Both pond creation and restoration provide long term biodiversity gains in agricultural landscapes: implications for conservation

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Both pond creation and restoration provide long term biodiversity gains in agricultural landscapes: implications for conservation

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ABSTRACT

Ponds are globally recognised for their unique contribution to freshwater biodiversity. However, due to agricultural intensification and urban development, many ponds within human-dominated landscapes have been lost, while many remaining ponds in such environments have become heavily terrestrialised, which has significantly reduced landscape-scale freshwater biodiversity. To reverse such trends, two main conservation approaches have been employed: pond creation and pond restoration. However, there remains a limited understanding on the longer-term effectiveness of these conservation techniques. This study aimed to quantify and compare long term responses of aquatic macrophyte communities among 56 created (28) and restored (28) ponds across an agricultural landscape in eastern England (United Kingdom). For both approaches, alpha and gamma richness were significantly higher 11+ years after intervention compared to 1–2 years following intervention, but their temporal trajectories differed. Plant colonisation was faster at restored compared to created ponds, with the former displaying a significantly higher taxonomic richness 1–2 and 3–6 years post-intervention. At 11+ years after pond creation or restoration, similar alpha and gamma diversity was recorded for the two conservation approaches. Successive time periods generally demonstrated more similar macrophyte communities within restored and created ponds, and macrophyte compositional differences between created and restored ponds decreased with time. Pond restoration and creation should be used as complementary approaches to create broader abiotic and biotic gradients, in turn supporting different species and community compositions across the landscape. Both approaches are urgently needed to bend the curve on global freshwater biodiversity losses.

1. Introduction

Ponds, both natural and human-made, are ubiquitous worldwide, and despite being historically understudied compared to other freshwater environments (e.g., lakes, rivers), are now being increasingly recognised for their important contribution to freshwater biodiversity (Williams et al., 2010a, 2010b; Hill et al., 2016; Vad et al., 2017). Pond biodiversity typically exhibits high spatiotemporal turnover, driven by high environmental heterogeneity, which results in many individual waterbodies across a pond network contributing to overall regional diversity (Hassall et al., 2012; Sayer et al., 2012; Hill et al., 2017). High environmental heterogeneity and associated ecological niches can result in pond networks often having a higher landscape-scale biodiversity compared to (i) a single larger lentic waterbody of the same size (Oertli et al., 2002), and, sometimes (ii) other freshwater habitats (e.g., streams and ditches; Williams et al., 2004; De Meester et al., 2005). The contribution of ponds to landscape-scale freshwater biodiversity patterns becomes particularly important in human-dominated environments where a large proportion of freshwater habitats have been lost or degraded (Ballut-Dajud et al., 2022). Moreover, in urban and agricultural environments ponds can act as islands of high-quality habitat for aquatic and terrestrial species in an otherwise unfavourable matrix (Sayer et al., 2012; Lewis-Phillips et al., 2019a, 2019b).

Despite their importance for biodiversity globally, many rural ponds

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have been in-filled and abandoned during the last century owing to agricultural intensification and urban development (Boothby and Hull, 1997; Wood et al., 2003; Thornhill et al., 2018). Thus, at the landscape scale, ponds have become increasingly isolated, with probable adverse effects for metapopulations and metacommunities (Joly et al., 2001; Jeffries, 2005; Hyseni et al., 2021). Where ponds remain, they have often been subjected to nutrient enrichment and other forms of chemical pollution (e.g., neonicotinoid inputs: Merga and Van den Brink, 2021), excessive physical disturbance, habitat simplification and invasive species colonisation, all of which lead to significant declines in pond biodiversity (Sun et al., 2019). In addition, due to the cessation of traditional grazing practices and/or management involving periodic scrub removal from ponds, agricultural pond networks worldwide have become dominated by wood-filled, late-succession ponds (Janssen et al., 2018; Sayer et al., 2012) – a so-called 'mass-terrestrialisation' effect (Sayer and Greaves, 2020). While generally species-poor late successional ponds that are overgrown by bushes, trees and fallen wood dominate agricultural landscapes, studies have shown major reductions in both aquatic and terrestrial biodiversity compared to landscapes where early open-canopy and mid-succession, macrophyte-rich ponds prevail (Lewis-Phillips et al., 2019a, 2019b; Sayer et al., 2012).

To address the degradation and terrestrialisation of agricultural pond networks, and to increase the density and environmental heterogeneity of ponds, two broad management approaches have typically been undertaken: pond creation and pond restoration (Williams et al., 2020b; Sayer et al., 2022). Pond creation has been the principal conservation approach in Europe, and occurs where new ponds are dug in the landscape and good water quality is prioritised in site selection. Previous research has demonstrated substantial benefits of creating new ponds for various aquatic faunal and floral groups (Coccia et al., 2016). For instance, Williams et al. (2020a) reported that pond creation increased total-catchment macrophyte richness by 26 %, and rare macrophyte species numbers by 181 %. Indeed, much is understood regarding the value of creating ponds for enhancing biodiversity in freshwater landscapes (Williams et al., 2020b) and there is a robust knowledge and evidence base on how best to design new ponds and pondscapes to maximise biodiversity (Biggs et al. 1994; Freshwater Habitats Trust, 2024; Sayer et al., 2023a). In addition, a new avenue for pond conservation is ghost pond resurrection, whereby ponds that have been deliberately in-filled are re-excavated, thus exposing long-lived (100+ years) seedbanks that can facilitate a fast (re)establishment of aquatic macrophyte communities (Alderton et al., 2017; Sayer et al., 2023b).

An alternative and complementary approach is to 'restore' ponds, which typically involves the re-setting of successional processes via pond de-watering (Lemmens et al., 2013), or for ponds at an advanced stage of terrestrialisation, removing major woody vegetation and pond sediment (Walton et al., 2021a; Sayer et al., 2022), followed by periodic management (Sayer et al., 2012). Recent research has highlighted the benefits of restoring late-succession ponds in the landscape for freshwater plant and macroinvertebrate species (Sayer et al., 2012; Janssen et al., 2018; Sayer et al., 2022; Ruse et al., 2025), and has also been shown to benefit a range of terrestrial taxa, including pollinators (Walton et al., 2021a, 2021b) and farmland birds (Davies et al., 2016; Lewis-Phillips et al., 2019a, 2019b). To date, however, few studies have directly compared pond creation and restoration to assess how they might differentially and/or complementarily influence aquatic biodiversity across the landscape. One notable exception is Minot et al. (2021), who studied larval odonate assemblages in Normandy, northwest France, across an equal number of created and restored ponds over a period of 2–3 years. The authors reported no significant difference in species richness or colonisation patterns between the two approaches, suggesting comparable contributions to odonate conservation. By understanding how different pond conservation/management approaches influence freshwater biodiversity, more ecologically effective management plans can be developed to maximise freshwater biodiversity within human-dominated landscapes.

To address this critical research gap and to contribute to future European pond conservation practice and policy, we aimed to quantify the temporal (1–2 years to 11+ years) responses of aquatic macrophyte communities to pond creation and pond restoration within an agricultural area of eastern England (United Kingdom). For this, we considered the following research questions: (1) what are the temporal responses of macrophyte richness patterns following pond restoration and creation? (2) do macrophyte communities become increasingly similar over time between restored and created ponds? (3) how does the conservation value of ponds change following restoration or creation?

2. Material and methods

2.1. Study sites

This study was undertaken in eastern England, United Kingdom, spanning the counties of Suffolk and Norfolk (Fig. 1). The study area is lowland (< 100 m.a.s.l), predominantly arable farmland, interspersed by meadows, small ancient and secondary woodland patches, with fields mostly enclosed by hedgerows. The study sites experience average annual maximum and minimum temperatures of 15 °C and 6 °C (1991–2020) respectively, with an annual average rainfall of 626 mm (1991–2020; UK Meteorological Office, 2022). The ponds are mostly perennial and are generally fed by shallow groundwater facilitating seasonally consistent water-level fluctuations: peaks in March–April and lows in September–October. Underlying geology largely comprises chalk (a fine powdered limestone) overlaid by chalky boulder clay.

In total, 56 ponds were examined that were equally split between created (28) and restored (28) ponds, the latter undergoing major woody vegetation and sediment removal (Fig. 2). These ponds were targeted at random from a wider dataset of 65 farm ponds subject to restoration as part of the Suffolk Wildlife Trust's Ponds Project. Some ponds were sampled multiple times after the creation/restoration intervention (e.g., 2, 6 and 11 years after intervention). However, to minimize temporal autocorrelation effects, where multiple surveys were collected from a single pond, only one of those surveys was included here. All ponds examined in this study were categorised into one of four time interval categories: 1–2 years, 3–6 years, 7–10 years and 11+ years post-intervention, with 7 created and restored ponds included in each time interval to ensure a balanced study design (Fig. 2). The restored ponds most likely originate from clay excavations undertaken in the 17th–19th centuries. All study ponds are small in area (mean: 307 m^2, min: 28 m^2, max: 8102 m^2), and shallow (mostly <2 m max. depth) (Fig. 2).

2.2. Macrophyte data collection

Wetland plants were surveyed visually by walking the entire perimeter of each pond, with a double-headed rake used to collect plants from deeper areas that could not be easily assessed. A species list (presence-absence) was made in-situ at each site covering all emergent, floating and marginal wetland vascular plants, including stoneworts (Characeae). Mosses were not included in this study.

2.3. Statistical analysis

2.3.1. Alpha and gamma diversity

All statistical analysis was conducted in R (R Development Core Team, 2022). Alpha diversity was defined as the taxonomic richness within an individual pond site, and gamma diversity as the overall number of species among the created or restored ponds. A Kruskal Wallis test (using the function *Kruskal.test* – non-normality prevented regression-based analyses) was used to test alpha diversity differences between: (i) each intervention type (i.e., restored versus created ponds) across each time interval period (1–2, 3–6, 7–10 and 11+ years) and (ii) across time periods within each intervention type. Pairwise comparisons

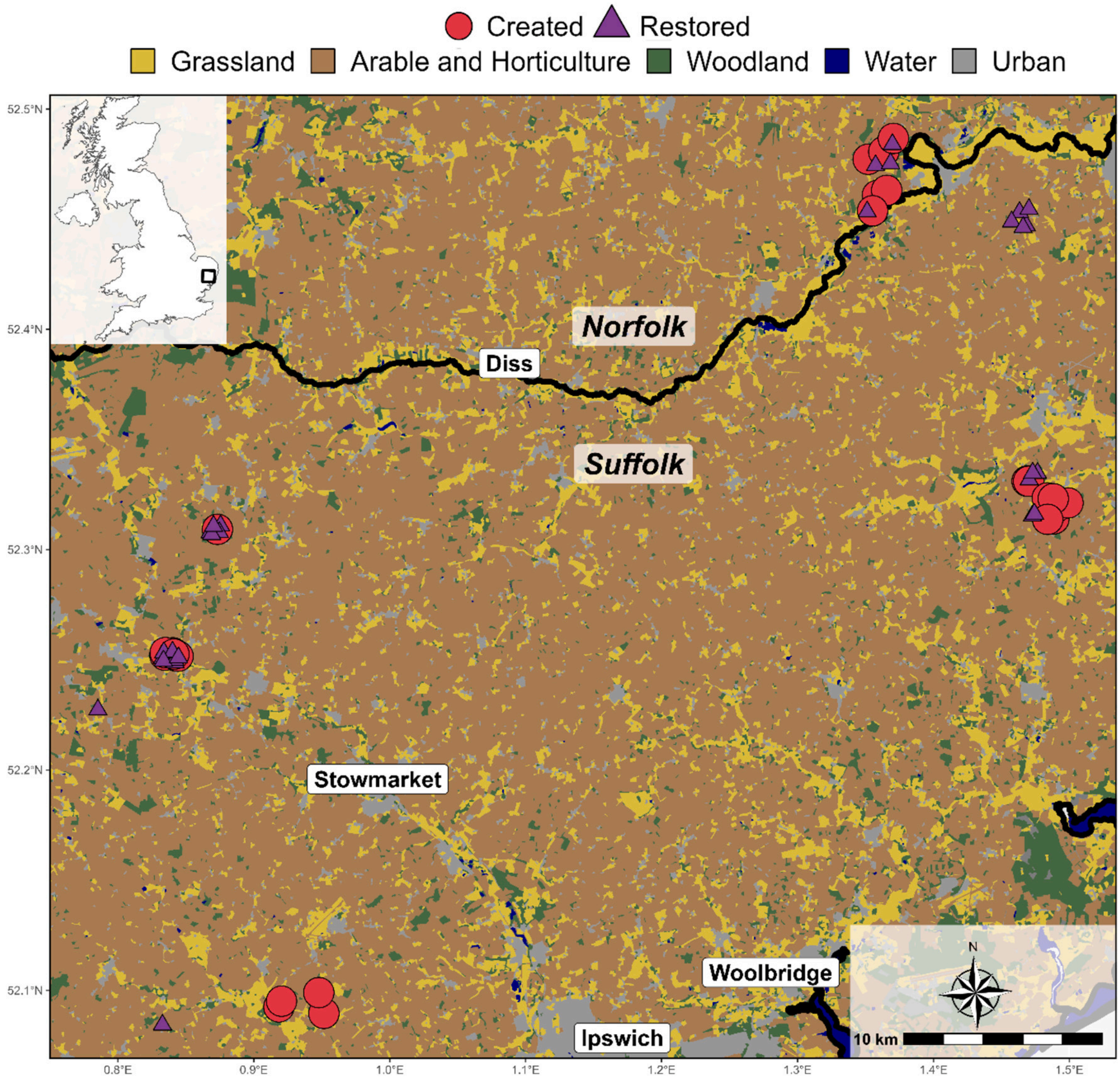

Fig. 1. Location of the 56 studied ponds in Norfolk and Suffolk, eastern England (inset).

using Nemenyi post hoc tests (using the *kwAllPairsNemenyiTest* function in the PMCMR package in R: Pohlert, 2022) were undertaken to determine where significant differences among the different study periods occurred for created and restored ponds.

2.3.2. *Macrophyte community composition*

Beta-diversity was defined here as the spatial variation in plant communities among study sites within a selected space/time (Socolar et al., 2016). To visualise changes in macrophyte compositional changes across time intervals for both intervention types, a centroid NMDS plot was constructed. A permutational multivariate analysis of variance (PERMANOVA) was undertaken using the *adonis2* function in the vegan package (Oksanen et al., 2022) to statistically test differences in macrophyte compositions between: (i) created versus restored ponds across each time interval period, (1–2, 3–6, 7–10 and 11+ years) and (ii) each time interval within either created or restored ponds. To examine the heterogeneity of macrophyte compositions within created and restored pond for each time interval, Permutational Multivariate Analysis of Dispersion (PERMDISP) values were calculated using the *betadisper* function in vegan. Statistical differences in PERMDISP values between the same comparisons as (i) and (ii) above were undertaken using a one-way Analysis of Variance (residual diagnostics were inspected to ensure assumptions of normality and homoscedasticity were satisfied). Tukeys Honest Significant Difference posthoc tests were subsequently undertaken to identify where significant pairwise differences in PERMDISP values occurred. For NMDS, PERMDISP and PERMANOVA analyses, the Sorensen dissimilarity measure was employed.

Total beta-diversity including species replacement and nestedness components were calculated (based on the Baselga family Jaccard-based indices) for restored and created pond macrophyte communities across each time interval, using the *beta.div.comp* function in the aedspatial package (Dray et al., 2021). Species replacement reflects the turnover of species between sites (ponds), while nestedness occurs when communities in species poor sites represent subsets of the communities in species rich sites (Hill et al., 2017). To determine the contribution of species replacement and nestedness to total beta-diversity between created and restored ponds for each time period, pairwise dissimilarity matrices for each time period, were initially calculated (based on the Baselga family, Jaccard-based indices) using the beta.div.comp function. Subsequently, mean pairwise total beta-diversity, and the mean pairwise contribution of species replacement and nestedness for each pairwise created vs. restored pond comparison for each time period was calculated. Comparisons of total beta-diversity, turnover and nestedness across the different time periods were also examined within each intervention (created and restored).

Fig. 2. Created farm ponds 2 years (a,b) and 10 years (c) after creation and restored farm ponds before (d), 2 years (e) and 10 years after restoration (f).

2.3.3. Conservation value

To quantify the conservation value of created and restored ponds, the Species Rarity Index (SRI) was calculated. For this, each recorded macrophyte was assigned a rarity value based on UK Joint Nature Conservation Committee (JNCC) criteria (Biggs, 2005). The SRI value for each pond was calculated by summing the rarity value assigned to each macrophyte species in a pond sample and dividing it by taxonomic richness (see Biggs, 2005). Differences in SRI scores between restored and created ponds among each of the time intervals were examined using a Kruskal Wallis test.

3. Results

3.1. Macrophyte richness

In total, 84 macrophyte species were recorded in this study, with 66 and 58 species recorded from restored and created ponds, respectively. The most commonly recorded of these were *Juncus inflexus* which was recorded from 37 ponds, followed by *Agrostis stolonifera* (36 ponds), *Potamogeton natans* (36 ponds), *Lemna minor* (23 ponds), *Typha latifolia* (23 ponds), *Juncus effusus* (22 ponds), and *Epilobium hirsutum* (21 ponds).

Restored ponds supported a greater total richness (gamma diversity) 1–2 years (34 species), 3–6 years (41 species) and 7–10 years (37 species) after intervention compared to the created ponds (1–2 years: 11 species, 3–6 years: 22 species, 7–10 years: 29 species) (Fig. 3a). Total richness increased rapidly among restored ponds 1–2 and 3–6 years after intervention and then plateaued across the remaining time intervals. Created pond total richness increased more slowly initially but maintained this trajectory consistently across successive time intervals (Fig. 3a). After 11+ years, created (39 species) and restored (40 species) ponds supported a similar macrophyte total richness (Fig. 3a). The dominant species in terms of the different intervention types (i.e., created versus restored) and time intervals are outlined in Supplementary Material Table S1.

For both restored and created ponds, median species richness (alpha diversity) increased over time after the intervention, with the lowest median macrophyte richness recorded 1–2 years after intervention (median macrophyte richness – restored = 8, created = 6) and the highest median macrophyte richness recorded at 11+ years after intervention (median macrophyte richness – restored = 13, created = 10: Table 1, Fig. 3b). Compared to the created ponds, macrophyte richness was significantly higher in restored ponds 1–2 years (Kruskal Wallis test, $\text{Chi}^2 = 6.6$, df = 1, $p = 0.01$) and 3–6 years (Kruskal Wallis test, $\text{Chi}^2 = 6.9$, df = 1, $p = 0.009$) after intervention (Fig. 2b). No significant difference in macrophyte richness was evident, however, between restored and created ponds after 7–10 years (Kruskal Wallis test, $\text{Chi}^2 = 1.3$ df = 1, $p = 0.249$) and 11+ years (Kruskal Wallis test, $\text{Chi}^2 = 0.5$ df = 1, $p = 0.479$) after intervention.

Alpha diversity patterns were broadly congruent with those reported for gamma diversity, with macrophyte richness among restored ponds increasing rapidly 1–2 and 3–6 years post-intervention and stabilising after 7–10 and 11+ years (Fig. 3b). Conversely, created ponds exhibited a low macrophyte richness 1–2 and 3–6 years post-intervention, followed by consistent increases 7–10 and 11+ years after creation (Fig. 3b). Significant differences in macrophyte richness were recorded between the time interval groups among the created ponds (Kruskal Wallis test, $\text{Chi}^2 = 9.599$, df = 3, $p = 0.002$). Post hoc Nemenyi tests indicated that macrophyte diversity 11+ years after pond creation was significantly higher than 3–6 years (q value = 3.676, $p = 0.046$). Among restored ponds, no significant differences were recorded between time intervals (Kruskal Wallis test, $\text{Chi}^2 = 4.03$, df = 3, $p = 0.258$).

3.2. Macrophyte community composition

Successive time intervals (e.g., years 1–2 and 3–6, or 7–10 and 11+ after intervention) showed more similar macrophyte communities across both created and restored pond categories, with greater macrophyte heterogeneity evident with increased time between sampling periods (e.g., 1–2 and 11+ years after intervention; Fig. 4a). In addition, created and restored pond macrophyte communities became increasingly similar through time, as demonstrated by the closer proximity of created and restored pond NMDS centroids for 11+ years after intervention versus earlier time intervals (Fig. 4a). Reinforcing this, pairwise PERMANOVA tests showed (a) macrophyte composition 1–2 years after pond creation to be significantly different ($p < 0.05$) to created ponds 7–10 years and 11+ years after creation, and to restored ponds 3–6 and 7–10 years after restoration, (b) macrophyte composition 3–6 years after pond creation was significantly different to macrophyte composition 11+ years after creation, and to restored ponds 11+ years after restoration and (c) macrophyte composition 7–10 years after pond creation was significantly different to macrophyte composition 11+ years after pond creation and to restored ponds 11+ years after pond restoration (see Supplementary Material Table S2 for full PERMANOVA results).

Broadly (apart from 1 to 2 years after intervention), the heterogeneity (multivariate dispersion – PERMDISP values) of macrophyte communities within each sample time period was similar for both created and restored ponds (Fig. 4b) and no significant differences ($p > 0.05$) were recorded between all studied years within created or restored ponds or between created or restored ponds across different time periods (Fig. 4b, see Supplementary Material Table S3 for multivariate dispersion for created and restored ponds for each time period and Tukey pairwise test results).

Moderate beta-diversity was recorded across all study periods for created and restored ponds (Fig. 5a). Among restored ponds, total beta diversity declined with increasing time since intervention, and the compositional variation of macrophytes was almost entirely explained by species replacement across all sample periods for the restored ponds (Fig. 5a). By contrast, among created ponds, beta diversity increased with time since intervention. Species replacement explained the majority of total beta-diversity compared to nestedness in created ponds, although there was an increased contribution of nestedness 7–10 years after creation (Fig. 5a). Relatively high numbers of species were gained and lost between each sampling time interval (Table 2), demonstrating high turnover of species at the landscape scale.

When macrophyte composition was compared between the restored and created ponds across the different time intervals, significant differences (average pairwise dissimilarity) were recorded. Compositional heterogeneity increased from 1 to 2 to 3–6 years between restored and created ponds, but then decreased subsequently (Fig. 5b). The greatest differences in macrophyte composition between created and restored ponds was recorded 3–6 years (total beta diversity: 0.88) after intervention, while the lowest macrophyte heterogeneity was evident 11+ years (total beta diversity: 0.78) after intervention. Increasing similarity of macrophyte composition through time was demonstrated by the close proximity of the created and restored pond NMDS centroid 11+ years after intervention (Fig. 4a). Species replacement contributed most to total macrophyte beta diversity across all time periods (Fig. 5b). Restored ponds supported more unique species (taxa recorded only from one pond type), 1–2, 3–6 and 7–10 years after intervention, although the proportion of unique taxa in created ponds increased consistently through time (Fig. 6, Table S4). At 11+ years after intervention a similar proportion of macrophyte species were unique to both created and restored ponds, and the number of taxa present in both the created and restored ponds increased with time.

3.3. Conservation value

In total, three species with a conservation designation were recorded from the studied ponds: *Chara aculeolata* (nationally scarce; recorded from one created pond 11+ years after intervention), *Tolypella intricata* (RDB vulnerable; recorded from one restored pond 7–10 years after intervention) and *Oenanthe fistulosa* (RDB vulnerable; recorded from one restored pond 7–10 years after intervention, see Table 2). The highest SRI score was recorded from a restored pond 7–10 years after intervention (SRI: 3.66, *very high conservation value*) but 75 % of all study samples recorded a score of 1 (*low conservation value:* Table 3). No statistically significant difference in SRI scores were recorded between restored and created ponds across any time period: 1–2 years (created pond mean SRI: 1, restored pond mean SRI: 1.018, Kruskal Wallis test, $\text{Chi}^2 = 1$, df = 1, $p = 0.317$), 3–6 years (created pond mean SRI: 1.038, restored pond mean SRI:1.038, Kruskal Wallis test, $\text{Chi}^2 = 0$, df = 1, $p = 1$), 7–10 years (created pond mean SRI: 1.06, restored pond mean SRI: 1.63, Kruskal Wallis test, $\text{Chi}^2 = 0.892$, df = 1, $p = 0.640$) and 11+ years (created pond mean SRI: 1.07, restored pond mean SRI: 1.02, Kruskal Wallis test, $\text{Chi}^2 = 0.387$, df = 1, $p = 0.539$; Table 3). No significant differences in conservation value (based on the SRI) were found between survey intervals for restored ponds (Kruskal Wallis test, $\text{Chi}^2 = 2.4267$, df = 3, $p = 0.489$) or created ponds (Kruskal Wallis test, $\text{Chi}^2 = 3.514$, df = 3, $p = 0.319$).

A total of three non-native species (based on the Global Register of introduced and invasive species – Great Britain) were recorded across the study area and period; *Crassula helmsii* (recorded from one created ponds 11+ years after intervention), *Epilobium ciliatum* (recorded from

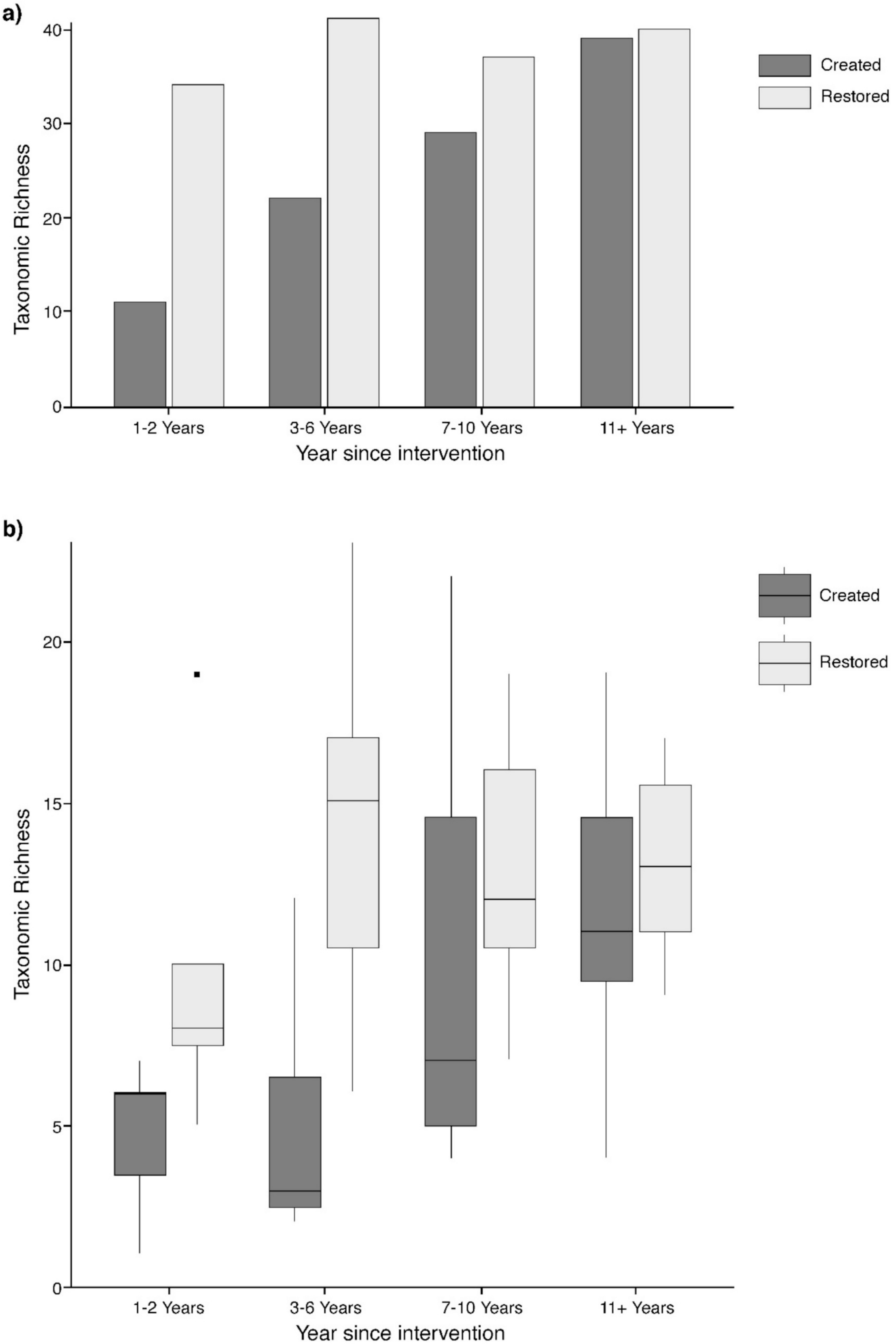

Fig. 3. (a) Total macrophyte richness (gamma diversity) for ponds sampled 1–2 years, 3–6 years, 7–10 years and 11+ years after pond creation or restoration and (b) boxplots of macrophyte richness (alpha diversity) for ponds sampled 1–2 years, 3–6 years, 7–10 years and 11+ years after pond creation or restoration (boxes show 25th, 50th and 75th percentiles, upper whiskers shows 75th percentile +1.5 * IQR, and the lower whisker shows the 25th percentile −1.5 * IQR.

Table 1
Summary statistics for aquatic macrophyte richness recorded from restored and created ponds across 1–2 years, 3–6 years 7–10 years and 11+ years since the management intervention.

Macrophyte richness		1–2 years	3–6 years	7–10 years	11+ years
Created	Mean	4.7	5	10.3	11.6
	Median	6	3	7	10
	Std. Deviation	3.1	3.9	7.8	4.9
	Min	1	2	4	4
	Max	7	12	22	19
Restored	Mean	9.6	14.1	13	13.1
	Median	8	15	12	13
	Std. Deviation	4.5	6.1	4.2	3.1
	Min	5	6	7	9
	Max	19	23	19	17

one created pond 1–2 years after intervention), *Lemna minuta* (recorded from 2 restored ponds 3–6 years after intervention).

4. Discussion

In recent years, there has been increasing recognition of the vital contributions that pond networks make to global freshwater biodiversity (Hill et al., 2021). However, due to agricultural intensification, urban development and a broader loss of historic pond uses (e.g., a water source for livestock), many ponds in human-dominated landscapes have been lost due to deliberate infilling (Wood et al., 2003; Swartz and Miller, 2021), or degraded due to water quality deterioration and/or terrestrialisation (Janssen et al., 2018; Sayer and Greaves, 2020; Sayer et al., 2022). Such pressures have resulted in widespread fragmentation and landscape-scale biodiversity declines in pond environments worldwide. Aside from the resurrection of infilled 'ghost ponds' (Alderton et al., 2017), two major approaches have been employed to increase the number of high-quality ponds in the landscape - pond creation (Williams et al., 2020a) and pond restoration (Sayer et al., 2022). This study compared the longer-term response of macrophyte communities to pond creation and restoration and found both approaches to be highly beneficial within an agriculturally-dominated landscape.

4.1. *Macrophyte richness responses to pond creation and restoration over time*

Pond restoration, which included major woody vegetation and sediment removal, facilitated more rapid increases in macrophyte richness than created ponds. Specifically, restored ponds supported a higher median (alpha) and total (gamma) richness than created ponds 1–2 and 3–6-years post-intervention. Woody vegetation clearance immediately reduces shade and de-silting removes poorly-consolidated leaf-dominated muds deposited under a dense tree canopy. Both of these changes will favour macrophyte development by increasing light availability for emergent as well as open-water plants (Sayer et al., 2012) and by increasing sediment cohesion and oxygenation (Schutten et al., 2005; Woodward and Hofstra, 2024). The rapid assembly of wetland plants in these restored ponds is also highly likely due to the disturbance and exposure of long-lived sediment seed banks. Previous research has demonstrated decadal-centennial scale viability of wetland plant propagules in pond sediments, spanning many species (including *Chara* spp. *Potamogeton* spp., *Ranunculus* sect. *Batrachium*), which allows for the re-establishment of plants following sediment removal (Kaplan et al., 2014; Stobbe et al., 2014; Alderton et al., 2017; Poschlod and Rosbakh, 2018). In turn, comparisons of sediment core plant macro-remains and post-restoration vegetation surveys have shown pond restoration by sediment removal to rapidly re-establish historic wetland plant communities (Walton et al., 2021c).

Whilst pond creation recorded slower initial gains in macrophyte richness, this increased rapidly 7–10 years post-intervention. The slower colonisation of created ponds has been reported elsewhere, including Barnes (1983) who identified <10 macrophyte species in colonised ponds in south-west England up to four years post-creation. This most likely reflects the absence of an established seedbank and hence the requirement for plant dispersal from nearby waterbodies (Vári, 2013; Lovas-Kiss et al., 2019; van Leeuwen et al., 2022; Green et al., 2023). However, more rapid macrophyte (re)establishment has been reported for created ponds elsewhere, such as Williams et al. (2010b) who found 34 species after 6 months (and 64 species after 7 years) in 40 newly created ponds in southern England. Differences in colonisation rates between the current study and Williams et al. (2010b) could potentially be explained by contrasts in connectivity and land use. This study was undertaken in a fragmented agricultural matrix, while Williams et al. (2010a, 2010b) studied ponds within a floodplain that had a high proportion of wetlands present. The fragmentation and relative isolation of freshwaters within agricultural landscapes undoubtedly results in greater dispersal distances for propagules. Digging ponds where there is high connectivity to other local waterbodies can thus help aid initial recovery trajectories, especially through hydrochorous transfer during flood events (Nilsson et al., 2010; Salgado et al., 2018). Other studies have also demonstrated the importance of proximity to other freshwaters for pond macrophyte dispersal, finding that ponds further apart were less likely to share similar species (García-Girón et al., 2019). It is equally likely that digging new ponds into floodplain and other wetland soils disturbs and uncovers old wetland seed banks, which, could greatly accelerate plant species accumulation.

Despite contrasting temporal trajectories of macrophyte recovery between restored and created ponds, taxonomic richness (both median richness and total richness) was comparably high 11+ years after intervention. This indicates that both pond restoration and creation result in comparable long-term biodiversity gains. While there have been no previous studies that have examined the long-term effects of pond restoration or creation on aquatic macrophyte communities, one examined how pond restoration and creation influenced odonate biodiversity (Minot et al., 2021). This focused on Tancat de la Pipa reserve, Spain, reporting no differences in species richness 3 years after pond creation or restoration. In the present study, it is unclear whether total macrophyte richness within the created and restored ponds had peaked within the study time period. Sø et al. (2020) found macrophyte species richness peaked approximately 20 years after Danish shallow lakes were created, which was followed by a decline, likely due to eutrophication development. Longer-term studies are clearly required to fully evaluate the temporal development of macrophyte species diversity after both pond creation and restoration. Beyond long-term monitoring of ponds created or restored either recently or in the future, further research could aim to target more historic interventions whereby plant communities have had sufficient time to (re)establish. In such instances, space-time substitutions (as employed in this study) could help elucidate the temporal influences of management interventions in different environments.

Disturbance caused by freshwater management can promote the establishment of non-native invasive species, as it creates newly available niches for colonisation (van Der Loop et al., 2023). However, the establishment and proliferation of non-native invasive species after creation or restoration did not occur in this study, as only two non-native species were present after 11 years (1) *Crassula helmsii* (one restored pond) and (2) *Lemna minuta* (present in two restored ponds 3–6 years after intervention). *C. helmsii*, native to Australia and New Zealand, is a highly invasive plant in the UK which suppresses macrophyte biodiversity and biomass through intense competition (Smith and Buckley, 2020; van Kleef et al., 2024). The limited presence of *C. helmsii* in the restored and created ponds most likely reflects the discrete nature of the ponds in this study and their location within an agricultural matrix which hence hinders *C. helmsii* dispersal into them via its stem fragmentation dispersal strategy (Smith and Buckley, 2020) and direct human introduction (Chapman et al., 2020). *L. minuta* (native to several

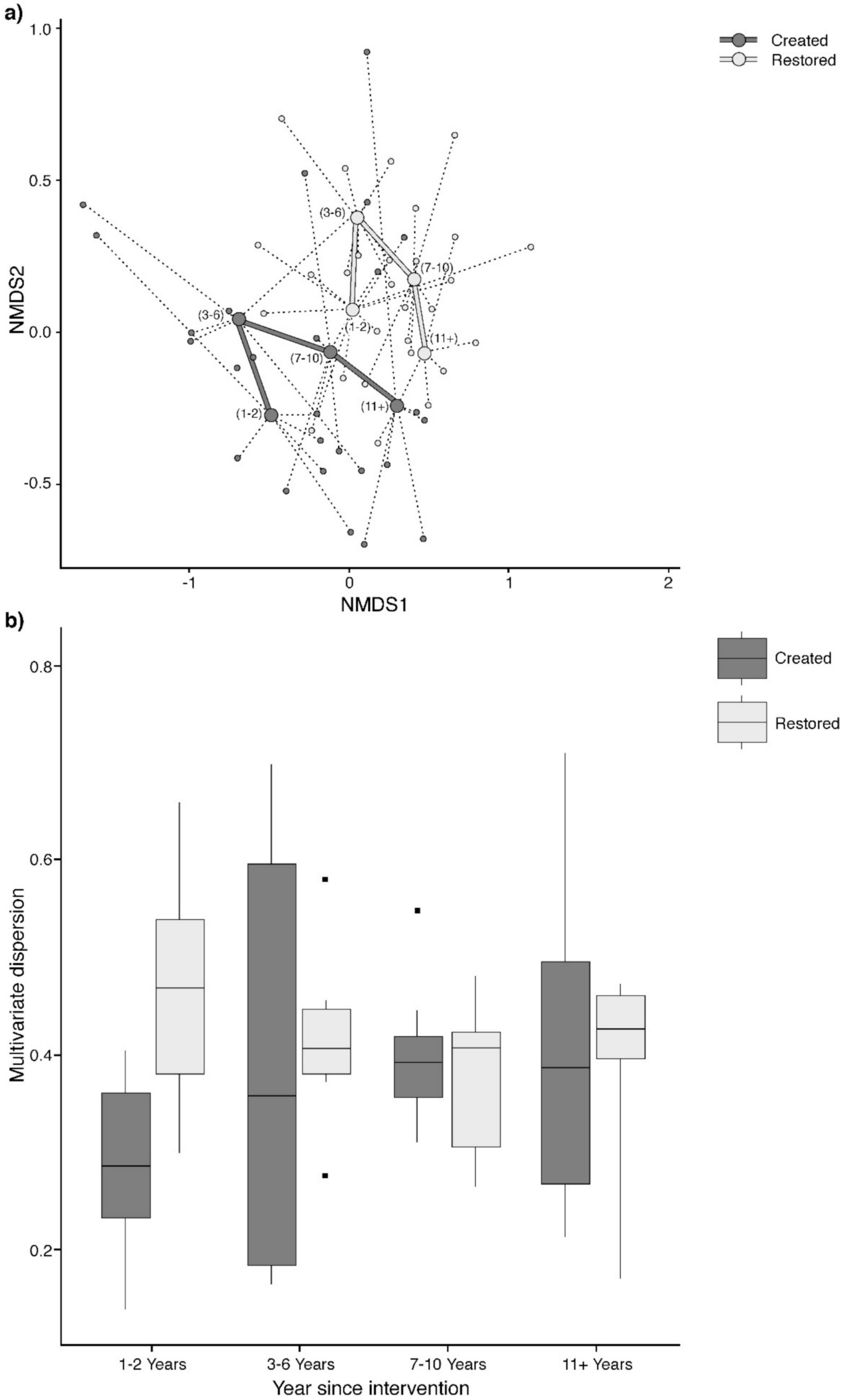

Fig. 4. Centroid NMDS plot of macrophyte communities created (blue points) and restored ponds (red points) across the different sampling periods (Sample years are presented in parentheses) (a) and boxplots of multivariate dispersion distances for macrophyte communities (Boxes show 25th, 50th and 75th percentiles, upper whiskers shows 75th percentile +1.5 * IQR, and the lower whisker shows the 25th percentile −1.5 * IQR) (b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

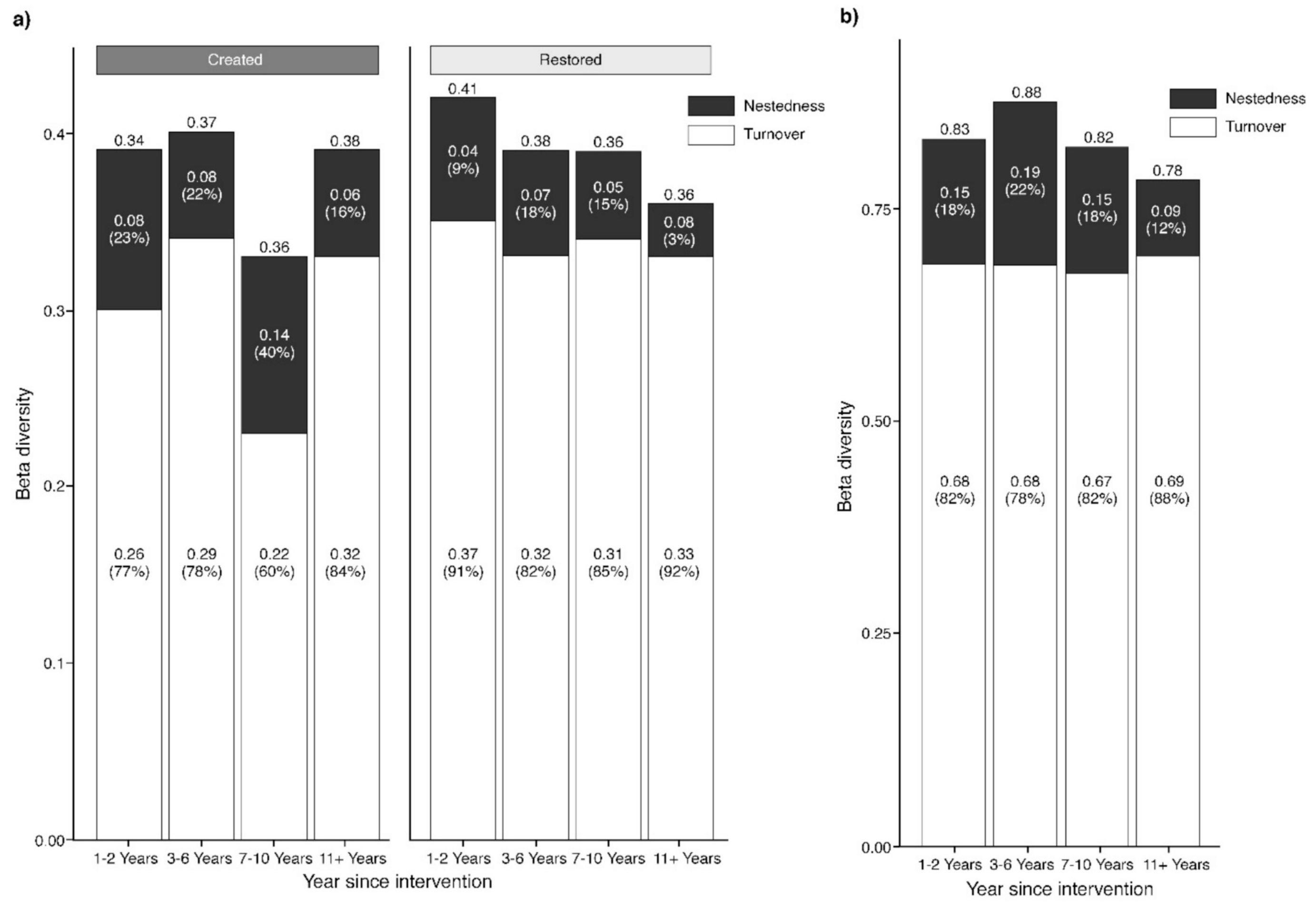

Fig. 5. The (a) relative contribution of nestedness and species replacement to total beta diversity within created and restored ponds 1–2, 3–6, 7–10 and 11+ years after the management intervention, and (b) heterogeneity of macrophyte communities (average pairwise dissimilarity) between restored and created ponds for each study time period. The relative contribution of species replacement and nestedness to the total beta-diversity between created and restored ponds in each sample year is presented. The dissimilarity value and percentage contribution are presented in parentheses.

regions in South and North America: Duenas 2009) is a free-floating duckweed species which can rapidly grow to cover the surface of ponds, outcompeting other surface macrophytes and reducing light and oxygen to pelagic and benthic species, resulting in losses of faunal and floral diversity (Peeters et al., 2013; Ceschin et al., 2019; Ceschin et al., 2020). However, among the created and restored ponds in this study *L. minuta* rarely dominated, most likely due to improved abiotic conditions after intervention, and competition with species-rich native plant communities (Paolacci et al., 2018).

4.2. Macrophyte composition responses to pond creation and restoration

Successive time intervals (e.g., years 1–2 and 3–6, and 7–10 and 11+ after intervention) had more similar macrophyte communities among the restored and created ponds, with greater macrophyte heterogeneity occurring between samples collected from ponds with increasing post-intervention time differences. This finding was not unexpected, and at least partially reflects predictable successional dynamics following management with early dominance of quick to colonise pioneer species in created ponds (e.g. Characeae) combined with species that have long-lived propagules in the sediments of restored ponds, (e.g., Characeae, Potamogetonaceae, *Ranunculus* sect. *Batrachium*) followed by a competition driven established community (Stage Sø et al., 2020). In the later time periods after intervention there was greater prevalence of the most common species (e.g., *Juncus inflexus*, *Lycopus europaeus* and *Potamogeton natans*) across the study ponds, and greater variability (gains and losses across study periods) among less common macrophyte species, as might be expected from stochastic extinction processes (Granath et al., 2024). High turnover (species gains and losses) recorded between study years may also be due to the environmentally dynamic nature of pond habitats and constantly changing environmental conditions (especially water levels), which may be suitable for particular macrophytes in one year, and unsuitable in the next (Jeffries, 2008; Boschilia et al., 2016; Fernández-Aláez et al., 2020). Compositional variation of macrophytes between restored and created ponds was almost entirely explained by species replacement, which was evident within all sample periods. This finding corroborates previous research showing high temporal turnover of macrophytes in lentic waterbodies (Boschilia et al., 2016; Sø et al., 2020). Thus, even at 11+ years after intervention, individual ponds supported distinct communities, with the majority of ponds contributing to regional richness. Similarly, in the wider landscape, ponds have been shown to make the greatest contribution to faunal and floral biodiversity at a landscape scale, with each pond contributing to overall regional richness (Williams et al., 2004; Hill et al., 2016).

Beta-diversity increased through time for created ponds, whilst for restored ponds it was highest 1–2 years after intervention and declined thereafter. High early beta-diversity for restored ponds may reflect inter-pond variation in seed bank composition, with increasing dominance of common species over time resulting in beta diversity decline in later time periods. For created ponds, where species colonisation was much slower, progressive species arrival via stochastic dispersal events and an absence of early species dominance effects likely contributed to pond

Table 2
Total diversity among restored and created ponds after 1–2, 3–6, 7–10 and 11+ years after management. The species gained category refers to taxa present in one year group and absent in the previous year group (e.g., a species would be gained if absent after 1–2 years but present after 3–6 years), and species loss refers to taxa present in the previous year group and absent in the next (e.g., a species would be lost if present in years 3–6 but absent in years 7–10).

	Restored				Created			
	Year 1–2	Year 3–6	Year 7–10	Year 11+	Year 1–2	Year 3–6	Year 7–10	Year 11+
Total diversity	34	41	37	40	11	22	29	39
Species gained	n/a	*Berula erecta* *Carex hirta* *Deschampsia cespitosa* *Eleocharis palustris* *Galium palustre* *Lemna gibba* *Lemna minor* *Lemna minuta* *Lycopus europaeus* *Oenanthe aquatica* *Phragmites australis* *Potamogeton crispus* Potamogeton trichoides *Pulicaria dysenterica* *Ranunculus trichophyllus* *Zannichellia palustris*	*Apium nodiflorum* Callitriche obtusangula *Carex pseudocyperus* *Carex riparia* *Carex vesicaria* *Chara vulgaris* *Myosotis scorpioides* *Oenanthe fistulosa* *Tolypella intricata* Epilobium spp.	*Carex flacca* *Carex remota* *Chara hispida* *Cirsium palustre* *Equisetum palustre* *Filipendula ulmaria* *Hippuris vulgaris* *Hypericum tetrapterum* *Juncus acutiflorus* *Linum catharticum* *Phragmites australis* *Pulicaria dysenterica* *Veronica beccabunga* Carex sp.	n/a	*Alisma plantago-aquatica* *Carex otrubae* *Epilobium hirsutum* *Equisetum palustre* *Juncus articulatus* *Lemna trisulca* *Lycopus europaeus* *Mentha aquatica* *Myriophyllum spicatum* *Phalaris arundinaceae* *Potamogeton crispus* *Ranunculus aquatilis* *Ranunculus flammula* *Solanum dulcamara* *Spirodela polyrhiza*	*Carex flacca* *Ceratophyllum demersum* *Chara globularis* *Eleocharis palustris* *Glyceria fluitans* *Juncus effusus* *Myosotis scorpioides* *Oenanthe aquatica* *Pulicaria dysenterica* nasturtium, officinale *Rumex crispus* *Schoenoplectus lacustris* *Schoenoplectus tabernaemontani* *Sparganium erectum* *Veronica catenata*	*Angelica sylvestris* *Apium nodiflorum* *Berula erecta* *Carex pseudocyperus* Chara aculeolata *Chara hispida* *Chara virgata* *Cirsium palustre* *Crassula helmsii* *Epilobium parviflorum* *Equisetum palustre* *Eupatorium cannabinum* *Filipendula ulmaria* *Galium palustre* *Lycopus europaeus* *Myriophyllum spicatum* *Potamogeton crispus* *Ranunculus trichophyllus* *Scrophularia auriculata* *Lychnis flos-cuculi* *Carex paniculata* Epilobium spp. *Juncus conglomeratus*
Secies lost	n/a	*Carex pendula* *Carex riparia* *Chara vulgaris* *Filipendula ulmaria* *Phalaris arundinacea* *Rumex crispus* *Scrophularia auriculata* Epilobium spp. *Riccia fluitans*	*Carex flacca* *Carex hirta* Chara spp. *Deschampsia cespitosa* *Lemna gibba* *Myriophyllum spicatum* *Oenanthe aquatica* *Phragmites australis* *Pulicaria dysenterica* *Ranunculus aquatilis* *Veronica beccabunga*	*Apium nodiflorum* Callitriche obtusangula *Carex pseudocyperus* *Carex vesicaria* *Oenanthe fistulosa* Potamogeton trichoides *Ranunculus sceleratus* *Ranunculus trichophyllus* *Tolypella intricata* *Veronica catenata* *Zannichellia palustris*	n/a	*Epilobium ciliatum* *Juncus effusus* Epilobium spp. Stratiodes aloides	Chara spp. *Equisetum palustre* *Lycopus europaeus* *Myriophyllum spicatum* *Phalaris arundinacea* *Potamogeton crispus* *Ranunculus flammula* *Spirodela polyrhiza*	*Ceratophyllum demersum* *Chara globularis* *Eleocharis palustris* *Glyceria fluitans* *Lemna trisulca* *Myosotis scorpioides* *Oenanthe aquatica* *Ranunculus aquatilis* *Rorippa nasturtium-aquaticum* *Schoenoplectus tabernaemontani* *Sparganium erectum* *Veronica catenata*

No macrophyte information is provided here as it cannot be confirmed which species were present prior to restoration and as a result which species colonised post restoration (the species present 1–2 years after restoration are presented in Table S5).

plant beta diversity increases through time. Previous research has demonstrated that dispersal, competition and local environmental conditions are important in structuring macrophyte community composition in pond networks (Akasaka and Takamura, 2011; García-Girón et al., 2019). In the case of created and restored ponds more long-term comparative studies are required to help understand how beta diversity changes on decadal scales, that also consider occasional necessary management events aimed at re-setting succession (Sayer et al., 2012).

A clear finding in this study was that created and restored ponds had

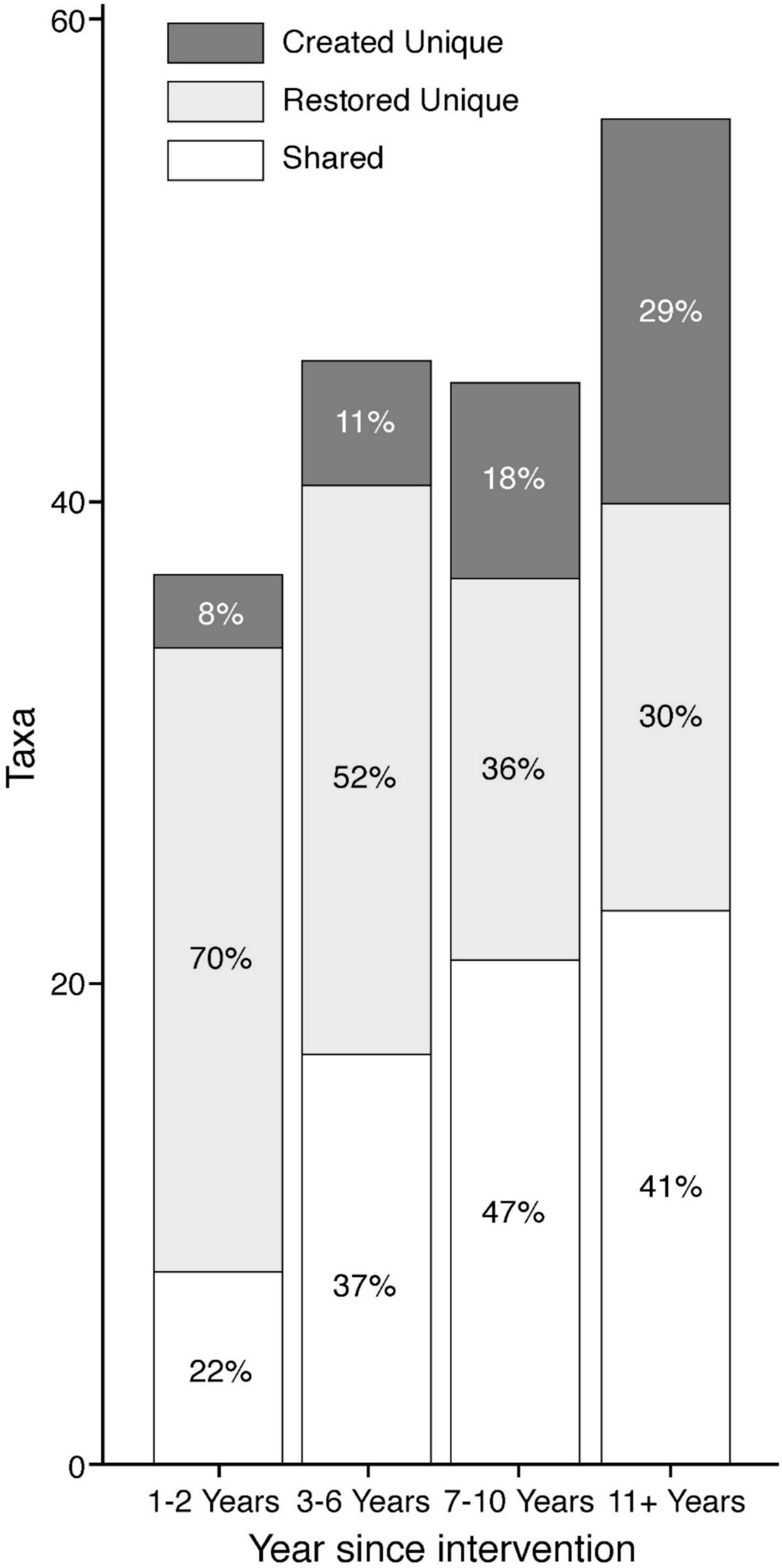

Fig. 6. The number of unique and shared macrophyte species among created and restored ponds 1–2, 3–6, 7–10 and 11+ years after the management intervention. The proportion of taxa unique to created or restored ponds, and the proportion of macrophyte taxa shared among created and restored ponds are presented in parentheses.

Table 3
The number created and restored ponds from each sampling time identified as very high, high, moderate and low conservation value (based on the SRI scores). Percentages in parentheses represent the percentage of restored or created ponds of that conservation value for that year group.

		Low	Moderate	High	Very High
1–2 years	Created	7 (100 %)	0	0	0
	Restored	6 (86 %)	0	1 (14 %)	0
3–6 years	Created	5 (71 %)	1 (14 %)	1 (14 %)	0
	Restored	5 (71 %)	2 (28 %)	0	0
7–10 years	Created	4 (57 %)	3 (43 %)	0	0
	Restored	4 (57 %)	1 (14 %)	0	2 (28 %)
11+ years	Created	5 (57 %)	1 (14 %)	1 (14 %)	0
	Restored	6 (86 %)	1 (14 %)	0	0

more similar contributions to biodiversity conservation as time progressed. The greatest dissimilarity in macrophyte community composition between restored and created ponds was recorded 1–2 and 3–6 years after intervention with a decline in dissimilarity thereafter, and with 11+ years after intervention exhibiting the lowest macrophyte heterogeneity between restored and created ponds. A far greater number of shared species among created and restored ponds over a decade after management may reflect the dispersal and colonisation of common and competitively superior macrophyte species (e.g. *P. natans*, *Sparganium erectum* in this study) across the restored and created ponds. The number of unique species was high in restored ponds 1–2 years post-intervention due to rapid plant emergence from the seed bank, with low uniqueness recorded from created ponds that most likely reflected the limited time for macrophyte (re)colonisation (Barnes, 1983). Despite having increasingly similar communities through time, several species were unique to created and restored ponds 11+ years after intervention, demonstrating similar benefits to landscape-scale biodiversity for pond creation and restoration.

4.3. Implications for pond management and conservation

This study has demonstrated that both pond restoration and creation have short to intermediate term positive effects on macrophyte diversity at the landscape-scale. Pond creation and restoration both increase the availability of high-quality freshwater habitat in agricultural landscapes, effectively emulating natural pond formation (pond creation) and natural disturbances (e.g. floods, tree fall and the activities of large herbivores like beavers) that would have re-set pond succession (pond restoration). The finding that newly created and restored ponds became increasingly compositionally similar over time, but that ponds managed at different time recorded greater macrophyte heterogeneity, suggests that creating and restoring a proportion of the ponds in the landscape across different years will create a wider gradient of abiotic and biotic conditions, in turn supporting different species and species compositions in the landscape. Pond restoration and creation undertaken across different years may also generate the environmental conditions needed to support the recolonisation and establishment of rare aquatic species in the wider landscape, as demonstrated in this study by *T. intricata* and *O. fistulosa* which were recorded in ponds 7–10 years after intervention, whilst *C. aculeolata* was recorded in a pond 11+ years after works. Although not in the selection of Suffolk restored ponds used in this study, one restored pond in the wider dataset was found to support the previously UK extinct (last recorded in 1959) charophyte *Nitella capillaris*, reflecting the disturbance of buried, still viable oospores of this species during the restoration process (Hawkins, 2019). Once brought back in the landscape opportunities then become available for rare species population expansion via dispersal into neighbouring restored or created ponds. Providing that unpolluted, clean water is present, either created or restored waterbodies can operate as important stepping stones for rare species (Williams et al., 2020a).

Pond conservation interventions should ideally reflect the specific requirements of a landscape, and both approaches should not be used without careful planning at a landscape-scale. For example, in some agricultural landscapes, where conservation projects can be financially constrained and therefore short-lived, and where rapid results are required, pond restoration may be most suitable as species diversity has a greater likelihood of rapidly increasing. Pond restoration may provide opportunities for incorporating high-quality ponds into intensively farmed landscapes, as some farmers are less keen to sacrifice land for pond creation. By contrast, in areas where the presence of ponds is low, creation may be most important to increase the density and availability of high-quality freshwater habitat and more efforts should be placed on this approach. Trees and scrub often take longer to overshade created ponds, and therefore woody vegetation management is required less quickly in created ponds (likely 10–20 years) compared to restored ponds (3–10 years: Sayer et al., 2023a). It can be concluded, however, that conservation projects should take up pond creation and restoration opportunities wherever possible, with the overriding aim of achieving environmentally heterogenous mosaics of ponds at different stages of succession hence maximising co-existence of wildlife and intensive agriculture (Sayer and Greaves, 2020; Williams et al., 2020a).

The techniques for both pond restoration and creation are well established (Sayer et al., 2023a, 2023b), and there are vast swathes of landscape across Europe that would benefit from combining creation, restoration and indeed ghost pond resurrection (Alderton et al., 2017) to establish high quality pond networks. In particular, ponds within agricultural landscapes provide an important space where pond creation and restoration could result in profound improvements in freshwater biodiversity (Sayer and Greaves, 2020; Williams et al., 2020a). Despite the increasingly recognised importance of ponds for freshwater diversity, they largely remain absent from freshwater conservation policy (Hill et al., 2018; Williams et al., 2020a). Given the clear benefits and cost effectiveness of both pond restoration and creation, it is clear that both should be included in wider freshwater conservation plans and policy to hopefully help reverse the current trajectory of freshwater biodiversity loss in Europe and beyond.

CRediT authorship contribution statement

Matthew J. Hill: Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **James C. White:** Writing – review & editing, Methodology. **Juliet Hawkins:** Writing – review & editing, Methodology. **Neema Binu:** Writing – review & editing, Methodology, Conceptualization. **Eleanor Baker:** Writing – review & editing. **Helen M. Greaves:** Writing – review & editing. **Carl D. Sayer:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization.

Declaration of competing interest

The authors confirm they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111279.

Data availability

Data will be made available on request.

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