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RESEARCH ARTICLE

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Large woody debris "rewilding" rapidly restores biodiversity in riverine food webs

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Abstract

1. Extensive habitat destruction and pollution have caused dramatic declines in aquatic biodiversity at local to global scales. In rivers, the reintroduction of large woody debris is a common method aimed at restoring degraded ecosystems through "rewilding." However, causal evidence for its effectiveness is lacking due to a dearth of replicated before–after control-impact field experiments.
2. We conducted the first replicated experiment of large woody debris rewilding across multiple rivers and organisational levels, from individual target species populations to entire food webs.
3. For the first time, we demonstrate causal links between habitat restoration, biodiversity restoration and food web responses. Populations of invertebrates and an apex predator, brown trout (*Salmo trutta*), increased, and food web analysis suggested increased biomass flux from basal resources to invertebrates and subsequently fishes within restored reaches.
4. *Synthesis and applications*. This study contributes significant new evidence demonstrating that large woody debris rewilding can help to restore human-impacted river ecosystems, primarily through altering the abundance and biomass of consumers and resources in the food web. We also outline a means to gauge the magnitude of ecological responses to restoration, relative to environmental stressors, which could help to prioritise the most effective conservation efforts.

KEYWORDS
BACI, biodiversity, biomonitoring, field experiment, food webs, rewilding, river restoration, river systems, trivariate analysis, woody debris

1 | INTRODUCTION

Overexploitation, pollution and habitat destruction are causing global declines in freshwater biodiversity (Strayer & Dudgeon, 2010; Vörösmarty et al., 2010), especially in running waters (Nilsson, Reidy, Dynesius, & Revenga, 2005; Stein & Kutner, 2000). Despite widespread improvements in water quality in the developed world, ecological recovery in rivers has often been patchy, slow or even entirely lacking (Battarbee, Shilland, Kernan, Monteith, & Curtis, 2014; Langford, Shaw, Ferguson, & Howard, 2009). This suggests that environmental drivers, which were previously subordinate to poor water quality, are now acting as principal bottlenecks where chemical conditions have improved. Foremost among these is habitat degradation associated with river straightening, channelisation, impoundment and clearance of large woody debris (also termed large wood, henceforth LW), which has been ongoing around the world for many centuries (Downs & Gregory, 2014). These modifications restrict natural river dynamics, such as LW processes that determine the frequency of pools and riffles, with often deleterious implications for ecosystems (Brooker, 1985; Gurnell & Sweet, 1998).

Large wood has been used to enhance in-river habitat throughout the world for over a century in tens of thousands of projects (Bernhardt et al., 2005; Feld et al., 2011; Roni, Beechie, Pess, Hanson, & Jonsson, 2015). In recent times, "rewilding" approaches, such as reintroducing beavers or felling whole trees into the river to replicate natural treefall, have been increasingly used as a means to reinstate natural processes, restore biodiversity and thus recover degraded river ecosystems (Baker & Eckerberg, 2016; Hood & Larson, 2015; Roni & Beechie, 2012). LW-based habitat restoration has been linked to increases in fish and invertebrate populations (Kail, Hering, Muhar, Gerhard, & Preis, 2007; Roni et al., 2015; Schneider & Winemiller, 2008), increases in allochthonous and autochthonous resources for invertebrates (Cashman, Pilotto, & Harvey, 2016; Gurnell, Gregory, & Petts, 1995), and increased provision of refugia for organisms from high flows (Borchardt, 1993) and predation (Everett & Ruiz, 1993). However, the assumed biodiversity enhancement following the restoration of habitat diversity is strongly contested in the absence of unequivocal evidence (Feld et al., 2011; Lepori, Palm, Brännäs, & Malmqvist, 2005; Palmer, Menninger, & Bernhardt, 2010; but see Kail, Brabec, Poppe, & Januschke, 2015; Pilotto, Bertoncin, Harvey, Wharton, & Pusch, 2014).

Due to a lack of replication and standardisation of monitoring techniques, the suitability of proxies (e.g. river habitat quality or the abundance of key taxa) as surrogates for effective ecosystem restoration remains unverified (Bernhardt & Palmer, 2011; Feld et al., 2011; Palmer et al., 2010). Where biomonitoring has been undertaken to assess restoration success, invertebrates or fish have often been the sole bioindicators used (Matthews, Reeze, Feld, & Hendriks, 2010; Whiteway, Biron, Zimmermann, Venter, & Grant, 2010; but see Kail et al., 2015). Despite being repeatedly advocated (Feld et al., 2011; Friberg et al., 2011; Pander & Geist, 2013), a more holistic, system-based view of restoration responses at higher levels of biological organisation is still lacking. Furthermore, no study to our knowledge has compared both control (i.e. unrestored) and target conditions (i.e. those naturally created which the intervention aims to replicate) across rivers in a multiple before–after control-impact (MBACI; sensu Downes et al., 2002) framework. This is nonetheless the only way to isolate potentially confounding drivers of ecological change in both space and time to test whether ecosystems are consistently restored to target conditions.

We address this knowledge gap by comparing ecological patterns between control reaches (i.e. those with no LW), reaches with naturally fallen LW prior to restoration (i.e. "target"), and those containing felled LW (i.e. "restored") in a MBACI experiment. This was conducted across five British lowland rivers that have been subjected to river habitat degradation and pollution typical for such systems (Environment AgencyEnglish Nature, 2004; WWF-UK, 2015). Recent studies (Hering et al., 2015; Kail et al., 2015) suggest that river restoration can affect biota quickly, the effects of restoration can diminish over time, and that restoration scale is a weak determinant of restoration effect. Thus, by comparing control, target and restored reaches, our aim was to assess short-term (<1 year post-restoration) responses to individual LW structures, while also giving a longer-term perspective on the trajectory of ecological recovery, as restored reaches develop from a degraded to a more fully restored "target" state. Such an approach is vital in a field where monitoring resources are limited and extended temporal sampling (>2 years) is rarely feasible (Feld et al., 2011).

To understand reach-scale effects of restoration on the community, we investigated changes in the mass and abundance of species populations and the links between them (trophic interactions) in food webs using "trivariate analyses" (sensu Cohen, Schittler, Raffaelli, & Reuman, 2009), as well as their more traditional univariate and bivariate component measures (e.g. linkage density and mass-abundance scaling exponents, respectively). Because invertebrate assemblages respond to habitat change (Demars, Kemp, Friberg, Usseglio-Polatera, & Harper, 2012), form the intermediate nodes in aquatic food webs, and are widely used as bioindicators in habitat restoration studies (Matthews et al., 2010; Palmer et al., 2010), we investigated assemblage-level response to LW restoration across reaches and between local habitat patches. We tested the following hypotheses: (1) LW restoration affects multiple levels of biological organisation, from species' populations to entire food webs: species with many predators and those especially sensitive to deteriorating environmental conditions will prosper from the increased refugia and restored conditions provided by LW; an increase in species richness will result in increases in both feeding-link diversity and new feeding pathways in restored food webs; (2) food webs in the recently restored reaches are intermediate between control and target conditions as small, vagile, fast-growing species (e.g. invertebrates) respond to elevated resources (i.e. refugia and available energy) before large, long-lived species (e.g. fish); (3) LW restoration increases invertebrate species richness (i.e. α-diversity) at the reach-scale and enhances invertebrate community dissimilarity (i.e. β-diversity) within reaches as habitat-specific assemblages colonise LW. Where frequently used control-impact designs cannot establish causation and standard BACI designs are unable to reveal the consistency of recovery patterns, the MBACI approach is perfectly suited to address these hypotheses.

2 | MATERIALS AND METHODS

2.1 | Study sites, restoration and experimental design

We sampled five UK lowland chalk rivers (Figure 1; Table S1) that span a range of nutrient concentrations representative of such systems (i.e. ortho-phosphate concentrations of 37.7–308.5 $\mu g\ l^{-1}$ representing relatively low to moderately enriched waters; UKTAG, 2013). On each river, we surveyed an "impact" reach, designated for restoration, and an unrestored "control" reach, which resembled the channel form and riparian surroundings that existed in the (pre) impact reach. We also surveyed a "target" reach where naturally fallen trees had been in place for 3–5 years prior to restoration on four of the rivers. There were no available target conditions at the R. Wensum, however. This meant we had two temporal controls at four of our rivers (i.e. control

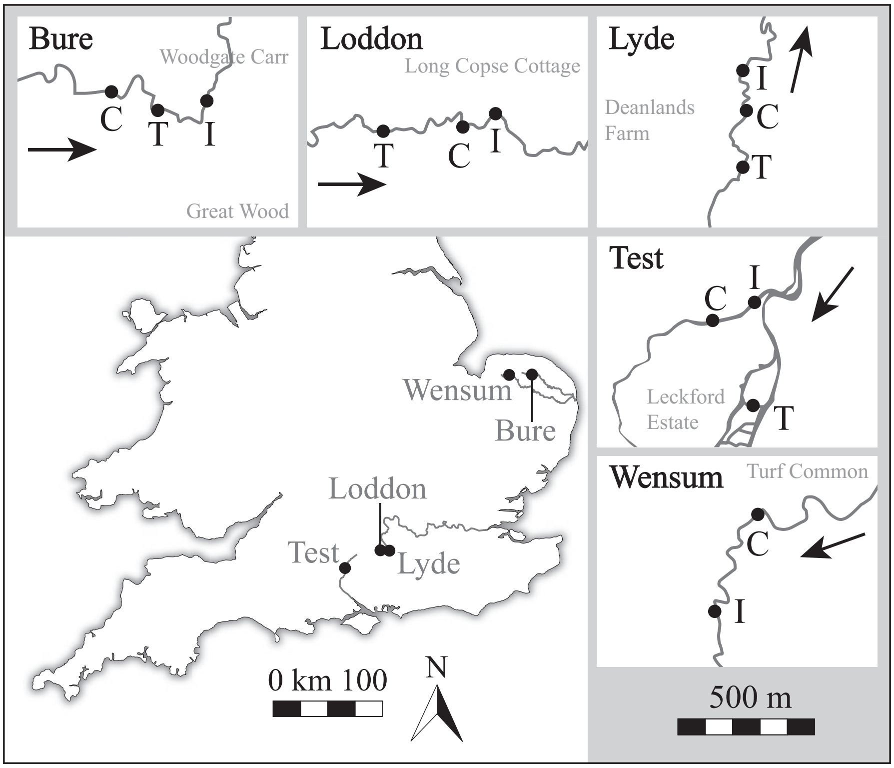

FIGURE 1 Locations of rivers used in this study in the United Kingdom. Upper and right panel shows control (C), impact (I) and target (T) reach arrangement in each river in relation to direction of flow (indicated by arrows). There were no suitable target reaches near the restoration on the River Wensum

and target reaches), which is considered an important, but often overlooked, requirement in BACI designs (Underwood, 1994).

Reaches were 25 m in length, 100–500 m apart in each river to maintain independence, and ordered randomly to avoid potentially confounding longitudinal effects (Harrison et al., 2004). Restorations were undertaken in late October and early November 2010. In each river we replicated, as closely as possible, the LW structure found in target conditions, that is, by felling the same size and species of tree, which were either whole Alder (*Alnus glutinosa* L.) or White Willow (*Salix alba* L.) at least 7 m tall and of 0.3 m diameter at the base of the trunk. Felled trees were tethered to stakes fashioned from their own branches.

2.2 | Sampling protocol

Across all reaches, biological, physical and chemical surveys were undertaken in spring (mid-March to mid-April) 2010 before restoration and during the same period in 2011 following restoration. Estimates were made of the conditions and extent of LW, river-edge (i.e. up to 1 m from the bank) and mid-river habitats across a grid of fifteen 1 m^2 quadrats divided between five equally spaced transects per reach (Figure S1). Using a bathyscope, proportions of silt, sand and gravel substrate were estimated visually to the nearest 5%, and coarse woody debris (<10 cm diameter), LW (>10 cm diameter) and plant occupancy were measured using the "percentage volume infested" (PVI) system (Canfield et al., 1984). Water velocity ($m\ S^{-1}$) was measured at 60% depth using a Valeport BFM002 flow meter at each survey point. Physical river reach characteristics (e.g. river width, altitude, gradient) were collated alongside annual averages of water temperature and chemistry (e.g. ortho-phosphate, total oxidised nitrogen, dissolved oxygen, pH and alkalinity) collected by the UK Environment Agency.

2.3 | Population abundance, community structure and trophic interactions

Epilithic biofilm was sampled from eight cobbles selected haphazardly at each reach. Each cobble was photographed and its upper surface area calculated using Image-J software (version 1.42) to provide data per unit area. Three cobbles were scraped on site, preserved in Lugol's iodine and prepared for diatom identification following Battarbee, Jones, Flower, and Cameron (2001). The first 100 diatom valves encountered within a 100-μm wide transect crossing the centre of each cover slip were identified to species, resulting in 300 valve identifications per reach that is considered optimal for determining community composition (Besse-Lototskaya, Verdonschot, & Sinkeldam, 2006). Full details of diatom abundance and dry mass estimation are given in Supporting Materials and Methods (see also Table S2). The remaining five cobbles were stored in the dark at −20°C. Biofilm was removed from the upper surface of each stone using a toothbrush. Chlorophyll-*a* (a proxy for algal biomass) was cold-extracted using 90% acetone and its concentration determined using a spectrophotometer (Ritchie, 2006).

Invertebrates were sampled from edge, mid and LW habitats in order to assess restoration effects within reach, as well as between reaches (Figure S1). We used these habitat types as the sampling unit because this allowed a fully replicated stratified design across reaches and years. A Hess sampler (0.017 m^2) with 335-μm mesh was used to collect invertebrates and coarse (CPOM) and fine particulate organic matter (FPOM). The Hess sampler had a row of teeth on the base in order to cut through branches, and thus sample LW habitat and the underlying benthos, in a comparable way to edge and mid habitats. Sampling followed a random stratified design in each reach: five samples were collected from mid-channel (the largest habitat by area and thus expected to have highest heterogeneity), three from channel edge, and three from LW (n = 263). Samples were preserved in 70% industrial methylated spirits. CPOM and FPOM, retained on 1 mm and 335 μm sieves, respectively, were determined by weighing oven dried (80°C) organic material from each Hess sample. Invertebrates were identified to the highest possible taxonomic resolution (usually species) and counted to provide data per unit area. Organism body size spanned many orders-of-magnitude in the communities studied here (i.e. from diatoms to fish, 3.93×10^{-8} to 9.88×10^{5} mg, respectively), thus we deemed river-specific estimates of invertebrate taxon mean body size sufficient to assess community-level responses. Measurements were made using all invertebrates collected from the control reaches in 2011, supplemented with specimens of rare taxa from other reaches. A list of regression equations used to determine individual invertebrate dry masses from linear dimensions (e.g. head-capsule widths or body lengths) is provided in Table S3.

Quantitative depletion electrofishing was undertaken at the reach-level, and all fish captured were identified to species and measured to fork length. Abundance (individuals per m^2) was estimated using iterative maximum weighted likelihood statistics (Carle & Strub, 1978). Dry-mass estimates were made for each species using length-mass regression equations and wet-to-dry mass conversions (Thompson et al., 2016). A large Hess sampler (0.14 m^2) was used at the Wensum impact reach due to the relatively low sampling efficiency of bullhead (*Cottus gobio* L.), as catches did not reduce on consecutive runs during electrofishing (Lauridsen et al., 2012). This approach was not necessary for the other reaches where bullhead densities were successfully depleted by electrofishing. Full details of fish abundance and dry mass estimation can be found in Supporting Materials and Methods.

At least three randomly selected fish gut-content samples were taken from individuals of each species from each reach (i.e. up to nine per river) in both years where numbers permitted (n = 132). Gut contents were identified to the highest possible taxonomic level (usually species). As gut content analysis captures only a snapshot of a predator's diet, we pooled all observed feeding links and combined these with feeding links published in the literature and in a recently collated database of trophic interactions from UK freshwaters (Gray et al., 2015). We assumed that if a trophic interaction between two species was directly observed or reported in the literature, and those same species were present within a reach, then that trophic interaction also occurred. This approach has been widely applied (e.g. Mulder & Elser, 2009; Pocock, Evans, & Memmott, 2012; Strong & Leroux, 2014), especially in the construction of river food webs (Gray et al., 2015; Layer, Hildrew, & Woodward, 2013; Layer, Riede, Hildrew, & Woodward, 2010; Thompson et al., 2016). The percentage of directly observed links that were also reported in the literature was 99%: i.e., only 1% of the 4,535 observations from gut contents analysis were new records. Further details of food web construction can be found in Thompson et al. (2016) and Gray et al. (2015), with feeding links observed here for the first time presented in Table S4.

2.4 | Food web analysis

Considering that species rare for their size (i.e. those with negative residuals from the general mass-abundance scaling relationship that spans the food web in Figure 2a) have been shown to be sensitive to deteriorating environmental conditions (Woodward et al., 2012), we expected increases in these species as environmental stressors were relieved following restoration (Figure 2b). In addition, species with many predators (i.e. those with elevated "vulnerability") were expected to prosper from the increased refugia provided by LW. Feeding-link diversity was measured using changes in the number of links, linkage density (i.e. the number of links divided by the number of species)

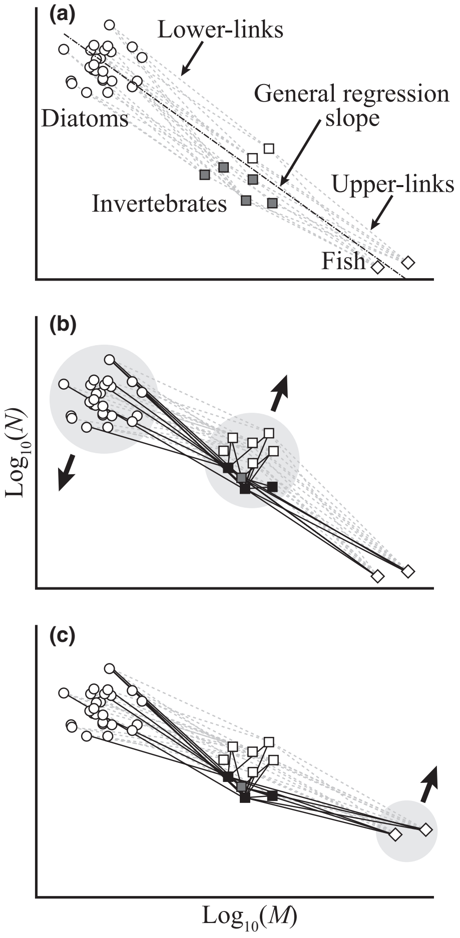

FIGURE 2 Hypothetical aquatic trivariate food webs on double-Log_{10} axes. Nodes represent mean body mass (M) and numerical abundance (N) of individual taxa; grey squares = rare-for-size invertebrate taxa, black squares = taxa found only in restored and target food webs, solid black line = new feeding-link. (a) Control or impact-before reach; (b) following habitat restoration invertebrate N and/or M increases, especially taxa rare for their size, and those with many predators prospering from increased refugia provided by LW; (c) target reaches following longer-term recovery of fish

and connectance (i.e. the proportion of realised links; Martinez, 1991). Increases in consumer nodes, links between consumers and increased predator generality (e.g. in the proportion of resource links to each fish node; sensu Schoener, 1989) were used to assess the potential for network "rewiring" via alternative feeding pathways. We tested whether small, vagile, fast-growing invertebrate taxa responded faster than large long-lived fish taxa by comparing food webs in the restored reaches with those in target reaches (see Figure 2b,c). Changes in feeding "link angles" (sensu Cohen et al., 2009; Thompson et al., 2016) and biomass stocks (e.g. fish biomass per reach) were used to test whether the inferred biomass flux increased following restoration, and whether this resulted in increases in consumer and predator biomass (i.e. bottom-up effects and/or release from top-down control). Where there were increases in species richness which may have masked changes in link angles across a common core of species (e.g. treatment level increases in rare-for-size taxa with more negative link angles could bias results), we re-ran the analysis after removing links unique to a given reach. All food web statistics were calculated in R using *Cheddar* (Hudson et al., 2012).

2.5 | Data analysis

We used principal components analysis and non-metric multidimensional scaling (NMDS) to ordinate the environmental and invertebrate data, respectively. Due to the nested and unbalanced design, data for multivariate analyses were split into four subsets: (1) temporal variation, unrelated to the restoration, was assessed using control-before and control-after data; and (2) spatial variation, unrelated to the restoration, was assessed using control-before and impact-before data; (3) control-after and impact-after data were used to test for restoration effects; and (4) impact-after and target-after data were used to test for differences between restored and target conditions. We used an NMDS of the chord-normalised expected species shared index of dissimilarity (CNESS, calculated in COMPAH96; Gallagher, 1999) on the largest common sample size to provide a measure of β-diversity not confounded by the number of individuals encountered (Trueblood, Gallagher, & Gould, 1994; Legendre & Gallagher, 2001). Permutation tests ($n = 999$) were then used to evaluate the significance of observed differences between rivers, reach- and habitat-types. All multivariate analyses were performed in R using *vegan* (Oksanen et al., 2015). Estimates of α-diversity (i.e. Hill number ^{q}D, where $q = 0$) were made in R using *iNEXT* (Hsieh, Ma, & Chao, 2014). By setting a base sample size and using rarefaction based on Hill numbers, this approach represents a robust way of comparing species richness where sample sizes differ (Chao et al., 2014). Taxa that were not resolved to species, and which could therefore represent multiple species, were removed from analyses of α- and β-diversity.

General linear mixed effect models (GLMM; simulating binomial or Poisson distributed responses), linear mixed effect models (LMM; modelling normally distributed responses) and linear models (LM; modelling normally distributed response without random terms) were used to test for ecological responses, besides invertebrate dissimilarity, to environmental drivers. Strictly positive, non-integer data (e.g. biomass) were Log_{10} transformed, with $x + 1$ when data included values <1. All mixed effect models were constructed in R using *lme4* (Bates, Maechler, Bolker, & Walker, 2015). Targeted tests for differences between group means were carried out using Tukey's all-pairwise comparisons that corrects for multiple comparisons in R using *multcomp* (Hothorn, Bretz, & Westfall, 2008). Habitat conditions in control reaches were significantly different between rivers (see Supporting Results; Figure S2a). Thus, to account for between-river differences, river identity was fitted as a random term in all initial models and restored and target reaches were compared to unrestored (control and before-impact) reaches to test for restoration effects. To assess the spatial scale of the restoration effect on invertebrates, and to disentangle potentially confounding variables, those models included the additional fixed terms of habitat-type (i.e. edge, mid and LW), resource (i.e. algae and detritus) and predator (i.e. fish) biomass. Where there was evidence of over-dispersion in GLMM (i.e. where residual deviance was substantially greater than the residual degrees of freedom), each datum row was fitted as an additional random term (Bolker, 2008). Only significant variables were retained in the final models (Table S5), as determined using the likelihood-ratio test on nested models compared with a χ^2 distribution.

3 | RESULTS

3.1 | Responses across multiple levels of biological organisation

Following LW restoration, which successfully replicated target environmental conditions (see Supporting Results, Table S6), there was an increase in nodes (species) in restored reach food webs only within the invertebrate assemblages (Table 1; Table S7). These "new" taxa found in the restored reaches, but not in their respective controls, were rare for their size (i.e. they had more negative residuals from the general regression slope when compared with taxa common to all reaches; LM, $F_{1519} = 118.1$, $p < .001$; Figure 3), and there was no difference in this response between restored and target reaches (LM, $F_1 = 0.213$, $p = .64$). Higher invertebrate vulnerability and fish generality revealed that "new" invertebrate taxa also had many potential predators, and their presence in the restored and target reaches was linked to an increase in both intermediate links between invertebrates and the diversity of feeding interactions (i.e. linkage density) within those food webs (Table 1).

The abundance, but not biomass, of *Salmo trutta* increased in restored and target reaches by 186% and 127%, respectively, compared with control reaches (Table 1). Increases in invertebrate abundance and biomass were restricted to LW habitat, irrespective of reach type (Table S5), indicating that the restoration effect was localised, and that increases were similar in magnitude in both, restored and target reaches. Invertebrate abundance across reach types was 102% (GLMM; $z = 5.22$; $p < .001$) and 185% ($z = 7.28$; $p < .001$; Figure S5f) higher in LW vs. mid and edge habitat, respectively, while biomass was 62% (LMM; $z = 2.35$; $p = .048$) and

TABLE 1 Tukey's all-pairwise comparisons of ecological responses between control (Con), target (Tar) and restored (Res) reaches following linear mixed effect model (LMM) Significant findings highlighted in bold

Response	Test	Estimate	*SE*	*z* value	*p*
Number invertebrate nodes	Tar–Con	16.05	2.66	6.03	**<.001**
	Res–Con	14.73	3.05	4.83	**<.001**
	Res–Tar	−1.32	3.43	−0.38	.921
Invertebrate vulnerability	Tar–Con	2.18	0.78	2.81	**.014**
	Res–Con	2.49	0.89	2.78	**.015**
	Res–Tar	0.3	1	0.3	.951
Fish generality	Tar–Con	9.01	2.78	3.24	**.003**
	Res–Con	10.09	3.2	3.16	**.005**
	Res–Tar	1.08	3.59	0.3	.95
Number between invertebrate links	Tar–Con	305.52	54.70	5.59	**<.001**
	Res–Con	301.20	62.82	4.79	**<.001**
	Res–Tar	−4.32	70.46	−0.06	.998
Linkage density	Tar–Con	2.58	0.89	2.89	**.011**
	Res–Con	3.04	1.03	2.96	**.009**
	Res–Tar	0.46	1.15	0.4	.915
Log_{10} (*Salmo trutta* abundance + 1) (100 m^2)	Tar–Con	0.27	0.11	2.54	**.029**
	Res–Con	0.36	0.12	2.90	**.010**
	Res–Tar	0.09	0.14	0.61	.811
Invertebrate α-diversity	Tar–Con	4.96	1.69	2.94	**.009**
	Res–Con	4.61	1.93	2.39	**.044**
	Res–Tar	−0.34	2.17	−0.16	.986

131% ($z = 3.84$; $p < .001$) higher. Fish biomass, the number of diatom and fish nodes, the number of invertebrate upper and lower links, and whole network metrics of connectance, general regression slope and intercept were all similar across reach types (see Tables S7, S8).

3.2 | Transitional responses within restored reaches

Algal biomass was lower (LMM; $z = -3.42$; $p = .002$) and fish abundance was higher in target relative to control reaches (LMM; $z = 2.46$; $p = .036$), and both were intermediate in restored reaches (Figure 4; Table S7). Both invertebrate lower- (LMM; $z = 13.04$; $p < .001$) and upper-link angles increased (LMM; $z = 2.47$; $p = .031$) relative to controls, but not target reaches, indicating the potential for increased biomass flux from basal resources to invertebrates, and subsequently to fish in restored food webs. The significance of our link-angle test results were not affected when we removed invertebrate links unique to each reach (Table S7). These responses suggest that restored reach food webs were in transition, moving from control to target conditions, as biomass was redistributed across the network.

3.3 | Invertebrate community structure

After controlling for differences in abundance (i.e. at base sample size of 1,388), invertebrate α-diversity increased by five species (approximately 9%) in restored and target reaches relative to controls (Table 1, Figure 5a), and this was chiefly due to increases in chironomid taxa (Table S7). Differences in invertebrate assemblages between habitat types (NMDS, $r^2 = 0.28$, $p = .001$) revealed that the addition of LW habitat enhanced overall β-diversity within restored and target reaches relative to controls (Figure 5b, see also Supporting Results, Figure S4; Tables S9,S10).

4 | DISCUSSION

By adopting a MBACI design, we successfully demonstrated the positive causal relationships between LW introduction, invertebrate α-diversity and β-diversity, and linked these with changes across river food webs, from basal resources through to an apex predator, *S. trutta*. The observed consistent ecological responses to restoration across rivers contradict many earlier inferential non-MBACI studies which questioned the link between restoring habitat diversity and increasing biodiversity (e.g. Harrison et al., 2004; Jähnig et al., 2010; Palmer et al., 2010). Moreover, by linking habitat restoration with changes across the food web, our study provides a more holistic system-based view that has been repeatedly called for (Feld et al., 2011; Friberg et al., 2011; Pander & Geist, 2013), and which supports the concept of LW rewilding as a means to recover and conserve river ecosystems degraded by anthropogenic activities.

Analysis of community mass-abundance scaling relationships and food web properties revealed that repopulation following restoration was largely driven by invertebrate taxa rare for their size (i.e. those considered particularly sensitive to deteriorating environmental

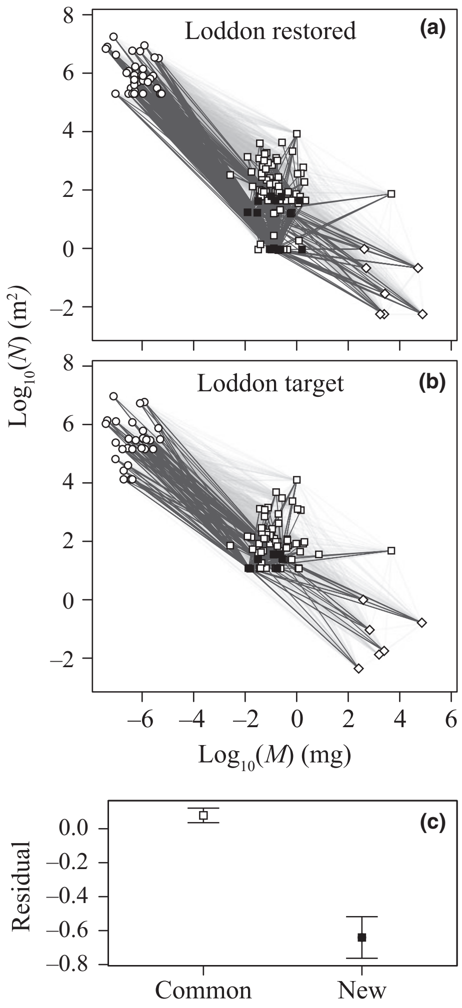

FIGURE 3 Trivariate food webs for the River Loddon, with new invertebrate nodes (black fill) and links (dark grey) highlighted in the (a) restored and (b) target reaches that were not present in the control reaches. Nodes represent mean body mass (*M*) and numerical abundance (*N*) of individual taxa; circles = diatom taxa, squares = invertebrate taxa, diamonds = fish taxa, grey lines = feeding-links. See Figure S3 for all food web plots. Differences in (c) residuals from the general regression slope between invertebrate nodes present in all reaches (common) compared with those found only in restored or target reaches (new) in all rivers. Error bars represent 95% confidence intervals

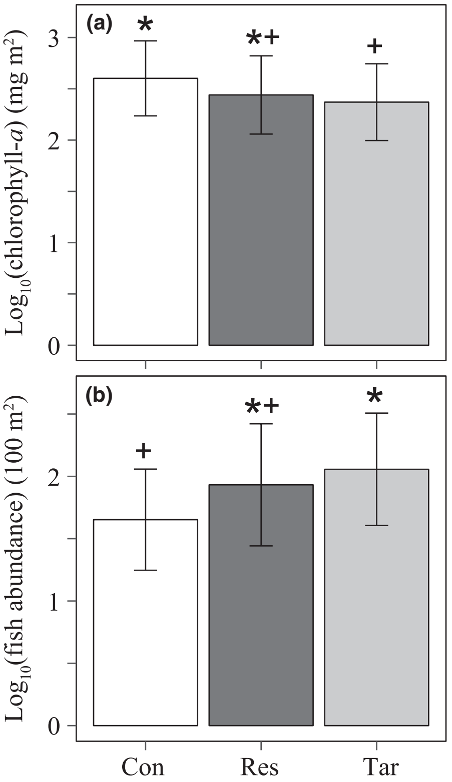

FIGURE 4 Differences in (a) algal biomass (as chlorophyll-*a*) and (b) fish abundance between control (Con), restored (Res) and target (Tar) reaches, evident following linear mixed effect modelling (LMM). Error bars represent 95% confidence intervals, * and + indicate significant differences at the α = 0.05 level

conditions) and with many potential predators. The persistence of these patterns in target reaches indicated that these taxa remained rare despite having had more time to repopulate older target reaches. Our analysis, therefore, provides novel insights into recovery processes across multiple levels of organisation, from individual species populations to the wider food web, and represents a useful new method for assessing the success of ecological restoration.

By using a system-based approach, we can begin to interpret how an increase in invertebrate α-diversity may influence restored ecosystems. First, reaches restored with LW have a higher number of species which may respond differently to fluctuating environmental conditions, and thus could provide higher ecological redundancy than in unrestored reaches (Yachi & Loreau, 1999). Second, the elevated potential for network rewiring via alternative intermediate nodes and the increase in feeding-link diversity may help to conserve species and ecosystem processes in restored webs in the face of environmental change (Lu et al., 2016; Staniczenko, Lewis, Jones, & Reed-Tsochas, 2010; Tylianakis, Laliberté, Nielsen, & Bascompte, 2010). Therefore, river sections rewilded with LW may be both more robust and resilient to environmental stressors. Moreover, because univariate, bivariate and trivariate analyses have allowed the quantification of an array of network responses to environmental stressors in recent years (Layer et al., 2010; O'Gorman et al., 2012; Thompson et al., 2016; Woodward et al., 2012), this more synthetic approach could provide a new and widely applicable means of gauging the ecological impacts of a range of drivers, including habitat restoration, pollution and warming, for example. In light of current and forecast environmental change, this is valuable information for practitioners and stakeholders aiming to focus resources to the most effective conservation interventions.

Our findings complement those of previous studies that have documented increases in economically important salmonid populations following LW restoration (e.g. Cederholm et al., 1997; Kail et al., 2007; Roni et al., 2015). We were able to show that this response was both rapid and persistent, driven by the presence of small *S. trutta* in both the restored and target reaches. This suggests that LW provides refugia or nursery habitat. Our analyses also indicate

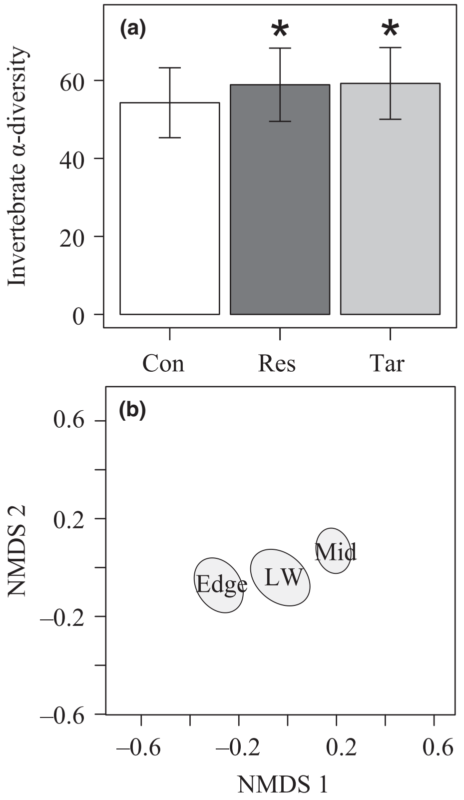

FIGURE 5 Differences in (a) invertebrate α-diversity in control (Con), target (Tar) and restored (Res) reaches (base sample size = 1,388), evident following linear mixed effect model (LMM). Error bars represent 95% confidence intervals. *A significant difference at the $\alpha = 0.05$ level. (b) Within reach differences in invertebrate β-diversity between habitat types using non-metric multidimensional scaling (NMDS) of chord-normalised expected species shared index of dissimilarity (CNESS) dissimilarity ($m = 16$) based on restored and target data represented by *SE* ellipses

that some biotic responses were in transition in the restored reaches. Elevated fish abundance, but not biomass, in the target reaches relative to controls was intermediated in restored reaches suggesting that other fish species, besides *S. trutta*, use LW as refugia or nursery habitat, but this response requires several years to develop. Power (1992) showed that increased habitat complexity, and consequently increased invertebrate abundance via provision of refugia from predation, increased top-down effects of invertebrates on producers. In this study, algal biomass in restored reaches was also intermediate between control and target conditions. This could mean elevated invertebrate populations in target reaches had increased top-down effects on their resources, but that this also takes several years to develop. The shallowing of feeding link angles provides further evidence of transitional effects, as biomass was redistributed across the network in restored reaches, and highlights the potential for increased biomass flux between resources and invertebrates and invertebrates and fishes. These findings pave the way for future experimental investigations using similar methods, combined with measures of ecosystem processes and extended temporal and spatial sampling. Such an approach could investigate: the causes of variation across restorations (e.g. as seen in Figures 4 and 5a, S6); conflicting effects of restoration on biota (e.g. Langford, Langford, & Hawkins, 2012); how restoration alters bottom-up and top-down effects, biomass flux and the distribution of taxa across the food web at the habitat level (e.g. use of LW as refugia and additional substrate by fishes and diatoms, respectively); and how longer-term alterations to restored food web structure (e.g. transient, cyclical or successional assembly dynamics) relate to the spatial and temporal frequency of treefall events.

By using a rigorous MBACI design to establish causative responses, this study contributes substantially to the evidence base that LW rewilding can help to restore human-impacted river ecosystems. Critically, we were able to isolate variation caused by confounding ecological drivers, enabling us to get closer to a mechanistic understanding of ecosystem responses to habitat restoration. If this approach were adopted in future studies, conducted across a range of restoration projects and river systems with extended temporal monitoring, a valuable open-source database of the short- and longer-term outcomes of ecological river restoration could be developed. Such an approach would offer a powerful means of improving understanding of ecological processes, help to mitigate negative human impacts on river ecosystems and enhance global biodiversity conservation.

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AUTHORS' CONTRIBUTIONS

M.T., S.B., C.S. and G.W. conceived the ideas and designed methodology; M.T. collected the data; M.T., J.A., C.G. and D.P. analysed the data; M.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Cefas datahub https://doi.org/10.14466/cefasdatahub.43 (Thompson, 2017).

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