

RESEARCH ARTICLE

A co-development approach to conservation leads to informed habitat design and rapid establishment of amphibian communities

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Abstract

1. Effective wildlife restoration is a critical requirement of many conservation actions. The outcome of conservation interventions can be optimized through knowledge of species' habitat requirements, but few studies consider the impact of using explicit evidence from dedicated local research to inform the design phase of habitat management. Furthermore, interventions administered externally from the top down, whilst simpler than those developed in discussion with multiple stakeholders including land managers (i.e. co-development), run the risk of failing to engage local people.

2. In this study, we focus on interventions in the Scottish Highlands to improve the availability and suitability of breeding ponds for local amphibian assemblages. We collected and analysed data based on 129 ecological variables across 88 reference ponds to quantify the local habitat preferences. We used the findings from these analyses to inform the construction or restoration of 25 intervention ponds co-developed in partnership with stakeholders (landowners, foresters, citizen scientists and government agencies). Following the interventions, we monitored amphibian communities at these sites over 4 years. We assessed presence and abundance of all five native amphibians (the anurans *Rana temporaria* and *Bufo bufo*, and the salamanders *Lissotriton helveticus*, *L. vulgaris* and *Triturus cristatus*) using egg searching, dip-netting, torching and trapping.

3. The new habitats were overall characterized by ecological conditions more favourable to amphibians than the reference ponds. We recorded a total of 51 colonization events. Within two breeding seasons after construction or restoration, the intervention ponds hosted the full complement of species, mirroring amphibian diversity patterns found in the local reference ponds.

4. Our study shows that ecological research to quantify local habitat requirements and working with commercial landmanagers to ensure equitable benefits prior to designing conservation actions can promote rapid and efficient recovery of wildlife.

KEYWORDS

conservation intervention, Evidence-based conservation, habitat management, land sharing, pond, recovery, wetland

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1 | INTRODUCTION

Increased recognition of the global biodiversity crisis and the need for biodiversity conservation have in the 21st century coincided with higher economic uncertainties (Díaz et al., 2019; IMF, 2020), leading to reduced investment in conservation (Hirsch et al., 2020). As conditions worsen, there is an increasing need for effective interventions that are well-executed and supported by empirical evidence (Addison et al., 2013). Co-development of projects by land managers, local citizens, conservation practitioners, policy makers and researchers has been proposed as a means of implementing successful and efficient conservation actions (Vercammen & Burgman, 2019; Wauters & Mathijs, 2013). The evidence-based conservation approach appears to be a good fit with co-development as it recommends the systematic evaluation of peer-reviewed and grey literature along with practitioners' and local people's experience (Sutherland, Pullin, Dolman, & Knight, 2004). Conservation research that is both practical and focuses on finding solutions is likely to appeal to a broad range of stakeholders, as is a systematic approach that includes social and economic, as well as ecological, considerations (Gilby et al., 2020).

The decline of amphibians is a major global biodiversity concern and has been linked to anthropogenic drivers including habitat loss, land use change, pollution, over-exploitation, disease and invasive species (Beebee & Griffiths, 2005; Scroggie et al., 2019), often acting in combination. Remediation of such threats can be particularly challenging outside of protected areas such as in places primarily managed for economic purposes (Denoël et al., 2019; Hartel, Scheele, Rozyłowicz, Horcea-Milcu, & Cogălniceanu, 2020). Indeed, land managed for forestry and agriculture, rather than for conservation *per se*, comprises a greater proportion of rural land globally and provides vital habitat for many species (e.g. Irwin et al., 2014; Pywell et al., 2012). Amphibians in particular are characterized by limited powers of dispersal, and land managed for economic gain may thus be the only connection between nature reserves and other sites managed for conservation (Pickett & Thompson, 1978). In such situations, proactive habitat management outside protected areas benefits a range of amphibian species and aids in population recovery (Sterrett et al., 2019).

One widely promoted, and effective, form of intervention in agricultural areas, where traditional nature reserves may be too prescriptive, is the conservation or creation of 'pondscapes' (ecologically meaningful clusters of ponds) designed to support local wildlife, including aquatic-breeding amphibian communities (Hill et al., 2018; Peterman, Anderson, Drake, Ousterhout, & Semlitsch, 2013; Rannap, Löhmus, & Briggs, 2009). Pondscapes may be funded through agri-environmental incentive schemes, or as part of mitigation measures following anthropogenic developments. However, such interventions can appear to be piecemeal, particularly for amphibians, which has led to calls for landscape scale conservation planning to consider the ecological requirements and connectivity needs of target species (Brown, Street, Nairn, & Forstner, 2012; Rannap et al., 2009).

Interventions for amphibian conservation must generally take account of both aquatic and terrestrial habitats to provide breeding, feeding and dispersal opportunities (Schmidt, Arlettaz, Schaub,

Lüscher, & Kröpfli, 2019). However, pond construction and restoration projects have had mixed success, and relatively few have been evaluated for their overall effectiveness (Smith, Meredith, & Sutherland, 2019). Ecological features of constructed and restored ponds can significantly influence the species richness and viability of residing amphibians (Peterman et al., 2013; Shulse, Semlitsch, Trauth, & Gardner, 2012), which is important for intervention projects because these features can markedly differ between established and newly created sites (Dayer & Richter, 2016; Korfel, Mitsch, Hetherington, & Mack, 2010). Studies which document the colonization and temporal persistence of amphibians in created or restored ponds indeed show that such sites often fail to reach typical community composition or might not attain community diversity index values typical of more established ponds (Lesbarrères, Fowler, Pagano, & Lodé, 2010). Even when available, empirical information is rarely considered in the design phase of habitat management.

This study summarizes a two-step research and restoration effort on a five-species amphibian assemblage in a rural area in Northern Scotland. The two sequential objectives are to (i) quantify local amphibian habitat preferences to inform the design of constructed and restored ponds and (ii) document amphibian community diversity of these ponds in comparison with existing sites, to determine whether habitat assessment-based design promotes their rapid colonization.

2 | MATERIALS AND METHODS

2.1 | Study area and study design

The study was based on 88 reference ponds and 25 intervention ponds (five restored and 20 newly constructed), all situated in the Moray Firth-Aviemore area of the Scottish Highlands, UK (4°35'–3°35'W, 57°38'–57°11'N; Figure 1, Table 1). Reference ponds included both glacial and constructed ponds, the latter ranging from prior to the earliest detailed maps (surveyed c. 1870) to ponds created approximately 15 years ago. A previous study had found no differences between species composition based on origin or age of pond (Miró, O'Brien, Hall, & Jehle, 2017). They consisted of 40 ponds which had post-1990 records of the European Protected Species *Triturus cristatus* (see below), and 48 ponds which were selected by surveying the nearest pond to a randomly generated grid reference within the area (3°35'–4°35'W, 57°11'–57°38'N; see Miró et al., 2017, for more details). The construction or restoration of intervention ponds was based on two amphibian conservation projects co-developed by practitioners (including two of the authors, DOB and KOB), local farmers, foresters, a golf club, governmental organizations and a regional conservation NGO (Highland Amphibian and Reptile Project – HARP). Lengthy discussions were held with each potential stakeholder to explain the rationale for amphibian conservation and to understand the constraints and opportunities that conservation measures might pose for their businesses. Interventions took place at four nodes within the study area, which were selected using criteria including connectivity, soil/geology and compatibility with economic use (Figure 1; Table A1 in the

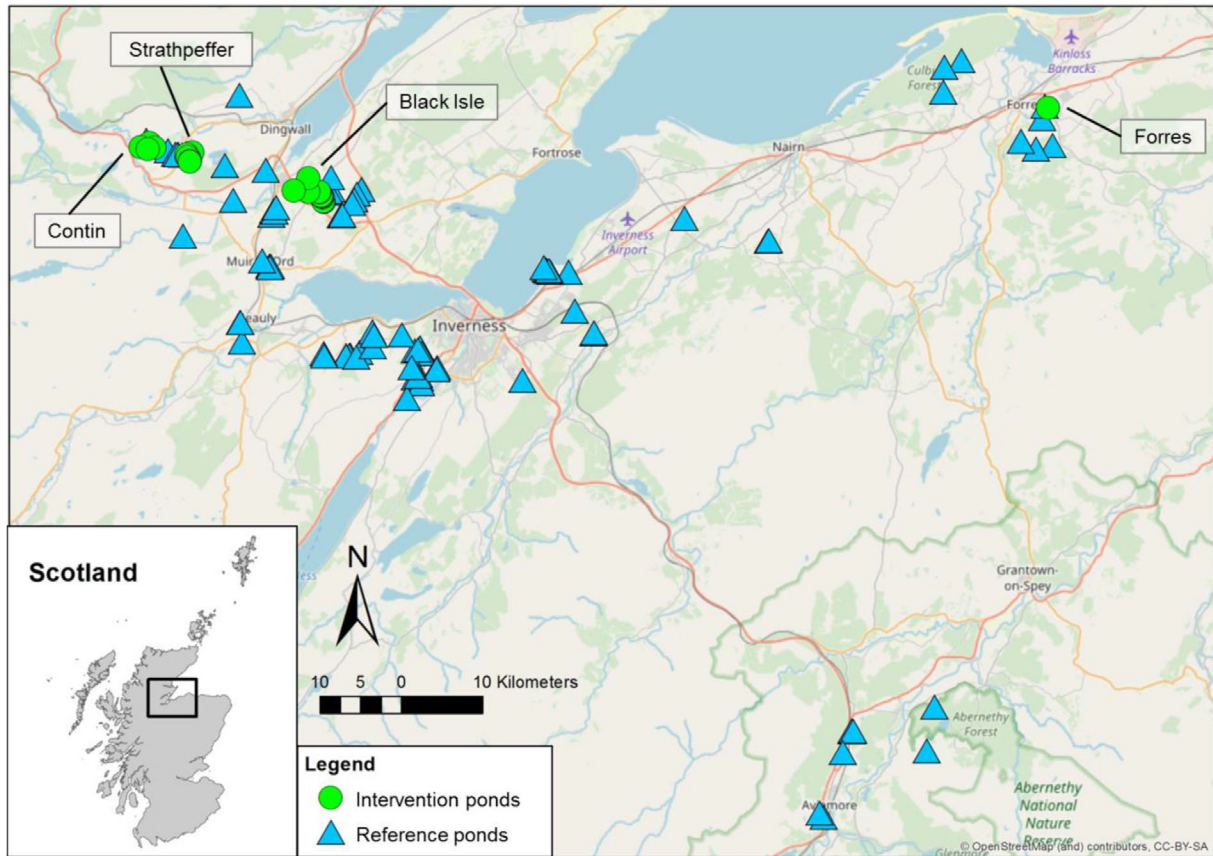


FIGURE 1 Distribution of intervention and reference ponds across the study area. The four pond nodes are named in the map, and magnified below (the complete list of intervention ponds is shown in table A1 in the online Appendix A).

TABLE 1 Selected designable habitat characteristics of the reference ponds used for the statistical analyses. Abbreviations used in Figure 2 are given in brackets. Detailed information about all variables is given in Appendix A in the Supporting Information

Variable type	Variable name	Description
Potential predators	Fish presence (FISH)	Binary factor determined by fish presence in the pond, dummy transformed
Aquatic vegetation	Macrophytes surface coverage (MACROPH)	Percentage coverage of the pond surface occupied by submerged or emergent macrophytes, logit transformed
Bank slope	Slightly sloping bank (BANK_SLIGHTLY)	Percentage of pond perimeter with slightly sloping banks (20–30° slope), $\log(x + 1)$ transformed
	Very sloping bank (BANK_VERY)	Percentage of pond perimeter with very sloping banks (70–80°), $\log(x + 1)$ transformed
Pond substrate	Substrate organic mud (SUBS_ORMUD)	Percentage of pond substrate comprising organic mud (mainly decaying stem and leaf debris), logit transformed
Shore habitat	Shore tree coverage (SHORE_TREE)	Percentage of tree coverage of the pond shore, square root transformed
Terrestrial habitat	Adjacent mixed woodland (TERR_MIXEDWOOD)	Percentage of adjacent terrestrial habitat comprising mixed <i>Pinus sylvestris</i> - <i>Betula</i> woodland, logit transformed
	Adjacent thickets and scrub (TERR_SCRUB)	Percentage of adjacent terrestrial habitat comprising temperate thickets and scrub, $\log(x + 1)$ transformed
	Terrestrial habitat richness (TERR_N)	Number of habitats present in the adjacent terrestrial area, 500 m from the pond shore (European Environment Agency, 2019)

Supporting Information). None of the source populations or intervention areas were nature reserves, although two sites (on the National Forest Estate) are managed partly for conservation. Pond construction was designed to improve connectivity between ponds known to have high amphibian diversity. Construction was funded by government partners (Forest and Land Scotland and NatureScot) which directly hired the contractors. Landowners received no financial incentives to take part.

2.2 | Assessment of local amphibian habitat preferences

The 88 reference ponds served as a basis to quantify local habitat preferences, before applying these findings to develop criteria to the design and siting of the intervention ponds (see below). Pond surface areas ranged from 2 to 168,500 m² (median 975 m²), and altitudes ranged from 10 to 248 m a.s.l. (median 91.5 m). They were surveyed at least three, and generally four, times annually between 2014 and 2018 during the breeding season (March–June). All five amphibian species found in the region were recorded (McInerney & Minting, 2016): two anurans, the European common frog (*R. temporaria*) and the common toad (*Bufo bufo*), together with three salamanders, the smooth newt (*Lissotriton vulgaris*), the palmate newt (*L. helveticus*) and the European protected species great crested newt (*T. cristatus*). Survey techniques following the British National Amphibian and Reptile Recording scheme (NARRS) protocol, was carried out by experienced licensed surveyors in suitable weather conditions (night water temperature $\geq 6^{\circ}\text{C}$, low wind disturbance of water surface). The NARRS protocol standardizes survey effort by pond perimeter and encompassed egg

searching, dip netting, torching (flashlighting) and minnow traps (ARG-UK, 2013; Griffiths & Langton, 2003; Langton, Beckett, & Foster, 2001). Sewell, Beebee, and Griffiths (2010) had found this combination of methods and survey frequency to minimize risk of imperfect detection. Data from surveys were combined for a given year to determine the presence or absence of amphibian species at given ponds. All surveying followed NatureScot guidance to ensure welfare of amphibians and other species, and the biosecurity and non-native species control measures advised for amphibian field workers (ARG-UK, 2008).

To investigate which habitat features were most important for amphibian community composition, we collected habitat data from 129 variables for these ponds, 88 derived through fieldwork in 2014 and 41 through desk study (for further details on habitat descriptors, see Appendix A in the Supporting Information and Miró et al., 2017). Topographical features were obtained from GIS using 1:25,000 maps from the British mapping agency Ordnance Survey. Given the conservation management context of the study and the proximity of occupied and non-occupied control ponds, we did not include spatial autocorrelation variables to avoid unnecessarily complexity and collinearity in the models.

2.3 | Intervention pond construction and surveys

The 25 intervention ponds were constructed or restored (i.e. former ponds identified from historic maps) for amphibian conservation in Autumn–Winter 2014–2015 (except one pond constructed in Winter 2017–2018), using a 13-t excavator on low-pressure tracks. Based on the findings from habitat preferences for the reference ponds (see below), particular attention was paid to land use, soil type, bank slope,

and terrestrial habitat when constructing or restoring these ponds (Table A1 in the Supporting Information). There was no planting or introduction of species: all ponds were naturally colonized. Pond surface areas ranged from 4 to 500 m² (median 150 m²), at altitudes between 46 and 163 m a.s.l. (median 141 m).

We monitored amphibian breeding community composition from 2014 to 2018 in restored ponds, and from 2015 to 2018 in constructed ponds, following the survey protocols as outlined for the reference ponds above. Habitat characteristics of intervention ponds were also assessed following the same protocol, during the 2016 breeding season, that is in the second year after construction or restoration, except for the pond constructed in Winter 2017–2018 which was surveyed in Summer 2019.

2.4 | Statistical analyses

The relative importance of habitat characteristics in shaping amphibian communities was assessed by redundancy analysis (RDA; Wollenberg, 1977), using amphibian community as response variable, and habitat features as explanative variables. To focus on community composition (and colonization events in later analyses), we used amphibian species presence/absence, coded as 1/0. Calculations were based on the Euclidean distance of Hellinger transformed amphibian data, which allows the computing of indices for community and beta diversity comparisons based on occurrence (1/0) data (Legendre & De Cáceres, 2013; Legendre & Legendre, 2012). First, we performed individual RDAs for each variable, retaining the 25 variables that were significant ($p < 0.05$). Second, we identified linear dependencies among the 25 retained variables, since collinearity could render the RDA regression coefficients unstable (Legendre & Legendre, 2012). We sequentially computed a variance inflation factor (VIF) for all variables and rejected the ones with the highest value until none of them was above 3. Seventeen variables obtained VIF values below 3, the threshold indicative of worrisome collinearity in regression analyses (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The detailed RDA variable selection procedure can be found in Appendix A in the Supporting Information.

Since the design of intervention ponds was based on reference ponds, we tested for the similarity of habitat characteristics between both groups of ponds by applying Kruskal–Wallis non-parametric tests for group homogeneity, followed by *post hoc* pairwise comparisons with Bonferroni adjustment. Since *B. bufo* is favoured by different variables than the other amphibian species and prefers larger, deeper ponds commonly containing fish (Hartel et al., 2007; Knapp, 2005; Miró, Sabás, & Ventura, 2018; Winandy, Darnet, & Denoë, 2015), we split the reference ponds into two groups: with amphibians present, and without amphibians or with *B. bufo* only. We illustrated the data using violin plots (Hintze & Nelson, 1998).

We investigated temporal changes of diversity patterns in the intervention ponds by computing 3 yearly diversity measures. First, amphibian richness was computed as the number of amphibian species per pond, based on all records for a given year. Second, amphibian pooled richness was defined as the total number of species found in the

pool of intervention ponds. Finally, amphibian community dissimilarity (or beta diversity) was defined as the total variance of the site-by-species (rows and columns, respectively) amphibian community table and computed as the total sum of the matrix squared deviations from the column means (Legendre & De Cáceres, 2013), again using the Euclidean distance of Hellinger transformed data (Legendre & Gallagher, 2001). To avoid bias caused by different sample sizes of reference and intervention ponds, we computed diversity values on the means of 999 random equally sized subsamples ($n = 15$) for each year. To allow comparisons with intervention ponds, we also included a category 'reference' computed on 999 randomizations of 15 subsamples from the 88 reference ponds. To build meaningful comparisons of individual ponds and pooled richness across years, we kept the surveys where no amphibians had been found in the dataset. We tested for statistical differences among years and reference ponds by applying a Kruskal–Wallis non-parametric test for group homogeneity, followed by *post hoc* pairwise comparisons. Due to the large sample size, we applied a significance level of $\alpha = 0.001$ to reduce the probability of type I errors (Cohen, 1988).

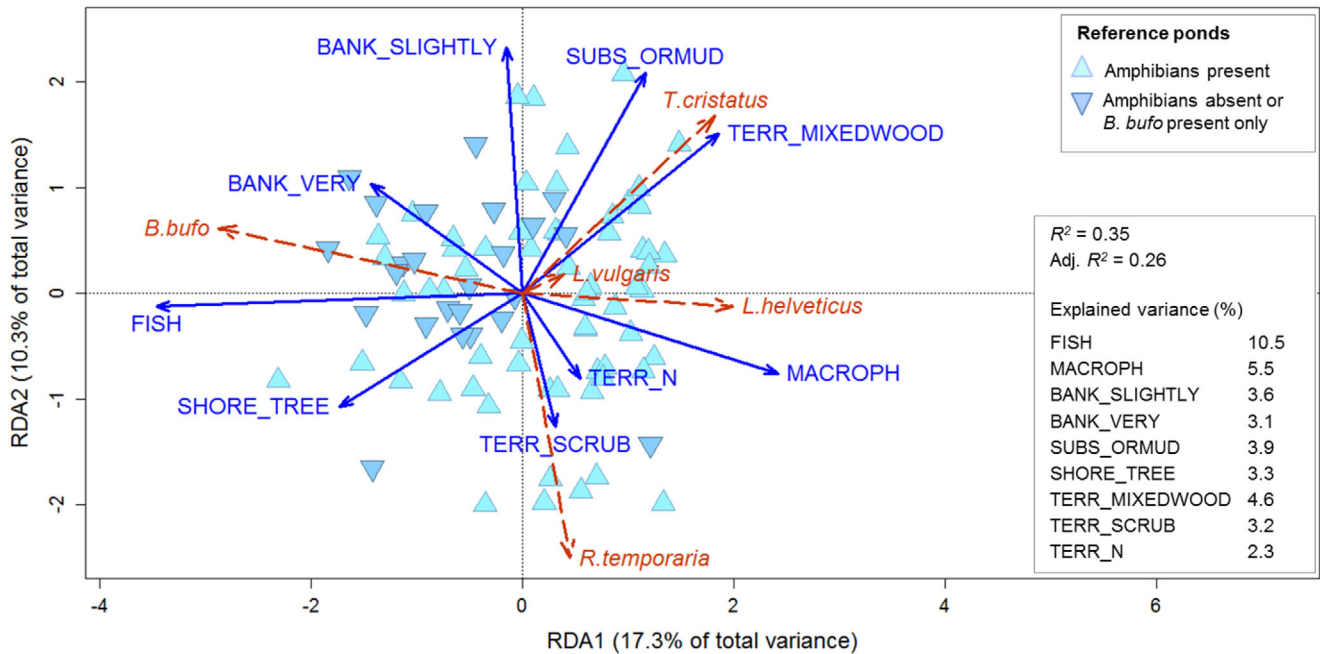
We investigated temporal changes in amphibian community composition in the 25 intervention ponds by performing a permutational multivariate analysis of variance (PERMANOVA; Anderson & Gorley, 2008) against year as a factor. We again divided the intervention sites into ponds with amphibian presence and ponds with amphibian absence or *B. bufo* presence only, and computed a *post hoc* pairwise test with Bonferroni correction. Computations were again performed based on amphibian species occurrence coded as 1/0 and normalized through a Hellinger transformation (Legendre & Gallagher, 2001). The PERMANOVA analysis was illustrated on a Principal Component Analysis (PCA) space built using the Euclidean distance matrix obtained from the 88 reference ponds as described for RDAs. We then projected the yearly (2014–2018) community centroids (mean and SE) from the intervention ponds in this PCA space. To allow for visual comparisons, the centroids of the reference pond presence/absence categories were marked differentially in the PCA graphics. We computed PERMANOVAs with PERMANOVA+ for PRIMER software (Anderson & Gorley, 2008), applying 9999 permutations and a significance level of $\alpha = 0.05$. All other statistical analyses were performed with R statistical software (R Core Team, 2018) using the basic functions and the packages *adespatial* (Dray et al., 2018) *vegetarian* (Charney & Record, 2012) *vegan* (Oksanen et al., 2018) and *vioplot* (Adler & Kelly, 2018).

3 | RESULTS

3.1 | Habitat assessments based on reference ponds

Analysing the pond habitat characteristics most associated with the taxonomic structure of the amphibian community in the reference ponds, we obtained a significant RDA ($F = 4.681$, $p = 0.001$), which explained 35.1% of the total variance (Figure 2a). All nine variables identified by the forward selection process were significant, and most

(a) Habitat characteristics associated with amphibian community for reference ponds



(b) Habitat characteristics for reference and intervention ponds

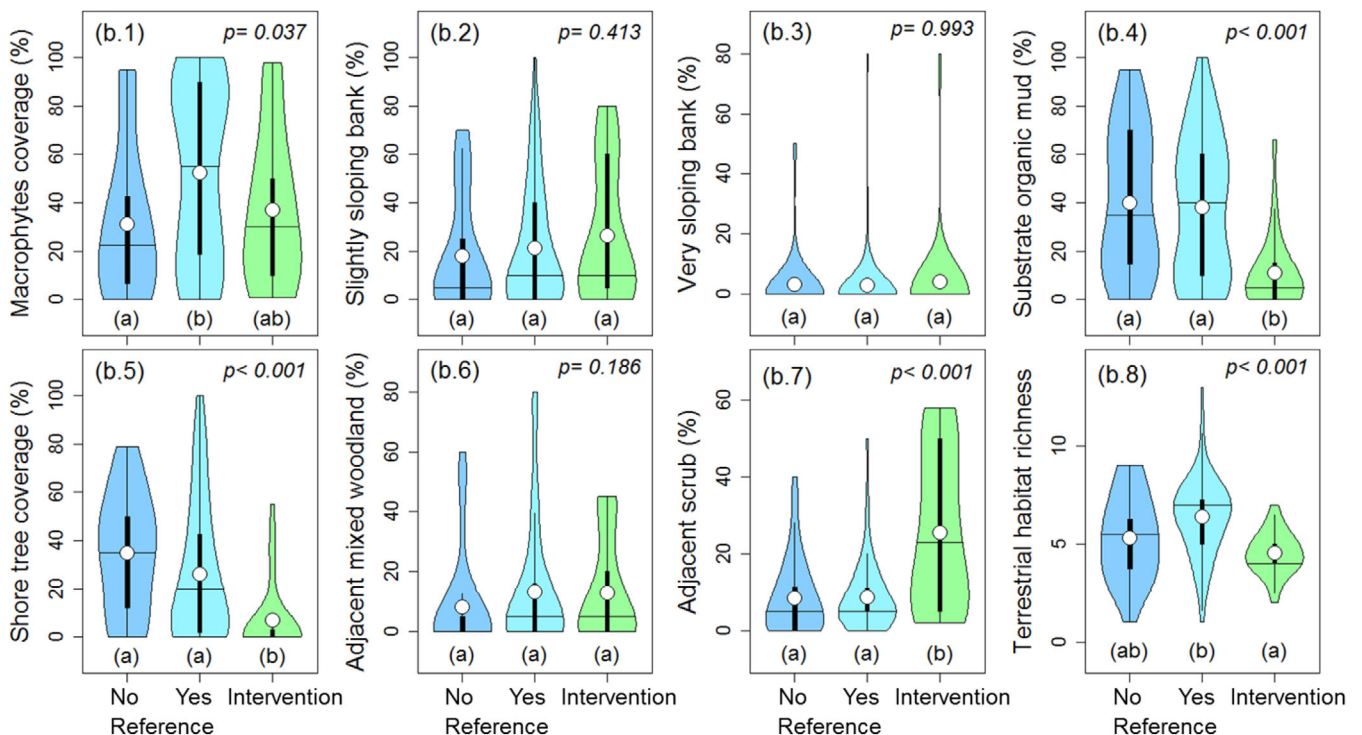


FIGURE 2 Habitat characteristics of reference and intervention ponds. Upper panel (a) shows the RDA correlation triplot computed on the amphibian community for the 88 reference ponds. Adjustment and relative importance of each selected habitat variable are shown. Abbreviations used are: fish presence (FISH), macrophytes surface coverage (MACROPH), slightly sloping bank (BANK_SLIGHTLY), very sloping bank (BANK_VERY), Substrate organic mud (SUBS_ORMUD), Shore tree coverage (SHORE_TREE), Adjacent mixed woodland (TERR_MIXEDWOOD), Adjacent temperate thickets and scrub (TERR_SCRUB) and Terrestrial habitat richness (TERR_N). Lower panel (b) shows violin plots comparing the distribution of the eight continuous variables selected in the RDA among reference ponds not occupied by amphibians or only occupied by *B. bufo* (Reference No), ponds occupied by amphibians (Reference Yes) and intervention ponds (Intervention). Sample sizes were: Reference No (24), Reference Yes (64) and Intervention (25). The p values of the main Kruskal-Wallis tests are shown in the top right corner of each chart. Different letters below the violins show significant differences in the post-hoc Kruskal-Wallis pairwise tests. NB there is no violin plot for fish as none were present in the intervention ponds.

prominently included fish presence and macrophyte coverage, as well as habitat features such as proportion of adjacent mixed woodland, organic mud substrate and slightly sloping banks (Figure 2a).

From the single-species perspective, *B. bufo* showed contrasting habitat preferences compared to the other amphibians (Figure 2a; Table A2 in the Supporting Information). Occurrence of *B. bufo* was positively associated with fish presence and proportion of very sloping bank, and negatively associated with proportion of macrophyte surface coverage (Table A2). The occurrence of *R. temporaria* was positively linked to terrestrial habitat richness and proportion of adjacent thickets and scrub, and negatively linked to proportion of organic mud substrate (Table A2). Among salamanders, *L. helveticus* was positively associated with macrophyte surface coverage and proportion of adjacent mixed woodland, and negatively associated with fish presence, proportion of tree coverage of the shore, and adjacent thickets and scrub (Table A2). The occurrence of *T. cristatus* was positively linked to proportion of slightly sloping bank, organic mud substrate and adjacent mixed woodland, and negatively linked to fish presence (Table A2). *L. vulgaris* was found in insufficient sites to allow a clear evaluation of habitat preferences.

3.2 | Habitat characteristics of intervention ponds

Once favourable amphibian habitat in the study area was assessed, the 25 intervention ponds were constructed or restored in line with these findings. Interventions targeted locations with adjacent mixed woodland, thickets and scrub, and ponds were constructed with a high proportion of slightly sloping bank (Figure 2b). By the second year after construction or restoration, macrophyte coverage was already higher in the intervention ponds compared to reference ponds, and the values of most other habitat variables favourable for amphibians showed similar or better values (Figure 2b, excluding ponds with *B. bufo* presence only). No intervention ponds contained fish. For reference ponds, 76.6% of ponds with amphibians, and 50% without amphibians or with *B. bufo* only, were fishless ($\chi^2 = 16.85, p < 0.001$). Intervention and reference ponds were indiscernible for proportion of very sloping bank, a favourable variable for *B. bufo* only, whereas intervention ponds had lower proportions of shore tree coverage than reference ponds, an unfavourable characteristic for *L. helveticus*. Organic mud substrate and terrestrial habitat richness, two desirable habitat characteristics linked to pond maturation, showed less favourable values for intervention ponds in comparison to reference ponds (Figure 2b).

3.3 | Diversity patterns and community composition in intervention ponds

We recorded 51 colonization events in the 25 intervention ponds over 4 years (Table 2). Forty-three colonizations (84%) were recorded in the 2 years after the intervention (21 in 2015, and 22 in 2016). The species responsible for the most rapid and frequent colonizations were *R. temporaria* and *L. helveticus* (Table 2). *Rana temporaria* colonized 20 inter-

TABLE 2 Yearly amphibian colonization events registered in the 25 intervention ponds

Amphibian species	Year				Total
	2015	2016	2017	2018	
<i>Rana temporaria</i>	13	5	1	1	20
<i>Bufo bufo</i>	0	1	1	0	2
<i>Lissotriton helveticus</i>	7	9	1	0	17
<i>Lissotriton vulgaris</i>	0	5	0	0	5
<i>Triturus cristatus</i>	1	2	2	2	7
Total	21	22	5	3	51

vention ponds, 13 of them the first year (2015). *L. helveticus* colonized 17 intervention ponds, seven in 2015 and nine in 2016. Fourteen colonizations were recorded for the other three amphibian species during the study period: two for *B. bufo*, five for *L. vulgaris* and seven for *T. cristatus*.

Amphibian species richness of intervention ponds exceeded that of reference ponds 2 years after construction or restoration (2016; median 1.93 and 1.66 species per pond, respectively) and continued to increase to a value of 2.3 in 2018 (Kruskal–Wallis chi-squared = 5144.7, $p < 0.001$; Figure 3a). Pooled amphibian richness in intervention ponds also significantly increased over time (Kruskal–Wallis chi-squared = 4873, $p < 0.001$; Figure 3b), to reach a median of five species (the maximum value possible in the area) in line with reference ponds also in 2016. Beta diversity of intervention ponds also significantly increased over time (Kruskal–Wallis chi-squared = 3454.6, $p < 0.001$; Figure 3c) before reaching stable values 3 years after intervention works (2017), at however still lower levels than the reference ponds (median 0.69 and 1.05 squared deviations, respectively). Amphibian community dissimilarity could not be calculated for 2014 (the year before intervention works), due to lack of variation in the site-by-species matrix.

PERMANOVA confirmed that intervention ponds reached stable amphibian community compositions in 2016 (pseudo- $F = 9.6228, p = 0.0001$; Figure 3e in reference to Figure 3d). Furthermore, between 2014 and 2016 the intervention ponds had higher occupancies than reference ponds for all species except *B. bufo* (Figure 2b; Table A3 in the Supporting Information).

4 | DISCUSSION

Our study found a total of 43 colonizations across the 25 intervention ponds during the first and the second breeding season after intervention works, increasing to 51 by 2018. In addition, intervention ponds reached amphibian diversity patterns and community compositions comparable with reference ponds in the study area by the second breeding season after intervention, a generally more rapid increase compared to other restoration projects (e.g. Lesbarrères et al., 2010; Petranka, Harp, Holbrook, & Hamel, 2007; Rannap et al., 2009). We propose that this rapid recovery is mostly due to our application

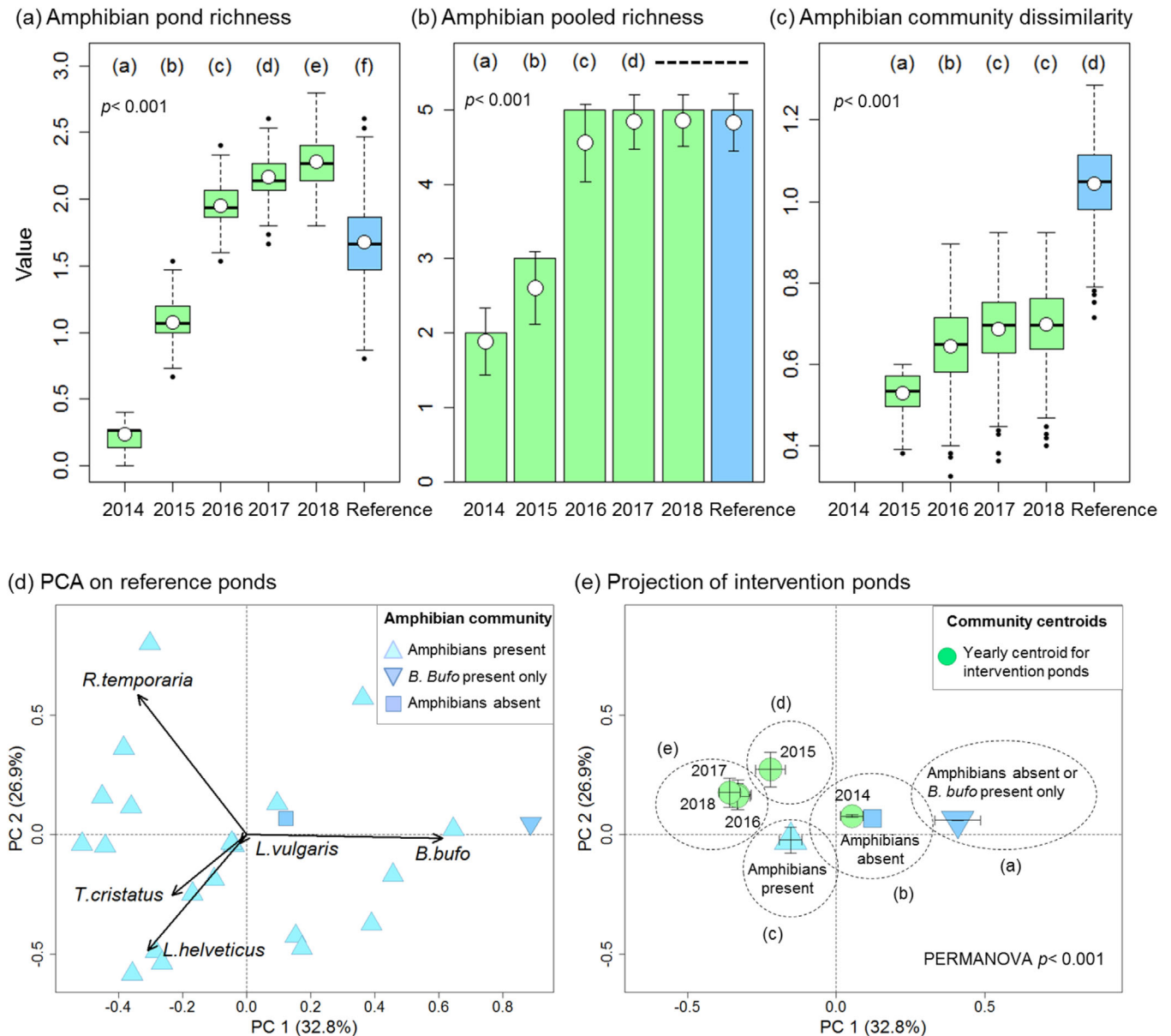


FIGURE 3 Changes in the amphibian diversity patterns (upper panel) and community composition (lower panel), across the study period, in the 25 intervention ponds compared to reference ponds. Upper panel shows the average amphibian pond richness (a), the total number of species found in the pool of intervention ponds (b), and the amphibian community dissimilarity as amphibian species matrix total variance (c). Boxes and bars are based on mean values from 999 random subsamples. Middle boxes line and upper bars line show median values, while white circles show mean values. Error bars in the bar chart show SD of the mean. Amphibian community dissimilarity could not be computed for year 2014 due the lack of variation in the community matrix. Years with different letters showed significant differences in the post-hoc Kruskal-Wallis pairwise tests. Lower panel shows the Principal Component Analysis (PCA) performed on the amphibian community composition of the 88 reference ponds (d), and the projection, in the same PCA space, of the yearly centroid (mean and SE) for the community composition of the intervention ponds across the study period (e). In graphic b1, we highlight the position occupied by the lakes without amphibians (square), and without amphibians or with *B. bufo* present only (inverted triangle). In graphic e, we add the two reference categories of amphibians absent, and amphibians absent or *B. bufo* present only, and the p -value of the permutational multivariate analysis of variance (PERMANOVA) main analysis. Groups of categories with different letters showed significantly different amphibian communities in the post-hoc pairwise PERMANOVA test.

of knowledge of local amphibian habitat preferences as acquired through a quantitative analysis prior to intervention. This has made the project effective in biodiversity terms, and efficient in financial (the total project cost was under £20,000, although we estimate the cost in volunteer time for monitoring the intervention project as being

around 400–500 worker-hours, excluding survey of the reference ponds, which had been carried out as a previous project) and land-use terms.

We suggest that the project's success is also due to bringing together co-development and conservation evidence approaches.

Three out of the five landowners had not previously undertaken conservation work on their land, and only one (the state forest managers at FLS) had done so on a formal basis. Participants had different motivations. Land managers wished to be seen as good stewards, protecting habitats and species whose survival represents part of a legacy of traditional land-management systems handed down from their ancestors; one of the families has owned the land since at least the 17th century. For both farm managers, there was desire not only to integrate conservation with profitable businesses, but to be seen to be doing so by their peers. Indeed, one of the participants joined the project after being convinced by another land manager. Whilst economic considerations were important, neither had participated in formal agri-environmental schemes due to the bureaucracy involved. A major attraction of the current work was the lack of form-filling, or any perception of loss of control over their own land.

The intervention at the golf club was more challenging, and ultimately depended on the relationship built with the club professional and ground staff. Some members were opposed to pond creation because of negative publicity about the presence of great crested newts limiting people's control over their land (Jehle, Thiesmeier, & Foster 2011). However, the club professional, a local man who remembered catching newts as a boy, was able to persuade members that a new water feature would benefit the game, without adverse impacts on site management. As with the farming community, the respect of local stakeholders was vital to implementation.

Government agency staff wanted to protect biodiversity whilst ensuring prudent use of public money. Volunteers were motivated by the desire to protect local species and the challenges of wildlife recording. With any co-development, failure includes the risk not only of wasting money and other resources (such as land removed from production and volunteer surveyors' time), but also of dampening enthusiasm for future biodiversity interventions. These motivations are complimentary but could easily have led to a project based on methods that were inefficient or ineffective. Evidence-based interventions are more likely to be effective as they build on a rigorously compiled knowledge base (Sutherland et al., 2004). However, any expert-based system runs the risk of alienating people living in the area of the intervention, as they are seen as something external being done to them and their land, and failing to consider their values and objectives. This criticism has in the past been levelled at evidence-based conservation (Adams & Sandbrook, 2013). By combining the two methodological approaches, we believe we have avoided their principal drawbacks.

4.1 | Habitat assessment and design of intervention ponds

Although widespread generalist species like *R. temporaria* and *B. bufo* have been well-studied, knowledge of species' habitat needs often relates to their core range and may not be relevant throughout their distribution (Arntzen & Themudo, 2008; Gomez-Mestre & Tejedo, 2003; Zanini, Pallet, & Schmidt, 2009). For example, a previous study of *T. cristatus* habitat preferences in the Scottish Highlands revealed

differences from its core range (Miró et al., 2017). An assessment and analysis of amphibians' local habitat preferences was therefore needed to select potential intervention sites likely to be colonized and then retain breeding populations. Our selection of reference ponds was only partly randomized, and one subset was biased towards *T. cristatus* presence, including ponds with especially rich amphibian communities rather than a random selection. This should not have markedly affected our inferences, as *T. cristatus*, while otherwise rare in Scotland, most commonly occurs in ponds in agricultural areas (e.g. Miró et al., 2017; Orchard, Tessa, & Jehle, 2019) and regularly co-occurs with all other investigated amphibians whenever their ranges overlap (e.g. Arntzen, Abrahams, Meilink, Iosif, & Zuiderwijk, 2017; Denoël, Perez, Cornet, & Ficetola, 2013). However, the corollary is that we have compared our intervention ponds with a set of reference ponds with higher than average amphibian diversity, making the rapid establishment of rich communities more remarkable.

Colonization by *T. cristatus* was seen as a particular success. The species has special protection under European and UK law, and prior to the intervention was found in only 44 ponds in the region. *B. bufo* was not a specific target of the project, although it colonized two ponds: this species is locally typical of large lochs of glacial origin and artificial water bodies created for fishing. It is common and often abundant in these habitats, and there is no evidence of any local declines (McInerny & Minting, 2016).

Pond design needed to both meet amphibians' ecological needs and complement local hydrology. Land-managers provided hydrological knowledge, based on experience of which areas were most likely to be waterlogged. The habitat needs revealed through our study, for example a large proportion of gently sloping banks, were easily incorporated by the construction operative. Sloping banks create shallow margins where water warms quickly, thus speeding larval development and, later, offer easy egress for metamorphs (e.g. Parris, 2006; see also Shulse et al., 2012 for constructed ponds). Such banks also make ponds less dangerous for livestock and humans, an important safety consideration on land managed for agriculture or where recreational access is likely.

Fish presence had been identified as an important negative factor for all local amphibians except *B. bufo*. Outside of flood plains, small water bodies in the region tend to be fishless, with human introduction seemingly the most common means of spread (Maitland, 1977). Whilst all stakeholders are aware of the need to keep ponds fish-free, introduction of fish by others, particularly in public access lands remains a risk. For some of these ponds, we have tried to keep visitors at a distance through allowing development of dense vegetation such as the spikey shrub *Ulex europaeus* between the pond margin and adjacent paths. In the long term, succession to wet woodland may become an issue. Subject to licensing, this may potentially be mitigated by re-excavating ponds on a rotational basis, thus keeping a variety of successional stages within the pondscape at each site which offer a variety of habitats.

Of the 20 newly created ponds, only one has not been colonized by amphibians and is unlikely to be suitable for them due to miscommunication during construction. Forestry staff assumed that lying

deadwood is often beneficial for wildlife and thus piled large quantities of brash along the margins. However, the species in question (the non-native Sitka spruce *Picea sitchensis*) produces highly acidic runoff, which resulted in low pH, sphagnum-dominated waters. Removing the brash would be logistically challenging, with an adverse impact on the acidophilous plants and invertebrates which have colonized the pond, potentially including the nationally endangered dragonfly *Leucorrhinia dubia* (unpublished data).

Not all characteristics of intervention ponds were more favourable for specific amphibians than the characteristics of reference ponds (for a similar finding, see, e.g. Korfel et al., 2010), although some of these will improve with time as the ponds mature. As the ponds were excavated with a digger, substrates are largely composed of mineral soils. Proportions of organic mud should increase through natural processes over time. Terrestrial habitat diversity can also be expected to increase, particularly in the forestry sites. Prior to construction, nine of the 13 forest sites (site codes beginning 'B' in Table A1 in the Supporting Information) were areas of clear-fell following harvesting of non-native Sitka spruce (*Picea sitchensis*). Regeneration is already taking place, with a broader variety of habitats developing, for example temperate thickets and scrub (EUNIS code F3.1), mixed *Pinus sylvestris* – *Betula* woodland (G4.4), broadleaved deciduous woodland (G1), *Pinus sylvestris* woodland (G3.4), along with surface running waters (C2), mires, bogs and fens (D). The farmland sites have seen less of a change as they were already adjacent to habitats that we had determined to favour amphibians, and the pond restorations have led to a more natural ecotone transition from grassland through mire to standing water.

4.2 | Diversity and community composition in the intervention ponds

Amphibians now breed in 24 out of 25 (96%) intervention ponds compared with 83% of reference ponds. This compares favourably to a recent review, which found that only five out of nine studies showed similar or higher numbers of species and reproductive activities in created ponds relative to natural ponds (occupancy of created ponds was 64–100%, with reproductive activity in 64–68% of them; Smith et al., 2019). All colonization events were within 600 m of known populations, with the exception of one *T. cristatus* colonization at 1840 m from the nearest known pond. This is further than the known colonization range for the species (Haubrock & Altrichter, 2016), and may have originated from an undocumented source, as there are unsurveyed ponds nearby.

The dominant species in our intervention ponds were *R. temporaria* (23 ponds, 92%) and *L. helveticus* (20 ponds, 80%; see Table A3 in the Supporting Information), both representing a higher occupancy than that documented for amphibian ponds across Scotland (70% and 42%, respectively (Table A4 in Appendix A in the Supporting Information; Wilkinson & Arnell, 2013). The proportions of ponds with breeding *L. vulgaris* and *T. cristatus* were both an order of magnitude higher than in the Scotland-wide survey (Wilkinson & Arnell, 2013; Table A3 in the Supporting Information). However, both species have very restricted

ranges in Scotland and so conclusions from such a comparison are limited. *B. bufo*'s low occupancy rate (two ponds, 8% relative to 35% of Scottish ponds, Wilkinson & Arnell, 2013) was unsurprising, as the species has different habitat preferences to the other native amphibians; typically breeding in larger, deeper ponds where fish are present (Minting, 2016). Indeed, Harper et al. (2020) found a negative association between *T. cristatus* and *B. bufo* in a study of over 500 ponds in England. Overall amphibian species richness was also greater in intervention ponds than in the reference group (Table A4 in the Supporting Information), despite the high proportion of the latter known to hold the European protected species *T. cristatus* (Miró et al., 2017). Thus, our comparison was with high biodiversity value ponds, rather than with already degraded ecosystems. A random sample would likely have included species-depleted ponds and possibly would have led to a failure to identify a shifting baseline resulting from biodiversity losses that occurred in past generations (Papworth, Rist, Coad, & Milner-Gulland, 2009).

The lower beta-diversity of the intervention ponds was expected, as they were constructed to be within a perceived ideal size and geological range for amphibians, rather than representing the wider range of natural ponds. That said, medium-sized ponds appear to be the size-class most likely to have been lost in the last hundred years or so (Wood, Greenwood, & Agnew, 2003) and confirmed by our review of historic maps. Indeed, small ponds (<400 m²) may even have increased in number through the creation of garden ponds (Banks & Laverick, 1986; Williams et al., 2007) and, at the other end of the scale, large water bodies tend not to be drained, despite often being heavily modified for power generation or water abstraction. Although created for amphibians, a pondscape featuring medium-sized ponds may host a range of species with similar habitats preferences and would benefit from detailed study of their fauna and flora (see e.g. Sayer et al., 2012).

4.3 | The future

A key factor in any conservation intervention is its long-term stability. While agri-environmental schemes can deliver benefits, they can be inflexible and include constraints which make them unsustainable after the initial funding period (Burton & Paragahawewa, 2011). Our development approach allowed land managers to allocate land that was unproductive, or where a pond would be an asset. Ponds can add to the aesthetic appeal of locations (Milburn, Brown, & Mulley, 2010), encouraging tourism (two of the sites offer cabin rentals), or be used for hunting water birds. Two farmers neighbouring the project sites have subsequently constructed ponds for amphibians without any incentivization (DOB, personal observation). Globally, not all amphibians breed in ponds, however, we believe that the approach we have used is equally applicable to other habitat types.

The project, although highly successful, will need continued monitoring and adaptive management to manage habitat changes that might threaten future amphibian persistence in the intervention ponds (e.g. Petranka et al., 2007). Examples of potential changes include

macrophyte surface coverage (Fardell et al., 2018), shore tree coverage/shading (Oldham, Keeble, Swan, & Jeffcote, 2000), emergence of shrubs leading to long-term pond loss (Erős, Maloş, Horváth, & Hartel, 2020), frequency of desiccation/ hydroperiod (Swartz, Lowe, Muths, & Hossack, 2020) and fish introductions (Hazell, Hero, Lindenmayer, & Cunningham, 2004). While land managers are aware of the need to avoid such developments, ongoing monitoring is carried out by volunteers from the local citizen science group HARP. At the date of submission (2020), management at all 25 ponds and their surrounding terrestrial habitats remain appropriate for wildlife conservation and all landowners remain committed to the project.

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AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; all authors took part in field work including data collection; DOB and KOB led on pre-intervention surveys and project management; AM analysed the data; DOB and JH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data are available through the Dryad Digital Repository <https://doi.org/10.5061/dryad.s1rn8pk6d> (O'Brien et al., 2020). Original species records, including records of non-target species are also publicly available via the National Biodiversity Network (<https://nbnatlas.org/>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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