

Does river restoration work? Taxonomic and functional trajectories at two restoration schemes

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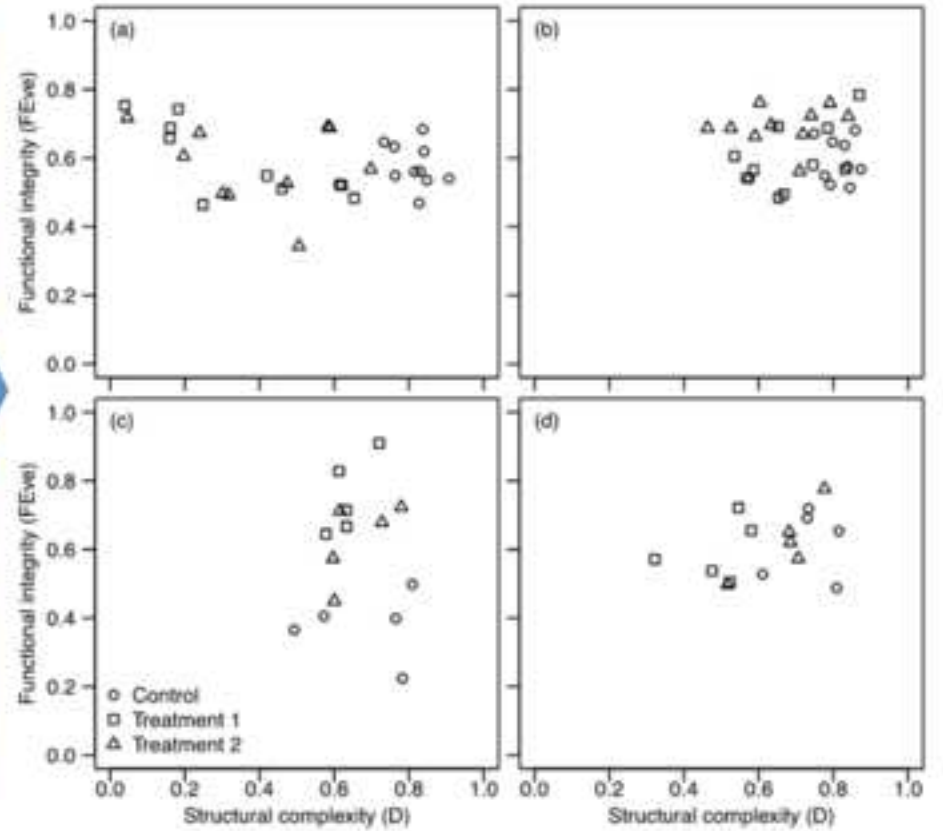
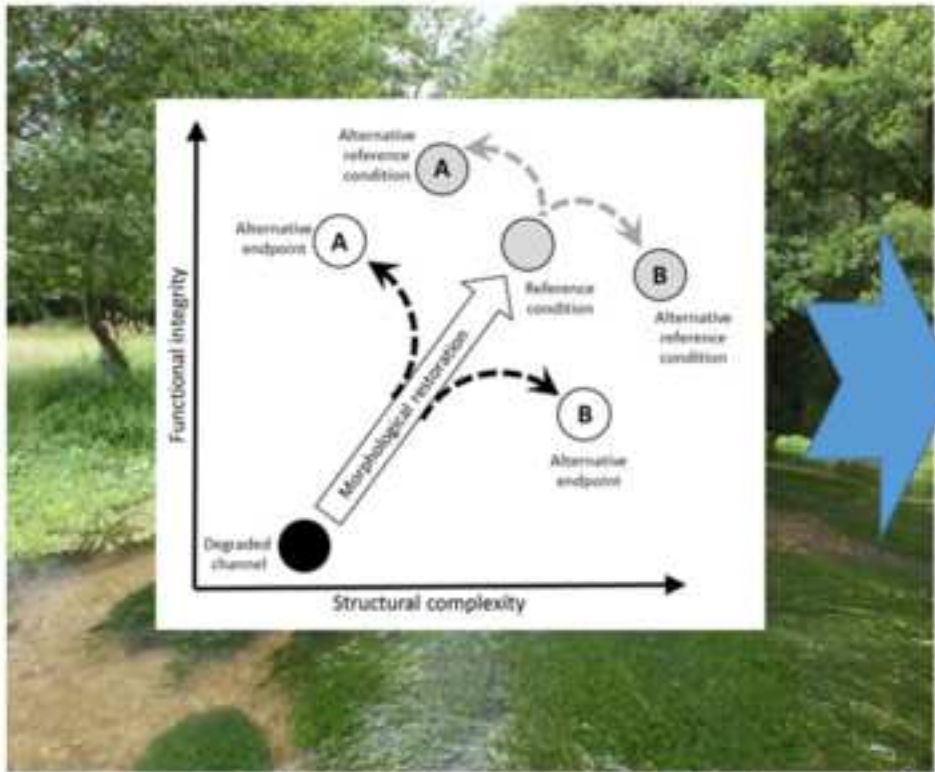
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Highlights

- Restoration of natural process was the aim of two river restoration case studies.
- The projects restored physical habitat composition.
- Rehabilitation of macroinvertebrate structural complexity was limited.
- Restoration of functional integrity was more difficult to achieve.
- Functional traits are useful in evaluating river restoration projects.

Does river restoration work? Taxonomic and functional trajectories at two restoration schemes

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ABSTRACT

Rivers and their floodplains have been severely degraded with increasing global activity and expenditure undertaken on restoration measures to address the degradation. Early restoration schemes focused on habitat creation with mixed ecological success. Part of the lack of ecological success can be attributed to the lack of effective monitoring. The current focus of river restoration practice is the restoration of physical processes and functioning of systems. The ecological assessment of restoration schemes may need to follow the same approach and consider whether schemes restore functional diversity in addition to taxonomic diversity. This paper examines whether two restoration schemes, on lowland UK rivers, restored macroinvertebrate taxonomic and functional (trait) diversity and relates the findings to the Bradshaw's model of ecological restoration. The study schemes are considered a success in terms of restoring physical processes, longitudinal connectivity and the resulting habitat composition. However, the rehabilitation of macroinvertebrate community structure and function was limited and inconsistent, varying over time, depending on the restoration measure applied and the taxonomic or functional index considered. Resampling of species pools at each site revealed a role for functional redundancy, meaning that increases in functional diversity are more difficult to achieve than outcomes based on taxonomic analyses. Our results highlight the usefulness of applying functional traits alongside taxonomic indices in evaluating river restoration projects.

Keywords: river restoration, process based restoration, taxonomic diversity, functional diversity

1. Introduction

Extensive changes to land management and river modifications have substantially changed our river systems (Allan, 2004; Newson, 1992; Petts, 1995). In response to this, recent

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decades have seen river restoration activity documented (e.g. Bernhardt et al., 2005; Smith et al., 2014) with in-stream habitat restoration being the primary focus of many schemes (Bernhardt et al., 2007; Smith et al., 2014). Schemes have often been undertaken on the assumption that restoring physical habitat heterogeneity will increase biodiversity—the “field of dreams” hypothesis: if you build it, they will come (Palmer et al., 1997). However, restoration scheme assessments have reported variable success, with some studies finding limited evidence of ecological benefits to macroinvertebrates (e.g. Feld et al., 2011; Friberg et al., 2014; Haase et al., 2013; Palmer et al., 2010) and others recording positive effects (e.g. Kail et al., 2015; Miller et al., 2010;). The low effectiveness of restoration on macroinvertebrates has been attributed to the limited scale of most restoration projects (Jähnig et al., 2010; Sundermann et al., 2011a), inappropriate design or measures which do not create the habitats and/or spatiotemporal arrangement needed for the life cycles of targeted organisms to be fulfilled (Lepori et al., 2005; Lorenz et al., 2009). To ensure more successful restoration schemes, incorporating process-based principles to re-establish physical, chemical, and biological processes have been proposed to promote the sustainable recovery of dynamic river ecosystems (Beechie et al., 2010). Other reasons for failure may include the lack of consideration as to the importance of dispersal as a driver of stream invertebrate composition (Kitto et al., 2015) and the order in which the species colonise, especially in the context of invasive species (Pander et al., 2016).

Fundamental to the monitoring and assessment of the restoration effectiveness is that we are monitoring the correct elements. The aims and objectives associated with many schemes are based on the underlying assumption that biodiversity will respond predictably to morphological restoration (Miller et al., 2010). Studies, such as Feld et al. (2014), have shown that biodiversity response to hydromorphological degradation was modest, supporting the conclusions reached in previous studies (e.g. Gerisch et al., 2011; Marchant, 2007). This inability to detect hydromorphological pressure impacts through assessing taxonomic diversity questions whether we should use this diversity as a measure to restoration success. However, Ruben et al. (2017)

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suggest that monitoring undertaken with more rigor or over a longer timescale would increase the likelihood of detecting statistically significant increases in diversity. Consideration of how biota in river systems respond to the disturbance of restoration and the recovery pathways that may occur can help us to understand the success or failure of restoration schemes and what are the most appropriate elements to measure to assess these changes.

The classic model of ecological restoration proposed by Bradshaw (1988) considers system trajectories after restoration in two dimensions—structural complexity (e.g. taxonomic composition) and functional integrity (e.g. trait composition) (Fig. 1). The model has been refined since its inception, particularly through the addition of ‘natural development’, i.e. drift in reference conditions over time (Newson and Large, 2006). This importance of catchment processes in understanding trajectories of change is well documented (e.g. Gurnell et al., 2016a) and their relevance to river management noted (Gurnell et al., 2016b; Kail et al., 2016⁵).

Bradshaw’s concept remains a keystone in the theory of ecological restoration and especially river restoration, where a pragmatic objective is to ‘improve’ ecosystem structure and function rather than return a system to some pre-disturbance condition (Brierley et al., 2010; Palmer et al., 2005). Yet, whilst a large number of studies have investigated the response of taxonomic diversity to river restoration, very few have considered functional diversity (FD) (Miller et al., 2010; Palmer et al., 2010). This is important because functional redundancy and community assembly processes mean that FD contains important information not captured by taxonomic assessments alone. Specifically, careful work has shown that FD can be described by three basic aspects (Mason et al., 2005). Firstly, functional richness (FRic) describes the volume of functional space occupied by the community. Secondly, functional divergence (FDiv) or functional dispersion (FDis) are abundance-weighted indices representing the proportion of the community with extreme trait combinations and the mean distance between pairs of taxa in functional space, respectively. Finally, functional evenness (FEve), which describes the regularity of abundances within the total functional space occupied by the community. A fourth type of FD index, Rao’s quadratic entropy (FEnt), contains a

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mixture of information on both the extent of functional space and the distribution of abundances within it (Mouillot et al., 2013).

To test the approach of combining taxonomic and functional diversity to assess trajectories of change, we undertook a detailed assessment of the results of monitoring of the restoration of two lowland rivers in the UK. We addressed the research question: does morphological restoration lead to the recovery of both structure and function?

Since species loss has been associated with degradation in many studies (e.g. Armitage et al., 1995; Feld and Hering, 2007; Friberg, 2010), we hypothesized that restoration would result in increased taxon richness (as found by Miller et al., 2010) and taxonomic diversity (if we assume species diversity is related to habitat heterogeneity, e.g. Ricklefs and Schluter, 1993). In addition, we hypothesized that the response of FRic would be more muted due to redundancy in the traits of colonising taxa. Feld et al. (2014) found redundancy within lowland river systems when assessing hydromorphological degradation, with ecologically similar species replacing those lost through environmental change, and we expected that a similar response may be seen within restoration schemes. We further hypothesised that FDiv, FDis, FEve and FEnt would increase, reflecting the establishment of greater habitat quality and complexity, driving community assembly processes based on niche differentiation (Cadotte et al., 2015).

2. Materials

2.1. Study reaches and field study design

The research focused on two rivers within the River Lee catchment, located north of London, UK (Fig. 2). The schemes selected for study are located on lowland, low-energy rivers (altitude < 75 m; slope < 3 m/km^{0.003}) underlain by chalk. The river restoration projects were selected because they incorporated morphological restoration measures that are commonly

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applied in temperate river systems—the removal of impoundments, narrowing of over-widened channels and the introduction of gravel to compensate for deepening caused by historic dredging. The River Rib restoration scheme incorporated weir lowering to reduce an impoundment and restoration of flowing water conditions to the upper section of the restored reach. The longitudinal profile of the lower section was restored through the introduction of gravel to compensate for over-deepening. The substrate added to the river was “as-dug” gravel from a local gravel pit. The channel was narrowed through the creation of marginal shelves, which were not planted but left to colonise naturally. The River Mimram restoration scheme also incorporated the lowering of a small weir, channel narrowing and the introduction of gravel, however, two types of gravel were incorporated within the restoration scheme: a ‘standard’ size of 40-20 mm and a ‘special’ mixed particle size distribution selected to match the gravel composition found within the river (supplementary material Table S1). Both schemes were designed to restore physical river processes. The sampling design for each scheme was based on a Before-After-Control-Impact (BACI) approach. Within each scheme two impact sites were monitored in addition to a control site. In each case, the control site was selected as the more naturally functioning (least impacted) section of channel, with no discharges or tributaries entering the channel between the sites.

2.2. Stream habitat quality

River Rib

Three reaches were assessed: the control; a site with reduced impoundment (‘drink’); and one within the section of introduced gravel (‘sluice’). Within each of the reaches, a representative 20 m section was mapped using a metre grid system to measure velocity (slack < 10 cm s⁻¹; slow 10-25 cm s⁻¹; moderate 25-50 cm s⁻¹; fast 50-100 cm s⁻¹; and spate >100 cm s⁻¹), depth and

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substrate (cobbles 64-256 mm; gravel 2-64 mm; sand 0.0625-2 mm; and silt < 0.0625m). Detailed measurements of stands of vegetation were made. The vegetation was assessed both as the species present and the vegetation type, classified as emergent narrow leaf vegetation, emergent broad leaf vegetation or submerged vegetation.

River Mimram

For the second scheme, three reaches were also assessed: the control; a site within the section where standard gravel was introduced ('standard'); and a third site where the special mix of gravel was introduced ('special'). At each site, visual assessment of the functional habitat coverage was made (following Harper et al., 1992), average depth measured and substrate compositions visually assessed. Representative substrate composition was measured using the residual from the macroinvertebrate core samples (see section 2.3). Habitat assessments were made and substrate composition assessed in July 1998 prior to the restoration work, two months post-restoration (October 1999) and one (June 2000) and two years (September 2001) following restoration.

2.3. Benthic invertebrate assessment

River Rib

The macroinvertebrate assemblage was assessed at the same three sites ('control', 'drink' and 'sluice'). Within each reach, 10 macroinvertebrate samples were collected using a modified Surber sampler—0.05 m² with a 900 µm mesh net (after Surber, 1937). The location of each sample was determined by the generation of random coordinates. Samples were collected in September 1996 prior to the restoration work and two (September 1998) and three (September

1999) years following restoration. At each sampling point, the near-bed velocity and depth were also measured. All macroinvertebrate samples were sorted in the laboratory and identified to species level (where possible) using standard keys (see Murray-Bligh et al., 1997) with the exception of Chironomidae and Oligochaeta. Abundances (number of individuals per m²) were enumerated for each taxon.

River Mimram

For the second scheme, the macroinvertebrate assemblages were assessed at each of the three sites ('control', 'standard' and 'special') to assess the change in invertebrate composition. Five invertebrate samples were collected on each sampling occasion using a large (25 cm diameter ~ 0.05 m²) metal core by agitating the sediment to a standard depth of 5 cm in order to obtain samples comparable with the samples from the River Rib. Within each core, the substrate was agitated to mobilize the invertebrates and these were collected using a 900 µm mesh net. The location of each core was determined by the generation of random coordinates. At each sampling point, the water depth and near-bed velocity were also measured. Samples were collected in September 1998 and July 1999 prior to the restoration work, in October 1999 (two months post-restoration) and one (June 2000) and two years (September 2001) following restoration.

2.4. Data analysis

For each of the samples, species diversity, (Simpson's D, after Simpson, 1949), density (individuals per m²) and taxon richness were calculated. To calculate FD, information from the widely-used database of Tachet et al. (2010) was combined with the well-established distance-based functional diversity (dbFD) approach of Laliberté and Legendre (2010) using the dbFD function in R 3.2.3 (R Core Team, 2015). This focused on 63 individual trait modalities across 11

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fuzzy coded categories of 'true' traits (Statzner & Běche 2010; Verberk et al. 2013), incorporating body length, life cycle duration, voltinism, aquatic life stages, reproduction mode, dispersal mode, resistance forms, respiration mode, locomotion or relation to the substrate, diet and feeding mode. The traits were applied at the same taxonomic level at which taxa were identified or the lowest resolution provided within Tachet et al. (2010). Details of the taxa and traits applied are presented within Table S2. Varying fuzzy coding levels between trait categories were controlled by expressing trait values as percentages within each trait category. For example, if a taxon had a fuzzy score of 1 for both annual and perennial life cycle durations, this was expressed the trait values as 50% for each of the two trait modalities within the life cycle duration category. The full trait database used can be found in the Supplementary Material online (Table S2). In calculating the five commonly reported FD indices (FRic, FDiv, FDis, FEve, FEnt), the maximum number of synthetic trait axes that allowed the number of taxa > number of traits condition to be maintained were used. FRic was standardised by dividing through the maximum FRic of a hypothetical community containing all species observed at a site (i.e. River Rib, River Mimram) throughout the whole study period.

To explore trends in the results, boxplots and correlation matrices were created. Possible differences between sites and sampling occasions were analysed using a two-way ANOVA followed by Bonferroni-corrected pairwise t-tests when the time * site interaction was significant. To further analyse the relationship between taxonomic and functional diversity, we randomly sampled (without replacement) taxa from the species pool at each site and calculated standardised FRic at values of taxon richness ranging from one to the total number of taxa in the species pool. This resulted in a null distribution of FRic for each value of taxon richness. Because macroinvertebrates were sampled from a variety of habitats at the River Rib, the random sampling was stratified by dominant substrate size category, defining two separate species pools for gravel and sand habitats. Other habitat types (i.e. silt) were not included since there were too few samples. The two restoration schemes assessments have a different number of samples per site

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(Rib 10 and Mimram 5). To avoid comparing different sampling efforts, comparisons were made within a scheme rather than between schemes. All analyses were performed in R 3.2.3 (R Core Team, 2015).

3. Results

3.1. Stream habitat quality

River Rib

The depth profiles, vegetation and velocity contour maps are shown in Fig. S1 and S2. Prior to the restoration work the 'drink' site had a deep homogenous channel with a uniform depth averaging 65 and 77 cm during June and September 1996. At the time of the post-project appraisal, the channel was shallower and more heterogeneous, reflecting the reduced impoundment, averaging 16 and 27 cm deep (t-test; significant at $P < 0.001$). Similarly, the 'sluice' site was a uniform trapezoidal channel averaging 45 and 39 cm deep during the baseline survey changing to a more heterogeneous, shallower depth averaging 28 and 24 cm reflecting the reduced impoundment and introduction of gravel to restore the longitudinal profile (t-test; significant at $P < 0.05$). The control site showed little variation in depth through the different surveys, averaging 11 cm deep on each occasion. The control site remained the shallowest of sites within the survey. A summary of the habitat composition in terms of flowing water functional habitat and substrate composition is presented in Fig. S3.

River Mimram

The functional habitat composition for the Mimram sites is presented in Fig. S4. Prior to the restoration the channel was over-wide and deep as a result of channelization and historic dredging. The scheme reduced the channel width and raised the bed level to reinstate the longitudinal profile, creating a shallower, more heterogeneous channel. The control site showed little variation through the different surveys. Changes in substrate composition over time were examined using the particle size data collected from the core samples and are presented in Fig. S5. The results from the baseline survey confirm that the substrate within the section of channel selected for restoration was dominated by fine sediment. By contrast, the control site showed a more mixed substrate composition. The first post-project appraisal showed the change in substrate as a result of the restoration work with the standard substrate still dominating where it had been placed and the special gravel showing a more mixed substrate. Although the special gravel introduced aimed to mimic the natural substrate within the channel, the substrate lacked some of the finer sediment particles (sand and fine gravel) found within the river. At the time of the second post-project appraisal there was a slight change in the sediment as a result of geomorphological processes moving finer sediment down the channel. This change resulted in the special gravel sediment being comparable with that of the control site as seen by the overlapping grain-size distribution curves. Circumstances were similar during the third post-project appraisal. This demonstrates that the intention of the restoration to recreate the natural substrate composition within the restoration scheme was successful where the special gravel was introduced but that little sediment transport in the river meant that the standard gravel remained dominated by a uniform size.

3.2. Invertebrate communities

Taxonomic and functional diversity indices are presented in Fig. 3 with comparisons using paired t-tests given in Tables 1 and 2. Results of two-way ANOVA tests revealed significant time *

treatment interactions for all indices except FEve in the River Rib (Table S3) and FDiv in the River Mimram (Table S4). In the River Rib, most taxonomic and functional indices suggested that the pre-restoration conditions for both treatments were significantly degraded with reference to the control site. During the post-project surveys, diversity, FDis and FEent were comparable with the control site suggesting some success from the restoration scheme. However, by the second sampling occasion (1999), the values of other indices were lower in at least one treatment site than in the control site. For example, taxon richness and FRic were significantly lower in the 'drink' site and FDiv was significantly lower in the 'sluice' site. Similar post-restoration results were observed for the River Mimram, where diversity, FRic, FDis and FEent fluctuated. Pre-restoration, there were no significant differences between treatment sites and the controls for diversity, density, FDis and FEent in the River Mimram.

Jaccard and Bray-Curtis similarities (Anderson et al., 2011) indicated that communities in restored sites initially became more similar to the corresponding control sites (Fig. 4). However, communities of both treatments on the River Rib and the special gravel treatment on the Mimram later diverged from the control communities.

Correlation matrices (Figs. S6, S7) indicated close correlations between taxon richness and FRic, and between Simpson's diversity and FDis. FEent was almost perfectly correlated with FDis (for this reason FEent is excluded from the boxplots in Fig. 3). Two indices were selected for further comparison: Simpson's diversity (structural complexity) and FEve (functional integrity), since they were relatively independent and incorporate information on both taxon occurrence and abundance (Fig. 5). Furthermore, FEve is suitable for indexing functional integrity since higher values reflect a more even distribution of niches, which has been linked to greater response diversity, and hence resilience, in a variety of ecosystems (Joseph et al., 2015; Morelli et al., 2017; Schriever et al., 2015). In the River Rib, the results show that restoration was successful in terms of moving restoration sites along the structural axis towards control sites, but there was relatively

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little vertical movement along the functional axis, suggesting that while taxonomic diversity was restored in comparison with the control sites, functional integrity was not. In the River Mimram, structural complexity was initially similar between control and pre-restored treatment sites. Three years after restoration, treatments and the control had converged along the functional axis, with a tendency for the functional integrity of treatment sites to decline. In both cases the treatment samples moved closer to the control samples after restoration work suggesting that the restored section was more similar to the control section and that the schemes can be considered a partial success.

Although taxon richness and FRic were closely correlated ($R \sim 0.8$) (Figs. S6, S7), random sampling from species pools showed that many samples had FRic values significantly lower than expected at random for a given taxon richness (Fig. 6.), demonstrating the occurrence of functional redundancy. The effect is stronger for the River Rib. In the River Mimram, the tendency for FRic to be significantly lower than expected increased with time since restoration (Fig. 6c).

4. Discussion

The assessment of the habitat composition of the restoration sites following the implementation of the morphological restoration shows that the schemes had been successful in creating a habitat composition comparable with the control sites. Mesohabitat assessment has been used as a cost-effective way to link ecology with morphology and hydrology in river channel restoration (Kemp et al., 1999). However, to demonstrate restoration success, the macroinvertebrate assemblages in relation to habitat composition must be considered.

4.1. Community response to restoration

This study demonstrated that, following morphological restoration measures, 'recovery', as defined by community indices, was largely incomplete and inconsistent in terms of treatment and taxonomic/functional index. Thus, there is no support for our hypothesis that FDiv, FDis, FEve and FEnt would increase, reflecting the establishment of greater habitat quality and complexity. These results are consistent with other studies which indicate variable response of benthic invertebrates to morphological restoration measures (e.g. Friberg et al., 2014; Jähnig et al., 2008; Leps et al., 2016; Palmer et al., 2010,)), and that traditional diversity indices may not be an appropriate measure of hydromorphological quality (Feld et al., 2014). Verdonschot et al. (2016) found that the general lack of the effect of restoration on microhabitat composition and diversity could be a key factor explaining the lack of response in the overall comparisons of the selected macroinvertebrate metrics they examined. They also concluded that several of the functional trait relationships they found were not detected using the taxonomic metrics. This emphasises the importance of considering functional indices in addition to structural indices and is supported by our findings.

This study found that there was a general tendency for taxa occurrences and abundances to become more similar between treatments and their corresponding controls over time, yet by the end of the study period treatment communities were only around 60% similar to controls. This also indicates that 'recovery', defined in terms of species identity and community structure, was largely incomplete, which may reflect the relatively short timescale of the monitoring and a time-lag in the ecological recovery as the restored sites adjust (Jones and Schmitz, 2009; Winking et al., 2014). Whilst restoration age is a crucial factor to consider when monitoring the results of restoration on riverine communities (Bash and Ryan, 2002), it may not be the ultimate reason for missing community recovery (Leps et al., 2016) and over time, restoration effects may vanish (Kail et al., 2016, 2015). The loss of restoration effects is often associated with unsustainable restoration that does not work with natural processes (Beechie et al., 2010); the combined influence of both local and regional hydromorphological quality (Leps et al., 2016) or not in keeping with catchment

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processes (Gurnell et al., 2016b). Miller et al. (2010), in their meta-analysis of in-stream habitat restoration projects, found that within 1 year of restoration, significant, positive effects on macroinvertebrate richness and inconclusive effects on density could be detected. Within this study the sources of colonists for the restoration schemes were in close proximity, so are unlikely to be a restricting factor. However, the pattern of initial colonisation is important (Pander et al., 2016) with strong dispersers known to colonise first and with species with low dispersal capacity needed longer time ~~reducing over time as weak dispersers continue~~ to colonise (Li et al., 2016).

These continuing adjustments could explain the incomplete recovery within this study.

When considering results from the River Rib in the context of Bradshaw's classic model of ecological restoration, the treatment sites moved further along the structural complexity axis than the functional integrity axis, suggesting that it is more challenging to achieve functional rehabilitation. This may indicate that the control sites are not true reference sites but are also subject to stressors; the treatment samples had a similar functional integrity to the control site prior to the restoration work supporting the notion that the control site was subject to other stressors. Following restoration we may have expected functional integrity at the restored site to exceed that of the control. This may mean that other stressors, maybe acting at a catchment scale, are continuing to limit functional integrity throughout the river. When undertaking restoration measures, it is important that catchment processes are considered, both from a physical (Gurnell et al., 2016a, 2016b) and ecological perspective (e.g. Leps et al., 2016). This is more likely to ensure that the restoration measures will be successful and a realistic target endpoint is identified which may deviate from the original reference condition. Not establishing reference condition benchmarks and evaluation endpoints against which to measure success is one of the common

problems or reasons for restoration project failure identified by Cowx et al. (20152013). In addition to considering the endpoints, it is important to understand the degraded nature of the system identified for restoration and their context within the catchment since they may influence the extent and pathway of recovery. Provided there is a suitable connectivity with an intact

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species pool, more degraded ecosystems are more likely to show the greatest responses (Miller et al., 2010). However, if the ecosystem had entered an alternative state, this may preclude recovery (Jones and Schmitz, 2009) and is more likely to result in an alternative endpoint.

We hypothesized that restoration would result in increased taxon richness and taxonomic diversity but that the response of FRic would be more muted due to redundancy in the traits of colonising taxa. Whilst we found little support for the first part of this hypothesis, results of random sampling from carefully defined species pools (Fig. 6) suggested that it is more difficult to increase functional diversity than taxonomic diversity because there is often significant functional redundancy. As taxon richness increases, the probability of colonisation by a species with a different or unique trait profile decreases (Petchey and Gaston, 2002). The fact that this effect was stronger in the River Rib may reflect a greater role for environmental filtering at this site (Poff, 1997). We defined two sets of species pools based on substrate composition for the River Rib because communities of sand habitats were a subset of those of gravel habitats, leading to inflation of null distributions of FRic when both substrates were lumped together. However, macroinvertebrates also have discrete distributions with respect to hydraulics (Doledec et al., 2007), yet we did not define separate species pools based on discrete categories of water depth and velocity, which were varied in the River Rib, especially after restoration (Supplementary Material). This could partially explain the results, but given our use of the occurrence-based FRic index, as well as the strong role played by mass effects in lotic macroinvertebrates (Stoll et al., 2016), it is likely that our results reflect true functional redundancy at the mesohabitat scale studied. Functional redundancy was also noted by Feld et al. (2014) when assessing hydromorphological degradation across Europe, supporting our conclusion.

4.2. Does morphological restoration lead to the recovery of both structure and function?

Overall, our findings suggest there was limited restoration success in both schemes and that neither structure nor function were successfully restored within the timescale of the monitoring. Furthermore, the application of the 'Bradshaw model' to our results and our resampling of the species pool revealed that functional rehabilitation is more difficult to achieve than structural improvement. Functional measures have proved successful in detecting hydromorphological pressure at different spatial scales (Feld and Hering, 2007) and our findings support the recommendation that functional indices are used alongside structural indices in the assessment of river restoration schemes (Kail et al., 2016, 2015; Mouchet et al., 2010; Watts and Mason, 2015). Their routine use in future evaluations of restoration schemes may help us to investigate the effect of measures and to infer causal relationships (Kail et al. 2016), identify barriers to full restoration of community composition (Watts and Mason, 2015), help us to understand how biodiversity interacts with ecosystem processes and environmental constraints (Mouchet et al., 2010) and identify effective restoration measures (Muhar et al., 2016). Greater insight may be provided by considering trait identity, rather than only trait diversity (Vandewalle et al., 2010), multiple rather than single traits (Piliere et al., 2016), the refinement and development of trait databases (Wilkes et al., 2017) and application across larger spatial scales where trait-based measures are more consistent than taxonomic measures (Pollard and Yuan, 2010). However, assessment should not be restricted to biological indices alone (Geist and Hawkins, 2016) and it is important to quantitatively measure habitat heterogeneity changes (Rubien et al., 2017).

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5. Conclusions

The results of our work support the conclusions of Feld et al. (2014) that traditional whole-community-based taxonomic diversity indices are not the ideal measures to detect and assess the various aspects of biodiversity loss. We recommend that both functional and structural diversity

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are measured, allowing the trajectories of change within the communities to be tracked. Monitoring may need to be undertaken over a longer timescale which increases the likelihood of detecting statistically significant increases in diversity (Rubin et al., 2017). The development and testing of novel indicators of biodiversity, capable of detecting biodiversity changes in response to hydromorphological degradation (Feld et al., 2014) and subsequent restoration, should be a priority. An increasingly structured approach to monitoring and appraisal of restoration schemes, which implements rigorous study designs, monitoring abiotic and biotic changes including functional approaches and following a multiple BACI approach, is to be encouraged, so that lessons can be learnt from successes and failures to inform best practice (Bernhardt et al., 2005; Geist and Hawkins, 2016; Miller et al., 2010). Understanding the catchment context and applying long-term monitoring will allow a better understanding of trajectories of change caused by restoration measures and to identify which measures are sustainable (Gurnell et al., 2016a, 2016b; Kail et al., (2016)2015).

Comment [A35]: Lacking in the list of references.

Comment [A36]: Spelling corrected to Rubin

Comment [A37]: Lacking in the list of references.

Comment [A38]: Corrected to Kail et al. 2015

Acknowledgements

We thank Richard Chadd for his helpful comments on the draft of this paper. We are very grateful to the two anonymous reviewers whose comments have helped us improve our manuscript. The views expressed in this paper are those of the authors and do not necessarily represent the views of their organizations.

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Comment [A45]: Add information about DOI.

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Comment [A47]: Add information about DOI.

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Field Code Changed

Comment [A49]: Abandon this old-fashioned doi which will take half a page to publish.

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Comment [A57]: It is unclear whether these are two positions (Murray-Bligh et al. 1997 and ISO 2012) or Murray-Bligh et al. 1997 is cited after ISO 2012. Please clarify.

Comment [A58]: Additional text included in error – this has been deleted.

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Figure captions:

Fig. 1. A general model of ecological restoration, including shifting reference conditions. Adapted from Newson and Large (2006), [reproduced with permission of Wiley](#), after Bradshaw (1988).

Fig. 2. Location of the restoration projects.

Fig. 3. Boxplots of taxonomic and functional diversity results from the River Rib (left diagrams) and the River Mimram (right diagrams). For the River Rib, treatment 1 was the 'drink' site (D) and treatment 2 was the 'sluice' site (S). For the Mimram, treatment 1 was the 'special' gravel (spc) and treatment 2 was the 'standard' gravel (std). [Horizontal lines show medians, boxes show the interquartile range, whiskers the range \(up to 1.5 times the interquartile range\), and closed circles denote outliers beyond 1.5 times the interquartile range.](#)

Fig. 4. [Comparison of](#) Jaccard and Bray-Curtis similarity [indices](#) within the River Rib (a, b) and the River Mimram (c, d).

Fig. 5. 'Bradshaw plots' comparing structural complexity (Simpson's diversity, D against functional integrity (functional evenness, FEve) for the two restoration schemes. Symbols represent replicates from the River Rib (a, b) and the Mimram (c, d) pre-restoration (a, c) and three years' post-restoration (b, d). For the River Rib, treatment 1 was the 'drink' site and treatment 2 was the 'sluice' site. For the Mimram, treatment 1 was the 'special' gravel and treatment 2 was the 'standard' gravel.

Fig. 6. Taxon richness in comparison with functional richness (FRic) of sample replicates in restored sites for the River Rib gravel habitats (a), sand habitats (b) and the River Mimram (c).

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Confidence intervals from random sampling of FRic are shown for a given taxon richness. Dashed lines represent the mean of null distributions. For the River Rib, treatment 1 was the 'drink' site and treatment 2 was the 'sluice' site. For the Mimram, treatment 1 was the 'special' gravel and treatment 2 was the 'standard' gravel.

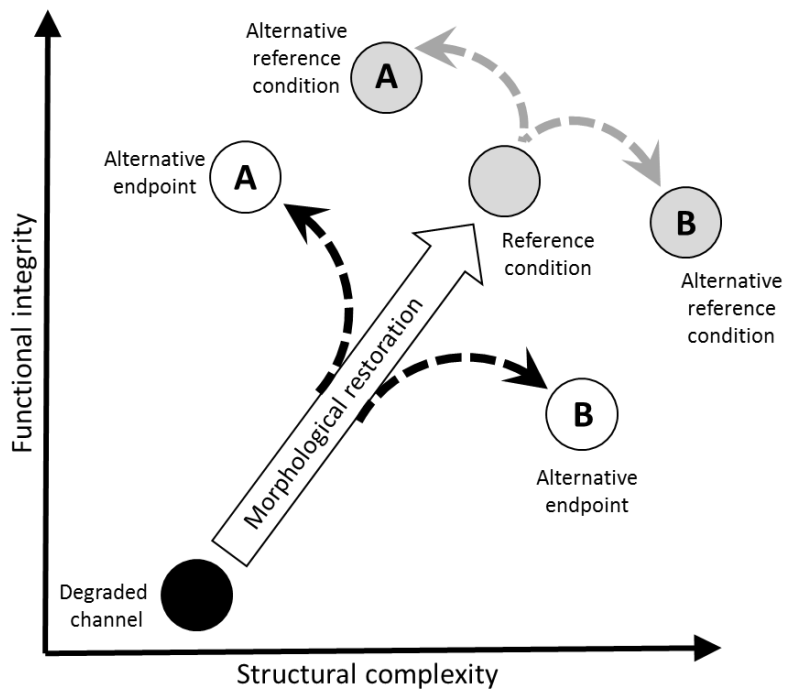


Fig. 1. A general model of ecological restoration, including shifting reference conditions. Adapted from Newson and Large (2006), reproduced with permission of Wiley, after Bradshaw (1988).

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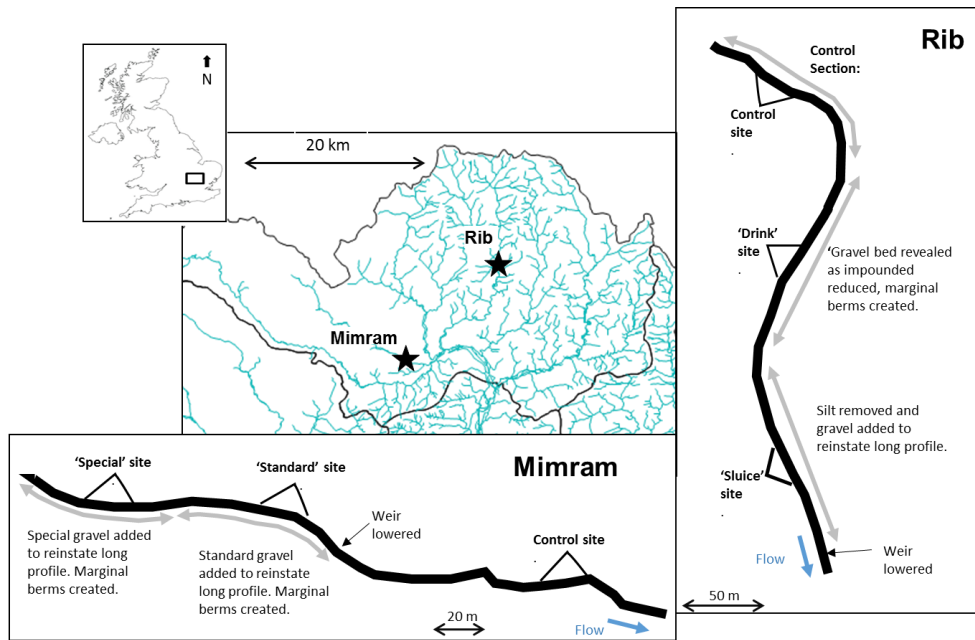


Fig. 2. Location of the restoration projects.

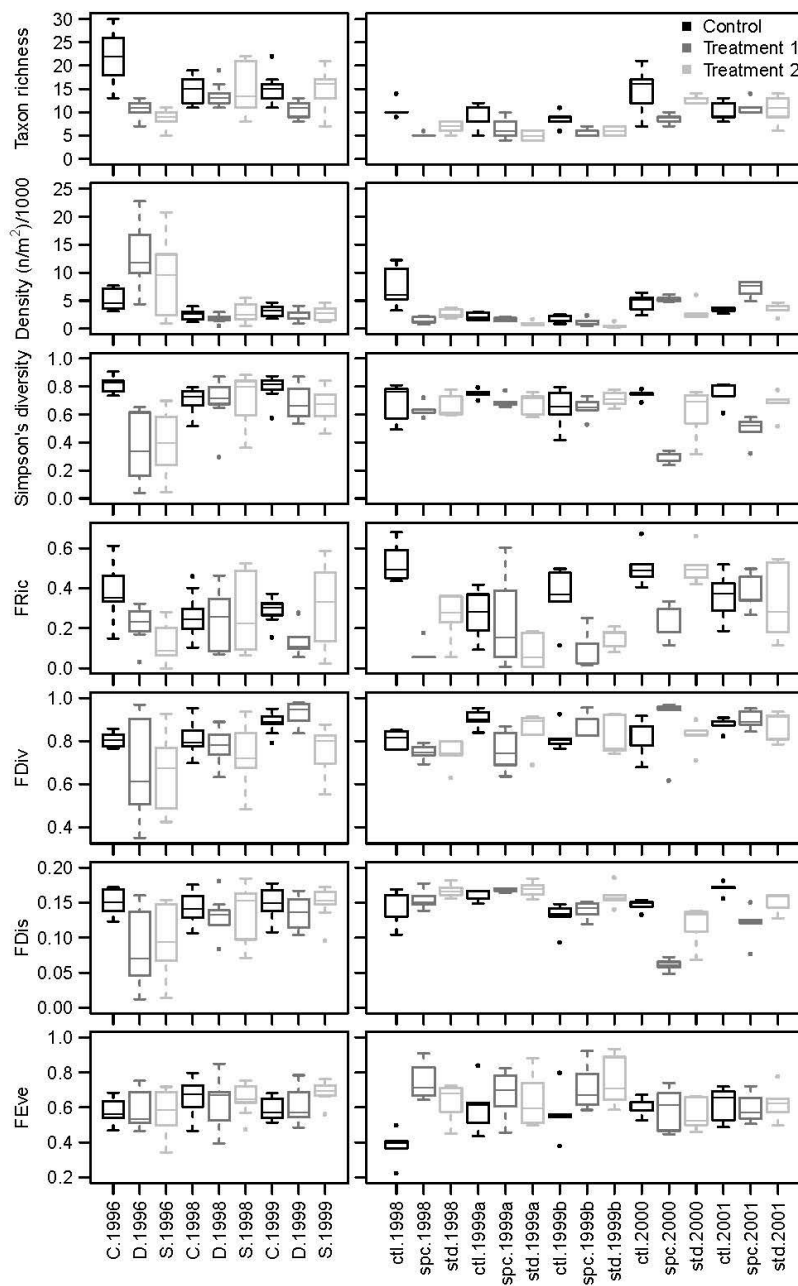


Fig. 3. Boxplots of taxonomic and functional diversity results from the River Rib (left diagrams) and the River Mimram (right diagrams). For the River Rib, treatment 1 was the ‘drink’ site (D) and treatment 2 was the ‘sluice’ site (S). For the Mimram, treatment 1 was the ‘special’ gravel (spc) and treatment 2 was the ‘standard’ gravel (std). Horizontal lines show medians, boxes show the

Comment [A75]: The paper will be published in electronic form in colour and in printed form in greyscale. However, the colours used here are not distinguishable when the figure is printed in greyscale. Please modify colours so as to obtain visibility in greyscale (e.g. black and two colours that yield ca. 70% and 30% black when changed to greyscale).

Comment [A76]: See new grayscale version pdf

Comment [A77]: Add a sentence explaining elements of the boxplots. This is necessary because particular elements may have different meaning (for instance, the line inside boxes may indicate either mean or median). I also suggest to use solid rather than dashed line for whiskers.

Comment [A78]: Sentence added to improve clarity

interquartile range, whiskers the range (up to 1.5 times the interquartile range), and closed circles denote outliers beyond 1.5 times the interquartile range.

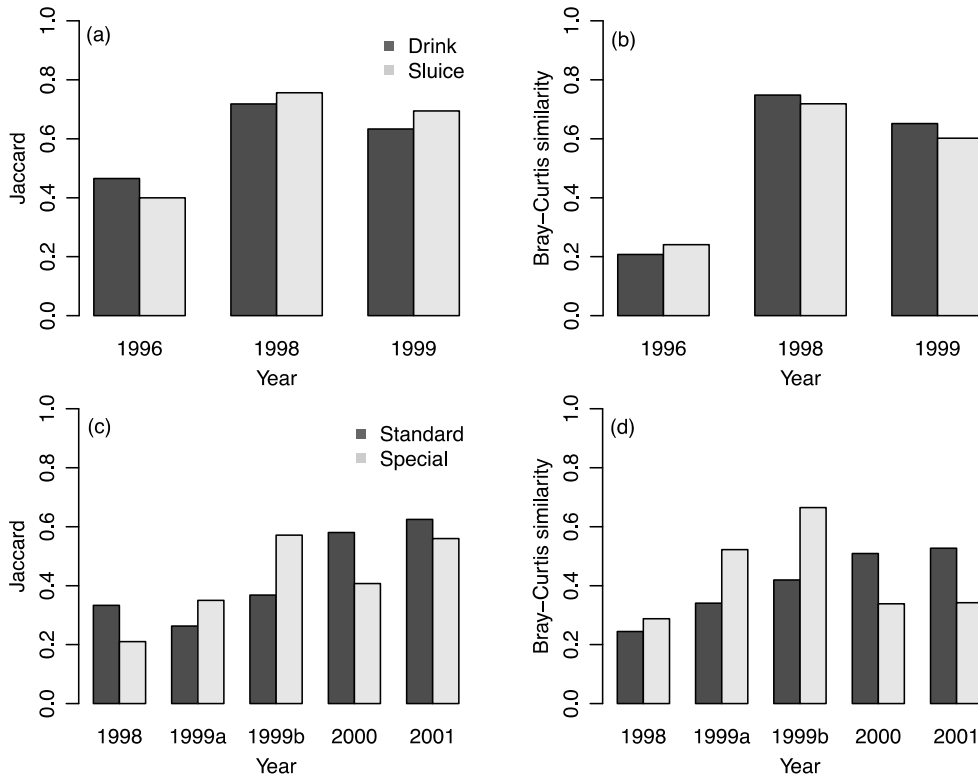


Fig. 4. Comparison of Jaccard and Bray-Curtis similarity coefficients/indices within the River Rib (a, b) and the River Mimram (c, d).

Comment [A79]: Similarity of what? Please complete the sentence.

Comment [A80]: Text amended to improve clarity. Also added a reference in the text for background on similarity indices (Anderson et al., 2011).

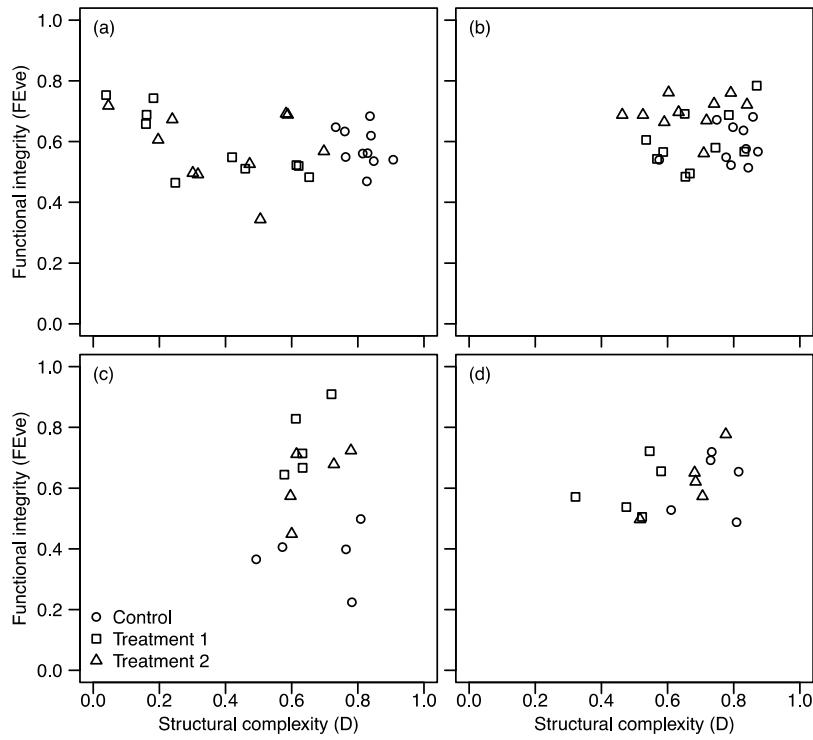


Fig. 5. ‘Bradshaw plots’ comparing structural complexity (Simpson’s diversity, D against functional integrity (functional evenness, FEve) for the two restoration schemes. Symbols represent replicates from the River Rib (a, b) and the Mimram (c, d) pre-restoration (a, c) and three years’ post-restoration (b, d). For the River Rib, treatment 1 was the ‘drink’ site and treatment 2 was the ‘sluice’ site. For the Mimram, treatment 1 was the ‘special’ gravel and treatment 2 was the ‘standard’ gravel.

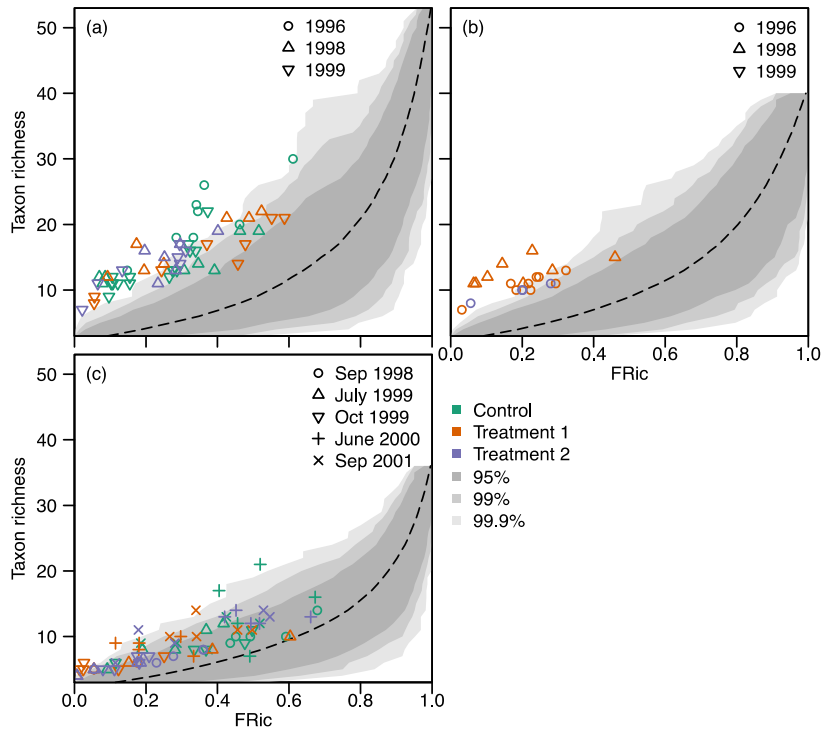


Fig. 6. Taxon richness in comparison with functional richness (FRic) of sample replicates in restored sites for the River Rib gravel habitats (a), sand habitats (b) and the River Mimram (c). Confidence intervals from random sampling of FRic are shown for a given taxon richness. Dashed lines represent the mean of null distributions. For the River Rib, treatment 1 was the ‘drink’ site and treatment 2 was the ‘sluice’ site. For the Mimram, treatment 1 was the ‘special’ gravel and treatment 2 was the ‘standard’ gravel.

Does river restoration work? Taxonomic and functional trajectories at two restoration schemes

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ABSTRACT

Rivers and their floodplains have been severely degraded with increasing global activity and expenditure undertaken on restoration measures to address the degradation. Early restoration schemes focused on habitat creation with mixed ecological success. Part of the lack of ecological success can be attributed to the lack of effective monitoring. The current focus of river restoration practice is the restoration of physical processes and functioning of systems. The ecological assessment of restoration schemes may need to follow the same approach and consider whether schemes restore functional diversity in addition to taxonomic diversity. This paper examines whether two restoration schemes, on lowland UK rivers, restored macroinvertebrate taxonomic and functional (trait) diversity and relates the findings to the Bradshaw's model of ecological restoration. The study schemes are considered a success in terms of restoring physical processes, longitudinal connectivity and the resulting habitat composition. However, the rehabilitation of macroinvertebrate community structure and function was limited and inconsistent, varying over time, depending on the restoration measure applied and the taxonomic or functional index considered. Resampling of species pools at each site revealed a role for functional redundancy, meaning that increases in functional diversity are more difficult to achieve than outcomes based on taxonomic analyses. Our results highlight the usefulness of applying functional traits alongside taxonomic indices in evaluating river restoration projects.

Keywords: river restoration, process based restoration, taxonomic diversity, functional diversity

1. Introduction

Extensive changes to land management and river modifications have substantially changed our river systems (Allan, 2004; Newson, 1992; Petts, 1995). In response to this, recent

decades have seen river restoration activity documented (e.g. Bernhardt et al., 2005; Smith et al., 2014) with in-stream habitat restoration being the primary focus of many schemes (Bernhardt et al., 2007; Smith et al., 2014). Schemes have often been undertaken on the assumption that restoring physical habitat heterogeneity will increase biodiversity—the “field of dreams” hypothesis: if you build it, they will come (Palmer et al., 1997). However, restoration scheme assessments have reported variable success, with some studies finding limited evidence of ecological benefits to macroinvertebrates (e.g. Feld et al., 2011; Friberg et al., 2014; Haase et al., 2013; Palmer et al., 2010) and others recording positive effects (e.g. Kail et al., 2015; Miller et al., 2010;). The low effectiveness of restoration on macroinvertebrates has been attributed to the limited scale of most restoration projects (Jähnig et al., 2010; Sundermann et al., 2011), inappropriate design or measures which do not create the habitats and/or spatiotemporal arrangement needed for the life cycles of targeted organisms to be fulfilled (Lepori et al., 2005; Lorenz et al., 2009). To ensure more successful restoration schemes, incorporating process-based principles to re-establish physical, chemical, and biological processes have been proposed to promote the sustainable recovery of dynamic river ecosystems (Beechie et al., 2010). Other reasons for failure may include the lack of consideration as to the importance of dispersal as a driver of stream invertebrate composition (Kitto et al., 2015) and the order in which the species colonise, especially in the context of invasive species (Pander et al., 2016).

Fundamental to the monitoring and assessment of the restoration effectiveness is that we are monitoring the correct elements. The aims and objectives associated with many schemes are based on the underlying assumption that biodiversity will respond predictably to morphological restoration (Miller et al., 2010). Studies, such as Feld et al. (2014), have shown that biodiversity response to hydromorphological degradation was modest, supporting the conclusions reached in previous studies (e.g. Gerisch et al., 2011; Marchant, 2007). This inability to detect hydromorphological pressure impacts through assessing taxonomic diversity questions whether we should use diversity as a measure to restoration success. However, Ruben et al. (2017) suggest

that monitoring undertaken with more rigor or over a longer timescale would increase the likelihood of detecting statistically significant increases in diversity. Consideration of how biota in river systems respond to the disturbance of restoration and the recovery pathways that may occur can help us to understand the success or failure of restoration schemes and what are the most appropriate elements to measure to assess these changes.

The classic model of ecological restoration proposed by Bradshaw (1988) considers system trajectories after restoration in two dimensions—structural complexity (e.g. taxonomic composition) and functional integrity (e.g. trait composition) (Fig. 1). The model has been refined since its inception, particularly through the addition of ‘natural development’, i.e. drift in reference conditions over time (Newson and Large, 2006). This importance of catchment processes in understanding trajectories of change is well documented (e.g. Gurnell et al., 2016a) and their relevance to river management noted (Gurnell et al., 2016b; Kail et al., 2015). Bradshaw’s concept remains a keystone in the theory of ecological restoration and especially river restoration, where a pragmatic objective is to ‘improve’ ecosystem structure and function rather than return a system to some pre-disturbance condition (Brierley et al., 2010; Palmer et al., 2005). Yet, whilst a large number of studies have investigated the response of taxonomic diversity to river restoration, very few have considered functional diversity (FD) (Miller et al., 2010; Palmer et al., 2010). This is important because functional redundancy and community assembly processes mean that FD contains important information not captured by taxonomic assessments alone. Specifically, careful work has shown that FD can be described by three basic aspects (Mason et al., 2005). Firstly, functional richness (FRic) describes the volume of functional space occupied by the community. Secondly, functional divergence (FDiv) or functional dispersion (FDis) are abundance-weighted indices representing the proportion of the community with extreme trait combinations and the mean distance between pairs of taxa in functional space, respectively. Finally, functional evenness (FEve), which describes the regularity of abundances within the total functional space occupied by the community. A fourth type of FD index, Rao’s quadratic entropy (FEnt), contains a

mixture of information on both the extent of functional space and the distribution of abundances within it (Mouillot et al., 2013).

To test the approach of combining taxonomic and functional diversity to assess trajectories of change, we undertook a detailed assessment of the results of monitoring of the restoration of two lowland rivers in the UK. We addressed the research question: does morphological restoration lead to the recovery of both structure and function?

Since species loss has been associated with degradation in many studies (e.g. Armitage et al., 1995; Feld and Hering, 2007; Friberg, 2010), we hypothesized that restoration would result in increased taxon richness (as found by Miller et al., 2010) and taxonomic diversity (if we assume species diversity is related to habitat heterogeneity, e.g. Ricklefs and Schluter, 1993). In addition, we hypothesized that the response of FRic would be more muted due to redundancy in the traits of colonising taxa. Feld et al. (2014) found redundancy within lowland river systems when assessing hydromorphological degradation, with ecologically similar species replacing those lost through environmental change, and we expected that a similar response may be seen within restoration schemes. We further hypothesised that FDiv, FDis, FEve and FEnt would increase, reflecting the establishment of greater habitat quality and complexity, driving community assembly processes based on niche differentiation (Cadotte et al., 2015).

2. Materials

2.1. Study reaches and field study design

The research focused on two rivers within the River Lee catchment, located north of London, UK (Fig. 2). The schemes selected for study are located on lowland, low-energy rivers (altitude < 75 m; slope 0.003) underlain by chalk. The river restoration projects were selected because they incorporated morphological restoration measures that are commonly applied in

temperate river systems—the removal of impoundments, narrowing of over-widened channels and the introduction of gravel to compensate for deepening caused by historic dredging. The River Rib restoration scheme incorporated weir lowering to reduce an impoundment and restoration of flowing water conditions to the upper section of the restored reach. The longitudinal profile of the lower section was restored through the introduction of gravel to compensate for over-deepening. The substrate added to the river was “as-dug” gravel from a local gravel pit. The channel was narrowed through the creation of marginal shelves, which were not planted but left to colonise naturally. The River Mimram restoration scheme also incorporated the lowering of a small weir, channel narrowing and the introduction of gravel, however, two types of gravel were incorporated within the restoration scheme: a ‘standard’ size of 40-20 mm and a ‘special’ mixed particle size distribution selected to match the gravel composition found within the river (supplementary material Table S1). Both schemes were designed to restore physical river processes. The sampling design for each scheme was based on a Before-After-Control-Impact (BACI) approach. Within each scheme two impact sites were monitored in addition to a control site. In each case, the control site was selected as the more naturally functioning (least impacted) section of channel, with no discharges or tributaries entering the channel between the sites.

2.2. Stream habitat quality

River Rib

Three reaches were assessed: the control; a site with reduced impoundment (‘drink’); and one within the section of introduced gravel (‘sluice’). Within each of the reaches, a representative 20 m section was mapped using a metre grid system to measure velocity (slack < 10 cm s⁻¹; slow 10-25 cm s⁻¹; moderate 25-50 cm s⁻¹; fast 50-100 cm s⁻¹; and spate >100 cm s⁻¹), depth and

substrate (cobbles 64-256 mm; gravel 2-64 mm; sand 0.0625-2 mm; and silt < 0.0625m). Detailed measurements of stands of vegetation were made. The vegetation was assessed both as the species present and the vegetation type, classified as emergent narrow leaf vegetation, emergent broad leaf vegetation or submerged vegetation.

River Mimram

For the second scheme, three reaches were also assessed: the control; a site within the section where standard gravel was introduced ('standard'); and a third site where the special mix of gravel was introduced ('special'). At each site, visual assessment of the functional habitat coverage was made (following Harper et al., 1992), average depth measured and substrate compositions visually assessed. Representative substrate composition was measured using the residual from the macroinvertebrate core samples (see section 2.3). Habitat assessments were made and substrate composition assessed in July 1998 prior to the restoration work, two months post-restoration (October 1999) and one (June 2000) and two years (September 2001) following restoration.

2.3. Benthic invertebrate assessment

River Rib

The macroinvertebrate assemblage was assessed at the same three sites ('control', 'drift' and 'sluice'). Within each reach, 10 macroinvertebrate samples were collected using a modified Surber sampler—0.05 m² with a 900 µm mesh net (after Surber, 1937). The location of each sample was determined by the generation of random coordinates. Samples were collected in September 1996 prior to the restoration work and two (September 1998) and three (September

1999) years following restoration. At each sampling point, the near-bed velocity and depth were also measured. All macroinvertebrate samples were sorted in the laboratory and identified to species level (where possible) using standard keys (see Murray-Bligh et al., 1997) with the exception of Chironomidae and Oligochaeta. Abundances (number of individuals per m²) were enumerated for each taxon.

River Mimram

For the second scheme, the macroinvertebrate assemblages were assessed at each of the three sites ('control', 'standard' and 'special') to assess the change in invertebrate composition. Five invertebrate samples were collected on each sampling occasion using a large (25 cm diameter ~ 0.05 m²) metal core by agitating the sediment to a depth of 5 cm in order to obtain samples comparable with the samples from the River Rib. Within each core, the substrate was agitated to mobilize the invertebrates and these were collected using a 900 µm mesh net. The location of each core was determined by the generation of random coordinates. At each sampling point, the water depth and near-bed velocity were also measured. Samples were collected in September 1998 and July 1999 prior to the restoration work, in October 1999 (two months post-restoration) and one (June 2000) and two years (September 2001) following restoration.

2.4. Data analysis

For each of the samples, species diversity, (Simpson's D, after Simpson, 1949), density (individuals per m²) and taxon richness were calculated. To calculate FD, information from the widely-used database of Tachet et al. (2010) was combined with the well-established distance-based functional diversity (dbFD) approach of Laliberté and Legendre (2010) using the dbFD function in R 3.2.3 (R Core Team, 2015). This focused on 63 individual trait modalities across 11

fuzzy coded categories of 'true' traits (Statzner & Běche 2010; Verberk et al. 2013), incorporating body length, life cycle duration, voltinism, aquatic life stages, reproduction mode, dispersal mode, resistance forms, respiration mode, locomotion or relation to the substrate, diet and feeding mode. The traits were applied at the same taxonomic level at which taxa were identified or the lowest resolution provided within Tachet et al. (2010). Details of the taxa and traits applied are presented within Table S2. Varying fuzzy coding levels between trait categories were controlled by expressing trait values as percentages within each trait category. For example, if a taxon had a fuzzy score of 1 for both annual and perennial life cycle durations, this was expressed the trait values as 50% for each of the two trait modalities within the life cycle duration category. The full trait database used can be found in the Supplementary Material online (Table S2). In calculating the five commonly reported FD indices (FRic, FDiv, FDis, FEve, FEnt), the maximum number of synthetic trait axes that allowed the number of taxa > number of traits condition to be maintained were used. FRic was standardised by dividing through the maximum FRic of a hypothetical community containing all species observed at a site (i.e. River Rib, River Mimram) throughout the whole study period.

To explore trends in the results, boxplots and correlation matrices were created. Possible differences between sites and sampling occasions were analysed using a two-way ANOVA followed by Bonferroni-corrected pairwise t-tests when the time * site interaction was significant. To further analyse the relationship between taxonomic and functional diversity, we randomly sampled (without replacement) taxa from the species pool at each site and calculated standardised FRic at values of taxon richness ranging from one to the total number of taxa in the species pool. This resulted in a null distribution of FRic for each value of taxon richness. Because macroinvertebrates were sampled from a variety of habitats at the River Rib, the random sampling was stratified by dominant substrate size category, defining two separate species pools for gravel and sand habitats. Other habitat types (i.e. silt) were not included since there were too few samples. The two restoration schemes assessments have a different number of samples per site

(Rib 10 and Mimram 5). To avoid comparing different sampling efforts, comparisons were made within a scheme rather than between schemes. All analyses were performed in R 3.2.3 (R Core Team, 2015).

3. Results

3.1. Stream habitat quality

River Rib

The depth profiles, vegetation and velocity contour maps are shown in Fig. S1 and S2. Prior to the restoration work the 'drink' site had a deep homogenous channel with a uniform depth averaging 65 and 77 cm during June and September 1996. At the time of the post-project appraisal, the channel was shallower and more heterogeneous, reflecting the reduced impoundment, averaging 16 and 27 cm deep (t-test; significant at $P < 0.001$). Similarly, the 'sluice' site was a uniform trapezoidal channel averaging 45 and 39 cm deep during the baseline survey changing to a more heterogeneous, shallower depth averaging 28 and 24 cm reflecting the reduced impoundment and introduction of gravel to restore the longitudinal profile (t-test; significant at $P < 0.05$). The control site showed little variation in depth through the different surveys, averaging 11 cm deep on each occasion. The control site remained the shallowest of sites within the survey. A summary of the habitat composition in terms of flowing water functional habitat and substrate composition is presented in Fig. S3.

River Mimram

The functional habitat composition for the Mimram sites is presented in Fig. S4. Prior to the restoration the channel was over-wide and deep as a result of channelization and historic dredging. The scheme reduced the channel width and raised the bed level to reinstate the longitudinal profile, creating a shallower, more heterogeneous channel. The control site showed little variation through the different surveys. Changes in substrate composition over time were examined using the particle size data collected from the core samples and are presented in Fig. S5. The results from the baseline survey confirm that the substrate within the section of channel selected for restoration was dominated by fine sediment. By contrast, the control site showed a more mixed substrate composition. The first post-project appraisal showed the change in substrate as a result of the restoration work with the standard substrate still dominating where it had been placed and the special gravel showing a more mixed substrate. Although the special gravel introduced aimed to mimic the natural substrate within the channel, the substrate lacked some of the finer sediment particles (sand and fine gravel) found within the river. At the time of the second post-project appraisal there was a slight change in the sediment as a result of geomorphological processes moving finer sediment down the channel. This change resulted in the special gravel sediment being comparable with that of the control site as seen by the overlapping grain-size distribution curves. Circumstances were similar during the third post-project appraisal. This demonstrates that the intention of the restoration to recreate the natural substrate composition within the restoration scheme was successful where the special gravel was introduced but that little sediment transport in the river meant that the standard gravel remained dominated by a uniform size.

3.2. Invertebrate communities

Taxonomic and functional diversity indices are presented in Fig. 3 with comparisons using paired t-tests given in Tables 1 and 2. Results of two-way ANOVA tests revealed significant time *

treatment interactions for all indices except FEve in the River Rib (Table S3) and FDiv in the River Mimram (Table S4). In the River Rib, most taxonomic and functional indices suggested that the pre-restoration conditions for both treatments were significantly degraded with reference to the control site. During the post-project surveys, diversity, FDis and FEnt were comparable with the control site suggesting some success from the restoration scheme. However, by the second sampling occasion (1999), the values of other indices were lower in at least one treatment site than in the control site. For example, taxon richness and FRic were significantly lower in the 'drink' site and FDiv was significantly lower in the 'sluice' site. Similar post-restoration results were observed for the River Mimram, where diversity, FRic, FDis and FEnt fluctuated. Pre-restoration, there were no significant differences between treatment sites and the controls for diversity, density, FDis and FEnt in the River Mimram.

Jaccard and Bray-Curtis similarities (Anderson et al., 2011) indicated that communities in restored sites initially became more similar to the corresponding control sites (Fig. 4). However, communities of both treatments on the River Rib and the special gravel treatment on the Mimram later diverged from the control communities.

Correlation matrices (Figs. S6, S7) indicated close correlations between taxon richness and FRic, and between Simpson's diversity and FDis. FEnt was almost perfectly correlated with FDis (for this reason FEnt is excluded from the boxplots in Fig. 3). Two indices were selected for further comparison: Simpson's diversity (structural complexity) and FEve (functional integrity), since they were relatively independent and incorporate information on both taxon occurrence and abundance (Fig. 5). Furthermore, FEve is suitable for indexing functional integrity since higher values reflect a more even distribution of niches, which has been linked to greater response diversity, and hence resilience, in a variety of ecosystems (Joseph et al., 2015; Morelli et al., 2017; Schriever et al., 2015). In the River Rib, the results show that restoration was successful in terms of moving restoration sites along the structural axis towards control sites, but there was relatively

little vertical movement along the functional axis, suggesting that while taxonomic diversity was restored in comparison with the control sites, functional integrity was not. In the River Mimram, structural complexity was initially similar between control and pre-restored treatment sites. Three years after restoration, treatments and the control had converged along the functional axis, with a tendency for the functional integrity of treatment sites to decline. In both cases the treatment samples moved closer to the control samples after restoration work suggesting that the restored section was more similar to the control section and that the schemes can be considered a partial success.

Although taxon richness and FRic were closely correlated ($R \sim 0.8$) (Figs. S6, S7), random sampling from species pools showed that many samples had FRic values significantly lower than expected at random for a given taxon richness (Fig. 6.), demonstrating the occurrence of functional redundancy. The effect is stronger for the River Rib. In the River Mimram, the tendency for FRic to be significantly lower than expected increased with time since restoration (Fig. 6c).

4. Discussion

The assessment of the habitat composition of the restoration sites following the implementation of the morphological restoration shows that the schemes had been successful in creating a habitat composition comparable with the control sites. Mesohabitat assessment has been used as a cost-effective way to link ecology with morphology and hydrology in river channel restoration (Kemp et al., 1999). However, to demonstrate restoration success, the macroinvertebrate assemblages in relation to habitat composition must be considered.

4.1. *Community response to restoration*

This study demonstrated that, following morphological restoration measures, 'recovery', as defined by community indices, was largely incomplete and inconsistent in terms of treatment and taxonomic/functional index. Thus, there is no support for our hypothesis that FDiv, FDis, FEve and FEnt would increase, reflecting the establishment of greater habitat quality and complexity. These results are consistent with other studies which indicate variable response of benthic invertebrates to morphological restoration measures (e.g. Friberg et al., 2014; Jähnig et al., 2008; Leps et al., 2016; Palmer et al., 2010), and that traditional diversity indices may not be an appropriate measure of hydromorphological quality (Feld et al., 2014). Verdonschot et al. (2016) found that the general lack of the effect of restoration on microhabitat composition and diversity could be a key factor explaining the lack of response in the overall comparisons of the selected macroinvertebrate metrics they examined. They also concluded that several of the functional trait relationships they found were not detected using the taxonomic metrics. This emphasises the importance of considering functional indices in addition to structural indices and is supported by our findings.

This study found that there was a general tendency for taxa occurrences and abundances to become more similar between treatments and their corresponding controls over time, yet by the end of the study period treatment communities were only around 60% similar to controls. This also indicates that 'recovery', defined in terms of species identity and community structure, was largely incomplete, which may reflect the relatively short timescale of the monitoring and a time-lag in the ecological recovery as the restored sites adjust (Jones and Schmitz, 2009; Winking et al., 2014). Whilst restoration age is a crucial factor to consider when monitoring the results of restoration on riverine communities (Bash and Ryan, 2002), it may not be the ultimate reason for missing community recovery (Leps et al., 2016) and over time, restoration effects may vanish (Kail et al., 2015). The loss of restoration effects is often associated with unsustainable restoration that does not work with natural processes (Beechie et al., 2010); the combined influence of both local and regional hydromorphological quality (Leps et al., 2016) or not in keeping with catchment

processes (Gurnell et al., 2016b). Miller et al. (2010), in their meta-analysis of in-stream habitat restoration projects, found that within 1 year of restoration, significant, positive effects on macroinvertebrate richness and inconclusive effects on density could be detected. Within this study the sources of colonists for the restoration schemes were in close proximity, so are unlikely to be a restricting factor. However, the pattern of initial colonisation is important (Pander et al., 2016) with strong dispersers known to colonise first with species with low dispersal capacity needed longer time to colonise (Li et al., 2016). These continuing adjustments could explain the incomplete recovery within this study.

When considering results from the River Rib in the context of Bradshaw's classic model of ecological restoration, the treatment sites moved further along the structural complexity axis than the functional integrity axis, suggesting that it is more challenging to achieve functional rehabilitation. This may indicate that the control sites are not true reference sites but are also subject to stressors; the treatment samples had a similar functional integrity to the control site prior to the restoration work supporting the notion that the control site was subject to other stressors. Following restoration we may have expected functional integrity at the restored site to exceed that of the control. This may mean that other stressors, maybe acting at a catchment scale, are continuing to limit functional integrity throughout the river. When undertaking restoration measures, it is important that catchment processes are considered, both from a physical (Gurnell et al., 2016a, 2016b) and ecological perspective (e.g. Leps et al., 2016). This is more likely to ensure that the restoration measures will be successful and a realistic target endpoint is identified which may deviate from the original reference condition. Not establishing reference condition benchmarks and evaluation endpoints against which to measure success is one of the common problems or reasons for restoration project failure identified by Cowx et al. (2013). In addition to considering the endpoints, it is important to understand the degraded nature of the system identified for restoration and their context within the catchment since they may influence the extent and pathway of recovery. Provided there is a suitable connectivity with an intact species

pool, more degraded ecosystems are more likely to show the greatest responses (Miller et al., 2010). However, if the ecosystem had entered an alternative state, this may preclude recovery (Jones and Schmitz, 2009) and is more likely to result in an alternative endpoint.

We hypothesized that restoration would result in increased taxon richness and taxonomic diversity but that the response of FRic would be more muted due to redundancy in the traits of colonising taxa. Whilst we found little support for the first part of this hypothesis, results of random sampling from carefully defined species pools (Fig. 6) suggested that it is more difficult to increase functional diversity than taxonomic diversity because there is often significant functional redundancy. As taxon richness increases, the probability of colonisation by a species with a different or unique trait profile decreases (Petchey and Gaston, 2002). The fact that this effect was stronger in the River Rib may reflect a greater role for environmental filtering at this site (Poff, 1997). We defined two sets of species pools based on substrate composition for the River Rib because communities of sand habitats were a subset of those of gravel habitats, leading to inflation of null distributions of FRic when both substrates were lumped together. However, macroinvertebrates also have discrete distributions with respect to hydraulics (Doledec et al., 2007), yet we did not define separate species pools based on discrete categories of water depth and velocity, which were varied in the River Rib, especially after restoration (Supplementary Material). This could partially explain the results, but given our use of the occurrence-based FRic index, as well as the strong role played by mass effects in lotic macroinvertebrates (Stoll et al., 2016), it is likely that our results reflect true functional redundancy at the mesohabitat scale studied. Functional redundancy was also noted by Feld et al. (2014) when assessing hydromorphological degradation across Europe, supporting our conclusion.

4.2. Does morphological restoration lead to the recovery of both structure and function?

Overall, our findings suggest there was limited restoration success in both schemes and that neither structure nor function were successfully restored within the timescale of the monitoring. Furthermore, the application of the 'Bradshaw model' to our results and our resampling of the species pool revealed that functional rehabilitation is more difficult to achieve than structural improvement. Functional measures have proved successful in detecting hydromorphological pressure at different spatial scales (Feld and Hering, 2007) and our findings support the recommendation that functional indices are used alongside structural indices in the assessment of river restoration schemes (Kail et al., 2015; Mouchet et al., 2010; Watts and Mason, 2015). Their routine use in future evaluations of restoration schemes may help us to investigate the effect of measures and to infer causal relationships (Kail et al. 2016), identify barriers to full restoration of community composition (Watts and Mason, 2015), help us to understand how biodiversity interacts with ecosystem processes and environmental constraints (Mouchet et al., 2010) and identify effective restoration measures (Muhar et al., 2016). Greater insight may be provided by considering trait identity, rather than only trait diversity (Vandewalle et al., 2010), multiple rather than single traits (Piliere et al., 2016), the refinement and development of trait databases (Wilkes et al., 2017) and application across larger spatial scales where trait-based measures are more consistent than taxonomic measures (Pollard and Yuan, 2010). However, assessment should not be restricted to biological indices alone (Geist and Hawkins, 2016) and it is important to quantitatively measure habitat heterogeneity changes (Rubin et al., 2017).

5. Conclusions

The results of our work support the conclusions of Feld et al. (2014) that traditional whole-community-based taxonomic diversity indices are not the ideal measures to detect and assess the various aspects of biodiversity loss. We recommend that both functional and structural diversity are measured, allowing the trajectories of change within the communities to be tracked.

Monitoring may need to be undertaken over a longer timescale which increases the likelihood of detecting statistically significant increases in diversity (Rubin et al., 2017). The development and testing of novel indicators of biodiversity, capable of detecting biodiversity changes in response to hydromorphological degradation (Feld et al., 2014) and subsequent restoration, should be a priority. An increasingly structured approach to monitoring and appraisal of restoration schemes, which implements rigorous study designs, monitoring abiotic and biotic changes including functional approaches and following a multiple BACI approach, is to be encouraged, so that lessons can be learnt from successes and failures to inform best practice (Bernhardt et al., 2005; Geist and Hawkins, 2016; Miller et al., 2010). Understanding the catchment context and applying long-term monitoring will allow a better understanding of trajectories of change caused by restoration measures and to identify which measures are sustainable (Gurnell et al., 2016a, 2016b; Kail et al., 2015).

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Figure captions:

Fig. 1. A general model of ecological restoration, including shifting reference conditions. Adapted from Newson and Large (2006), reproduced with permission of Wiley, after Bradshaw (1988).

Fig. 2. Location of the restoration projects.

Fig. 3. Boxplots of taxonomic and functional diversity results from the River Rib (left diagrams) and the River Mimram (right diagrams). For the River Rib, treatment 1 was the 'drink' site (D) and treatment 2 was the 'sluice' site (S). For the Mimram, treatment 1 was the 'special' gravel (spc) and treatment 2 was the 'standard' gravel (std). Horizontal lines show medians, boxes show the interquartile range, whiskers the range (up to 1.5 times the interquartile range), and closed circles denote outliers beyond 1.5 times the interquartile range.

Fig. 4. Comparison of Jaccard and Bray-Curtis similarity indices within the River Rib (a, b) and the River Mimram (c, d).

Fig. 5. 'Bradshaw plots' comparing structural complexity (Simpson's diversity, D) against functional integrity (functional evenness, FEve) for the two restoration schemes. Symbols represent replicates from the River Rib (a, b) and the Mimram (c, d) pre-restoration (a, c) and three years' post-restoration (b, d). For the River Rib, treatment 1 was the 'drink' site and treatment 2 was the 'sluice' site. For the Mimram, treatment 1 was the 'special' gravel and treatment 2 was the 'standard' gravel.

Fig. 6. Taxon richness in comparison with functional richness (FRic) of sample replicates in restored sites for the River Rib gravel habitats (a), sand habitats (b) and the River Mimram (c). Confidence intervals from random sampling of FRic are shown for a given taxon richness. Dashed lines represent the mean of null distributions. For the River Rib, treatment 1 was the 'drink' site and treatment 2 was the 'sluice' site. For the Mimram, treatment 1 was the 'special' gravel and treatment 2 was the 'standard' gravel.

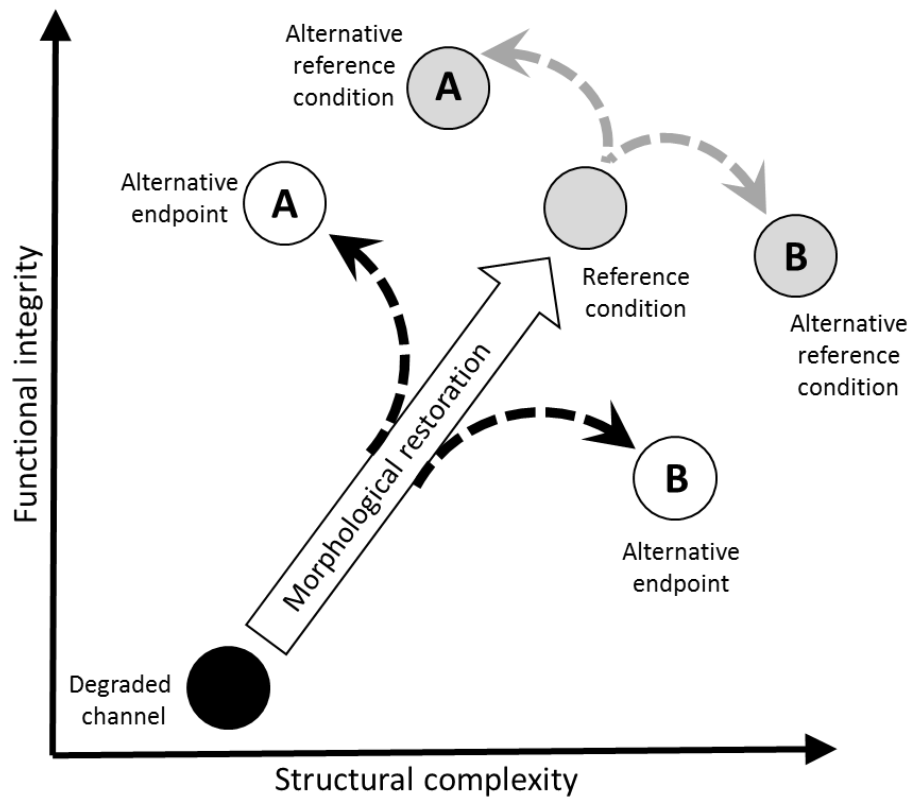


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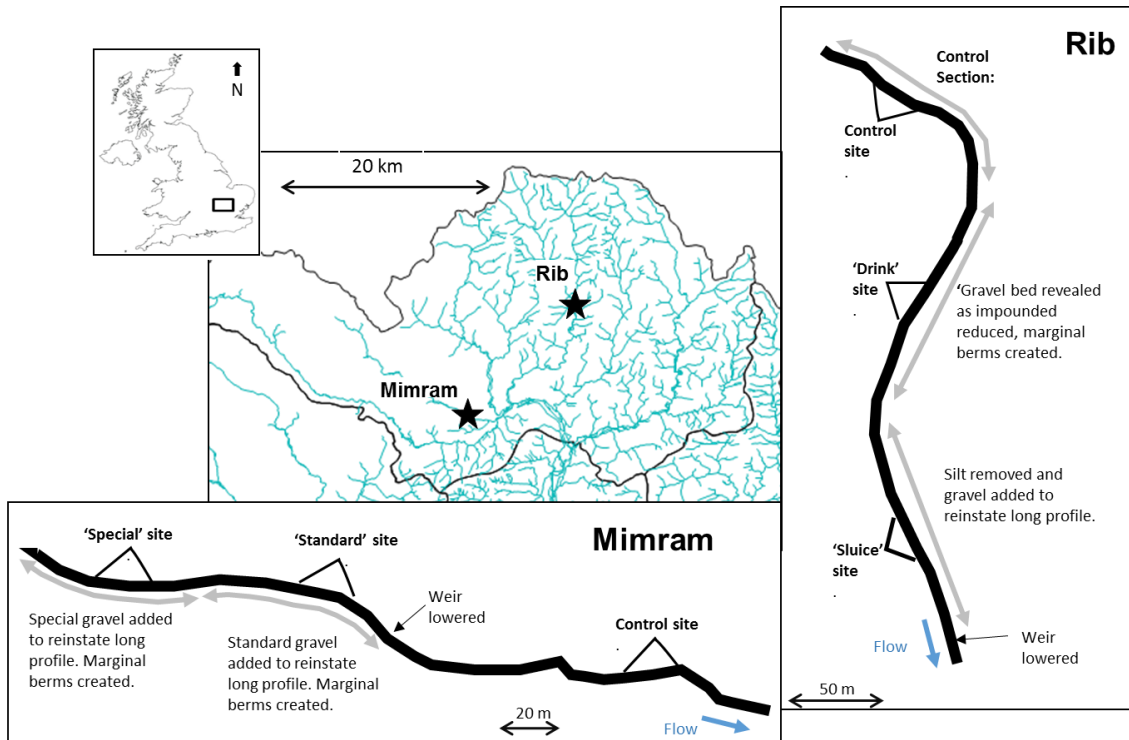


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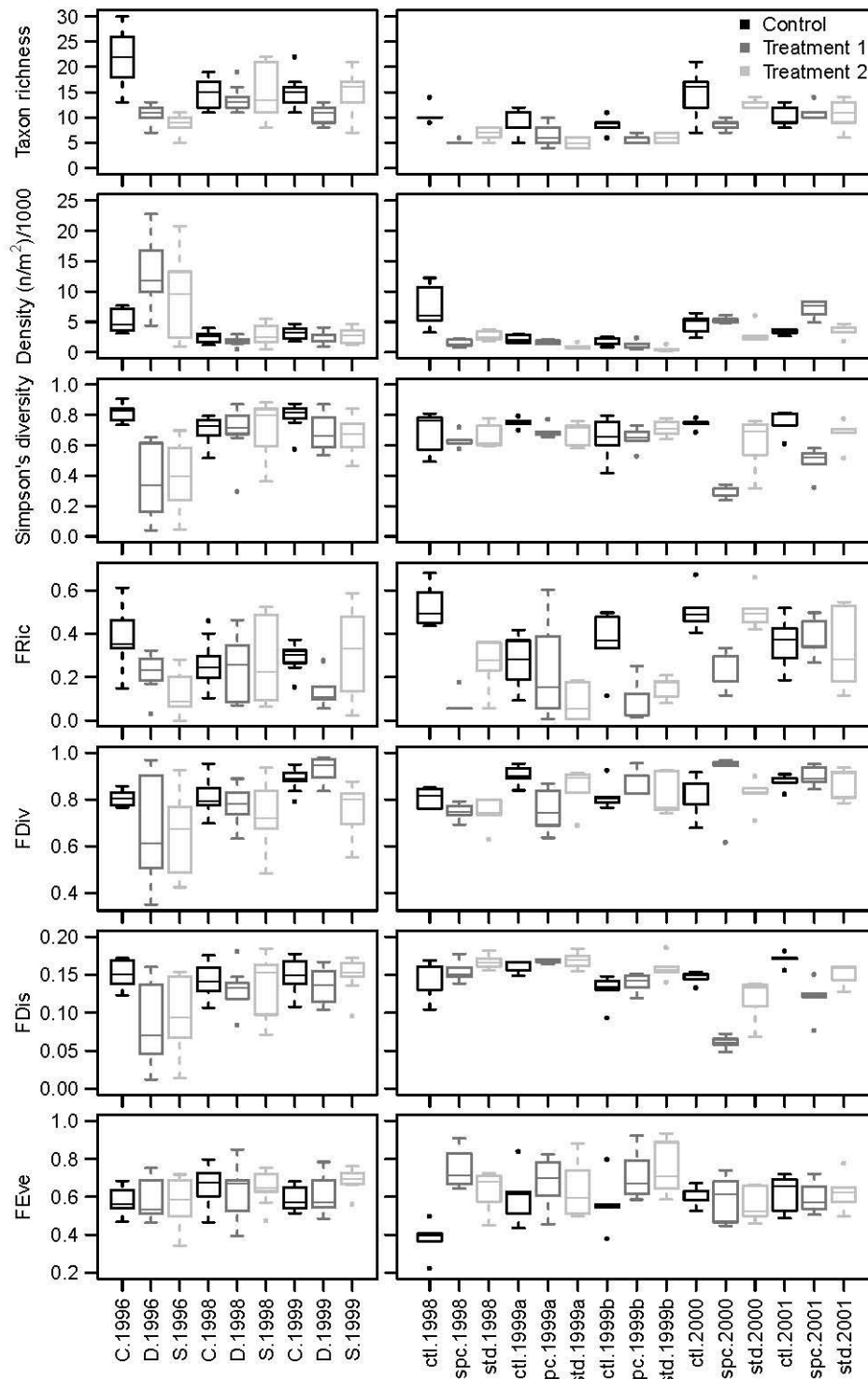


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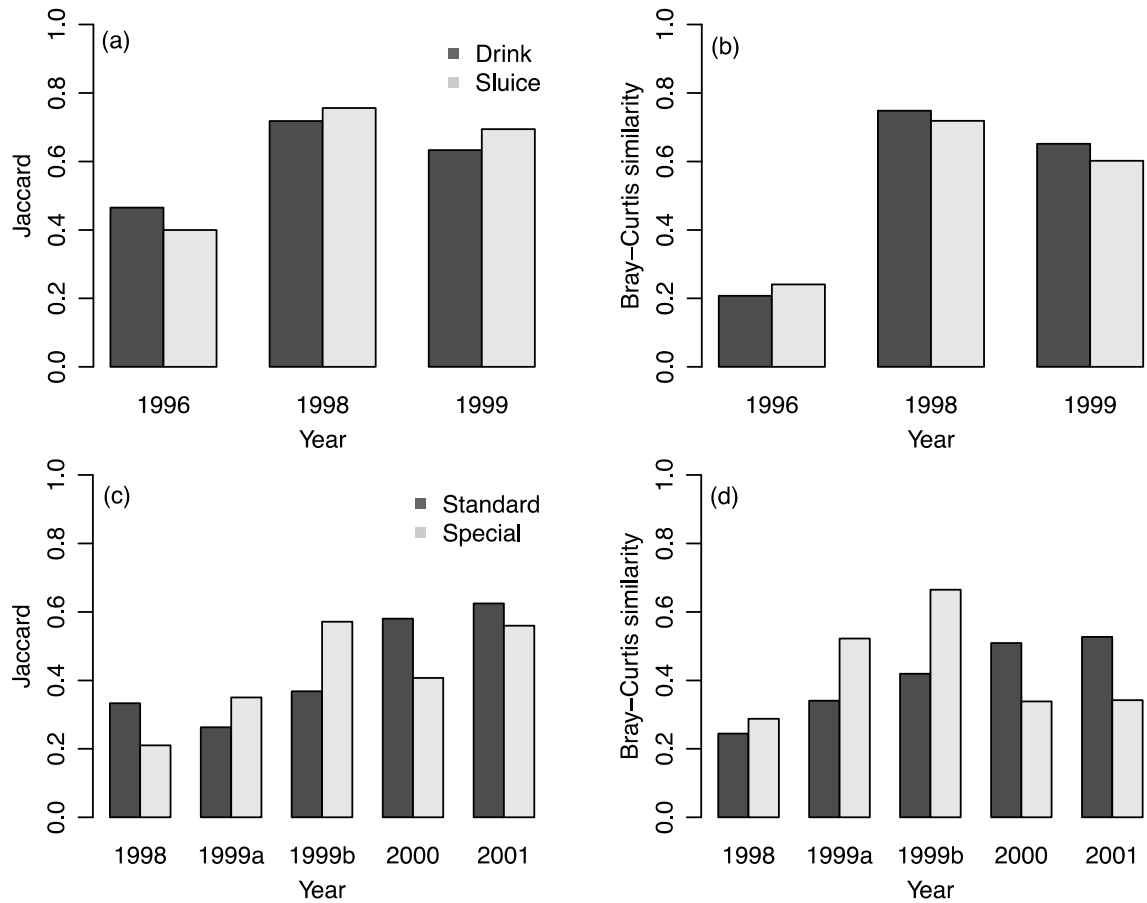


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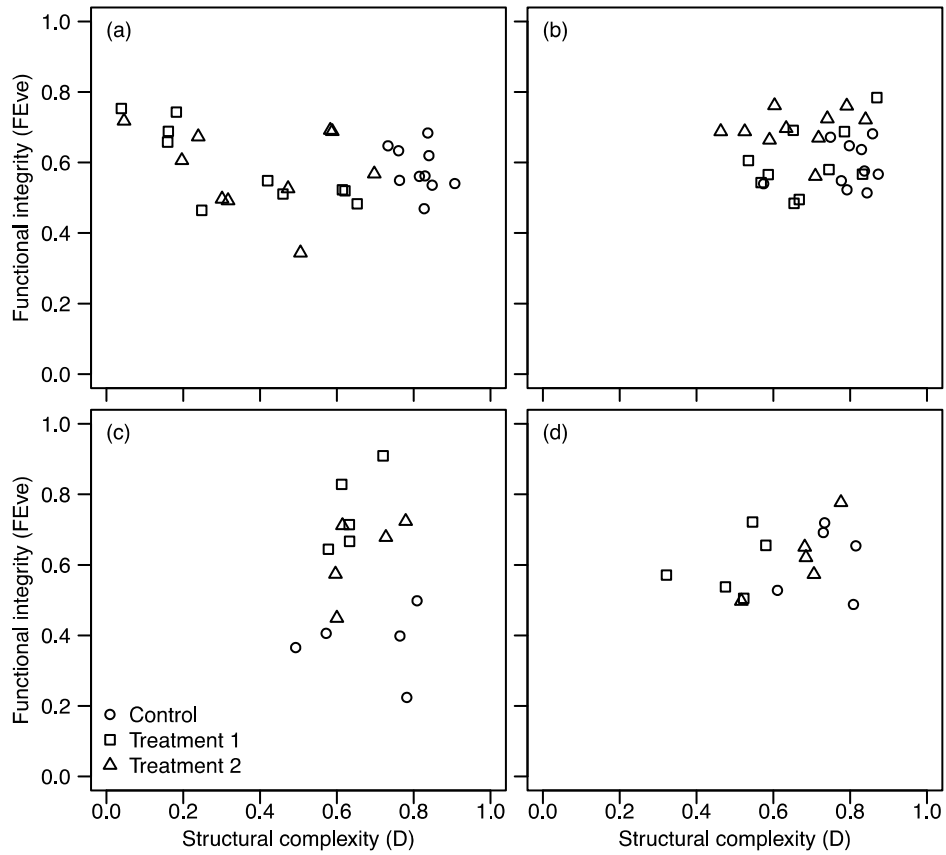


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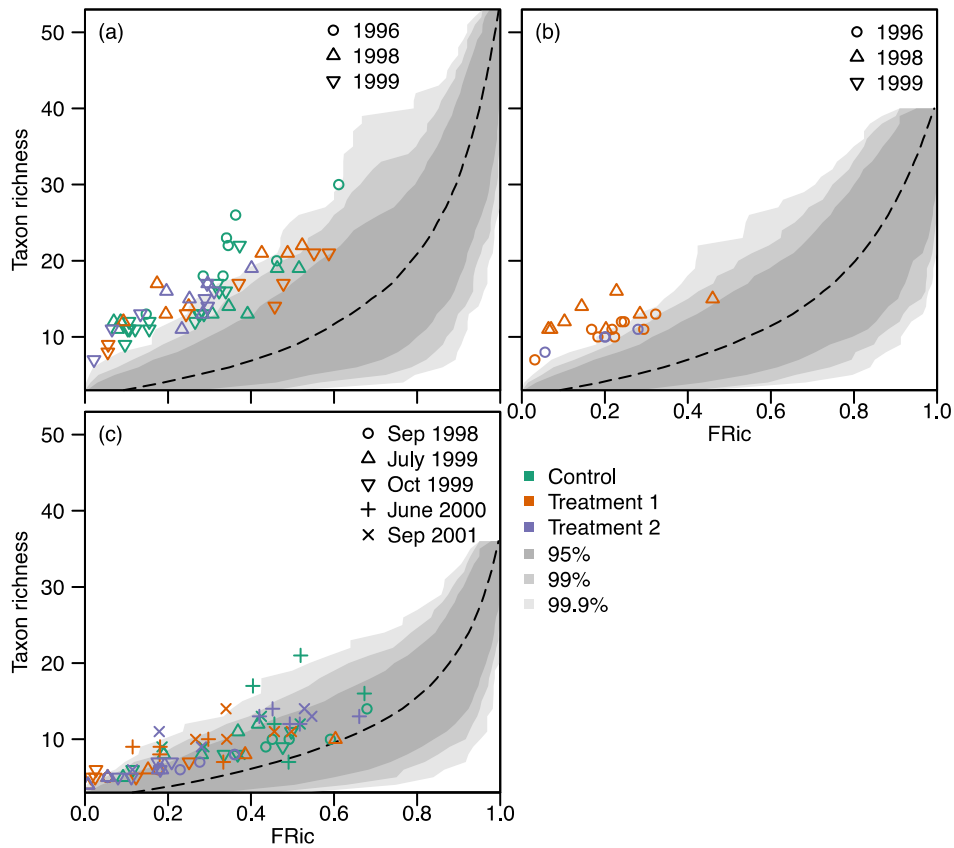


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Table 1

Comparisons of taxonomic and functional diversity indices using paired t-tests for the River Rib. Results for functional evenness (FEve) are not reported as time * treatment interaction term was not significant. Asterisks indicate results significant at: ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05.

Index	Year of survey		
	1996	1998	1999
Diversity	Drink < Control*** Sluice < Control***	Drink = Control Sluice = Control	Drink = Control Sluice = Control
Density	Drink > Control** Sluice = Control	Drink = Control Sluice = Control	Drink = Control Sluice = Control
Richness	Drink < Control*** Sluice < Control***	Drink = Control Sluice = Control	Drink < Control* Sluice = Control
Functional richness (FRic)	Drink < Control* Sluice < Control**	Drink = Control Sluice = Control	Drink < Control** Sluice = Control
Functional divergence (FDiv)	Drink = Control Sluice = Control	Drink = Control Sluice = Control	Drink = Control Sluice < Control*
Functional dispersion (FDis)	Drink < Control* Sluice = Control	Drink = Control Sluice = Control	Drink = Control Sluice = Control
Functional entropy (FEnt)	Drink < Control* Sluice = Control	Drink = Control Sluice = Control	Drink = Control Sluice = Control

Table 2

Comparisons of taxonomic and functional diversity indices using paired t-tests for the River Mimram. Results for functional diversity (FDiv) are not reported as time * treatment interaction term was not significant. Asterisks indicate results significant at: ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05.

Index	Date of survey				
	September 1998	July 1999	October 1999	June 2000	September 2001
Diversity	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special < Control*** Standard = Control	Special < Control* Standard = Control
Density	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control
Richness	Special < Control** Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control
Functional richness (FRic)	Special < Control** Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special < Control* Standard = Control	Special = Control Standard = Control
Functional dispersion (FDis)	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special < Control*** Standard = Control	Special = Control Standard = Control
Functional evenness (FEve)	Special > Control** Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control
Functional entropy (FEnt)	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard = Control	Special = Control Standard < Control***	Special = Control Standard = Control

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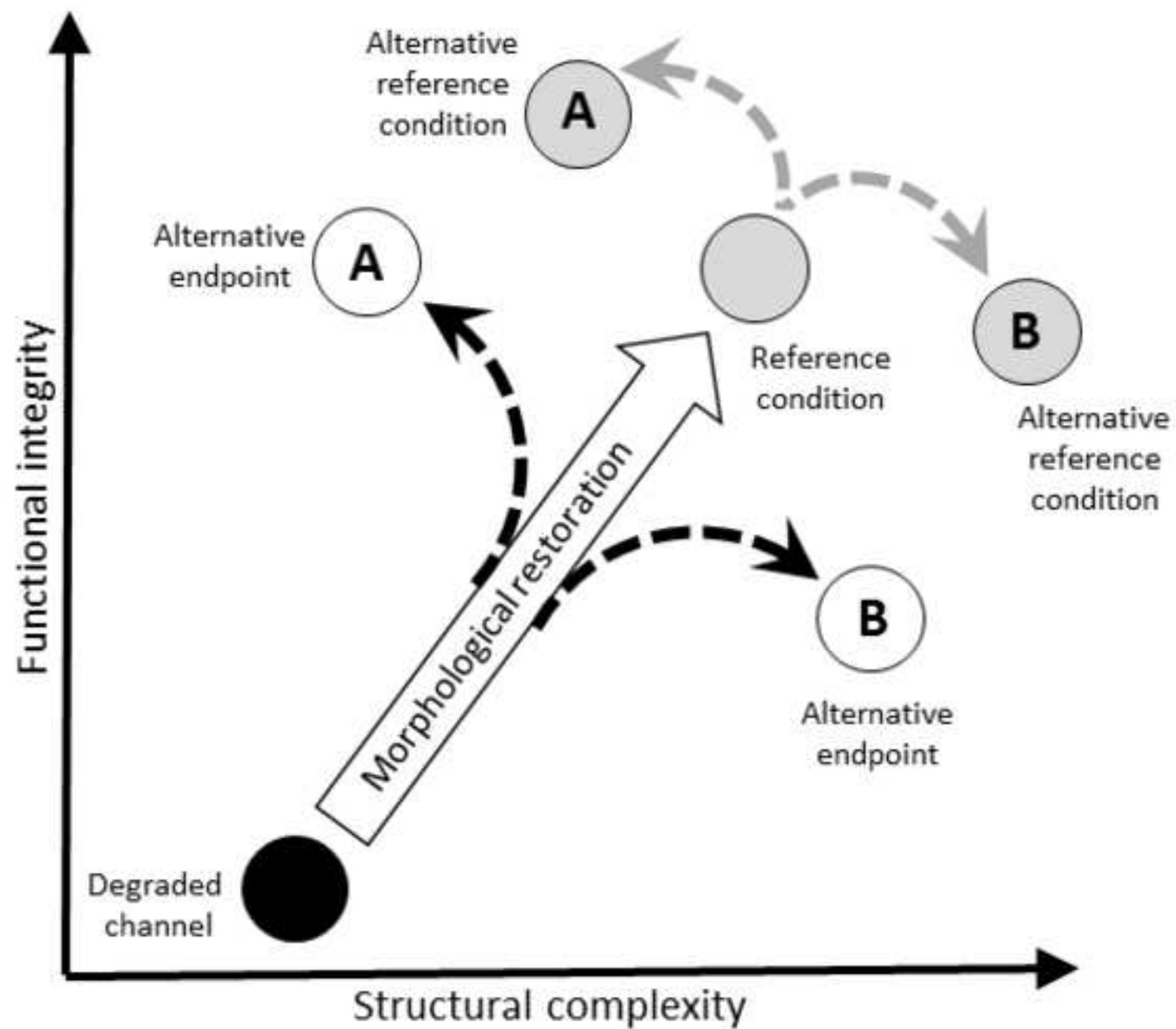
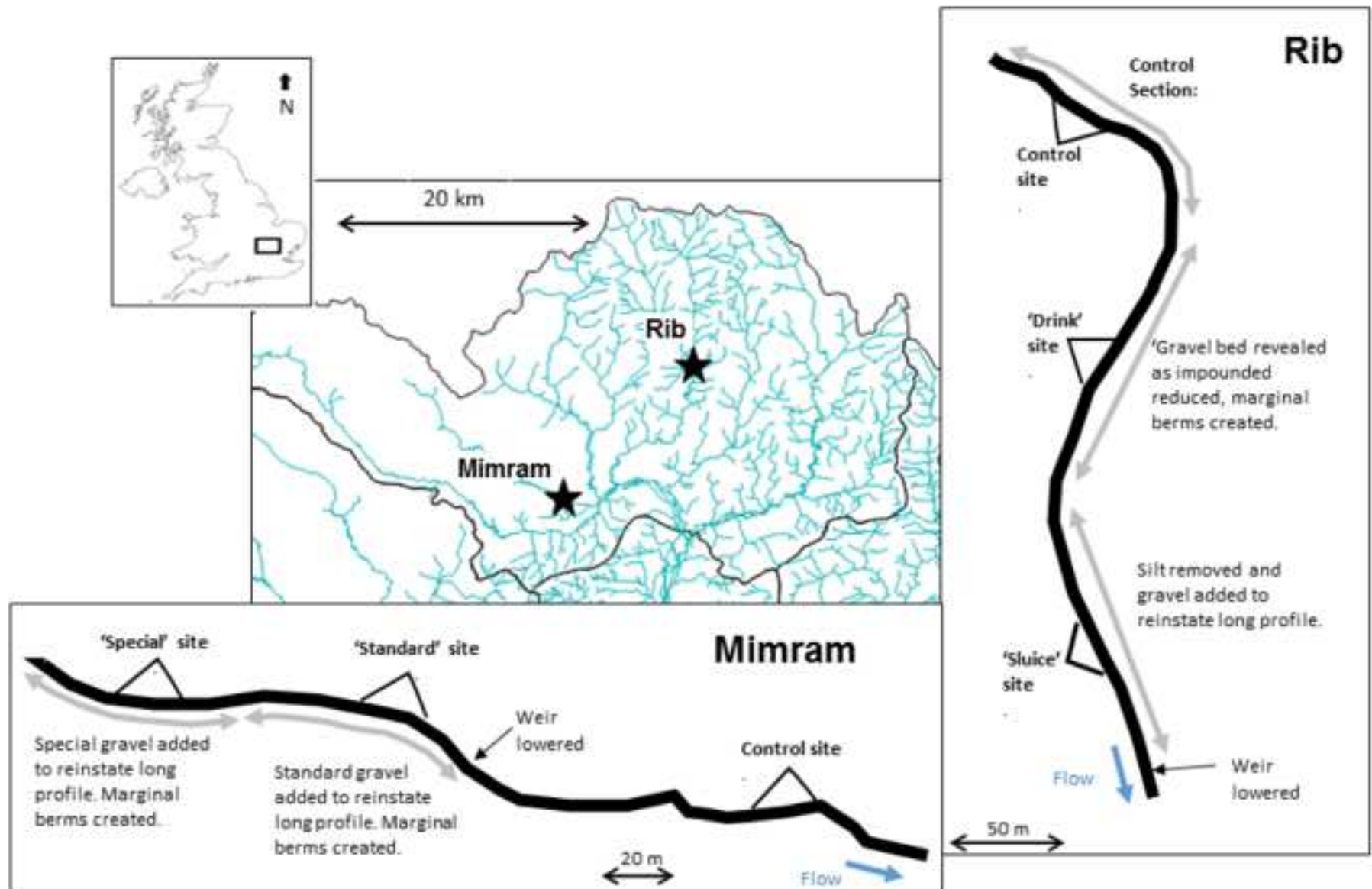


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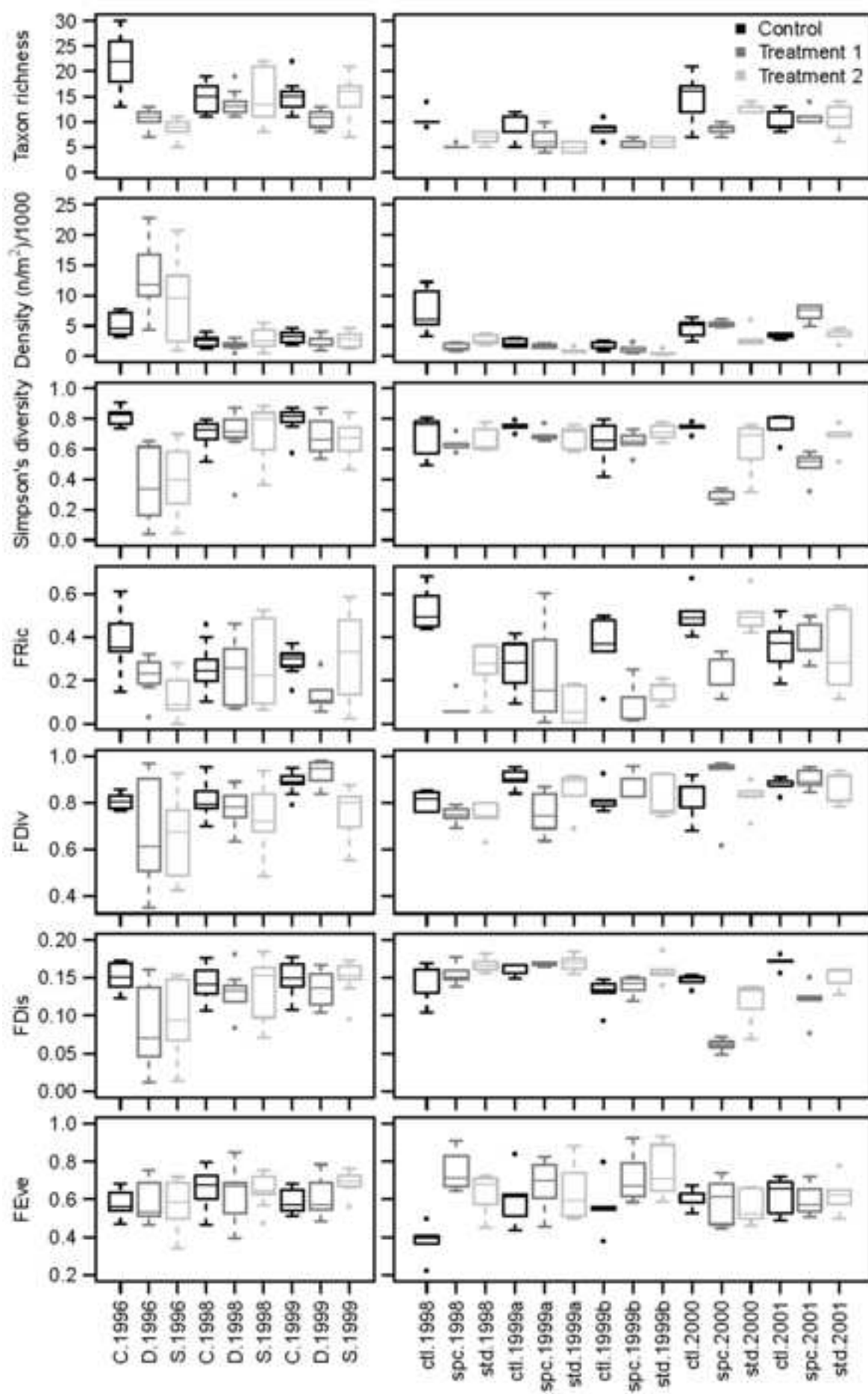
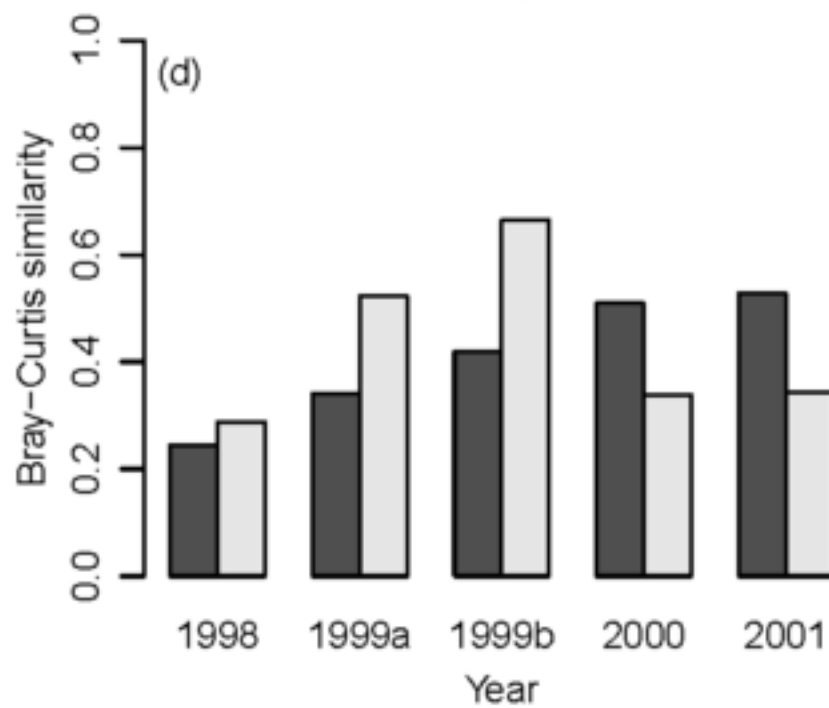
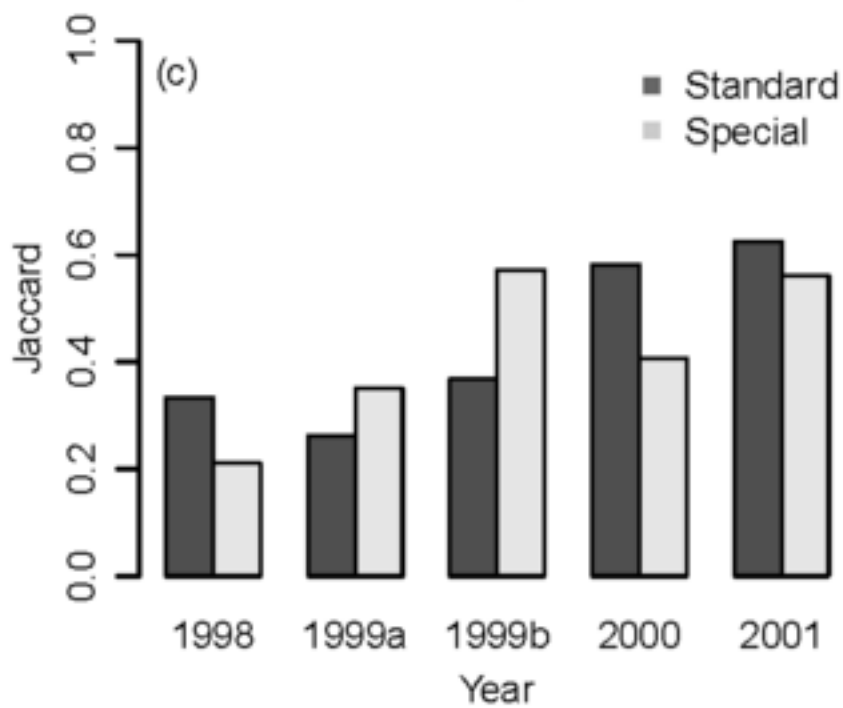
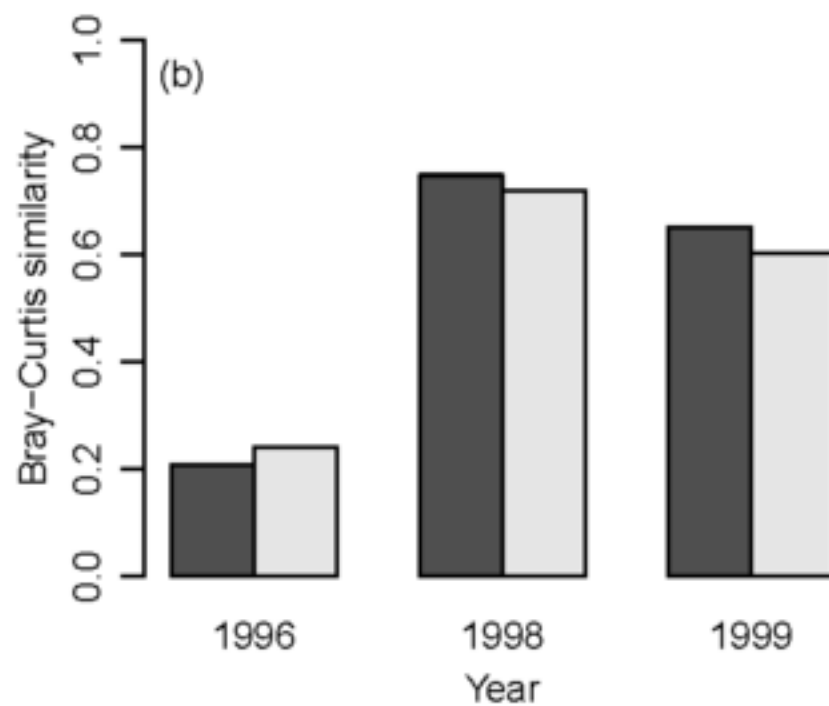
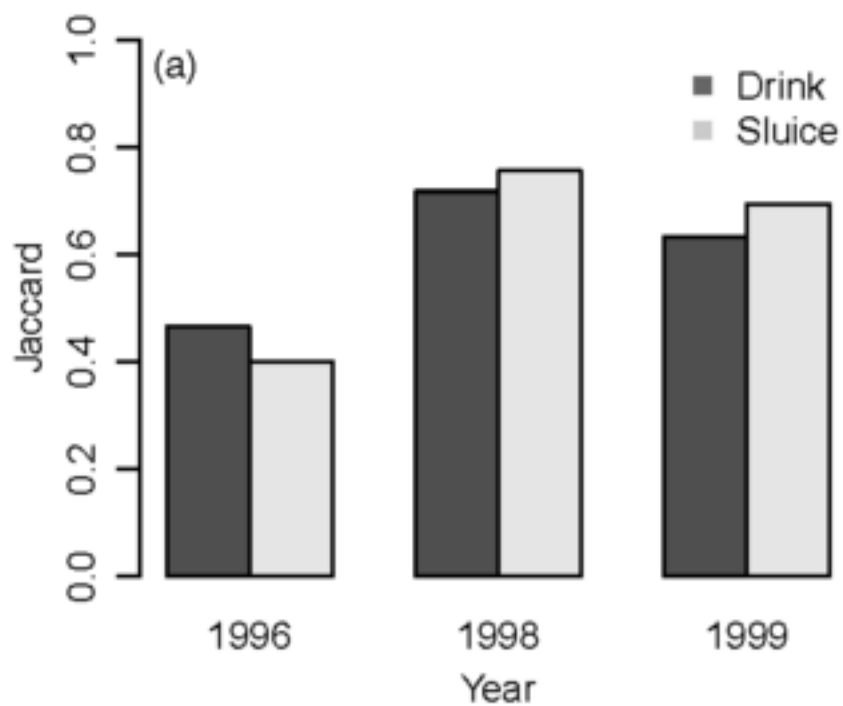


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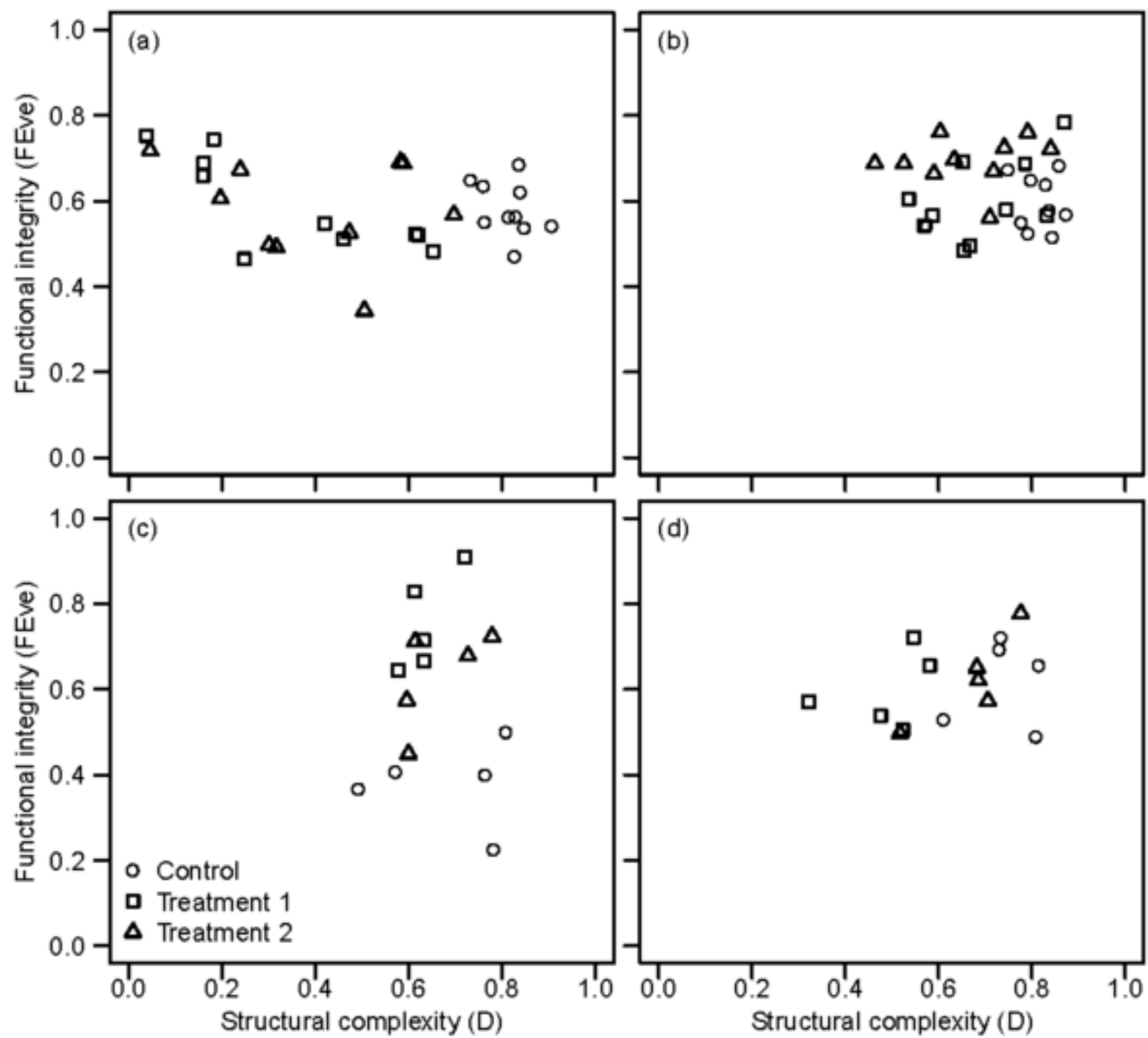
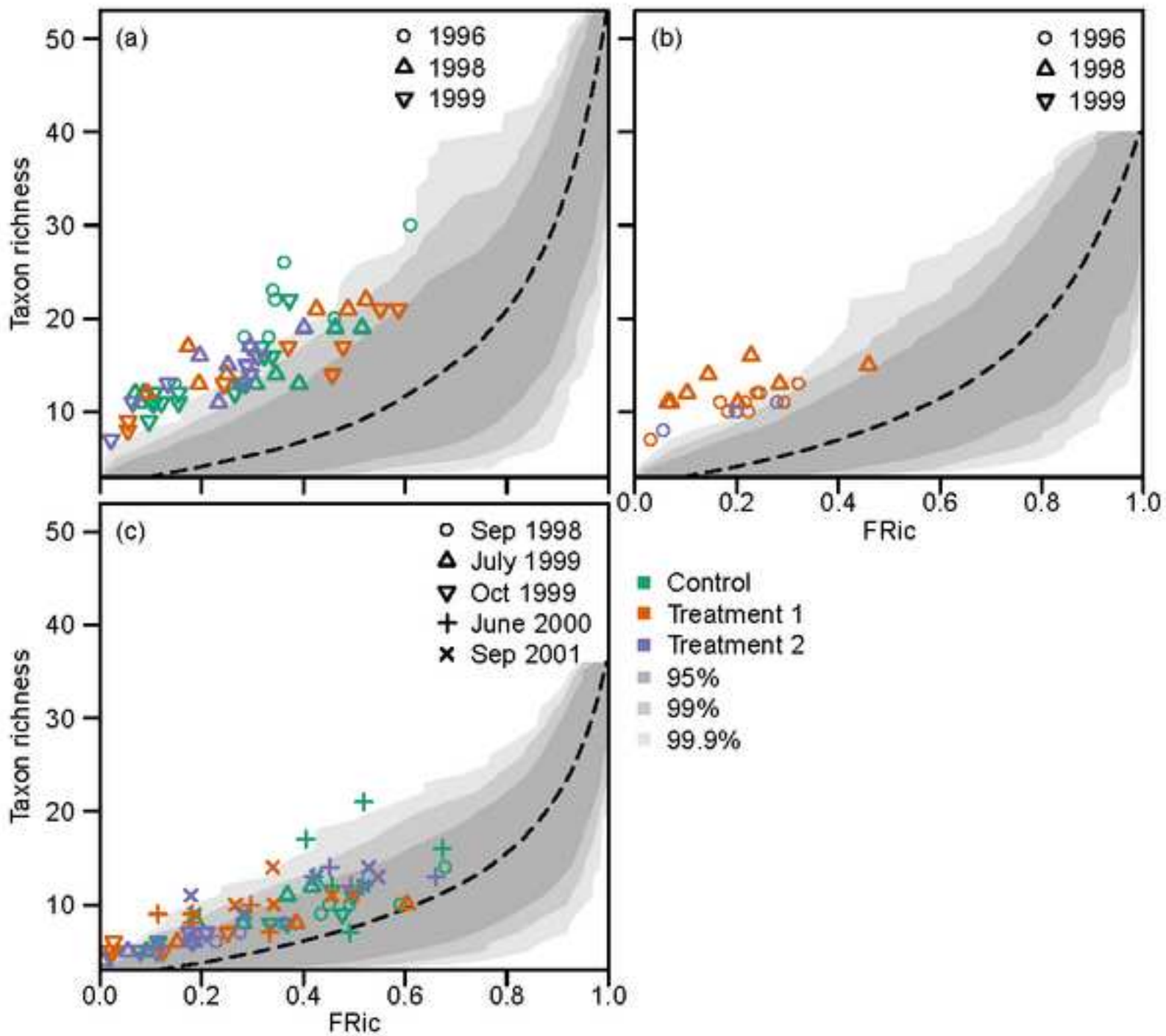


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