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RESEARCH ARTICLE

Agricultural pond restoration enhances species richness in non-biting midges (Diptera: Chironomidae)

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Agricultural ponds are biodiversity hotspots, especially when restored to open-canopy conditions. Studies comparing pre- and post-restoration pond diversity are rare, however, and have widely focused on "easy-to-identify" taxa. Chironomids have so far been neglected in pond restoration studies, but are a highly speciose group critical to aquatic ecosystem functioning. This makes them good potential indicators of ecological change. Despite a reputation for being taxonomically challenging, the final molts of chironomid pupae, the exuviae, can be reliably sampled and identified using the Chironomid Pupal Exuvial Technique (CPET). For a lowland farmland pond landscape in eastern England, we used CPET sampling in a Before-After Control-Impact study encompassing nine ponds restored by major removal of woody vegetation and sediment, four terrestrialized control ponds and two open-canopy control ponds. Species richness was significantly greater in the restored and open-canopy control ponds compared to the terrestrialized ponds, likely due to structurally complex plant communities in the former. Few chironomid species preferred the wood and organic matter-dominated conditions afforded by the terrestrialized ponds, while the restoration of these ponds to open-canopy, macrophyte-dominated condition strongly increased chironomid diversity. To maximize landscape-scale chironomid diversity, agricultural landscapes should ideally contain ponds at different stages of succession, including a high proportion of ponds restored to an early successional macrophyte-filled state. As for many other taxonomic groups, we show that pond restoration is essential to the maintenance of species-rich chironomid communities in farmland pondscapes.

Key words: biodiversity, chironomid pupal exuviae, farmland, management, succession

Implications for Practice

- As sensitive indicators of aquatic ecological change, chironomids can be employed to track pond responses to management and restoration.
- Restoring overgrown, terrestrialized farm ponds by major woody vegetation and sediment removal substantially increases landscape-scale chironomid diversity.
- Conservation projects that result in pondscapes that contain a mix of successional stages, including a high proportion of early succession, open-canopy ponds, will maximize chironomid diversity and their associated ecosystem functions.

Introduction

Ponds are biodiversity hotspots in agricultural landscapes (Ruggiero et al. 2008; Gioria et al. 2010). In many lowland European farmland regions, agricultural intensification since the 1950s has led to a major loss of ponds due to deliberate infilling (Alderton et al. 2017; Curado et al. 2011; Ferreira & Beja 2013; Smith et al. 2022), as well as the degradation of existing ponds due to the abandonment of traditional woody vegetation management (Sayer et al. 2012; Janssen et al. 2018). The latter has led to a "mass-terrestrialization" effect, whereby entire farmed landscapes have become dominated by heavily terrestrialized "late-succession" ponds overgrown by woody vegetation and filled by poorly decomposed leaf litter and woody material (Sayer & Greaves 2020). Previous work has shown that pond terrestrialization results in low landscape-scale habitat heterogeneity, coupled with low biodiversity across multiple aquatic and terrestrial species groups (Sayer et al. 2022). Compared to terrestrialized ponds, ponds regularly managed or restored to open-

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canopy conditions by a combination of woody vegetation and sediment removal, are known to support a higher coverage of aquatic macrophytes (Sayer et al. 2022), as well as significantly elevated wetland plant (Sayer et al. 2012, 2023), invertebrate (Sayer et al. 2012; Janssen et al. 2018), and amphibian diversity (Skelly et al. 2014; Arntzen et al. 2017). Increased abundances of emerging aquatic insects (Lewis-Phillips et al. 2020) and more diverse and flower-rich habitat structures at restored open-canopy ponds have also been shown to strongly benefit farmland bird (Davies et al. 2016; Lewis-Phillips et al. 2019a, 2019b) and diurnal pollinator (Walton et al. 2021a, 2021b) communities.

Previous studies investigating the consequences of farmland pond restoration for aquatic biodiversity and species assemblages have largely focused on cross-comparisons of sites at different successional stages (chronosequence studies) to infer changes through time as a response to restoration (Sayer et al. 2012). In contrast, studies directly examining the consequences of pond restoration for species diversity before and after restoration interventions are rare. Furthermore, past studies reporting positive effects of pond restoration have tended to focus on relatively easily identifiable taxa, such as Odonata and Coleoptera (Raebel et al. 2012; Sayer et al. 2012; Janssen et al. 2018), leaving the possibility of neglecting other taxonomic groups (e.g. Sialidae and Dipterans) that may potentially favor terrestrialized ponds (Biggs et al. 1994).

The Chironomidae (Order: Diptera, “non-biting midges”) have been widely ignored in pond conservation and restoration studies. With 608 species listed for Britain and Ireland by Langton and Pinder (2007) and with at least an additional 30 species reported since their publication, the Chironomidae are an extremely species-rich family. Indeed, their known species richness represents a larger pool than that of all known non-dipteran aquatic macroinvertebrate species in Britain and Ireland combined. Chironomids form an integral part of aquatic food webs, mediating energy transfer from bacteria and decomposing organic matter to fish and birds (Tokeshi 1995; Lewis-Phillips et al. 2020). Among aquatic insects, only chironomid species and a few notonectid bugs possess hemoglobin. Hemoglobin in chironomids has a particularly strong affinity to oxygen, enabling those species that possess it to survive highly anoxic conditions (Cranston 1995). Hemoglobin therefore tends to make chironomids physiologically adapted to poorly aerated, highly organic, or even desiccated habitats. While larvae in the family represent free-living species as well as silk-spinning tube and net builders and miners residing in plant material, including wood, a large proportion of chironomid species are tube-dwelling in soft sediments, in which they undulate their bodies to drive water through the tubes—an activity known to increase with falling oxygen concentrations (Pinder 1995). Chironomid tube-building activity also significantly increases sediment surface area and associated oxygen penetration and uptake (Lock 1994). Hence, many chironomid species might be expected to thrive in tree-covered late-succession ponds characterized by low oxygen levels.

All chironomid species must rise to the water surface in order to eclose (Langton 1995), so that the collection of floating exuviae is a highly representative sampling technique reflecting chironomid emergence. Members of this family have a reputation for being difficult to identify because the aquatic larval stage lacks easily discriminating features. Nonetheless, in the aquatic phase, the final molts of the pupae, the exuviae, can be reliably identified to species. Pupal exuviae furthermore remain afloat for 1–2 days following the emergence of the adult (Wilson & Bright 1973). Exploiting the easy collection and identification of pupal exuviae discarded by emerging adults, the Chironomid Pupal Exuvial Technique (CPET; Wilson & Ruse 2005) allows for reliable ecological assessments (CEN 2006). CPET has been previously used successfully to classify rivers (Wilson & Bright 1973; Wilson 1980), assess and classify the ecological status of lakes (Ruse 2010, 2011), and to characterize gradients of biological structure variation across lotic and lentic habitats in river-floodplain systems (Gandouin et al. 2006).

Here, we employ CPET in an agricultural pondscape located in Norfolk, eastern England, United Kingdom, with the aim of studying the effects of pond restoration by major removal of woody vegetation and pond sediment on chironomid community structure and species richness. We test the following two hypotheses: (1) Due to specific adaptations of chironomid larvae that allow them to cope with low levels of oxygen and the inability of many other invertebrate taxa to do this, chironomids have high species richness in terrestrialized ponds, whereas competitive pressures from other highly diverse macroinvertebrate assemblages in open-canopy ponds may limit chironomid species richness. (2) As a consequence of (1), pond restoration leads to reductions in chironomid species richness in the landscape.

Methods

Pond Location and Sampling Strategy

This study exploits a farmland pond landscape composed of four ponds acting as terrestrialized controls, two ponds acting as open-canopy, macrophyte-dominated controls (hereafter open control ponds), seven ponds that were sampled before and after restoration by major woody vegetation and sediment removal, with an additional two ponds sampled only post-restoration (hereafter restored ponds). All ponds were small (<488 m^2), shallow (<2 m maximum depth), and located within a radius of 1.5 km of Baconsthorpe Castle, near Bodham, Norfolk, eastern England (52°54′N, 1°09′E; Fig. 1). The farm landscape is typical of lowland eastern England, being dominated by arable agriculture, interspersed by small patches of deciduous woodland and grassland used for cattle grazing, with fields mostly enclosed by hedgerows. Soils in the region are predominately free-draining, sandy, and slightly acidic (LandIS 2023), and average (1991–2020) monthly temperatures range from 7.4°C in January to 20.8°C in July, with annual precipitation at approximately 640 mm (Met Office 2023). Pond restorations were undertaken by the Norfolk Ponds Project partnership (Sayer & Greaves 2020), with two of the study ponds restored in 2011 (SABA and MYST) and five restored in 2018 (NROAD, CHFA2, CHFA3, SKYLA, and BAWO2), while the two remaining restored ponds (BECK and SHOOT) that both lacked

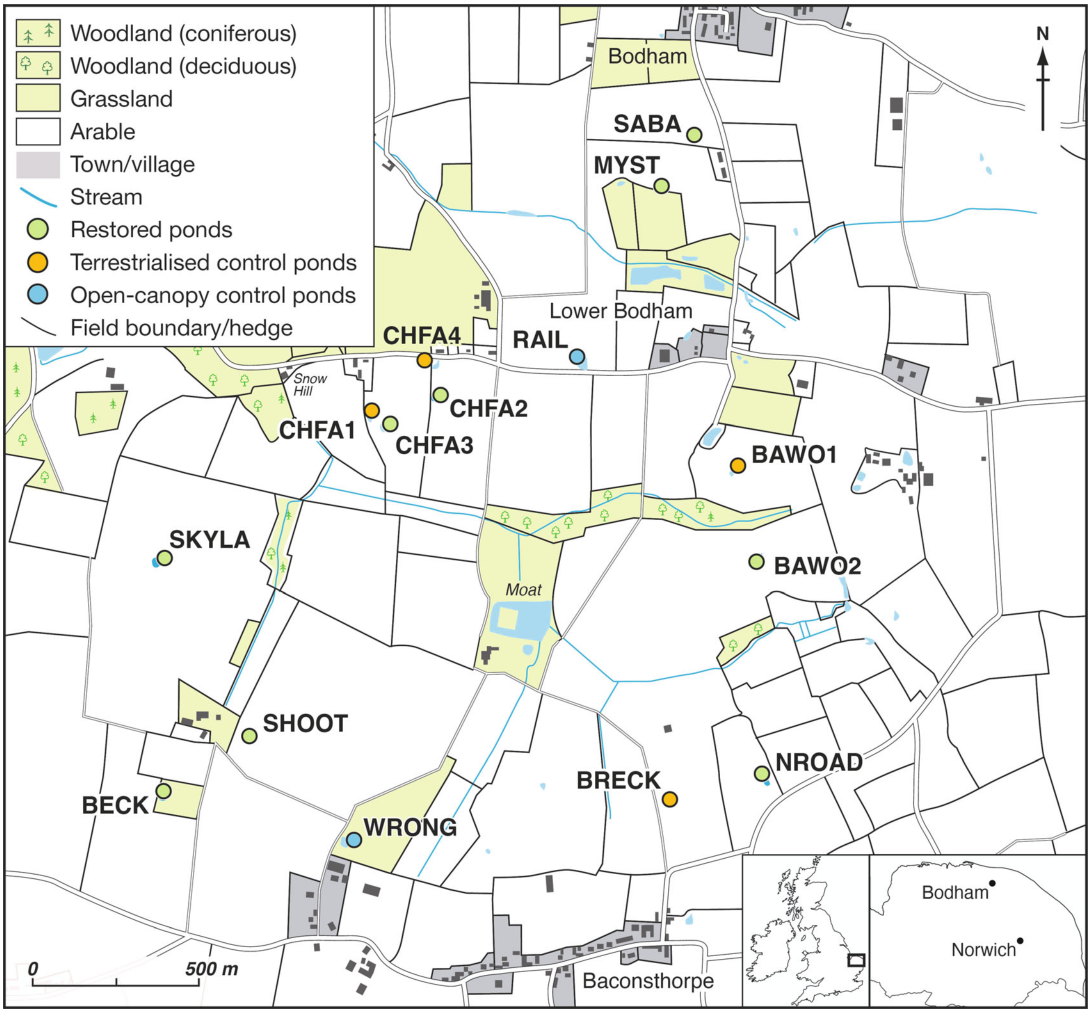

Figure 1. Map of the study area showing the location of terrestrialized control ponds, open-canopy control ponds, and ponds restored from a terrestrialized to an open state within the Bodham-Baconsthorpe restored pond landscape, North Norfolk, eastern England (note that no pre-restoration data was available for BECK and SHOOT).

pre-restoration sampling were restored in 2014. Pond restorations (Fig. 2A & 2B) were undertaken between the months of September and November (Table 1). Chironomid sampling spanned 2010–2021, with sampling periods for each pond given in Table 1. The sampling aimed to cover inter-annual variability in chironomid communities and emergences, with MYST and SABA sampled on nine occasions before restoration and 11 times after restoration, and the five remaining restored ponds with available pre-restoration data sampled on three occasions before restoration and four following restoration. The two remaining restored ponds (BECK and SHOOT) were sampled seven times, and the open control ponds five (WRONG) and 20 times (RAIL), respectively. The terrestrialized control ponds CHFA1, CHFA4, BAWO1, and BRECK were all sampled 6 times, but each pond was dry on one sampling occasion in late summer.

Floating chironomid pupal skins were collected with a 0.25 mm mesh pond net from all accessible parts of each pond (Fig. 2C). Pupal skins can remain afloat for 1–2 days and accumulate at the downwind side of waterbodies. Shoreline water surface-skimming of pupal skins is hence generally representative of all parts of a waterbody. To account for changes in wind direction prior to sampling, as well as the sheltered nature of small ponds, exuviae were collected with a 0.25 mm mesh net, supported by an extendable pole (Fig. 2C), from all accessible bankside areas of each pond. Sampling was not timed but continued until all areas were deemed sufficiently sampled. Where possible, the netted sample was sieved on site to facilitate transport in a 150 mL plastic jar. Removal of bulky material was achieved by passing the sample through 4 and 0.25 mm mesh sieves, with the residue of the coarse sieve refloated and passed again through the sieve stack before repeating at least once more. All chironomid pupal skins were then sorted and identified, wherever possible, to species level in the laboratory with reference to Langton and Visser (2003).

Figure 2. Overgrown control pond BAWO1 (A), restored pond CHFA2 3 years after restoration by major woody vegetation and sediment removal (B) and the lead author (LR) undertaking sampling of floating pupal chironomid exuviae in an open-canopy, macrophyte-dominated pond with a long-handled net (C).

Table 1. Study ponds with details on Chironomid Pupal Exuvial Technique (CPET) sampling period, pond category, restoration year (where appropriate), and surrounding habitat. OCC, open-canopy control pond; R, restored pond; TC, terrestrialized control pond. Note that ponds BECK and SHOOT (OCC) were restored to open-canopy conditions in 2014, but were not sampled for chironomids prior to restoration. Ponds RAIL and WRONG were not subjected to restoration and were pre-existing open-canopy ponds. A, arable; M, meadow; W, near woodland.

Pond code	*Sample period (M/Y)*	*Pond category and restoration year*	*Surrounding habitat*	*Terrestrialized pond*	*Open-canopy pond*
CHFA2	6/2016–5/2021	R 2017	A	x	x
CHFA3	6/2016–5/2021	R 2017	A	x	x
BAW02	6/2016–5/2021	R 2017	A	x	x
NROAD	6/2016–5/2021	R 2017	A	x	x
SKYLA	6/2016–5/2021	R 2017	A	x	x
MYST	5/2010–5/2015	R 2011	A	x	x
SABA	5/2010–5/2015	R 2011	A	x	x
BECK	6/2016–5/2021	R 2014	M	—	x
SHOOT	6/2016–5/2021	R 2014	A	—	x
CHFA1	6/2016–5/2021	TC	A	x	—
CHFA4	6/2016–5/2021	TC	A	x	—
BAWO1	6/2016–5/2021	TC	A/W	x	—
BRECK	6/2016–5/2021	TC	A	x	—
WRONG	4/2017–5/2021	OCC	M	—	x
RAIL	5/2010–5/2015	OCC	A	—	x

Data Analysis

Comparisons were made of chironomid richness and distribution across four different pond categories: terrestrialized control ponds, restored ponds pre-restoration, restored ponds (ponds restored to open-canopy conditions), and the other open-canopy ponds in the landscape (open control ponds). For individual ponds sampled before and after restoration, species counts were amalgamated into pre- and post-restoration totals. Species counts for terrestrialized ponds that were not restored during this study were amalgamated for each pond, respectively. As a high number of species were represented by one or a few skins only in our samples, these samples were considered to be highly incomplete. To account for this issue, we used "Total Expected Species" (TES) numbers (Zou et al. 2023) in addition to the observed species richness to estimate the total number of chironomid species likely to occur in a complete sample from the respective ponds and pond treatments. TES uses asymptotic parametric approximation models for individual-based rarefaction, offering a robust estimate of species richness in communities with partial sampling (Zou et al. 2023). Both observed and estimated species richness values for the different treatments (terrestrialized, restored, and open-canopy controls) were then used in an Analysis of Variance (ANOVA) to test for significant between-treatment differences (at $p < 0.05$).

We finally used the Chord-Normalized Expected Species Shared (CNESS)-measure to calculate the dissimilarity in chironomid assemblages between ponds. CNESS has been developed specifically to estimate similarity between incompletely sampled assemblages (Zou & Axmacher 2020). Two different rarefied sample sizes, represented by m values in CNESS, were selected for analysis: $m = 1$, which focuses on compositional dissimilarity for dominant species, and $m = 36$ (as the second lowest sample size of all sites) that focuses more strongly on dissimilarities in overall assemblage composition. Nonmetric multi-dimensional scaling (NMDS) was then used to visualize the CNESS dissimilarity matrix as an unconstrained ordination. The TES richness was calculated by the R functions "TES()" (Zou et al. 2023). The CNESS dissimilarity matrix was calculated using the function "ESS()" from Zou and Axmacher (2020), and the NMDS ordination was conducted using the "vegan" package (Oksanen et al. 2018). ANOVA and post hoc tests were undertaken using SPSS 27. Our sampling design overall followed the Before-After-Control-Impact (BACI) approach, with controls both of the pre-restoration (terrestrialized) and open-canopy pond stages, and with the majority of restored ponds sampled both before and after restoration.

Results

Of the 123 chironomid species identified from the 15 study ponds (Table S1), 9 species were exclusively recorded at terrestrialized ponds. In contrast, 56 chironomid species were exclusively recorded at ponds restored to an open-canopy state, 5 from the open control ponds, with a further 20 species found in both open control and restored ponds. This means that, in total, 81 species (71.5%) were only recorded from open-canopy ponds. The remaining 33 species were found in both terrestrialized and open ponds. One species, *Glyptotendipes caulicola* (Kieffer), collected exclusively from restored pond CHFA2 following its restoration, has not previously been recorded in the British Isles. This species is morphologically very similar to *G. foliicola* Kieffer as found in restored ponds BECK, SHOOT, and SKYLA. The adult syntype series of *G. caulicola*, held at the Zoologische Staatssammlung München (ZSM) in Germany, was collected by Kieffer from material derived from several populations. Additionally, a Diptera specialist at the ZSM alerted us to the possibility that the syntype comprises more than one species (M. Spies, 2023, ZSM personal communication). The situation with *G. foliicola* Kieffer is even more confusing, as almost none of the numerous applications of this name were derived from appropriate original sources, as indicated by Spies and Sæther (2004). In this paper, the two species have been identified on the basis of pupal exuviae descriptions sensu Langton and Visser (2003).

The number of observed species, as well as the TES number in ponds following restoration, greatly exceeded that observed at the same ponds before restoration (Fig. 3). This pattern was further consolidated by the terrestrialized control pond records and the open-canopy controls, with observed and expected species richness also significantly higher in the latter pond category.

The unconstrained ordination plots, based on an NMDS of CNESS for $m = 1$ (Fig. 4A) and $m = 36$ (Fig. 4B), reflected a differentiation of the terrestrialized ponds from both the restored ponds and the open-canopy control ponds. The latter two groups formed a loose cluster, with open-canopy control ponds not strongly differentiated from the restored ponds in relation to chironomid community composition (Fig. 4B). When focusing on dominant species (Fig. 4A), the differentiation between the different pond categories was less strict, with some of the restored ponds dominated by the same species also dominant in the overgrown ponds. In both ordination plots, open-canopy control

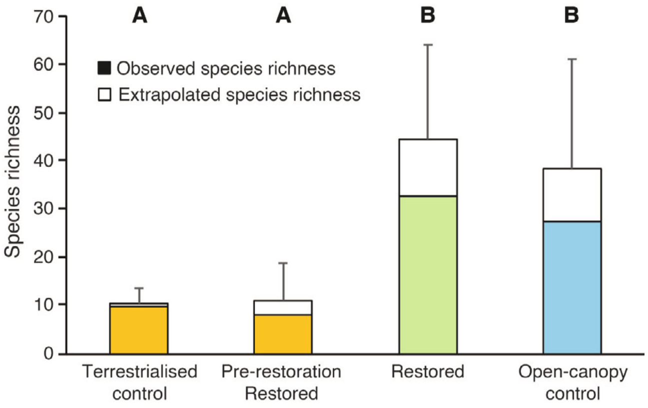

Figure 3. Mean observed (solid) and estimated (white, with error bars representing standard deviation) chironomid species richness per pond at terrestrialized control ponds (terrestrialized control), restored ponds sampled in the terrestrialized state before restoration (pre-restoration), restored ponds following restoration (restored) and open-canopy control ponds (open Control). The different letters (A, B) indicate significant ($p < 0.05$) differences in diversity for both observed and estimated species richness between chironomid assemblages of the respective pond treatments, while error bars represent ± SD for the extrapolated species richness measures.

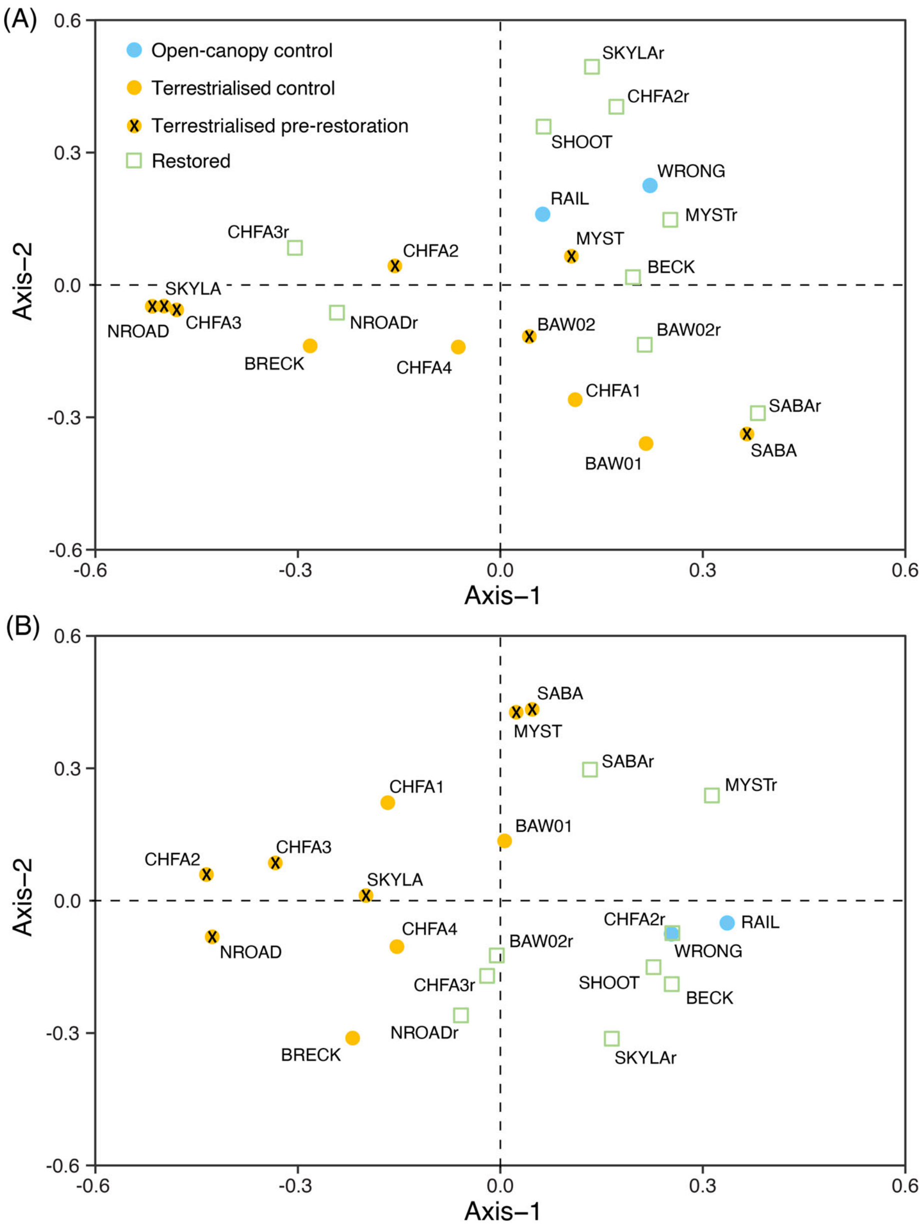

Figure 4. NMDS ordination plots for chironomid assemblages in the study ponds, based on a CNESS dissimilarity matrix (see text) for $m = 1$ (A), emphasizing similarity in dominant species, and $m = 36$ (B) showing similarity in overall species composition. Orange circles represent terrestrialized ponds (including overgrown control ponds and open-canopy restored ponds before restoration, with the latter marked with a black X), open green squares represent open-canopy restored ponds (denoted also by a small r at the end of the pond code where pre-restoration data exists) and blue circles represent open-canopy control ponds.

ponds showed a strong similarity in assemblage structure, while terrestrialized ponds were characterized by substantial inter-pond variation in species assembly both in terms of dominant species and overall species composition.

Discussion

The notable increase in actual and estimated chironomid species numbers in the restored farmland ponds, and the higher number of species found in the open-canopy control ponds compared to terrestrialized farmland ponds dominated by woody vegetation, contradicts our first hypothesis that chironomid species diversity might be reduced in open-canopy macrophyte-filled ponds. Instead, the chironomid diversity response aligns with patterns observed for other aquatic invertebrate taxa (Odonata, Trichoptera, Coleoptera, and Mollusca) that have shown much higher diversity in early succession ponds with abundant aquatic plants compared to highly shaded, late-succession ponds with sparse macrophyte cover (Hassall et al. 2011; Raebel et al. 2012; Janssen et al. 2018), a pattern similarly demonstrated for ponds within our wider study area (Sayer et al. 2012). Thus, at least in farmland ponds, and despite the ability of many chironomid larvae to cope with extremely low oxygen levels in the water bodies, chironomids do not exhibit a positive diversity response to pond terrestrialization. Instead, most chironomid species appear to thrive in macrophyte-filled, open-canopy ponds with low shading—a situation that quickly arises in formerly terrestrialized ponds following restoration (Sayer et al. 2022). While a small number of chironomid species were exclusively recorded from the terrestrialized ponds in this study ($n = 9$), many more were uniquely encountered in the open-canopy, macrophyte-dominated pond condition ($n = 81$). Our second hypothesis that pond restoration results in a reduction of chironomid species richness in the landscape can therefore also be rejected. The mechanisms that favor enhanced chironomid richness in restored, macrophyte-filled ponds compared to heavily wooded terrestrialized ponds are obscure, as it was not possible to undertake a detailed characterization of water chemistry and hydrological fluctuation in this study. Nonetheless, it can be speculated that improved habitat structure (plants), increased oxygenation, and changes to hydrological regimes (with ponds becoming more permanent following the removal of trees) are key. Further research is required to more clearly identify direct drivers of the observed chironomid species richness increases.

To help infer patterns in chironomid composition across the studied terrestrialized and open-canopy study ponds, as well as changes in community assembly before and after restoration, it is instructive to consider available knowledge of chironomid ecology, although this is relatively scarce, especially for pond communities. Generally, Céréghino et al. (2008) found that differences in aquatic vegetation structure and age between ponds played an important role in selecting for invertebrate species traits related to population dynamics and feeding habits. For a set of shallow eastern English lakes, Langdon et al. (2010) showed that aquatic macrophyte density and, importantly, their species richness were primary controls on chironomid community distribution in surface sediment samples. In palaeoecological studies of both Danish (Brodersen et al. 2002) and English (Davidson et al. 2013) shallow lakes subject to eutrophication, sub-fossil chironomid assemblages have been found to again strongly co-vary with changes in macrophyte abundance and structure as inferred from plant macro-remains. If we apply this knowledge gained from lakes, it might hence be expected that aquatic vegetation represents a key driver of chironomid composition in our study ponds and, in turn, a major influence over community changes through time.

Of the nine species uniquely found in terrestrialized ponds, *Chironomus lacunarius* was only found at terrestrialized control pond BAWO1 and in pond BAWO2 before restoration. As this species has previously been associated with alpine and upland lakes (Langton & Visser 2003; Moller Pillot 2009), its occurrence in ponds in this lowland study region extends our knowledge of its environmental preferences. Two other species only found in terrestrialized pond SKYLA were not recorded from this pond after its restoration. One of these is the deposit feeder/scraper *C. anthracinus*, which is tolerant of prolonged anoxia and requires thick sediments for tube burrows (Pinder 1995; Moller Pillot 2009). The apparent loss of *C. anthracinus* might therefore be linked to the extensive sediment removal that was undertaken during the restoration of SKYLA, resulting in a loss of appropriate habitat. The second species, *Neozavrelia* Pe1 (either *Neozavrelia fuldensis* or *N. luteola*, their exuviae cannot be separated), is a periphyton grazer found previously in five upland lakes in Wales and Scotland, and in an English Midlands lake by Ruse (2011). As a grazer, this species might have been expected to thrive in the macrophyte-dominated conditions prevalent in SKYLA following its restoration, and its absence from post-restoration samples is hard to explain.

Expected early returners (within 4 months as in Ruse 2002) to ponds subject to restoration were the multivoltine *Psectrocladius limbatellus*, *Acricotopus lucens*, and *C. riparius*. These are known rapid colonizers of muddy habitats, as is the parthenogenetic detritivore/algal-feeding *Paratanytarsus laccophilus* (Langton 1995). First-time colonizers of the restored ponds also included *Tanypus kraatzi*, an algal/detritus feeder, which can turn to carnivory when early instars of chironomid larvae from other species become available (Vallenduuk & Moller Pillot 2007). Further, post-restoration mud-dwelling detritophages and possible microcarnivores were *Cladopelma viridulum* and *Micropsectra junci*. Predatory colonizers included the organic silt-dwelling final instar of *Psectrotanypus varius* (common to most ponds) and later instars of *Procladius choreus*, *P. sagittalis*, *Cryptochironomus obreptans*, and *Harnischia curtilamellata*, as well as the facultative predator *Parachironomus arcuatus*—species all exclusively recorded at open-canopy, macrophyte-dominated ponds. Predatory chironomids likely have an advantage in freshly excavated, standing water bodies that are devoid of fish and macrophyte stands due to low top-down predation pressure and ease of hunting in a structureless habitat (Ruse 2002). New colonizers of restored ponds also included species intolerant of pond drying and consequent desiccation, such as the predatory *Ablabesmyia longistyla*, the grazer *Polypedilum nubens*, as well as *Corynoneura gratias*, an algal/detritus feeder associated with aquatic macrophytes.

The importance of macrophyte habitat is clearly key to explaining the 81 chironomid species unique to open-canopy ponds (combining open control and restored ponds) in our study area. Extensive emergent, floating, and submerged vegetation communities develop rapidly (6 months to 1 year) following the restoration of terrestrialized ponds (Sayer et al. 2022) and provide complex structures for invertebrates to live in. When submerged and floating plants colonized the study ponds (after around 8 months), chironomid species that mine leaves and stems such as *Endochironomus albipennis* started to occur. Other open-pond leaf-mining colonizers, *E. tendens* (intolerant of low oxygenation and drying out) as well as *Glyptotendipes foliicola*, *G. caulicola*, *G. cauliginellus*, and *G. scirpi* also arrived. These species spin silk nets at constructed tunnel entrances to collect suspended algae and are commonly associated with the floating-leaved plant *Potamogeton natans*, which quickly became abundant at many study ponds following restoration in less than 1 year.

Other plant-feeding, shredder species found exclusively in the open-canopy study ponds included *Monopelopia* *tenuicalcar* and *Cricotopus ornatus*. Diatoms and detritus attached to stem and leaf surfaces of aquatic macrophytes appear to have attracted a further, diverse range of grazing chironomid species, including *Xenopelopia falcigera*, *Psectrocladius obvius*, *G. barbipes* (also a filterer), *Tanytarsus mancospinosus*, *T. medius*, and *T. niger*. Colonization by bryozoans on hard surfaces such as plants then appears to have attracted the chironomid *Parachironomus frequens*, which strongly depends on them (Moller Pillot 2009). This species was only recorded at restored open-canopy control pond SHOOT. *Dicrotendipes lobiger* has similarly been associated with bryozoans and was found in all but one of the open-canopy ponds. When a restored pond is colonized by snails, it can start to support populations of the parasitic *P. mauricii*; this species colonized restored pond SABA 12 months after restoration. Young larvae in this species enter a snail's shell and feed on its body fluid. The prepupa then leaves the host before pupation, so it can eclose at the water surface.

Some three chironomid species were restricted to open-canopy control pond RAIL. This pond possesses dense beds of aquatic plants, and evidence from sediment core macrofossil analysis suggests that this has been so for at least two centuries (Emson 2015). In keeping with centuries of macrophyte cover stability in RAIL, the tanypod *Guttipelopia guttipennis* is strongly associated with aquatic vegetation and with long-established waterbodies (Vallenduuk & Moller Pillot 2007). The large thoracic horns of the pupa from this species make it buoyant and vulnerable to predation at the surface, so it clings to submerged vegetation with strong finger-like thoracic combs (Langton 1995). This species might be expected to appear in the recently restored ponds in the study area as they mature. The orthoclad *Psectrocladius brehmi*, which was also unique to RAIL, is found creeping on leaf blades. It is rare and was only found in four upland tarns among 240 U.K. lakes surveyed by Ruse (2011). It is clear, therefore, that long-established plant-dominated ponds (due to frequent management or the chance of absence of invading wet-loving shrubs and trees) may be important for enhancing chironomid diversity in the landscape.

Chironomids form an important component of aquatic ecosystems, having a significant impact on water chemistry at the sediment/water interface through bioturbation, particularly in shallow waterbodies (Benelli et al. 2018). They are critical to ecological functioning and food webs in both aquatic and terrestrial ecosystems, providing an important link between primary producers and secondary consumers (Tokeshi 1995). In this respect, studies have shown that chironomids are an important food source for farmland birds (Lewis-Phillips et al. 2020), as well as bats (Vaughan 1997; Vesterinen et al. 2020), both of which are in decline on a global scale, with declines in insect prey considered causal (Inger et al. 2015; Vesterinen et al. 2020). Given their exceptional ecological diversity and occurrence across the full array of wetland habitats and their key functional role, chironomids clearly afford great potential for detecting and monitoring ecological change, including in ponds. Chironomids are, however, widely absent in aquatic conservation discourses. In the future, it is hence entirely appropriate to consider how best to conserve and enhance chironomid communities and populations in farm pond landscapes, as studied here.

Inevitably, in the absence of natural disturbance and/or management intervention (e.g. grazing and scrub removal), farm ponds become heavily overgrown by trees and bushes after a few decades (Sayer et al. 2013). It is clear from this study that very few chironomid species prefer the resulting semi-terrestrial conditions, while the opening up of terrestrialized ponds through pond restoration dramatically increases chironomid diversity, leading to colonization by species currently considered rare in the United Kingdom. While the benefits of pond restoration to chironomid communities are clear, some species were apparently lost from the terrestrialized ponds post-restoration. Given this pattern, it seems sensible that landscape-scale pond restoration plans should retain a number of ponds in a late-succession state. Such an approach has recently been advocated for other species groups associated with farmland ponds, spanning freshwater invertebrates (Hassall et al. 2012; Sayer et al. 2012), pollinating insects (Walton et al. 2021a) and farmland birds (Lewis-Phillips et al. 2019a, 2019b). In our view, landscape-scale pond conservation should hence seek to use restoration and subsequent woody vegetation management to maintain a mosaic of ponds in different stages of succession, from recently excavated open-canopy ponds to mature and semi- and fully terrestrialized ponds, but with a clear dominance of early successional ponds. We emphasize the key importance of pond restoration for chironomid conservation in farmland pond landscapes.

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LITERATURE CITED

Alderton E, Sayer CD, Davies R, Lambert SJ, Axmacher JC (2017) Buried alive: aquatic plants survive in 'ghost ponds' under agricultural fields. Biological Conservation 212:105–110. https://doi.org/10.1016/j.biocon.2017.06.004

Arntzen JW, Abrahams C, Meilink WRM, Losif R, Zuiderwijk A (2017) Amphibian decline, pond loss and reduced population connectivity under agricultural intensification over a 38 year period. Biodiversity and Conservation 26:1411–1430. https://doi.org/10.1007/s10531-017-1307-y

Benelli S, Bartoli M, Zilius M, Vybernaite-Lubiene I, Ruginis T, Petkuviene J, Fano EA (2018) Microphytobenthos and chironomid larvae attenuate nutrient recycling in shallow-water sediments. Freshwater Biology 63:187–201. https://doi.org/10.1111/fwb.13052

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

Brodersen KP, Odgaard BV, Vestergaard O, Anderson NJ (2002) Chironomid stratigraphy in the shallow and eutrophic lake Sobygaard, Denmark: chironomid-macrophyte co-occurrence. Freshwater Biology 46:253–267. https://doi.org/10.1046/j.1365-2427.2001.00652.x

Céréghino R, Ruggiero A, Marty P, Angélibert S (2008) Influence of vegetation cover on the biological traits of pond invertebrate communities. Annales de Limnologie 44:267–274. https://doi.org/10.1051/limn:2008010

Comité Européen de Normalisation (CEN) (2006) Water quality – guidance on sampling and processing of the pupal exuviae of Chironomidae for ecological assessment. European Committee for Standardization, Standard EN15196, Brussels, Belgium.

Cranston PS (1995) Introduction. In: Armitage PD, Cranston PS, Pinder LCV (eds) The Chironomidae. Chapman and Hall, London, United Kingdom. https://doi.org/10.1007/978-94-011-0715-0_1

Curado N, Hartel T, Arntzen JW (2011) Amphibian pond loss as a function of landscape change – a case study over three decades in an agricultural area of northern France. Biological Conservation 144:1610–1618. https://doi.org/10.1016/j.biocon.2011.02.011

Davidson TA, Reid MA, Sayer CD, Chilcott S (2013) Palaeolimnological records of shallow lake biodiversity change: exploring the merits of single versus multi-proxy approaches. Journal of Paleolimnology 49:431–446. https://doi.org/10.1007/s10933-013-9696-8

Davies SR, Sayer CD, Greaves H, Siriwardena GM, Axmacher JC (2016) A new role for pond management in farmland bird conservation. Agriculture, Ecosystems and Environment 233:179–191. https://doi.org/10.1016/j.agee.2016.09.005

Emson D (2015) The ecology and palaeoecology of diatom-duckweed relationships. Doctoral dissertation. University College London, London, United Kindom. https://discovery.ucl.ac.uk/id/eprint/1462713/

Ferreira M, Beja P (2013) Mediterranean amphibians and the loss of temporary ponds: are there alternative breeding habitats. Biological Conservation 165:179–186. https://doi.org/10.1016/j.biocon.2013.05.029

Gandouin E, Maasri A, Van Vliet-Lanoe B, Franquet E (2006) Chironomid (Insecta: Diptera) assemblages from a gradient of lotic and lentic waterbodies in river floodplains of France: a methodological tool for paleoecological applications. Journal of Paleolimnology 35:149–166. https://doi.org/10.1007/s10933-005-8149-4

Gioria M, Schaffers A, Bacaro G, Feehan J (2010) The conservation of farmland ponds: predicting water beetle assemblages using vascular plants as a surrogate group. Biological Conservation 143:1125–1133

Hassall C, Hollinshead J, Hull A (2011) Environmental correlates of plant and invertebrate species richness in ponds. Biodiversity and 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 and Conservation 21:829–852. https://doi.org/10.1007/s10531-011-0223-9

Inger R, Gregory R, Duffy JP, Stott I, Voříšek P, Gaston KJ (2015) Common European birds are declining rapidly while less abundant species' numbers are rising. Ecology Letters 18:28–36. https://doi.org/10.1111/ele.12387

Janssen A, Hunger H, Konold W, Pufal G, Staab M (2018) Simple pond restoration measures increase dragonfly (Insecta: Odonata) diversity. Biodiversity and Conservation 27:2311–2328. https://doi.org/10.1007/s10531-018-1539-5

LandIS (2023) Soilscapes viewer. https://www.landis.org.uk/soilscapes/ (accessed 31 Jan 2024)

Langdon PG, Ruiz Z, Wynne S, Sayer CD, Davidson TA (2010) Ecological influences on larval chironomid communities in shallow lakes: implications for palaeolimnological interpretations. Freshwater Biology 55:531–545. https://doi.org/10.1111/j.1365-2427.2009.02345.x

Langton PH (1995) The pupa and events leading to eclosion. Pages 169–193. In: Armitage PD, Cranston PS, Pinder LCV (eds) The Chironomidae. Chapman and Hall, London, United Kingdom

Langton PH, Pinder LCV (2007) Keys to the adult male Chironomidae of Britain and Ireland. Freshwater Biological Association Scientific Publication no. 64. Vol 1. Freshwater Biological Association, Ambleside, UK.

Langton PH, Visser H (2003) Chironomid exuviae. A key to pupal exuviae of the west Palaearctic region. University of Amsterdam, Amsterdam, the Netherlands https://chironomidae-exuviae.linnaeus.naturalis.nl/linnaeus_ng/app/views/key/?epi=77 (accessed 5 Sep 2024)

Lewis-Phillips J, Brooks S, Sayer CD, McCrea R, Siriwardena G, Axmacher JC (2019*a*) Pond management enhances 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

Lewis-Phillips J, Brooks SJ, Sayer CD, McCrea R, Siriwardena G, Robson H, Harrison A, Axmacher JC (2019*b*) Seasonal benefits of farmland pond management for birds. Bird Study 66:342–352. https://doi.org/10.1080/00063657.2019.1688762

Lewis-Phillips J, Brooks SJ, Sayer CD, Patmore IR, Hilton G, Harrison A, Robson H, Axmacher JC (2020) Ponds as insect chimneys: restoring overgrown farmland ponds benefits birds through elevated productivity of emerging aquatic insects. Biological Conservation 241:108–253. https://doi.org/10.1016/j.biocon.2019.108253

Lock MA (1994) Dynamics of particulate and dissolved inorganic matter over the substratum of water bodies: bioturbation. Pages 137–160. In: Wotton RS (ed) The biology of particles in aquatic systems. 2nd edition. CRC Press, Boca Raton, Florida

Met Office (2023) Location-specific long-term averages. https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/u12v1xhdm (accessed 11 Apr 2024)

Moller Pillot HKM (2009) Chironomidae larvae: biology and ecology of the Chironomini. KNNV Publishing, Zeist, the Netherlands

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. (2018) vegan: community ecology package. R package version 2.5-6. http://CRAN.R-project.org/package=vegan (accessed 10 Aug 2023)

Pinder LCV (1995) The habitats of chironomid larvae. Pages 107–135. In: Armitage PD, Cranston PS, Pinder LCV (eds) The Chironomidae. Chapman and Hall, London, United Kingdom

Raebel EM, Merckx T, Feber RE, Riordan P, MacDonald DW, Thompson DJ (2012) Identifying high-quality pond habitats for Odonata in lowland England: implications for agri-environment schemes. Insect Conservation and Diversity 5:422–432. https://doi.org/10.1111/j.1752-4598.2011.00178.x

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

Ruse LP (2002) Colonisation of gravel lakes by Chironomidae. Archiv für Hydrobiologie 153:391–407. https://doi.org/10.1127/archiv-hydrobiol/153/2002/391

Ruse LP (2010) Classification of nutrient impact on lakes using the chironomid pupal exuvial technique. Ecological Indicators 10:594–601. https://doi.org/10.1016/j.ecolind.2009.10.002

Ruse LP (2011) Lake acidification assessed using chironomid pupal exuviae. Fundamental and Applied Limnology 178:267–286. https://doi.org/10.1127/1863-9135/2011/0178-0267

Sayer CD, Andrews K, Shilland E, Edmonds N, Edmonds-Brown R, Patmore IR, Emson D, Axmacher JC (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, Burningham H, Alderton E, Axmacher JC, Robinson P, Greaves H, Hind A (2023) Bringing lost ponds back to life: the art of ghost pond resurrection. Conservation Land Management 21:25–31

Sayer CD, Greaves H (2020) Making an impact on UK farmland pond conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 30:1821–1828. https://doi.org/10.1002/aqc.3375

Sayer CD, Hawkins J, Greaves H (2022) Restoring the ghostly and the ghastly: a new golden age for British lowland farm ponds? British Wildlife 33:477–487

Sayer C, Shilland E, Greaves H, Dawson B, Patmore I, Emson D, et al. (2013) Managing Britain's ponds – conservation lessons from a Norfolk farm. British Wildlife 25:21–28

Skelly DK, Bolden SR, Fridenburg LK (2014) Experimental canopy removal enhances diversity of vernal pond amphibians. Ecological Applications 24:340–345. https://doi.org/10.1890/13-1042.1

Smith LP, Clarke LE, Weldon L, Robson HJ (2022) An evidence-based study mapping the decline in freshwater ponds in the Severn Vale catchment in the UK between 1900 and 2019. Hydrobiologia 849:4637–4649. https://doi.org/10.1007/s10750-022-05000-w

Spies M, Sæther OA (2004) Notes and recommendations on taxonomy and nomenclature of Chironomidae. Zootaxa 752:1–90. https://doi.org/10.11646/zootaxa.752.1.1

Tokeshi M (1995) Production ecology. Pages 269–296. In: Armitage PD, Cranston PS, Pinder LCV (eds) The Chironomidae. Chapman and Hall, London, United Kingdom

Vallenduuk HJ, Moller Pillot HKM (2007) Chironomidae larvae: general ecology and Tanypodinae. KNNV Publishing, Zeist, the Netherlands

Vaughan N (1997) The diets of British bats (Chiroptera). Mammal Review 27: 77–94. https://doi.org/10.1111/j.1365-2907.1997.tb00373.x

Vesterinen EJ, Kaunisto KM, Liley TM (2020) A global class reunion with multiple groups feasting on the declining insect smorgasbord. Scientific Reports 10: 16595. https://doi.org/10.1038/s41598-020-73609-9

Walton RE, Sayer CD, Bennion H, Axmacher JC (2021*a*) Open-canopy ponds benefit diurnal pollinator communities in an agricultural landscape: implications for farmland pond management. Insect Conservation and Diversity 14:307–324. https://doi.org/10.1111/icad.12452

Walton RE, Sayer CD, Bennion H, Axmacher JC (2021*b*) Improving the pollinator pantry: restoration and management of open farmland ponds enhances the complexity of plant-pollinator networks. Agriculture, Ecosystems and Environment 320:107611. https://doi.org/10.1016/j.agee.2021.107611

Wilson RS (1980) Classifying rivers using Chironomid pupal exuviae. Pages 209–216. In: Murray DA (ed) Chironomidae ecology, systematics, cytology and physology. Pergamon Press, Oxford, United Kingdom

Wilson RS, Bright PL (1973) The use of chironomid pupal exuviae for characterizing streams. Freshwater Biology 3:283–302. https://doi.org/10.1111/j.1365-2427.1973.tb00923.x

Wilson RS, Ruse LP (2005) Guide to the identification of genera of Chironomid pupal exuviae occurring in Britain and Ireland and their use in monitoring lotic and lentic freshwaters. Freshwater Biological Association Special Publication. Vol 13. Freshwater Biological Association, Ambleside, UK.

Zou Y, Axmacher JC (2020) The Chord-normalized expected species shared (CNESS)-distance represents a superior measure of species turnover patterns. Methods in Ecology and Evolution 11:273–280. https://doi.org/10.1111/2041-210X.13333

Zou Y, Zhao P, Axmacher JC (2023) Estimating total species richness: fitting rarefaction by asymptotic approximation. Ecosphere 14:e4363. https://doi.org/10.1002/ecs2.4363

Supporting Information

The following information may be found in the online version of this article:

Table S1. Total species counts (names sensu Langton & Visser 2003)—restored pond names with suffix “r.”

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