Evidence of Taxonomic and Functional Recovery of Macroinvertebrate Communities Following River Restoration

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Abstract: River ecosystems have been heavily degraded globally due to channel hydromorphological modifications or alterations to catchment-wide processes. Restoration actions aimed at addressing these changes and restoring ecological integrity are increasing, but evidence of the effectiveness of these actions is variable. Using a rare 7-year before-after-control-impact (BACI) study of restoration of a lowland groundwater-fed river in England, UK, we explore changes in the macroinvertebrate community following the removal of impoundments and channel narrowing to aid restoration of physical processes. Restoration activity prompted significant taxonomic and functional responses of benthic invertebrate communities in the 4 years post-restoration. Specifically, significant gains in taxonomic and functional richness were evident following restoration, although corresponding evenness and diversity measures did not mirror these trends. Restoration activities prompted a shift to more rheophilic taxa and associated traits matching the physical changes to the channel and habitat composition. Temporal changes were clearer for taxonomic compositions compared to the functional properties of macroinvertebrate communities, indicating a functional redundancy effect of new colonists inhabiting restored reaches following restoration. The results highlight the value of long-term BACI studies in river restoration assessments, as well as project appraisals incorporating both taxonomic and functional observations. We highlight the urgent need of such studies to provide evidence to inform effective river restoration strategies to address future changes such as adaption to climate change and the biodiversity crisis.

Keywords: groundwater fed river; diversity; BACI; connectivity; hydromorphology

1. Introduction

Freshwater ecosystems comprise <1% of the earth's surface but support up to 12% of the world's biodiversity [1] and are under threat from a multitude of anthropogenic stressors [2,3]. One of the primary pressures degrading riverine systems is morphological change [3] stemming from physical modifications to the channel or alteration of catchment condition and processes [4], which simplifies river habitats and ecosystems [5,6].

River restoration activities focussed on addressing physical degradation are increasingly being applied [7]. While historically, river restoration activities entailed the creation of stable channels mimicking natural forms, there has been a shift in recent years to a process-based hydromorphological ideology, where restoration techniques are designed to re-establish the lateral, longitudinal and vertical connectivity of river systems [8]. From an ecological standpoint, biomic river restoration practices [9] have been widely advocated, reconnecting healthy biomes to realise the benefits of biological interactions in river processes. Bradshaw's [10] classic model of ecological restoration considers system trajectories after restoration in two dimensions—structural complexity (e.g., taxonomic composition) and

functional integrity (e.g., trait composition). Aligning well with process-based and biomic restoration approaches, Bradshaw's concept remains fundamental to river restoration, aiming to restore ecosystem structure and function [11,12].

Restoration projects are often implemented based on the assumption that if the habitat quality of the stream is restored, then the biological diversity will benefit—the "Field of Dreams Hypothesis" assuming that "if you build it, they will come" [13]. However, the history of the ecological success of restoration activities is inconsistent, with some researchers reporting success (e.g., [7]), whilst others report mixed results (e.g., [14,15]). Differences have been attributed to restoration activity not being undertaken at the same scale as the causes of degradation [15,16], varying timescales of ecological response [17], proximity to sources of colonists [18], limiting factors degrading riverine ecosystems not being addressed [16] and/or interactions with other anthropogenic stressors [19,20].

Part of the mixed picture of restoration success can be attributed to the lack of monitoring and appraisal [21,22] or a poorly planned inappropriate monitoring strategy that provides meaningless or misleading information [23,24]. Whilst the number of restoration appraisals published is increasing [15], there is often a focus on short-term recovery, with most studies investigating only 1 or 2 years or seasons post-restoration [25], with longer-term monitoring still rare (but see [25–27]). However, monitoring undertaken with more rigor or over a longer timescale will increase the likelihood of accurately and effectively detecting changes in community change [28].

With logistical issues and limited financial resources available to undertake scientific assessment of restoration effectiveness, targeted appraisals or demonstration projects can be used to assess hydromorphological and ecological responses, which could in turn guide other restoration activities [29,30]. Barrier removal is a well-established restoration technique that aims to enhance longitudinal connectivity to restore natural processes [31–33]. The rate and response of geomorphological processes to the connectivity being restored depends on the energy within the river to drive the physical processes [33,34]. Groundwater-fed river systems, such as the UK's chalk streams, are low-energy systems, and relying on natural physical processes to modify physical habitats may be expected to take longer [35,36]. To assess the timescale of responses to barrier removal in a lowland groundwater-fed chalk stream, we applied a before-after-control-impact (BACI) approach to a UK case study to investigate the effects of removing impoundments on benthic macroinvertebrates. We hypothesised that following the removal of infrastructure, restored sites would become more hydromorphologically and ecologically similar to the control sites. Following Bradshaw's model of restoration [10], we hypothesised that these changes would be reflected in both structural complexity (e.g., taxonomic composition) and functional integrity (e.g., trait composition) of macroinvertebrate communities [37].

2. Materials and Methods

2.1. Study Area

The river Kennet is one of the main tributaries in the river Thames catchment (southeast England, UK). It is a lowland, groundwater-fed chalk stream, approximately 70 km long, with multiple interconnected channels and upper reaches that dry seasonally forming winterbourne sections [35]. The Kennet has been designated for its conservation value as a Site of Special Scientific Interest (SSSI [38]). Historic modification to the Kennet has resulted in sections of the river being over-widened and impounded by a series of weir and sluice structures. To address the physical modifications, a catchment-wide river restoration plan was developed in 2011 and is ongoing [39].

The restoration activity under assessment here took place in a perennial section of the river (Figure 1a) and involved the alteration or bypassing of a series of sluices and weir structures, which were historically used primarily to supply flow to a water meadow system. The removal of the impounding influences was accompanied by channel narrowing to restore natural river processes by improving hydraulic and sediment connectivity. The restoration took place in October and November 2013.
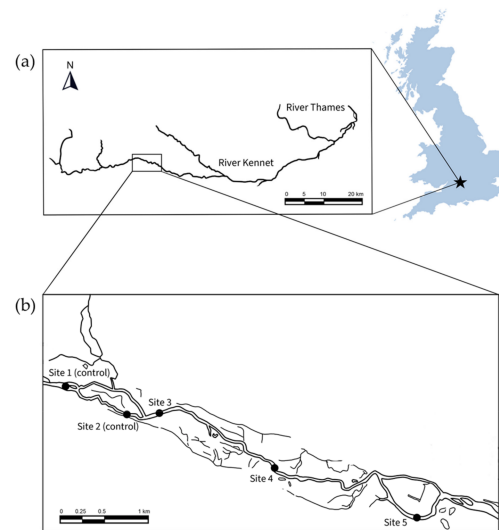
Figure 1. Location of the Kennet River restoration scheme (**a**) and the monitoring sites (**b**).

Routine Environment Agency data from a monitoring site 1.5 km downstream of the study area confirm that throughout the study period, the water quality of the Kennet was good to high, apart from dissolved oxygen, which was moderate in 2016 (Supplementary Material Table S1).

2.2. Sampling Strategy

To assess the effects of the restoration activity on the benthic macroinvertebrate community, we monitored two control sites and three restoration sites (Figure 1b). The control sites were located upstream of the previous impounding influences, with no tributaries or discharges entering the channel between the control sites and the restored sites. The control sites represent sections of the watercourse considered to be representative of a healthy chalk stream, containing no impounding structures and narrower channel widths more akin to unmodified chalk systems (Appendix A).

Each site was sampled annually in spring (April–May) and autumn (September– November), starting in autumn 2011 through to autumn 2017, with the exception of control site 1, where sampling started in autumn 2012. The samples from autumn 2013 were collected prior to the start of the restoration work. On each sampling occasion, macroinvertebrate samples were collected following the standard approach used by UK regulatory agencies [40,41]: a 3 min kick/sweep technique using a pond net, where the bed of the river is disturbed by kicking the substrate and vegetation whilst zig-zagging in an upstream direction, sampling all available habitats in proportion to their occurrence. This is supplemented by a 1 min hand search. Visual estimates of channel substrate composition within the survey site (% boulders, cobbles, pebbles, gravel, sand and silt) were made in association with each macroinvertebrate sample, and the mean substrate size summarised as the mean substrate (MSUB) in phi units [42,43]. Coarse-grained dominated substrates are represented by low MSUB values, and fine-grained dominated substrates by high MSUB values. Channel widths and depths (averaged across 3 measurements taken at a quarter, half and three-quarter river width) were recorded at cross sections representative of predominant hydromorphological conditions in the sampling area.

2.3. Data Analysis

2.3.1. Deriving Macroinvertebrate Community Compositions

All data processing and statistical analyses reported herein were performed in R studio (operated within R version 3.3.1 [44]). Functional traits were derived from a European database, which adopts a fuzzy-coding procedure, whereby faunal affinities to individual traits range from zero (indicating no affinity) to three or five (indicating high affinity, the

upper limit depending on the amount information reported in existing literature [45]). Trait information in the database is typically available at the genus or species level. Taxa resolved to a coarser resolution than specified within the database were excluded from the functional analyses, while some 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; for nomenclature, see [46]) were examined that contain information on the biological properties of invertebrate taxa (see Table S2). Prior to the functional analyses, trait values of all qualifying taxa were standardised across all grouping features so that traits summed to 1, thus ensuring equal taxonomic weighting. These standardised values were then used to calculate univariate functional diversity indices (see below). To calculate multivariate functional trait compositions, standardised values were multiplied by $\ln(x + 1)$ transformed community abundances (see [47]) to create a trait-abundance array. Finally, each trait was averaged across all sampled taxa and standardised across all grouping features to account for spatially and temporally driven changes in taxonomic abundances [48].

2.3.2. Deriving β-Diversity Community Responses

Taxonomic and functional β-diversity values were calculated to assess differences in communities between samples driven by restoration, which were derived via the beta.pair and functional.beta.pair functions, respectively, in the betapart package [49]. Both of these functions subdivide the total β-diversity into turnover and nestedness-resultant components. Turnover represents the replacement of species and traits between samples, while nestedness-resultant indicates the extent to which low-diversity sites contain taxonomic and trait combination subsets of those inhabiting high-diversity sites. Taxonomic β-diversity values were derived using a Sørensen dissimilarity measure performed on the original taxonomic composition matrix (i.e., not modified for functional analyses) in a presence–absence format. The functional β-diversity approach requires both taxonomic and functional trait data inputs. For this, a presence–absence taxonomic dataset (formatted to match the taxonomic resolution available in the traits database) was inputted alongside trait information that was characterised by two PCoA trait vectors (to reduce dimensionality [50]); the latter was processed using the cmdscale function, whereby a Sørensen dissimilarity matrix was constructed from standardised trait values.

2.3.3. Calculating α-Diversity Community Response Metrics

Ten community response metrics reflecting the α-diversity of taxonomic and functional compositions were examined. Initially, six community response metrics representing the α-diversity were derived that captured the richness, evenness and diversity of both taxonomic and functional compositions within each sample. Taxonomic richness and evenness (Pielou's metric) were calculated using base functions, while the taxonomic diversity (Simpson's metric) was derived using the diversity function in the Vegan package [51]. The functional richness (FRic), evenness (FEve) and diversity (Rao's quadratic entropy) were calculated using the dbFD function in the FD package [52] and were derived from a Bray–Curtis dissimilarity matrix created from standardised trait values (see above). In addition, four additional metrics were derived, whereby the taxonomic richness was subdivided into categories characterising the number of taxa preferring specific flow velocities (fast and slow) and substrate sizes (coarse and fine). For this, flow groups assigned to taxa within the Lotic-invertebrate Index for Flow Evaluation (LIFE [53]) metric calculation were used to identify the richness of rheophilic taxa (flow groups 1 and 2) and those preferring slow flow velocities (flow groups 3 and 4). Similarly, macroinvertebrate fine sediment sensitivity ratings assigned to taxa within the Proportion of Sediment-sensitive Invertebrates (PSI [54]) metric calculation were used to identify the richness of taxa preferring coarse substrates (A and B ratings) and fine sediments (C and D ratings).

2.3.4. River Restoration Effects on Hydromorphological Properties

The average channel width, depth and MSUB were used to test hydromorphological responses to river restoration activity. Each of these was used as a response variable in a linear model, whereby treatment (control or restored), time period (before or after) and their interactive effects (testing the influence of restoration) were modelled as covariates alongside the additive influence of season. In addition, the same formulae were repeated within a linear mixed-effect model design using the study site as a random effect to capture potential temporal autocorrelation effects. For each response variable, the Akaike information criterion (AIC) values derived from the linear and linear mixed-effect models were compared. Subsequently, statistical outputs and model predictions (for graphical outputs) from the linear model (i.e., the simpler model) were used unless the linear mixed-effect model possessed an AIC value at least 4 units lower [55]. For all linear or linear mixed-effect models, residual plots were inspected to ensure the assumptions of normality and homoscedasticity were satisfied, with up to 4 outliers being removed during this process. The significance values of all covariates comprising linear or linear mixed-effect models were derived via an analysis of variance, the latter using the Anova function in the Car package [56]. The statistical explanatory power of all covariates was identified through partial r^2 values calculated via the etasq (heplots package [57]) and r2glmm (using the Kenward–Roger approach; r2beta package [58]) functions for linear and linear mixed-effect models, respectively.

2.3.5. River Restoration Effects on Macroinvertebrate Community Compositions

Differences in the taxonomic and functional compositions of macroinvertebrate communities between BACI levels were analysed via principal coordinate analysis (PCoA) plots performed on a Bray–Curtis dissimilarity matrix using the cmdscale function (it should be noted that this PCoA used to visualise compositional changes differs from that derived from standardised trait values used to reduce functional dimensionality; see above). The total variation explained by each PCoA axis was calculated 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 functional community values). To identify the traits driving differences in functional composition, Pearson correlation tests were performed between individual traits and PCoA axes processed from functional compositions.

2.3.6. River Restoration Effects on Macroinvertebrate β-Diversity Values

The pairwise β-diversity functions performed on taxonomic and functional community responses produced six pairwise distance matrices, which accounted for their total β-diversity values, as well as their turnover and nestedness-resultant components. Subsequently, values from all pairwise comparisons between "before control" versus "after control" and "before restoration" versus "after restoration" samples within all six matrices were retained to examine temporal changes separately for control and restored reaches. These values were used as a response variable and examined against treatment (control or restored) in a Kruskal–Wallis to test whether restoration effects on β-diversity properties were significant (QQ plots indicated normality did not exist).

2.3.7. River Restoration Effects on Macroinvertebrate α-Diversity Metrics

The statistical procedures undertaken for hydromorphological responses to restoration (i.e., linear and linear mixed-effect models incorporating the individual and interactive effects of time period and treatment alongside season) were replicated to test for the effects of river restoration on the 10 α-diversity metrics (response variables). To ensure model assumptions were satisfied, functional richness values were ln(x)-transformed. In addition, individual traits (making up the functional compositional matrix) associated with taxa preferring specific flow velocities (i.e., rheophilic taxa or taxa preferring slower velocities) and substrate sizes (i.e., taxa preferring coarse substrates or fine sediments)

were statistically tested via a group-equalised indicator value (IndVal) analysis. This was performed across 999 permutations to determine to determine its significance using the multipatt function in the indicspecies package [59]. This IndVal analysis was also performed for both taxonomic and functional trait compositions (response matrices) that were tested against season (independent variable) to explore the significance of individual taxa and traits associated with spring and autumn months.

3. Results

3.1. Hydromorphological Changes Following Restoration

Restoration yielded a significant effect on the channel width, as evidenced by the significant two-way interaction between treatment and time period (F-value = 18.60; p-value $\leq$ 0.001; Table 1). The average width of restored sites declined on average from 17.0 to 11.9 m before and after restoration activity was undertaken, respectively, while channel widths in the control sites broadly remained stable over time (Figure 2). The interaction between treatment and time period did not yield a significant effect on either the average channel depth or the mean substrate (MSUB; Table 1). However, the MSUB displayed an overall decline after activity was undertaken in restored sites, reflecting an increase in substrate size, and displayed the opposite trend in control sites (Figure 2). Channel depths were consistently higher in restored sites but displayed comparable temporal trends as control sites (Figure 2), thus indicating why treatment yielded a significant effect on channel depth (F-value = 4.36; p-value = 0.037*) but neither time period nor its interaction with treatment did (Table 1).

Table 1. Hydromorphological responses to river restoration indicated by linear model or linear mixed-effect model outputs; the significance tests for these, respectively, use X^2 and F-values (the latter have been italicised). Stars denote the degree of significance: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS, non-significant.

Model	Covariate	Partial r²	X² or *F*-value	*p*-Value
Width	Season	0.14	9.41	0.002 **
	Treatment	0.15	0.09	0.763 (NS)
	Time period	0.28	58.38	<0.001 ***
	Treatment × Time period	0.25	18.60	<0.001 ***
Depth	Season	0.11	10.84	<0.001 ***
	Treatment	0.38	4.36	0.037 *
	Time period	0.00	10.76	0.001 **
	Treatment × Time period	0.02	0.65	0.419 (NS)
MSUB	Season	0.00	*0.24*	0.627 (NS)
	Treatment	0.12	*8.11*	0.006 **
	Time period	0.04	*4.69*	0.034 *
	Treatment × Time period	0.03	*1.83*	0.181 (NS)
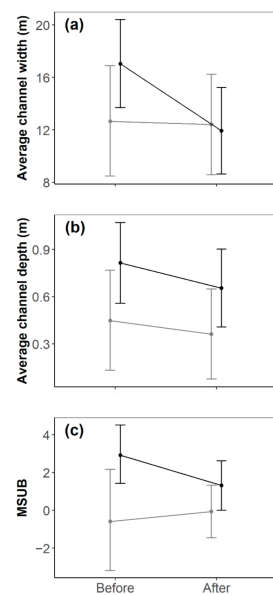
Figure 2. Statistical model outputs (mean and 95% confidence intervals) indicating the effects of restoration on hydromorphological properties. Control = grey; restored = black. Linear mixed-effect models were used to test (**a**) the average channel width and (**b**) the average channel depth, while a linear model was used to test (**c**) the mean substrate (MSUB).

3.2. Community Compositional and β-Diversity Responses to River Restoration

Principal coordinate analysis (PCoA) highlighted a greater shift in the taxonomic and functional composition centroids over time in restored sites relative to control sites, with communities after restoration shifting closer to the control site communities (Figure 3a,b). Taxonomic communities prior to restoration were positively associated with axis 1 and negatively associated with axis 2, which explained 26.1% and 14.8% of the statistical variation, respectively. This trend then reversed following restoration, and communities shifted towards community compositions inhabiting control sites, though they displayed a greater degree of heterogeneity (Figure 3a).
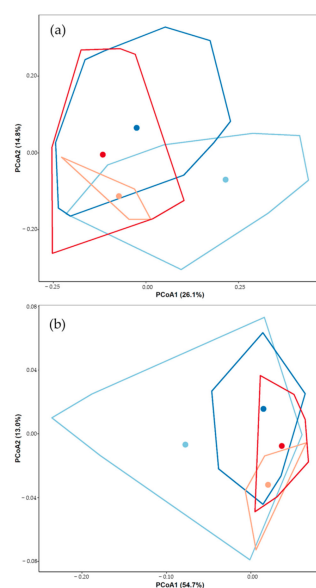
Figure 3. Principal coordinates analysis (PCoA) indicating the average (centroid) and spread (convex hull) of macroinvertebrate community compositions displayed by each BACI level. Before control = orange; after control = red; before restoration = light blue; and after restoration = dark blue. (**a**) Taxonomic compositions and (**b**) functional compositions.

For functional compositions, the before-restoration sites displayed a greater degree of heterogeneity in comparison to post-restoration and control sites (Figure 3b). This was evidenced by samples from before-restoration sites occupying more extreme negative values along axis 1 (54.7% statistical variation), which was characterised by traits of taxa that are ovoviviparous adults, burrow and are passive aquatic dispersers with life cycles of >1 year. (Table 2). Conversely, taxa with life cycles of ≤1 year, aerial dispersers, those laying clutches of eggs that are cemented or fixed (e.g., to cobbles) and taxa that produce one brood per year were positively associated with axis 1 and were thus more typical of restored sites post-restoration and the control sites (Table 2).

Table 2. Five strongest positive and negative Pearson correlation values between PCoA axes 1 and 2 versus individual functional traits.

PCoA Axis	Direction	Grouping Feature	Trait	R
1	Negative	Reproduction	Ovoviviparity	−0.98
		Dispersal	Aquatic passive	−0.93
		Life cycle	>1 year	−0.92
		Aquatic stage	Adult	−0.87
		Locomotion	Burrower	−0.80
	Positive	Life cycle	≤1 year	0.93
		Dispersal	Aerial active	0.87
		Reproduction	Clutches, cemented or fixed	0.86
		Aquatic stage	Nymph	0.85
		Voltinism	1	0.84
2	Negative	Resistance	Cocoons	−0.65
		Reproduction	Clutches, free	−0.61
		Respiration	Tegument	−0.61
		Locomotion	Temporarily attached	−0.56
		Feeding group	Parasite	−0.52
	Positive	Respiration	Gill	0.75
		Food	Living macrophytes	0.62
		Reproduction	Isolated eggs, cemented	0.61
		Feeding group	Deposit feeder	0.54
		Reproduction	Isolated eggs, free	0.49

Restoration yielded a significant increase in the total β-diversity of macroinvertebrate communities over time compared to control sites (Table 3 and Figure 4). This was predominantly driven by a turnover in taxa and traits, which displayed significantly higher rates over time (i.e., before versus after) in restored sites relative to control sites (Table 3). For both the total β-diversity and its turnover component, temporal differences between control and restored sites were clearer for taxonomic compositions compared to the functional properties of macroinvertebrate communities. Conversely, restoration had no significant effect on the nestedness-resultant component of β-diversity for either taxonomic or functional compositions.

Table 3. Kruskal–Wallis statistical outputs indicating the effects of restoration on different β-diversity components. Stars denote the degree of significance: ** $p \leq 0.01$; *** $p \leq 0.001$; NS, non-significant.

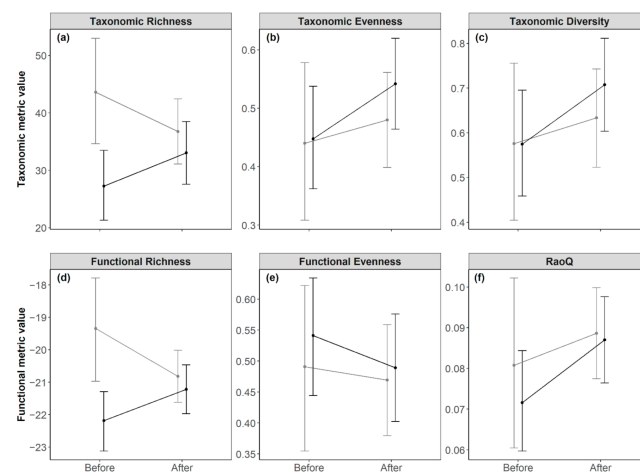|	Taxonomic		Functional	
	X^2	*p*-Value	X^2	*p*-Value
Nestedness-resultant	0.48	0.490 (NS)	1.35	0.244 (NS)
Turnover	91.62	<0.001 ***	11.85	<0.001 ***
Total β-diversity	124.69	<0.001 ***	7.53	0.006 **
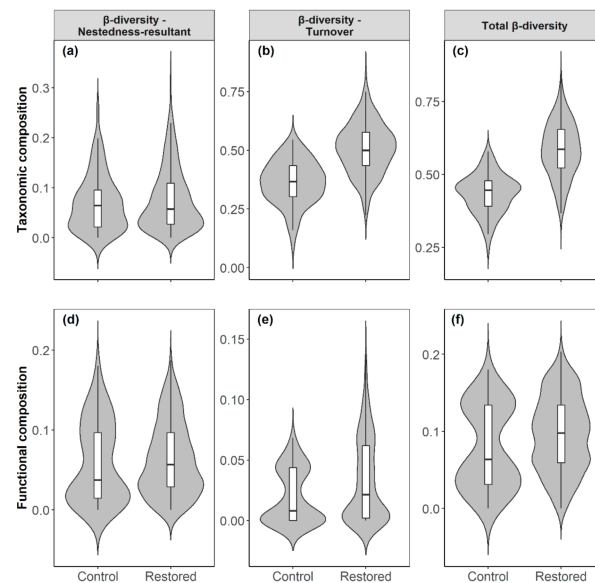
Figure 4. Violin and boxplots (whiskers indicate the range, while boxes indicate the 25th, 50th and 75th percentiles) showing differences in how taxonomic (**a**–**c**) and functional (**d**–**f**) β-diversity properties changed temporally (before versus after) between control and restored sites. The total β-diversity (**a**,**d**) was measured along with the turnover (**b**,**e**) and nestedness-resultant (**c**,**f**) components.

3.3. α-Diversity Responses to River Restoration Activity

Of the six α-diversity metrics examining the richness, evenness or diversity of taxonomic and functional compositions, only the two richness measures displayed significant responses to restoration (taxonomic richness: F-value = 8.66, *p*-value = 0.005; functional richness: F-value = 6.48, *p*-value = 0.014; Table 4). Both taxonomic and functional richness measures increased after works were conducted in restored sites, whilst they yielded decreases in control sites across the same time period (i.e., before versus after; Figure 5). Although not statistically significant, the taxonomic evenness, taxonomic diversity and Rao's quadratic entropy (RaoQ) did display greater increases over time in restored sites compared to control sites (Figure 5). Season yielded a significant influence on all taxonomic metrics and a notably high effect on functional evenness, individually explaining 24% of the model (partial r^2 = 0.24; F-value = 18.52; *p*-value < 0.001; Table 4). The taxonomic richness was significantly greater during the spring months, while the functional evenness was significantly higher during autumn (Supplementary Material 2, Figure S1). Various Ephemeroptera (e.g., *Seratellaignita*, *Caenisrivulorum* and *Baetisscambus*) and Trichoptera (e.g., *Athripsodesalbifrons*, *Lepidostomahirtum* and *Limnephiluslunatus*) species were significantly associated with the spring sampling season, along with various life cycle traits associated with such taxa (e.g., egg-laying reproduction strategies, aerial dispersal mechanisms, larval and nymph forms; see Table 5). Conversely, fewer taxa were significantly associated with autumn months and were spread across multiple orders. Specific resistance traits (diapause/dormancy and cocoons) and specialist respiratory (hydrostatic vesicle and spiracle) mechanisms were significantly associated with the autumn months (Table S1).

Table 4. Macroinvertebrate α-diversity responses to river restoration indicated by linear model outputs. Significant models are indicated in bold, and stars denote the degree of significance: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS, non-significant.

| Response	Covariate	Partial r^2	F-Value	p-Value
Taxonomic richness	Season	0.10	5.77	**0.020 ***
	Treatment	0.19	12.78	**<0.001 ****
	Time period	0.03	6.29	**0.015 ***
	Treatment × Time period	0.13	8.66	**0.005 ****
Taxonomic evenness	Season	0.10	6.06	**0.017 ***
	Treatment	0.05	2.85	0.097 (NS)
	Time period	0.14	9.37	**0.003 ****
	Treatment × Time period	0.01	0.82	0.386 (NS)
Taxonomic diversity	Season	0.08	4.69	**0.034 ***
	Treatment	0.05	3.61	0.062 (NS)
	Time period	0.12	7.26	**0.009 ****
	Treatment × Time period	0.01	0.69	0.409 (NS)
Functional richness	Season	0.00	0.14	0.715 (NS)
	Treatment	0.09	5.66	**0.021 ***
	Time period	0.01	1.49	0.228 (NS)
	Treatment × Time period	0.10	6.48	**0.014 ***
Functional evenness	Season	0.24	18.52	**<0.001 ****
	Treatment	0.02	1.11	0.300 (NS)
	Time period	0.06	7.41	**0.009 ****
	Treatment × Time period	0.01	0.32	0.574 (NS)
RaoQ	Season	0.01	0.44	0.509 (NS)
	Treatment	0.01	0.42	0.518 (NS)
	Time period	0.10	8.35	**0.005 ****
	Treatment × Time period	0.01	0.40	0.527 (NS)

Figure 5. Linear model outputs (mean and 95% confidence intervals) indicating the effects of restoration on taxonomic (**a**–**c**) and functional (**d**–**f**) metrics. Control = grey; restored = black. (**a**) Taxonomic richness, (**b**) taxonomic evenness, (**c**) taxonomic diversity, (**d**) functional richness, (**e**) functional evenness and (**f**) RaoQ.

Table 5. Macroinvertebrate α-diversity responses to river restoration indicated by linear model outputs. Significant models are indicated in bold, and stars denote the degree of significance: * $p \leq 0.05$; *** $p \leq 0.001$; NS, non-significant.

Response	Covariate	Partial r^2	F-Value	*p*-Value
Rheophilic taxa richness	Season	0.29	21.29	**<0.001 *****
	Treatment	0.28	20.90	**<0.001 *****
	Time period	0.22	34.12	**<0.001 *****
	Treatment × Time period	0.17	12.10	**<0.001 *****
Slow-flow taxa richness	Season	0.09	5.46	**0.023 ***
	Treatment	0.01	0.47	**0.495 (NS)**
	Time period	0.13	12.70	**<0.001 *****
	Treatment × Time period	0.00	0.01	**0.911 (NS)**
Coarse substate taxa richness	Season	0.23	15.25	**<0.001 *****
	Treatment	0.34	28.17	**<0.001 *****
	Time period	0.13	23.69	**<0.001 *****
	Treatment × Time period	0.23	17.14	**<0.001 *****
Fine sediment taxa richness	Season	0.00	0.26	0.611 (NS)
	Treatment	0.00	0.00	0.946 (NS)
	Time period	0.07	4.93	0.030 *
	Treatment × Time period	0.00	0.05	0.819 (NS)

The richness of rheophilic taxa (F-value = 12.10, *p*-value $\leq$0.001) and taxa preferring coarse substrates (F-value = 17.14, *p*-value $\leq$0.001) displayed a positive, significant association with river restoration (Table 5), increasing over time in restored sites, whilst control sites displayed the opposing trend (Figure 6a,c). Conversely, taxa preferring slower flow velocities and fine sediments did not respond significantly to restoration and displayed a negative trend over time in both control and restored sites (Figure 6b,d). Indicator species analysis highlighted various individual traits significantly associated with both rheophilic taxa and taxa preferring coarse substrates, as well as taxa preferring slower flow velocities and fine sediments (Table 6). In addition, many of these traits mirrored those reported for seasonal variation above, with specific aquatic stages (larvae and nymph) and dispersal strategies (aerially active and passive) being associated with rheophilic taxa and taxa preferring coarse substrates (Table 6). Conversely, taxa preferring slower flow velocities and fine sediments were significantly characterised by surface water swimmers and taxa reproducing via ovoviviparity (as with taxa associated with autumn months; see Table S1).
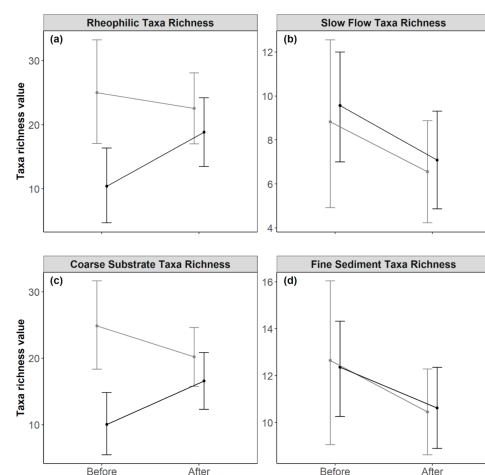
Figure 6. Linear model outputs (mean and 95% confidence intervals) indicating the effects of restoration on the richness of taxa preferring different flow velocity or sedimentological conditions. Control = grey; restored = black. (**a**) Rheophilic, (**b**) slow flow taxa, (**c**) coarse substrate taxa and (**d**) fine sediment taxa richness.

Table 6. Indicator species analysis quantifying the association of individual taxa and functional traits with taxa preferring specific flow velocities and substrate sizes. Stars denote the degree of significance: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS, non-significant.

Grouping Feature	Trait	Rheophilic Taxa		Coarse Substrate Taxa	
		Indicator Value	*p*-Value	Indicator Value	*p*-Value
Dispersal strategy	Aerially active	0.79	0.001 ***	0.7	0.011 *
Aquatic stages	Larvae	0.75	0.004 **	-	-
Resistance form	None	0.73	0.014 *	0.75	0.005 **
Food consumed	Detritus < 1 mm	0.66	0.027 *	-	-
Aquatic stages	Nymph	0.63	0.001 ***	0.59	0.007 **
Dispersal strategy	Aerially passive	0.60	0.047 *	0.6	0.034 *
Locomotion and substrate relation	Temporarily attached	0.54	0.016 *	0.57	0.008 **
		Slow-Flowing Taxa		Fine Sediment Taxa	
		Indicator Value	*p*-Value	Indicator Value	*p*-Value
Aquatic stages	Adult	0.78	0.001 ***	0.7	<0.001 ***
Resistance form	Diapause or dormancy	0.65	0.005 **	0.65	0.011 *
Food consumed	Dead animal ≥ 1 mm	0.59	0.008 **	0.56	0.012 *
Locomotion and substrate relation	Surface swimmer	0.48	0.014 *		
Reproduction strategy	Ovoviviparity	0.42	0.045 *		

4. Discussion

Our BACI assessment of river restoration measures on the groundwater-fed river Kennet, south-eastern England, UK, demonstrated that the removal of impoundments and the restoration of physical processes changed both the habitat composition as well as the taxonomic and functional properties of macroinvertebrate communities in the 4 years post-restoration.

We hypothesised that following restoration, the sampling sites within the restored section would become more hydromorphologically and ecologically similar to the control sites. Our assessment of the physical changes found that the channel was narrower post-restoration, but there were no significant changes in the channel depth. There was an overall increase in substrate size in the restored sections, which may reflect, but the change was not significant relative to the control sites. These results suggests that under the same discharge, there is a concentration of flow into areas of faster-velocity hydraulic habitats, flushing out fine sediment and creating central areas of gravel with silt-dominated vegetated margins. This change in habitat composition was confirmed by the before and after photograph changes (Appendix A) and suggest that the removal of impounding structures and channel narrowing has been partially successful in restoring physical processes within this low-energy groundwater river [35,36].

Restoration activity facilitated an ecological trajectory that shifted both the taxonomic and functional community compositions to be more akin to those of the control sites. The decrease in taxonomic and functional richness at the control sites may reflect the slight deterioration in the water quality of the river (Supplementary Material, Table S1). These findings support our hypothesis that changes would be reflected in both structural complexity and functional integrity following Bradshaw's classic model, where restoration acts to increase both taxonomic and functional integrity. The response was demonstrated by shifts in multivariate location (i.e., the community centroid) of macroinvertebrate commu-

nity abundances (taxonomic) and functional trait compositions. Restoration also yielded a significant increase in the total β-diversity, indicating that there were greater taxonomic and functional differences over time (i.e., before versus after) in restored sites compared to control sites. The fact that changes in β-diversity were largely driven by turnover, and not nestedness, highlights that new taxa colonised the restored sites at the expense of those that existed prior to restoration, which mirrors the findings of [60]. The presence of new taxa and trait combinations in restored sections following works being undertaken likely represents favourable environmental conditions that were not present previously. Such taxa likely colonised restored reaches from nearby habitats (e.g., control sites) possessing comparable habitat conditions. This reinforces the fundamental role of proximal sources of rich species pools in underpinning successful reach-scale restoration measures [16]. The loss of various taxa inhabiting the restored sites prior to works taking place could be due to new environmental conditions being unfavourable or those species that were there initially being outcompeted by the new taxa. For both the total β-diversity and its turnover component, temporal differences between control and restored sites were clearer for taxonomic compositions compared to the functional properties of macroinvertebrate communities. This potentially indicates a functional redundancy effect of new colonists inhabiting restored reaches after works were implemented and supports the findings of other studies examining the effectiveness of other restoration projects in the region [37].

Our findings highlight a clear increase in the taxonomic and functional richness in restored sites following works being implemented. The positive ecological effect associated with the restoration activity here joins a growing body of evidence of invertebrate response reporting varying success. Whilst some studies report limited evidence of ecological benefits following river restoration activity (e.g., [14,61–63]), others record positive effects (e.g., [7,64,65]). The success of ecological recovery following restoration depends on the following barriers being overcome: (i) dispersal limitation, (ii) abiotic resistance, (iii) resource limitation and (iv) biotic resistance [66]. Our analyses indicating that taxa colonised restored reaches from other sections of the Kennet (e.g., upstream control sites), as well as the absence of large-scale abiotic stressors (e.g., flow regime, water quality [67] or filters [68]), suggests that (i) and (ii) were not barriers to ecological recovery, although understanding whether (iii) and (iv) were overcome within the studied restoration projects is more challenging. It is likely that biotic resistance was at least limited, given the turnover in new species in restored reaches at the expense of taxa initially established prior to works being undertaken.

Despite increases in the taxonomic and functional richness, the responses of evenness and overall α-diversity did not respond significantly to restoration activity. This highlights that whilst restoration activity increased the number of taxa, the distribution of taxonomic abundances and trait proportions did not respond significantly. This may be due to the demographical responses of taxa being more difficult to detect relative to presence/absence responses, such as through stochastic colonisation mechanisms [69]. The differing response of community evenness and overall α-diversity could be due to variations in resources (see iii above) in restored reaches relative to controls. Alternatively, pre-established taxa may have persisted at restored sites after works were implemented, which could have produced different community structures relative to control sites (iv above). These results could also indicate the ecological response is still underway as the restored sites continue to adjust, as found by other researchers [70,71]. Comparable results to those reported here in rivers were observed in a New Zealand study [60]. Within the study, nearly 20 years after restoration, the macroinvertebrate communities had broadly converged with those inhabiting reference sites via a turnover in species; however, the authors indicated restored communities displayed a reduced inter-annual variability compared to natural systems, and thus concluded that the community dynamics of restored sites may be slower to recover [60]. Such findings may help explain the responses of community evenness and α-diversity in this study and indicate the need for long-term monitoring to assess fully the effectiveness of river restoration activities [16,67]. Our findings also indicate the importance of adopting multi-seasonal sampling strategies when assessing macroin-

vertebrate communities within river restoration post-project appraisals. Spring samples were dominated by various Ephemeroptera and Trichoptera taxa, which contained mature larvae representatives during this season prior to emergence. This represents an important finding, given that such taxa represent valuable bioindicators from biodiversity, functional diversity and ecosystem service standpoints [68,69]. However, the autumn months supported macroinvertebrate communities, yielding a greater functional evenness, whereby the influence of Ephemeropterans and Trichopterans were less pronounced. Such findings may have been due to recently hatched larvae not developing or widely establishing, which allowed alternative taxa possessing different trait combinations to prevail. Alternatively, lower-flow conditions during the autumn (relative to spring months) would tend to favour taxa preferring slower flow velocities and fine sediments. As such, both spring and autumn samples provided complementary ecological information underpinning macroinvertebrate community responses to river restoration.

The exploration of functional traits is often neglected within river restoration post-project appraisals [7]. However, their assessment provides a way of understanding the link between habitat preference, habitat heterogeneity and specific biotopes [72] as well as aiding the understanding of the effects of river restoration [73]. In this study, prior to restoration, macroinvertebrates communities were characterised by taxa displaying resistance/resilience strategies (e.g., ovoviviparity that prevents the vulnerability of eggs being laid and washed away, burrowing into the fine sediment). After restoration, the recovery of Ephemeroptera and Trichoptera (and the associated biological traits, e.g., nymphs, eggs, aerially active) occurred, indicating a community favouring faster-flowing water and coarser substrates, whilst excluding those preferring slower-flowing waters and fine sediments. This matches with the physical changes to the channel and the observed habitat composition. Increases in rheophilic taxa preferring coarser substrates in restored works did not correspond with trends observed in control sites, where an overall decrease has occurred, reflecting background changes within the catchment. Such temporal changes at the control sites highlights the influence that catchment processes have on biological communities [67,68]. Our analyses indicate that improvements in habitat conditions can offset the negative ecological effects of coarser-scale environmental pressures; for example, a greater range of habitats can alleviate the ecological implications of hydrological extremes through providing refuges [74–76]. Such findings indicate the importance of applying a BACI approach to river restoration appraisals to place ecological responses within the context of catchment-wide processes and assess biological recovery trends over time relative to non-restored sites [7,30,64].

5. Conclusions

This study uses a rare BACI dataset to demonstrate the ecological benefits of restoration activity on a lowland groundwater-fed river. Our findings provide empirical evidence regarding how the removal of impoundments and channel-narrowing techniques prompt statistically significant taxonomic and functional responses of invertebrate communities. Most notably, the taxonomic and functional richness of invertebrate communities increased following restoration works, despite decreasing over time within control sites. The monitoring approach highlights the value of well-planned appraisal strategies. Given a global paucity in long-term studies of the effects of river restoration activities, studies such as this are essential to provide the evidence to inform effective river restoration strategies to address future changes such as climate change and the biodiversity crisis.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/w13162239/s1, Environment Agency routine water quality data. Figure S1: Boxplots indicating differences in (a) taxonomic richness and (b) functional evenness between seasons. The boxes indicate the 25th, 50th and 75th percentiles, while whiskers indicate the data range except for extreme outliers, which are indicated by points, Table S1: River Kennet water quality data, Table S2: Indicator species analysis quantifying the association of individual taxa and functional traits with sampling seasons, Table S3: River Kennet bio indices & env variables.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Control Section	
Pre-Restoration—November 2011	**Post-Restoration—June 2021**

Site 1

Site 2

Restored Section	
Pre-Restoration—November 2011	**Post-Restoration—June 2021**

Site 3

Site 4

Site 5

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