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Going to the archives: Combining palaeoecological and contemporary data to support river restoration appraisals

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Abstract

River restoration practices are being increasingly implemented to help offset the global degradation of freshwater ecosystems. The ecological success of such projects is typically determined via post-project appraisals comparing restored conditions against specified baselines (e.g., pre-project and/or non-restored data), but such approaches can overlook broader ecosystem recovery patterns. Using freshwater macroinvertebrate communities, this study examined ecological responses to river restoration that are seldom assessed: (i) sub-annual temporal trajectories and (ii) palaeoecological versus contemporary community comparisons. Palaeoecological samples contained assemblages that existed prior to major anthropogenic pressures, which were collected from a sinuous palaeochannel that was restored and reconnected during the study; after which contemporary macroinvertebrate samples were collected. The restored channel initially supported an impoverished community, but taxonomic richness and densities were comparable to non-restored conditions after 13-months. The freshwater shrimp (*Gammarus pulex*) and non-native New Zealand mud snail (*Potamopyrgus antipodarum*) proliferated 7-months post-restoration, and follow-up biomonitoring highlighted their dominance prevailed 5-years later. Such evidence indicates how ecosystem dynamics in the aftermath of restoration can shape longer-term recovery. Palaeoecological communities exhibited higher biodiversity and conservation values compared with contemporary samples. This highlights that escalating anthropogenic pressures since the mid-20th Century degraded macroinvertebrate communities, notably constraining marginal-dwelling and lentic specialists. With palaeochannel reconnections being widely applied worldwide, this study demonstrates the value in collecting palaeoecological data before restoration works to provide valuable baseline information. As the global anthropogenic footprint increasingly degrades suitable “reference” river environments, palaeoecological data can better characterize biodiversity losses and potentially provide target conditions informing effective restoration activities.

KEYWORDS

biomonitoring, conservation, lotic ecosystems, palaeochannel, reconnection, reference conditions, river rehabilitation

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1 | INTRODUCTION

Riverine environments are subjected to a myriad of anthropogenic pressures that are driving severe freshwater biodiversity declines globally (Lynch et al., 2023; Tickner et al., 2020). This includes physical habitat degradation, hydrological modifications (e.g., water abstraction, flow regulation), various forms of pollution (e.g., eutrophication, plastic, and metal inputs), invasive species, land cover transformation (e.g., urbanization, agricultural intensification) and climate change (Lynch et al., 2023). The morphological integrity of river environments is fundamental to freshwater ecosystem health as naturally functioning and diverse habitats help sustain ecosystem dynamics, allow freshwater biota to complete their life cycles and increase ecosystem tolerance to adverse environmental conditions (Ciotti et al., 2021; Tickner et al., 2020; White et al., 2017).

River restoration projects have been widely implemented to help promote lotic habit diversity. Such practices typically aim to improve the environmental and ecological health of degraded systems to make them more akin to target or “reference” conditions (Ciotti et al., 2021). Restoration projects are implemented with the view to improving the hydrological, morphological, and/or ecological health of riverine systems, which are linked to various ecosystem services (e.g., natural flood management, bank erosion protection, community engagement and appreciation—Gilvear et al., 2013). While some studies have reported river restoration benefitting freshwater ecosystem health (e.g., Kail et al., 2015; Lu et al., 2019), others have recorded modest ecological responses that are incongruent with physical habitat improvements (e.g., Al-Zankana et al., 2020; Palmer et al., 2010). Such outcomes have often been linked to unresolved abiotic pressures (e.g., poor water quality or flow regime modifications) and instream barriers inhibiting natural recolonization processes. However, other factors including the biodiversity of local and regional species pools, biotic pressures (e.g., invasive species) and dispersal limitations may also affect ecological recovery following restoration (Frame et al., 2016; Palmer et al., 2010).

Biota colonizing recently restored reaches can significantly influence the subsequent trajectory of ecological change and may vary considerably depending on the restoration techniques implemented (Gilvear et al., 2013). For instance, taxa colonizing reaches restored via in-channel works (e.g., weir removal, large woody material introductions) will face predation and competition from pre-established biotic communities (Frame et al., 2016), although this may be reduced if the works had a destructive effect on habitats and biota in its aftermath (Gilvear et al., 2013). Alternatively, freshwater species colonizing (re)created freshwater habitats (e.g., palaeochannels or newly engineered channels) will initially face reduced biotic pressures, but also limited resources (Barrett et al., 2021). Subsequently, communities often experience high compositional turnover over time as established and newly colonizing species interact with existing communities and changing environmental conditions (Dézerald et al., 2023), and typically subside in the long term as communities stabilize (Graham & Quinn, 2020). Biotic influences in the aftermath of river restoration can have significant implications for ecosystem recovery trajectories,

but short-term ecological trajectories have not been widely considered in post-project appraisals.

Ecological appraisals of river restoration projects typically utilize contemporary biological data, often comparing restored environmental conditions and biotic communities against those observed at non-restored sites used as baseline; these could reflect conditions encountered prior to restoration (i.e., “control” reaches) or those observed in environments minimally or less impacted by anthropogenic influences (i.e., “reference” sites; Ciotti et al., 2021). Control sites typically reflect conditions that the restored reach should be ideally moving away from following intervention, while observations from reference sites are often used as targets to aspire to. The latter poses potential problems given that human pressures affect most, or arguably all, of the world's freshwater habitats (Tickner et al., 2020). Moreover, many anthropogenic pressures on riverine environments have occurred for several centuries or even millennia (Davidson et al., 2018; Tickner et al., 2020). Therefore, sites considered to be minimally impacted in contemporary landscapes in many regions worldwide are unlikely to reflect river conditions prior to anthropogenic pressures. Palaeoecological approaches provide a means of identifying pre-disturbed freshwater ecosystem characteristics (Davidson et al., 2018; Seddon et al., 2019). Historically, such research in riverine systems has been limited due to the relatively short and interrupted time sequences available caused by dynamic erosion and deposition processes (Greenwood et al., 2006). Sampling sediments in palaeochannels affords the opportunity to examine the sub-fossilized remains of the faunal communities that inhabited the river system before it became isolated from the main channel, which can often reflect time periods prior to major human interventions (Seddon et al., 2019). Such research has often utilized subfossilized macroinvertebrate community groups, including dipterans like Chironomidae (Howard et al., 2010) that are typically challenging to resolve to high taxonomic resolutions compared with other faunal groups. The same issues arise with other invertebrate taxa like Simuliidae (Heiri, 2004) and Cladocera (Pióciennik et al., 2020) also used in riverine palaeoecological research. However, various Snails (Gastropods), mussels (Bivalvia), caddisfly larvae (Trichoptera), adult beetles (Coleoptera), and alderfly larvae (Megaloptera) that also occur at high abundances within riverine palaeochannel sediments are readily identifiable to species-level; such taxa are also commonly found in contemporary freshwater macroinvertebrate samples and display a range of environmental preferences and tolerances (Greenwood et al., 2006; Howard et al., 2009; Seddon et al., 2019). Comparing the palaeoecological and contemporary assemblages of these faunal groups could be used to support the ecological appraisal of river restoration schemes by characterizing pre-disturbed communities and providing information on the environmental conditions they inhabited. However, to our knowledge, such palaeoecological information has never been incorporated within a river restoration post-project appraisal.

This study compared contemporary and palaeoecological macroinvertebrate community data to appraise the ecological effectiveness of a river restoration scheme that reconnected the watercourse to its former channel (i.e., a palaeochannel). Specifically, we aimed: (i) to

assess the temporal trajectories of contemporary communities following restoration over 13-months and (ii) to compare the contemporary and palaeoecological communities to assess the ecological outcomes of river restoration.

2 | METHODS

2.1 | Study area

The study was undertaken in the lowland region of the River Wensum in eastern England (Norfolk, United Kingdom; catchment area = 162 km²; Figure 1). Much of the catchment is underlain by Senonian Chalk (a fine-grained limestone), which facilitates a groundwater-dominated flow regime and high width:depth channel ratios due to its low stream power (Coombes et al., 2007). The Wensum catchment was historically dominated by floodplain forests and possessed a sinuous planform with a wide floodplain that was regularly flooded. Most woodland in the catchment has now been replaced by arable agriculture and some urban development. Large parts of the Wensum have been subjected to extensive morphological modifications (e.g., channel straightening, dredging, and over-deepening) for local drainage and flood alleviation purposes, the majority of which has taken place since new policies were introduced in the aftermath of the Second World War—post 1945 (Allen et al., 2019). Other contemporary, catchment-wide pressures include excessive ponding and

siltation from abandoned mill structures, colonization by non-native species (notably signal crayfish—*Pacifastacus leniusculus*, and Himalayan balsam—*Impatiens glandulifera*) and macronutrient enrichment from agriculture and effluent water returns (Coombes et al., 2007; Cooper & Hiscock, 2023). Just c. 1 km upstream of the study site, a major sewage treatment plant was established in 1975 that drastically increased macronutrient concentrations until phosphate (or “P”) stripping techniques were introduced in 1999, which yielded significant water quality and ecological improvements (Coombes et al., 2007; Cooper & Hiscock, 2023).

Some parts of the Wensum have been subjected to less intense anthropogenic pressures where healthy ecological conditions have prevailed. As a result, the Wensum has been designated as a “Special Area of Conservation” and a “Site of Special Scientific Interest” due to it supporting flora (*Ranunculus fluitans*) and fauna (e.g., *Austropotamobius pallipes*, *Lampetra planeri*) of high national and international conservation significance. The varying threats to such biota (see above) resulted in the Wensum being the focus of the first ever “whole river” restoration strategy in the UK (Coombes et al., 2007).

At the study site, the channel was artificially straightened and dredged in 1946 as part of a land drainage improvement scheme, leading to the studied meander bend being cut off. This was replaced by a uniform and over-deepened stretch of the river (“control” reach herein) that possesses sluggish flows and a silt-dominated riverbed. The relict meanders gradually filled with sediment over time and

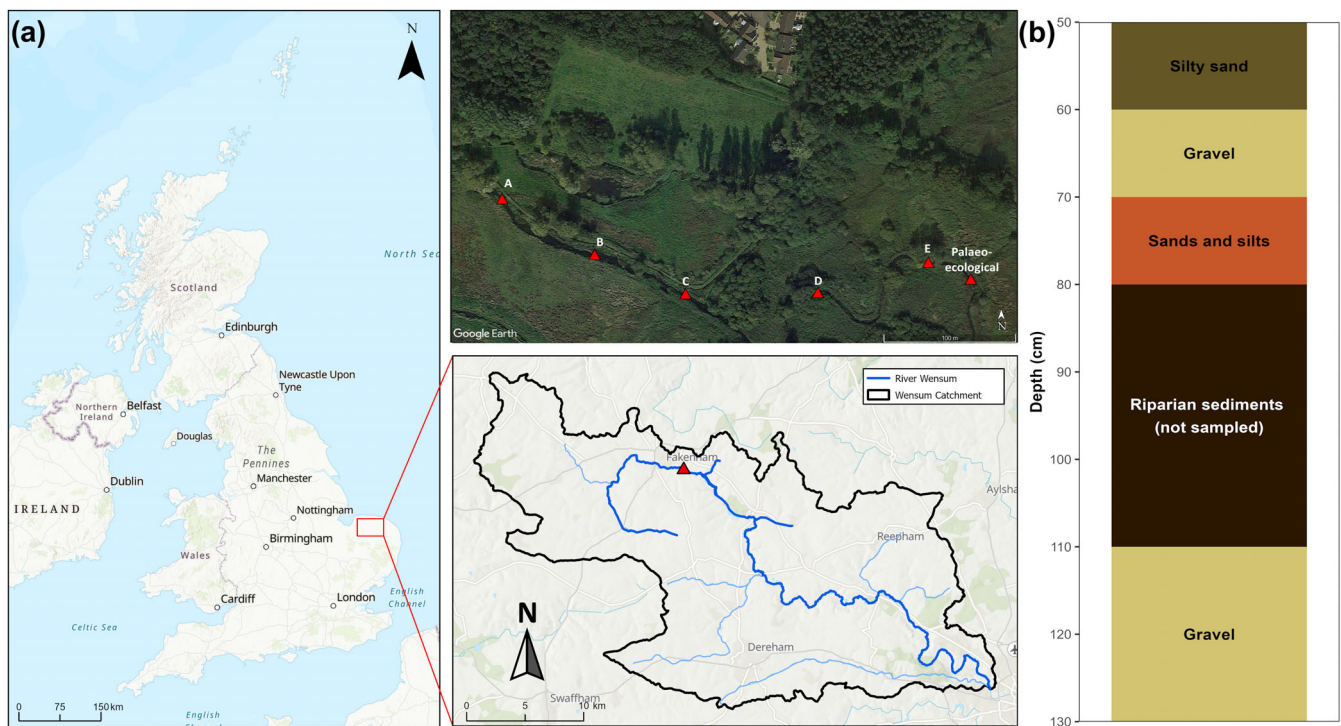


FIGURE 1 Contextual information on the study site. (a) The location on the River Wensum (Norfolk) within the UK and the sampling sites therein. Contemporary sample sites are indicated by capitalized letters (A–C = control samples and D–E = restored samples); (b) A stratigraphic diagram of the lithological profile used for palaeoecological sampling (note—stratigraphic section starts at 50 cm below ground surface). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/1365-3113.12111)]

became a palaeochannel, preserving the sub-fossilized remains of the faunal communities that it supported at the time of its disconnection (used in “palaeoecological” samples—see below). In 2010, the palaeochannel was excavated and the following morphological adjustments were implemented: gravels from the old riverbed were left intact; coarse substrates were added to some parts of the reach; deep pools were excavated in some sections; and the reach was narrowed in parts (to increase flow velocities) by installing bunds along the bank that were seeded with native flora. Once these works had been finalized in November 2010, the main channel was diverted into the “restored” reach by blocking the modified stretch (the downstream limit of the control reach) using excavated materials (photographs of the study site are displayed in Appendix A).

For this study, five contemporary sampling sites were identified, three of which (sites A-C) were located along the control reach, and two (sites D-E) in the restored section. The palaeoecological sampling site was located in the restored reach and was sampled before it was excavated (Figure 1).

2.2 | Faunal community data collection

Contemporary macroinvertebrate communities were sampled on five occasions during June 2010 (only control), November 2010 (within 1-week of restoration—but no macroinvertebrates had colonized Site E at this point), February 2011, June 2011, and December 2011 (due to excessive flow depths, Site B was not sampled during the last three sampling events, and Site C was not surveyed during February 2011). Five 1-minute Surber sample replicates (0.09 m², 250- μ m mesh size) were collected along a cross-section for each site within each sampling period by disturbing benthic material within the frame for 1 min ($n = 90$). Samples were preserved in the field with 4% formaldehyde solution and subsequently identified to species level in the laboratory wherever possible, with the exception of some immature mayfly (Ephemeroptera) and caddisfly (Trichoptera) larvae (genus), mollusca (Bivalvia; Sphaeriidae—family), beetle (Coleoptera) larvae (Halipilidae, Dytiscidae, and Gyrinidae—family), some true fly larvae (e.g., Tupilidae, Simuliidae, and Chironomidae—family), and Oligochaeta that were recorded as such.

For the palaeoecological samples (collected in June 2010), a sediment pit was initially excavated along the restored reach prior to it being reconnected. Subsequently, c. 5 kg of sediment samples were extracted from the pit (to provide a monolith/core section) at 10 cm intervals (sensu Greenwood et al., 2003) at depths between 50 and 80 cm. For this, 50–60 cm comprised of a mixture of lentic sediments and organic matter grading into sand, 60–70 cm contained a distinct gravel layer (representing the channel immediately prior to its disconnection), 70–80 cm comprised sand and finer fluvial sediments. The next 30 cm of the core comprised peaty material characterizing lentic or riparian conditions, so were not sampled. However, beneath this there was a second larger gravel layer (110–130 cm deep) representing a second, older palaeochannel from which a single bulk was sampled to compare with the lotic sediments above it. The samples were

returned to the laboratory immediately after collection and refrigerated at 4°C to prevent decay before processing. Specimens were extracted using the paraffin flotation method (sensu Coope, 1986) but with the addition of 125- and 90- μ m sieves to retain smaller Trichoptera fragments (sensu Greenwood et al., 2003). Preserved Trichoptera and Coleoptera fragments were mounted on slides in water-soluble Hoyer's medium (to allow recovery of specimens if required). Identification of subfossil Trichoptera fragments and larvae were made using the keys prepared by Edington and Hildrew (1995) and Wallace et al. (2003), as well as photographic reference collections compiled by Malcom Greenwood (used in Greenwood et al., 2003). Coleoptera (fragments and complete specimens) were identified using Duff (2008) and Friday (1988) and through comparison with reference collections at the Leicestershire Museum at Barrow upon Soar, Leicestershire (UK). Megaloptera (exclusively *Sialis* sp.) were identified using the key of Elliott (2009). Gastropoda and Bivalves (subfossil and contemporary) were identified using Macan (1977).

2.3 | Temporal trajectories of contemporary macroinvertebrate communities following restoration

All statistical analyses reported herein were performed in R studio (R Development Core Team, 2014). Samples from the control reach collected in June 2010 (i.e., prior to restoration) were excluded from the temporal trajectory analyses (i.e., contemporary communities examined in aim 1; 75 samples were assessed). The α -diversity of each Surber sample was characterized via six univariate metrics. These comprised the (i) total taxonomic richness; (ii) total taxonomic density; rheophilic taxa; (iii) richness and (iv) density; and non-rheophilic taxa (v) richness and (vi) density. Rheophilic and non-rheophilic taxa groupings were based on “individual flow scores” (fs) assigned to UK freshwater macroinvertebrate species within the Lotic Invertebrate index for Flow Evaluation (LIFE—sensu Extence et al., 1999). Rheophilic taxa were identified as those belonging to fs groups 1 or 2 (taxa typically preferring moderate to rapid flow velocities $>0.2 \text{ m s}^{-1}$), and non-rheophilic taxa as those in fs groups 3 to 6 (preferring sluggish flow velocities to drought-impacted conditions).

To address aim 1, the temporal trajectories of the six α -diversity metrics were compared between the control and restored reaches (“reach”). This was achieved via separate linear models testing the additive and interactive effects of sampling date (“time”) and reach, whereby each response was $\log(x + 1)$ transformed and up to nine outliers were removed to satisfy assumptions of normality and homoscedasticity (inspected via residual diagnostic plots). Subsequently, a two-way ANOVA was performed on each model to determine the significance of each independent variable.

A pairwise “Total β -diversity” (between sample variability) dissimilarity matrix of contemporary macroinvertebrate communities was derived that quantified the ecological similarity between each pairwise combination of Surber samples. Pairwise “richness difference” and “replacement” matrices were also calculated, the product of these making up the initial Total β -diversity dissimilarity matrix. All three of

these matrices were derived using the *beta.div.comp* function (Podani family decomposition of Jaccard-based indices) in the *adespatial* package (Dray et al., 2023). Subsequently, two sets of pairwise comparisons were conducted: (i) those between consecutive sampling periods within each reach (“time comparisons”; e.g., control samples in November 2010 vs. February 2011) and (ii) those between reaches within each sampling period (e.g., control vs. restored samples in November 2010). For these, (i) enabled the temporal changes in different β -diversity components within each reach to be assessed and compared, while (ii) provided an understanding of how ecologically (dis)similar the control versus restored reaches became over time. These pairwise comparisons were used as dependent variables within six linear regression models, whereby response variables were obtained for both (i) and (ii) for the three dissimilarity matrices used. The regression-based models followed the same procedures described for α -diversity metrics, although no response variables were transformed and the formulae were slightly modified: (i) the additive and interactive effects of time comparisons and reach were modeled; (ii) the independent effect of time was assessed.

2.4 | Quantifying ecological differences between contemporary and palaeoecological communities

Prior to comparing control, restored, and palaeoecological samples (i.e., three “treatment” effects; aim 2), taxonomic communities required harmonizing. This entailed only considering Gastropoda, Bivalvia, Coleoptera, Megaloptera, and Trichoptera (GBCMT) taxa in the contemporary datasets as only these groups could be identified from the remains from the paleochannel data. Surber sample replicates (i.e., those collected from the same sampling site/event) were then pooled. Subsequently, macroinvertebrate communities from all three treatments were transformed to presence-absence data given the difference in sampling methodologies and associated taxa counts. Subsequently, nine ecological metrics were calculated for each sample. This included the taxonomic richness and “Community Conservation Index” (CCI), the latter indicating the national and international rarity (and hence conservation value) of macroinvertebrate species (sensu Chadd & Extence, 2004). “Permutational Multivariate Analysis of Dispersion” (PERMDISP) was performed to characterize the heterogeneity of macroinvertebrate communities for each treatment by calculating the multivariate distance from each sample to the centroid of the corresponding reach (this was calculated using *betadisper* in the *Vegan* package—Oksanen et al., 2022). Three commonly employed lotic biomonitoring metrics used nationally in the UK were also calculated to characterize macroinvertebrate communities based on their preferences and tolerances to nutrient enrichment (average Walley, Hawkes, Paisley and Trigg score per taxon—WHPT-ASPT; Paisley et al., 2014), flow velocities (as a surrogate for river discharges; LIFE—see above) and fine sediment pressure (Empirically-weighted Proportion of Sediment-sensitive Invertebrates—E-PSI; Turley et al., 2016) respectively. Lastly, the percentage of taxa in each sample comprising Gastropoda, Trichoptera, and Coleoptera representatives were

calculated (Bivalvia and Megaloptera were not assessed as they only comprised a single taxa). Non-parametric Kruskal-Wallis tests were undertaken (due to non-normality in the data) to test whether each of the nine univariate metrics differed significantly between treatment effects (independent variable). In addition, the number of taxa expressing various guilds were calculated and differences between treatments were explored. Specifically, we summed the number of taxa that are: sensitive and tolerant to nutrient enrichment (“WHPT PO” taxon scores ≥ 6 and < 6 , respectively—these are used to calculate WHPT-ASPT); rheophilic and non-rheophilic (see above); and sensitive and tolerant to fine sediment (“species-specific sensitivity weightings” ≥ 0.5 and < 0.5 , respectively—these are used to calculate E-PSI).

Multivariate differences in GBMCT compositions between each reach were explored via a Permutational Multivariate Analysis of Variance (PERMANOVA) using the *adonis2* function in *Vegan*. A pairwise PERMANOVA was then undertaken to test whether communities differed between reach combinations via the *pairwise.adonis* function in the *pairwiseAdonis* package (Martinez Arbizu, 2017). Compositional differences between each reach were visualized using a Principal Coordinate Analysis (PCoA) using the *cmdscale* function in *Vegan*. Pearson correlation coefficient (*r*) values were calculated between PCoA axis scores and various ecological metrics (WHPT-ASPT, LIFE, E-PSI, Gastropoda [%], Trichoptera [%], and Coleoptera [%]) using *cor.test*.

3 | RESULTS

3.1 | Temporal trajectories in contemporary macroinvertebrate communities following restoration

The control reach supported a higher taxa richness than the restored reach between November 2010 (when restoration had taken place <1-week before) and June 2011. Both reaches displayed consecutive increases in overall taxa richness between sampling periods, but these were more pronounced in the restored channel. Subsequently, the overall taxa richness declined in both the control and restored reaches in December 2011 (13-months after restoration—the study period end), but this was less marked in the latter. These trends resulted in comparable taxa richness values between the control and restored reach by December 2011 (Figure 2a,b). The differences in temporal trajectories between the two reaches were evident from a significant “time” (factor) \times “reach” interactive effect identified within a two-way ANOVA ($F = 5.5$, p -value = 0.006). A significant time \times reach interactive effect was also detected for rheophilic taxa richness ($F = 8.8$, p -value < 0.001) and non-rheophilic taxa richness ($F = 6.6$, p -value = 0.003; see Appendix B for complete model results).

Temporal changes in the overall taxa density in the control reach displayed a stepped pattern, with values in November 2010 and February 2011 being about half those observed in June 2011 and December 2011. These trends were largely driven by changes in non-rheophilic taxa density, with the rheophilic taxa density remaining broadly comparable between sampling periods (Figure 2c).

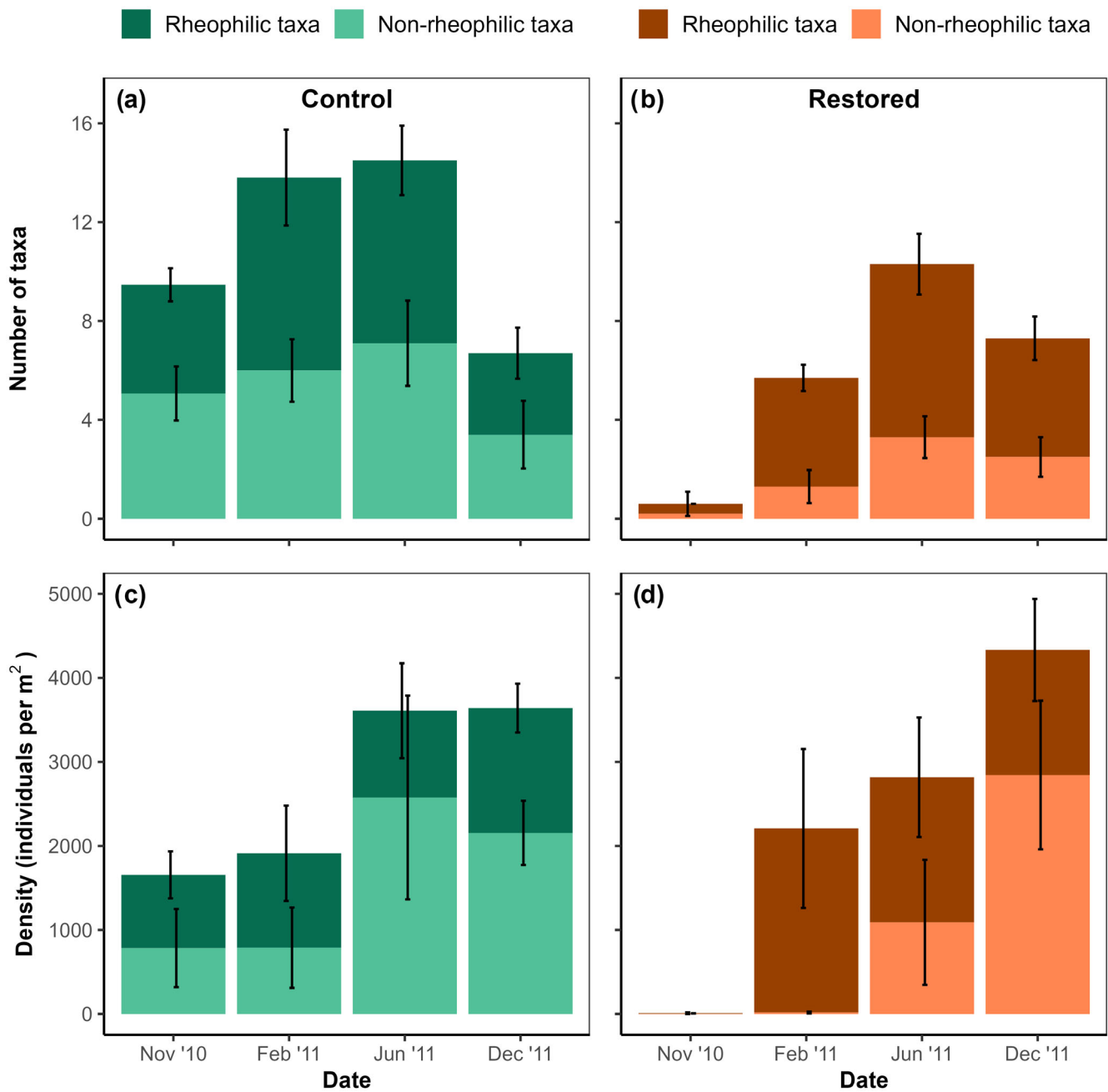


FIGURE 2 Stacked bar charts of mean averaged (± 2 standard errors) richness (a, b) and density (c, d) of rheophilic and non-rheophilic macroinvertebrate taxa across different sampling dates (time), shown for control (a and c) and restored (b and d) reaches. [Color figure can be viewed at wileyonlinelibrary.com]

Conversely, overall taxa density in the restored reach displayed consecutive increases, displaying lower values in November 2010 and surpassing the control reach by December 2011 (Figure 2d). Rheophilic taxa density increased sharply between November 2010 and February 2011, and slightly declined between sampling periods thereafter. Non-rheophilic taxa density was low between November 2010 and February 2011, and then increased dramatically over the latter two sampling events (Figure 2d; these trends were predominantly driven by the New Zealand mud snail—*Potamopyrgus antiopodarum*; freshwater shrimp—*Gammarus pulex*; and blackfly larvae—*Simuliidae*—

see Appendix B). The time \times reach interaction indicated a non-significant influence on overall taxa density ($F = 1.4$, p -value = 0.267) and rheophilic taxa density ($F = 2.5$, p -value = 0.094), but did have a highly significant effect on non-rheophilic taxa density ($F = 27.9$, p -value < 0.001).

Total β -diversity displayed greater variability between sampling dates (i.e., “time comparisons”) in the restored reach compared with the control (Figure 3a–c). This was reflected in a highly significant two-way ANOVA testing a time comparison \times reach interaction ($F = 113.2$, p -value < 0.001; see Appendix B for the full model results).

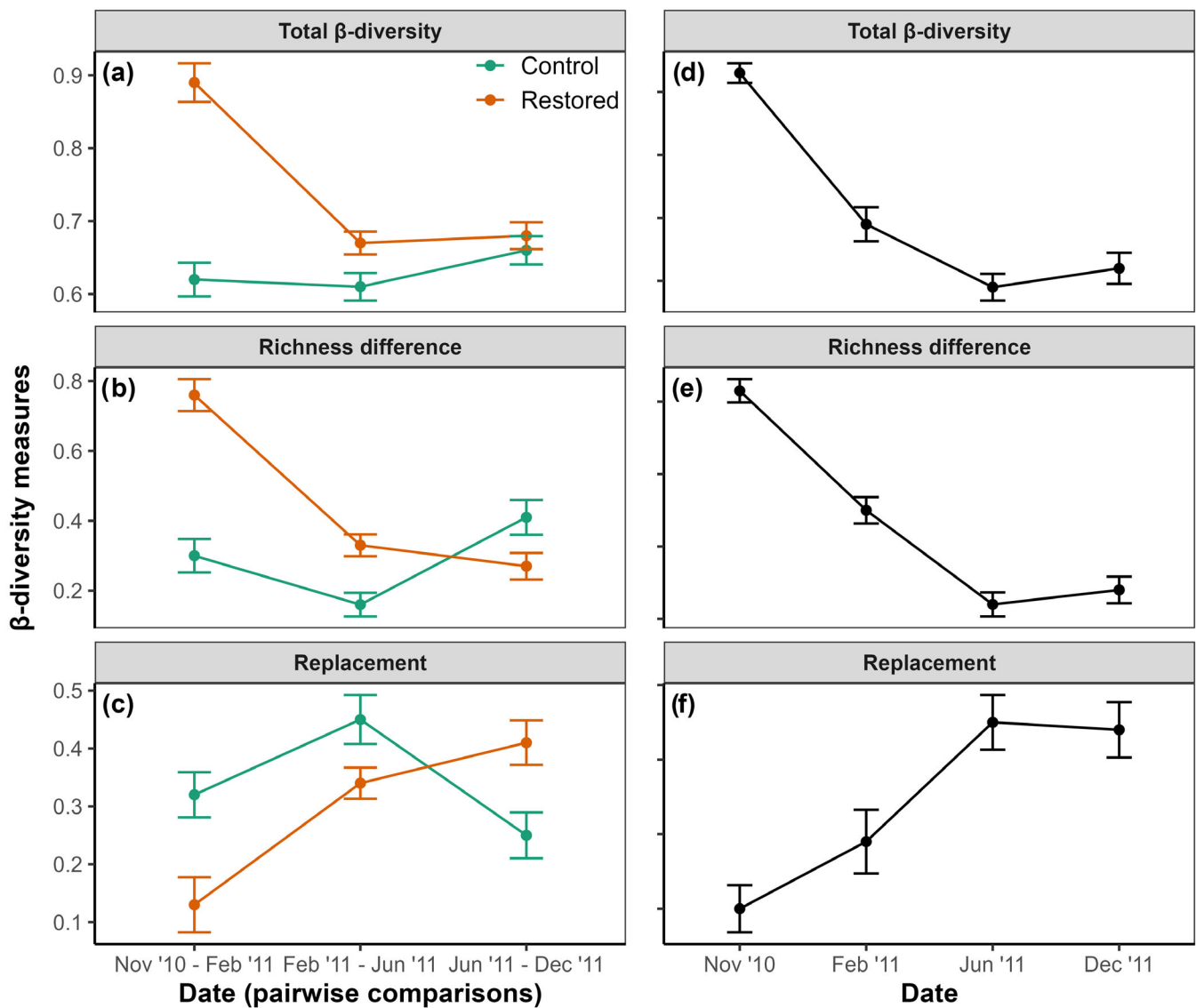


FIGURE 3 Temporal changes in mean averaged (± 2 standard errors) β -diversity values derived from pairwise comparisons: (a–c) those between consecutive sampling periods (“time comparisons”) within each reach; and (d–f) those between the control and restored reaches within each sampling period. The Total β -diversity (a and d) are displayed along with its richness difference (b and e) and replacement (c and f) components. [Color figure can be viewed at wileyonlinelibrary.com]

Specifically, the restored reach displayed notably higher Total β -diversity values relative to the control between November 2010 and February 2011, which was largely driven by richness difference (85% on average). The Total β -diversity in the restored reach declined markedly between February 2011 and June 2011 and plateaued between June 2011 and December 2011, displaying comparable values to the control reach during this latter time comparison (Figure 3a). A similar temporal pattern was observed for richness difference, but such values also decreased between June 2011 and December 2011 in the restored reach when it accounted for its lowest proportion of the Total β -diversity (40% on average; Figure 3b). Taxa replacement values increased consecutively between each time comparison in the restored reach but peaked between February 2011 and June 2011 in the control (Figure 3c). Changes in richness

difference ($F = 99.3$, p -value < 0.001) and replacement ($F = 44.7$, p -value < 0.001) displayed significantly different variations across time comparisons between the control and restored reach.

β -diversity pairwise comparisons between each reach for each sampling period (Figure 3d–f) highlighted that the Total β -diversity ($F = 215.9$, p -value < 0.001) and richness difference ($F = 231.3$, p -value < 0.001) both decreased consecutively between November 2010 and June 2011, and displayed small increases in December 2011. These Total β -diversity patterns broadly indicated greater ecological similarity between the control and restored reach over time. Taxa replacement displayed the opposite temporal trend (increasing until June 2011 and decreasing after) and varied significantly over time ($F = 40.5$, p -value < 0.001). The Total β -diversity between reaches was largely driven by richness difference in the earlier

sampling periods (89% on average in November 2010) before taxa replacement became more influential later (55% on average in December 2011).

3.2 | Ecological differences between control, restored, and palaeoecological samples

In total, 40 taxa belonging to Gastropoda, Bivalvia, Coleoptera, Megaloptera, and Trichoptera (GBCMT) were recorded across the contemporary (i.e., control and restored reaches—pooled Surber samples) and palaeoecological samples. The control reach supported 28 GBCMT taxa and was dominated by Gastropoda ($n = 11$) and Trichoptera ($n = 14$). The palaeoecological samples also supported 28 GBCMT taxa but were more evenly spread across different taxonomic orders (9 Gastropoda, 11 Trichoptera, and 6 Coleoptera). Only 15 GBCMT taxa were recorded from the restored reach and primarily consisted of Trichoptera ($n = 9$). The control and palaeoecological treatments respectively supported 5 (3 Gastropoda and 2 Trichoptera) and 12 (4 Gastropoda, 3 Coleoptera, 1 Megaloptera, and 3 Trichoptera) unique GBCMT taxa (i.e., not recorded in any other treatment; Table 1); the restored reach did not support any unique GBCMT taxa.

A Kruskal-Wallis test indicated that taxa richness differed significantly between treatments ($\chi^2 = 8.42$, p -value = 0.014). Taxa richness was highest in palaeoecological samples and lowest in the restored reach (Figure 4a; mean average values for the latter were suppressed by earlier samples—see above, although no GBCMT taxa were recorded in November 2010, so restored samples were not assessed). A Nemenyi post-hoc test only indicated significant differences between palaeoecological versus restored samples (p -value = 0.011). CCI values were highest and lowest in

palaeoecological and restored treatments, respectively (Figure 4b), although no statistically significant differences were recorded ($\chi^2 = 4.27$, p -value = 0.118). The palaeoecological samples displayed the lowest values for the multivariate distance to centroid (PERMDISP— $\chi^2 = 3.99$, p -value = 0.136), WHPT-ASPT ($\chi^2 = 4.65$, p -value = 0.100), LIFE ($\chi^2 = 7.57$, p -value = 0.022), and E-PSI ($\chi^2 = 10.2$, p -value = 0.006; see Figure 4c–f); although only LIFE and E-PSI demonstrated significant differences. Post-hoc comparisons indicated that LIFE (p -value = 0.023) and E-PSI (p -value = 0.005) scores differed significantly between restored and palaeoecological treatments, while E-PSI also differed significantly between palaeoecological and control samples (p -value = 0.048). Gastropoda (%) (i.e., percentage of this taxonomic class comprising each sample) was broadly comparable across the three treatments ($\chi^2 = 2.47$, p -value = 0.291), but palaeoecological samples supported higher Coleoptera (%) ($\chi^2 = 3.91$, p -value = 0.142) and lower Trichoptera (%) values ($\chi^2 = 3.43$, p -value = 0.180; Figure 4g,h); although none of these latter three responses differed significantly.

Greater numbers of taxa that are more tolerant to nutrient enrichment (Figure 5a), non-rheophilic (Figure 5b) and better adapted to fine sediment (Figure 5c) were observed in the palaeoecological samples compared with the contemporary control and restored samples (the former less so). These resulted in the lower WHPT-ASPT, LIFE, and E-PSI scores observed (see Figure 4d–f). Comparable numbers of taxa more sensitive to nutrient enrichment, preferring higher flow velocities (i.e., rheophilic), and intolerant to fine sediment were observed across the three treatments.

PERMANOVA indicated significantly different GBCMT community composition between treatments ($F = 6.3$, p -value < 0.001), which explained 40% of the statistical variation ($r^2 = 0.40$). A pairwise PERMANOVA indicated significantly different compositions between palaeoecological versus control ($F = 9.2$, p -value = 0.003) and restored ($F = 10.9$, p -value = 0.006) reach samples, explaining 40% ($r^2 = 0.40$) and 55% ($r^2 = 0.55$) of the statistical variation, respectively. However, non-significant trends were observed between control versus restored samples ($F = 1.64$, p -value = 0.420, $r^2 = 0.10$). The 1st PCoA axis scores explained 39.4% of the ecological variability, with contemporary and palaeoecological samples being associated with lower and higher values (i.e., clustered on the left and right), respectively (Figure 6). PCoA1 values displayed significant, negative correlations with LIFE ($r = -0.55$, p -value = 0.008), Gastropoda (%) ($r = -0.46$, p -value = 0.032), and E-PSI ($r = -0.39$, p -value = 0.007), but demonstrated a significant positive correlation with Coleoptera (%) ($r = 0.68$, p -value < 0.001). The 2nd PCoA axis scores explained 18.1% of the statistical variability and generally encompassed all treatments along this axis gradient, but palaeoecological samples did not occur at lower PCoA2 scores (Figure 6). PCoA2 scores displayed significant, negative correlations with WHPT-ASPT ($r = -0.78$, p -value < 0.001), Trichoptera (%) ($r = -0.71$, p -value < 0.001), E-PSI ($r = -0.54$, p -value = 0.008), LIFE ($r = -0.51$, p -value = 0.016), and Coleoptera (%) ($r = -0.43$, p -value = 0.046), but were positively correlated with Gastropoda (%) ($r = 0.68$, p -value < 0.001).

TABLE 1 Taxa that were unique to control, restored (i.e., contemporary) or palaeoecological samples (i.e., three “treatments”).

Control	Palaeoecological
<i>Theodoxus fluviatilis</i> (G)	<i>Stagnicola palustris</i> (G)
<i>Anisus leuctosoma</i> (G)	<i>Anisus vortex</i> (G)
<i>Gyraulus albus</i> (G)	<i>Bathyomphalus contortus</i> (G)
<i>Lepidostoma hirtum</i> (T)	<i>Planorbium corneum</i> (G)
<i>Athripsodes albifrons</i> (T)	<i>Brychius elevatus</i> (C)
	<i>Haliplus</i> sp.(C)
	<i>Nebiroporus depressus</i> (C)
	<i>Helophorus</i> sp.(C)
	<i>Sialis lutaria</i> (M)
	<i>Hydropsyche angustipennis</i> (T)
	<i>Potamophylax cingulatus</i> (T)
	<i>Molanna angustata</i> (T)

Abbreviations: C, Coleoptera; G, Gastropoda; M, Megaloptera; T, Trichoptera (no Bivalvia taxa were unique to a specific treatment).

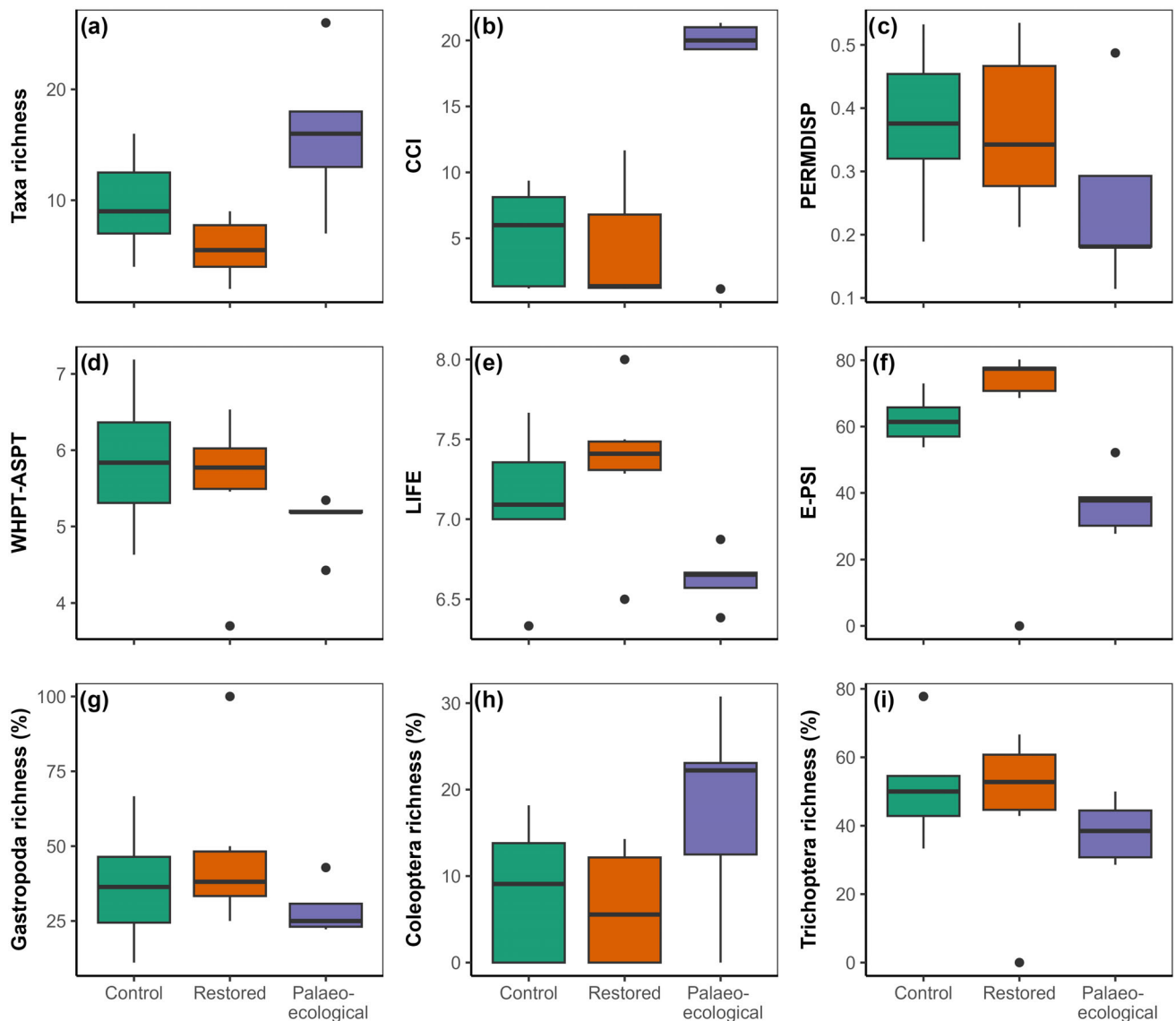


FIGURE 4 Boxplots displaying the range (whiskers), 25th, 50th, and 75th percentiles (boxes) of ecological metric values between different sample types (control, restored and palaeoecological—the former two being contemporary samples). (a) Taxa richness; (b) Community Conservation Index (CCI); (c) Permutational Multivariate Analysis of Dispersion (PERMDISP); (d) average Walley, Hawkes, Paisley, and Trigg score per taxon (WHPT-ASPT); (e) Lotic Invertebrate index for Flow Evaluation (LIFE); (f) Empirically-weighted Proportion of Sediment-sensitive Invertebrates (E-PSI); (g–i) the percentage of Gastropoda, Trichoptera, and Coleoptera comprising each sample. [Color figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | The temporal trajectories of macroinvertebrate communities following river restoration

Various studies have called for longer-term monitoring to better understand the temporal dynamics of river ecosystems following the implementation of restoration schemes and how this translates to project success (e.g., Kail et al., 2015; Lu et al., 2019). However, the shorter-term (e.g., sub-seasonal to seasonal) temporal dynamics of freshwater ecosystems following river restoration works have seldom

been explored. Such sub-annual information may help in understanding how river ecosystems are likely to recover in the long-term. For instance, “biotic resistance” may arise when competitively superior taxa establish early in the aftermath of restoration works and subsequently inhibit the (re)colonization of diverse biotic communities (i.e., priority effects; Frame et al., 2016). Alternatively, “resource limitations” could limit or delay ecological recovery if a restored reach supports insufficient energy sources (e.g., primary producers, invertebrate prey—Barrett et al., 2021).

This study provided rare insights into the temporal trajectory of freshwater macroinvertebrate communities in the 13-months following a river restoration project, which entailed reconnecting a

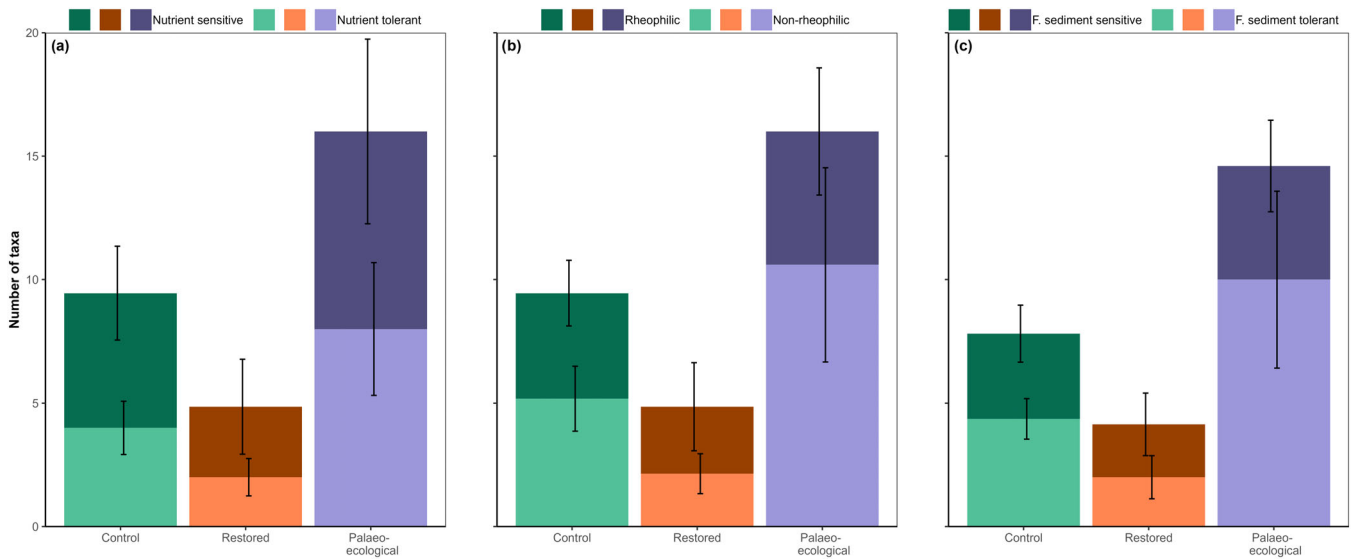


FIGURE 5 Stacked bar charts of the mean average (± 2 standard errors) number of taxa displaying different ecological guilds between control, restored, and palaeoecological samples (i.e., three “treatments”). (a) taxa sensitive and tolerant to nutrient enrichment; (b) rheophilic and non-rheophilic taxa; (c) taxa sensitive and tolerant to fine sediment (“F. sediment”). [Color figure can be viewed at wileyonlinelibrary.com]

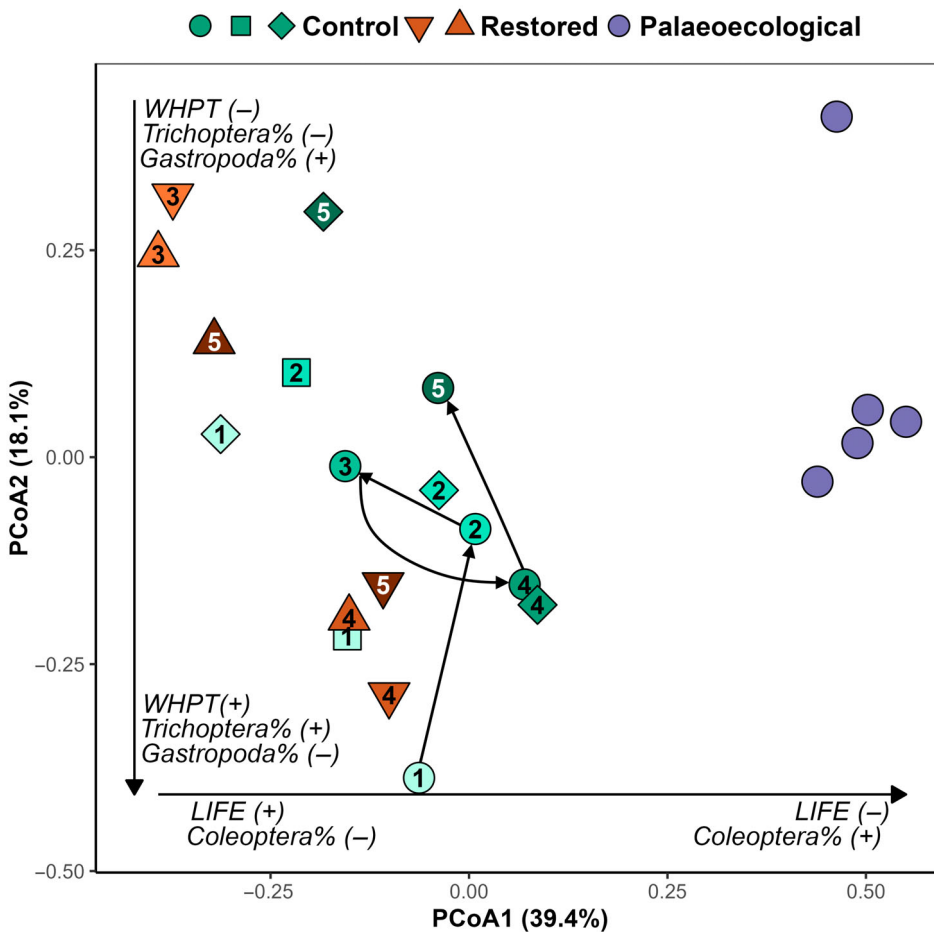


FIGURE 6 Principal Coordinates Analyses (PCoA) of Gastropoda, Bivalvia, Coleoptera, Megaloptera, and Trichoptera (GBCMT) communities across different treatments (control = green circles, diamonds and squares; restored = orange triangles, palaeoecological = purple circle). Each shape indicates a specific study site, while each number denotes a sampling period: 1 = June 2010; 2 = November 2010; 3 = February 2011; 4 = June 2011; 5 = December 2011. Arrows have been drawn between consecutive sampling periods for Site A (control reach) for esthetic purposes. No data is presented in the restored site for first and second sampling periods, with the former predating the palaeochannel reconnection (i.e., no samples collected) and the latter containing impoverished communities devoid of GBCMT taxa (<1 week after restoration works). Sites B and C (control reach) were not sampled during certain events due to excessive flow depths. WHPT, Walley, Hawkes, Paisley, and Trigg. [Color figure can be viewed at wileyonlinelibrary.com]

straightened watercourse to its former palaeochannel that possesses a naturally more sinuous morphology. α -diversity analyses highlighted that the restored reach initially (<1-week post-works) supported an

impoverished community. This resulted in richness difference driving β -diversity patterns in the earlier stages of the study, both in terms of pairwise comparisons between the control versus restored reach

samples, and those between consecutive sampling periods within the restored reach (“time comparisons”; i.e., a higher richness in subsequent sampling periods). For such time comparisons, the increasing influence of taxa replacement over time illustrated how new species continued to (re)colonize, and in some instances displace established taxa within the restored reach. This could suggest community instability due to ecological recovery not yet being complete, as reported by Dézerald et al. (2023) in the three-years following a dam removal. Despite this, the taxa richness and density gains in the restored channel observed over time outpaced the control reach and were comparable between the two reaches by the end of the study period, with ecologically similar communities across this timeframe also being indicated by decreasing Total β -diversity values.

From a practical perspective, more ecologically comparable samples between the control and restored reaches is not necessarily desirable given that the former was a straightened, over-deepened system that supported a low biodiversity. However, detecting signals of complete ecological “restoration” in this study was unlikely given its relatively short timeframe, with few studies demonstrating this level of recovery within c. 1 year following project completion (Leps et al., 2016; but see Thompson et al., 2018 for a notable exception). Further, long-term evidence would be required from the study site to better appraise its overall ecological effectiveness. No unique taxa were sampled in the restored reach, which indicates that ecological responses to the works were confined by one or more of the following (all discussed further below): dispersal limitations of taxa within the catchment-wide species pools over the 13-month time period examined (Sundermann et al., 2011); local species pools (i.e., those inhabiting proximal freshwater habitats) exhibiting a low biodiversity or being dominated by competitively superior taxa (Frame et al., 2016; Sundermann et al., 2011); or adverse upstream catchment properties (e.g., water quality, flow regime variations; Palmer et al., 2010). It should however be noted that the restored channel supported modestly higher numbers of rheophilic taxa by the end of the study period, albeit with all of these also being found in the control section. Such patterns indicate that restoration can still enhance the heterogeneity of biotic communities (e.g., co-occurrence patterns) within the confines of a limited species pool (White et al., 2017).

Rheophilic taxa densities peaked 3 months after restoration when Simuliidae (blackfly arvae) proliferated, but then sharply declined by the following sampling period. Simuliidae can rapidly recolonize freshwater habitats (Aspin & House, 2022) and are filter-feeders that would have benefitted from the increased flow velocities in the restored reach (Extence et al., 1999). Subsequent Simuliidae declines may be linked to increased *Gammarus pulex* (freshwater shrimp) abundances, which is a habitat generalist that widely displaces established fauna (including Simuliidae) through direct predation or competition for space and resources (Aspin & House, 2022). High non-rheophilic taxa densities in the restored reach at the end of the study period reflected the propagation of the non-native gastropod *Potamopyrgus antipodarum* (New Zealand mud snail). *P. antipodarum* is also a habitat generalist and is readily capable of inhabiting faster flow conditions (Geist et al., 2022; the LIFE metric used to classify hydraulic

preference does not account for such plasticity—Extence et al., 1999). Interestingly, routine biomonitoring undertaken c. 5 years after restoration indicated both contemporary reaches were dominated by *G. pulex* and *P. antipodarum* (see Appendix C). Such taxa can potentially negatively influence freshwater ecosystem health, including overconsumption of basal resources like coarse particulate organic matter and algae that limits resources available for other taxa (Aspin & House, 2022; Geist et al., 2022). Further investigation spanning multiple years would be required to examine whether the dominance of such competitive taxa may have exerted biotic resistance effects and thus influenced the ecological effectiveness of the river restoration works in the long-term.

4.2 | Contemporary versus palaeoecological macroinvertebrate communities

The palaeoecological samples collected in this study provided a “snapshot” of macroinvertebrate communities inhabiting a meander bend prior to it being disconnected in 1946. Although anthropogenic pressures existed across the River Wensum at this time (e.g., mill structures harnessing water; agricultural pollution—Coombes et al., 2007), far more severe morphological and water quality stressors were to follow in later years associated with agricultural intensification following the Second World War (Allen et al., 2019). As such, palaeoecological samples captured freshwater ecosystem characteristics prior to major human disturbance at this study site, which was supported by these containing a greater number of Gastropoda, Bivalvia, Coleoptera, Megaloptera, and Trichoptera (GBCMT) taxa relative to their contemporary counterparts (both control and restored reaches). Palaeoecological communities also comprised a greater conservation value (i.e., a higher number of less nationally common taxa), as indicated by the higher Community Conservation Index (Chadd & Extence, 2004).

Assessing biomonitoring indices in isolation would indicate that the palaeochannel displayed greater nutrient enrichment, slower flow velocities and increased fine sediment loads compared with the contemporary reaches (based on lower WHPT-ASPT, LIFE, and E-PSI scores, respectively). However, palaeoecological samples contained a greater number of taxa displaying a broader range of corresponding ecological guilds relative to the contemporary samples, which highlights potential issues when interpreting averaged-based metrics. There were several taxa unique to the palaeoecological samples that displayed preferences for sluggish flow environments, including gastropods (*Stagnicola palustris*, *Anisus vortex*, *Bathymorphus contortus*, *Planorbium corneum*) that often inhabit instream macrophytes, as well as *Helophorus* sp. (Coleoptera), *Sialis lutaria* (Megaloptera) and *Molanna angustata* (Trichoptera; Extence et al., 1999). However, some rheophilic taxa were also unique to the palaeoecological samples (e.g., *Brychius elevatus*—Coleoptera; *Hydropsyche angustipennis*—Trichoptera; *Potamophylax cingulatus*—Trichoptera). These multiple lines of ecological evidence indicate that former channel (i.e., prior to 1946) contained large areas of slow flowing, fine sediment dominated

habitats, interspersed with coarser substrate habitats associated with fast flow velocities and abundant growth of instream macrophytes.

This study indicated that habitat changes via river restoration did not facilitate the establishment of biotic communities akin to those recorded in the palaeochannel within 13 months of works being undertaken. The increasing ecological similarity between control and restored contemporary communities (see above) in spite of their contrasting morphologies indicates that physical habitat characteristics are unlikely to be a primary limiting factor driving a lower biodiversity compared with palaeoecological conditions. Such findings support other studies indicating that reach-scale restoration can have limited effects when placed in the context of catchment-scale pressures (Palmer et al., 2010). Contemporary reaches did support taxa requiring higher water quality conditions (e.g., *Lepidostoma hirtum*—Trichoptera; Nemouridae—Plecoptera; *Sericostoma personatum*—Trichoptera; Paisley et al., 2014) that resulted in higher WHPT-ASPT scores. Moreover, the “P stripping” infrastructure employed at the sewage treatment plant discharging c. 1 km upstream indicates that Phosphate concentrations (a significant issue across the studied catchment—Coombes et al., 2007; Cooper & Hiscock, 2023) is also unlikely to be a key environmental filter limiting the biodiversity of the contemporary system. However, other abiotic stressors may have limited contemporary samples versus paleoecological conditions, including various other pressures associated with sewage treatment works (e.g., modified flow or thermal regimes, pharmaceuticals or microplastics—Lynch et al., *In Press*), but no empirical data exists for this and further investigation on these influences would be required. It is also plausible that biological mechanisms may be driving less diverse contemporary communities compared with palaeoecological conditions, including the presence of non-native fauna (e.g., *P. antipodarum*—see above; *Pacifastacus leniusculus*, the signal crayfish has also been recorded in the catchment) or dispersal limitations of upstream assemblages (Sundermann et al., 2011), the latter potentially being further exacerbated by weirs and mill structures in the catchment.

4.3 | Using palaeoecological information to guide river restoration practices

Palaeoecological information has been widely utilized in lake environments to quantify the extent of ecosystem degradation and to provide targets within management frameworks (i.e., “reference” conditions—Davidson et al., 2018). Such research has been less widely explored and utilized in riverine systems due to the comparably short timescales involved and interrupted sequences available caused by fluvial erosion and deposition processes (Greenwood et al., 2006). However, palaeochannels can provide important ecological information on faunal assemblages that inhabited watercourses prior to being disconnected from the main channel (Seddon et al., 2019). Moreover, palaeochannels are a widely occurring fluvial landform and have been used to characterize biotic communities from centuries (Seddon et al., 2019; or decades in this study) to

millennia prior to the present day (Greenwood et al., 2006; Howard et al., 2009, 2010).

Palaeoecological information can be most effectively incorporated within freshwater management strategies when considering a range of past pre-disturbed conditions, rather than assuming a single set of target objectives (Davidson et al., 2018). However, such evidence requires careful consideration of appropriate and attainable time periods, as well as the availability of appropriate sampling locations. In this study, pre-1946 was deemed to reflect conditions prior to the intensification of human disturbances, which is in keeping with many other European rivers exposed to mounting anthropogenic pressures following the Second World War (Haase et al., 2023). However, other river systems experienced significant degradation earlier than this and the time period assessed here would therefore provide unsuitable target conditions elsewhere (e.g., some rivers in the English Midlands were so polluted in 1945 that freshwater life was completely absent from some reaches—Langford et al., 2010). Conversely, Seddon et al. (2019) collected palaeoecological macroinvertebrate communities from a meander bend that was disconnected in the 1850s, which exhibited a higher biodiversity than its contemporary counterparts. However, the authors reported that such evidence indicated a sluggish environment nested within a landscape of riparian marshlands that would be unattainable and impractical to use as target conditions within a contemporary river restoration scheme. In the present study, the palaeoecological samples scrutinized could feasibly be used alongside other comparable evidence to guide a range of target conditions, but this would require further evidence from comparable river environments (i.e., chalk streams/rivers) across different time periods to provide a more complete overview of pre-disturbed community variability and dynamics. Notwithstanding, the palaeoecological information examined in this study reliably indicated that contemporary communities are ecologically poor relative to those that existed prior to major anthropogenic disturbances, and highlights that further management would be required to truly “restore” the study site.

This study illustrates how palaeoecological data from disconnected river channels can provide valuable information on the extent of degradation within freshwater ecosystems and potentially provides restoration targets. Given that re-connecting palaeochannels is a popular river restoration technique implemented globally (Gilvear et al., 2013), extracting sub-fossilized faunal assemblages prior to reconnection could provide more appropriate target conditions compared with contemporary samples taken from “reference” sites identified via space–time substitutions. The latter is widely adopted in post-project appraisals, despite these sites potentially being subjected to contemporary anthropogenic pressures and/or may display natural environmental and ecological differences compared with restored sections. Palaeoecological information should thus be investigated more widely alongside other forms palaeo (e.g., hydrological/sedimentological indicators, geochronology to age samples—Sear & Arnell, 2006) and contemporary evidence (e.g., ecological and geomorphological—see England, Angelopoulos, et al., 2021, England, Hayes, et al., 2021; River Restoration Centre, 2023) to appraise the effectiveness of meander reconnection schemes. Further palaeoecological research

focusing on riverine systems is required that encompasses varying time periods and environmental contexts to provide robust pre-disturbed ecological data that can be incorporated within different restoration projects and post-project appraisals.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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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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