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RESEARCH ARTICLE

Initial ecological recovery post-weir removal amidst catchment-wide improvements, in a groundwater-dominated chalk stream

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Abstract

Physical habitat modification is one of the main pressures affecting river environments, impacting their ecosystem health and compromising their ability to adapt to the effects of climate change. Addressing the impacts of physical modification through reinvigorating natural processes has become a globally established river restoration technique. Here, we appraised such an approach by assessing ecological responses to a weir removal project on an English groundwater-dominated 'chalk' stream. Using a Before-After-Control-Impact (BACI) approach, we found that 3 years post-restoration the macroinvertebrate communities are moving towards those of the target community both in terms of structural complexity (e.g., taxonomic composition) and functional integrity (e.g., trait composition). The progress is ongoing and has occurred alongside wider catchment improvements. Our results indicate that ecological responses to passive restoration undertaken on low energy streams, such as chalk streams, may be gradual, and thus longer-term assessment is needed to fully appraise ecological recovery. We highlight the importance of a BACI approach to understand the local responses to restoration in a catchment context. Our findings also provide further evidence highlighting complementary ecological information provided by assessing taxonomic and functional properties concurrently in post-project appraisals. A better understanding of ecological recovery times should be incorporated into future restoration planning. Such evidence would help develop robust assessments over appropriate timescales, increasing the likelihood of accurately and effectively appraising restoration project success, and helping to build support to increase the scale and pace of restoration actions needed to address biodiversity loss.

KEYWORDS

BACI, barrier, chalk stream, groundwater, process-based, recovery, restoration

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1 | INTRODUCTION

Rivers are biodiversity hot spots compared to other habitats globally (Reid et al., 2019), yet such environments and the species they contain are amongst the most threatened (Dudgeon, 2019). Human alterations to the riverscape that degrade ecological systems include: physical modification (Brookes et al., 1983), reduced lateral, longitudinal and vertical connectivity (Jansson et al., 2007), abstraction and flow regulation (Dunbar et al., 2010), water quality (Whelan et al., 2022) and invasive species (Gallardo et al., 2016). Such human pressures negatively affect the ability of river ecosystems, biotic communities and species to resist or be resilient to extreme events (Woodward et al., 2016). Climate change is expected to alter the frequency and intensity of extreme events such as floods and drought (Collet et al., 2017; Garner et al., 2015; Watts et al., 2015), which in turn will affect the processes that govern freshwater habitats and the ecosystems they support (Poff et al., 1997). Addressing human alterations, including physical modifications, that restore diverse and functional ecosystems is essential for human well-being and to help river landscapes adapt to a changing climate (Science Task Force for the UN Decade on Ecosystem Restoration, 2021). Re-establishing natural riverine processes is considered one of the most effective restoration approaches to address physical modification (Beechie et al., 2010; Wheaton et al., 2019), whereby restoring natural geomorphic processes promotes habitat heterogeneity (Wohl et al., 2024), which in turn facilitates recovery following disturbances from extreme hydrological events (Chester & Robson, 2011; Dunbar et al., 2010; Townsend & Hildrew, 1994).

The removal of barriers is a well-established restoration technique to enhance longitudinal connectivity and restore natural processes (Birnie-Gauvin et al., 2018; O'Hanley, 2011). The response of a river system to barrier removal will depend on the energy of the river system driving the natural physical processes (Bellmore et al., 2019; O'Hanley, 2011). Higher energy systems respond rapidly in terms of geomorphological processes (Wang & Kuo, 2016) and can help facilitate faster ecological responses (Claeson & Coffin, 2016). However, in low energy river systems, including England's groundwater-fed 'chalk' (a fine-powdered limestone) streams, relying on natural physical processes to modify physical habitats is expected to take longer (England, Hayes, et al., 2021; Sear et al., 1999). Such natural processes include the important role of ecosystems engineers in driving geomorphological change and creating heterogeneous habitat in chalk streams (Gurnell & Grabowski, 2016; Johnson et al., 2020).

The success of many restoration schemes remains uncertain due to a lack of project monitoring and appraisals worldwide (Angelopoulos et al., 2017). When appraisals are completed, they often span a limited timescale, although a few exceptions to this have been reported in recent years (Al-Zankana et al., 2020). Understanding the long-term recovery of restoration projects is crucial for predicting the trajectories of change (Kail et al., 2015), especially for process-based restoration (Beechie et al., 2010), and quantifying responses to extremes such as droughts and floods (Poff et al., 1997).

Post-project ecological appraisals that have been undertaken have primarily assessed the taxonomic responses of biotic

communities (Lorenz, 2021; Stoll et al., 2016). This has provided a detailed understanding of how river restoration schemes have influenced community compositions and the diversity of species underpinning this (e.g., rare taxa or those of high conservation value; species with varying ecological guilds) (Kail et al., 2015). Moreover, the diversity of individual biotic groups (e.g., macroinvertebrates) can reliably indicate wider ecosystem health (Lin et al., 2020). Assessing functional responses can offer additional insights on ecological responses to river restoration, including: more spatially transferrable trends (traits are less influenced by biogeographic constraints); greater certainty inferring ecological mechanisms underpinning trends; more obvious linkages to wider ecosystem functions and services; and potentially more statistically robust findings (White et al., 2017).

This study aimed to assess the taxonomic and functional responses of freshwater macroinvertebrate communities to the removal of a historic gauging station weir in a lowland groundwater-fed chalk stream. We hypothesised that the macroinvertebrate communities would become more similar to the Control site (depicting 'target' morphological and ecological conditions) in both structural complexity (e.g., taxonomic composition) and functional integrity (e.g., trait composition).

2 | METHODOLOGY

2.1 | Study area

This study was located on the River Lambourn, a 26 km tributary of the River Kennet within the Thames catchment in southern England (United Kingdom). It is a Special Area of Conservation and Site of Special Scientific Interest (SSSI), designated for its characteristic chalk stream vegetation (*Ranunculus fluitans* and *Callitriche-Batrachion*) and wildlife; Brook lamprey (*Lampetra planeri*), Bullhead (*Cottus gobio*) and abundant aquatic invertebrates (Natural England, 2022). The region has a temperate oceanic climate (Cfb: Kottek et al., 2006), with mean annual minimum and maximum air temperatures of 6.9 °C and 14.9 °C, respectively, and mean annual rainfall of 658 mm (Met Office, 2022). The mean annual discharge is 1.7 m³/s, dominated by chalk groundwater resulting in a baseflow index of 0.97 (National River Flow Archive, 2019). It is within a primarily rural catchment dominated by agricultural land use—predominantly arable 53.7% and grassland 30.3% (National River Flow Archive, 2019).

The restoration scheme studied here is part of an extensive programme of work to achieve 'Favourable Condition' for the Lambourn SSSI (Environment Agency, 2011). The works entailed removing a 10.7 m wide, 0.85 m high Crump weir in 2019, replacing it with an ultrasonic gauge, to improve the connectivity of the watercourse and restore natural processes (see Supporting information for information, photographs and location—Figure S1). Prior to its removal the weir impounded water for approximately 0.4 km. Three sampling sites were monitored in this study. Two sites were initially positioned within the impounded section of the Lambourn, located 0.25 km (Restored A) and 0.05 km (Restored B) upstream of the flow

gauging weir. The Control site was located 0.5 km upstream of the former weir location, and was unaffected by its impounding influences. The Control site was selected to represent a more naturally functioning chalk stream and the conditions that were expected to be recreated within the restored section - hence used as 'target' conditions here. Sites were surveyed twice per year in spring (April–May) and autumn (October–November) starting in autumn 2011 and ending in autumn 2022 (although no data were collected in 2018 or 2019).

Mean average channel widths remained broadly similar within each site regardless of the weir removal, while the restored section became shallower following the works and more comparable to the Control site (Figure S2a). Prior to restoration, the impounded section exhibited a finer substrate than the Control, but became significantly coarser following restoration (most notably at Restored B—Figure S2a).

Our study employed a Before-After-Control-Impact (BACI) approach, whereby temporal trajectories in ecological responses from restored sites could be assessed relative to background (or baseline) changes from the Control site. Physico-chemical quality elements (ammonia, dissolved oxygen, phosphate, temperature and pH) were Good to High throughout the study period (Catchment data explorer, Environment Agency, 2024).

2.2 | Survey methods

We collected one freshwater macroinvertebrate from each site. Samples were collected using a 3-min kick sample, supplemented with a 1-min hand search, sampling all habitats present in proportion to their occurrence (Murray-Bligh & Griffiths, 2022). In the laboratory we identified specimens to the lowest practical taxonomic resolution, predominantly species- or genus-level, although some taxa were identified or harmonised to family-level (mainly dipterans—Chironomidae, Empididae, Psychodidae, Ceratopogonidae, Syrphidae—but also Chydoridae and Hydridae), while Nematoda, Oligochaeta, Hydracarina, Ostracoda and Copepoda were identified as such.

2.3 | Data analysis

We derived functional traits from a European database that adopts a fuzzy-coding procedure, with faunal affinities to individual traits ranging from zero (no affinity) to three or five (high affinity—the upper limit depending on the amount of information reported in existing literature; Tachet et al., 2010). Trait information in the database is typically available at the genus or species level. We excluded taxa resolved to a coarser resolution than specified within the database from the functional analyses, while taxa resolved to a finer taxonomic resolution were aggregated (e.g., multiple species combined to the genus level). In total, 11 grouping features (a functional trait category—e.g., maximum body size) comprising 63 traits (modalities residing within grouping features—e.g., ≤ 0.25 cm, ≥ 8 cm) were

examined that contain information on the biological properties of invertebrate taxa (Table S1). Prior to the functional analyses, we standardised trait values of all qualifying taxa across all grouping features so that traits summed to 1, thus ensuring equal taxonomic weighting. We used these standardised values to calculate univariate functional diversity indices (see below). To calculate multivariate functional trait compositions, standardised values were multiplied by $\ln(x + 1)$ transforming community abundances to create a trait-abundance array. Finally, we averaged each trait across all sampled taxa and standardised across all grouping features to account for spatially and temporally driven changes in taxonomic abundances (sensu White et al., 2017).

All data processing and statistical analyses reported herein were performed in R studio (operated within R version 3.3.1—R Development Core Team, 2014). We calculated 10 univariate community response metrics characterising different diversity measures of taxonomic and functional compositions. This included six metrics that captured the richness, evenness and diversity of the taxonomic and functional compositions within each sample. For this, we used the diversity function in the Vegan package (Oksanen et al., 2022) to obtain taxa richness, evenness (Pielou's metric) and diversity (Simpson's metric). To calculate functional richness, evenness and diversity (Rao's quadratic entropy) we used the dbFD function in the FD package (Laliberté et al., 2023) performed on a Bray–Curtis dissimilarity matrix from standardised trait values (see above). We derived four additional metrics, whereby the taxa richness was subdivided into categories characterising the number of taxa generally preferring fast and slow flow velocities and coarse (inferred from those being sensitive to fine sediments) and fine substrate sizes. For this, we used taxa assigned to flow groups within the Lotic-invertebrate Index for Flow Evaluation (LIFE—Extence et al., 1999) metric to calculate the 'rheophilic taxa richness' (flow groups 1 and 2) and 'non-rheophilic taxa richness' (flow groups 3–6). Similarly, we used macroinvertebrate fine sediment sensitivity ratings assigned to taxa within the Empirically-weighted Proportion of Sediment-sensitive Invertebrates index (E-PSI) biomonitoring index to derive the 'coarse substrate taxa richness' and 'fine sediment taxa richness' based on taxa possessing 'species-specific sensitivity weightings' ≥ 0.5 and < 0.5 , respectively (sensu Turley et al., 2015).

We used each of the 10 response metrics as response variables within linear models that tested the interactive effects of 'Time Period' (i.e., 'before' or 'after' restoration) and 'Site'; this interaction quantified whether pre versus post changes in response variables differed between sites, and hence whether restoration was a statistically probable cause of ecological change ('Restoration Effect' herein). We incorporated the influence of Season as an additive influence within these models. For each linear regression, we inspected model diagnostics to ensure that assumptions of homoscedasticity and normality were satisfied, with non-rheophilic taxa richness and fine sediment taxa richness being $\log_{10}(x+1)$ transformed to meet these requirements. Additionally, up to four outliers were removed to meet model assumptions and reduce the possibilities of anomalous data points shaping statistical outcomes (see Zuur et al., 2010). We performed a

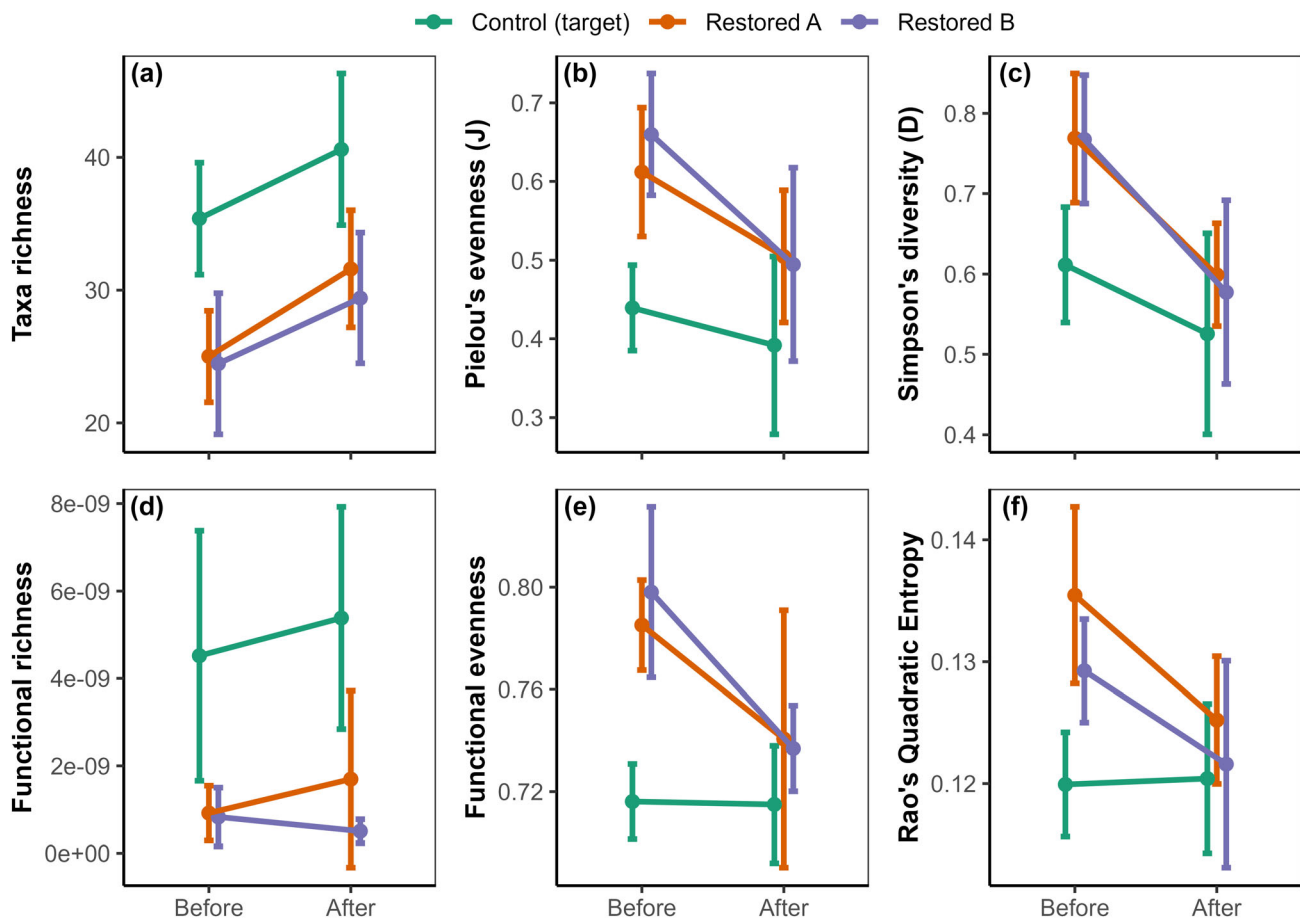


FIGURE 1 Error plots (mean \pm 2 standard errors) indicating changes in different univariate ecological metrics (a–c = taxonomic; d–f = functional) before and after restored across the three sites assessed. (a) taxa richness; (b) Pielou's evenness (J); (c) Simpson's diversity (D); (d) functional richness; (e) functional evenness; and (f) Rao's Quadratic Entropy (denoting functional diversity). [Color figure can be viewed at wileyonlinelibrary.com]

two-way analysis of variance (ANOVA) on these linear models to determine the significance of the model and the individual parameters that it comprised (including the interactive effect). Partial r^2 values captured the statistical power of individual parameters using the *etasq* function using the 'heplots' package (Friendly et al., 2023). Lastly, we performed Tukey honest significant difference (HSD) post hoc tests to assess whether response variables differed significantly between pairwise Site-Time Period combinations (e.g., Restored A-Before vs. Restored A-After).

We analysed differences in macroinvertebrate taxonomic and functional compositions between Site-Time Period pairwise combinations (indicating the Restoration Effect) using principal coordinate analysis (PCoA) plots, which were performed on a Bray-Curtis dissimilarity matrix using the *cmdscale* function in Vegan. We calculated the total variation explained by each PCoA axis by dividing its eigenvalue by the sum of all eigenvalues. These plots enabled the shift in compositions to be identified (via the centroid) in addition to any changes in community heterogeneity (via the convex hull—the minimum-possible area enclosing all values in ordination space). For the latter, we identified outliers for PCoA

axis 1 and 2 scores from interquartile range (IQR) values (values below $Q1 - 3 \times IQR$ or above $Q3 + 3 \times IQR$) and removed from the plot to aid visual interpretation (samples from Control and Restored B sites in spring 2014 samples prior to works were removed, as was the autumn 2022 sample at Restored A site after the works). We performed Pearson correlation tests between individual taxa and traits versus corresponding PCoA axis scores. We explored multivariate differences in taxonomic and functional compositions between the overall Restoration Effect alongside Season (as with the linear regression models) via a permutational multivariate ANOVA (PERMANOVA) using the *adonis2* function in Vegan. We then used a pairwise PERMANOVA to assess the significance of multivariate differences between pairwise Site-Time Period combinations using the *pairwise.adonis* function in the *pairwiseAdonis* package (Arbizu, 2020).

Lastly, we tested individual taxa and traits associated with specific Site-Time Period combinations using a group-equalised 'Indicator Value' (IndVal) analysis. This was conducted via the 'multipatt' function in the 'indicpecies' package and performed across 999 permutations to determine its significance.

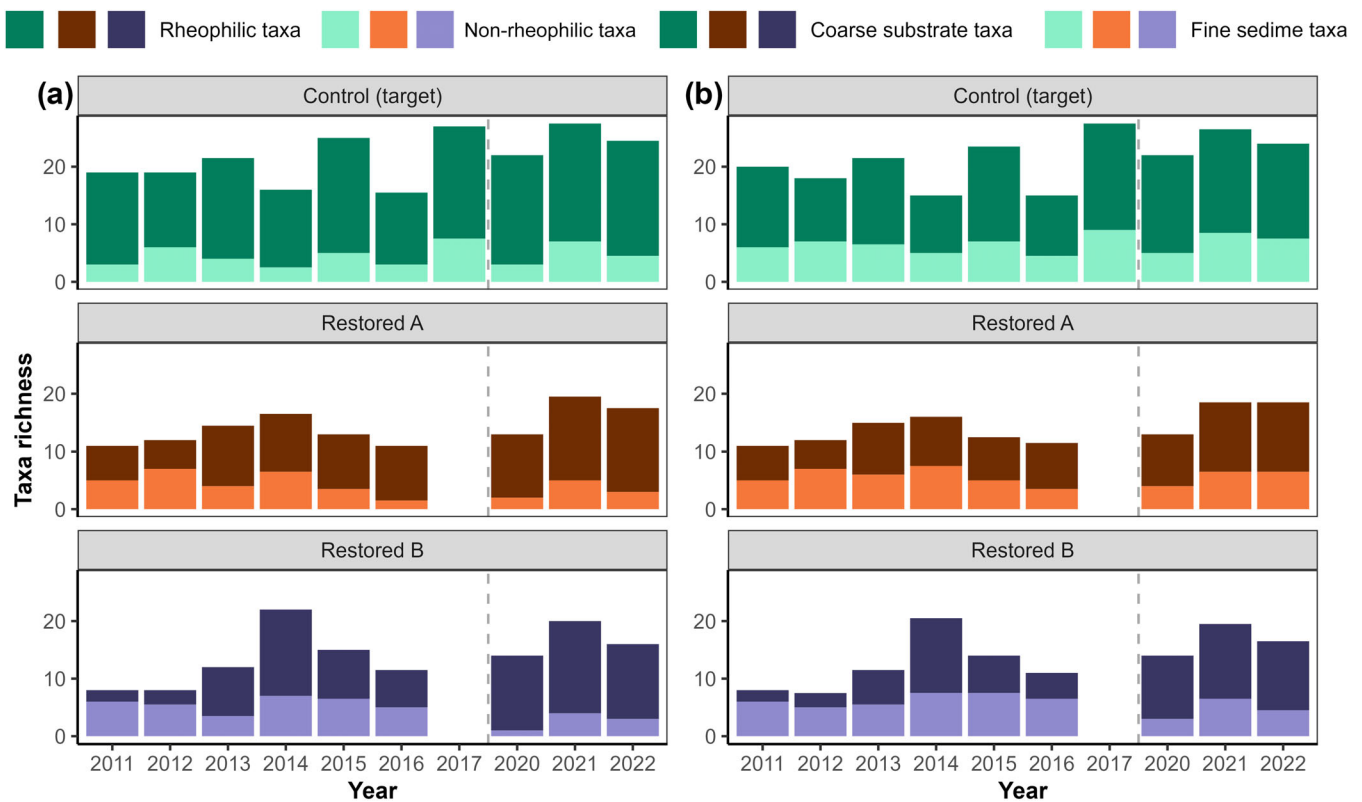


FIGURE 2 Stacked bar charts highlighting the mean averaged number of taxa expressing different ecological guilds across different years and sites. (a) velocity conditions and (b) benthic sediment characteristics. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

3 | RESULTS

3.1 | Taxonomic and functional macroinvertebrate responses

Two-way ANOVA highlighted that eight (of the 10) univariate metrics displayed a significant Restoration Effect, while the non-rheophilic taxa richness and fine sediment taxa richness were non-significant (see Table S2).

Taxa richness broadly increased in the years following restoration across all sites, but this was most prominent in Restored A (Figures 1a and 2). These differences in taxa richness increases over time between sites resulted in the significant Restoration Effect ($r^2 = 0.43$; $F = 6.5$; p -value < 0.001). The Tukey's HSD posthoc analyses highlighted that taxa richness differed significantly between the Control versus both the Restored A and Restored B sites prior to, but not after, restoration (Table 2). However, while taxa richness values were more comparable between sites after restoration (relative to pre-works), these are still higher on average in the Control site throughout the study period (Figures 1a and 2). A significant Restoration Effect on Pielou's Evenness ($r^2 = 0.43$; $F = 6.3$; p -value < 0.001) and Simpson's Diversity ($r^2 = 0.39$; $F = 5.1$; p -value < 0.001) reflects steeper declines in values over time in the Restored A and Restored B sites compared to the Control (Figure 1b,c). As with taxa richness, posthoc analyses indicated that Pielou's Evenness differed significantly

between the Control versus both the Restored A and Restored B sites before the weir removal and not after (Table 1). Simpson's Diversity also differed significantly between Control versus Restored B prior to the works, and while the corresponding pairwise comparison Restored A was marginally non-significant, this was far more statistically robust (i.e., lower p -values) compared to the post-restoration comparison (Table 1).

The functional richness, evenness and diversity (Rao's Quadratic Entropy) were broadly comparable within the Control site before and after the weir removal (Figure 1d-f), although the former displayed a slight increase on average. A slight upward trend in functional richness was also observed in Restored A, but this was highly variable and far less pronounced compared to corresponding taxa richness increases (Figure 1d). Conversely, functional richness values in Restored B declined following restoration. The disparities in how functional richness varied between Time Periods across the different sites explained the significant Restoration Effect ($r^2 = 0.33$; $F = 4.2$; p -value = 0.004). No significant differences were observed in Tukey's HSD test for functional richness, likely due to the large variability in such values between sites and Time Periods. In keeping with the corresponding taxonomic measures, the Restoration Effect had a significant influence on functional evenness ($r^2 = 0.53$; $F = 9.0$; p -value = < 0.001) and Rao's Quadratic Entropy ($r^2 = 0.44$; $F = 6.7$; p -value = < 0.001) whereby such values declined in restored sites after the weir removal (Figure 1e,f). Tukey's HSD indicated significant and

Ecological response	Site	Before	After
Taxa richness	Control versus Restored A	0.009	0.336
	Control versus Restored B	0.005	0.135
	Restored A versus Restored B	1.000	0.996
Pielou's evenness (J)	Control versus Restored A	0.016	0.666
	Control versus Restored B	0.001	0.747
	Restored A versus Restored B	0.930	1.000
Simpson's diversity (D)	Control versus Restored A	0.054	0.963
	Control versus Restored B	0.044	0.993
	Restored A versus Restored B	1.000	1.000
Functional richness	Control versus Restored A	0.063	0.409
	Control versus Restored B	0.067	0.138
	Restored A versus Restored B	1.000	0.989
Functional evenness	Control versus Restored A	<0.001	0.905
	Control versus Restored B	<0.001	0.956
	Restored A versus Restored B	0.971	1.000
Rao's quadratic entropy	Control versus Restored A	<0.001	0.909
	Control versus Restored B	0.076	1.000
	Restored A versus Restored B	0.330	0.971
Rheophilic taxa richness	Control versus Restored A	<0.001	0.007
	Control versus Restored B	<0.001	0.013
	Restored A versus Restored B	0.729	1.000
Non-rheophilic taxa richness	Control versus Restored A	0.999	0.820
	Control versus Restored B	0.999	0.547
	Restored A versus Restored B	0.983	0.997
Coarse substrate taxa richness	Control versus Restored A	<0.001	0.014
	Control versus Restored B	<0.001	0.047
	Restored A versus Restored B	0.437	0.997
Fine sediment taxa richness	Control versus Restored A	0.941	0.863
	Control versus Restored B	1.000	0.388
	Restored A versus Restored B	0.972	0.964

TABLE 1 Tukey's honest significant difference test calculating the significance in differences in various ecological metrics across different pairwise combinations of Site and 'Time Period' (i.e., before vs. after restoration works).

Note: Significance differences are highlighted with bold text. Non-rheophilic taxa and fine sediment taxa richness exhibited non-significant trends in the two-way analysis of variance (see Table S2), but have been included here for completeness.

marginally non-significant differences between Control versus Restored A and Restored B sites in the before Time Period (respectively), and considerably higher p -values (indicating lower statistical significance) after the restoration (Table 2).

A significant Restoration Effect was observed for both rheophilic taxa richness ($r^2 = 0.73$; $F = 21.6$; p -value = <0.001) and coarse substrate taxa richness ($r^2 = 0.71$; $F = 20.3$; p -value = <0.001). The Control site consistently supported higher numbers of taxa preferring fast flow velocities (i.e., rheophilic) and coarser substrates, while this typically only occurred in both restored sites after the weir removal (Figures 2 and 3). These two responses displayed similar differences between Time Periods to the overall taxa richness (see Figure 1a), although Restored B displayed stronger increases than Restored A (Figure 3). Tukey's HSD test highlighted that the Restored A and Restored B sites displayed significantly lower rheophilic taxa richness

and coarse substrate taxa richness values versus the Control site in both the before and after Time Periods, which were the only significant post hoc results observed after restoration. The restored sites supported a high relative proportion of taxa preferring slower flow velocities (i.e., non-rheophilic species) and fine sediments prior to works, most notably in 2011 and 2012 (Figure 2). The number of non-rheophilic taxa evidently declined in both restored sites after the weir removal, which was also observed for fine sediment taxa richness in Restored B but not Restored A (Figure 3). However, the non-significant two-way ANOVA (Restoration Effect) and Tukey's HSD outputs highlight the large variability in how non-rheophilic and fine sediment taxa richness varied between sites and over time. Season exerted a significant influence on only the rheophilic taxa richness and coarse substrate taxa richness, with the spring months supporting evidently higher values (Table S2 and Figure S3).

TABLE 2 Indicator species analysis characterising taxa and functional trait associations with different Site-Time Period (i.e., before vs. after restoration) combinations.

Site-Time Period combinations	Taxa	Indicator Species value	p-Value	Functional grouping feature	Functional trait	IS value	p-Value
Control (before), Control (after), Restored A (before), Restored B (before), Restored B (after)—Common species/traits that declined in the upper restored reach after works	<i>Baetis rhodani/atlanticus</i>	0.89	0.025	Reproduction	Clutches, terrestrial	0.91	0.023
Control (before), Restored A (before), Restored B (before)—Taxa that declined across all reaches in recent years.	<i>Sigara</i> sp.	0.78	0.010				
Control (before), Control (after)—Taxa consistently associated with 'target' conditions (not restored sites).	<i>Rhyacophila dorsalis</i>	0.81	<0.001				
	<i>Limnius volckmari</i>	0.77	0.006				
	<i>Hydropsyche siltalai</i>	0.77	<0.001				
Control (after)—Taxa only associated with 'target' conditions (not restored site) in recent years.	<i>Polycelis felina</i>	0.86	<0.001				
	<i>Hydropsyche pellucidula</i>	0.70	0.010				
	<i>Hydraena</i> sp.	0.63	0.019				
	<i>Agraylea multipunctata</i>	0.63	0.019				
Control (after), Restored A (after)—Taxa associated with target conditions in recent years and upper restored site after works.	<i>Lype</i> sp.	0.78	0.005				
Control (after), Restored B (after)—Taxa associated with target conditions in recent years and lower restored site after works.	<i>Calopteryx virgo</i>	0.67	0.018				
Control (after), Restored A (after), Restored B (after)—Taxa associated with target conditions in recent years and both restored sites after works.	<i>Antocha vitripennis</i>	0.97	<0.001				
	<i>Heptagenia sulphurea</i>	0.93	<0.001				
Control (before), Control (after), Restored A (after)—Taxa consistently associated with target conditions and upper restored site after works.	<i>Riolus subviolaceus</i>	0.71	0.008	Reproduction	Asexual	0.77	0.003
Control (before), Control (after), Restored B (after)—Taxa consistently associated with target conditions and lower restored site after works.	<i>Ancylus fluviatilis</i>	0.89	<0.001				
Control (before), Control (after), Restored A (after) and Restored B (after)—Taxa consistently associated with target conditions and both restored sites after works.	<i>Agapetus</i> sp.	0.98	<0.001	Locomotion	Permanently attached	0.94	<0.001
	<i>Silo</i> sp.	0.97	<0.001	Resistance	Builds cocoons	0.94	<0.001
	<i>Ithytrichia</i> sp.	0.82	0.008	Reproduction	Clutches, free	0.82	0.039
	<i>Baetis scambus</i>	0.71	0.031				
	<i>Orectochilus villosus</i>	0.71	0.039				

Note: Grey boxes indicate positive ecological effects of restoration works.

3.2 | Macroinvertebrate indicator species responses

Indicator species analyses highlighted various taxa and some traits that were significantly associated with different Site-Time Period combinations (Table 2). Various rheophilic taxa were recorded more consistently and in greater abundances in the Control site, either throughout the study period (e.g., *Rhyacophila dorsalis*) or specifically in the years following restoration (despite not being directly affected by works; e.g., *Polycelis felina*). Additionally, a variety of rheophilic taxa

were associated with restored sites and the Control site after the weir removal, including *Lype* sp.—Restored A, *Calopteryx virgo*—Restored B, and *Heptagenia sulphurea* and *Antocha vitripennis* both restored sites. Various traits were associated with the Control site throughout the study period, as well as both restored sites after the weir removal. Specifically, taxa that are permanently attached to substrates, build cocoons (as a form of resistance) and lay clutches of eggs freely in the water were significantly associated with these Site-Time period combinations (Table 2). *Sigara* sp. (a non-rheophilic taxa) was significantly associated with the before Time Period in all three sites. *Baetis*

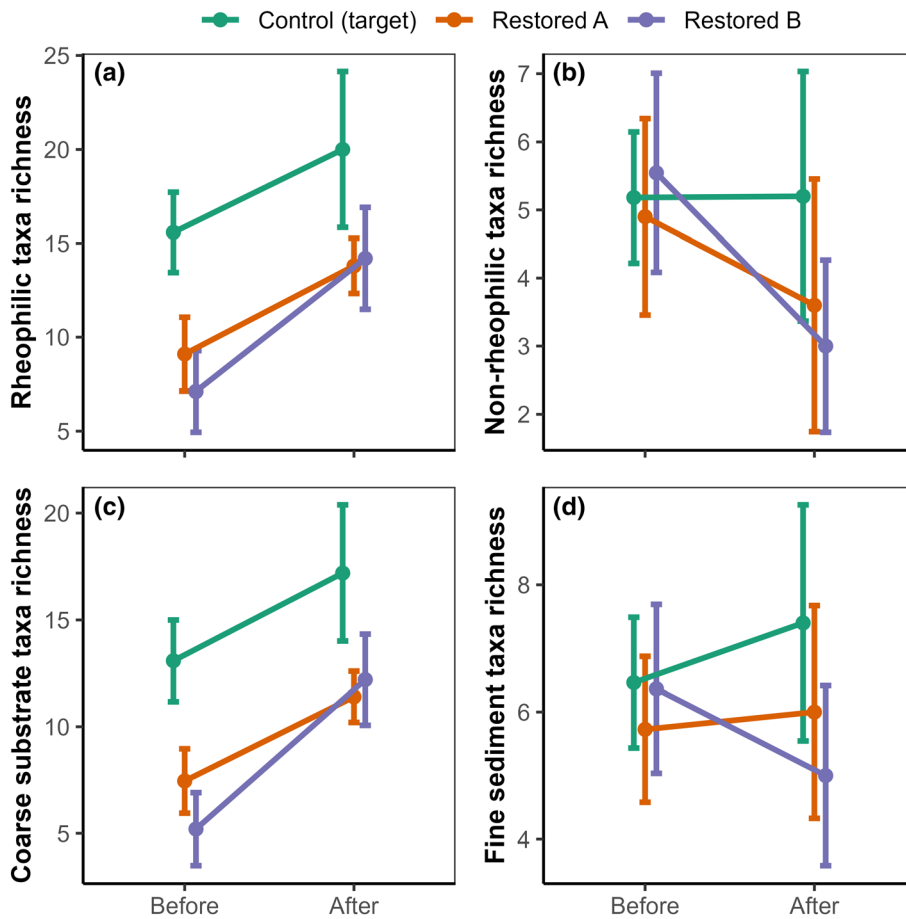


FIGURE 3 Error plots (mean \pm 2 standard errors) indicating changes in univariate metrics denoting the richness of taxa expressing ecological guilds. (a) Rheophilic taxa richness; (b) Non-rheophilic taxa richness; (c) Coarse substrate taxa richness; and (d) Fine sediment taxa richness. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Pairwise permutational multivariate analysis of variance indicating the significance (highlighted with bold text) of taxonomic and functional trait compositional differences across different Time Periods (i.e., before and after restoration works).

Composition	Reach	Before	After
Taxonomic	Control (target) versus Restored A	0.015	0.390
	Control (target) versus Restored B	0.015	0.705
	Restored A versus Restored B	1.000	1.000
Functional	Control (target) versus Restored A	0.015	0.270
	Control (target) versus Restored B	0.015	1.000
	Restored A versus Restored B	1.000	1.000

rhodani/atlanticus and taxa reproducing via clutches of eggs laid in terrestrial vegetation were significantly associated with all Site-Time Period pairwise combinations except for samples taken Restored A following restoration, suggesting these species/traits were commonly found but were less suited to the upper restored site following the restoration (Table 2).

3.3 | Community macroinvertebrate responses

PERMANOVA highlighted a significant Restoration Effect on both taxonomic ($r^2 = 0.34$; $F = 4.6$; p -value = <0.001) and

functional trait ($r^2 = 0.36$; $F = 5.6$; p -value = <0.001) compositions. The pairwise PERMANOVA highlighted that the Control site supported significantly different taxonomic and functional compositions compared to each restored site before the weir removal, but non-significant trends were observed after works were undertaken (Table 3). Such trends were reinforced by the PCoA analyses, whereby the taxonomic and functional compositions of Restored A and Restored B sites prior to restoration (lower PCoA axis 1 scores) were distinctly separated from corresponding samples collected at the same sites after the works, as well as from all samples from the Control site (higher PCoA axis 1 scores; Figure 4; Figure S4).

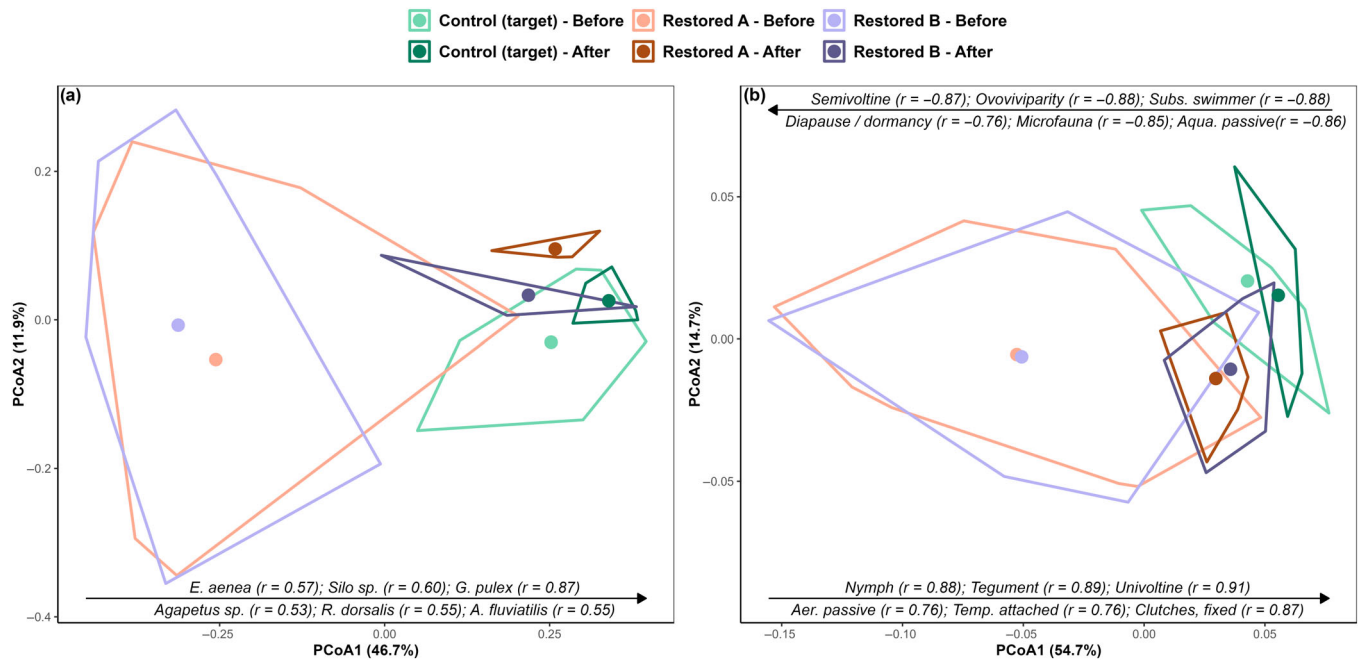


FIGURE 4 Principal coordinate analysis (PCoA) indicating the average (centroid) and spread (convex hull) of macroinvertebrate community taxonomic (a) and functional (b) compositions displayed by across each Reach-Time period (i.e., before vs. after restoration) pairwise combination. The strongest correlations between individual taxa and traits versus PCoA axis 1 scores are displayed (no strong negative correlations were observed for individual taxa and are therefore not displayed: Minimum $r = -0.32$). For the individual traits (grouping feature; see Table S1): ‘Subs. Swimmer’ = full water swimmer (locomotion); ‘Ovoviviparity’ (reproduction); ‘Semivoltine’ = >1 brood per year (voltinism); ‘Aqua. passive’ = aquatic, passive (dispersal); ‘Microfauna’ = macroinvertebrates (food); ‘Diapause/dormancy’ (resistance); ‘Univoltine’ = 1 brood per year (voltinism); ‘Tegument’ (respiration); ‘Nymph’ (aquatic stage); ‘Clutches, fixed’ = (reproduction); ‘Temp. attached’ = Temporarily attached (locomotion); and ‘Aer. Passive’ = aerially passive (dispersal). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

4 | DISCUSSION

English ‘chalk’ streams are internationally recognised and prized for their biodiversity (Mainstone, 1999). However, many chalk streams have been degraded by multiple human pressures, leading to calls for their restoration (Rangle-Wilson et al., 2021). Attempts to improve and reverse morphological degradation of river environments is typically expected to increase ecological resilience to further disturbance (Woodward et al., 2016). In this study, we assessed whether river restoration via weir removal facilitated the (re)establishment of macroinvertebrate communities comparable with those of the Control site.

Our univariate and multivariate analyses highlighted greater taxonomic and functional similarity between the Control site versus the two restored sites after the weir removal, and thus a shift in macroinvertebrate communities towards target ecological conditions. These assemblages were typified by a higher taxonomic and functional richness, but lower corresponding evenness and diversity values. Such findings indicate that the Control site, and now the restored sites, support a greater number of macroinvertebrate species that are more dominated by a smaller number of taxa. The shift in communities in the restored sites is likely to reflect the change in habitat composition observed, with a more diverse habitat composition supporting a greater richness of species (Townsend & Hildrew, 1994).

Importantly, our analyses suggest that recovery is underway, but not yet complete. This was most evident from patterns in taxa richness, which remained lower in both restored reaches compared to the Control site after the weir removal. Timescales of ecological responses to river restoration are highly variable (Stoll et al., 2016) depending on factors like physical habitat adjustments following works (Al-Zankana et al., 2020); the proximity of restored reaches to colonist sources and potential barriers restricting their dispersal (Sundermann et al., 2011); biotic pressures for established communities, including competition for food resources (Barrett et al., 2021); and the presence of other prevailing abiotic pressures (flow regime modifications, water quality issues; Leps et al., 2015).

Our study presents macroinvertebrate assessments for 3 years post-restoration. Whilst this is longer than the 1 or 2 years or seasons following restoration in many post-project appraisal studies (Lorenz, 2021), it was likely insufficient to document complete recovery following the restoration scheme. Various other studies have reported ongoing or incomplete ecological recovery within 3 years of river restoration schemes, as highlighted in different meta-analyses (Kail et al., 2015; Lu et al., 2019). More specifically, Dézerald et al. (2023) reported high levels of community instability 3 years following a dam removal, while England, Hayes, et al. (2021) highlighted ongoing biotic community responses 4 years after a weir removal on a comparable chalk stream. Physical habitat and ecological responses to

passive process-based restoration such as weir removal can be slow (Beechie et al., 2010; Wohl et al., 2024), especially in lowland ground-water dominated rivers where typically flow variability is buffered and sediment movement is slow (Sear et al., 1999). Where more active restoration measures are employed, physical habitat and ecological responses can typically be detected more rapidly, even in low energy environments. For instance, Thompson et al. (2018) identified rapid biodiversity improvements only 1-year after woody material was introduced along various English chalk streams.

Ecological improvements observed in this study would have been aided by diverse regional species pools within the catchment that could (re)colonise and (re)establish following the implementation of larger scale management interventions (Patrick et al., 2021; Sundermann et al., 2011). Biodiversity improvements were observed in the Control and restored sites, although this occurred at slightly (but significantly) higher rates in the latter (i.e., those directly affected by the weir removal). This highlights that even after accounting for wider background ecological improvements in recent years, physical habitat changes from the restoration works also accounted for ecological recovery within the formerly impounded reach. These results highlight the importance in BACI designs and long-term monitoring before and after restoration, whereby the temporal trajectories of ecological recovery following restoration can be placed within the context of wider causes of ecological change (England, Angelopoulos, et al., 2021). Wider biodiversity recovery in the Lambourn may have stemmed from upstream restoration works (Environment Agency, 2011; for another example, see England, Hayes et al., 2021), but in other instances may involve wider catchment management practices like water quality improvements or environmental flow strategies (Lynch et al., 2023). Studies quantifying the ecological responses to river restoration schemes in the context of broader catchment initiatives have not been widely reported, and fewer still have demonstrated the complementary ecological benefits of restoration alongside other management interventions. Rare exceptions include Nicol et al. (2021), who reported that woody material introductions were unlikely to yield notable ecological benefits within wider environmental flow strategies, while Williams et al. (2020) reported that debris dam introductions did not facilitate additional biodiversity benefits on top of those linked to catchment-scale water storage interventions. Given the dramatic biodiversity losses encountered in freshwater ecosystems globally, multiple management initiatives will be increasingly required to address the different anthropogenic pressures within river environments (Lynch et al., 2023; Reid et al., 2019). Further evidence like that provided in this study is required to highlight when different management initiatives applied simultaneously can effectively facilitate ecological recovery.

The ecological trajectories of taxonomic and functional properties differed slightly between the restored sites, despite being located within the same formerly impounded section of river 200-metres apart. Specifically, both restored sites experienced considerable increases in rheophilic taxa that typically inhabit coarser substrates, but this was more prevalent in Restored B that was closer (0.05 km

upstream) to former weir. Such findings likely reflected the former ponding effect of the weir that made the site uninhabitable for such species prior to works (England, Angelopoulos, et al., 2021), while its removal promoted faster flowing conditions. It may be that ongoing natural biogeomorphic processes will result in marginal deposition of sediment, consolidated by the colonisation by plants, which could promote habitat and ecological diversity by creating these new conditions while focusing flows in mid-channel areas (Gurnell & Grabowski, 2016). Continued monitoring of the scheme presented here is recommended to document future development of habitat composition and ecological communities. A better understanding of recovery following passive process-based restoration in low energy streams can inform suitable 'goals' and therefore more targeted and effective assessments in future (England, Angelopoulos, et al., 2021). It will also allow better discussions with stakeholders about expected timescales of recovery as wide stakeholder support is considered an important component of successful restoration schemes (Angelopoulos et al., 2017).

Despite taxonomic richness increases after the weir removal, taxonomic evenness and diversity declined across all sites, and most notably in the restored section. This indicates that environmental improvements can allow a subset species to dominate, but not at the peril of the wider ecosystem. This depicts a key finding as other studies have reported the dominance of competitively superior taxa that can inhibit ecological recovery following restoration (Barrett et al., 2021). Functional responses displayed comparable, but more variable trends relative to their taxonomic counterparts. For instance, functional richness increased in the Control and Restored A sites after the weir removal (albeit less profoundly than taxa richness). Functional richness is typically highly correlated with taxa richness, although the former can start to plateau at higher species numbers due to functional redundancy effects, which likely explained the modest functional richness increases observed over time (across the Control and restored sites) in this study (see England & Wilkes, 2018). The declines in functional richness observed after the weir removal in Restored B are likely due to the more marked (re)colonisation of rheophilic taxa (with more broadly comparable functional properties) and potentially simultaneous losses of non-rheophilic taxa, the latter not being observed in the Control or Restored A sites (although this trend was non-significant). Functional evenness and diversity (Rao's Quadratic Entropy) measures responded comparably over time compared to their corresponding taxa metrics. While this intuitively suggests that greater taxa dominance resulted in lower diversity being reflected in their associated functional trait properties, such congruency is often not observed in other freshwater macroinvertebrate research (England, Angelopoulos, et al., 2021; White et al., 2019). The restored site studied created environmental conditions that allowed species exhibiting specific functional properties (specifically univoltine, tegument-breathing insect nymphs, including *Silo* sp., *Rhyacophila dorsalis* and *Agapetus* sp.) to dominate. By exploring the taxonomic and functional responses concurrently, our study demonstrates the additional insight that it

brings to understanding ecological recovery, thus improving our understanding of the effects of river restoration (White et al., 2017). Functional assessments also provide insight into habitat preference, habitat heterogeneity and specific biotopes (Verdonschot et al., 2016) which can improve our ability to predict ecological response to river restoration. Our findings support our hypothesis that the macroinvertebrate communities would become more similar to the Control site in both structural complexity (e.g., taxonomic composition) and functional integrity (e.g., trait composition). However, it is clear that the ecological recovery process is ongoing (as evidenced by taxa and functional richness trends) and the restored sites are not yet comparable with the Control site.

5 | CONCLUSIONS

Our study tracks initial ecological (macroinvertebrate) response to the removal of a historical barrier, on a lowland groundwater-fed chalk stream in the context of other catchment-wide improvements. We found that the macroinvertebrate communities are moving towards those of the target community both in terms of structural complexity (e.g., taxonomic composition) and functional integrity (e.g., trait composition). This ecological recovery progress is ongoing and reflects the time that process-based restoration can take in lower energy systems such as chalk streams. Additional, longer-term assessment is needed before ecological responses to the removal of this weir can be more comprehensively understood. However, we highlight the importance of a BACI approach to understand the local responses to restoration in a catchment context. Our research may serve to inform design of more targeted and robust river restoration assessments with an increased likelihood of accurately and effectively detecting ecological change.

Consideration of the physical and ecological response time needs to be made when planning restoration schemes, as to whether to apply (a) passive process-based restoration and let nature take its course or (b) more active approaches which may be quicker but more expensive. This evidence base is needed urgently to deliver ecosystem restoration at the scale needed to address current physical modification and adapt to a changing climate and its hydroecological impacts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Environment Agency Ecology and Fish Data Explorer at <https://environment.data.gov.uk/ecology/explorer>.

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SUPPORTING INFORMATION

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

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