



PRACTICAL ARTICLE

Once a pond in time: employing palaeoecology to inform farmland pond restoration

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The restoration of highly terrestrialized farmland ponds that combines the removal of woody vegetation and pond sediment greatly enhances aquatic biodiversity. Nonetheless, questions remain regarding the historical precedent of pond restoration, and particularly if post-restoration aquatic macrophyte communities resemble pre-terrestrialization assemblages. We used a paleoecological approach to address these questions for a typical, recently restored farmland pond in Norfolk, eastern England. Plant and animal remains in pond sediment cores were used to infer decadal-centennial scale changes to pond communities and to identify past pond management events. We then evaluated the resemblance of restored and historical assemblages by comparisons with contemporary post-restoration vegetation data. Based on changes in the abundance of terrestrial leaf remains and other indicators (increases followed by declines of aquatic organisms), the study pond appears to have a long history (going back to the early-1800s) of canopy management (at least three inferred management events), but after the mid-1970s, steady and substantial increases in terrestrial indicators suggest cessation of management resulting in uninterrupted terrestrialization. Aquatic macrophyte communities arising after restoration showed some similarities with historical assemblages, but also contained apparently new species. This study demonstrates how paleolimnological methods can improve understanding of pond ecological histories to better inform restoration targets and practices.

Key words: agriculture, ecological succession, freshwater conservation, macrofossils, paleolimnology

Implications for Practice

- Paleolimnological methods can be successfully employed at small, human-made ponds to assess past biological communities and trajectories of ecological change.
- Restoration of heavily terrestrialized farmland ponds through major woody vegetation and sediment removal mimics periodic management activities undertaken over past centuries and is essential to the maintenance of open canopy conditions and biodiversity conservation.
- Caution must be taken when setting restoration targets for farmland ponds as rare macrophyte species indicative of high water quality may not necessarily return to restored pond habitats due to fragmentation effects associated with the loss of local populations and/or in-pond eutrophication development.

species-poor matrix (Davies et al. 2008), despite their small spatial footprint (Biggs et al. 1994).

As a consequence of agricultural intensification and associated land consolidation, since the 1940s–1950s many farmland ponds have been lost to in-filling (Pienkowski 2003; Alderton et al. 2017), while the landscape surrounding remaining ponds has changed dramatically due to, among other changes, increases in field sizes (Robinson & Sutherland 2002), hedgerow destruction (Baudry et al. 2000), and a general fragmentation of semi-natural habitats (Tscharntke et al. 2005). Additionally, modern agricultural intensification has seen increased use of agro-chemicals and together these landscape-scale changes have negatively affected agricultural

Introduction

Ponds have been a widespread component of United Kingdom and European lowland agricultural landscapes for centuries (Rackham 1986; Céréghino et al. 2008). Largely of anthropogenic origin (Prince 1964), farmland ponds and their margins act as important semi-natural habitats for aquatic and terrestrial organisms, acting as biodiversity hotspots in an otherwise

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ponds and their communities (Declerck et al. 2006; Williams et al. 2010).

Pond succession leading to terrestrialization represents an additional environmental stressor on farmland pond communities. In the United Kingdom, cessation of traditional pond management practices (combining scrub and sediment removal) and a resulting mass-terrestrialization of ponds since ~1960s–1970s (Sayer et al. 2013) is thought to have resulted in an overwhelming dominance of highly shaded, macrophyte-free, late-successional ponds, with few aquatic macrophyte-dominated, mid- and early-successional ponds remaining (Sayer et al. 2012). This loss of macrophyte-rich ponds and associated structured habitat has in turn resulted in declines across multiple species groups, including invertebrates and amphibians (Sayer et al. 2012; Janssen et al. 2018).

Pond restoration and subsequent management that combines removal of encroaching woody vegetation and pond sediment greatly increases the biodiversity of farmland ponds (Sayer et al. 2012; Janssen et al. 2018). In restoration ecology, success is commonly assessed by comparing post-restoration assemblages with those existing prior to habitat degradation (Sayer et al. 2012). Previous research focused on the resurrection of deliberately infilled farmland "ghost ponds" has revealed long-term seed viability of many macrophyte species in pond sediments (Alderton et al. 2017). This work, in conjunction with observations of rapid macrophyte re-colonization of restored ponds (Sayer et al. 2013; Hawkins 2019), suggests that pond restoration may reestablish components of historic wetland plant communities, but research comparing historical and post-restoration plant assemblages is lacking. Furthermore, although scrub and tree management is thought to have occurred in the past (Boothby & Hull 1997; Upex 2004; Janssen et al. 2018), and has inspired pond restoration activities presently (Sayer et al. 2012, 2013), historical evidence for these activities is at best sparse and anecdotal.

Paleoecology has hitherto rarely been used to establish the past ecological dynamics of small farmland ponds (see Emson et al. 2018). Nonetheless, extensive paleoecological studies of shallow lakes suggest tremendous potential for detecting longterm changes in both aquatic and surrounding terrestrial vegetation (Birks 1973; Madgwick et al. 2011), and for demonstrating the impact of changing agricultural practices (Brush & Hilgartner 2000; Bradshaw et al. 2005) and other land use changes (Tolonen 1978; Riera et al. 2006) on aquatic ecosystems. We address this research gap with a paleoecological study of plant and animal macrofossils for the Bodham Mystery Pit (hereafter Mystery Pit), a typical farmland pond in North Norfolk, eastern England (Fig. 1). Mystery Pit was subjected to restoration by major scrub and sediment removal in 2011. We hypothesized that our study would reveal a history of periodic management events involving woody vegetation removal, followed by a more recent period of steady terrestrialization. Furthermore, we hypothesized that a high proportion of macrophytes found in the sediment record and subsequently lost through terrestrialization would characterize post-restoration pond communities. Our study shows how a





Figure 1. Photographs of the Bodham Mystery Pit in (A) October 2008 when the pond was heavily terrestrialized, and (B) in June 2014, 3 years post-restoration.

paleoecological approach can assist understanding of the need for and success of ecological restoration for farmland ponds.

Methods

Study Site and Sediment Coring

Mystery Pit is a small (535 m²), shallow (mean pre-restoration summer water depth: 135 cm, range: 75–178 cm) "marl-pit" pond located along an old hedgerow in an arable setting in the village of Bodham, North Norfolk. A single sediment core (MYST1) was collected from the pond using an adapted Livingstone coring system (71 mm internal diameter) from a central location (water depth ~107 cm at core site) in November 2011. Given its small size, and as a number of studies of shallow lakes have shown a single core to reliably capture changes in dominant macrophyte species in larger shallow lakes (Davidson et al. 2005; Salgado et al. 2010; Sayer et al. 2010), a single core was deemed sufficient to characterize long-term macrophyte dynamics for the pond. Core MYST1 was 124 cm

long and extruded in the field at 1 cm intervals with the resulting 124 subsamples immediately placed in cold storage.

Analysis of Sediment Subsamples

Core MYST1 was dated using Lead-210 (210 Pb) and Cesium-137 (137 Cs) analysis of 38 sediment subsamples (at 3–4 cm intervals) from along the length of the core using direct gamma assay in the Environmental Radiometric Facility at University College London (UCL), but only 18 subsamples, covering the uppermost 67 cm of the sequence, yielded 210 Pb and 137 Cs results. Dates were calculated using the constant rate of 210 Pb supply (CRS) dating model (Appleby 2001), but below 61–62 cm depth (date: 1867 ± 27 years), sediment ages were extrapolated from the average sedimentation rate of the lowermost three dated sediment samples (at 50–51, 56–57, 61–62 cm) and must therefore be interpreted with caution (Binford 1990).

Macrofossil, Organic Matter, and Carbonate Content Analysis

A total of 34 sediment subsamples from MYST1 were analyzed for macro-remains of aquatic plants, shrubs, trees, and key aquatic animals. A minimum wet sediment volume of 20 cm³, as determined by water displacement (Birks 2001), was gently washed through sieves of 355 and 125 µm, with the retent analyzed for macrofossils under a dissecting microscope at 10-40× magnification. Macrofossils were identified to the lowest achievable taxonomic level using a seed reference collection housed at UCL combined with Schoch et al. (1988) and Cappers et al. (2012). Leaf fragments of fine-leaved Potamogeton species probably representing either Potamogeton pusillus L. or Potamogeton berchtoldii Fieb. were aggregated as "fine-leaved Potamogeton spp." Animal remains were limited to mollusk fragments, cladoceran ephippia, trichopteran case fragments. and scale fragments from fish. Identified taxa were expressed as numbers per 100 cm³ wet sediment (Birks 2001). Organic matter and carbonate content of core samples were estimated using the loss-on-ignition procedure (Heiri et al. 2001).

Data Analysis

Plant macro-remains were grouped into aquatic, emergent, and woody vegetation types. The aquatic group comprised fossils from submerged, floating-leaved, and free-floating plants, the emergent group included pond margin-associated helophytes, and the woody vegetation group comprised leaves and woody remains (twigs/thorns) from trees and shrubs.

Stratigraphic plots for core MYST1 were generated using the C2 program (Juggins 2016). Due to the differential production and preservation of remains from different plants and animals (Zhao et al. 2006; Salgado et al. 2010), meaningful zonation of macrofossil data is notoriously difficult. Hence, in this study, aquatic macrophyte assemblage changes, as well as pond management episodes (arrows in Fig. 2), were inferred "by eye" on the basis of major shifts in remains from submerged and floating-leaved plants and from shrubs and trees respectively.

To assess the similarity of current and historic aquatic macrophyte assemblages, data from MYST1 were compared with data for extant aquatic macrophyte communities collected during three surveys prior to (2008–2011), and five after (2012–2017) the pond restoration in 2011, during summer (May–July) by one observer (Sayer unpublished data).

Results

MYST1 Dating and Biostratigraphy

Total 210 Pb reached equilibrium with supported 210 Pb at a depth of around 67 cm in the core (Table S1; Figs S1 and S2A & S2B). 137 Cs peaked at 29–32 cm (Table S2; Fig. S2C), likely marking the 1963 fallout maximum associated with the global peak in atmospheric nuclear weapons testing. The CRS model placed 1963 at between 26.5 and 29.5 cm (Table S3; Fig. S1) aligning with the depth estimated for 1963 (29–32 cm) by the 137 Cs profile. This gives high confidence in the chronology for this period. The lowest obtainable date for the 210 Pb profile was 1867 (\pm 27 years) at a depth of 61.5 cm. Based on extrapolation the age of the core base (116.5 cm) was \sim 1652.

Four distinct zones were identified in the macrofossil data for MYST1 (Fig. 2).

Zone 1 (117–84 cm; ~1652–1757). Zone 1 is dominated by remains of submerged and floating-leaved macrophytes (Fig. 2A). Decadal-scale shifts are evident between *Potamogeton natans* L. → *Chara* spp. → *P. natans* in this zone with later phases of increased fine-leaved *Potamogeton* spp., *Myriophyllum spicatum* L., and aquatic moss prevalence. Remains of Mollusca, especially of *Planorbis*, *Lymnaea*, and *Bithynia* spp., ephippia of *Daphnia pulex* Leydig 1860, scale fragments of crucian carp *Carassius carassius* Linnaeus 1758 (over 108–103 cm, ~1687–1702), and trichopteran cases are abundant in this zone. Undifferentiated terrestrial tree leaves, a *Salix* sp. seed capsule, and an increase of organic matter from 5 to 19%, suggest limited encroachment of pioneer woody vegetation (Fig. 2B). Emergent plant species appearing during this phase include *Typha* spp. and *Epilobium hirsutum* L.

Zone 2 (83–57 cm; ~1780–1904). Sediments in this zone are co-dominated by remains of fine-leaved *Potamogeton* spp., *P. natans*, and the shallow-water emergent *Alisma plantago-aquatica* L. Seeds of free-floating *Lemna minor* L. are abundant at 84–80 cm (~1780–1791), and *Oenanthe fistulosa* L. seeds occur exclusively over 73–66 cm (~1822–1846). Initial increases at the start of the zone and subsequent decreases (at 73 cm, ~1822) in remains of *Crataegus monogyna* Jacq., *Salix* spp. and *Rubus fruticosus* agg. may signal a woody vegetation management event. Animal remains are variably abundant in this zone with *D. pulex* generally decreasing in abundance and molluskan and trichopteran remains sparse through many intervals, but with some infrequent instances of high abundance.

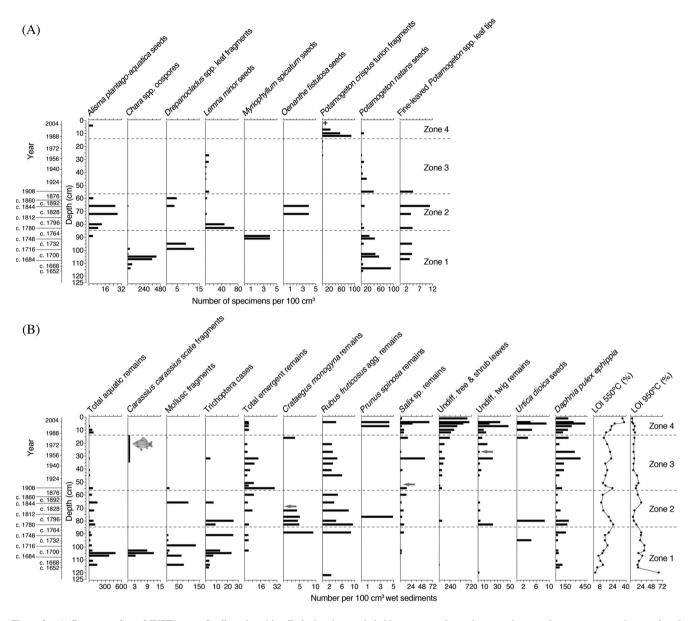


Figure 2. (A) Summary of core MYST1 macrofossil stratigraphies displaying three main habitat types: total aquatic macrophyte, total emergent macrophyte, and total woody vegetation, as well as fish and cladoceran remains. Organic content (LOI 550°C) and carbonate content (LOI 950°C) are displayed as percentages and zones are denoted by a dashed line. Arrows denote periods of suspected canopy management. Fish symbol represents known occurrence of crucian carp in the Mystery Pit (C. Sayer pers. obs.). (B) MYST1 macrofossils of the aquatic macrophyte assemblage. Zones denoted by dashed line. Cross in (A) indicates the occurrence of *Potamogeton crispus* during contemporaneous surveys. Differences in the number of remains for each type resulted in a variable scale along the *x*-axis in each figure.

Zone 3 (56–16 cm; 1907–1981). This zone sees abundant remains of *P. natans*, fine-leaved *Potamogeton* spp., and *L. minor* at 56–55 cm (1907 \pm 16 years), followed by a decline, with aquatic macrophyte remains completely absent at 54–51 cm (1911–1916 \pm 16 years). At 28 cm (1961 \pm 5 years), *Potamogeton crispus* L. turions were detected for the first time. Two potential management interventions are evident at approximately 53 cm (1911 \pm 16 years) and 27 cm (1961 \pm 5 years) as indicated by rapid reductions in *Salix* spp. and undifferentiated twig remains respectively. By 16–17 cm (1981 \pm 4 years), however, remains of aquatic macrophytes are largely absent, while substantial increases in woody vegetation remains (especially

undifferentiated terrestrial leaf and twig remains) occur over 46–16 cm (1930–1981), co-incident with a steady increase in organic matter content to a maximum of 22%. Macrofossils from pond margin-associated plants, including *Lycopus europaeus* L. and the wet ground disturbance indicator *Juncus bufonius* L., are moderately abundant in this zone. Aside from *D. pulex*, aquatic animal remains are generally sparse.

Zone 4 (15–01 cm; 1989–2008). This zone sees a marked increase in woody vegetation indicators including remains of *Quercus* spp. and *Salix* spp. as well as undifferentiated terrestrial

leaves and twigs with a corresponding steep increase in sediment organic matter to 38%. Aquatic macrophyte remains included *P. crispus* over 13–7 cm (1989–1997) and *A. plantago-aquatica* at 5–4 cm (2002 \pm 2 years). Animal remains continue to be dominated by *D. pulex*.

Comparisons With Macrophyte Surveys

Of the 20 species recorded in post-restoration macrophyte surveys (2012-2017), some 9 were also recorded as macrofossils in core MYST1 (Table 1) indicating relatively good representation (45%) of the historical community in the pond following the restoration works. Plants found in zones 1-3 (pre-terrestrialization) that were also well represented in post-restoration surveys were P. natans, Chara spp., A. plantago-aquatica, E. hirsutum, L. minor, P. crispus, Sparganium erectum L., and Juncus spp. (Table 1). Although M. spicatum and O. fistulosa were recorded twice in the core at 92-89 cm (\sim 1749-1757) and 73-66 cm (~1822–1846) respectively they were absent from the postrestoration surveys. Pre-restoration surveys during 2008–2011 showed three aquatic species were present, namely Ceratophyllum submersum L., L. minor, and P. crispus (Table 1), the latter limited to small patches in the southern pond margins. C. submersum was not recorded in core MYST1, however.

Discussion

The macrofossil data permit a centennial-decadal scale reconstruction of changes in near-pond terrestrial vegetation and both semi-aquatic and aquatic plant dynamics. Key indicators of terrestrialization (that tend to change in synchrony) in the Mystery Pit core are increases in undifferentiated leaves and woody plant material, increased sediment organic matter content (most likely a reflection of increased leaf litter inputs), and higher abundances of the cladoceran *D. pulex*, which prefers macrophytefree conditions (Davidson et al. 2010) as typical of heavily shaded ponds.

In the initial 200 years of its history, Mystery Pit appears to have been a largely open-canopy, macrophyte-filled pond, with a generally rich and abundant plant-associated invertebrate community. In the pond's early history (~pre-1780), in particular, decadal-scale shifts between P. natans \rightarrow Chara spp. \rightarrow $P. natans \rightarrow \text{fine-leaved } Potamogeton \text{ spp. suggest that aquatic}$ vegetation composition was dynamic, as observed in long-term pond monitoring data locally (Emson et al. 2018). Woody marginal vegetation, including C. monogyna, Salix spp., and the shrub R. fruticosus agg., was likely present during the first century of the pond's history, but, given the clear dominance of submerged and floating-leaved plants, it seems likely that scrub encroachment, and hence shading, was minimal. Shallow ponds can undergo rapid succession (Hassall et al. 2012) with an open-canopy succeeding to a fully terrestrialized state in \sim 20–30 years, meaning it is highly likely that periodic scrub management took place over much of the Mystery Pit's history. Prior to the 1950s-1960s, farmland ponds were likely used for livestock watering, fishing (e.g. crucian carp), and hemp-retting (Rackham 1986; Upex 2004; Sayer et al. 2013), while nutrient-rich pond sediment was sometimes used as organic fertilizer on neighboring fields, with records of such activity in the region dating back to the 16th century (Tusser 2013). Thus, as at the Mystery Pit, periodic woody vegetation and sediment removal probably prevented full terrestrialization at many ponds. Certainly the core data suggest that, due to one or a number of the aforementioned pond uses, robust management of encroaching woody vegetation occurred at the Mystery Pit on at least three occasions (\sim 1803, 1911 \pm 16 years, 1961 \pm 5 years) as variously evidenced by prior increases and subsequent dramatic decreases in woody vegetation remains, D. pulex abundance, and organic matter content.

The increase in woody vegetation remains in the core after around 1940, and especially after the mid-1970s supports anecdotal evidence for reductions in pond management across the region during the latter half of the 20th century (Sayer et al. 2013). This period of terrestrialization is marked by a decrease in aquatic plant species in the core, further supporting previous studies showing declines in pond biodiversity with increases in tree canopy-cover (Williams et al. 2010; Sayer et al. 2012). While no fish remains were found in the core for this period, crucian carp are known to have been present in the Mystery Pit during the 1960s-1970s. Consistent with the idea of progressive terrestrialization since this time, a survey of fish in 2008 failed to capture this species suggesting extirpation over the 1980s-2000s due to prevalence of anoxic conditions (Sayer et al. 2011). Thus, overall, the sediment record suggests that the most recent period of terrestrialization is historically unprecedented, in turn again strongly indicating that periodic management of woody vegetation had kept the pond in an open state for centuries. Importantly, while sediment removal may have taken place in the past, given a lack of evidence for a hiatus in the core from the radiometric dating, such activities do not appear to have disturbed the sediments of the central core site.

Restoration resulted in the re-occurrence of a number of key submerged, floating and emergent aquatic plants characteristic of the pond pre-1907, especially P. natans and Chara spp. In particular, P. natans affords excellent habitat for dragonflies (perching and oviposition) (Martens 1994) and amphibians, especially newts (egg-laying) (Gustafson et al. 2006), while Chara spp., along with C. submersum (which expanded significantly following restoration), provide complex-structured habitat known to support species-rich invertebrate communities (Hargeby 1990). Rapid post-restoration colonization of the Mystery Pit by Chara sp. (in this case Chara globularis Thuill.) and P. natans is likely due to resurrection of these plants from propagule banks disturbed by the restoration works as these species have long-lived (centennial timescales) oospores (Stobbe et al. 2014) and seeds (Alderton et al. 2017) respectively. It is likely, however, that several species found post-restoration are "new colonists" to the pond, potentially via passive dispersal mechanisms such as wildfowl-based endozoochory (Soons et al. 2008; Green et al. 2016) and regurgitation (Kleyheeg & van Leeuwen 2015). Some ancestral species did not return to Mystery Pit, including the submerged plant M. spicatum and the nationally rare O. fistulosa. M. spicatum is found locally in lakes and ponds (Sayer et al. 2012; Clarke et al. 2014), but has generally declined in agricultural landscapes due to

Table 1. Comparison of aquatic plant species recorded in the Mystery Pit pond in pre- and post-restoration surveys and in core MYST1. Pre-restoration surveys were conducted 2008–2011. Post-restoration surveys were conducted 2012–2017. Plants with macro-remains in the sediment core but not present in post-restoration surveys are highlighted in bold. * = Chara globularis.

Macrophyte Species	<i>Present in Core Zone</i> 1 (~1652−1757)	<i>Present in Core Zone</i> 2 (∼1780–1904)	Present in Core Zone 3 (1907–1981)	Present in Core Zone 4 (1989–2008)	Present Before Restoration	Present After Restoration
Agrostis	_	_	_	_	_	✓
stolonifera						
Alisma plantago-	✓	✓	_	✓	_	✓
aquatica						
Calamagrostis	✓	_	_	_	_	_
canascens						
Carex riparia	_	_	✓	_	_	_
Chara spp.	✓	✓	_	_	_	/ *
Ceratophyllum submersum	_	_	_	_	✓	✓
Cladophora spp.	_	_	_	_	✓	✓
Eleocharis palustris	_	_	_	_	_	✓
Epilobium	✓	✓	✓	✓	_	✓
hirsutum Filipendula ulmaria	_	_	_	_	-	1
Fontinalis anitpyretica	-	-	_	_	-	✓
Juncus articulatus	_	_	✓	_	-	1
Juncus bufonius	_	_	✓	_	_	✓
Juncus effusus	_	_	_	_	_	✓
Juncus inflexus	_	_	_	_	_	✓
Lemna minor	✓	✓	✓	_	✓	✓
Lemna trisulca	_	_	_	_	_	✓
Lycopus	_	_	✓	_	_	_
europaeus						
Myriophyllum spicatum	1	_	_	_	_	_
Oenanthe	_	/	_	_	_	_
fistulosa		•				
Potamogeton	_	_	1	1	/	1
crispus			•	•	•	•
Potamogeton natans	✓	✓	✓	✓	-	✓
Fine-leaved Potamogeton spp.	✓	✓	✓	_	-	
Ranunculus sceleratus	-	_	-	-	_	1
Sparganium erectum	✓	_	✓	✓	-	1
Typha spp.	✓	_	_	_	_	_
Veronica spp.	_	✓	_	_	_	_

eutrophication (Sayer et al. 2010; Sayer et al. 2016). Indeed this may explain its early loss from Mystery Pit, with its disappearance immediately followed by appearance of the duckweed *L. minor* (which may have shaded out *M. spicatum*), a plant known to be indicative of advancing eutrophication (Sayer et al. 2010; Emson 2015; Emson et al. 2018). Meanwhile *O. fistulosa* has declined to localized patches in the study region during the last 50–100 years due to changes in farming practices and an associated loss of fen habitat (Southam & Wigginton 2002).

It is likely, therefore, that compared to *M. spicatum*, *O. fisulosa* has a reduced potential for dispersal into the pond and would therefore need to be re-introduced. A further limiting factor for the return of these species might be reduced seedbank viability (Vécrin et al. 2007) making spatial dispersal or planned reintroduction the only return route. As a caveat, absence of some contemporary plant species (e.g. *Callitriche* spp. and *C. submersum*) from the sediment record may be due to poor preservation or low seed production (Zhao et al. 2006) and it is

recognized that, as observed elsewhere (Madgwick et al. 2011; Clarke et al. 2014), a single core study cannot afford a full reflection of past aquatic plant diversity, especially when species were rare in the past.

Macrofossil analysis of sediment cores is widely used for setting restoration targets for lakes, and to establish if historically important species benefit from management and restoration activities (Sayer et al. 2012; Bennion et al. 2018). This study demonstrates that similar methods can be applied to small farmland ponds. Further research utilizing additional sites is needed to shed greater light on farmland pond management histories. Despite this limitation, our study shows that the pond restoration undertaken at Mystery Pit in 2011 appears to mimic management actions of the past. In addition, it is clear that pond restoration by woody vegetation and sediment removal results in the return and/or resurrection of many former species, thereby greatly enhancing pond macrophyte diversity.

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Supporting Information

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

Table S1. ²¹⁰Pb concentration outputs for 18 upper core sub-samples.

Table S2. Artificial fallout radionuclide concentrations in core MYST1.

 $\textbf{Table S3}. \ Lead-210 \ chronology \ for \ core \ MYST1.$

Figure S1. Radiometric chronology of core MYST1.

Figure S2. Fallout radionuclide concentrations in core MYST1.

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