Agriculture, Ecosystems and Environment 273 (2019) 130–140

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Pond management enhances the local abundance and species richness of farmland bird communities

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A R T I C L E I N F O

Keywords:
Aquatic habitat restoration
Biodiversity conservation
Bird behaviour
Invertebrates
Trophic links

A B S T R A C T

Agricultural intensification and the associated loss of non-cropped habitats have caused a major decline in UK farmland bird populations since the 1970s. As a consequence, there is an urgent need to implement effective conservation and habitat restoration measures in agricultural landscapes. Over the last 40–50 years, due to the cessation of traditional management practices, the majority of UK farmland ponds have become highly terrestrialised, resulting in major reductions in the diversity and abundance of aquatic plant and invertebrate assemblages. Recent research undertaken at farmland ponds in early summer, has shown restored open-canopy, macrophyte-dominated ponds support an increased abundance and diversity of farmland birds, compared to non-managed, overgrown ponds.

Here, we expand on this previous research with a year-long field study to assess the implications of pond management for farmland birds by comparing bird diversity, abundance and activity at managed open-canopy ponds with those at unmanaged overgrown ponds. Driven strongly by pond management and connectivity to semi-natural landscape features such as hedgerows and woodland patches, bird abundance and species richness, as well as foraging and parental behaviour, were all significantly higher at managed open-canopy ponds. Further, a wider landscape analysis found that terrestrial land-use patterns in the vicinity of the ponds were not significant predictors of bird communities at the pond sites.

In light of the numerous potential benefits to conservation-listed birds and other wildlife, we conclude that farmland pond management has been undervalued as a conservation measure to assist farmland birds. Consequently, we conclude that future agri-environment schemes, should more fully embrace farmland ponds.

1. Introduction

Populations of many farmland bird species have declined across Europe over the last quarter of the 20th century (Tucker and Heath, 1994). In line with this wider trend, UK farmland bird species have experienced severe decreases in their populations, with an overall drop in farmland bird populations of 56% since 1970 (Defra, 2018). Changes in agricultural practices, especially the widespread loss of semi-natural non-cropped habitats, are thought to be a main driver behind European farmland bird decline, as determined by large-scale declines in food resources (invertebrates, seeds) and in the availability of suitable nesting habitat (Barker, 2004; Aebischer et al., 2015).

The availability of invertebrate and seed-based food sources have been negatively impacted by agro-chemical use (Aebischer, 1991; Newton, 2004; Bright et al., 2008; Hallmann et al., 2014), the switch from spring-sown to autumn-sown crops (Crick et al., 1994; Vickery et al., 2001; Robinson and Sutherland, 2002; Evans et al., 2004; Newton, 2004), removal of non-cropped features such as hedgerows, woodland patches, meadows and farmland trees (Benton et al., 2002; Robinson and Sutherland, 2002; Wood et al., 2003; Benton et al., 2003; Bright et al., 2008) and major farmland drainage schemes (Newton, 2004).

Agri-environment schemes (AES) were introduced by the European Union in part to alleviate the negative impacts of intensive agriculture

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https://doi.org/10.1016/j.agee.2018.12.015
Received 16 August 2018; Received in revised form 15 November 2018; Accepted 24 December 2018
Available online 30 December 2018

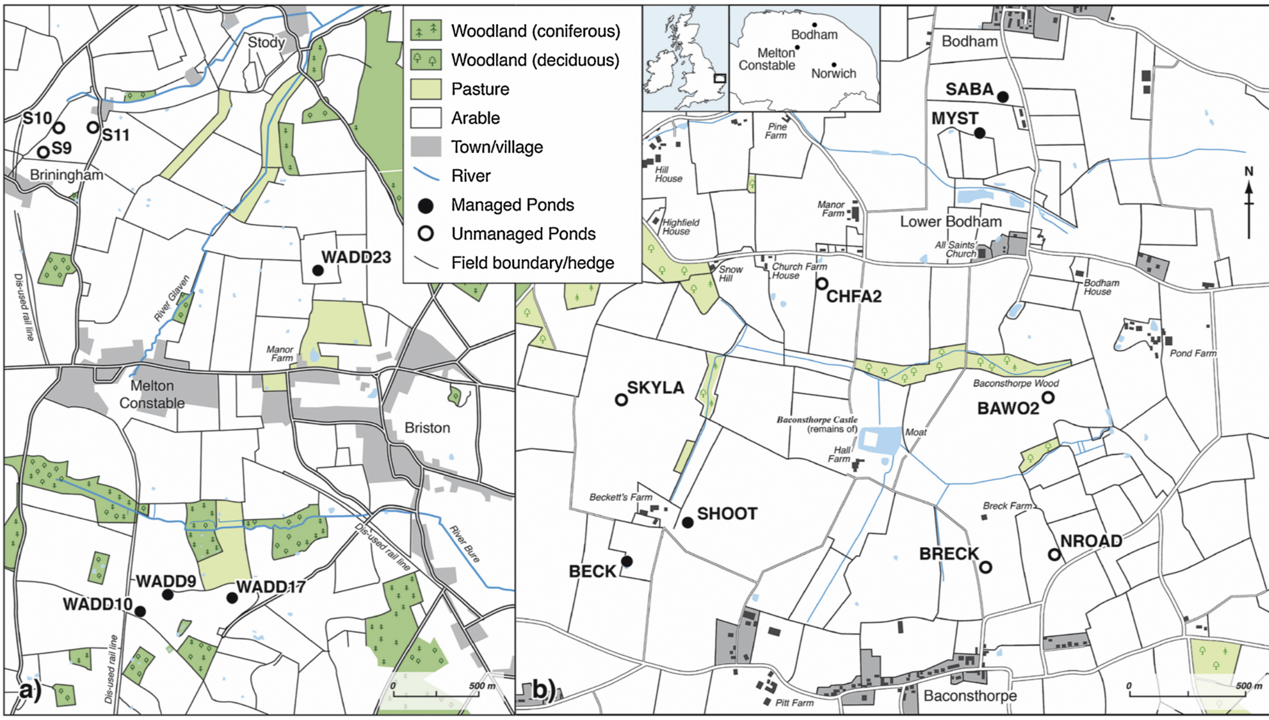

Fig. 1. The farmland study ponds and surrounding landscape near to Briston (a) and Bodham (b) in North Norfolk, eastern England.

on biodiversity (Natural England, 2009; Davey et al., 2010). Nevertheless, farmland bird populations have continued to decline, suggesting that current approaches in AES have largely failed, probably due to a mismatch between the requirements of local bird populations and the type and quantity of AES measures adopted by farmers (Vickery et al., 2008; Risely et al., 2010; Chaudhary et al., 2016). One criticism of AES has been a general lack of emphasis on wet habitat provision, with ponds, streams and wetland habitats rarely mentioned in government annual reporting on farmland bird population declines (Bradbury and Kirby, 2006; Defra, 2015). Further, despite the proven potential of ponds to support a wide range of aquatic and semi-aquatic species in an otherwise species-poor landscape (O'Connor and Shrubb, 1986; Davies et al., 2008), farmland pond management and creation are particularly poorly subscribed measures in comparison to other AES options (Natural England, 2009).

Over the last 40–50 years, many UK farmland ponds have been lost due to deliberate in-filling (Alderton et al., 2017) while, due to the general cessation of traditional scrub management over the same time period, many remaining ponds have succeeded to seasonally flooded wet woodland habitats (Sayer et al., 2013). As a result, open-canopy ponds currently occupy a low percentage of the total pond resource in agricultural areas (Sayer et al., 2012; Sayer, 2014; Thornhill, 2017). Recent research has shown that farmland pond restoration by scrub and sediment removal, aimed at increasing the number of open-canopy ponds, significantly increases the diversity of aquatic macrophytes and invertebrates in ponds and pond landscapes (Sayer et al., 2012). Thus, via restoration it is possible to relatively quickly (within 1 year) return open-canopy ponds to the landscape, with periodic scrub removal (perhaps every 3–6 years) needed to maintain the ponds in this state.

The benefits of ponds and other aquatic habitats can also extend to terrestrial species through numerous aquatic-terrestrial ecological interactions (Baxter et al., 2005). Adult flying life stages of aquatic invertebrates, often emerging simultaneously in vast numbers, can provide an important food source for many nesting and fledging bird species (Baxter et al., 2005; Bradbury and Kirby, 2006; Schummer et al., 2012; Popova et al., 2017). For example, yellow wagtail *Motacilla flava* chicks feed on damselflies (Zygoptera) (Nelson et al., 2003), swallow *Hirundo rustica* chicks consume mayflies (Ephemeroptera) (Loske, 1992) and tree sparrow *Passer montanus* chick diet consists of a high proportion of aquatic midges (Diptera) (Anderson et al., 2002); consequently, tree sparrows are more likely to adopt nest boxes situated next to aquatic habitats (Field and Anderson, 2004).

In a preliminary study of pond management benefits for UK farmland birds, Davies et al. (2016) demonstrated that, in the month of June, avian species richness and abundance were significantly higher at managed open-canopy agricultural ponds compared to unmanaged overgrown ponds. These patterns, it was hypothesised, were related to higher habitat complexity and food availability at managed open-canopy pond sites. Expanding on this preliminary research, the present study provides an integrated, year-round, insight into bird activity patterns at a different configuration of restored and overgrown farmland ponds in the same study area, in combination with a more in-depth analysis of pond margin and wider landscape influences on birds. We firstly hypothesised that, in line with the patterns observed by Davies et al. (2016), managed open-canopy ponds will generally harbour a significantly higher species diversity and bird abundance than unmanaged overgrown ponds. Secondly, we hypothesised that habitats afforded by the pond margin, that vary between open-canopy and overgrown ponds, including scrub, tall grasses, herbaceous plants and bramble, will provide an additional influence on birds via the provision of food and nesting habitat. Finally, we hypothesised that bird foraging, territorial and parental behaviour will be enhanced at managed open-canopy ponds.

2. Methods

2.1. Study area

The study was conducted at 16 farmland ponds, distributed over five farms in North Norfolk, eastern England (Fig. 1). The study ponds were created as a by-product of marl extraction and to provide water for livestock (Sayer et al., 2013) and all ponds were featured on 1836 tithe maps, with most likely significantly older than this date. The area investigated is representative of wider UK lowland agricultural

Fig. 2. A managed open-canopy pond (a) and an unmanaged overgrown highly terrestrialised pond (b) surveyed in the study.

landscapes (especially south-east England), where arable land dominates alongside a combination of hedgerows, woodland patches and grassland. Four of the five farms participate in AES and have implemented a range of conservation measures such as installation of wild bird cover crops and conservation headlands. The ponds are all surrounded by agricultural fields and situated on loamy free-draining soil (Landis, 2018). They are surrounded by grassland buffers of at least 7 m width, mostly established as part of existing AES agreements. All study ponds are shallow (average depth < 1.5 m), have an average water surface area of 303 m^2 ± 31 m^2, and a total average footprint, including the margins, of 2694 m^2 ± 464 m^2.

The study ponds can be broadly divided into two categories: ‘managed open-canopy’ and ‘unmanaged overgrown’ ponds (Fig. 2), with eight study ponds in each group. Managed open-canopy ponds have been subject to restoration by scrub and mud removal or have been subject to long-term scrub management within the last five years and have < 10% canopy shading of the water surface. These ponds support species-rich aquatic communities (Fig. 2a) with frequent dominance of *Potamogeton natans* and/ or *Ceratophyllum submersum* in open water, and are all, at least in part, fringed by emergent vegetation including *Sparganium erectum*, *Typha latifolia* and *Epilobium hirsutum*. By contrast, the unmanaged ponds are overgrown by willow (*Salix* spp.) and or *Alnus glutinosa* due to a lack of scrub management for at least 20–30 years, resulting in high shading (> 85%) and the absence of submerged, floating and emergent macrophytes (Fig. 2b). This later terrestrialised pond state is typical of the wider study area.

2.2. Bird monitoring

Bird species richness and abundance were recorded at each study pond between May 2016 and April 2017. Point count surveys were conducted as per Davies et al. (2016), but the survey methodology was slightly modified to broaden the range of bird species recorded and to increase identification accuracy. Two types of bird survey were used throughout; ‘Main’ and ‘Snapshot’. ‘Main’ surveys consisted of three five-minute point count surveys with a 2-minute gap between individual survey events (Voříšek et al., 2008). This survey length was selected to maximise bird detection, whilst minimising the chance of duplicating individual recordings (Bibby et al., 1998). In combination with the point count surveys, ‘snapshot’ surveys were conducted in the 2-minute intervals between the ‘main’ surveys to obtain recordings of aerial insectivores, chiefly swallow, swift *Apus apus* and house martin *Delichon urbicum*. The snapshot surveys recorded aerial species directly interacting with the pond (e.g. feeding directly above the water surface) at a set moment in time, exactly one minute after the ‘main’ survey was completed. Birds were recorded to species level, conservation status (Eaton et al., 2015), and according to Defra habitat and generalist/ specialist groups (Defra, 2018). Wherever possible, the sex and life stage of bird individuals was also determined. In addition, the location of each bird within the pond, such as emergent aquatic vegetation, open water, overhead, tree or herbaceous margin was recorded alongside behavioural activities such as foraging, travelling, singing (territorial) and call displays, courtship and parental behaviour, with the latter including observations of birds provisioning young, foraging alongside young or travelling in a family group.

All surveys were conducted between 05:00 and 10:30 and between 12:00 and 17:30. The morning surveys were consistent with the protocol employed in the British Trust for Ornithology (BTO) Breeding Bird Survey (BTO, 2011). The inclusion of afternoon surveys increased the opportunity to record avian use of the ponds over a wide range of species. For example, foraging frequency of swallow peaks around midday, such that omitting early afternoon surveys would probably lead to an underestimation of their interaction with the ponds (Zielinski and Wojciechowski, 1999).

One set of morning and afternoon ‘main’ and ‘snapshot’ surveys were completed at each pond every month. Surveys were conducted during good weather in the absence of significant rain to avoid bias from lowered bird activity due to poor weather (BTO, 2011). A minimum distance of 200 m between study ponds was maintained and pond visit order was randomised in order to reduce replicate records of bird individuals moving between the pond sites (Ralph et al., 1995) and thus resulting spatial autocorrelation. To eliminate potential detection bias due to habitat differences between managed and unmanaged ponds, birds were recorded by both sight and sound. Recording individuals by sound decreases potential detectability bias as sound suffers less attenuation than sight in enclosed habitats. Furthermore, the BTO found that habitat-specific detectability does not differ greatly within small habitat areas, such as ponds (A. Johnston, pers. comm.). Surveys were conducted using a viewing telescope and binoculars from a set location that maximised the visibility of the pond open surface area and margin (Bibby et al., 1992). Birds flushed on approach were recorded within the first survey (Voříšek et al., 2008). All individual birds observed at the pond, including in shrubs, trees and in the surrounding herbaceous margins, were recorded. Flying individuals were included when observed within 10 m of the water surface and if observed to be interacting with the pond or pond margin habitat.

2.3. Pond environment and wider landscape analysis

Environmental data for each pond, including management status, connectivity with other key semi-natural habitat features (distance to nearest hedgerow or woodland feature), total water area, open water area, enclosed (shaded) water area, % aquatic macrophyte cover, herbaceous margin area, bramble area, tree area and pond permanence were recorded in summer 2017. Aerial photographs were captured for each pond using a DJI Mavik Pro drone. Land-use within a 500 m radius of each pond, including the area of arable land, grassland, open water, residential land, AES cover crops, woodland and hedgerow length was assessed. The area of the main habitat types within each pond (e.g. open water, shaded water, tree cover and other terrestrial vegetation) and in

Table 1
Bird species richness and observations comparing avian alpha diversity of open and overgrown ponds and gamma diversity of birds from all ponds, where figures for the alpha diversity measures represent mean values ± standard error of the mean. Statistical significance of independent samples t-tests comparing alpha diversity means of managed open-canopy and unmanaged overgrown ponds are based on a p-value threshold of $p < 0.05$ denoted as $p < 0.001$ (***), $p < 0.01$ (**) and $p < 0.05$ (*).

Pond category	Species richness (x ± SE)	Observations (x ± SE)	Shannon Diversity (exp)	Simpson's Diversity (1/D)
Alpha diversity				
Managed	34.00 ± 0.5***	288.13 ± 23.16**	20.20 ± 0.64***	14.98 ± 0.56***
Unmanaged	15.63 ± 1.62***	142.75 ± 22.89**	9.13 ± 0.85***	7.32 ± 0.72***
Gamma diversity				
All Ponds	66	3447	22.05	14.8
Combined managed	64	2305	25.52	17.3
Combined unmanaged	37	1142	12.67	9.53

the wider landscape was then calculated using Photoshop Creative Cloud 2017.

2.4. Data analysis

2.4.1. Bird abundance and species richness

Bird abundance, represented as the total number of individual bird observations, combined across species, recorded at each pond, species richness and Simpson's exponential and Shannon's diversity indices were used to characterise alpha and gamma diversity (Crist et al., 2003; Jost, 2006). Because bird flocks or family groups do not behave independently, they were treated as a single visit event in all analyses to avoid statistical bias by artificially inflating the sample size (i.e. a single species flock of 10 birds arriving together was counted as one visit, as was a single bird arriving alone). This approach underestimates bird abundance, and therefore the results provide a conservative response to pond management. The 'vegan' package (Oksanen et al., 2013) in R-software 1.1.423 (R Core Team, 2017) was used to calculate diversity values and to complete Hellinger transformations (Oksanen et al., 2013). iNEXT online (Hsieh et al., 2016) was used to create rarefaction curves.

2.4.2. Environmental controls on bird community compositions

Bird community responses to pond type were investigated using GLMMs of assemblage-level indices, with species-specific variations in response then being analysed using Redundancy Analysis (RDA). We determined those environmental factors related to bird abundance and bird species richness using Generalised Linear Mixed Models (GLMMs), with both the individual pond and 'pond nested within date' set as random effects using the lme4 package (Bates and Maechler, 2010) in R-software 1.1.423 (R Core Team, 2017). This approach controls for temporal autocorrelation associated with ponds being surveyed repeatedly throughout the year, alongside potential multiple observations per date-pond combination.

Pearson's correlation analysis showed significant correlations ($p < 0.05$) between some in-pond and wider landscape variables (Appendix A). Correlated variables (shaded water area, open water area, macrophyte cover, grassland area, woodland area, open water area and woodland area) were removed, and the variables pond management, pond landscape connectivity, pond water area, herbaceous margin, bramble, tree, arable land, residential land and cover crops as well as hedge length were subsequently selected for GLMM analysis (Bates and Maechler, 2010). Model averaging was conducted, and Akaike's information criterion (AICc < 2) was used to select the best predictive models (Burnham and Anderson, 2002; Grueber et al., 2011) with full average results reported (Bolker et al., 2009).

Principal Components Analysis (PCA) was conducted to distil the main gradients for the full set of predictor variables including management, macrophyte cover, open water area, shaded water area, waterline perimeter, pond connectivity, bramble area, tree area and herbaceous margin area. RDA was conducted to examine the direct links between the resulting principal components and the bird assemblages using Hellinger-transformed bird species richness and abundance data. SPSS (IBM Corp, 2016) was used to calculate PCA values and CANOCO 5 (Morris, 2015) was used to generate all ordination plots.

2.4.3. Foraging activity

Total observations of foraging activity and territorial and parental behaviour patterns were compared between the pond management types using a two-proportions Z-test using R-software 1.1.423 (R Core Team, 2017).

3. Results

3.1. Bird observations

In total, 66 bird species were observed at the 16 farmland ponds (Table 1) (Appendix B). Of these, 64 were recorded at managed open-canopy ponds compared to 37 at unmanaged overgrown ponds (Table 1). Both overall bird species richness and bird abundance were significantly higher at managed open-canopy ponds, compared to unmanaged overgrown ponds (Table 1). Similarly, rarefaction estimated total species richness was higher at managed open-canopy ponds compared to unmanaged overgrown ponds, with rarefaction curves indicating that γ-diversity across the agricultural pondscape did not exceed estimated diversity values for the combined data from the managed ponds (Fig. 3).

Apart from two species, treecreeper *Certhia familiaris* and woodcock

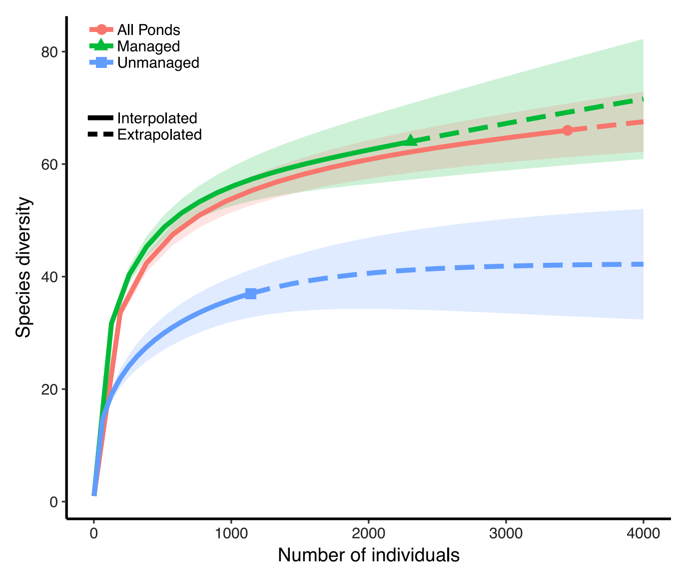

Fig. 3. Rarefaction curves with 95% confidence intervals for managed open-canopy ponds and unmanaged overgrown ponds and all ponds combined. The number of individuals sampled are plotted against number of species.

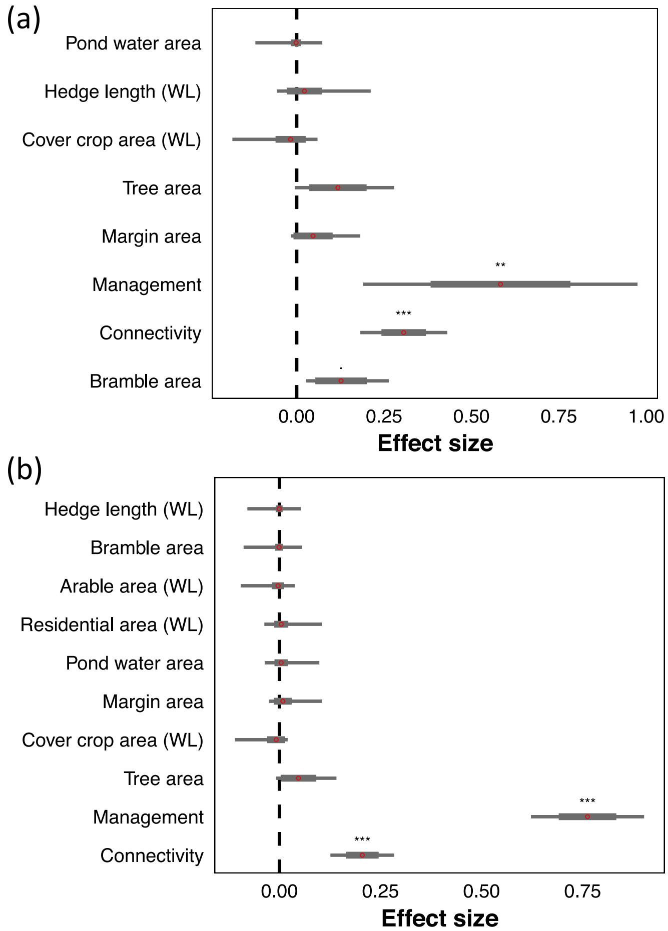

Fig. 4. (a) effect size plot for bird abundance and (b) bird species richness. Significance value codes: < 0.001 '***', 0.001 '**', 0.05 '*', 0.1 '.' WL denotes a wider landscape variable. Estimated effect size with standard error, upper and lower limits included.

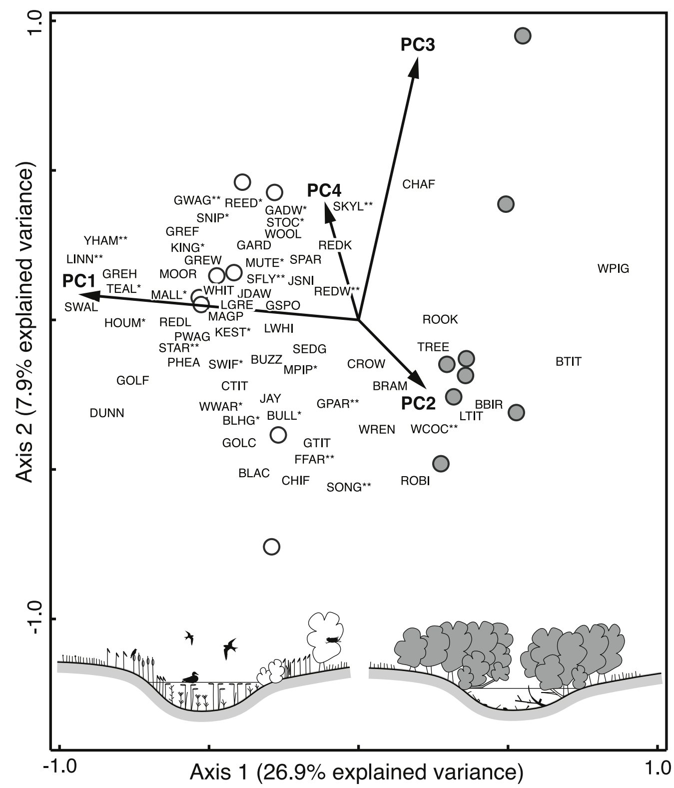

Fig. 5. Redundancy Analysis (RDA) of bird assemblages recorded at managed open canopy ponds (white, non-filled circle) and unmanaged overgrown ponds (grey circle). Amber listed species annotated with *, red listed bird species **. Key to species codes: BLHG: black-headed gull, BBIR: blackbird, BLAC: blackcap, BTIT: blue tit, BRAM: brambling, BULL: bullfinch, BUZZ: common buzzard, CHAF: chaffinch, CHIF: chiffchaff, CTIT: coal tit, CROW: carrion crow, DUNN: dunnock, FFAR: fieldfare, GADW: gadwall, GARD: garden warbler, GOLC: goldcrest, GOLF: goldfinch, GTIT: great tit, GSPO: great-spotted woodpecker, GREW: green woodpecker, GREF: greenfinch, GREH: grey heron, GPAR: grey partridge, GWAG: grey wagtail, HOUM: house martin, JSNI: jack snipe, JDAW: jackdaw, JAY: jay, KEST: kestrel, KING: kingfisher, LWHI: lesser whitethroat, LINN: linnet, LGRE: little grebe, LTIT: long-tailed tit, MAGP: magpie, MALL: mallard, MPIP: meadow pipit, MOOR: moorhen, MUTE: mute swan, PHEA: pheasant, PWAG: pied wagtail, REDK: red kite, REDL: red-legged partridge, REDW: redwing, REED: reed bunting: ROBI: robin, ROOK: rook, SEDG: sedge warbler, SKYL: skylark, SNIP: snipe, SONG: song thrush, SPAR: sparrowhawk, SFLY: spotted flycatcher, STAR: starling, STOC: stock dove, SWAL: swallow, SWIF: swift, TEAL: teal, TREE: treecreeper, WHIT: whitethroat, WWAR: willow warbler, WPIG: woodpigeon, WCOC: woodcock, WOOL: woodlark, WREN: wren, YHAM: yellowhammer (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Scolopax rusticola, all species recorded at the unmanaged overgrown ponds were also found at managed open-canopy ponds. By contrast, 31 bird species were exclusively recorded at the open-canopy managed ponds.

GLMMs showed that, of the parameters tested, pond management and connectivity to hedgerows and woodland areas were significant predictors of overall avian abundance, with both pond management and high connectivity having a positive effect on bird abundance (Fig. 4) (Appendix C). These two parameters were also significant predictors of overall bird species richness (Fig. 4). No variables recorded at the landscape-scale showed any significant link to bird abundance or species richness at the ponds. Area of bramble showed a close to significant positive relationship with abundance ($p = 0.08$), but not the species richness of birds encountered at the ponds.

Four main principal components were distilled from the set of predictor parameters in the PCA, together explaining 90.9% of total variance (Appendix D). The first principal component (PC1) chiefly represents the management gradient, with higher values indicative of open-canopy ponds with large areas of aquatic macrophyte-filled open water as a result of recent management. Higher values for PC2 are associated with ponds that are highly connected to landscape features such as hedgerows or small woodland patches, as well as representing an increase in overall pond size. PC3 chiefly represents areas with high bramble and tree cover at the pond margin, whereas PC4 finally increases in line with the pond margin area occupied by herbaceous plants.

As reflected by their association with PC1 in the RDA ordination plot (Fig. 5), many bird species, including conservation priority farmland, woodland and water specialists, showed a clear preference for managed, open-canopy ponds (Table 2). These species included aerial insectivores like house martin and swallow, granivores like linnet *Carduelis cannabina* and yellowhammer *Emberiza citrinella*, dabbling ducks like teal *Anas crecca* and mallard *Anas platyrhynchos* and other obligate wetland species like kingfisher *Alcedo atthis*, grey heron *Ardea cinerea*, moorhen *Gallinula chloropus*, and snipe *Gallinago gallinago*. A smaller group of generalist species, woodpigeon *Columba palumbus,* blue tit *Cyanistes caeruleus* and rook *Corvus frugilegus,* displayed a preference for unmanaged overgrown ponds (Fig. 5).

Several woodland species, including robin *Erithacus rubecula*, wren *Troglodytes troglodytes*, blackbird *Turdus merula,* long-tailed tit *Aegithalos caudatus,* woodcock and brambling *Fringilla montifringilla*, appear also loosely associated with increased connectivity between the pond and woody landscape elements (PC2), in addition to their

Table 2
Specialist bird species, subdivided into Defra habitat category, observed at managed and unmanaged ponds. Number indicates number of times the species was observed as opposed to abundance. Red listed species notated with † †, amber with †.

Habitat	Common name	Species name	Managed	Unmanaged
Farmland	Goldfinch	Carduelis carduelis	96	16
	Greenfinch	Chloris chloris	32	4
	Grey partridge ††	Perdix perdix	1	0
	Linnet ††	Linaria cannabina	64	1
	Skylark ††	Alauda arvensis	14	2
	Starling ††	Sturnus vulgaris	5	0
	Stock dove †	Columba oenas	1	0
	Whitethroat	Sylvia communis	60	8
	Yellowhammer ††	Emberiza citrinella	79	0
Woodland	Blackcap	Sylvia atricapilla	33	16
	Chiffchaff	Phylloscopus collybita	132	80
	Coal tit	Periparus ater	2	0
	Garden warbler	Sylvia borin	3	0
	Goldcrest	Regulus regulus	8	1
	Greater spotted woodpecker	Dendrocopos major	1	0
	Green woodpecker	Picus viridis	3	0
	Jay	Garrulus glandarius	4	1
	Sparrowhawk	Accipiter nisus	1	0
	Treecreeper	Certhia familiaris	0	1
	Willow warbler †	Phylloscopus trochilus	13	0
Water/ wetland	Grey wagtail ††	Motacilla cinerea	4	0
	Kingfisher †	Alcedo atthis	5	0
	Little grebe	Tachybaptus ruficollis	4	0
	Sedge warbler	Acrocephalus schoenobaenus	4	0
	Snipe †	Gallinago gallinago	14	0
	Teal †	Anas crecca	15	0

preference for unmanaged overgrown pond habitats. Chaffinch *Fringilla coelebs* showed a clear preference for ponds with increased tree and bramble cover (PC3) while grey partridge *Perdix perdix*, fieldfare *Turdus pilaris*, meadow pipit *Anthus pratensis*, and sedge warbler *Acrocephalus schoeniclus,* displayed a preference for ponds with low tree and bramble cover.

3.2. Bird behaviour

Observations of foraging activity and parental behaviours were significantly higher ($p < 0.001$) at managed open-canopy ponds than at the unmanaged overgrown ponds (Table 3). By contrast, observations of territorial behaviour did not differ significantly between the pond management types.

4. Discussion

4.1. Drivers of avian diversity and abundance

Expanding on the study of Davies et al. (2016), our investigations provide a year-long integrated analysis of farmland bird interactions with open-canopy and overgrown ponds and a more in-depth consideration of wider landscape influences. In support of our first hypothesis, the results show that managed open-canopy ponds support a higher bird diversity and abundance than their unmanaged counterparts, hence solidifying evidence of pond management benefits for farmland bird conservation. We show open ponds to attract a suite of bird species across a wide range of families and guilds. Our data expand on previous research identifying ponds as important wildfowl habitats (O'Connor and Shrubb, 1986; Sebastián-González et al., 2010; Newton, 2017), and indicate that beneficiaries of open pond habitats extend to a range of farmland and woodland habitat specialist bird species, including a number of declining species included on UK red and amber lists (Table 2). Importantly, as well as showing a preference for open-canopy ponds, conservation priority farmland and woodland species currently experiencing significant declines also showed a preference for ponds with high connectivity to hedgerow or woodland habitats and with wide herbaceous pond margins. The association of such a wide range of species with open-canopy managed ponds, combined with behavioural observations of increased foraging and parental interactions further lend support for our hypothesis that birds are gaining benefits from increased resource availability at open-canopy ponds.

Table 3
Bird behavioural observations at managed open-canopy and unmanaged overgrown ponds.

Pond management	Behaviour	No. behavioural observations	Total observations	X^2	df	P
Managed	Foraging	595	2305	52.806	1	< 0.001
Unmanaged		170	1142			
Managed	Territorial	457	2305	0.576	1	0.45
Unmanaged		214	1142			
Managed	Parental	59	2305	9.782	1	0.001
Unmanaged		11	1142			

4.2. The importance of the aquatic ecosystem

Our results show that pond management is a significant predictor of both bird abundance and species richness in the local vicinity of farmland ponds, with a further significant positive correlation between management and bird activity. The process of pond management has been shown to result in high levels of aquatic plant diversity (Sayer et al., 2012), with managed open-canopy study ponds characterised by extensive stands of submerged and emergent macrophytes in contrast to unmanaged terrestrialised ponds which are generally free of all macrophyte vegetation. Macrophytes play a key role in pond ecology and importantly the high structural complexity provided by plants is known to alter the density and community structure of aquatic invertebrates (Gregg and Rose, 1985; Declerck et al., 2011). A positive link between macrophytes and farmland birds at our ponds seems likely to stem from increased invertebrate abundance and emergence in plant-dominated ponds and hence an important source of food to birds. Indeed, a positive response of birds to increased aquatic macrophyte coverage has been identified previously for waterfowl (Knapton and Petrie, 1999; McKinstry and Anderson, 2002; Santoul et al., 2009; Sebastián-González et al., 2010) with the same true for streams and birds via aquatic-terrestrial subsidies (Baxter et al., 2005).

Overall, observed bird foraging levels were significantly higher at managed open-canopy ponds than at unmanaged overgrown ponds. Invertebrate emergence trapping experiments at the study ponds indicate that levels of emergent invertebrates, especially of Ephemeroptera and Chironomidae, are significantly higher at the managed open-canopy ponds than at unmanaged overgrown ponds (Lewis-Phillips et al. in prep). This suggests that the higher levels of bird abundance, species richness and foraging observations at managed open-canopy ponds are a direct response to increased invertebrate food associated with mass-emergences of Ephemeroptera and Chironomid individuals (Bradbury and Kirby, 2006), as well as a more constant flux of emerging dragonflies. These high-quality aquatic food sources may be especially important over the breeding season, when bird nutritional requirements are particularly high. Parental observations were also significantly higher at managed open-canopy ponds with adults observed repeatedly provisioning juveniles with invertebrates emerging directly from the pond. Pond-side nest sites, including yellowhammer and chiffchaff *Phylloscopus collybita,* were observed at open-canopy ponds with pairs likely drawn to high-quality local foraging opportunities. In contrast, only a single nest, occupied by a pair of woodpigeons was encountered at the unmanaged overgrown ponds. Birds may also benefit from refuge and abundant perching habitat provided by the heterogenous vegetation structure with exposed mud also affording nest-building material (Davies et al., 2016).

Our results show that pond size was not a strong predictor of bird abundance or diversity at the farmland pond sites. This is in line with the findings of Santoul et al. (2009), but contrasts with observations from other studies (Sebastián-González et al., 2010; Davies et al., 2016). However, sites used in the Sebastián-González study were considerably larger, with an average area of 6000 m^2, in comparison to an average water surface area of 303 m^2 per pond in this study.

4.3. The importance of pond margins

While the area of herb-dominated pond margin was not found to have a significant effect on either bird abundance or species richness, PCA indicates a positive association of this feature with a number of individual bird species, including the UK conservation priority species skylark and redwing. Davies et al. (2016) hypothesised that herb rich patches in pond margins were likely inhabited by large numbers of invertebrates, and pan trapping experiments at the study sites confirm that the diversity of invertebrate groups was indeed significantly higher at managed open-canopy ponds (Lewis-Phillips et al. in prep). In addition, the herbaceous margins of managed open-canopy ponds support a number of seed-rich plants, including species from the *Polygonaceae* and *Asteraceae*, that form an important diet component for farmland specialist species (McCracken and Tallowin, 2004; Holland et al., 2006), whilst also providing nesting habitat for species such as reed bunting that nest in tall, non-woody vegetation (Redhead et al., 2018), alongside cover from predators (Bradbury and Kirby, 2006). Overgrown ponds are often also encircled by herb-dominated margins, but these areas did not appear to offer the same resources to birds, potentially because of lowered plant diversity, shading by scrub over large portions of the wet pond margin, or avoidance of foraging on the ground next to dense woody vegetation that could harbour predators.

Increased bramble area (*Rubus* spp.) was found to provide a near-significant effect on bird abundance. Bramble development is driven by the removal of shading at open-canopy ponds, leaving large open spaces available for rapid colonisation by this strongly competitive species. In comparison, the heavily shaded environment of overgrown ponds tended to impede bramble growth (Harmer et al., 2012). While bramble is known to supress plant diversity (Harmer, 2006) it nevertheless provides a complex habitat structure and offers a range of benefits to birds, including food resources, especially fruit and insects (Harmer, 2006; Charman et al., 2009), cover from predators and again nesting habitat for specialist farmland and woodland species (Peakall 1960; Rodrigues and Crick, 1997).

4.4. Influence of the wider landscape on bird diversity and abundance

Lawton et al. (2010) advocated the key importance of landscape connectivity for wildlife. In support of this idea, our results show pond sites connected to, or in close proximity to tree-dominated landscape features (hedges and woodland patches) support a significantly higher bird abundance and species richness. Connectivity with landscape features such as hedgerows has been regularly shown to represent an important factor for birds and a range of plant, invertebrate and mammal species (Bennett et al., 1994; Parish et al., 1994; Joyce et al., 1999; Wehling & Diekmann 2009; Sullivan et al., 2017), with hedges acting as corridors and stepping stones by which individuals move through the landscape. Birds may also gain benefits from the resources provided by linear connecting features, such as hedgerows (Whittingham et al., 2009) via increased provision of food in the form of seeds and invertebrates, in addition to increased shelter, nest site provision and protection from predators. The majority of species that appear to benefit from greater connectivity to woodland and hedgerow patches were woodland generalist species such as robin and blackbird but other species, such as bullfinch *Pyrrhula pyrrhula* and willow warbler *Phylloscopus trochilus* also showed similar preferences.

Apart from connectivity to hedges and woodland, the wider landscape analysis suggests that terrestrial land-use patterns in the vicinity of the ponds were not significant predictors of bird abundance or species richness at the pond sites. This may be because the land-use surrounding the study sites was consistent, with all ponds surrounded by a mixture of arable and grassland. Therefore, it appears that managed farmland ponds are locally influencing bird abundance and species richness, rather than the responses being driven solely by the surrounding landscape matrix.

4.5. Pond management and farmland bird conservation

Open-canopy farmland ponds with abundant aquatic and wetland-emergent plants clearly play an important role in supporting both local aquatic and terrestrial biodiversity (O'Connor and Shrubb, 1986; Sayer et al., 2012; Céréghino et al., 2014; Davies et al., 2016). Our study emphasises the potential for managed open-canopy ponds to provide significant cross-system subsidies between aquatic and terrestrial environments, providing stronger evidence for the important value of pond management to farmland birds. The provision of abundant invertebrate food resources at managed open-canopy ponds may be significant for a number of farmland bird species that have suffered severe declines over the last decades. Terrestrial habitats typically surrounding open ponds, such as herbaceous margins, bramble thickets and connecting hedgerows, are also highlighted as potentially important habitat patches for farmland birds. Our results accordingly highlight that bird diversity supported by managed ponds on their own is very similar to that of all ponds, including open-canopy and overgrown ponds, across the agricultural pondscape. Therefore, while our results still place an emphasis on maintaining a mosaic of pond successional states, they suggest that, for bird conservation within a farmed landscape, emphasis should be strongly placed on generating a larger number and proportion of open-canopy managed ponds. We suggest that farmland ponds, and in particular their potential contribution to terrestrial conservation, have been greatly undervalued as a conservation tool. A landscape-scale approach incorporating urban and floodplain ponds (Hill et al., 2016), farmland pond restoration (Sayer et al., 2013), pond creation (Williams et al., 2010), and, where possible, resurrection of infilled farmland 'ghost' ponds (Alderton, 2016; Alderton et al., 2017) has the potential to benefit birds alongside aquatic species over large areas. As such, as elsewhere (Sayer, 2014), we call for ponds to be given a higher priority in an AES context at the landscape scale. An opportunity to make such revisions in the UK is presented by the development of a new agricultural subsidy structure following the country's exit from the European Union.

Funding

Funding for this research was provided by the NERC London Doctoral Training Programme studentship to Jonathan Lewis-Phillips (Grant code: NE/L002485/1).

Declarations of interest

None.

Acknowledgements

This paper is dedicated to Richard Waddingham, the owner of Manor Farm in Briston, Norfolk, who inspired this research through years of careful management and bird observations at his ponds. We would also like to thank Derek Sayer, Thomas and Amelia Courthauld, Peter Seaman, Paul Marsh and the Stody Estate for allowing us access to their farmland ponds and Rob Hawkes for his advice with GLMM analysis.

Appendix A. Correlation table

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	***			***	***	***										
2		***														
3			***	***												
4	***		***	***	***	***										
5	***			***	***	***	*									
6	***			***	***	***	*					*				
7					*	*	***					***				
8								***								
9									***							
10										***	***					
11										***	***					*
12						*	***					***				
13													***			
14														***		
15															***	*
16											*				*	***

Management: 1, Connectivity: 2, Water area: 3, Water area (open, non-shaded): 4, Water area (shaded): 5, Macrophyte area: 6, Bramble area: 7, Tree area: 8, Margin area: 9, Arable area (WL): 10, Grassland area (WL): 11, Open water area (WL): 12, Residential area (WL): 13, Cover crop area (WL): 14, Woodland area (WL): 15, Hedgerow length (WL): 16. Significance value codes: < 0.001 '***', 0.01 '**', 0.05 '*'. WL denotes wider landscape variable.

Appendix B. Full species list

Bird species observed at managed and unmanaged ponds. Number in brackets indicates number of times the species was observed as opposed to abundance. Codes for ponds: BECK: A. MYST: B, SABA: C, SHOOT: D, WADD9: E, WADD10: F, WADD17: G, WADD23: H, BAWO2: I, BRECK: *J*, CHFA2: K, NROAD: L, S9: M: S10: N, S11: O, SKYLA: P. Red listed species notated with † †, amber with †.

Family	*Common name*	*Species name*	*Managed ponds*	*Unmanaged ponds*
Accipitridae	common buzzard	*Buteo buteo*	A (2), B (6), E (1)	I (1)
	red kite	*Milvus milvus*	H (1)	
	sparrowhawk	*Accipiter nisus*	H (1)	
Aegithalidae	long-tailed tit	*Aegithalos caudatus*	A (4), D (1), E (1)	I (3), L (2), M (1), N (1), O (1)
Alaudidae	skylark † †	*Alauda arvensis*	A (1), C (1), D (7), E (2), G (3)	J (1), P (1)
Alcedinidae	kingfisher †	*Alcedo atthis*	C (3), F (1), H (1)	
Anatidae	gadwall †	*Anas strepera*	G (1)	
	mallard †	*Anas platyrhynchos*	A (5), D (2), F (8), G (12), H (11), E (4)	L (1), N (1)
	mute swan †	*Cygnus olor*	D (4)	
	teal†	*Anas crecca*	A (3), B (4), C (2), F (1), G (2), H (4)	
Apodidae	swift †	*Apus apus*	A (1), B (2), C (7)	
Ardeidae	grey heron	*Ardea cinerea*	A (1), B (3), C (4), D (3), G (2)	
Certhidae	treecreeper	*Certhia familiaris*		N (1)
Columbidae	stock dove †	*Columba oenas*	G (1)	
	woodpigeon	*Columba palumbus*	A (12), B (14), C (17), D (25), E (6), F (10), G (2), H (10)	I (14), J (14), K (16), L (17), M (23), N (26), O (27), P (12)
Corvidae	carrion crow	*Corvus corone*	B (5), C (1), D (1), E (1), H (1)	I (1), M (1), N (3), O (2)
	jackdaw	*Corvus monedula*	B (1)	
	jay	*Garrulus glandarius*	A (2), B (1), F (1)	L (1)
	magpie	*Pica pica*	B (8), C (10), D (3), F (2), G (1)	K (1), L (1), M (5)
	rook	*Corvus frugilegus*	A (1)	I (1)
Emberizidae	reed bunting †	*Emberiza schoeniclus*	C (2), E (1), G (12), H (11)	

	yellowhammer † †	*Emberiza citrinella*	B (9), C (22), D (4), E (7), F (15), G (2), H (20)	
Falconidae	kestrel †	*Falco tinnunculus*	A (2), B (2), E (1), F(2), G (1) H (1)	I (1), O (1)
Fringillidae	brambling	*Fringilla montifringilla*	C (1)	K (1), N (2)
	bullfinch †	*Pyrrhula pyrrhula*	A (8), B (1), C (5), D (6), H (10)	K (3), L (1), M (2), O (1)
	chaffinch	*Fringilla coelebs*	A (26), B (23), C (33), D (18), E (10), F (31), G (12), H (36)	I (1), J (3), K (12), L (24), M (23), N (4), O (19), P (22)
	goldfinch	*Carduelis carduelis*	A (6), B (8), C (20), D (15), E (20), F (5), G (10), H (12)	J (4), K (2), M (1), N (8), O (1)
	greenfinch	*Chloris chloris*	B (2), C (12), D (3), E (12), F (2), G (1)	K (4)
	linnet † †	*Linaria cannabina*	A (4), B (6), C (22), D (7), E (2), F (5), G (10), H (8)	N (1)
Hirundinidae	house martin †	*Delichon urbicum*	A (2), B (1), C (6), D (4), F (1), H (1)	
	swallow	*Hirundo rustica*	A (3), B (1), C (4), D (6), E (2), F (1), G (4), H (1)	
Laridae	black-headed gull †	*Chroicocephalus ridibundus*	A (2), D (2)	
Motacillidae	grey wagtail † †	*Motacilla cinerea*	F (1), G (3)	
	meadow pipit †	*Anthus pratensis*	A (1), E (1), F (1), G (2), H (1)	M (1), N (1)
	pied wagtail	*Motacilla alba*	A (1), D (2), E (4), F (5), G (3), H (1)	M (1)
Muscicapidae	spotted flycatcher † †	*Muscicapa striata*	D (3)	
Paridae	blue tit	*Cyanistes caeruleus*	A (28), B (19), C (18), D (18), E (12), F (4), G (2), H (15)	I (25). J (4), K (10), L (35), M (29), N (13), O (27), P (4)
	coal tit	*Periparus ater*	A (1), F (1)	
	great tit	*Parus major*	A (9), B (8), C (6), D (2), E (12), F (6), G (6), H (3)	I (3), K (4), L (1), M (2), N (10), O (11)
Phasianidae	grey partridge † †	*Perdix perdix*	E (1)	
	pheasant	*Phasianus colchicus*	A (1), B (4), C (4), D (2), E (3), G (6), H (2)	L (2), N (2), O (3)
	red-legged partridge	*Alectoris rufa*	A (4), E (3), F (3), G (7), H (2)	
Picidae	greater spotted woodpecker	*Dendrocopos major*	B (1)	
	green woodpecker	*Picus viridis*	E (1), G (2)	
Podicipedidae	little grebe	*Tachybaptus ruficollis*	B (4)	
Prunellidae	dunnock	*Prunella modularis*	A (12), B (11), C (31), D (11), E (33), F (9), G (12), H (7)	K (1), L (4), N (4), O (6)
Rallidae	moorhen	*Gallinula chloropus*	A (24), B (13), C (10), D (43), E (19), F (17), G (14), H (15)	J (1), K (1), L (14), M (6), N (7), P (3)
Scolopacidae	jack snipe	*Lymnocryptes minimus*	D (1)	
	snipe †	*Gallinago gallinago*	C (2), D (5), G (7)	
	woodcock † †	*Scolopax rusticola*		O (1)
Sturnidae	starling † †	*Sturnus vulgaris*	B (1), C (3), E (1)	
Sylviidae	blackcap	*Sylvia atricapilla*	A (9), B (1), C (1), D (8), E (2), F (4), G (1), H (7)	J (1), M (5), N (5), O (5)
	chiffchaff	*Phylloscopus collybita*	A (18), B (22), C (25), D (14), E (5), F (18), G (1), H (29)	J (4), L (10), M (25), N (19), O (22)
	garden warbler	*Sylvia borin*	G (3)	
	goldcrest	*Regulus regulus*	A (4), D (3), F (1)	O (1)
	lesser whitethroat	*Sylvia curruca*	B (9)	L (1)
	sedge warbler	*Acrocephalus schoenobaenus*	E (3), H (1)	
	whitethroat	*Sylvia communis*	B (10), C (8), D (5), E (10), F (6), G (7), H (14)	J (4), K (4)
	willow warbler †	*Phylloscopus trochilus*	A (2), D (8), E (3)	
Troglodytidae	wren	*Troglodytes troglodytes*	A (40), B (39), C (57), D (33), E (37), F (41), G (28), H (33)	I (19), J (14), K (26), L (24), M (30), N (37), O (24), P (3)
Turdidae	blackbird	*Turdus merula*	A (24), B (38), C (43), D (20), E (19), F (16), G (11), H (39)	I (4), J (16), K (22), L (38), M (30), N (13), O (31), P (6)
	fieldfare † †	*Turdus pilaris*	A (1), B (2), C (2), G (1)	M (1), N (1), O (1)
	redwing † †	*Turdus iliacus*	C (2), E (1), F (1), G (1), H (1)	K (2), L (2)
	robin	*Erithacus rubecula*	A (15), B (12), C (20), E (11), F (19), G (7), H (16)	I (2), J (15), K (20), L (2), M (29), N (21), O (31), P (1)
	song thrush † †	*Turdus philomelos*	A (5), E (1), F (2)	K (1), M (1)

Appendix C. GLMM analysis

Component models	df	loglik	AICc	delta	weight
4.6.9	7	−2890.11	5794.32	0	0.14
3.4.6.9	8	−2889.35	5794.83	0.51	0.11
4.6	6	−2891.57	5795.21	0.89	0.09
4.6.7	7	−2890.64	5795.37	1.05	0.08
4.6.7.9	8	−2889.75	5795.63	1.31	0.07
3.4.6.9.10	9	−2889.78	5795.72	1.4	0.07
4.6.9.10	8	−2889.84	5795.81	1.48	0.07
4.6.8.9	8	−2889.85	5795.82	1.5	0.07
1.4.6.9	8	−2889.89	5795.9	1.58	0.06
4.6.8	7	−2890.9	5795.9	1.58	0.06
2.4.6.9	8	−2890.02	5796.16	1.84	0.06
4.5.6.9	8	−2890.04	5796.2	1.87	0.06
1.4.6.7	8	−2890.07	5796.26	1.94	0.05

Term codes: 1: Arable area (WL), 2: Bramble area, 3: Covercrop area (WL), 4: Connectivity, 5: Hedge length (WL), 6: Management, 7: Margin area, 8: Residential area (WL), 9: Tree area, 10: Water area. WL denotes wider landscape variable.

Full average parameter estimates from the Generalized Linear Mixed models for bird abundance. Significance value codes: < 0.001 '***', 0.001 '**', 0.01 '*', 0.1 '.'. WL denotes wider landscape variable.

Bird abundance	Estimate	SE	Z	P	Sig.
(Intercept)	0.663	0.118	5.603		
Bramble area	0.127	0.074	1.725	0.085	.
Connectivity	−0.306	0.064	4.813	< 0.001	***
Management	0.583	0.2	2.911	0.004	**
Margin area	0.047	0.056	0.835	0.404	
Tree area	0.118	0.082	1.439	0.15	
Cover crop area (WL)	−0.017	0.043	0.403	0.687	
Hedge length (WL)	0.022	0.051	0.437	0.662	
Pond water area	−0.002	0.015	0.116	0.908	

Full average parameter estimates from the Generalized Linear Mixed models for bird species richness. Significance value codes: < 0.001 '***', 0.001 '**', 0.01 '*', 0.1 '.'. WL denotes wider landscape variable.

Bird species richness	Estimate	SE	Z	P	Sig.
(Intercept)	0.663	0.118	58.752		
Connectivity	−0.205	0.04	5.093	< 0.001	***
Management	0.762	0.071	10.675	< 0.001	***
Tree area	0.047	0.044	1.743	0.286	
Cover crop area (WL)	−0.008	0.022	1.347	0.717	
Margin area	0.008	0.022	1.191	0.707	
Pond water area	0.004	0.017	0.902	0.797	
Residential area (WL)	0.004	0.017	0.929	0.799	
Arable area (WL)	−0.003	0.015	0.843	0.82	
Bramble area	−0.001	0.01	0.437	0.924	
Hedge length (WL)	−0.001	0.009	0.393	0.931	

Appendix D. Principal Components Analysis

Component	Total	% of variance	Cumulative %
1	5.829	52.992	52.992
2	1.802	16.384	69.376
3	1.288	11.706	81.082
4	1.077	9.794	90.877
5	0.458	4.164	95.04
6	0.298	2.712	97.753
7	0.163	1.482	99.235
8	0.081	0.732	99.967
9	0.003	0.024	99.991
10	0.001	0.009	100
11	2.91e-17	2.91e-16	100

		Component		
	1	2	3	4
Management	−0.955	0.154	−0.143	0.007
Connectivity	−0.277	0.715	0.407	−0.283
Waterline perimeter	0.635	0.615	−0.322	0.067
Macrophyte cover %	0.938	−0.119	0.194	−0.03
Macrophyte cover area	0.984	0.101	−0.029	−0.034
Pond area (open, unshaded)	0.981	0.139	−0.045	−0.041
Pond area (shaded)	−0.868	0.401	−0.071	0.065
Pond water area total	0.665	0.664	−0.151	0.003
Bramble area	0.503	−0.283	0.668	−0.147
Tree area	−0.376	0.405	0.693	0.283
Margin area	0.252	−0.019	0.051	0.94

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