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Stream Invertebrate Responses to Fine Sediment Depend on the Organic and Inorganic Components

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ABSTRACT

1. Excess fine sediment (<2 mm) is a pervasive stressor of aquatic systems at a global scale. To date, most research quantifying ecological response to deposited fine sediment has been conducted without distinguishing between the organic and inorganic components of fine sediment, leaving mechanistic understanding of how fine sediment affects macroinvertebrates lacking.
2. To address this research gap, we examined the ecological responses of macroinvertebrates to various components of fine sediment stress (inorganic, organic and total mass). Using data collected from field surveys, first, we quantified invertebrate responses to fine sediment in two countries: New Zealand and the United Kingdom and second, we quantified whether ecological responses to the fine sediment components differed in spring and autumn in the United Kingdom.
3. Results indicated that the response of invertebrates varied dependent on both the component of fine sediment and the facet of community quantified (i.e., taxonomic or functional). The organic component was highly influential in structuring aquatic communities, particularly in New Zealand, whilst in the United Kingdom, there were less pronounced differences between the relative importance of organic and inorganic sediment. Ephemeroptera, Trichoptera and Plecoptera taxa (and derived indices) were consistently found to be strongly related to all fine sediment gradients. Further, according to threshold analysis, changes in taxonomic measures of the community in the United Kingdom occurred at lower quantities of fine sediment in autumn than in spring, particularly for the organic component. However, individual taxon and trait responses were more evident in spring.
4. Our study highlights several implications for the global monitoring and management of fine sediment. We have demonstrated that macroinvertebrates have distinctive responses to individual components of fine sediment (i.e., inorganic, organic and total mass) which may be missed from qualitative assessments of gross fine sediment coverage on streambeds alone. Further, aggregating multiple seasons into annual assessments may overlook important nuances in invertebrate responses to the different fine sediment components exhibited in individual seasons.

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1 | Introduction

Erosion, transportation and delivery of fine sediment (typically particles < 2 mm) is a natural process in river systems (Dubuis and De Cesare 2023). However, disruption to these natural processes associated with intensive land management practices has resulted in current loads far exceeding historic background levels (Collins et al. 2009a, 2009b). Whilst deposition of fine sediment is a natural process providing material to the streambed, excessive supply results in negative impacts on ecosystem processes and structure. As such, excess fine sediment is now regarded to be a pervasive stressor in aquatic environments globally (Dudgeon 2019). The effects of excess fine sediment in aquatic systems are extensive, spanning multiple trophic levels (Izagirre et al. 2009; Ramezani et al. 2016; Firmiano et al. 2021) and the implications for ecological communities are often complex (Wagenhoff et al. 2011; Blöcher et al. 2020; McKenzie et al. 2022a, 2022b). Macroinvertebrates are important components of aquatic ecosystems and are typically widely employed in international biological monitoring programmes, including those assessing fine sediment stress (Birk et al. 2012).

The broad functional diversity of macroinvertebrates makes their response to environmental stressors often non-linear (Friberg 2010), with responses to fine sediment dependent on a number of factors such as their relationship with the substratum, their feeding behaviour, and their respiration mode (Dolédec et al. 2009; Wagenhoff et al. 2012; Lange et al. 2014). The settling and ingress of fine sediments into gravel beds reduce habitat heterogeneity, clog interstitial pore space, and limit intragravel flows and hydraulic connectivity (Sear 1993; Yarnell et al. 2006; Boulton 2007). These processes alter the availability and quality of substratum for some taxa, limit the vertical exchange of oxygen and removal of excreta, increase invertebrate dispersal via drift, and can affect respiration and feeding activities, all of which ultimately shape the structure and diversity of macroinvertebrate communities (Larsen and Ormerod 2010; Descloux et al. 2014). To date, the taxonomic and functional responses of macroinvertebrates to fine sediment have been examined extensively at the individual and community level (Lange et al. 2014; Piggott et al. 2015; Doretto et al. 2018; McKenzie et al. 2022a, 2022b). However, understanding the mechanisms underpinning these ecological responses is further complicated when considering the composition (i.e., organic and inorganic components) as opposed to simply the quantity of excess fine sediment deposition in river systems.

Deposition of instream fine sediment provides an essential source of both organic and inorganic material to the riverbed. Whilst the total mass of fine sediment deposited on the riverbed is important, the relative proportions of organic and inorganic material can also control how this shapes the structure and function of ecological communities (McKenzie et al. 2022a, 2022b). Despite this, most research on fine sediment has been conducted without differentiating between these two components (Turley et al. 2015; Doretto et al. 2018; Gieswein et al. 2019); but see Murphy et al. (2015) and more recently Mathers et al. (2023, 2024) who demonstrate the importance of discriminating between organic and inorganic components when considering macroinvertebrate responses. The lack of detailed mechanistic research has resulted in a constrained understanding of the implications of excess fine sediment for aquatic biota, which is crucial for implementing effective monitoring and management of this global stressor.

The supply of organic matter to river systems is vital, providing a food source and habitat for benthic organisms (Jones et al. 2012). Organic matter can be introduced to river systems through natural (e.g., leaf litter and woody material) or anthropogenic (e.g., agricultural runoff and wastewater inputs) sources. Some systems, such as exposed deforested upland areas, can be limited in organic matter supporting only simple trophic systems dependent on autotrophic production (Tank et al. 2010). However, excess organic sediment can negatively alter the trophic state of river systems. Increases in microbial activity through decomposition of the organic material reduces the availability of oxygen, increasing the rate of anaerobic processes, thereby altering the metabolic balance of the riverbed (Zhu et al. 2022). When coupled with naturally high inorganic fine sediment substratum, pore space is sufficiently reduced which increases the entrapment of organic matter further (Sear et al. 2014). This ultimately limits hydraulic exchange and further reduces oxygen availability (Bjornn and Reiser 1991), with many species sensitive to oxygen depletion and the associated chemical changes (Von Bertrab et al. 2013).

Excess quantities of inorganic sediment can affect food availability and reduce the feeding efficiency of filter feeders (through rapid gut filling; Lemly 1982; Strand and Merritt 1997; Fossati et al. 2001), grazers and scrapers (through burial of biofilms and coarse particulate organic matter; Couceiro et al. 2010; Doretto et al. 2016), and moreover, can directly reduce interstitial habitat availability (Descloux et al. 2014; Mathers et al. 2019a). Sediment particles also have the potential to clog gill surfaces, affecting respiratory and osmoregulatory processes (McKenzie et al. 2020). Numerous authors have concluded that although macroinvertebrate responses could be observed using quantitative data, disentangling the direct and indirect effects and the specific mechanisms driving the responses was not possible (Connolly and Pearson 2007; Cover et al. 2008; Buendia et al. 2013c; Culp et al. 2013) meaning that further research is urgently required (Conroy et al. 2016). Investigating the responses to the individual components of fine sediment (i.e., organic, inorganic and total sediment) driving changes to the structure and function of macroinvertebrate communities is warranted to elucidate the different mechanisms responsible.

The flux of organic matter to riverine systems is dependent on a range of landscape and climatic factors which influence the supply and delivery of organic material (Owens et al. 2005; Collins et al. 2014). As such, landscape context has been demonstrated to be highly important when considering ecological responses to fine sediment (Mathers et al. 2022, 2024). For example, fine sediment inputs from mining and construction sources typically deliver lower quantities of organic matter compared with those from agriculture (dos Reis Oliveira et al. 2019, 2020). Yet, there is variation in fine sediment inputs from agriculture. Davis et al. (2022) observed that variations in the input of fine sediment differed in accordance with land use intensity. Further, partitioning of agriculture by the relative contributions of arable vs. pastural land use has been found to be a key factor in controlling macroinvertebrate community responses (Schürings et al. 2022). In addition to landscape context, managers and researchers must also consider the influence of season in controlling both fine sediment dynamics (both delivery and storage) and the lifecycle of macroinvertebrates. Seasonal variation in instream sediment dynamics is highly influenced by the catchment hydrological regime and antecedent flow characteristics, with the presence of organic material further influenced by riparian and instream sources such as leaf litter and macrophyte breakdown (Collins et al. 2013; Wohl et al. 2015). Macroinvertebrate assemblages themselves also demonstrate natural annual or multi-annual fluctuations intrinsically linked to biological traits, such as the aquatic stages of their life cycle and the number of generations of an organism per year (voltinism) (Tachet et al. 2010), which likely influence the strength of the fine sediment association (Mathers et al. 2017). Recent research has also illustrated that resource partitioning of silt deposits, which are often richer in organic matter, varies with season, with much greater occupancy (abundance and richness) by macroinvertebrates in autumn compared with spring (Mathers et al. 2023). In combination, these factors can make it difficult to separate the effects of excess fine sediment on macroinvertebrates from the natural seasonal changes in community assemblage (Buendia et al. 2013a).

To address the knowledge gaps identified above, we sought to provide evidence as to the potential influence of the different components of fine sediment (inorganic, organic and total mass) in structuring macroinvertebrate communities and how these may vary as a function of season. We predicted that:

1. Taxonomic and functional facets of the macroinvertebrate communities would respond to organic and inorganic components of fine sediment differentially; specifically, communities will be more sensitive to the organic component of fine sediment.
2. Taxonomic and functional macroinvertebrate responses to the organic and inorganic components would vary as a function of season (spring vs. autumn); specifically, communities will demonstrate a lower change point in autumn than in spring.

Prediction 1 was tested using field-survey data from the United Kingdom and New Zealand as examples, whilst prediction 2 was examined using field-survey data from the United Kingdom only due to data availability.

2 | Methods

2.1 | Data Collection

Paired fine sediment and macroinvertebrate data were aggregated for rivers in the United Kingdom ($n = 337$) and New Zealand (Southland region; $n = 422$). Data from the former were collected for academic purposes (to support national policy) whilst the latter was a combination of academic research and via Environment Southland (a regional government agency) regulatory monitoring. All data were collected in summer (December to February, or into early autumn where flows restricted sampling access) in New Zealand, and in spring (May to July, $n = 174$) and autumn (September to November, $n = 163$) in the United Kingdom. All sites comprised wadeable streams and both sediment and macroinvertebrate sampling were carried out following standardised methods within each respective region (Murray-Bligh et al. 1997; Stark et al. 2001). Limited availability of paired invertebrate and fine sediment data which also included the composition of fine sediment (organic and inorganic components) narrowed the spatial scope of our study, particularly in New Zealand where such data was only available for the South Island. Detailed information on data sources and site selection can be found in Appendix S1.

Fine sediment was sampled using the same fully quantitative method; known either as the disturbance method in the United Kingdom (Collins et al. 2005; Duerdoth et al. 2015) or the 'Quorer' method in New Zealand (Quinn and Cooper 2010). Both methods rely on the isolation of a patch of riverbed and overlying water column by pushing an open-ended cylinder (of known diameter) into the riverbed to achieve a seal from the adjacent flow. In both methods, the top 10 cm of bed sediment within the cylinder was vigorously agitated to resuspend any deposited fine sediment and homogenise fine sediment distribution in the water column, the volume of the water column measured, and a known volume of water sampled. Water samples were filtered, dried and weighed to calculate the total sediment mass and mass of organic sediment obtained via Loss On Ignition (LOI) at 500 C–550°C. Subsequently, individual sample mass was converted to mass of sediment per unit area of riverbed using the volume of water within the cylinder (Duerdoth et al. 2015). Background water samples were taken to correct for turbidity levels outside of the cylinder, although sampling in high flow events was avoided. The two techniques in each country (New Zealand vs. United Kingdom) differ in the duration of agitation (15 s vs. 1 min), number of samples collected per site (six vs. four) and calculation of reach average sediment quantities (arithmetic vs. geometric). However, both provide quantitative data on the mass ($\mathrm{g\,m^{-2}}$) of inorganic sediment (SIS), organic sediment (SOS) and total fine sediment (total) at the stream reach scale using well developed methods which have been tested for their accuracy (Clapcott et al. 2011; Duerdoth et al. 2015) and we only consider results within their respective country. Additionally, we calculated the proportion (%) of organic sediment (SOS.prop) which has been shown to be related to macroinvertebrate community diversity but not yet extensively examined between seasons (Murphy et al. 2017).

Macroinvertebrates were collected using standardised methods and taxa were identified to mixed taxon level (largely species or genus) following the respective standard practice for monitoring macroinvertebrate communities nationally. In New Zealand, data were collected either via Surber sampling or kick net sampling methods in riffle areas according to standard protocols (Stark et al. 2001). In the United Kingdom, a 3 min multi-habitat kick sample, followed by a 1 min hand search for taxa likely to be missed by the kick-sampling method (e.g., taxa found on tree roots or large boulders) was conducted (Murray-Bligh et al. 1997). Data were converted to relative abundance to ensure comparability (Chen and Olden 2020;

Chen et al. 2023) and resolved to family level to account for the mixed levels of identification (Everall et al. 2017; Stubbington et al. 2022). The publication of a new multi-national harmonised trait database (Kunz et al. 2022) allowed the comparison of functional measures of the community using the same combination of individual traits in each country (Table S2). A total of 71 taxa (out of 123) from the United Kingdom and 42 taxa (of 108) from New Zealand were assigned traits at the family level. The trait database was acquired as proportional traits (rather than fuzzy coded traits). The community weighted means (CWM) of each individual trait were calculated using the *FD* package in R (Laliberté et al. 2014).

2.2 | Data Analysis

All analyses were conducted in the R environment (R Development Core Team 2022). Accounting for variation in data collection methods between the United Kingdom and New Zealand, data were not combined for analysis, and we did not aim to draw direct comparisons between each country from the results. Instead, we aimed to determine overall patterns of macroinvertebrate responses and how these varied between sediment components within each country. The following analyses were carried out for all data (global) and individually by season (spring or autumn) for the United Kingdom only. Ten taxonomic and functional metrics were calculated to determine macroinvertebrate responses across the fine sediment gradients using commonly employed biodiversity metrics. Taxonomic metrics calculated comprised taxon richness, the richness of Ephemeroptera, Plecoptera and Trichoptera (EPT), EPT (relative) abundance, Simpson's index and Pielou's eveness. Functional diversity metrics (Botta-Dukát 2005; Villéger et al. 2008) were calculated using the *FD* package (Laliberté et al. 2014) and comprised functional richness (FRic–the minimum trait space encompassing all species), functional dispersion (FDis–the mean distance of each species in trait space to the centroid of all species), functional evenness (FEve–evenness in the distribution of abundance in functional trait space), functional divergence (FDiv–the relationship between trait values of the most abundant species and the centroid of the assemblage) and Rao's quadratic entropy (RaoQ–the sum of pairwise functional distances between species weighted by their relative abundances). Each functional diversity metric represents a distinct aspect of the variation in the functional trait community and incorporating all available metrics into analysis can help contribute to the mechanistic understanding of the invertebrate community responses to stressor gradients such as fine sediment (Mason et al. 2013). Spearman's rank correlations (due to non-normal data distribution) were applied to assess the performance of the metrics against each component of fine sediment. Pairwise correlations were corrected for multiple comparisons using the Holm-Bonferroni correction (Holm 1979).

Quantifying macroinvertebrate community compositional change across the gradients of the various sediment components (and the points on each gradient where community change were greatest) was carried out using two analyses suitable for non-linear responses to environmental gradients: Threshold Indicator Taxa Analysis (TITAN) and Gradient Forest (GF). Both analyses were conducted on taxonomic (as relative abundance) and functional (as community weighted means) measures of macroinvertebrate community data. For the TITAN analysis, analysis of each component of fine sediment is conducted individually. For Gradient Forest, SIS, SOS and Total sediment were included as a combined model, with SOS.prop excluded to avoid circularity.

TITAN (using the *TITAN2* package: Baker et al. 2015) is a nonparametric method which uses a resampling technique to detect abrupt changepoints in abundance and/or occurrence across an environmental gradient. Function parameters were set as 250 random permutations (*numPerm*) and 500 bootstrap (*nBoot*) replicates (Porter-Goff et al. 2013; Khamis et al. 2014; Lencioni 2018). A taxon or trait modality is identified as either responding positively ($z+$) or negatively ($z-$) to the fine sediment component if: (a) the change in frequency and abundance is the same for ≥ 95% of all bootstrap samples (i.e., pure) and (b) ≥ 95% of all bootstrap samples are significantly different from a random distribution ($p < 0.05$: i.e., reliable). The sum of all z scores (sum$z$) can be used as an indicator of taxonomic or functional community level threshold by identifying peaks along the gradient associated with the maximum decline or increase in frequency and/or abundance of negative and positive responders, respectively (Monk et al. 2007; King et al. 2016).

GF (*gradientForest* package; Ellis et al. 2012) is an extension of random forest (Breiman 2001) and applies a regression tree approach to quantify thresholds using nonlinear responses across an environmental gradient. First, separate random forests (ntree = 1000) are constructed for each taxon (or trait modality for functional community analysis). Next, GF aggregates the split value of each individual tree and their fit improvement across all taxa (or traits) with model fits of $R^2 > 0$. When quantifying the overall compositional change across the gradient, each split in the GF contributes relative to its fit improvement, and each taxon (or trait modality) contributes relative to its variance (as R^2) explained by the environmental predictors (Ellis et al. 2012; Compton et al. 2013; Chen and Olden 2020; Chen et al. 2023). One of the benefits of GF is that it is robust to unevenly distributed data across the environmental gradient, which is often the case with field survey data, as it standardises split density by the density of observed values across the gradient (Ellis et al. 2012; Wagenhoff et al. 2017). With the standardisation expressed as a ratio, points where the value is > 1 represent areas where compositional change is highest compared to the turnover occurring elsewhere across the gradient. Points across the gradient where the ratio exceeded 1:1 were identified using the R package *pracma* (Borchers 2019; Chen and Olden 2020).

3 | Results

3.1 | Taxonomic and Functional Responses to Individual Components of Fine Sediment Within New Zealand and the United Kingdom

Ephemeroptera, Plecoptera and Trichoptera (EPT) relative abundance (negative correlation) and taxonomic richness (positive correlation) were significantly correlated with most components of deposited fine sediment in both New Zealand and the United Kingdom (Figure 1, Table S1). Only the proportion (%) of

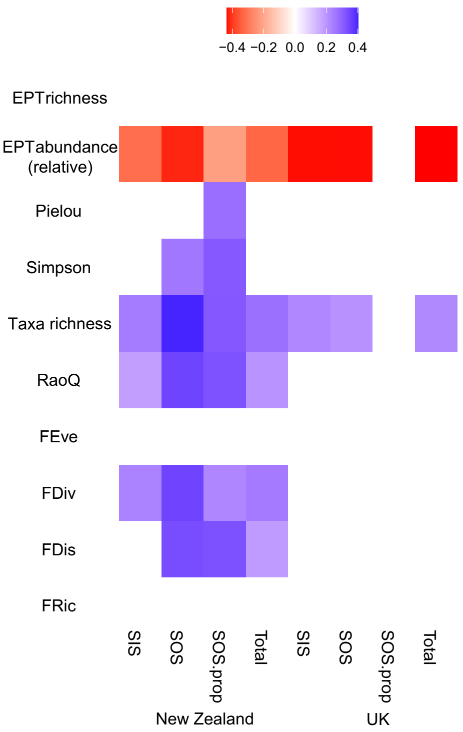

FIGURE 1 | Correlation matrix for taxonomic and functional metrics of community composition for the mass of inorganic sediment (SIS), mass of organic sediment (SOS), organic sediment proportion (SOS prop) and total mass of fine sediment (Total) in New Zealand and the United Kingdom. Colour ramp depicts the direction and strength of the Spearman's rank correlation coefficient. Only significant pairwise correlations ($p < 0.05$) are presented.

organic sediment (SOS.prop) in the United Kingdom was not significantly correlated with either metric. EPT relative abundance demonstrated the only negative correlation coefficient (i.e., response decreases as quantity of sediment increases) of all ten metrics tested. In contrast, taxonomic richness displayed a positive response. Regardless of the quantity of fine sediment, EPT relative abundance was higher overall in New Zealand and taxonomic richness was higher in the United Kingdom (Figure S1). No other macroinvertebrate metric was significantly correlated with any component of fine sediment in the United Kingdom.

In New Zealand, five other macroinvertebrate metrics displayed significant positive correlations which varied by sediment component, but in general, the responses were predominantly driven by the organic component. SOS and SOS.prop were correlated with the greatest number of macroinvertebrate metrics (six and seven, respectively, out of a total of ten). Functional metrics demonstrated a mixed response to fine sediment, with Rao's Quadratic Entropy (RaoQ) and functional divergence (FDiv) being significantly correlated with all sediment components, whereas functional evenness (FEve) and functional richness (FRic) were not significantly correlated with any component of fine sediment in either country.

In New Zealand, when considering the location of the change points determined by TITAN, there was a differential response between the positively (fsumz+) and negatively (fsumz−) responding trait groups for the SOS component (with the change point of negatively responding traits being considerably higher), but the change points were determined to be similar between groups for the inorganic sediment (SIS), SOS.prop and total components (Figure 2). In contrast, in the United Kingdom, positively and negatively responding trait change points were similar for the SOS and SOS.prop components but exhibited discrepancies for the SIS and total components. However, all functional communities (with the exception of SOS.prop in New Zealand) for both countries had wide confidence intervals, suggesting uncertainty in the change point location. In the United Kingdom, there was a greater differential response between the positively and negatively responding taxonomic communities for the SOS and SOS.prop components than for SIS and total sediment (Figure 2b,d,f,h). By contrast, in New Zealand, the change points of the positively and negatively responding taxonomic communities for SOS were similar, but SOS.prop had a large differential response between positively and negatively responding taxa (Figure 2a,c,e,g).

For interpretation of the individual taxon and trait modality responses, we only considered three sediment components (SIS, SOS, total sediment; not SOS.prop). In the United Kingdom, an equal number of taxa were identified as indicators of SOS, SIS and total sediment components. In contrast, in New Zealand, more taxa were identified as indicators of the SOS component in comparison to SIS and total (which were equal; Figures S2–S17). Most taxa/trait modalities were allocated by TITAN to the same group identity (i.e., *z*− or *z*+) across all three components of deposited sediment. In almost all cases, where a taxon or trait modality was identified as an indicator of the SIS component, the same taxon/trait modality was also identified as an indicator of the total sediment mass. By contrast, several taxa/trait modalities identified as indicators of SOS were not identified by any other sediment component.

In NZ, seven taxa were identified as indicators of SOS only (Table 1), five of which were positively responding and two as negatively responding. Functionally, shredders, filterers and burrowers were all identified as responding positively to only the SOS component, whilst no trait modalities were identified as responding negatively to SOS only. Sessile macroinvertebrates were identified as positively responding to both SOS and the total deposited sediment component. In the United Kingdom, seven taxa were identified as indicators of SOS only (Table 1), with five of these responding positively and two responding negatively. Seven taxa were identified as indicators of both the SIS and total deposited sediment components. Functionally, predators and small macroinvertebrates were identified as indicators of deposited SOS only, with predators identified as positively responding and small macroinvertebrates identified as negatively responding. Swimmers (negatively responding), semivoltine and bi/multivoltine taxa (positively responding) were identified as indicators of both the SIS and total deposited sediment component.

Overall, for both countries and across all three components of deposited sediment, more indicator taxa were identified by TITAN as positively responding to fine sediment than negatively responding. A smaller proportion of taxa was identified as negatively responding to deposited sediment in New Zealand than in the United Kingdom (Figures S2–S9). The 17 taxa responding positively to all sediment components in New Zealand belonged

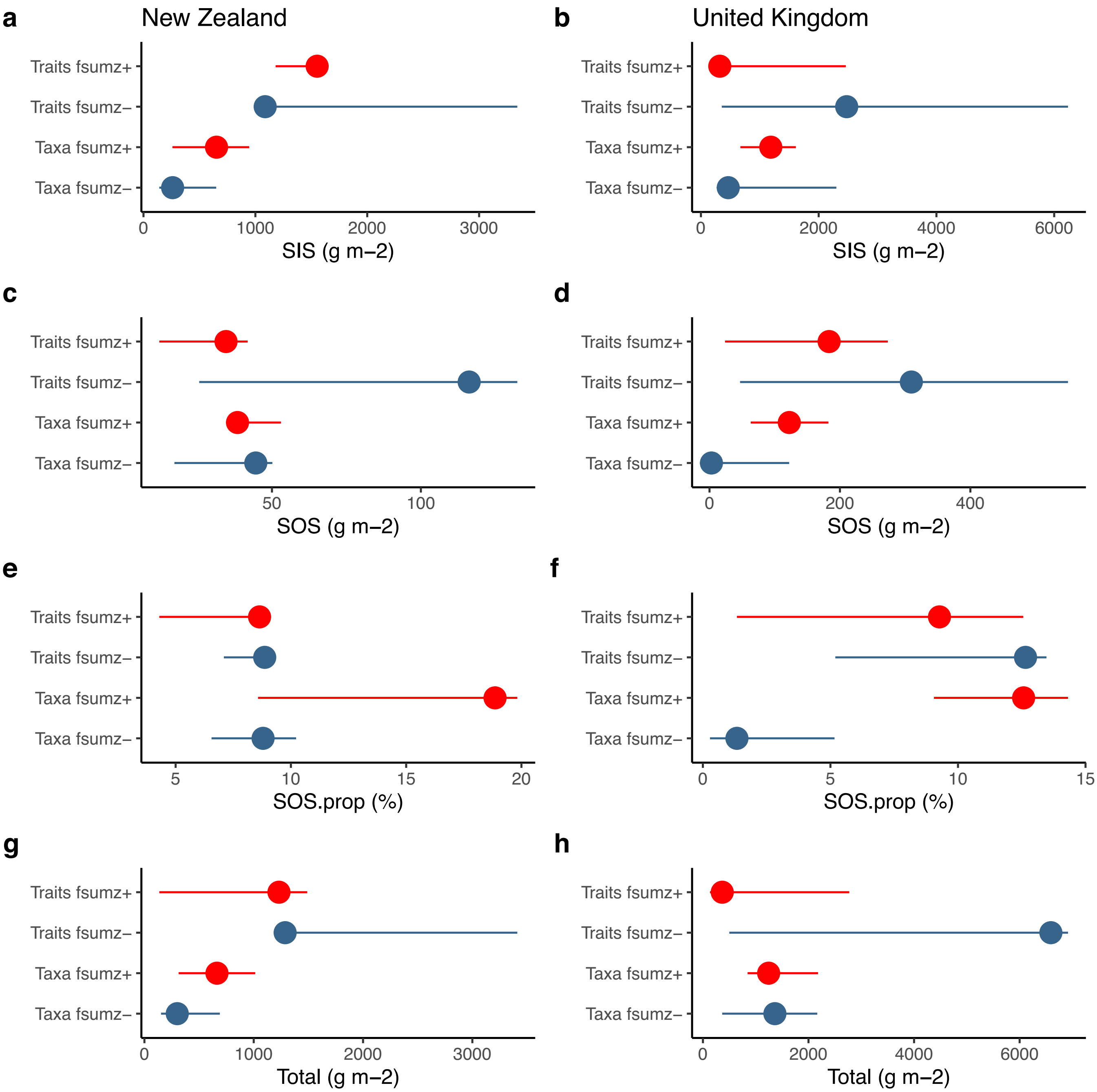

FIGURE 2 | Observed sum*z*– (blue) and sum*z*+ (red) maxima (i.e., change points) identified by Threshold Indicator Taxa Analysis (TITAN) of taxonomic (taxa) and functional (traits) macroinvertebrate communities in New Zealand (a,c,e,g) and the United Kingdom (b,d,f,h) for inorganic sediment (SIS), organic sediment (SOS), organic sediment proportion (SOS.prop) and total mass of fine sediment (Total). The sumz– or sumz+ represents the community level threshold (or change point) of taxa/traits identified as either negatively or positively to fine sediment respectively. Community change points depicted as circles with 5th and 95th percentile distributions as horizontal lines. Change points are filtered to show only pure and reliable taxon/traits. Taxa and trait TITAN community change points have been plotted together for comparison. Note the change in scale on the X axis.

to a wide variety of macroinvertebrate orders. Of the nine taxa which were identified as negatively responding, seven belonged to EPT orders with one Diptera (Limoniidae) and one Coleoptera (Elmidae). Of the taxa responding positively across the three deposited sediment components in the United Kingdom (28 taxa), Diptera (seven taxa) had the highest occurrence compared with all other orders represented. In comparison, of the 21 taxa identified as responding negatively to all deposited components, 14 were families from EPT orders (Ephemeroptera–four, Plecoptera–three and Trichoptera–seven; Figures S10–S17).

Considering the Gradient Forest models, the importance of each sediment component (as individual predictor variables in the model) was consistent within both countries and between the taxonomic and functional models (Table 2). SOS was determined to be the most important component, with the SIS component being the least important. However, the difference between the importance of the two components was more pronounced in New Zealand. Only a few taxa/trait modalities were identified as having positive fits (i.e., $R^2 > 0$) by GF (Table S2).

TABLE 1 | Observed group identity (z− or z+) of TITAN results for New Zealand and the United Kingdom where individual taxon/trait modality response varies between inorganic sediment (SIS), organic sediment (SOS) and total mass of fine sediment (Total).

Taxa	SIS	SOS	Total	Trait	SIS	SOS	Total
New Zealand							
Ceratopogonidae		z−		Shredder		z+	
Conoesucidae	z−		z−	Filter feeder		z+	
Helicopsychidae		z+		Burrower		z+	
Hirudinea		z+		Sessile		z+	z+
Hydraenidae	z−						
Isopoda		z+					
Muscidae		z−	z−				
Polycentropodidae		z−					
Staphylinidae		z+					
Stratiomyidae		z+					
The United Kingdom							
Calopterygidae		z+		Predator		z+	
Ceratopogonidae	z+		z+	Swimmer	z−		z−
Chironomidae	z+		z+	Small size		z−	
Cordulegastridae		z+		Semi-voltine	z+		z+
Dixidae		z+		Bi/multi-voltine	z+		z+
Empididae		z−					
Hydraenidae	z−		z−				
Hydroptilidae	z−		z−				
Nematomorpha		z+					
Perlodidae	z−		z−				
Physidae		z+					
Psychomyiidae	z+		z+				
Simuliidae		z−					
Tabanidae	z+		z+				

Note: Taxon/trait modalities that were identified as being a pure and reliable indicator of all three components of fine sediment were excluded. Only the three sediment components measured on the same scale (i.e., not SOS.prop) are included for individual taxon/trait modality interpretation.

3.2 | Seasonal Variation in Taxonomic and Functional Responses to Individual Components of Fine Sediment in the United Kingdom

When comparing spring and autumn in the United Kingdom, EPT relative abundance was significantly associated with all components of sediment (except for SOS.prop) in both spring and autumn (Figure S18). Taxonomic richness demonstrated a significant correlation in autumn for all components of sediment (except for SOS.prop) but was not associated with any fine sediment component in spring. Both EPT relative abundance and taxonomic richness scores were slightly higher in spring than in autumn (Figure S19). The gradient of each fine sediment component was similar in both spring and autumn, although autumn demonstrated greater maximum values in all instances (Figure S2). As SOS.prop was not observed to be related to the invertebrate community in the United Kingdom (Figure 1), this component is not presented further for the seasonal analysis.

TABLE 2 | Overall importance (in descending order) of organic sediment (SOS) and inorganic sediment (SIS) for each Gradient Forest model, weighted across ecological indicator outputs (i.e., R^2 weighted importance).

New Zealand		The United Kingdom	
Taxonomic	***Functional***	***Taxonomic***	***Functional***
SOS (0.023)	SOS (0.011)	SOS (0.003)	SOS (0.003)
SIS (0.007)	SIS (0.005)	SIS (0.002)	SIS (0.002)

Taxonomic community responses determined by TITAN were comparable across all sediment components (SIS, SOS and Total) for both spring and autumn (Figure S20). In contrast, there were variations in functional community responses between the two seasons, with change points for both positive and negative responders being slightly lower in autumn than in spring. When considering seasonal differences, in spring there were more taxa and trait modalities identified as indicators of only one or two components of fine sediment (Table 3). In spring, 12 taxa were identified as indicators of SIS and total deposited sediment and six taxa were identified as indicators of SOS only (Figures S21—S26). This finding was in contrast to autumn, where six taxa were identified as indicators of the SIS and total sediment components and four taxa were identified as indicators of the SOS component only (Figures S27—S32). The trait responses were more complex in spring, with two modalities being indicators of SIS only, two modalities being indicators of SOS only, two modalities being indicators of total sediment only and two modalities being indicators of both SIS and SOS. In autumn, two trait modalities were identified as indicators of the organic component only. There were no taxa or modalities that were identified in opposing groups (i.e., positive/negative) between the two seasons. However, more taxa were identified as indicators in spring (SIS = 41 indicators, SOS = 35, total mass = 42) compared to autumn (SIS = 34, SOS = 31, total mass = 33). For both seasons, the SOS component had the lowest number of taxa identified as indicators compared to the SIS and total components.

The gradient forest models for individual seasons in the United Kingdom followed the same pattern as the global responses (SOS >SIS: Table S3). When comparing the change in community structure between the seasons for each component, the peak thresholds (i.e., the point across the gradient with the highest ratio of density) for the taxonomic community were consistently lower in autumn than determined for spring (Table 4). Whilst the functional community depicted distinct peak thresholds for each component in spring, for autumn these were less apparent (particularly for SIS), with both components displaying multiple lower density peaks across the entire gradient (Figures S33–S36). There were more taxa identified by GF for the individual season models than the combined global model. Seven taxa and five trait modalities were identified in spring, and three taxa and three modalities were identified in autumn (Table S4).

4 | Discussion

4.1 | Taxonomic and Functional Responses to Individual Components of Fine Sediment in New Zealand and the United Kingdom

This study sought to enhance the knowledge base of macroinvertebrate responses to different components of fine sediment. Results demonstrate differential responses dependent on the facet of the community quantified (taxonomic or functional). Furthermore, the association with various components of fine sediment was not consistent within New Zealand nor the United Kingdom, thus confirming our first prediction. The organic content of fine sediment was found to be highly influential in structuring aquatic communities, particularly in New Zealand, whilst in the United Kingdom there were less pronounced differences between the relative importance of organic and inorganic sediment. It is likely that landscape scale factors (Buendia et al. 2013b; Mathers et al. 2022) are highly influential in structuring the delivery of fine sediment and subsequently the response of aquatic communities.

Agricultural land use in the catchments surrounding sampling sites was high in the United Kingdom (69%). Most sampling locations in the United Kingdom were located in headwater catchments of rural areas (first order streams), with agriculture being the predominant source of fine sediment (Zhang et al. 2014; Murphy et al. 2015; Jones et al. 2017). Pre-2005, the European Union Common Agricultural Policy subsidies were coupled with production levels, and this led to a period of intensive non-sustainable land management practices which resulted in elevated loss of topsoil from farmed land (Defra 2009; Graves et al. 2015). Whilst the proportion of pastoral land is roughly equal in the two countries, significantly more land is used as cropland (arable) in the catchments sampled in the United Kingdom (22% compared to 5% in New Zealand). Cropland has been found to supply less organic material through runoff than pasture (Collins and Zhang 2016; dos Reis Oliveira et al. 2018, 2020), and this coupled with a greater total mass of fine sediment in the sampled river systems may provide an explanation as to why the UK rivers demonstrated macroinvertebrate responses that were less specific to the organic content of fine sediment. Moreover, whilst it was previously thought that eroding arable topsoil was the dominant source of fine sediment in most UK rivers, recent sediment sourcing methods suggest that eroding channel banks delivering inorganic material are often the dominant source, again perhaps providing evidence as to why the macroinvertebrate community reacted less strongly to the organic component (Pulley and Collins 2023).

The macroinvertebrate communities in the Southland Region of New Zealand were found to be primarily related to the organic component of fine sediment. Streams in New Zealand have typically been shown to have poor retention of coarse organic material and therefore communities which rely on the direct utilisation of coarse particulate organic matter, such as leaves, rarely exist (Winterbourn et al. 1981). As such, macroinvertebrate communities in New Zealand differ from their Northern Hemisphere counterparts, with communities often being composed of fewer shredders and more predators (Winterbourn et al. 1981). Shredders, filter feeders and burrowers, which all rely on organic matter for either feeding or habitat preferences, demonstrated a positive response to organic sediment in this study, most likely reflecting that New Zealand streams are typically limited in organic matter. We also found evidence that more taxa responded exclusively to the organic component of fine sediment and that by only considering the inorganic or the total mass, we risk missing key ecological responses. For example, Ceratopogonidae and Polycentropodidae both responded negatively to the organic component, whereas Helicopsychidae, Hirudinea, Isopoda, Staphylinidae and Stratiomydiae all responded positively. These observations are confounded by methodological details, with invertebrate monitoring protocols in the Southland Region only targeting riffle habitats, therefore sampling taxa which are more likely to be 'sensitive' to the organic

TABLE 3 | Observed group identity (z– or z+) of TITAN results in spring and autumn in the United Kingdom where individual taxon/trait modality response varies between inorganic sediment (SIS), organic sediment (SOS) and total mass of fine sediment (Total).

Taxa	SIS	SOS	Total	Trait	SIS	SOS	Total
Spring							
Acarina		z+		Predator		z+	
Asellidae	z+		z+	Burrower			z−
Calopterygidae	z+		z+	Sessile			z+
Chloroperlidae	z−		z−	Swimmer	z−		
Cordulegastridae	z+		z+	Small size		z−	
Crangonyctidae		z+		Semi-voltine	z+	z+	
Enchytraeidae	z−		z−	Uni-voltine	z−	z−	
Ephemeridae	z+		z+	Bi/Multi-voltine	z+		
Gammaridae	z+		z+				
Glossiphoniidae	z+		z+				
Heptageniidae	z−		z−				
Hydraenidae	z−		z−				
Leptoceridae		z−					
Nemouridae		z+					
Ostracoda		z+					
Pediciidae		z+					
Planorbidae			z+				
Simuliidae	z−		z−				
Autumn							
Ancylidae		z−		Medium size		z−	
Athericidae			z−	Terrestrial oviposition		z+	
Chloroperlidae	z−		z−				
Dixidae		z+					
Ephemeridae	z+		z+				
Haliplidae	z+		z+				
Hydraenidae	z−		z−				
Lepidostomatidae		z−					
Lymnaeidae	z+	z+					
Physidae		z+					
Polycentropodidae	z−		z−				
Psychomyiidae	z+						

Note: Change points are filtered to show only pure and reliable taxon/trait modalities.

component of fine sediment (both in excess and/or limitation in these higher flow habitats). The organic component of fine sediment has rarely been considered in New Zealand with the majority of research using the 'Quorer' method focusing on inorganic sediment (e.g., Lange et al. 2014; Magbanua et al. 2016; Ramezani et al. 2016). Notably, the legal definition of sediment stress in some territories, including the European Union, is inclusive of both inorganic and organic components. However, New Zealand refers specifically to only '*inorganic particles deposited on the streambed that are less than 2mm in size*' (Clapcott et al. 2011). We demonstrate here that invertebrate communities likely respond strongly to the organic

TABLE 4 | Threshold change values ($g\,m^{-2}$) of inorganic sediment (SIS) and organic sediment (SOS) for macroinvertebrate communities in spring and autumn in the United Kingdom identified by Gradient Forest.

	Spring		Autumn	
	Taxonomic	Functional	Taxonomic	Functional
SIS	896, 1333, 2395, 8519, **9081***, 9914	2437, 2958, 4457, 5874, 8560, **9102***, 9831	**720***, 4628	489, 1234, 2108, 4756 **7250***
SOS	162, **1423***	265, 492, 661, **1423***	**93***	78, 214, 335, **1434***, 1797

Note: Threshold values are defined as locations where compositional change is highest compared to the turnover occurring elsewhere across the gradient. The largest (i.e., the point at which the ratio of densities is largest) change point for each individual model is indicated in bold. Models with distinct individual peak thresholds are identified with an asterisk (*).

component, and future research and management efforts should consider all fine sediment components to avoid misclassifying the ecological implications of excess fine sediment.

EPT derived metrics have been shown to reliably display close relationships with fine sediment (Conroy et al. 2016), second only to the performance of certain sediment specific metrics (e.g., EPSI and CoFSI; Turley et al. 2015; Murphy et al. 2015). In our study, the relative abundance of EPT taxa was consistently found to be most strongly related to all three fine sediment gradients. Moreover, most taxa identified as sensitive (i.e., responding negatively) to fine sediment in both countries comprised taxa from these orders. One study suggested EPT taxa respond negatively to the organic content of fine sediment (Conroy et al. 2016), with most EPT species preferring well oxygenated environments with low organic inputs. However, in our study, EPT taxa were sensitive across all components of fine sediment, not just the organic component. A reduction in coarse streambed substratum availability and associated interstices from fine sediment ingress has been shown to result in a shift from EPT taxa to non-insect macroinvertebrates such as molluscs and worms (Burdon et al. 2013). This shift may be why EPT metrics generally demonstrate strong relationships with increasing fine sediment gradients measured using visual assessments, even those that do not incorporate any element of sediment quality (McKenzie et al. 2022a, 2022b).

4.2 | Seasonal Variation in Taxonomic and Functional Responses to Individual Components of Fine Sediment

Our results confirmed our second prediction, that in the United Kingdom, there was a complex seasonal influence on the response of macroinvertebrate communities to individual components of fine sediment. Changes in the taxonomic measures of community occurred at lower quantities of fine sediment in autumn than in spring, particularly for the organic component. However, individual taxon and trait responses were more evident in spring. It is likely that both the natural seasonal and cyclical patterns in macroinvertebrate communities, coupled with temporal variations in fine sediment supply and retention, influence the community response (Mathers et al. 2017, 2019b; Davis et al. 2024).

Sediment supply from the catchment is influenced by significant flow events and discharge peaks throughout the hydrological year (Delmas et al. 2011; Mckenzie et al., 2021). In the United Kingdom, flow typically becomes more stable from late spring through to early autumn (Worrall et al. 2014). Overlying sediment is likely to accumulate on surface gravels through summer and into autumn due to a lack of mobilising flows (Wood and Armitage 1999). A large proportion of the accumulated material will be the finest fraction of sediments (i.e., silt $< 63\,\mu m$) which will account for a relatively small proportion of the total sediment mass. Whilst in our study, we found no overall difference in the mass of each sediment component (SIS vs. SOS) between seasons, autumn samples demonstrated the greatest maximum of sediment quantities (for all components). Conversely, in spring, where frequent fluctuations in discharge occur (Harris et al. 2000), the accumulation of finer fractions will be increasingly transient in nature, leading to much more dynamic and variable invertebrate communities (Mathers et al. 2023). In our combined analysis, the organic and inorganic components were equally as important for structuring the macroinvertebrate community in the United Kingdom. However, the taxonomic community changepoint for both components was substantially lower in autumn compared to spring. Changing seasonal environmental conditions, such as flow and fine sediment, are thus inherently linked to differential changepoint effects when considering the implications of fine sediment on macroinvertebrate communities. Our results suggest that, in the United Kingdom, macroinvertebrate taxonomic compositional change occurs at a lower threshold of fine sediment, both for inorganic and organic components, in autumn than in spring, but that the changepoint of functional composition does not differ seasonally.

Aquatic macroinvertebrate communities demonstrate a temporally variable composition associated with naturally occurring annual or intra-annual (i.e., seasonal) cycles (Butler 1984; Malmqvist 2002). We found more individual taxa and trait modalities were identified by TITAN as indicators across all components of fine sediment in spring (18 taxa and eight traits) compared with autumn (12 taxa and two traits). In northern latitudes, such as the United Kingdom, spring is characterised by an increase in water temperatures, light, and nutrient supply, which results in a rapid rise in primary production (Šporka et al. 2006). In the United Kingdom, most macroinvertebrates with aquatic larval stages (freshwater insects) will emerge as flying, terrestrial adults in spring. Emergence is usually a highly synchronised occurrence and is triggered by environmental cues in order to maximise reproductive success (Corbet 1964; Woods et al. 2022). In autumn and winter, ambient temperatures fall, daylight hours decrease, and the breakdown of macrophytes and riparian leaf litter occurs, thus increasing particulate organic matter in the substratum (Šporka et al. 2006).

Currently, and in recognition of these annual fluctuations, standard national (the United Kingdom) monitoring practice is to sample macroinvertebrate communities during spring and autumn and an average score is provided for environmental health assessments (Water Framework Directive–United Kingdom Technical Advisory Group (WFD-UKTAG) 2014). While this practice may be sufficient to provide a generic health assessment, research has increasingly considered the importance of season when monitoring fine sediment pressures (Davis et al. 2024). Several studies examining macroinvertebrate responses to fine sediment, in line with current biomonitoring practices, have found no difference in macroinvertebrate response across seasons (Turley et al. 2014; McKenzie et al. 2022a, 2022b). However, at the multihabitat scale (e.g., reach scale), combining seasonal samples reduces inter-site variation by increasing the number of shared taxa, potentially masking pressure-response relationships (Furse et al. 1984; Johnson et al. 2012; Carlson et al. 2013). When measured at the habitat patch level, macroinvertebrate biodiversity, particularly in silt deposits, may be seasonally inconsistent. For example, Mathers et al. (2023) found that season explained a greater amount of variance in functional community composition than the individual habitat unit, with gravel and vegetation habitat units being functionally more stable over time compared with silt habitats. Silt and sand habitat units were found to support similar functional macroinvertebrate composition in spring, but not during other seasons. In contrast, in our study, we found the largest differences between spring and autumn were recorded for taxonomic measures of macroinvertebrate communities, whereas functional responses between seasons were similar. This may be a reflection of the multihabitat sampling methods in the United Kingdom, and thus the loss of the information at finer levels that enables interpretation of functional macroinvertebrate specialists inhabiting individual habitat units (Larsen et al. 2009). This may also suggest inaccuracies in biological trait assignments and their equivocal response to fine sediment (Wilkes et al. 2017). Recent research suggests ecological traits, as opposed to biological, may better reflect functional responses to anthropogenic stressors (Sinclair et al. 2024).

Abiotic conditions (e.g., temperature and flow) in UK spring can be more variable than in autumn, and therefore, the macroinvertebrate communities sampled in spring will likely be predominately structured by a range of antecedent abiotic conditions making responses to fine sediment more difficult to identify (Buendia et al. 2013a). In early autumn, when flow conditions are more stable (Harris et al. 2000; Worrall et al. 2014), the community will likely be structured much more prominently by fine sediment conditions (predominantly the clay and silt organic component). Therefore, the communities in low excess fine sediment sites are likely to be distinct from those with high sediment inputs, resulting in overall lower community thresholds.

5 | Conclusion

Our study presents the first instance of quantifying macroinvertebrate responses to multiple components of fine sediment (organic, inorganic and total mass) within two distinct regions: Southland Region, New Zealand and the United Kingdom. Our results demonstrate that ecological responses vary depending on the component of fine sediment and the facet of macroinvertebrate diversity (e.g., taxonomic or functional) quantified. Further, seasonal changes in both taxonomic and functional diversity and sediment supply and deposition, may influence the ecological response changepoints. Current monitoring practices of only measuring total sediment mass (i.e., not separating out organic and inorganic sediment) or aggregating multiple seasons into annual assessments may overlook important responses to each individual sediment component and how these vary between different seasons. Considering excess fine sediment represents a global threat to the health of freshwater systems, understanding these nuances is crucial to the implementation of appropriate monitoring methods.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available from the Authors upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.