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# Temporal effects of fine sediment deposition on benthic macroinvertebrate community structure, function and biodiversity likely reflects landscape setting

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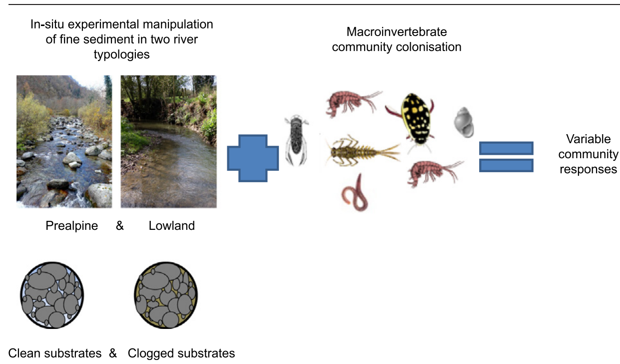
## HIGHLIGHTS

- Clogging effects on macroinvertebrates were examined in alpine and lowland rivers.
- Colonisation devices experimentally altered fine sediment content of substrates.
- Fine sediment typically resulted in nested taxonomic and functional communities.
- The biodiversity facet affected by fine sediment may differ by landscape setting.
- Monitoring and managing fine sediment likely requires context specific approaches.

## GRAPHICAL ABSTRACT

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## ABSTRACT

Globally, excessive fine sediment (particles <2 mm) deposition is acknowledged to have deleterious effects on aquatic biodiversity. However, the impacts are often equivocal possibly reflecting landscape context, although this is rarely considered. To address this, we examined the temporal response of macroinvertebrate taxonomic and functional diversity to experimental fine sediment clogging in a prealpine (Italy) and lowland setting (UK). Colonisation devices were installed *insitu* with either clean or clogged substrates and examined for short (7–14 days), medium (21–28 days) and long (56–63 days) timescales. Clogging resulted in altered taxonomic community composition in both the lowland and prealpine rivers and modified functional community composition in the prealpine river. Nestedness was consistently found to be the dominant process driving differences in taxonomic composition between the clean and clogged substrates in the prealpine environment, with clogged substrates forming a nested community. No dominant component structured lowland taxonomic communities. Functional community composition was driven by nestedness in both environments but was heavily dominant in the case of the prealpine river, possibly reflecting low functional redundancy. Widely employed community richness metrics (EPT, taxa and functional richness) only displayed a response to fine sediment loading in the prealpine environment but taxa characterized as sensitive to fine sediment as well as some functional feeding groups did exhibit differences in both settings. In the prealpine environment, the effects of fine sediment intensified over time for several community metrics. Although further research is required to corroborate our findings and extend our observations across more rivers and typologies, excessive fine sediment is a pervasive stressor affecting macroinvertebrate communities in prealpine and lowland environments. However, the biodiversity facets

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that responded to clogging differed between the two landscape settings probably reflecting wider environmental filtering. Monitoring and managing fine sediment loading likely requires context specific approaches to maximise ecological benefits.

## 1. Introduction

Excessive fine sediment (defined here as inorganic particles <2 mm) loading is widely considered to be one of the major threats to freshwater biodiversity globally (Dudgeon, 2019; Sánchez-Bayo and Wyckhuys, 2019). The negative ecological effects of fine sediment have been widely recognised for decades, however current sediment loading still exceeds historic levels (Collins and Anthony, 2008) and a mechanistic understanding of the abiotic and biotic controls driving the ecological implications of fine sediment for biodiversity is still lacking (Mathers et al., 2017a). The input, deposition and storage of fine sediment is a natural component of riverine ecosystem functioning, but anthropogenic modifications have significantly enhanced the delivery and storage of fines within lotic systems (Collins and Zhang, 2016). Moreover, climatic driven alterations to rainfall and runoff regimes are anticipated to intensify fine sediment pressures in the future (Burt et al., 2016).

In excessive quantities, fine sediment has deleterious implications for the entire trophic food web from algae through to macroinvertebrates and fish (see reviews in Wood and Armitage, 1997; Kemp et al., 2011; Jones et al., 2012a, 2012b, 2014). Reductions in interstitial pore space associated with the deposition and infiltration of fine sediment typically leads to impaired habitat quality and excessive sedimentation can ultimately result in habitat homogenisation (Burdon et al., 2013; Descloux et al., 2013). Where fine sediment clogs occur, it may also limit the transfer of resources and organisms between surface and groundwater dominated environments, with the hyporheic zone effectively being disconnected from benthic substrates (Hartwig and Borchardt, 2015; Mathers et al., 2014; Mathers et al., 2019a). Although fine sediment typically occurs in combination with other stressors (such as sediment-associated contaminants) recent research has identified that fine sediment is a master stressor and that catchment management practices should focus on alleviating fine sediment pressures to maximise ecological gains (Davis et al., 2018; Beermann et al., 2018).

Excessive fine sediment is widely acknowledged to alter the structure and function of macroinvertebrate communities (e.g., Mathers et al., 2017b; Descloux et al., 2014). Fine sediment can have direct physical effects on individuals such as the clogging of gills (McKenzie et al., 2020), burying of individuals (Wood et al., 2005; Conroy et al., 2018) and dislodging organisms during resuspension (Culp et al., 1986; Gibbins et al., 2007). Infilling of interstitial pore space can exclude larger bodied organisms (Mathers et al., 2019a; Peralta-Maraver et al., 2019) and may indirectly disadvantage some functional feeding groups due to impaired access to food or reduced food quality (Rabení et al., 2005; Doretto et al., 2016). As such, excessive fine sediment can act as environmental filter, with communities responding to fine sediment stress via the selection of taxa and biological traits that confer tolerance to elevated fine sediment conditions (Buendia et al., 2013; Murphy et al., 2017). However, research is still required to characterise the effects of taxa filtering associated with fine sediment on macroinvertebrate functional measures (but see Juvigny-Khenafou et al. (2021) for work in the multiple stressor literature).

Despite fine sediment representing a clear environmental filter on the distribution and diversity of macroinvertebrate communities (dos Reis Oliveira et al., 2020), few studies have examined the mechanistic process driving differences in beta diversity (the variation in community composition within a pre-defined area; Whittaker, 1960). Beta diversity can be separated into two distinct components: nestedness and turnover (Baselga, 2010). Nestedness refers to communities which represent a subset of the diversity of richer communities, whilst turnover represents the replacement of taxa or functional traits between the communities (Legendre, 2014). The small number of fine sediment studies which have directly decomposed beta diversity into its nestedness and turnover components suggest that nestedness is the primary process driving the changes in the communities due to a loss of sediment sensitive taxa (Doretto et al., 2017, 2021; Salmaso et al., 2021). However, to date these studies have focused solely on the taxonomic facet of biodiversity with the implications for functional communities lacking.

Environmental filtering may represent a key process to characterise the context-dependency and severity of fine sediment loading events for macroinvertebrate communities. Although fine sediment is widely acknowledged to result in negative ecological effects, specific responses to fine sediment are often equivocal (Wilkes et al., 2017). One reason for the apparent contradictory results between studies when individual taxa / groups or biological traits are examined may be the broad environmental context, which is rarely considered or reported. For example, lowland streams are typically subject to high levels of fine sediment input and deposition naturally due to their location and landscape setting. This means they may support communities which are better adapted to an abundance of fine sediment. In marked contrast, prealpine, upland and headwater streams typically support rheophilic taxa which display preferences towards coarser substrates subjected to limited fine sediment deposition. Both river types are under increasing fine sediment pressures but from differing anthropogenic stressors. Agricultural pressures in lowland rivers continue to deliver excessive diffuse fine sediment to rivers (Grabowski and Gurnell, 2016) whilst in prealpine rivers, climatic change, hydropower construction and land use change (forest management and agricultural practices) are driving increasing amounts of fine sediment runoff (Scheurer et al., 2009). Indeed, the high number of papers focusing on the availability, storage and effects of fine sediment in prealpine (and headwater) rivers in recent years (e.g., Gieswein et al., 2019; Doretto et al., 2018, 2021; Salmaso et al., 2021; Thollet et al., 2021; Misset et al., 2021) demonstrates the increasing need to consider context dependency when evaluating the ecological effects of fine sediment.

To date, much of the published research has focussed on fine sediment deposition and the subsequent ecological effects at scales specific to the study environment with little consideration of the context-specific effects on biota / biological traits or the transferability of results between locations. Moreover, transnational studies considering the ecological effects of fine sediment loading in rivers are absent. Therefore, we sought to investigate the importance of environmental context in controlling fine sediment effects by examining the temporal response of benthic macroinvertebrate community structure, function and biodiversity to experimental manipulation of fine sediment clogging in a lowland river (UK) and a prealpine river (Italy). Specifically, we sought to address the following research questions:

- Is the effect of increased fine sediment loading on macroinvertebrate taxonomic and functional composition consistent between prealpine and lowland rivers?
- Does fine sediment loading drive differences in the contribution of nestedness and turnover to total beta diversity; and is the contribution of these components consistent between lowland and prealpine rivers?
- If macroinvertebrate community taxonomic and functional effects are present due to fine sediment loading, are they temporally consistent?

## 2. Material and methods

### 2.1. Macroinvertebrate datasets

Two colonisation datasets were collated comprising macroinvertebrate samples collected from a prealpine environment (Doretto et al., 2017, 2018) and a lowland environmental setting (Mathers et al., 2017b). In both environments, colonisation devices (volume 0.65 $dm^{3,}$ surficial area of 60 and 65 mm) were installed in the riverbed and retrieved after three time periods (short, medium and long; see below and Appendix 1 for detailed sampling methods by location). All colonisation devices were filled with a gravel framework and assigned to two treatments; a) clean substrates which were free from fine sediment upon installation and thus acting as a control / reference condition, and b) clogged substrates in which fine sand (<2 mm) filled interstitial pore space (see Appendix 1 for more details by location). Prealpine colonisation devices were installed in a reach of the River Po (Paesana, Monviso Natural Park, NW Italy: 44°41′06" N, 7°14′04″ E; elevation 730 m a.s.l.) and retrieved 7 (short), 21 (medium) and 63 days (long) later. 15 replicated colonisation samples were installed for each treatment and sample period comprising a total of 90 samples. Lowland colonisation devices were installed in reaches on the River Chater (Rutland, UK, 52°37′29″N, 00°44′53″W, 96 m a.s.l.) and River Gwash (52°38′42″N, 00°44′ 42″W: elevation 105 m a.s.l.) both of which are tributaries of the River Welland, and retrieved after 14 (short), 28 (medium) and 56 days (long). Preliminary analyses indicated that the two lowland rivers reacted in a similar manner to sediment loading and as a result data from both lowland rivers were pooled to create a single dataset used throughout subsequent analyses. A total of 20 replicated colonisation samples were installed for each treatment and sample period across the two rivers, resulting in a total of 120 samples.

Both datasets were collected during baseflow conditions (prealpine pluvio-nival flow regime: 9th November - 11th January and lowland pluvial flow regime: 2nd July – 27th August). By conducting the experiments under comparable hydrological conditions in lowland and prealpine rivers, it was anticipated that taxa lifecycles would be as analogous as possible (see Breitenmoser-Würsten and Sartori, 1995; Bennett, 2007). In the UK, stable flow conditions were punctuated by small fluxes in river stage associated with summer rainfall events whilst in Italy minimal changes in river stage were observed during the study period when runoff is at it minimum. Natural substrate composition of the prealpine river consisted of boulders, cobbles and coarse gravels with localised fine sediment in depositional areas; and within the lowland rivers, substrate composition consisted of mixed cobbles and gravel with widespread fine sediment (ca. 20% of subsurface content). Approximate channel width and depth in the prealpine river were 6–7 m and 30 cm whilst lowland reaches were on average 4 m wide and 20 cm deep. Grassland and arable farming dominate the land use surrounding the lowland rivers whilst mixed broadleaf forest dominates in the prealpine river. Taxonomy across datasets was harmonised to ensure comparability between taxa lists providing a mixed resolution dataset. For further information on the individual sites and sampling methods please see Doretto et al. (2017, 2018), Mathers et al., 2017b; Mathers et al., 2019b and Appendix 1.

### 2.2. Functional traits

Macroinvertebrates were assigned to 11 biological 'grouping features' comprising 63 functional traits from the Tachet et al. (2010) European trait database (Table S1). The database employs a fuzzy coding procedure with faunal affinities to individual traits ranging from zero (no affinity) to three or five (high affinity). Trait values were therefore standardised so that each grouping feature summed to 1 (to ensure trait affinities had an equal weighting between taxa). For taxa recorded at a lower resolution than that of the trait database (family level), affinities of all genera recorded were averaged to provide a family score (sensu Gayraud et al., 2003). Taxa recorded at a higher resolution than family (e.g., Oligochaeta, Hydracarina) were excluded as were Chironomidae and Ceratopogonidae as these families demonstrate high trait variability (Serra et al., 2017; Tachet et al., 2010). A total of 52 (of 56) taxa were assigned functional traits. Subsequently a taxa x traits compositional matrix was constructed and used in subsequent analyses.

### 2.3. Statistical analysis

All analyses were conducted in the R Environment on abundance data (R Development Core Team, 2020).

#### 2.3.1. Taxonomic and functional composition associated with sediment treatment over time

Taxonomic and functional compositional differences between the two sediment treatments for each sampling period were visually examined via Principal Co-ordinates Analysis (PCoA) plots. Bray-Curtis dissimilarity matrixes were constructed for taxonomic communities and a Gower dissimilarity matrix (adapted for the fuzzy coded traits; Pavoine et al., 2009) was derived for functional communities. PCoA plots were subsequently created using the '*cmdscale*' function in the stats package. Statistical differences in community composition associated with sediment treatment (clean and clogged), time (short, medium and long) and their interaction were tested via permutational multivariate analysis of variance (PERMANOVA) using the '*adonis*' function in the vegan package (Oksanen et al., 2019). Where significant differences occurred by treatment, pairwise comparisons of differences were performed using the '*pairwise.adonis*' function (Arbizu, 2019).

Total beta diversity was decomposed into its nestedness and turnover components to investigate the dominant processes structuring taxonomic and functional differences in macroinvertebrate composition. Prior to functional beta analysis the taxa x traits matrix underwent hierarchical clustering using UPGMA with Gower distances following Cardoso et al. (2015). Taxonomic and functional total beta diversity, nestedness and turnover pairwise distance matrices were calculated for lowland and prealpine communities separately using the function '*beta*' in the BAT package (Cardoso et al., 2021). Subsequently, the mean total beta diversity, and mean contribution of nestedness and turnover for each clean vs clog comparison was calculated for each time period for prealpine and lowland communities. Mean taxonomic and functional total beta diversity were calculated and partitioned into mean turnover and nestedness components for clean, clogged and all substrates using the '*beta.multi*' function.

#### 2.3.2. Taxonomic and functional diversity associated with sediment treatment over time

Nine taxonomic and functional metrics known to respond to fine sediment stress were calculated from the raw data. Taxonomic metrics of community abundance, taxa richness, richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) and abundance of taxa characterized as sensitive to fine sediment according to sensitivity weightings provided in the Proportion of Sediment-Sensitive Invertebrates index (PSI; Extence et al., 2013) were calculated for each sample. Functional metrics of the abundance of shredders, collectors, and scrapers, functional richness and functional evenness were also calculated. Functional feeding groups were assigned based on the fuzzy coded Tachet et al. (2010) database and as a result some taxa were coded in more than one group. These three functional feeding groups were specifically examined as previous research has demonstrated their sensitivity to fine sediment (e.g., Relyea et al., 2000; Rabení et al., 2005; Doretto et al., 2016). Functional richness (FRic) represents the minimum convex hull encompassing all species and functional evenness (FEve) reflects the regularity in which species are distributed across functional space (Villéger et al., 2008). The two functional diversity metrics were computed using the '*dbFD'* function on a Gower dissimilarity matrix in the FD package (Laliberté et al., 2014) following 'fuzzy coding' standardisation (Chevene et al., 1994) using the '*prep.fuzzy'* function in the ade4 package (Thioulouse et al., 2018).

Linear models (LM) were constructed for each response variable by dataset and were fitted with the fixed interacting effects of sediment treatment and time using the '*lm*' function in the stats package. Where significant differences associated with sediment treatment occurred post-hoc pairwise comparisons of groups were performed using estimated marginal means, and *p-values* were adjusted for multiple comparisons via Tukey tests within the emmeans package (Lenth et al., 2020). All statistical models were validated by visually checking residuals (Zuur et al., 2009) and where necessary transformations performed (sediment sensitive, community abundance, shredders, scrapers and

FRic were sqrt transformed, collectors log + 1 transformed). Correlation between FRic and taxa richness (Villéger et al., 2008) was examined via spearman's rank correlation using the '*cor.test*' function in the stats package.

## 3. Results

A total of 10,861 individuals were recorded in the prealpine samples and 8,034 individuals in the lowland samples. 14 taxa were shared across

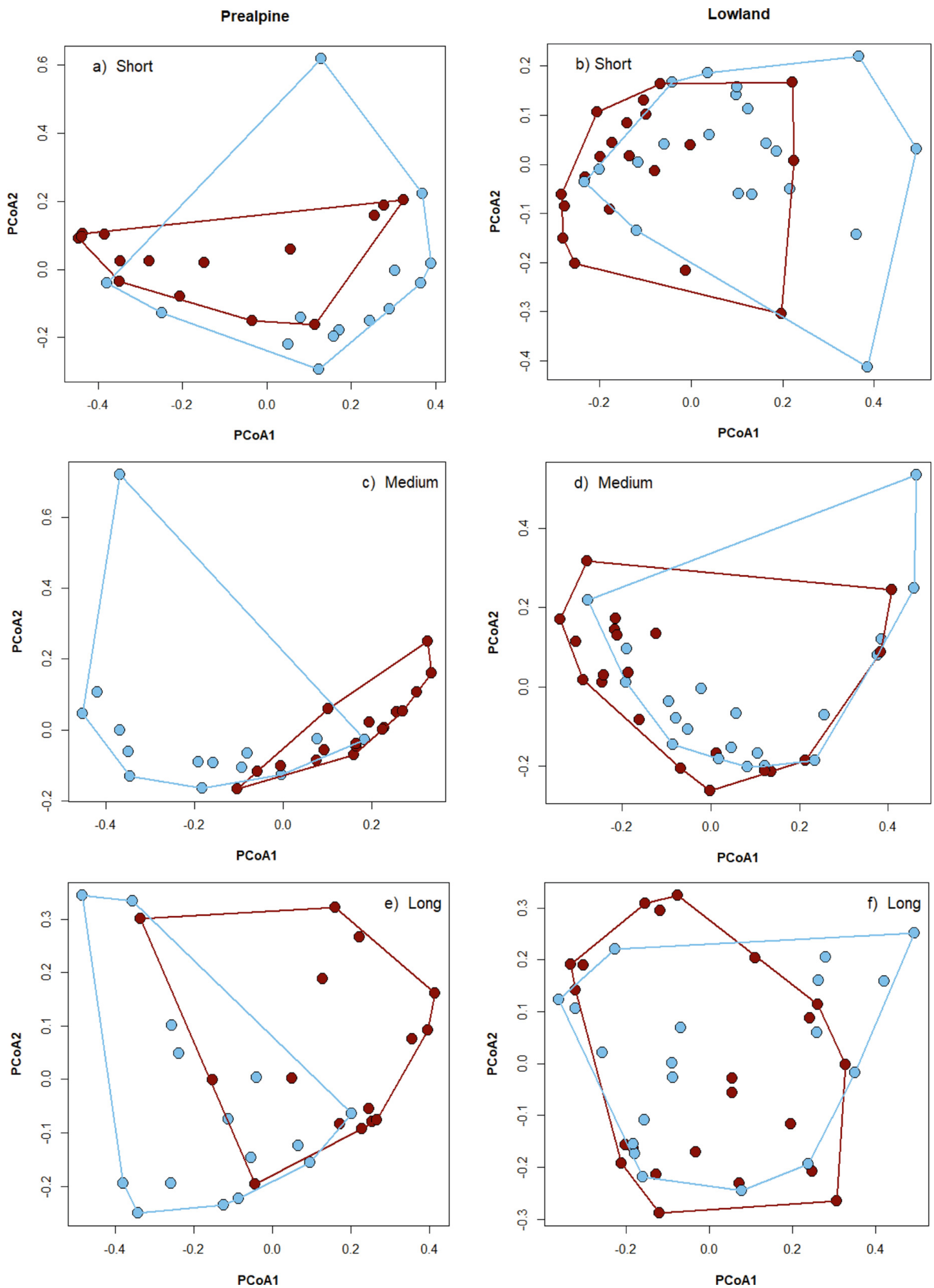


**Fig. 1.** Principal coordinates Analysis (PCoA) plots of macroinvertebrate taxonomic community composition from the prealpine (Italy) and lowland (UK) rivers by sediment treatment over time (short, medium, long). Red = clean substrates, and blue = clogged substrates.

**Table 1**
Summary of PERMANOVA testing the influence of sediment treatment, time and their interaction on taxonomic and functional community composition. Significant ($p < 0.05$) results are in bold.

| Factor | Prealpine | | | Lowland | | |
|---|---|---|---|---|---|---|
| | $R^2$ | F value | p | $R^2$ | F value | p |
| Taxonomic | | | | | | |
| Treatment | 12.39 | 15.41 | **<0.001** | 3.71 | 4.74 | **<0.001** |
| Time | 16.31 | 20.30 | **<0.001** | 3.62 | 4.64 | **0.003** |
| Treatment vs Time | 2.17 | 2.71 | **0.018** | 1.20 | 1.54 | 0.154 |
| Functional | | | | | | |
| Treatment | 7.57 | 7.30 | **<0.001** | 1.32 | 1.60 | 0.176 |
| Time | 3.05 | 1.47 | 0.148 | 3.29 | 2.00 | 0.071 |
| Treatment vs Time | 2.37 | 1.15 | 0.312 | 0.10 | 0.56 | 0.834 |

communities. Prealpine communities were dominated by *Leuctra* sp. (36.4%), *Amphinemura* sp. (19.9%), Chironomidae (22.3%) and Oligochaeta (7.2%) whilst lowland communities were dominated by *Gammarus pulex* (65.7%), *Potamopyrgus antipodarum* (9.6%) and Oligochaeta (5.3%). Taxa and functional richness demonstrated a strong and significant positive correlation ($r = 0.756, p < 0.001$).

### 3.1. Taxonomic and functional composition associated with sediment treatment over time

When the taxonomic facet of diversity was considered there was a statistically significant effect of sediment on macroinvertebrates in prealpine communities with differences in community composition evident for all three time periods (Fig. 1a,c,e; Table 1). In lowland communities the degree of separation between clogged and clean communities was less clear (Fig. 1b,d,f; Table 1). In prealpine communities, the effects of sediment persisted over time whilst in lowland communities, differences in community composition associated with fine sediment were evident only for the short and medium time-period and diminished over the longer time period (no significant differences between clean and clogged communities observed; Table 2). Functional community composition demonstrated differences associated with sediment treatment only for prealpine communities (Fig. 2; Table 1) with short and medium time periods being statistically different for pairwise comparisons between treatments (Fig. 2a, c,e: Table 2). In lowland communities there was little evidence of functional differences associated with sediment treatment (Fig. 2b,d,f).

When beta diversity was decomposed into its nestedness and turnover components, pairwise comparisons of clogged and clean substrates across the different time periods indicated that taxonomic prealpine communities recorded a strong contribution of nestedness (Fig. 3a; Table S2). Clogged communities demonstrated much lower diversity than clean substrates

**Table 2**
Summary of pairwise PERMANOVA testing for statistical differences between sediment treatment by time period for taxonomic and functional community composition. Significant ($p < 0.05$) results are in bold.

| Time period | Prealpine | | | Lowland | | |
|---|---|---|---|---|---|---|
| | $R^2$ | F value | p | $R^2$ | F value | p |
| Taxonomic | | | | | | |
| Short (7 and 14 days) | 14.42 | 4.55 | **0.005** | 3.71 | 4.74 | **0.001** |
| Medium (21 and 28 days) | 25.69 | 10.02 | **0.001** | 3.63 | 4.64 | **0.003** |
| Long (63 and 56 days) | 20.77 | 7.34 | **0.001** | 1.20 | 1.54 | 0.154 |
| Functional | | | | | | |
| Short (7 and 14 days) | 8.60 | 2.54 | **0.027** | 4.77 | 1.90 | 0.101 |
| Medium (21 and 28 days) | 16.67 | 5.80 | **0.002** | 1.46 | 0.56 | 0.717 |
| Long (63 and 56 days) | 5.29 | 1.57 | 0.179 | 1.09 | 0.43 | 0.773 |

(Fig. 4) and therefore formed a nested subset of clean communities across the three time periods (Table S3). Within the lowland environment, there was less dominance of either component of taxonomic beta diversity, although there was a slight tendency towards a greater contribution of nestedness for the medium time period (Fig. 3; Table S2). When functional beta diversity was decomposed, nestedness was also the dominant process structuring differences between control and clogged substrates in both prealpine and lowland communities, with this being highly evident in the prealpine environment (Fig. 3, Table 3; S3). In the prealpine setting, there was a temporal increase in the relative contribution of nestedness, whilst in the lowland setting nestedness was the greatest for the medium time period (Fig. 3b; Tables S3-S4).

Trait grouping features that were consistently affected by fine sediment in the prealpine river were body size (a total of 6 traits being >5% different compared to the control substrates over the three time periods when presence / absence is considered), reproduction (5 traits), respiration (5 traits) and locomotion (3 traits; Table S5). Taxa with a body size of >1-2 cm, that reproduce via cemented / fixed clutches of eggs and that respired by gills were consistently affected across all time periods with a loss of these traits in clogged substrates. In contrast, smaller taxa (>0.25–1 cm) and those that respired via spiracles were consistently more dominant in clogged substrates. The locomotion group of crawlers were lost in clogged substrates for the medium time period whilst burrowers increased in dominance for the medium and long time periods. Taxa which reproduce via isolated fixed eggs also increased in dominance in clogged substrates for short and long time periods (Table S5). Within lowland communities there was less consistency in traits affected by sediment loading, with different traits identified within each time period (Table S5).

### 3.2. Taxonomic and functional diversity associated with sediment treatment over time

Eight (of nine) of the community diversity metrics demonstrated a significant effect of fine sediment in the prealpine communities with only functional evenness displaying no statistical differences (Table 4). Five community diversity metrics demonstrated a sediment effect on lowland communities (Table 4). Within the prealpine environment, community abundance, taxa richness (Fig. 4a), EPT richness (Fig. 4b), sediment sensitive taxa abundance (Fig. 4c), shredder and scraper abundance and functional richness (Fig. 4d) all demonstrated increasing differences in values associated with fine sediment over time with clean communities displaying greater values (Table 5). In the case of prealpine functional richness, clogged and clean communities were not statistically different for the short time period, but for all other metrics all pairwise tests indicated a significant effect of sediment treatment (Table 5). Collector abundances displayed significant differences associated with fine sediment for all time periods but there was no temporal strengthening in sediment effects (with medium time period samples being most dissimilar to each other for sediment treatment) whilst scraper abundances were significantly different for short and long time periods with lower abundances in the clogged substrates (Table 5). For lowland communities, total abundance, sediment sensitive taxa abundance (Fig. 5c), shredder abundance, collector abundance and scraper abundance all demonstrated significant differences for the short and medium time periods, but differences between clean and sedimented substrates were not evident for the longer time period (Table 5). Taxa richness (Fig. 5a), EPT richness (Fig. 5b), functional richness (Fig. 5d) demonstrated no effect of fine sediment loading in lowland rivers.

## 4. Discussion

Our results clearly demonstrate that macroinvertebrate communities are affected by fine sediment clogging in both prealpine and lowland environmental settings. However, these effects varied between environmental setting (prealpine vs lowland) and for different biodiversity facets

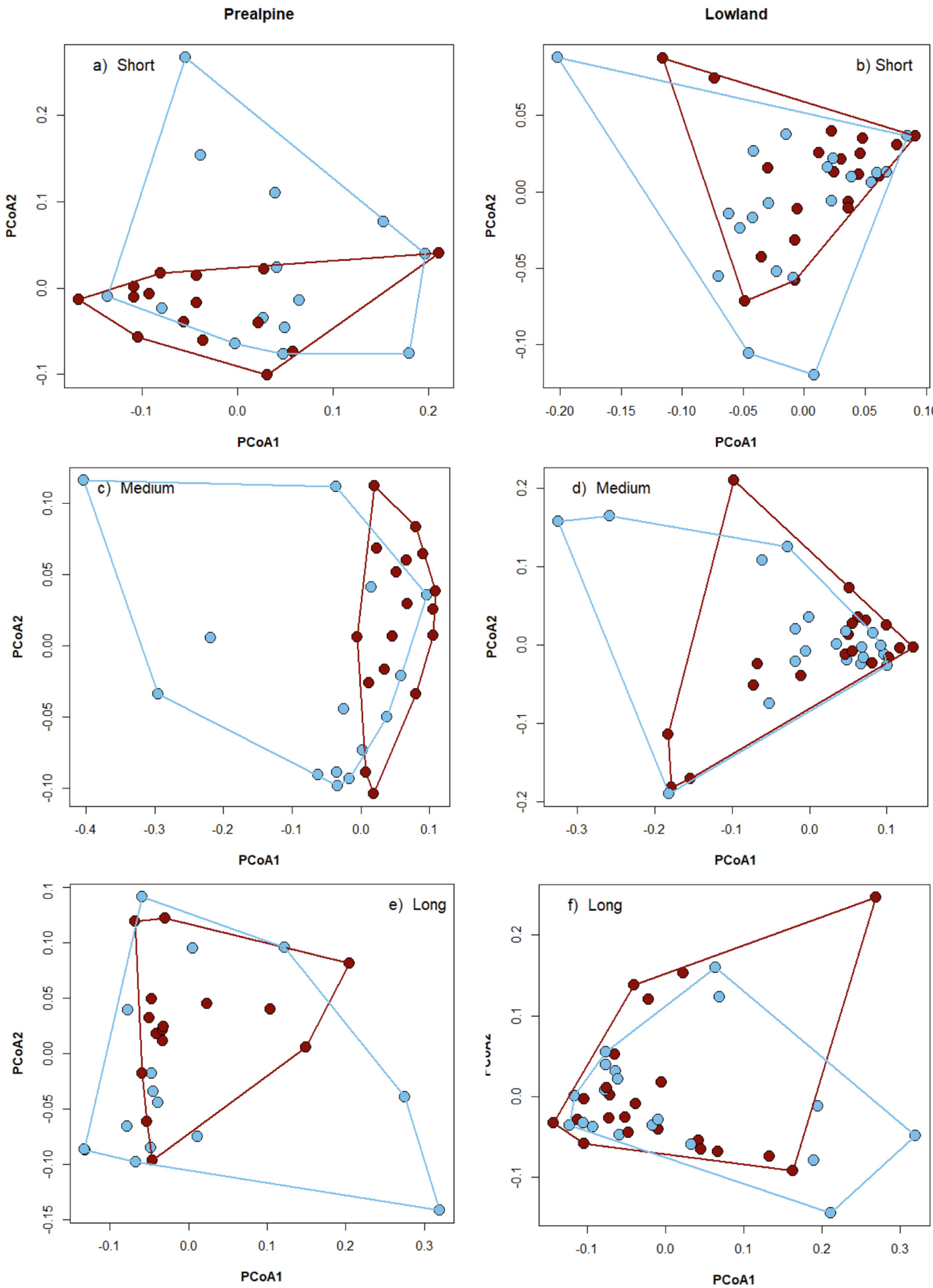


**Fig. 2.** Principal coordinates analysis (PCoA) plots of macroinvertebrate functional community composition from the prealpine (Italy) and lowland (UK) rivers by sediment treatment over time (short, medium, long). Red = clean substrates, and blue = clogged substrates.

suggesting that the effects of fine sediment loading are not always consistent and may be context specific. It should be noted that our results are based on one prealpine river and two lowland rivers and therefore further investigation is required to corroborate the validity and consistency of our findings. In the prealpine setting there was a significant effect of fine sediment on taxonomic and functional community composition with

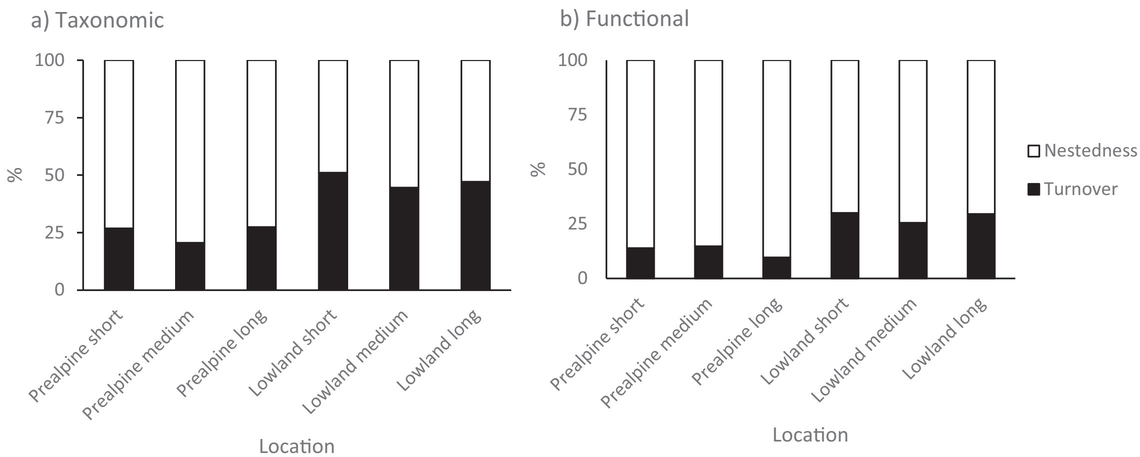


**Fig. 3.** Mean contribution of nestedness and turnover to the total beta diversity for pairwise comparisons between clean and clogged substrates for lowland and prealpine a) taxonomic and b) functional communities.

communities in clogged substrates comprising a distinct community relative to clean substrates. In marked contrast, lowland communities demonstrated some differences in taxonomic community composition (but not functional) for the short and medium time periods, but the effects of the fine sediment clogging treatment diminished over time; with no differences recorded for the long-time period (54 days). Given, that both environmental locations displayed a clear effect of fine sediment clogging in the short-term, it suggests that fine sediment loading has a strong filtering effect and represents an important stressor (Beermann et al., 2018; dos Reis Oliveira et al., 2020). It also provides additional evidence that fine sediment is highly influential in structuring macroinvertebrate community composition (Descloux et al., 2013; Mathers and Wood, 2016).

The longevity of fine sediment deposition effects on macroinvertebrate communities are less well documented but it is highly likely that the effects will also reflect the landscape context. The few studies that have examined the temporal effects of fine sediment loading on riverine faunal communities report equivocal results. In one instance, the effects of fine sediment remained temporally consistent (5 weeks) where additions were in streams with a naturally moderate fine sediment cover and that supported high taxa richness (Matthaei et al., 2006). In other contexts, such as streams that experience intensive pastural catchment land use and where fine sediment may be a consistent stressor, the temporal effects of sediment addition diminished over time (27 days – 5 weeks; Matthaei et al., 2006; Ramezani et al., 2014). However, recent work by Davis et al. (2021) reported that New Zealand rivers in intensive land-use settings displayed high variability in both deposited sediment and macroinvertebrate community composition over a 5-year period. The relative importance of fine sediment at the catchment scale may be linked to stream power and slope (Naden et al., 2016) with low-gradient streams potentially being equally affected if there is a diminished ability to remobilise deposited sediment.

In both study areas, there were no large discharge events during the study period that enabled a flushing of fine sediment from the colonisation devices and as such the clogged fine sediment remained *in-situ* for the entire experiment. As a result, the relative contribution of catchment context was evident in both environmental settings. Within the prealpine setting, the effect of fine sediment became accentuated over time, with six of the nine community diversity metrics (both functional and structural) displaying greater differences in values between clogged and clean substrates. The greatest implication of fine sediment loading on prealpine functional communities appeared to occur between the short and medium time-period, with no differences in functional richness between sediment treatments for the short time period, but which became increasingly evident over time with clean substrates supporting greater functional richness. It also appears that fine sediment impeded the functional gains seen in the clean substrates as colonisation progressed over time. It should be noted that colonisation times may be seasonally influenced being lowest in temperate rivers during winter months (Mackay, 1992). However, we envisage the implications of this to be limited within the prealpine river given that high initial colonisation rates were recorded in our study (see taxa / functional richness values) and that Matthaei et al. (1996) recorded rapid recolonisation following an artificial disturbance in a prealpine Swiss river associated with populations being adapted to frequent and high intensity disturbances.

In contrast, in the lowland setting, the effects of fine sediment loading were evident in the short term but dissipated over time when taxonomic structure and five (of nine) community metrics were considered. The breakdown in the long-term effect of fine sediment on lowland communities probably reflects the fact that the taxa present are adapted to fine sediment stress having already undergone some environmental filtering associated with landuse setting. This was evident in EPT richness with no marked differences between sediment treatment in the lowland river but that showed a strong sediment treatment effect that intensified over time in the prealpine setting. EPT taxa are widely acknowledged to be highly sensitive to fine sediment (Angradi, 1999) and therefore it is likely that some filtering of these taxa groups has already taken place at the landscape scale in the lowland environment. The lowland rivers were located predominately in arable / grassland whilst the prealpine river was surrounded by broadleaf forest. Land use has been shown to drive differences in community composition linked to instream fine sediment composition and ecosystem effects such as sediment oxygen demand (dos Reis Oliveira et al., 2018). This filtering may also provide some explanation as to why taxa richness was also only significantly affected by sediment treatment in the prealpine environment and not the lowland.

Despite the traditional community diversity metrics of EPT richness and taxa richness not detecting the fine sediment stress in the lowland setting, there were still clear patterns in the number of taxa that were classified as sediment sensitive (Extence et al., 2013) in both the prealpine and lowland environmental settings. Consistent and temporally strengthening differences in the number of sensitive taxa were evident in prealpine communities, whilst differences in lowland communities were observed for the short and medium time periods. The fact that differences due to fine sediment loading in a species poor sediment laden lowland river were clearly evident indicates the high-level effect that fine sediment exerts over lotic community structure and biodiversity. Although whether this was due to sediment clogging or the availability of clean substrate patches within a sediment rich river would require further examination.

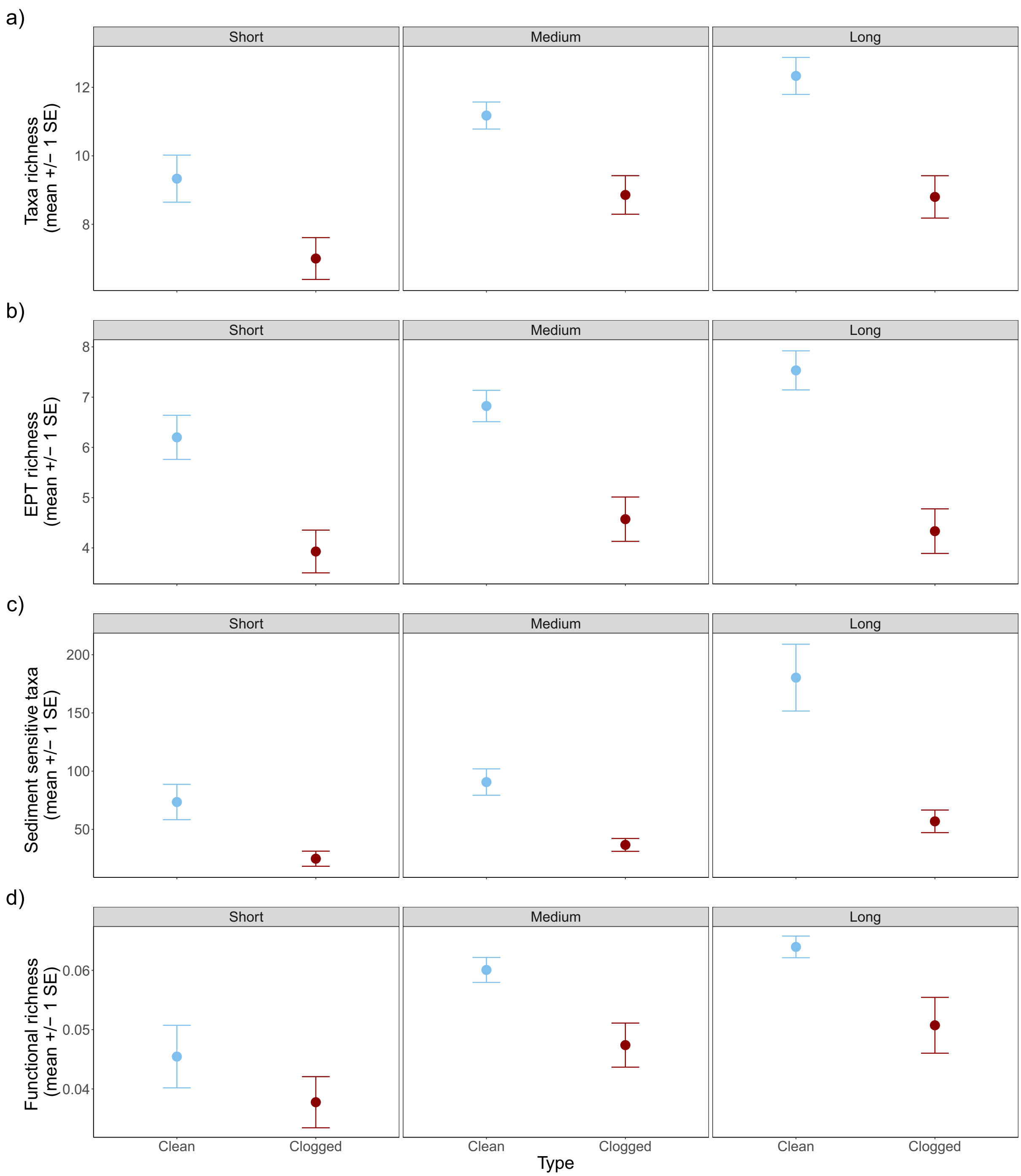


**Fig. 4.** Mean (±1 SE) prealpine a) taxa richness; b) EPT richness; c) sediment sensitive taxa and; d) functional richness by sediment treatment (clean or clogged substrates) over time (short, medium, long).

The difference in the strength of environmental filtering associated with fine sediment was also apparent when beta diversity was decomposed into nestedness and turnover components. In the prealpine environment, nestedness was consistently found to be the dominant process driving differences in taxonomic composition (mean overall contribution of 77%) between the clean and clogged substrates, with the latter forming a nested community. This nestedness of clogged communities most likely reflects the loss of sediment sensitive taxa including EPT groups (while taxa richness gains were observed over time in the clean substrates). The role of nestedness in structuring communities subjected to sediment loading supports recent findings in two other pluvio-nival rivers that have decomposed taxonomic beta diversity (Doretto et al., 2021; Salmaso et al., 2021) and earlier studies (one pluvio-nival and the other pluvial) which have examined nestedness only (Larsen and Ormerod, 2010; Buendia et al., 2013). In marked contrast, the contribution of turnover and nestedness was comparable for the lowland communities (although nestedness was still the most important process with an overall mean contribution of 54%). This suggests that there is no dominant process structuring total beta diversity in lowland rivers potentially reflecting the fact that these communities are

**Table 3**
Summary of pairwise taxonomic and functional beta, nestedness and turnover comparisons for clean, clogged, clean vs clogged and all substrates for lowland and prealpine communities.

| | Prealpine | | | | Lowland | | | |
|---|---|---|---|---|---|---|---|---|
| | Control | Clog | Clog vs Control | All | Control | Clog | Clog vs Control | All |
| Taxonomic | | | | | | | | |
| Total Beta | 0.51 | 0.58 | 0.62 | 0.58 | 0.48 | 0.48 | 0.49 | 0.49 |
| Nestedness | 0.39 | 0.43 | 0.47 | 0.44 | 0.27 | 0.23 | 0.27 | 0.26 |
| Turnover | 0.12 | 0.15 | 0.14 | 0.14 | 0.20 | 0.25 | 0.23 | 0.23 |
| Nestedness % | 77 | 74 | 77 | 76 | 57 | 47 | 54 | 53 |
| Turnover % | 23 | 26 | 23 | 24 | 43 | 53 | 46 | 47 |
| Functional | | | | | | | | |
| Total Beta | 0.44 | 0.53 | 0.54 | 0.53 | 0.40 | 0.42 | 0.42 | 0.41 |
| Nestedness | 0.38 | 0.44 | 0.51 | 0.46 | 0.30 | 0.27 | 0.30 | 0.29 |
| Turnover | 0.06 | 0.09 | 0.03 | 0.07 | 0.10 | 0.16 | 0.12 | 0.12 |
| Nestedness % | 86 | 83 | 94 | 87 | 74 | 63 | 75 | 71 |
| Turnover % | 14 | 17 | 6 | 13 | 26 | 37 | 25 | 29 |

already adapted to the presence of fine sediment in the environment and therefore did not react strongly to enhanced loading.

When functional beta diversity was decomposed, nestedness was found to be the dominant process structuring communities in both prealpine and lowland rivers. Like taxonomic communities, the functional communities in the clogged substrates represented a subset of those inhabiting the clean substrates in the prealpine system, with functional richness being significantly lower in clogged substrates at the medium and long time period (but not short). The positive correlation between taxonomic and functional richness, and the strong pattern of nestedness recorded within the prealpine system, may therefore reflect relatively low functional redundancy. As fine sediment loading selectively removes species the associated functional traits are also lost which most likely explains the high levels of nestedness observed in the prealpine setting. In contrast, lowland communities demonstrated no significant effect of fine sediment on functional composition or richness, being comparable between sediment treatments in all time periods. This may reflect relatively high functional redundancy within the lowland system associated with the strong environmental filtering that has already taken place from historical sediment loading. As such additional fine sediment in lowland settings may not alter community functioning despite having some implications for taxonomic structure and biodiversity.

In common with other studies that have considered the specific response of individual biological traits to fine sediment stress (Wilkes et al., 2017), the traits which are filtered and lost (based on P/A data) due to clogging were not consistent between the settings. However, in this instance it likely reflects the landscape context; in the prealpine stream, larger body sized taxa were consistently present less frequently in clogged substrates with smaller taxa becoming more dominant for both the short and long-time periods (Buendia et al., 2013; Larsen and Ormerod, 2010). As pore space is a key determinant in habitat accessibility, the infilling of interstitial spaces excluded larger bodied organisms (Mathers et al., 2019a; Peralta-Maraver et al., 2019), which may have been particularly important in the coarse-grained prealpine river. Respiration mode was also consistently affected in prealpine rivers, with taxa that respire by gills being lost in clogged substrates, whilst those that respire via spiracles increased their occurrence. This is in line with McKenzie et al. (2020) who provided mechanistic evidence to indicate that gill surfaces exposed to fine sediment become clogged driving macroinvertebrate sensitivity to fine sediment.

Many of the traits affected in the lowland and prealpine setting in this study were the same as those recorded in other studies (e.g., crawlers, burrowers, gill respiration, body size, Buendia et al., 2013; Rabení et al., 2005; Townsend et al., 2008). However, in marked contrast to the prealpine environment, there was no temporal consistency of affected traits lost in the lowland site. It is highly likely that as the lowland communities are more adapted to fine sediment that although these traits are susceptible to environmental filtering by fine sediment stress, the strength of this filtering is not a strong as in environments in which fine sediment is more temporally punctuated (e.g., flow related), diffuse in nature or localised as is the case in prealpine environments. As such the strength of these associations was less evident in the lowland environment, and when functional composition and functional richness was examined no significant response to fine sediment clogging was determined. Despite this there was some effect on functional feeding groups evident, with the abundance of shredders, scrapers and collectors being reduced in clogged substrates in both the prealpine and lowland environment setting. Within the lowland setting, these three feeding groups demonstrated differences between control and clogged substrates breaking down only for the long time period in line with the other affected community metrics (i.e., sediment sensitive taxa).

### 4.1. Wider implications of the study

The negative ecological effects of excessive fine sediment for aquatic diversity are unequivocal with habitat homogenisation acting as a filter on the wider species pool. However, the specific responses of taxa / traits and the severity of effects are often equivocal. Our results indicate that an understanding of the environmental context may be vital to disentangle the potential effects of fine sediment loading on instream ecology. Lowland stream communities, that are to some degree adapted to

**Table 4**
Summary of linear models testing the effect of treatment, time and their interaction on nine community metrics for prealpine and lowland communities. Significant ($p < 0.05$) results are in bold. D·F are provided in paratheses under each factor.

| Community metric | Prealpine | | | | | | Lowland | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Treatment (d.f. 1,84) | | Time (d.f. 2,84) | | Type × Time (d.f. 2,84) | | Treatment (d.f. 1,114) | | Time (d.f. 2,114) | | Type x Time (d.f. 2,114) | |
| | F value | p | F value | p | F value | p | F value | p | F value | p | F value | p |
| Community abundance | 47.55 | **<0.001** | 39.26 | **<0.001** | 1.53 | 0.130 | 8.07 | **0.005** | 4.59 | **0.012** | 1.142 | 0.323 |
| Taxa richness | 34.29 | **<0.001** | 9.55 | **<0.001** | 0.75 | 0.477 | 0.50 | 0.483 | 4.27 | **0.016** | 0.17 | 0.844 |
| EPT richness | 59.97 | **<0.001** | 2.40 | 0.097 | 0.89 | 0.416 | 0.42 | 0.520 | 0.52 | 0.597 | 0.21 | 0.809 |
| Sediment sensitive taxa | 49.72 | **<0.001** | 13.46 | **<0.001** | 1.69 | 0.191 | 8.54 | **0.004** | 0.77 | 0.463 | 0.95 | 0.400 |
| Shredder abundance | 53.62 | **<0.001** | 12.60 | **<0.001** | 1.59 | 0.210 | 9.25 | **0.003** | 1.21 | 0.303 | 1.51 | 0.226 |
| Collector abundance | 23.44 | **<0.001** | 17.59 | **<0.001** | 0.34 | 0.710 | 8.71 | **0.004** | 1.23 | 0.297 | 1.61 | 0.204 |
| Scraper abundance | 25.61 | **<0.001** | 12.68 | **<0.001** | 2.82 | 0.065 | 9.53 | **0.003** | 9.53 | 0.203 | 1.62 | 0.203 |
| Functional richness | 23.05 | **<0.001** | 10.77 | **<0.001** | 5.92 | **<0.001** | 1.26 | 0.265 | 0.95 | 0.391 | 0.09 | 0.914 |
| Functional evenness | 0.10 | 0.757 | 1.84 | 0.165 | 1.05 | 0.354 | 0.46 | 0.501 | 0.19 | 0.826 | 0.18 | 0.838 |

**Table 5**
Pairwise post-hoc comparisons between clogged and clean substrates for eight community metrics by each time period. Functional evenness was not significant in either river type and is not presented. Significant ($p < 0.05$) results are in bold. D.f of prealpine and lowland data are 84 and 114 respectively.

| Community metric | Prealpine | | Lowland | |
|---|---|---|---|---|
| | t ratio | p | t ratio | p |
| Community abundance | | | | |
| Short (7 and 14 days) | −2.79 | **0.007** | −2.34 | **0.021** |
| Medium (28 and 21 days) | −3.82 | **<0.001** | −2.17 | **0.032** |
| Long (63 and 56 days) | −5.31 | **<0.001** | −0.42 | 0.672 |
| Taxa richness | | | | |
| Short | −2.85 | **0.006** | −0.07 | 0.945 |
| Medium | −2.91 | **0.005** | 0.64 | 0.525 |
| Long | −4.38 | **<0.001** | 0.65 | 0.517 |
| EPT richness | | | | |
| Short | −3.88 | **<0.001** | 0.16 | 0.875 |
| Medium | −3.96 | **<0.001** | −0.63 | 0.530 |
| Long | −5.57 | **<0.001** | −0.65 | 0.515 |
| Sediment sensitive taxa | | | | |
| Short | −2.24 | **0.002** | −2.24 | **0.027** |
| Medium | −3.38 | **0.001** | −2.26 | **0.026** |
| Long | −3.97 | **<0.001** | −0.58 | 0.566 |
| Shredder abundance | | | | |
| Short | −3.36 | **0.001** | −2.29 | **0.024** |
| Medium | −3.63 | **<0.001** | −2.63 | **0.010** |
| Long | −5.69 | **<0.001** | −0.37 | 0.713 |
| Collector abundance | | | | |
| Short | −2.89 | **0.005** | 2.18 | **0.030** |
| Medium | −3.69 | **<0.001** | 2.66 | **0.009** |
| Long | −2.49 | **0.015** | 0.28 | 0.780 |
| Scraper abundance | | | | |
| Short | −2.07 | **0.042** | −2.41 | **0.018** |
| Medium | −1.84 | 0.070 | −2.51 | **0.014** |
| Long | −4.86 | **<0.001** | −0.45 | 0.655 |
| Functional richness | | | | |
| Short | −0.66 | 0.510 | 0.90 | 0.372 |
| Medium | −2.04 | **0.044** | 0.31 | 0.759 |
| Long | −5.50 | **<0.001** | 0.73 | 0.465 |

fine sediment loading due to their position in the landscape and river network, are likely to support a reduced species pool that may have already experienced some environmental filtering. In marked contrast, prealpine and upland streams which experience sediment loading that is intermittent (flow related), diffuse in nature or highly localised are likely to display stronger environmental filtering effects with a more sensitive species pool exposed to the fine sediment loading. These differences in environmental context likely determine the structural and functional components of the macroinvertebrate communities that respond to fine sediment pressures. For example, only the prealpine stream demonstrated strong functional community responses (composition and richness). Despite the reduced species pool however, lowland stream communities did respond to the sediment treatment over short time periods, with structural compositional changes being evident. Importantly, taxa classified as being sensitive to fine sediment (following Extence et al., 2013) clearly reflected the fine sediment stress in both environmental settings suggesting that despite potential landscape filtering, macroinvertebrate communities do respond to increased sediment loading (pollution) even in sediment rich streams.

Recent fine sediment-ecology research has focused on developing and refining sediment biomonitoring indexes that detect the pressure of fine sediment (e.g. Turley et al., 2016; Murphy et al., 2015; Doretto et al., 2018; Gieswein et al., 2019). However, this research suggests that although fine sediment does exert a pressure on the macroinvertebrate community, the specific effects are difficult to generalise and may reflect the environmental context which is rarely considered when such indexes are employed. As such we suggest that careful interpretation is required when interpreting the results of indices. In order, to accurately assess the potential effects of fine sediment loading it is likely that sediment indices should be calibrated or developed alongside distinct river typologies to account for the potentially overriding influence of environmental context. Such indices would then be better placed to accurately quantify fine sediment stress by identifying the specific components of diversity that are affected by excessive fine sediment loading, even when the local species pool may already have undergone environmental filtering at the landscape scale.

Although fine sediment stress is present in many locations globally, the results of this research suggest that it is vital to consider the context specificity of the river being studied / monitored. Sedimentation effects in prealpine streams (and most likely upland streams) were strong with eight (of nine) community diversity metrics and both taxonomic and functional community composition detecting fine sediment stress. In these environments we therefore suggest that management efforts should be targeted at minimising or preventing fine sedimentation within these sensitive ecosystems. However, it is also clear that lowland rivers are negatively affected by fine sediment with structural composition and five (of the nine) community metrics responding to fine sediment stress in the study. Patch-scale habitat diversity is likely important within these systems in maintaining a wider species pool (Wood et al., 1999). Efforts within lowland streams should therefore focus on limiting further fine sediment loading, identifying locations where fine sediment stress continues to exacerbate and structure the community and implementing management techniques that encourage patch scale habitat diversity. It is also likely that identification of fine sediment effects in both prealpine and lowland rivers would benefit from patch scale monitoring efforts rather than typically employed reach scale observations with fine sediment deposits often being localised even within lowland streams.

## CRediT authorship contribution statement

**Kate Mathers**: Funding acquisition, Project administration, Investigation, Conceptualization, Methodology, Formal Analysis, Visualization, Writing – original draft, Writing - review & editing. **Alberto Doretto:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Stefano Fenoglio:** Conceptualization, Methodology, Writing - review & editing. **Matthew Hill:** Conceptualization, Formal Analysis, Writing – original draft, Writing - review & editing. **Paul Wood:** Conceptualization, Methodology, Writing - review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.154612.

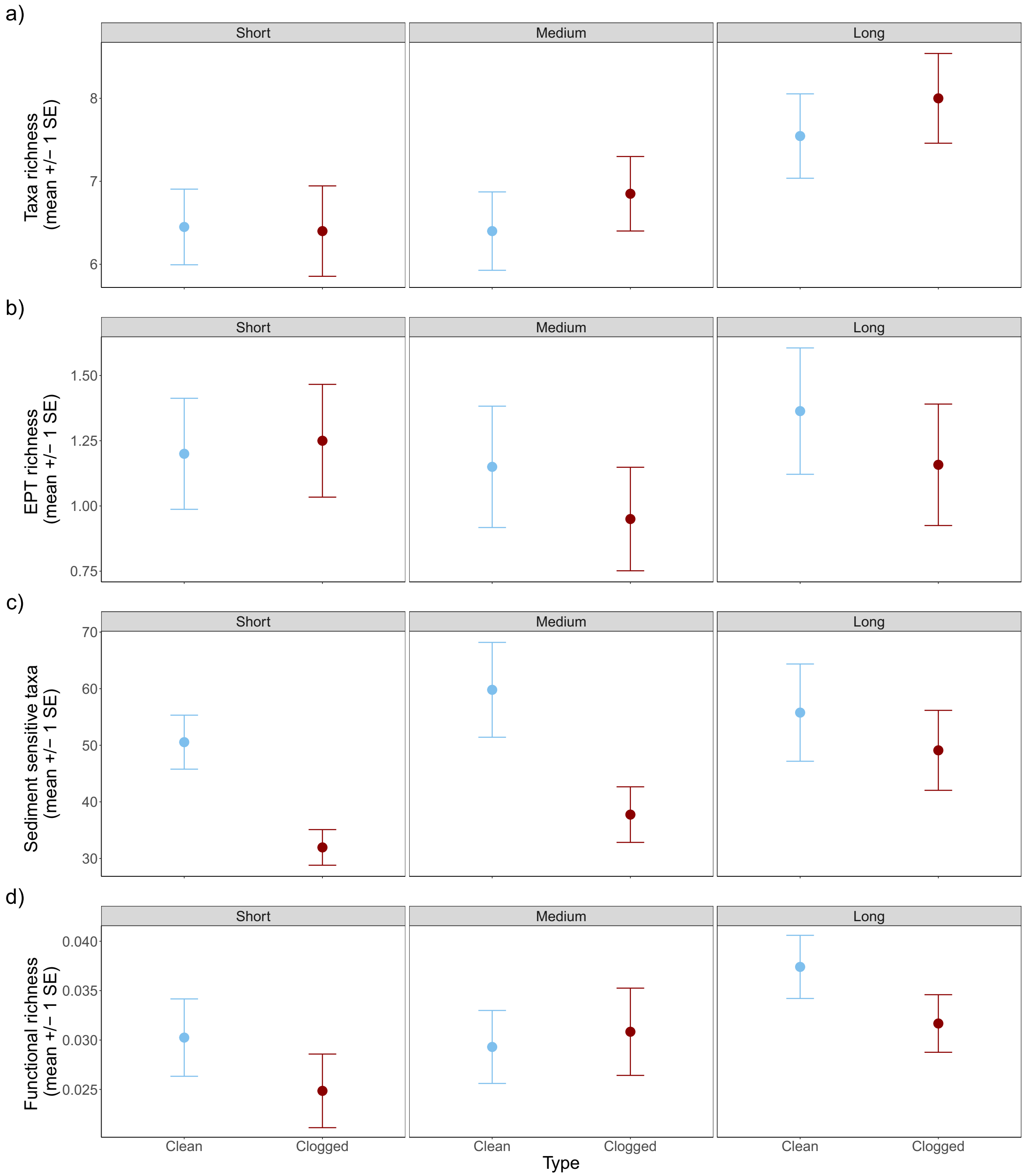


**Fig. 5.** Mean (±1 SE) lowland a) taxa richness; b) EPT richness; c) sediment sensitive taxa and; d) functional richness by sediment treatment (clean or clogged substrates) over time (short, medium, long).

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