (Booth *et al.*, 1994; Dormann *et al.*, 2013). Following this preparatory work, initial GLMM analyses were conducted using open, non-shaded water area (a direct result of pond management and other, highly correlated predictor variables, see Appendix B) and pond connectivity (Bates & Maechler 2010). For all GLMM analyses, Akaike's information criterion ($AICc < 2$) was used to select the most parsimonious models (Burnham & Anderson 2002; Grueber *et al.* 2011), with model averaging conducted and full average results reported (Bolker *et al.*, 2009). All explanatory variables were standardised prior to analysis.

Given the extreme differences in emergent insect abundance between managed open-canopy and unmanaged overgrown ponds, a second GLMM analysis was completed separately for the managed open-canopy ponds only to investigate the

relative strength of water surface area, open water area and mean water temperature in explaining the observed patterns in insect abundance.

Finally, a GLMM analysis was completed for all ponds to investigate the strength of daily water temperature on daily insect emergence and graphs plotted to visually display daily abundances of Ephemeroptera and Diptera emergence at the managed open-canopy ponds.

2.5.4. Environmental influences on bird abundance and species richness

The relative strength of links between environmental predictor variables and both bird abundance and bird species richness were estimated using GLMMs of assemblage-level indices, with individual pond set as a random effect. Emergent insect abundance, insect biomass, understory area, margin area, pond connectivity and tree canopy area within the margin were all included within the analysis (Bates & Maechler 2010) (Appendix C). We also tested links between environmental factors and Shannon diversity, but since these revealed the same patterns observed between bird species richness and environmental factors, we decided to not include this analysis in our paper.

3. Results

3.1. Emerging insects

3.1.1. Insect abundance and biomass

Diptera dominated all the pond samples over the survey period in terms of abundances, but for biomass, while Diptera dominated for the unmanaged overgrown ponds, Ephemeroptera dominated for the managed, open-canopy ponds. Odonata and Ephemeroptera were only recorded at managed open-canopy ponds. Total insect abundance and total insect biomass over the study period were significantly higher at managed open-canopy ponds, with a combined total of 4003 individuals weighing 6515.92 mg, in comparison to a combined total of 217 individuals with a weight of 252.63 mg at the unmanaged overgrown ponds (total insect abundance = $t(6) = 4.94$, $p = 0.003$, total insect biomass = $t(6) = 2.89$, $p = 0.028$) (Table 1). No significant differences were identified in the mean biomass of Diptera ($t(6) = -1.73$, $p = 0.135$) or Ephemeroptera ($t(6) = -0.71$, $p = 0.50$) individuals between the pond management types.

Table 1. Total emergent insect abundance and biomass at managed open-canopy and unmanaged overgrown ponds in May 2017. Significant differences between the two pond management types based on independent samples t-tests ($p < 0.05^*$ and $p < 0.01: **$). Significant differences are denoted highlighted in **bold**.

Pond category	Total insect abundance/ m^2	Total insect biomass (mg)/ m^2 ($\bar{x} \pm SE$)	Mean biomass (mg) Diptera individual ($\bar{x} \pm SE$)	Mean biomass (mg)/ Ephemeroptera individual ($\bar{x} \pm SE$)
Managed	1000.75 $\pm$ 189.87**	1628.98 $\pm$ 540.38*	0.63 $\pm$ 0.1	3.11 $\pm$ 0.26
Unmanaged	54.25 $\pm$ 29.58**	63.15 $\pm$ 32.21*	1.15 $\pm$ 0.3	3.41 $\pm$ 0.37

Abundance and biomass of Diptera, Ephemeroptera and Odonata differed significantly between the pond management types (Figure 4, Diptera abundance and

biomass: $p = 0.029$, Ephemeroptera abundance and biomass: $p = 0.029$, and Odonata abundance and biomass: $p = 0.029$). Trichoptera abundance ($p = 0.34$) and biomass ($p = 0.20$) were not significantly different between the pond management types.

Figure 4. Emergent insect order abundance (a) and emergent insect order biomass (mg) (b) per pond management type. Boxplots show median, upper and lower quartiles, with data falling outside Q1 – Q3 range plotted as outliers. Statistical significance of independent samples t-tests are denoted by: $P < 0.05$ (*) and ns = not significant. Order codes: Dip: Diptera, Eph: Ephemeroptera, Tri: Trichoptera and Odo: Odonata.

3.1.2. Environmental predictors of emerging insect productivity

Of the potential environmental predictors tested, GLMMs indicated that open, non-shaded water area significantly predicted emergent insect abundance and biomass for all the study ponds over the survey period (Table 2, appendix D).

Table 2. Average GLMM parameter estimates for emergent insect abundance and biomass at all ponds ($p < 0.001$: ***).

	<i>estimate</i>	<i>SE</i>	<i>Z</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Sig.</i>
Abundance						
Intercept	1.64	0.38	4.31	0.90	2.39	
Open, non-shaded water	1.62	0.39	4.09	0.85	2.40	***
Connectivity	0.19	0.34	0.55	-0.32	1.23	n.s.
Biomass						
Intercept	5.42	0.33	16.61	4.77	6.07	
Open, non-shaded water	1.75	0.34	5.21	1.09	2.41	***
Connectivity	0.09	0.23	0.39	-0.38	0.94	n.s.

When the managed open-canopy ponds were considered on their own, water area, open water area and mean water temperature did not significantly predict emerging insect abundance (Table 3, Appendix D).

In contrast, when analysed based on daily changes, water temperature showed a highly significant positive relationship with the emerging insect abundance (Table 4, Appendix D).

Table 3. Average GLMM parameter estimates for emerging insect abundance at managed ponds, only. Model: 1: Connectivity + water area, 2: connectivity + open, non-shaded water area & 3: connectivity + mean water temperature ($p < 0.05^*$: $p < 0.01$: ** and $p < 0.001$: ***).

<i>Model</i>		<i>estimate</i>	<i>SE</i>	<i>Z</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Sig.</i>
1	Intercept	6.84	0.16	40.56	6.52	7.18	
	Connectivity	0.01	0.09	0.18	-0.27	0.39	n.s.
	Total water area	0.01	0.08	0.09	-0.31	0.37	n.s.
2	Intercept	6.84	0.16	40.51	6.52	7.18	
	Connectivity	0.01	0.08	0.17	-0.26	0.39	n.s.
	Open, non-shaded water	0.01	0.09	0.09	-0.30	0.37	n.s.
3	Intercept	6.84	0.16	40.56	6.52	7.18	
	Mean water temperature	-0.014	0.166	0.82	-0.54	0.04	n.s.
	Connectivity	0.01	0.11	0.18	-0.04	0.32	n.s.

Table 4. Average GLMM parameter estimates for daily emerging insect abundance ($p < 0.05^*$: $p < 0.01$: ** and $p < 0.001$: ***).

	<i>estimate</i>	<i>SE</i>	<i>Z</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Sig.</i>
Intercept	1.63	0.7	2.33	0.26	2.99	
Daily water temperature	0.17	0.02	9.88	0.13	0.2	***

Finally, when Ephemeroptera and Diptera emergence were observed on a daily basis, emergence peaks occurred in asynchronous patterns within the different ponds sampled producing emerging invertebrate peaks on different days (Figure 5).

Figure 5. Emerging abundance of Ephemeroptera (a) and Diptera (b) at the managed open-canopy ponds over the survey period, May 2017.

3.2. Birds

3.2.1. Abundance and species richness comparison

In line with the year-round findings of Lewis-Phillips et al (2019) in this study bird species richness was significantly higher at the open-canopy ponds ($t(6) = 5.65$, $p = 0.001$) with 35 species recorded in comparison to 19 species at the overgrown

ponds. In total, 36 bird species were observed at the eight farmland ponds over the survey period (Table 5). Further, bird abundance was significantly higher at the open-canopy ponds ($t(6) = 5.43$, $p = 0.002$), with 1291 observations compared to 459 observations at the overgrown ponds (Table 6).

With the exception of little owl, *Athene noctua*, goldfinch *Carduelis carduelis* and great tit *Parus major*, all bird species were recorded in higher numbers at managed open-canopy pond sites. Bird visits to both pond management types were dominated by passerine species, with the majority of these visits from species that feed insects to their young (Table 5). All three hirundine species were recorded exclusively at managed open-canopy pond sites and similarly, the red and amber conservation priority species recorded were either entirely absent, or only recorded in low numbers, at unmanaged overgrown ponds (Table 5).

Table 5. Bird species and their visits to managed open-canopy farmland and unmanaged overgrown farmland ponds in May 2017. Species that feed young on invertebrates denoted with *, red listed and amber listed conservation priority species (RSPB, 2018) notated with ^{††} and [†] respectively.

Common name	Scientific name	Managed open-canopy	Unmanaged overgrown
Chiffchaff*	<i>Phylloscopus collybita</i>	149	60
Blackbird*	<i>Turdus merula</i>	102	79
Chaffinch*	<i>Fringilla coelebs</i>	107	67
Wood pigeon	<i>Columba palumbus</i>	100	56
Wren*	<i>Troglodytes troglodytes</i>	128	22

Whitethroat*	<i>Sylvia communis</i>	125	17
Dunnock*	<i>Prunella modularis</i>	76	40
Blue tit*	<i>Cyanistes caeruleus</i>	65	43
Moorhen*	<i>Gallinula chloropus</i>	70	21
Robin*	<i>Erithacus rubecula</i>	33	17
Blackcap*	<i>Sylvia atricapilla</i>	46	3
Linnet ^{††}	<i>Linaria cannabina</i>	41	0
Yellowhammer ^{*††}	<i>Emberiza citrinella</i>	37	2
Goldfinch*	<i>Carduelis carduelis</i>	12	16
Swallow*	<i>Hirundo rustica</i>	28	0
Mallard [†]	<i>Anas platyrhynchos</i>	23	2
Bullfinch ^{*†}	<i>Pyrrhula pyrrhula</i>	23	0
House martin ^{*†}	<i>Delichon urbicum</i>	22	0
Pheasant*	<i>Phasianus colchicus</i>	17	3
Magpie	<i>Pica pica</i>	19	0
Greenfinch*	<i>Chloris chloris</i>	13	0
Swift ^{*†}	<i>Apus apus</i>	13	0
Great tit*	<i>Parus major</i>	3	7
Skylark ^{*††}	<i>Alauda arvensis</i>	10	0
Carrion crow*	<i>Corvus corone</i>	6	2
Starling ^{*††}	<i>Sturnus vulgaris</i>	7	0
Lesser whitethroat*	<i>Sylvia curruca</i>	3	0
Red legged partridge*	<i>Alectoris rufa</i>	3	0
Grey heron	<i>Ardea cinerea</i>	2	0
Greylag Goose	<i>Anser anser</i>	2	0
Little Owl*	<i>Athene Noctua</i>	0	2

Sedge warbler*	<i>Acrocephalus schoenobaenus</i>	2	0
Jay	<i>Garrulus glandarius</i>	1	0
Kestrel†	<i>Falco tinnunculus</i>	1	0
Meadow pipit*†	<i>Anthus pratensis</i>	1	0
Willow warbler*†	<i>Phylloscopus trochilus</i>	1	0

Table 6. Bird abundance, species richness and Shannon Diversity at managed open-canopy and unmanaged overgrown ponds over May 2017, where figures represent mean values $\pm$ standard errors of the mean ($p < 0.01$: **).

Pond category	Abundance ($x \pm SE$)	Species richness	Shannon Diversity (exp)
Managed	$322.75 \pm 31.39^{**}$	$24.75 \pm 1.70^{**}$	$16.63 \pm 1.31^{**}$
Unmanaged	$114.75 \pm 21.91^{**}$	$11.75 \pm 1.54^{**}$	$7.81 \pm 1.21^{**}$

3.2.2. Predictors of bird abundance and species richness

Emergent insect abundance was a highly significant predictor of both bird abundance and species richness (Table 7, Figure 6, Appendix E).

Table 7. Average GLMM parameter estimates for bird abundance and species richness ($p < 0.001$: ***).

	<i>estimate</i>	<i>SE</i>	<i>Z</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Sig.</i>
Bird abundance						
Intercept	1.82	0.11	15.8	1.59	2.04	

Insect abundance	0.5	0.11	4.4	0.28	0.73	***
Margin area	0.049	0.09	0.53	-0.9	0.34	n.s.

Bird species richness

Intercept	1.58	0.12	12.9	1.35	1.82	
Insect abundance	0.51	0.14	3.44	0.22	0.81	***
Margin area	0.1	0.12	0.87	-0.13	0.34	n.s.
Connectivity	0.09	0.13	0.66	-0.17	0.34	n.s.
Insect biomass	0.09	0.14	0.6	-0.19	0.36	n.s.
Understory area	-0.09	0.22	0.38	-0.53	0.36	n.s.

Figure 6. Emerging insect abundance (log10) per survey and bird abundance/ survey at managed open-canopy and unmanaged overgrown ponds, with line of best fit and 95% confidence intervals shaded.

4. Discussion

4.1. Restoring ponds feeds farmland birds

Our study shows that restoration has a dramatic positive effect on insect abundance and biomass at farmland pond sites that in turn support a higher abundance and species richness of farmland birds. While we acknowledge the low number of pond sites sampled within this study, the extreme and uniform differences identified in both insect and bird communities between pond sites clearly demonstrate the significant impact pond management exerts on these groups.

Both pond management types were dominated (in terms of abundance) by Diptera spp., an order tolerant of a wide range of water temperatures (Cornette *et al.*, 2015) and oxygen conditions (Panis *et al.* 1996; Rasmussen 1996; Marziali *et al.* 2006). In comparison, Odonata and Trichoptera were only recorded at the open-canopy ponds. These orders are less tolerant of low dissolved oxygen and generally favour macrophyte-dominated conditions. For example, limnephilids, the most common trichopteran family associated with ponds, use macrophytes as material for case construction (FBA 2011), while adult Odonata show a preference for open, non-shaded ponds, with some species ovipositing onto submerged or floating-leaved aquatic plants (Corbet & Brooks 2008).

Following the substantial removal of woody vegetation from overgrown farmland ponds, an increased open, non-shaded water area results in major increases in aquatic vegetation cover (Sayer *et al.*, 2012, 2013). In turn the development of architecturally complex submerged, floating and emergent macrophyte structure in

ponds provides several benefits to invertebrates, including enhanced micro-habitat provision, increased food resources and refuge from predators (Brönmark 1995; Declerck *et al.* 2011). In particular adult dragonflies use emergent and floating-leaved macrophytes for perching and egg-laying (Corbet & Brooks 2008), while dragonfly larvae use submerged macrophytes for foraging and refuge (Goertzen and Suhling, 2013). Mayflies also exploit macrophytes for shelter and as a substratum for periphyton (Brittain, 1982), caddisflies use macrophytes for shelter (Skuja, 2011) and case building materials (Wallace, 2006) and many chironomids are known to have close habitat ties to plants, for example for laying eggs and as a food source (Kondo and Hamashima, 1992). Pond management also increases average water temperature which is known to be a key factor for the development and emergence patterns of aquatic insects (Egan *et al.* 2016; Twining *et al.* 2018), including influencing Ephemeroptera spp. egg development and larval growth rates (Brittain, 1982), Chironomidae spp. growth and development (Wiggins *et al.* 1980; Armitage *et al.* 1995) and larval growth rate in dragonflies (Odonata spp.) (Corbet 1999; Corbet & Brooks 2008). Thus, the pond restoration and management that directly increases macrophyte-dominated open water and water temperature, increases both emergent insect productivity and diversity at the order level.

The observed key role of emergent aquatic insect abundance in explaining both bird abundance and species richness could be linked to the benefits that these insects offer to birds, especially in comparison to terrestrial insects. Recent research has revealed that food quality is of key importance for birds (Oudman *et al.*, 2014) and in addition, major differences in the nutritional value of aquatic and terrestrial invertebrates have been identified (Twining *et al.* 2016a), with aquatic insects

containing significantly higher levels of highly unsaturated omega-3 fatty acids (HUFA) than their terrestrial counterparts (Gladyshev *et al.* 2013; Twining *et al.* 2016a; Twining *et al.* 2018). The biochemical importance of these compounds for birds has been demonstrated for tree swallow *Tachycineta bicolor*, with chicks raised on high-HUFA diets exhibiting better overall condition, faster growth, greater immunocompetence, lower basal metabolic rates and higher fledgling success than chicks raised on low HUFA diets (Twining *et al.* 2016b). Furthermore, long-term field studies on tree swallow have shown aquatic insect availability during chick development to be a strong predictor of fledging success, whereas terrestrial insect availability had no influence in this respect (Twining *et al.* 2018). Thus, HUFA availability could make aquatic insects even more important for some bird species than numbers alone would suggest. Further research is required to investigate HUFA contributions of aquatic invertebrates associated with farmland ponds and other agricultural freshwater areas, both in the breeding season and throughout the year, especially in terms of the breeding success of declining European farmland birds.

Our previous research showed that a significantly higher abundance and species richness of birds were found at open-canopy farmland ponds in comparison to overgrown ponds in comparable landscape settings (Lewis-Phillips *et al.*, 2019). However, pan-trapping studies showed no significant differences in the abundance of non-aquatic invertebrate communities between the two pond management types (Lewis-Phillips *et al.*, in prep). It seems highly likely, therefore, that the mechanism underpinning more abundant and complex bird communities at farmland pond sites is increased emergent aquatic insect availability. Indeed, alongside other bird species, chiffchaff *Phylloscopus collybita*, yellowhammer, whitethroat *Sylvia*

communis, chaffinch *Fringilla coelebs* and the three hirundine species were regularly recorded as feeding directly on insects emerging from the water surface at open canopy ponds during this study. The importance of emergent aquatic insects to farmland birds is supported by the fact that the majority of bird species that visited the study ponds feed insects to their young. For example, aquatic midges are an integral part of barn swallow diet and chick nutrition (Loske, 1992). A further key insight is the asynchronous nature of insect emergence with peaks occurring on different days at different pond sites (Figure 5). The implication here is that, on any one day, in a network of ponds containing several open-canopy sites, at least one pond locality could provide a rich food supply for local birds, with this especially true of aerial insectivores that move around the landscape.

4.2. Conservation implications

Our study clearly highlights a key role of managed open-canopy ponds as providers of insect food to birds within agricultural areas where chemicals are regularly applied and we conclude, therefore, that remaining open-canopy, macrophyte dominated ponds in European lowland farmed landscapes are likely of high importance to insect-eating birds (Newton, 2017). From a bird's perspective, open-canopy ponds provide a valued source of food. As individual ponds had mass emergences of Ephemeroptera and Diptera on different days, landscape complexes of restored ponds can grant extended periods of high food supply. It is very possible that, dependent on the scale of their home range and density of managed open-canopy ponds, that some bird species like barn swallow could easily shift around the landscape to fully exploit this resource. Our research therefore reconfirms the

importance of a landscape-scale approach to farmland pond management (Hassall et al. 2012; Sayer, 2014), that affords a mosaic of ponds at varying successional states, in order to provide opportunities for conservation and biodiversity gains for a range of farmland birds and other wildlife. It is clear that restoring open-canopy farmland ponds may greatly assist the conservation of declining farmland bird species and we strongly recommend that farmland pond restoration is re-evaluated and granted a higher priority within European agri-environment schemes.

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Appendix

Appendix A: Study pond habitat details

	Total water area	Shaded water area	Open water area	Macrophyte surface area	Herbaceous margin	Understory	Tree	Connectivity
COMBINED								
Unit	m ²	m ²	m ²	m ²	m ²	m ²	m ²	m
Mean	233.75375	73.50625	160.2475	156.57	2445.4775	177.125	466.96	27
Standard Deviation	126.342860721756	99.3762371621103	179.876213447709	183.18104845831	2250.76056552161	281.102135734124	381.197724547249	26.1315354094845
Range	426.94	254.25	488.79	488.79	5867.15	801	1191.98	71
MANAGED PONDS								
Unit	m ²	m ²	m ²	m ²	m ²	m ²	m ²	m
Mean	311.55	0	311.55	311.55	2799.5825	352.75	397.72	19.75
Standard Deviation	119.31	0	119.31	119.31	1989.60	319.55	312.76	23.83
Range	248.04	0	248.04	248.04	4249.35	756	722.25	48
UNMANAGED PONDS								
Unit	m ²	m ²	m ²	m ²	m ²	m ²	m ²	m
Mean	155.95	147.012	8.94	1.59	2091.37	1.5	536.2	34.25
Standard Deviation	82.88	92.92	14.59	3.00	2743.64	3	477.97	29.74
Range	197.66	222.92	30.52	6.1	5867.15	6	1076.67	71

Appendix B – correlation matrix for predictor variables for insect abundance

	1	2	3	4	5	6	7
1	1	-0.03	-0.74	-0.93	-0.85	-0.93	0.84
2	-0.3	1	0.44	0.34	0.1	0.34	-0.07
3	-0.074	0.44	1	0.87	0.44	0.88	-0.4
4	-0.93	0.34	0.87	1	0.78	1	-0.79
5	-0.85	0.1	0.44	0.78	1	0.76	-0.91

6	-0.93	0.34	0.88	1	0.76	1	-0.78
7	0.84	-0.07	-0.4	-0.79	-0.91	-0.78	1

Pearson correlation coefficient values for: Management: 1, Connectivity: 2, Water area: 3, Water area (open, non-shaded): 4, Macrophyte cover: 5, Mean water temperature: 6, Water area (open): 7, Water area (shaded).

Appendix C – correlation matrix for predictor variables for bird communities

	1	2	3	4	5	6	7	8	9
1	1	0.19	-0.33	-0.21	0.24	-0.18	-0.16	0.24	-0.17
2	0.19	1	-0.17	-0.77	-0.67	-0.75	-0.74	-0.3	-0.34
3	-0.33	-0.17	1	0.56	-0.09	-0.14	-0.28	0.19	-0.31
4	-0.21	-0.77	0.56	1	0.63	0.5	0.34	0.05	0.13
5	0.24	-0.67	-0.09	0.63	1	0.57	0.34	-0.03	0.32
6	-0.18	-0.75	-0.14	0.5	0.57	1	0.91	0.41	0.86
7	-0.16	-0.74	-0.28	0.34	0.34	0.91	1	0.44	0.72
8	0.24	-0.3	0.19	0.05	-0.03	0.41	0.44	1	0.35
9	-0.17	-0.34	-0.31	0.13	0.32	0.86	0.72	0.35	1

Pearson correlation coefficient values for: Tree area: 1, Pond management, 2, Margin area: 3, mean water temperature: 4, Understory area: 5, Insect abundance: 6, Water area: 7, Connectivity: 8, Insect biomass: 9.

Appendix D - GLMM

a) predicting overall insect abundance and biomass

<i>Component models</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
Abundance					
2	3	-1189.98	2386.06	0	0.6
1.2	4	-1189.33	2386.83	0.77	0.4
Biomass					
2	3	-911.20	1828.51	0	0.67
1.2	4	-910.88	1829.92	1.42	0.33
Term codes	1: Connectivity	2: Open water			

b) predicting insect abundance at managed ponds only

<i>Model</i>	<i>Component models</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
1		2	-539.39	1082.89	0	0.54
	1	3	-539.32	1084.85	1.96	0.2
	2	3	-539.37	1084.95	2.06	0.19
	1.2	4	-539.31	1086.98	4.09	0.07
2		2	-539.39	1082.89	0	0.58
	1	3	-539.32	1084.85	1.96	0.22

	2	3	-539.37	1084.95	2.06	0.21
3	2	3	-538.29	1082.8	0	0.35
		2	-539.39	1082.89	0.09	0.34
	1.2	1.2	-537.88	1084.1	1.31	0.18
	1	1	-539.32	1084.85	2.05	0.13

c) predicting daily insect abundance/ daily water temperature

<i>Component models</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
1	3	-1145.09	2296.28	0	1

Term codes: 1: Daily water temperature

Appendix E – GLMM for predicting birds

<i>Component models</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	<i>delta</i>	<i>weight</i>
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Abundance

1	3	-563.35	1132.79	0	0.61
1.2	4	-562.74	1133.65	0.85	0.39

Term codes 1: Insect abundance Margin area

Species richness					
Component models	df	logLik	AICc	delta	weight
3	3	-500.37	1006.84	0	0.36
3.5	4	-500	1008.17	1.33	0.19
2.3	4	-500.15	1008.47	1.63	0.16
3.4	4	-500.19	1008.56	1.71	0.15
1.3	4	-500.3	1008.77	1.92	0.14
Term codes	1: Bramble area	2: Connectivity	3: Insect abundance	4: Insect biomass	5: Margin area