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Go hard or go home: Major removal of woody vegetation and sediment greatly enhances wetland plant and water beetle diversity recovery in a farmland pond landscape

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Abstract

1. Ponds are important habitats for biodiversity conservation and ecosystem service provisions in farmland settings. Agricultural intensification and cessation of traditional management has resulted in a substantial loss of open-canopy farmland ponds across Europe, resulting in a decline of landscape-scale biodiversity. To recover biodiversity in agricultural pondscapes, recent studies have advocated restoration of overgrown, 'late-succession' ponds via the removal of woody vegetation and/or sediment. However, few studies have documented real-time pond and pondscape species responses to this kind of intervention. Crucially, evidence for how the intensity of intervention shapes biodiversity outcomes has been completely missing.

2. We investigated short-term (1-3 years) pond biodiversity responses to restoration at a typical, medium-sized, predominantly arable farm in eastern England. Wetland plants and water beetles (Coleoptera) were surveyed in 11 restored ponds and four control ponds before and twice following restoration, involving three management prescriptions: i) major woody vegetation removal, only; ii) major woody vegetation and minor sediment removal and iii) major woody vegetation and major sediment removal.

3. Pond restoration involving major woody vegetation and major sediment removal was associated with the greatest uplift in α-diversity for wetland plants. It was also most effective in restoring rare plant species, especially charophytes.

4. Water beetle diversity also responded positively to major woody vegetation and sediment removal, with a significant uplift being observed. Overall, six red-listed species returned to the studied pondscape following restoration interventions.

5. **Practical Implication**: Our small-scale, explorative study highlights the great potential value of implementing high intensity restoration interventions that combine major woody vegetation and sediment removal over lower intensity options, for maximising freshwater biodiversity and the conservation of rare species in agricultural landscapes.

Keywords: biodiversity conservation, Coleoptera, freshwater, macrophyte, restoration, terrestrialisation

1. Introduction

Ponds are frequently inhabited by highly diverse plant, invertebrate and vertebrate assemblages that include many conservation priority species (Florencio et al., 2014; Gee et al., 1997; Nicolet et al., 2004), highlighting their importance as aquatic refugia within agricultural landscapes (Ruggiero et al., 2008; Sayer et al., 2012). However, despite their established importance for aquatic biodiversity conservation, ponds lack effective legislative protection (Hill et al., 2018) and are thought to be in a poor ecological state in many areas of the globe. In the UK, for example, numerous ponds were actively in-filled to make additional space for crops and infrastructure developments after the 1940s-1950s (Smith et al., 2022; Wood et al., 2003). As in many other parts of Europe (Curado et al., 2011; Janssen et al., 2018), remaining UK agricultural ponds have seen a widespread cessation of traditional pond management since the 1950s, resulting in major encroachment of wetland trees and woody vegetation, for example by *Salix* spp. and *Alnus glutinosa* L. Gaertn, and rapid pond infilling. The resulting highly terrestrialised, heavily shaded ponds are mostly free of aquatic vegetation and dominated by poorly decomposed organic debris derived from leaves, branches and sometimes whole fallen trees (Sayer and Greaves, 2020). Accordingly, many UK pond landscapes have become overwhelmingly dominated by these late-succession ponds, with consequent reductions in landscape-scale biodiversity spanning multiple biological groups (Sayer et al., 2022). Currently, an estimated 80% of UK ponds are considered in poor ecological condition, with the number of sites categorised as poor or very poor increasing from 60% to 72% between 1996 and 2007 (Carey et al., 2008). In addition, recent reports have shown that even the UK's best "priority ponds" commonly located in semi-natural landscapes are undergoing a decline in wetland plants richness and rarity value, with scrub and tree encroachment identified as a key causal factor (Williams, 2018).

There is consensus in the pond conservation community that biodiversity is maximised where pond landscapes contain a mix of successional stages, including a high proportion of early succession open-canopy, macrophyte-dominated ponds known to support particularly high levels of biodiversity (Hassall et al., 2011; Sayer et al., 2012; Sayer et al., 2023a). As habitat conditions vary greatly between pond successional stages, a mixture of these stages in a pond network makes it suitable for a greater variety of flora and fauna.

Pond-based biodiversity conservation can take a number of forms. In Europe, recent decades have seen a strong focus on creating networks of unpolluted, new ponds (Minot et al., 2021; Williams et al., 2020) and much evidence suggests that adding new ponds to a landscape significantly increases species richness, potentially including rare species (Coccia et al., 2016; Williams et al., 2020). Further, newly created ponds have been observed to attain a good ecological condition relatively rapidly (<10 years) and retain their ecological value for many years (Oertli, 2018; Williams et al., 2008). A relatively rarer and newer restoration approach is the re-excavation of 'ghost ponds' lost to land reclamation and in-filling (Alderton et al., 2017; Sayer et al., 2023b). With this approach, the recovery of aquatic plants has been shown to be especially rapid due to the development of many species from long-lived propagules exposed during re-excavation (Alderton et al., 2017).

Pond restoration and management also needs to be employed to deal with the issue of mass pond terrestrialisation and consequent reductions in pond habitat heterogeneity (Sayer et al., 2022; Sayer and Greaves, 2020). Pond restoration aims to reset succession through removal of woody vegetation and potentially also sediment. Recent research has revealed major benefits for species diversity following the restoring of ponds to an early succession, open-canopy state. Aquatic taxa shown to benefit include macrophytes (Sayer et al., 2012, 2022; Hill et al., 2025), dragonflies (Janssen et al., 2018), chironomids (Ruse et al., 2025) as well as freshwater invertebrates in general (Sayer et al., 2012; Ruse et al., 2025; Hill et al., 2025), and amphibians (Skelly et al., 2014; Arntzen et al., 2017). Pond restoration benefits are also known to extend to terrestrial species, reflecting strong aquatic-terrestrial linkages for small waterbodies (Soininen et al., 2015). For example, almost twice as many farmland bird species visited restored open-canopy, macrophyte-filled ponds compared to overgrown ponds in Eastern England (Davies et al., 2016; Lewis-Phillips et al., 2019), a pattern linked to greatly enhanced hatches of emerging invertebrates from the open ponds (Lewis-Phillips et al., 2020). In addition, restored ponds have been shown to support more diverse diurnal pollinator communities (Walton et al., 2021a) and more complex plant-pollinator networks (Walton et al., 2021b) than overgrown ponds.

While pond restoration therefore can be highly effective, there is a lack of evidence on how differing types and intensities of restoration and management affect biodiversity outcomes, at both the pond and pondscape scales. For example, pond interventions can include management that removes excessive woody vegetation without interfering with the pond sediment, or it can combine both major wood and sediment removal. To inform and support future practitioner decision making, it is therefore crucial to understand which types and intensities of management-restoration intervention are most beneficial.

Previous research on pond restoration by removal of woody vegetation and/or sediment has largely been based on space-for-time substitution and comparisons of restored and non-restored ponds (Janssen et al., 2018; Sayer et al., 2012). Indeed, few studies have documented real-time pond and pondscape species responses to this form of pond restoration. Equally, as mentioned above and despite the existence of guidance (Sayer et al., 2023b), published science on how management intensity (especially removal of wood vs. wood and sediment) affects pond restoration outcomes is lacking. To fill these knowledge gaps, we studied a pond landscape in eastern England where a series of highly terrestrialised “late-succession” ponds were restored using different combinations and intensities of woody vegetation and sediment removal between 2015 to 2019. Given the time and effort involved in such studies, our investigations are based on a relatively small sample size and thus arguably only provide a “first impression” at the pond diversity responses to differing intensities of management, paving the way for larger studies in future years. We furthermore only report on the early years (years 1-3) following restoration in terms of wetland plants and water beetle (Coleoptera) responses. The hypothesises of this study are that, in line with earlier pond restoration studies (Sayer et al., 2022; Hill et al., 2025), all restoration approaches rapidly (within 1-2 years) and significantly increase macrophyte and coleoptera biodiversity in the pondscape, without resulting in major losses of rare species. Furthermore, we hypothesise that, based on the more fundamental disruption to the degraded pond ecosystems, high intensity restoration (woody vegetation removal combined with major sediment removal) triggers the most pronounced increases in biodiversity across the pond network when compared to ponds restored by removal of woody vegetation, only, or of woody vegetation combined with minor sedimental removal. This pattern might be further emphasized by the strongest seed-bank responses in wetland plants following exposure of old sediment layers under intensive management interventions.

2. Materials and Methods

2.1. Study area

The study was conducted at the Heydon estate, North Norfolk, eastern England (Fig. 1) between 2010 and 2019. The area spans 8.2 km^2 and contains upwards of 50 ponds, 15 of which were included here. The study area is located at 45-55 m above sea level and has freely-draining, slightly acidic, loamy soils (LandIS, 2023) that have developed on deposits of clay and silt overlying sand and gravel of the Wroxham Crag formation (British Geological Survey, 2023). The region's climate is temperate and dry when compared to the rest of the UK, with an annual (1991-2020) rainfall of 660 mm (Met Office, 2023). Typical of the wider area, most ponds on the estate were highly overgrown by trees and bushes, especially Grey Willow *Salix cinerea*, Blackthorn *Prunus spinosa* and Hawthorn *Crataegus monogyna* prior to restoration (Sayer et al., 2013). All study ponds are located in arable fields used for a variety of crops, including wheat, barley, oil-seed rape and sugar beet. The farmed fields are surrounded by hedgerows and interspersed with small patches of predominantly deciduous woodland. The ponds in the study area are all small (<550 m^2 with the exception of pond PYES1 at 2400 m^2) and, at the time of sampling, were surrounded by woody vegetation and/or rough grass margins ranging between 5 and 10 m width.

The study ponds were surveyed prior to restoration in 2010, 2013 and 2014, and following restoration in 2016, 2017, 2018 and 2019. 11 of the 15 ponds studied were restored, with restoration of ponds coded COLG1, COLG2, COLG3, COLG4, BONF1, PYES1, PYES2 in 2015, HEY93, HEY96 and HEY97 in 2016 and ponds HEY102 and DAIRY2 in 2018. The remaining two ponds on the Heydon estate (HEY89, BULLS2), as well as two additional ponds in the surrounding area (MYSTF, CHEST1), formed a control pond group of overgrown (>60% shading) ponds that were neither restored nor managed (Fig. 1). Information about the management of each can be found in Table 1 and Table S1.

2.2. Field Methods

Wetland plant surveys were undertaken at all 15 study ponds. Due to a lack of pre-restoration data for some ponds, only 11 ponds (seven restored and four control ponds) are included in the analysis of water beetle assemblages (Table S1). To generate both, the beetle and plant datasets, surveys were conducted pre-restoration, and at least once in years 1-3 post-restoration to look at short-term responses to management intervention. Data for years 2 and 3 were amalgamated as not all ponds were surveyed after 2 or 3 years, and the resulting relative scarcity of survey data for all ponds across both years. All surveys were conducted between May and August in a respective study year. Additional information regarding the survey years and restorative actions are given in Table S1.

Wetland plants were exhaustively surveyed by visual observation whilst wading and walking the perimeter of each pond, and with a double-headed rake used to collect macrophytes from deeper, central pond areas. The survey continued at each pond until at least 10 minutes had elapsed without a new species being found. All marginal and open water wetland species found in each pond were scored for abundance on the DAFOR scale (Bullock, 2006) as Dominant (5), Abundant (4), Frequent (3), Occasional (2) or Rare (1). *Callitriche* taxa were combined as *Callitriche* spp. due to the absence of diagnostic fruits in the collected material.

Water beetles were surveyed using a standard ISI pond net (1 mm mesh). A total of three minutes were spent sampling each pond as per Biggs et al. (1998), with efforts made to cover all major habitat types: areas shaded by large overhanging branches, patches of floating plants, beds of submerged plants and the shallow edge water with marginal plants. Following the procedure proposed by Biggs et al. (1998) and as recommended by Hill et al. (2016), the time apportioned to each pond habitat was roughly equivalent to the proportional area of the respective habitat. Water beetles were separated from the samples in the field by searching multiple trays of collected material until no further individuals were found. All invertebrates were transferred to plastic containers and preserved on site in 90% IMS.

Species were identified and recorded ex-situ. Species identification was based on Foster & Friday (2011) and Foster et al. (2014), with unclear identifications verified by Garth Foster, chair of the British Aquatic Coleoptera Conservation Trust.

2.3. Data Analysis

Wetland plant rarity was assessed at the national scale with reference to Stroh et al. (2014) and Stewart & Church (1992), while regional and local rarity was assessed using the approach adopted by Williams et al. (2020). For the latter assessment, records for all recorded plant species were extracted from the Botanical Society of Britain and Ireland database from 2000 to present. Local rarity was calculated as the percentage of 1x1 km grid squares (monads) where a species was recorded as present out of the 100 monads falling within a 100 km^2 area around the Heydon site. Regional rarity was calculated as the percentage of monads with species records out of all monads covering Norfolk (n=5498). Any plant species with a frequency below 5% in either metric was classified as ‘rare’ (Table S3). Rarity assessment of water beetles was based on the list of scarce and threatened British species compiled by Foster (2010), a local rarity assessment comparable to wetland plants was not possible due to a lack of comprehensive records (Table S4).

To determine the influence of management intensity on wetland plant and water beetle communities, ponds were divided into four management intensity groups (Table 1). Groups are described below, accompanied by the number of ponds with wetland plant and coleoptera surveys (X/Y), respectively. Group 0 represented control and unrestored sites, dominated by woody vegetation, with no intervention (4, 3), Group 1 were sites where management was limited to woody vegetation removal (2, 2), Group 2 ponds experienced major removal of woody vegetation and minor sediment removal (4, 2), while Group 3 sites experienced major removal of both, woody vegetation and sediment (5, 4).

As water beetle species richness is generally assumed to be incomplete in pond net samples, we used the bias-corrected formula for Chao 1 (Chao and Chiu, 2016) to generate estimates for the minimum number of water beetle species expected to occur in the ponds.

For each of the three management intensity groups, we then compared both the observed number of wetland plants and Chao 1-estimated species richness of water beetles using a series of one way Analysis of Variance (ANOVAs) with subsequent post-hoc Scheffé-tests to establish potential differences in species richness between groups. We used this approach firstly to determine potential temporal differences in species richness separately for each of the three management intensity groups, starting with the pre-restoration data for each of the respective ponds, and comparing this to data 1 year and 2/3 years since management. We then repeated this approach to compare the temporal differences in species richness for all ponds irrespective of management intensity, differentiated solely into control/pre restoration data, data for year 1 and data for years 2/3 post-restoration. Finally, we used two ANOVAs to compare the mean aquatic macrophyte species richness of ponds differentiated by management category, establishing treatment differences 1 year after restoration and 2/3 years after restoration, respectively.

Detrended Correspondence Analysis (DCA) was then employed to confirm that the data allowed the use of models assuming a unimodal distribution patterns across the pondscape (gradient length: 2.77). Subsequently, Correspondence Analysis (CA), based on presence-absence data of the aquatic macrophytes, was used to visually explore plant compositional changes and successional patterns. The ordinations were performed using CANOCO version 4.5 (Lepš and Šmilauer, 2003).

3. Results

3.1. Wetland plants

A large increase in wetland plant species was evident for the restored ponds post-intervention, with the greatest uplift associated with sites with major wood and sediment removal (Fig. 2, Table 2), which had significant differences in species richness between year 0 and year 1, and between year 0 and years 2-3 (P <0.01 in all cases, ANOVA $F_{2,12}$=23.7, $SS_{bg/wg}$: 1067/270, $MS_{bg/wg}$: 533/23). Ponds with wood and sediment removal only showed a significant (P<0.05) species richness increase between years 0 and years 2-3 post-restoration (ANOVA $F_{2,9}$=4.9, P=0.036, $SS_{bg/wg}$: 248/226, $MS_{bg/wg}$: 124/25) and sites with only wood removal did not show a significant increase in species richness between any groups (ANOVA $F_{2,6}$=0.2, P=0.82, $SS_{bg/wg}$: 3.6/51, $MS_{bg/wg}$: 1.8/8.4). The cumulative species richness across all restored ponds mirrored the major wood and sediment removal group with a significant increase between year 0 and year 1 (*P*<0.01) and year 0 and years 2-3 (*P* <0.01; ANOVA $F_{2,33}$=16.4, P<0.001, $SS_{bg/wg}$: 935/939, $MS_{bg/wg}$: 467/28). While there were no significant differences in the average plant species richness one year post-restoration between the three intervention intensity groups (ANOVA $F_{2,8}$=0.16, P=0.85, $SS_{bg/wg}$: 10.6/262, $MS_{bg/wg}$: 5.3/32.7), ponds in the most intensively managed group harboured a significantly higher plant species richness for years 2/3 when compared with ponds with only wood removal (P=0.03, ANOVA $F_{2,10}$=5.0, $SS_{bg/wg}$: 222/220, $MS_{bg/wg}$: 111/22).

Whilst the control sites are represented in a single box plot (Figure 2), the limited overall and interquartile ranges reflect consistently low species richness. Although this trend is not statistically significant (t=1.14, P=0.9), ponds in the control group often lost species when comparing their assemblages in pre- to post-restoration timeframes , with average species richness dropping from 6.5 to 2.75. This trend is most notable for pond HEY89, which supported 11 species in 2013, while no aquatic macrophytes at all were found in 2018 (Table S2). *Rorripa amphibia* was the only plant species recorded before, but not following restoration in any pond. In contrast, some 32 wetland plant species were added to the set of investigated ponds following pond restoration, 30 of which were exclusively found in the restored ponds. Average species richness per site increased from five to 15.5 from pre-restoration surveys to post-restoration sampling years 2-3. The total species richness increase across all sites was 118.5% (Table 2). A total of 21 rare species were gained across all restoration sites. The majority of new rare species (11) were found in the sites with major wood and sediment removal, with six species unique to this group (Table 2). Sites with wood and sediment removal gained eight rare species, four of which were unique to this group, including one nationally rare (Schedule 8 in 1981 British Wildlife & Countryside Act) species, namely *Najas marina*, which was recorded in PYES1. Finally, ponds with only wood removal gained 2 rare species, and only one was unique to the group.

Clear aquatic vegetation composition responses in relation to management intensity are reflected by the CA plot (Fig. 3). Some samples were excluded in this analysis as they had no recorded species, while control site CHEST1 was removed as an outlier due to the occurrence of just two species (*Lythrum salicaria* and *Myosotis scorpioides*). A group of three major wood and sediment removal sites is strongly separated from all other plots along CA Axis 1 (11.45% explained variance, see also supplementary table S5). Further, sites with major wood and sediment removal tend to move towards the centre of the plot as number of years since intervention increases. Sites with wood and sediment removal show smaller amounts of change along both axes with time since restoration but are markedly removed in general from their respective year 0 surveys. One pond in this group, PYES1), the largest pond in the dataset, is separated from the other sites by having a negative position on axis 2 due to the occurrence of three unique species post-restoration. Sites with only wood removal display little movement between survey years, even when compared with respective pre-restoration assemblages, suggesting that minor compositional change only. Control and pre-management pond surveys are mostly spread between Axis 1 values of 0 and -1.5, occupying the top left quadrant of the ordination plot.

Rare species (Table S3) are spread widely across the ordination plot, with many strongly associated with the major wood and sediment removal sites. In particular, charophyte species similarly are strongly associated with these sites in the CA, as are *Potamogeton berchtoldii, Oenanthe aquatica* and *Ranunculus aquatilis*. Overall, the CA suggests that high management intensity (major wood and sediment removal) results in assemblages that are distinctly different from other sites, but with this distinctiveness diminishing over time (years 2-3).

3.2. Water beetles

Restored ponds showed substantial increases in water beetle diversity and, similar to wetland plants, sites subject to major wood and sediment removal saw the most substantial increase (Fig. 4). Following restoration, mean water beetle species richness increased significantly (P=0.009, $F_{1,6}$=14.57, SSbg/wg: 880/362, MSbg/wg: 880/60) in ponds subject to this treatment, from 2.3 to 23.3 species. In contrast, no significant differences in beetle diversity pre- and post-restoration were observed for ponds with only wood removal (P=0.83, $F_{1,2}$=0.06) and 2 (P=0.16, $F_{1,2}$=4.7). The overall uplift across in the set of surveyed sites was 45.8% (Table 2). Some eight species were not found in post-restoration samples (including two nationally red-list taxa), but 19 species were recorded exclusively in the restored ponds, including six nationally red-listed species *Gyrinus natator, Helochares obscurus, Hydrochus megaphallus, Scarodytes halensis, Helophorus griseus* and *Hydraena nigrita* (Table 2). Additionally, there was a significant change (P=0.006) in mean water beetle abundance following pond restoration, with the mean and maximum number of beetle individuals captured during our standardized sampling at each pond survey increasing from four to 25, and from 11 to 64 individuals, respectively. The overall uplift of abundance for 623.8% (Table 2).

4. Discussion

4.1. Biodiversity uplift following restoration

Just one to two years following restoration the restored ponds achieved high plant coverage both in the water and around the pond margins, with the uplift being particularly strong for the ponds with major wood and sediment removal (Fig. 5). Consistent with previous space-for-time comparisons of terrestrialised and restored, open-canopy ponds (Sayer et al., 2012, 2022; Walton et al., 2021c), this study also showed major short-term increases in species diversity for both wetland plant and water beetle communities following pond restoration. At the pondscape level, management interventions across all sites resulted in a major boost to wetland plant communities, with over double the number of species recorded across the ponds following restoration interventions. Of the 32 species that were new to the restored pondscape, 21 were deemed locally or regionally rare, with one species, *Najas marina*, having statutory protection at a national level (Schedule 8 of the 1981 British Wildlife and Countryside Act). Furthermore, these major gains were accompanied by the loss of just one species, *R. amphibia*, notably from one of the control ponds, although it is generally widespread in the study area. In contrast, the majority of new rare species were gained in the ponds with minor (8) and major (11) sediment removal.

A post-restoration increase in beetle abundance (623.8%) and species richness (45.8%) in the pondscape, including the arrival of 19 new species, six of which are red-listed rare taxa, can be directly linked to an increase in the number of structurally-complex, vegetation-rich ponds as a response to restoration. Strong associations between aquatic vegetation structure and water beetle diversity and assembly have been reported in previous research (Nilsson, 1984; Fairchild et al., 2008; Gioria et al., 2010). For example, in a study of aquatic plant and water beetle diversity across 425 farm ponds in North-west England, Hassall et al. (2011) showed a significant positive relationship between plant coverage and water beetle richness, as well as negative relationships with shading. Thus, enhanced habitat availability, potentially combined with short flight distances between high quality, plant-dominated aquatic habitats (Iversen et al., 2017; Liao et al., 2022), is a likely explanation for increases in water beetle abundance and diversity. As for wetland plants, water beetle species gains were strongly concentrated in ponds restored by major woody vegetation and sediment removal. Whilst these sites clearly afforded viable habitat for new species to colonise, it is also notable that six of the new species, including one National Red List species (*Hydraena nigrita*), were additionally found in the overgrown control ponds. This highlights the importance of maintaining a heterogeneous pondscape supporting a mix of successional stages, including numerous early succession, open-canopy ponds and some late-succession, tree-shaded ponds (Brudvig et al., 2009; Hassall et al. 2011; Sayer et al., 2012).

4.2. Seed bank-driven vegetation recovery

The remarkable rapidity of wetland plant recovery in the farmland pondscape is worthy of discussion. While zoochorous wetland seed dispersal (via wildfowl and mammals) may potentially be enhanced through a shortening of the distance between ponds with abundant food resources (Clausen et al., 2002; Coughlan et al., 2017; Kleyheeg et al., 2017), the speed at which high plant cover was achieved in the restored ponds suggests an additional strong seed bank driver of vegetation recolonisation. A relatively consistent feature of the response amongst the ponds restored by major woody vegetation and sediment removal is an early dominance (high cover) of charophytes, Potamogetonaceae (especially *Potamogeton natans*) and *Ranunculus aquatilis*. Characean species are well known pioneer plants that are widely associated with disturbance events (Wade, 1990) due to abundantly produced oospores that form substantial sediment propagule banks (Bonis and Grillas, 2002; Rodrigo et al., 2010). Farm ponds in the region are generally >200-300 years old (Prince, 1962; Sayer et al., 2013; Emson et al., 2018), sometimes older, extending back to the 1500s-1600s (Walton et al., 2021c). This means that sediment removal work often exposes centuries old sediment layers, making it a key component of the management approach. A number of studies have shown that charophyte oospores can germinate even after burial for 10s to 100s of years (Wade & Edwards 1980; Beltman & Allegrini 1997; Tanaka et al. 2003; Rodrigo et al. 2010; Stobbe et al. 2014). Thus, by exposing deeper sediment layers, associated with former open-canopy, macrophyte-rich eras prior to major pond terrestrialisation (Walton et al. 2021c), substantial characean meadows can result after less than 1 year (Fig. 5d). Knowledge of propagule longevity amongst other wetland plants is patchy, but information is emerging. For example, Kaplan et al. (2014) were able to use the seed bank to re-establish a macrophyte (*Potamogeton coloratus*) that had been nationally extinct for at least 30 years. Additionally, tank-based microcosm and field-based studies undertaken on locally (<20 km from the study sites here) collected under-field sediment deposits (dated to a minimum of 50-150 years before present) from in-filled ‘ghost ponds’ showed that propagules of *P. natans, R. aquatilis, Juncus* sp., as well as six charophyte species, germinated and subsequently grew into substantial plants within 12 months

(Alderton et al., 2017). As many of these species were abundant in one or more the restored ponds following minor or major sediment removal and in turn much less prevalent (absent in the case of Characeae) from ponds subject to woody vegetation removal only, we confidently believe that early colonisation and high submerged and floating plant coverage of the former ponds was primarily driven by seed bank exposure. Such a conclusion is consistent with the observation that newly created farm ponds take at least a decade to achieve wetland plant coverage and species richness that is equivalent to restored ponds (Hill et al., 2025). That a more rapid rise in plant species richness and representing a distinct community was evident in the ponds subject to major wood and sediment removal (Fig. 3) may also reflect the prevalence of firmer better oxygenated bottom sediment following the removal of fluid, organic matter-rich muds associated with decades of terrestrial leaf and woody debris deposition. In shallow lakes many aquatic macrophytes have been shown to prefer firm sediments with high cohesive strength (Schutten et al., 2005) and low oxygen demand (Woodward and Hofstra, 2024) and it seems probable that this phenomenon may also apply to ponds, though this is an area needing further research.

We show that, by restoring and managing ponds to ensure that lowland farmland contains mosaics of ponds at different successional stages, and especially by increasing the number of early-succession, open-canopy, macrophyte-rich ponds, it is possible to rapidly and majorly increase wetland plant and water beetle diversity. The Heydon project also emphasises the importance of applying varying management intensity across ponds, especially including major sediment removal aimed at exposing species-rich seed banks . A recent study investigating the value of adding new ponds (newly created ponds) into a comparable farmland landscape in Leicestershire, English Midlands, showed a 26% increase in wetland plant richness at the catchment-scale, including (as in this study) a high proportion of locally scarce species (Williams et al., 2020). Our study, hints at an even stronger (118.5%) transformative effect of restoring ponds for aquatic plants. This, in turn, suggests that combining the restoration of pre-existing highly terrestrialised ponds with the construction of new ponds might be the most powerful pond conservation approach.

5. Recommendations and conclusions

Resonating with the results of several other studies (Declerck et al., 2006; Ruggiero et al., 2008; Gioria et al., 2010; Sayer et al., 2012, 2022), we emphasise that ponds in farmland settings, where sufficiently buffered from agricultural activities, are important contributors to aquatic biodiversity. As well as being one of the first before-after studies, it provides a 'first look' at the impact of differing management approaches on pond biodiversity outcomes. More extensive studies, that include larger numbers of ponds, are ideally required to bolster the conclusions that are made here in turn enabling fuller analysis of changes in gamma diversity and species turnover. Despite this, we confidently offer the following recommendations to the pond conservation field:

i) We urge practitioners and policymakers to centralise pond restoration in landscape-scale conservation plans and policy. It is vital that ponds are prominently featured in agri-environment policy and nature recovery strategies, in order to support wider freshwater biodiversity conservation efforts.

ii) High intensity restoration involving sediment removal has the greatest transformative effect on ponds. We recognise that major sediment removal can incur significant costs and present logistical challenges for practitioners, but for highly terrestrialised ponds, the advantages of doing so out-weighs these dis-benefits.

iii) Restoration involving sediment removal can make an important contribution to rare plant conservation by uncovering still viable wetland plant seed banks. We emphasise the need for monitoring of 5-10 year responses of wetland plants and water beetles to restoration to try and understand how conservation outcomes change in the longer term.

iv) We recommend those involved in pond restoration to undertake before-after control-impact studies of biological responses to help bolster the science evidence-base for pond restoration.

v) As emphasised in a recent practical guide to the restoration of ponds (Sayer et al., 2023b), we urge practitioners faced with a dominance of highly terrestrialised ponds to ‘go hard or go home’ and give a high proportion of these ponds the major disturbance and successional-rest that they need.

Author Contributions

Ben Siggery and Carl Sayer conceived and designed the study; Ben Siggery, Carl Sayer, Emily Alderton, Peter Robinson and Helen Greaves collected the data; Carl Sayer and Helen Greaves led on the pond restorations, Ben Siggery and Jan Axmacher analysed the data; Ben Siggery, Carl Sayer and Jan Axmacher led the writing of the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication.

Statement on Inclusion

This study was conducted in the UK, the country in which the authorship team is based. The authors engaged with local landowners and stakeholders within the North Norfolk region through the Norfolk Ponds Project to share research outcomes and support the restoration of ponds on their land.

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Conflict of Interest

The authors declare no conflicts of interest.

Data availability statement

The dataset used for the analysis of the paper is available from the authors upon request.

References

Alderton, E., Sayer, C. D., Davies, R., Lambert, S. J., Axmacher, J. C. (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, J. W., Abrahams, C., Meilink, W. R. M., Iosif, 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

Beltman, B., & Allegrini, C. (1997). Restoration of lost aquatic plant communities: New habitats for *Chara*. *Netherlands Journal of Aquatic Ecology*, *30*(4), 331–337. https://doi.org/10.1007/BF02085876

Biggs, J., Fox, G., & Nicolet, P. (1998). A guide to the methods of the National Pond Survey. *Pond Action*.

Bonis, A., & Grillas, P. (2002). Deposition, germination and spatio-temporal patterns of charophyte propagule banks: A review. *Aquatic Botany, 72*, 235–248. https://doi.org/10.1016/S0304-3770(01)00203-0

British Geological Survey. (2023). *BGS Geology Viewer*. British Geological Survey. https://www.bgs.ac.uk/map-viewers/bgs-geology-viewer/ (accessed September 21, 2023).

Brudvig, L. A., Damschen, E. I., Tewksbury, J. J., Haddad, N. M., & Levey, D. J. (2009). Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of the National Academy of Sciences, 106*, 9328–9332. https://doi.org/10.1073/pnas.0809658106

Bullock, J. M. (2006). Plants. In W. J. Sutherland (Ed.), *Ecological Census Techniques: A Handbook* (pp. 186–213). Cambridge University Press. https://doi.org/10.1017/CBO9780511790508.005

Carey, P. D., Wallis, S., Chamberlain, P. M., Cooper, A., Emmett, B. A., Maskell, L. C., McCann, T., Murphy, J., Norton, L. R., Reynolds, B., Scott, W. A., Simpson, Smart, S. M., & Ullyett, J. M. (2008). *Countryside Survey: UK Results from 2007*. Centre for Ecology and Hydrology.

Chao, A., & Chiu, C.-H. (2016). Species richness: Estimation and comparison. In *Wiley StatsRef: Statistics Reference Online* (pp. 1–26). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118445112.stat03432.pub2

Clausen, P., Nolet, B. A., Fox, A. D., & Klaassen, M. (2002). Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in northern Europe—a critical review of possibilities and limitations. *Acta Oecologica, 23*, 191–203. https://doi.org/10.1016/S1146-609X(02)01150-5

Coccia, C., Vanschoenwinkel, B., Brendonck, L., Boyero, L., & Green, A. J. (2016). Newly created ponds complement natural waterbodies for restoration of macroinvertebrate assemblages. *Freshwater Biology, 61*, 1640–1654. https://doi.org/10.1111/fwb.12804

Coughlan, N. E., Kelly, T. C., & Jansen, M. A. K. (2017). "Step by step": High frequency short-distance epizoochorous dispersal of aquatic macrophytes. *Biological Invasions, 19*, 625–634. https://doi.org/10.1007/s10530-016-1293-0

Curado, N., Hartel, T., & Arntzen, J. W. (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

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

Declerck, S., De Bie, T., Ercken, D., Hampel, H., Schrijvers, S., Van Wichelen, J., Gillard, V., Mandiki, R., Losson, B., Bauwens, D. (2006). Ecological characteristics of small farmland ponds: Associations with land use practices at multiple spatial scales. *Biological Conservation, 131*, 523–532.

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

Emson, D., Sayer, C. D., Bennion, H., Patmore, I. R., & Rioual, P. (2018). Mission possible: Diatoms can be used to infer past duckweed (lemnoid Araceae) dominance in ponds. *Journal of Paleolimnology, 60*, 209–221. https://doi.org/10.1007/s10933-017-0008-6

Fairchild, G., Faulds, A., & Matta, J. (2008). Beetle assemblages in ponds: Effects of habitat and site age. *Freshwater Biology, 44*, 523–534. https://doi.org/10.1046/j.1365-2427.2000.00601.x

Florencio, M., Díaz-Paniagua, C., Gómez-Rodríguez, C., & Serrano, L. (2014). Biodiversity patterns in a macroinvertebrate community of a temporary pond network. *Insect Conservation and Diversity, 7*, 4–21. https://doi.org/10.1111/icad.12029

Foster, G. N. (2010). *Species Status No. 1: A review of the scarce and threatened Coleoptera of Great Britain – Part 3: Water beetles of Great Britain*. Joint Nature Conservation Committee, Peterborough.

Foster, G. N., Bilton, D. T., & Friday, L. E. (2014). *Keys to adults of the water beetles of Britain and Ireland. Pt. 2: Coleoptera: Polyphaga: Hydrophiloidea - both aquatic and terrestrial species*. Royal Entomological Society.

Foster, G. N., & Friday, L. E. (2011). *Keys to adults of the water beetles of Britain and Ireland. 1: Coleoptera: Hydradephaga, Gyrinidae, Haliplidae, Paelobiidae; Noteridae and Dytiscidae (2nd ed.)*. Royal Entomological Society.

Gee, J. H. R., Smith, B. D., Lee, K. M., & Griffiths, S. W. (1997). The ecological basis of freshwater pond management for biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems, 7*, 91–104. https://doi.org/10.1002/(SICI)1099-0755(199706)7:2<91::AID-AQC221>3.0.CO;2-O

Gioria, M., Schaffers, A., Bacaro, G., & Feehan, J. (2010). The conservation value of farmland ponds: Predicting water beetle assemblages using vascular plants as a surrogate group. *Biological Conservation, 143*, 1125–1133. https://doi.org/10.1016/j.biocon.2010.02.007

Hassall, C., Hollinshead, J., & Hull, A. (2011). The effects of eutrophication on the biotic composition of freshwater ponds: An overview. *Hydrobiologia, 664*, 123–131. https://doi.org/10.1007/s10750-010-0435-5

Hill, M. J., Hassall, C., Oertli, B., Fahrig, L., Robson, B. J., Biggs, J., Samways, M. J., Usio, N., Takamura, N., Krishnaswamy, J., & Wood, P. J. (2018). New policy directions for global pond conservation. *Conservation Letters, 11*(e12447). https://doi.org/10.1111/conl.12447

Hill, M. J., Sayer, C. D., & Wood, P. J. (2016). When is the best time to sample aquatic macroinvertebrates in ponds for biodiversity assessment? *Environmental Monitoring and Assessment, 188*, 194. https://doi.org/10.1007/s10661-016-5178-6

Hill, M. J., White, J. C., Hawkins, J., Binu, N., Baker, E., Greaves, H. M., & Sayer, C. D. (2025). Both pond creation and restoration provide long term biodiversity gains in agricultural landscapes: Implications for conservation. *Biological Conservation*, *309,* 111279. https://doi.org/10.1016/j.biocon.2025.111279

Iversen, L. L., Rannap, R., Briggs, L., & Sand-Jensen, K. (2017). Time-restricted flight ability influences dispersal and colonization rates in a group of freshwater beetles. *Ecology and Evolution, 7*, 824–830. https://doi.org/10.1002/ece3.2680

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

Kaplan, Z., Šumberová, K., Formanová, I., & Ducháček, M. (2014). Re-establishment of an extinct population of the endangered aquatic plant *Potamogeton coloratus*. *Aquatic Botany, 119*, 91–99. https://doi.org/10.1016/j.aquabot.2014.08.005

Kleyheeg, E., Treep, J., de Jager, M., Nolet, B. A., & Soons, M. B. (2017). Seed dispersal distributions resulting from landscape-dependent daily movement behaviour of a key vector species, *Anas platyrhynchos*. *Journal of Ecology, 105*, 1279–1289. https://doi.org/10.1111/1365-2745.12738

LandIS. (2023). *LandIS Soilscapes Viewer* [WWW document]. https://www.landis.org.uk/soilscapes/ (accessed September 21, 2023)

Lepš, J., & Šmilauer, P. (2003). *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press. https://doi.org/10.1017/CBO9780511615146

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

Lewis-Phillips, J., Brooks, S. J., Sayer, C. D., Patmore, I. R., Hilton, G. M., Harrison, A., Robson, H., & Axmacher, J. C. (2020). Ponds as insect chimneys: Restoring overgrown farmland ponds benefits birds through elevated productivity of emerging aquatic insects. *Biological Conservation, 241*, 108253. https://doi.org/10.1016/j.biocon.2019.108253

Liao, W., Venn, S., & Niemelä, J. (2022). Diving beetle (Coleoptera: Dytiscidae) community dissimilarity reveals how low landscape connectivity restricts the ecological value of urban ponds. *Landscape Ecology, 37*, 1049–1058. https://doi.org/10.1007/s10980-022-01413-z

Met Office. (2023). Marham (Norfolk) UK climate averages [WWW document]. *Met Office*. https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/u127sby66 (accessed September 21, 2023)

Minot, M., Aubert, M., & Husté, A. (2021). Pond creation and restoration: Patterns of odonate colonization and community dynamics. *Biodiversity and Conservation, 30*, 4379–4399. https://doi.org/10.1007/s10531-021-02312-6

Nicolet, P., Biggs, J., Fox, G., Hodson, M. J., Reynolds, C., Whitfield, M., & Williams, P. (2004). The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. *Biological Conservation, 120*, 261–278. https://doi.org/10.1016/j.biocon.2004.03.010

Nilsson, A. N. (1984). Species richness and succession of aquatic beetles in some kettle-hole ponds in northern Sweden. *Ecography, 7*, 149–156. https://doi.org/10.1111/j.1600-0587.1984.tb01115.x

Oertli, B. (2018). Editorial: Freshwater biodiversity conservation: The role of artificial ponds in the 21st century. *Aquatic Conservation: Marine and Freshwater Ecosystems, 28*, 264–269. https://doi.org/10.1002/aqc.2902

Prince, H. C. (1962). Pits and ponds in Norfolk (Gruben und Teiche in der Grafschaft Norfolk). *Erdkunde*, 10–31.

Rodrigo, M. A., Alonso-Guillén, J. L., & Soulié-Märsche, I. (2010). Reconstruction of the former charophyte community out of the fructifications identified in Albufera de València lagoon sediments. *Aquatic Botany, 92*, 14–22.

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, L., Sayer, C.D., Zou, Yi., Greaves, H.M., Downes, D. & Axmacher, J.C. (2025). Agricultural pond restoration enhances species richness in non-biting midges (Diptera: Chironomidae). *Restoration Ecology*. **doi.org/10.1111/rec.70086**

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

Sayer, C. D., Biggs, J., Greaves, H. M., & Williams, P. (2023b). *Guide to the restoration, creation and management of ponds*. University College London.

Sayer, C., Burningham, H., Alderton, E., Axmacher, J., Robinson, P., Greaves, H. M., & Hind, A. (2023a). Bringing lost ponds back to life: The art of ghost pond resurrection. *Conservation Land Management, 21*, 25–31.

Sayer, C., Hawkins, J., & Greaves, H. M. (2022). Restoring the ghostly and the ghastly: A new golden age for British lowland farm ponds? *British Wildlife*, 477–487.

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

Sayer, C. D., & Greaves, H. M. (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

Schutten, J., Dainty, J., & Davy, A. J. (2005). Root anchorage and its significance for submerged plants in shallow lakes. *Journal of Ecology, 93*(3), 556–571. https://doi.org/10.1111/j.1365-2745.2005.00980.x

Skelly, D. K., Bolden, S. R., & Freidenburg, L. K. (2014). Experimental canopy removal enhances diversity of vernal pond amphibians. *Ecological Applications, 24*(2), 340–345. https://doi.org/10.1890/13-1042.1

Smith, L. P., Clarke, L. E., Weldon, L., & Robson, H. J. (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

Soininen, J., Bartels, P., Heino, J., Luoto, M., & Hillebrand, H. (2015). Toward more integrated ecosystem research in aquatic and terrestrial environments. *BioScience, 65*, 174–182. https://doi.org/10.1093/biosci/biu216

Stewart, N. F., & Church, J. M. (1992). *Red Data Books of Britain and Ireland: Stoneworts*. The Joint Nature Conservation Committee.

Stobbe, A., Gregor, T., & Röpke, A. (2014). Long-lived banks of oospores in lake sediments from the Trans-Urals (Russia) indicated by germination in over 300-year-old radiocarbon dated sediments. *Aquatic Botany, 119*, 84–90. https://doi.org/10.1016/j.aquabot.2014.07.004

Stroh, P. A., Leach, S. J., August, T. A., Walker, K. J., Pearman, D. A., Rumsey, F. J., Harrower, C. A., Fay, M. F., Martin, J. P., Pankhurt, T., Preston, C. D., Taylor, I. (2014). A vascular plant red list for England. Botanical Society of Britain and Ireland.

Tanaka, N., Momohara, A., Sakayama, H., & Uehara, K. (2003). Chara species that emerged from 40-year-old sediments from Lake Teganuma, Central Japan. *Nature History Research, 7*, 101–105.

Wade, P. M. (1990). The colonisation of disturbed freshwater habitats by Characeae. *Folia Geobotanica et Phytotaxonomica, 25*, 275–278. https://doi.org/10.1007/BF02913027

Wade, P. M., & Edwards, R. W. (1980). The effect of channel maintenance on the aquatic macrophytes of the drainage channels of the Monmouthshire levels, South Wales, 1840–1976. *Aquatic Botany, 8*, 307–322. https://doi.org/10.1016/0304-3770(80)90061-3

Walton, R. E., Sayer, C. D., Bennion, H., & Axmacher, J. C. (2021a). 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, R. E., Sayer, C. D., Bennion, H., & Axmacher, J. C. (2021b). Improving the pollinator pantry: Restoration and management of open farmland ponds enhances the complexity of plant-pollinator networks. *Agriculture, Ecosystems & Environment, 320*, 107611. https://doi.org/10.1016/j.agee.2021.107611

Walton, R. E., Sayer, C. D., Bennion, H., & Axmacher, J. C. (2021c). Once a pond in time: Employing palaeoecology to inform farmland pond restoration. *Restoration Ecology, 29*, e13301. https://doi.org/10.1111/rec.13301

Williams, P. (2018). What's happening to the quality of our best ponds? A re-survey of National Pond Survey sites after 24 years. *Freshwater Habitats Trust*.

Williams, P., Biggs, J., Stoate, C., Szczur, J., Brown, C., & Bonney, S. (2020). Nature-based measures increase freshwater biodiversity in agricultural catchments. *Biological Conservation, 244*, 108515. https://doi.org/10.1016/j.biocon.2020.108515

Williams, P., Whitfield, M., & Biggs, J. (2008). How can we make new ponds biodiverse? A case study monitored over 7 years. *Hydrobiologia, 597*, 137–148. https://doi.org/10.1007/s10750-007-9224-9

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

Woodward, K. B., & Hofstra, D. (2024). Submerged macrophyte root oxygen release reduces sediment oxygen demand: A positive feedback loop in shallow lakes. *Aquatic Botany*, *193*, 103776. https://doi.org/10.1016/j.aquabot.2024.103776

TABLES

Table 1: Management intervention categories and the ponds representing each respective management group. Shortened name used to refer to each group in results and discussion. Pond locations are provided in Fig. 1.

Group	Management / restoration	Shortened name	Sites
0	Non-managed (control) or pre-managed	Control	BULLS2, CHEST1, HEY89, MYSTF and all other ponds pre-restoration
1	Removal of overhanging woody vegetation	Only wood removal	BONF1, COLG1 post-restoration
2	Major removal of overhanging woody vegetation and minor sediment removal	Wood and sediment removal	HEY93, HEY97, PYES1, PYES2 post-restoration
3	Major removal of overhanging woody vegetation and major sediment removal	Major wood and sediment removal	COLG3, COLG4, DAIRY2, HEY96, HEY102 post-restoration

Table 2: Summary of wetland plant and water beetle species gained and lost in the pond landscape over the study period. (#) indicates number of species unique to that group. For a full wetland plant list see Table S2 and for water beetle species list see Table S4. *Schedule 8 protected species in 1981 British Wildlife and Countryside Act. Group 0 = Control sites and pre-restoration pond surveys, Group 1 = major woody vegetation removal only, Group 2 = major woody vegetation removal, minor sediment removal, Group 3 = major woody vegetation and sediment removal.

	No. of spp. lost	No. of spp. gained (unique to group)	Rare spp. lost (unique to group)	Rare spp. gained (unique to group)	Total no. spp. (average per site) no. of individuals]
Wetland Plants					
Before rest.	-	-	-	-	27 (5)
After rest.	1	32	1	21	59 (15.5)
Group 0	1 (1)	2 (2)	1 (1)	0	**% Increase**
Group 1	0 (0)	3 (1)	0	2 (1)	118.5%
Group 2	0 (0)	19 (10)	0	8 (4) (inc. *Najas marina)**	
Group 3	0 (0)	20 (10)	0	11 (6)	
Water beetles					
Before rest.	-	-	-	-	24 (4.9) [42]
After rest.	8	19	2	6	35 (14.4) [304]
Group 0	4 (4)	6 (6)	1 (*Hydroporus angustatus*)	1 (1) - *Hydraena nigrita*	**% Increase**
Group 1	2 (2)	3 (3)	1 (*Ilybius chalconatus*)	0 (0)	45.8% [623.8%]
Group 2	1 (1)	4 (2)	0 (0)	3 (1) - *Helochares obscurus, Scarodytes halensis, Helophorus griseus*	
Group 3	1 (1)	8 (6)	0 (0)	4 (2) - *Gyrinus natator, Helochares obscurus, Hydrochus megaphallus, Helophorus griseus*	