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Habitat-specific invertebrate responses to hydrological variability, anthropogenic flow alterations, and hydraulic conditions

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Abstract

1. Quantifying ecological responses to river flow regimes is a key scientific approach underpinning many environmental flow (e-flow) strategies. Incorporating habitat-scale influences (e.g. substrate composition and organic matter cover) within e-flow frameworks has the potential to provide a broader understanding of the causal mechanisms shaping instream communities, which may be used to guide river management strategies.
2. In this study, we examined invertebrate communities inhabiting three distinct habitat groups (HGs—defined by coarse substrates, fine sediments, and the fine-leaved macrophyte *Ranunculus* sp.) across four rivers (each comprising two study sites) within a single catchment. We tested the structural and functional responses of communities inhabiting different HGs to three sets of flow-related characteristics: (1) antecedent hydrological (discharge—m³/s) variability; (2) antecedent anthropogenic flow alterations (percentage of discharge added to or removed from the river by human activity); and (3) proximal hydraulic conditions (characterised by the Froude number). The former two were derived from groundwater model daily time series in the year prior to the collection of each invertebrate sample, while the latter was collected at the point of sampling.
3. While significant effects of hydrological and anthropogenic flow alteration indices were detected, Froude number exerted the greatest statistical influence on invertebrate communities. This highlights that habitat-scale hydraulic conditions to which biota are exposed at the time of sampling are a key influence on the structure and function of invertebrate communities.
4. Mixed-effect models testing invertebrate community responses to flow-related characteristics, most notably Froude number, improved when a HG interaction term was incorporated. This highlights that different mineralogical and organic habitat patches mediate ecological responses to hydraulic conditions. This can be attributed to HGs supporting distinct taxonomic and functional compositions

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and/or providing unique ecological functions (e.g. flow refuges), which alter how instream communities respond to hydraulic conditions.

5. While the individual importance of both flow and small-scale habitat effects on instream biota has been widely reported, this study provides rare evidence on how their interactive effects have a significant influence on riverine ecosystems. These findings suggest that river management strategies and e-flow frameworks should not only aim to create a mosaic of riverine habitats that support ecosystem functioning, but also consider the management of local hydraulic conditions within habitat patches to support specific taxonomic and functional compositions.

KEYWORDS

environmental flows, flow velocity, flow–ecology relationships, Froude number, groundwater abstraction

1 | INTRODUCTION

Flow regime variability is widely recognised as a primary factor shaping riverine ecosystems (Ledger & Milner, 2015; Monk et al., 2006; Poff, 2018; Thompson, King, Kingsford, Mac Nally, & Poff, 2018). However, land use changes (Chadwick et al., 2006; López-Moreno et al., 2014) and water resource management practices have profoundly altered river flow regimes (De Graaf, Van Beek, Wada, & Bierkens, 2014; Gleeson & Richter, 2018; Lehner et al., 2011), significantly threatening the integrity of lotic ecosystems globally (Bunn & Arthington, 2002; Poff et al., 2010; Vörösmarty et al., 2010). For example, groundwater abstraction substantially reduces river discharges worldwide (De Graaf et al., 2014) and profoundly alters lotic ecosystems (Bradley, Streetly, Farren, Cadman, & Banham, 2014; Bradley et al., 2017; Kennen, Riskin, & Charles, 2014). Conversely, some management activities elevate river discharges (e.g. effluent water returns and low-flow alleviation schemes), which also prompt significant ecological responses (Luthy, Sedlak, Plumlee, Austin, & Resh, 2015; Wright & Berrie, 1987). As such, there remains a pressing need to understand how water resources can be managed to meet human needs while conserving lotic ecosystems and the services they provide (Arthington, Naiman, McClain, & Nilsson, 2010; Poff, 2018; Poff, Tharme, & Arthington, 2017).

Environmental flows (e-flows) represent the management of river discharges aiming to conserve specific societal and ecological attributes (Arthington et al., 2010). Establishing statistical relationships between flow regime properties and targeted ecological responses (i.e. flow–ecology relationships) represents a key scientific process underpinning many e-flow methodologies (Davies et al., 2014; Poff, 2018; Poff & Zimmerman, 2010; Tharme, 2003). Scientists now widely advocate the construction of flow–ecology relationships to guide the implementation of region-wide e-flow strategies, in part due to limited resources restricting the collection of detailed ecological and hydrological information on a river by river basis (Arthington, Bunn, Poff, & Naiman, 2006; Chen & Olden, 2018; Poff et al., 2010).

As such, the functional properties of biotic communities are being increasingly utilised within flow–ecology relationships (e.g. Mims & Olden, 2013; Ruhi, Dong, McDaniel, Batzer, & Sabo, 2018), with such responses being more likely to transcend multiple river basins as they are not confined by the biogeographical constraints of individual species and community structural properties (Poff, 2018; White, Hannah, et al., 2017).

Despite the advantages of flow–ecology relationships in guiding regional e-flow strategies, such statistical relationships do not necessarily reflect the underlying mechanisms structuring instream communities (Acreman et al., 2014; Lancaster & Downes, 2010). Quantifying community responses to different flow-related characteristics (e.g. hydrological variability, flow alterations and hydraulic conditions) at the habitat-scale has the potential to provide more ecologically meaningful evidence to guide e-flow strategies (Acreman et al., 2014; Arthington, Kennen, Stein, & Webb, 2018; Rosenfeld, 2017). E-flow methodologies accounting for habitat-scale characteristics (e.g. *habitat simulation* techniques—see Tharme, 2003) often focus on channel areas defined by depth-velocity relationships because of the widely recognised influence of hydraulic conditions on fish species with a high socio-economic value (e.g. Bovee et al., 1998; Harby, Olivier, Merigoux, & Malet, 2007; Lamouroux & Jowett, 2005). At the regional scale, stream velocities often respond comparably to changes in discharge (Rosenfeld, 2017), which allows ecohydraulic principles (e.g. ecological preferences towards shear velocity conditions) to be integrated within studies utilising hydrological (river discharge) time series (e.g. Armanini et al., 2014; Monk, Wood, Hannah, & Wilson, 2008; Monk et al., 2006). However, directly examining ecological responses to hydraulic conditions has been advocated in order to facilitate a greater understanding of the underlying causal mechanisms structuring communities as they provide a proximal characterisation of the stream flow forces experienced by biota (Lamouroux, Hauer, Stewardson, & Poff, 2017; Monk et al., 2018; Turner & Stewardson, 2014).

The mineralogical (e.g. gravel and silt) and organic (e.g. macrophyte and macroalgae) habitat patches occurring in lotic environments are shaped by hydrological, hydraulic, and geomorphic controls (Kemp, Harper, & Crosa, 1999). Anthropogenic flow alterations have been shown to modify biotic communities indirectly via changes to habitat heterogeneity (e.g. Armitage & Pardo, 1995; Storey & Lynas, 2007). However, how communities inhabiting different mineralogical and organic habitat patches respond to different flow-related characteristics has not been widely explored (rare examples being Clarke, Mac Nally, Bond, & Lake, 2010; Lind, Robson, & Mitchell, 2006; Palmer, Arensburger, Martin, & Denman, 1996) and has been seldom incorporated within e-flow methodologies globally.

In this study, we examine invertebrate community responses to three sets of flow-related characteristics: antecedent hydrological variability (discharge— m^3/s), antecedent anthropogenic flow alterations (daily percentage of discharge added to or removed from the river by human activities) and hydraulic conditions. The former two were derived from daily time series outputted from a groundwater model over the year prior to the collection of each invertebrate sample, while the latter was measured at the point of invertebrate sampling. We tested whether community responses to these flow-related characteristics varied between distinct lotic habitat groups (HG—comprising fine and coarse substrate classes and *Ranunculus*

sp.—a fine-leaved macrophyte). This study aimed to quantify the structural and functional responses of invertebrate communities to: (1) differences in HGs; (2) the individual influence of each flow-related characteristic across different HGs; and (3) the most statistically influential (*optimal*) flow-related indices across different HGs.

2 | METHODS

2.1 | Study area

Four rivers, each comprising two sampling sites, were examined across the Hampshire Avon catchment (Hampshire, UK; Figure 1) between May 2015 and January 2016; a period characterised by intermediate river discharges within the context of long-term hydrological time series (Barker, Hannaford, Muchan, Turner, & Parry, 2016; White, 2018). The Hampshire Avon is classified as a Special Area of Conservation (SAC) under the EU Habitats Directives (92/43/EEC), with areas of the catchment also being designated as Sites of Special Scientific Interest (Natural England, 1996). The catchment is primarily underlain by a chalk lithology (Heppell et al., 2017), a fine-grained limestone that exhibits a relatively low specific yield, although it can develop high transmissivities as groundwaters move through small fissures (Soley et al., 2012). As such, chalk is considered a *highly*

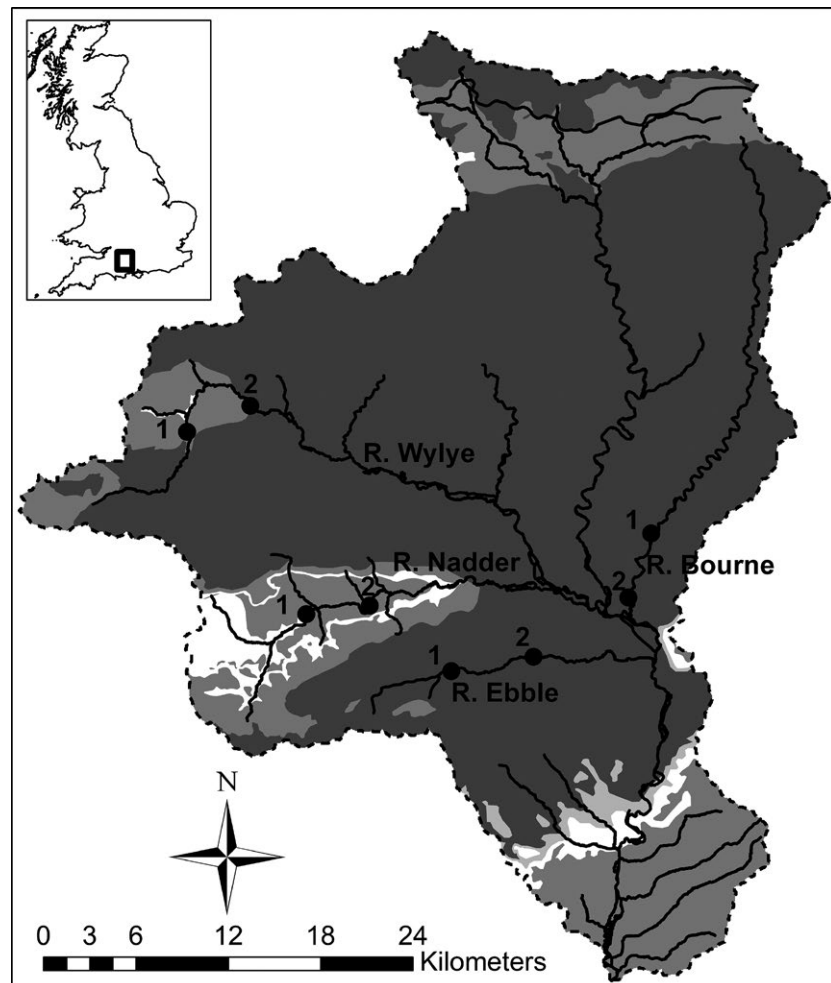


FIGURE 1 The location of the study sites within the Hampshire Avon. Square within the inset = study region; dashed line = Hampshire Avon catchment boundary; circles = sampling sites. Dark grey = highly productive aquifer; light grey = moderately productive aquifer; white = low productivity aquifer or rocks with essentially no groundwater (for classification, see British Geological Survey, 2018)

TABLE 1 Land use coverage (%) for each of the studied river catchments. The site names correspond to the identifiers outlined within the National River Flow Archive (NRFA, 2018)

	Ebble	Nadder	Wylve	Bourne
National River Flow Archive (NRFA) site	43011—Ebble at Bodeham	43006—Nadder at Wilton	43008—Wylve at South Newton	43004—Bourne at Laverstock
Woodland	6.00	15.98	9.38	10.07
Arable agriculture	55.83	48.94	31.01	40.45
Grassland	31.30	29.94	50.70	39.07
Heathland	0.51	0.80	0.17	0.00
Urban	2.86	3.18	2.70	4.54

Source: NRFA (2018).

productive aquifer (British Geological Survey, 2018; see Figure 1) and overlying rivers typically convey seasonally consistent flow regimes as groundwater levels rise and fall in accordance with antecedent climatic conditions (Sear, Armitage, & Dawson, 1999). However, the Hampshire Avon is also underlain by bands of greensand (a *moderately productive aquifer*) and clay (possessing *essentially no groundwater*) in the west of the catchment (Figure 1 and British Geological Survey, 2018 for nomenclature), which facilitate quicker hydrological responses to rainfall (Heppell et al., 2017). The land use across the four sub-catchments studied is predominantly arable agriculture (although the Wylve exhibits a higher proportion of grassland coverage) with minimal urban coverage (see Table 1). Rivers across the Hampshire Avon exhibit comparable physico-chemical properties due to the strong calcareous geological influence and similar land uses between sub-catchments. The rivers examined are characterised by alkaline waters and high electrical conductivity, dissolved oxygen and nutrient levels (Table 2).

Within the Hampshire Avon, groundwater abstraction is the primary water resource management mechanism reducing river discharges, with the regional water company (Wessex Water plc.) operating 21 groundwater supply wells across the catchment (White et al., 2018). However, outflows from effluent water returns and low flow alleviation strategies (which utilise groundwater to augment discharges in select river channels that fall below threshold discharge values) results in some river reaches conveying a greater volume of flow than would naturally occur. All study sites exhibit perennial flow regimes.

2.2 | Defining habitat groups

Three *habitat groups* (HGs) were established based on their prevalence over a 50-m reach for each of the study sites. Two HGs comprised different sedimentological characteristics, which were present across all study sites—(1) coarse substrates and (2) fine sediments. Coarse substrates included bare mineralogical coverings dominated by gravel and/or cobble sized substrates (between 2 and 64 mm—Kemp et al., 1999), while fine sediment habitats comprised sand and silts sized particles (<2 mm), often deposited between macrophyte stands growing in the river margins (e.g. *Apium nodiflorum*, *Callitriche* sp., *Sparganium erectum*). The third

HG comprised (3) *Ranunculus* sp., a fine-leaved, submerged macrophyte which is widespread within many calcareous rivers regionally (Westwood, Teeuw, Wade, Holmes, & Guyard, 2006). It is typically located in central areas of channel cross-sections conveying higher flow velocities (Westwood et al., 2006). *Ranunculus* sp. has been shown to support diverse invertebrate communities and is a key refuge for faunal assemblages during extreme hydrological conditions (Bickerton, Petts, Armitage, & Castella, 1993; Wright & Symes, 1999). *Ranunculus* sp. was sampled within five of the eight study sites.

2.3 | Biological data

Field sampling was undertaken during spring (May), summer (July), autumn (October) 2015, and winter (January) 2016, although high river levels prohibited sampling at one site along the River Nadder during winter 2016. Invertebrate samples were collected using a Surber sampler (0.03 m², 250- μ m mesh size), disturbing the sediment and/or plant material (at the base of the *Ranunculus* sp. bed where stems are most highly concentrated) for 15 s for each sample. Three replicate samples were collected from each HG present within each study site across all sampling occasions ($n = 237$; 48–69 samples taken from each river—which varied depending on the presence of *Ranunculus* sp. between study sites and seasons). Invertebrate samples were collected from separate HG patches within each study site (spanning the 50-m reach). A total of 93 samples were collected from both coarse substrates and fine sediments, while 51 samples were taken from *Ranunculus* sp. All samples were preserved using 4% formaldehyde solution in the field prior to being processed and stored within 70% industrial methylated spirit in the laboratory. Specimens were identified to lowest possible taxonomic level (typically species or genus), but in some cases taxa were resolved to family level (primarily Diptera larvae); while Hydracarina, Oligochaeta (class), Ostracoda (subclass), and Collembola (order) were identified as such.

2.4 | Velocity data

A 30-s averaged flow velocity reading was collected immediately adjacent to each invertebrate sample at 60% of the channel depth using

TABLE 2 Average water quality measurements collected from different study sites between January 2014 and January 2016. Site names correspond to those designated by the Environment Agency within their routine monitoring (Environment Agency, 2017)

Environment Agency WQ site	Ebble 1 SW-50250291	Nadder 1 SW-C0235000	Nadder 2 SW-50220284	Wylve 1 SW-50250634	Wylve 2 SW-50240461	Bourne 1 SW-50240226	Bourne 2 SW-50240116
pH	7.88	8.09	8.07	8.33	8.22	7.84	8.05
Conductivity ($\mu\text{s}/\text{cm}$)	551	496.25	507.85	455.49	580.17	535.97	551.25
Dissolved oxygen (% saturation)	95.57	95.28	94.08	103.73	105.34	NA	98.75
Nitrates (mg/L)	7.04	4.40	5.53	6.31	5.89	7.29	7.63
Orthophosphate (reactive; mg/L)	0.05	0.16	0.12	0.09	0.16	NA	0.05

All water quality (WQ) sites located within 2.5 km of the study sampling sites. There is no regulatory WQ monitoring site close to Ebble 2 and some WQ measurements are not routinely recorded at Bourne1. Source: Environment Agency (2017).

a Valeport Electromagnetic Current Meter. From this, the Froude number was calculated (Table 3) to enable a direct comparison of hydraulic measurements across different habitat conditions (Jowett, 1993), as well as between reaches and seasons, given that the influence of flow velocity is scaled by the channel depth (Wadeson & Rowntree, 1998).

2.5 | Wessex Basin groundwater model

The *Wessex Basin* regional groundwater model (Soley et al., 2012) was used to characterise the hydrological variability predicted to occur at each study site by modelling a *historic* discharge time series. Daily historic discharge time series were obtained from the model between 1 January 2014 and 31 January 2016 so that the hydrological variability could be derived from the 12-month period preceding all invertebrate samples. Outputs from the *Wessex Basin* model were also used to quantify antecedent anthropogenic flow alterations across the same time period. This was derived from the daily percentage difference between naturalised (i.e. modelled discharges subject to no hydrological alterations) and the historic discharge time series. This *anthropogenic flow alteration* time series accounts for any groundwater abstractions operated by Wessex Water plc., in addition to all hydrological inputs (e.g. effluent water returns or low flow alleviation strategies).

The hydrogeological mechanisms underpinning the *Wessex Basin* model have been described elsewhere (Heathcote, Lewis, & Soley, 2004; Soley et al., 2012; White et al., 2018) and are summarised here. The model divides the *Wessex Water* plc. region underlain by chalk and upper greensand into 250 × 250 m grid cells, with stream cells (for which discharge time series are outputted) being positioned along the valley floors. The *Wessex Basin* model has been adapted from the MODFLOW model (see McDonald & Harbaugh, 1988), with the interaction between stream cells and groundwater levels being calculated at c. 10-day intervals (three modelled outputs per month). This has been combined with daily outputs from a 4R (rainfall, recharge and runoff routing) hydrological model to provide an estimate of total daily discharge conveyed by each stream cell. Errors in mean long-term (1970–2013) historic discharges (outputted by the *Wessex Basin* model) were within $\pm 10\%$ of observed discharges (ENTEC, 2016), which were obtained from flow gauges (sourced from the National River Flow Archive (NRFA), 2018). As such, the *Wessex Basin* model was considered indicative of a *very good* hydrological model (see Hain et al., 2018; for additional hydrological model fit statistics of sampling sites positioned close to flow gauges, see Supporting Information Appendix S1: Table S1). In addition, the *Wessex Basin* model has been externally reviewed and is considered to accurately model daily river discharges by the environmental regulator within England (the Environment Agency). Although it should be noted that an incorrectly modelled 10-day drying event at the River Wylve 1 during September 2015 was excluded when deriving hydrological indices (see below) as a

Index	Flow-related characteristic	Flow regime components	Description
QMay	Hydrological (m ³ /s)	Magnitude Timing	Mean average discharge in May
QJulianMin	Hydrological (m ³ /s)	Magnitude Timing	Julian day of the minimum discharge occurrence
QMax30	Hydrological (m ³ /s)	Magnitude	Maximum discharge in the 30-days prior to sampling
QMin30	Hydrological (m ³ /s)	Magnitude	Minimum discharge in the 30-days prior to sampling
QMin90	Hydrological (m ³ /s)	Magnitude	Minimum discharge in the 90-days prior to sampling
AFMay	Anthropogenic flow alteration (%)	Magnitude Timing	The average flow alteration in May
AFJul	Anthropogenic flow alteration (%)	Magnitude Timing	The average flow alteration in July
AFJulianMin	Anthropogenic flow alteration (%)	Magnitude Timing	Julian day of the minimum percentage modified discharge
AFLPD	Anthropogenic flow alteration (%)	Magnitude Duration	The average duration that flow alterations <75th percentile
AbMax7	Anthropogenic flow alteration (%)	Magnitude	Maximum flow alteration in the 7 days prior to sampling
Froude	Hydraulic	NA	The ratio between inertial and gravitational forces within the water column. Fr = v / \sqrt{gD} . v = average velocity (ms ⁻¹); g = gravitational acceleration (ms ⁻²) and D = sample depth (m)

TABLE 3 Hydrological (Q), anthropogenic flow alteration (AF), and hydraulic (Froude) indices included within the final analyses

nearby flow gauge (positioned c. 3 km upstream from the River Wylfe 1—see Figure 1) indicated permanent flowing conditions throughout the study period (NRFA, 2018—site 43806, Wylfe at Brixton Deverill).

3 | DATA ANALYSIS

3.1 | Invertebrate community response metrics

Invertebrate taxonomic (community abundances) and functional trait multivariate compositions were examined. Functional traits were derived from the European database compiled by Tachet, Bournaud, Richoux, and Usseglio-Polatera (2010). The functional traits database adopts a fuzzy-coding procedure, whereby faunal affinities to individual traits range from zero (indicating no affinity) to three or five (indicating high affinity—the upper limit

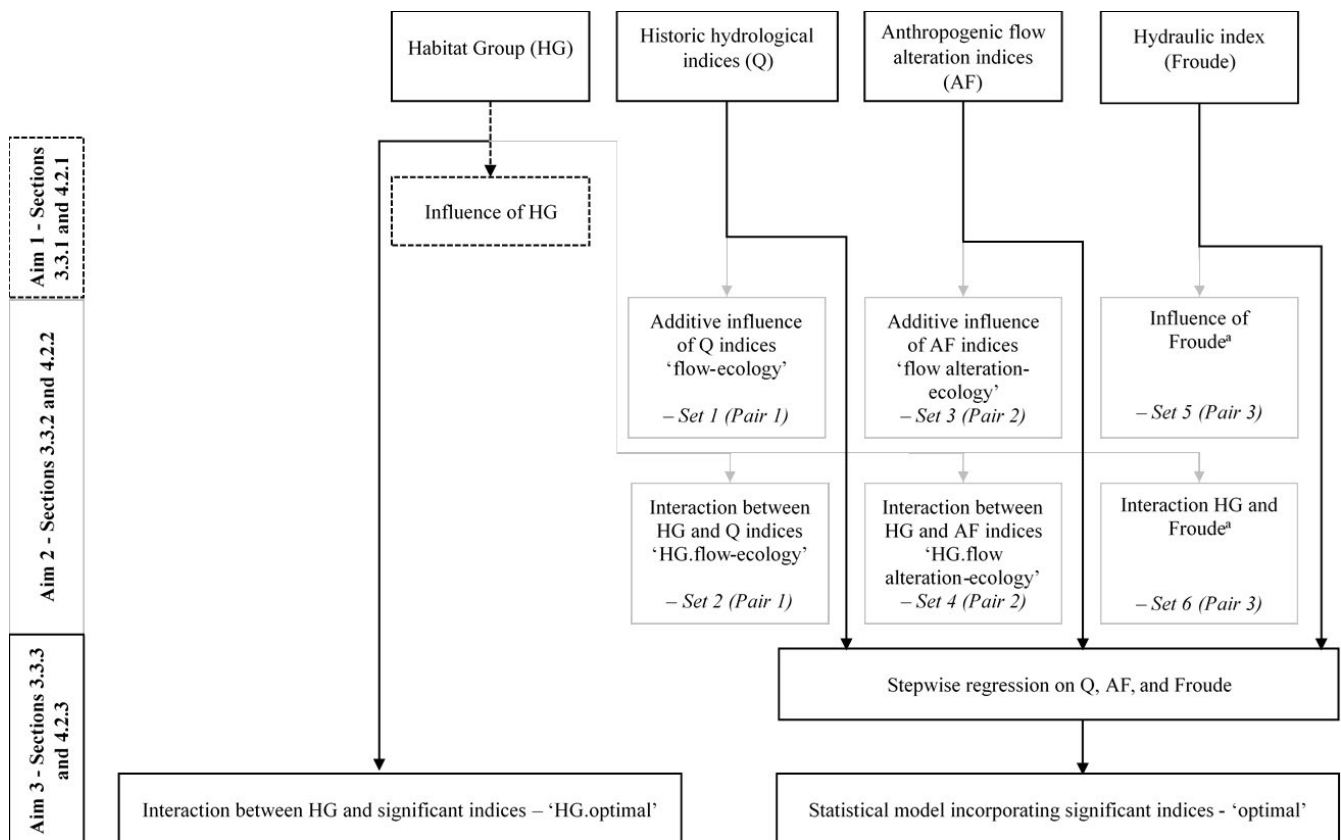
depending on the amount of available information reported in existing literature—Tachet et al., 2010). Trait information within the database is typically available at species- or genus-level and taxa resolved to a coarser resolution than that specified within the database were excluded from the trait analyses. Trait values for all qualifying taxa were standardised across all *grouping features* (a functional trait category—e.g. *maximum body size*) so that traits (modalities residing within grouping features—e.g. ≤ 0.25 cm, ≥ 8 cm; for nomenclature, see Schmera, Podani, Heino, Erős, & Poff, 2015) summed to 1 to ensure equal taxonomic weighting. These standardised values were then used to derive univariate functional diversity indices (see below). To calculate the multivariate functional trait compositions, standardised values were multiplied by $\ln(x + 1)$ transformed community abundances (see Schmera, Podani, Erős, & Heino, 2014) to create a trait-abundance array. Finally, each trait was averaged across all

sampled taxa and standardised across all grouping features to account for spatially and temporally driven changes in taxonomic abundances (Demars, Kemp, Friberg, Usseglio-Polatera, & Harper, 2012; Gayraud et al., 2003). Eleven grouping features comprising 63 traits were examined containing information on the biological properties of invertebrate taxa (see Supporting Information Appendix S2: Table S2).

Seven univariate community response metrics were derived and calculated within R studio (operated within R version 3.3.1; R Development Core Team, 2014). Five structural responses of invertebrate communities were examined: (1) total community abundance—*Abundance*; (2) taxonomic richness—*TaxRic*; (3) taxonomic diversity (obtained from the inverse Simpson's diversity index; Oksanen, 2016)—*TaxDiv*; (4) Berger–Parker index (Seaby & Henderson, 2007); and (5) the percentage of Ephemeroptera, Plecoptera, and Trichoptera taxa—%EPT. The functional richness *FRic* and functional evenness *FEve* metrics were calculated using the *dbFD* function in the *FD* package (Laliberté, Legendre, & Shipley, 2015) and were derived from a Bray–Curtis dissimilarity matrix created from standardised trait values (see above). *FRic* characterises the volume of functional space occupied by invertebrate communities and *FEve* describes the regularity of abundances within this space (Villéger, Mason, & Moullot, 2008).

3.2 | Antecedent hydrological and anthropogenic flow alteration indices

All subsequent statistical analyses were performed in R Studio. Given that some hydrological indices have been shown to be influenced by river catchment sizes (Monk et al., 2006), historic discharge time series from each study site were transformed to z-scores. As anthropogenic flow alterations are dimensionless (the percentage difference between naturalised and historic discharges), these were not transformed. Subsequently, 47 indices were derived to characterise both the hydrological (Q—derived from historic discharge time series) and anthropogenic flow alteration (AF) time series (94 indices in total) at each sampling site prior to each sampling event. These indices were calculated as they have been highlighted as ecologically influential within groundwater dominated rivers in the UK (see Worrall et al., 2014) and characterise different components of the flow regime (i.e. *magnitude, frequency, duration, timing, and rate of change*—see Poff et al., 1997). The indices derived included the 33 hydrological indices outlined in the *Indicators of Hydrological Alteration* methodology (Richter, Baumgartner, Powell, & Braun, 1996) and 14 additional variables which have been demonstrated to significantly influence invertebrate communities within UK groundwater dominated



a) To avoid repetition, these results are presented in the third sub-section of the results

FIGURE 2 A flow chart outlining the analytical framework adopted within this study. Dashed lines = first aim/results subsection; grey lines = second aim/results subsection; solid black lines = third aim/results subsection. The nomenclature for different sets of statistical models are indicated by apostrophes

streams (Wood, Agnew, & Petts, 2000; Wood & Armitage, 2004; Monk et al., 2006; Worrall et al., 2014; see Supporting Information Appendix S3: Table S3). Hydrological indices dominated by a single value (>50%) or with a lack of unique values ($n < 10$) were excluded from subsequent analyses (13 in total, leaving 81 Q and AF indices—see Supporting Information Appendix S3: Table S3).

Separate principal component analyses (PCAs) were performed on Q and AF indices using a correlation matrix (Olden & Poff, 2003). The statistical significance of each PCA axis was determined via a broken-stick method using the *PCAsignificance* function within the BiodiversityR package (Kindt, 2018). Subsequently, the dominant 25 Q and AF indices (50 in total) were derived following the data redundancy procedure outlined by Olden and Poff (2003) and Monk, Wood, Hannah, and Wilson (2007); with the number of indices selected from each significant PCA axis being proportional to the amount of statistical variation that the axis itself explained. This procedure accounts for the major sources of statistical variation and minimises redundancy between hydrological indices. To account for collinearity between the selected indices, variation inflation factors (VIFs) were calculated for the Q and AF indices derived from the PCA procedure, as well as two hydraulic metrics (mean velocity and Froude number), with variables being iteratively removed until all VIFs were below 3 (Zuur, Ieno, & Elphick, 2010).

3.3 | Analytical framework

The following statistical analyses are reported in three subsections corresponding to each study aim. An analytical framework for this is presented schematically in Figure 2 (although it should be noted that an alternative analytical framework was explored to test the influence of HGs and each set of flow-related characteristics on invertebrate communities—see Supporting Information Appendix S4: Table S4).

3.3.1 | Structural and functional community differences between habitat groups

Multivariate differences in the taxonomic and functional trait compositions of invertebrate communities between HGs were examined by pooling the three replicate samples from each HG within each study site (taxonomic abundances were summed; functional traits were averaged). This was tested via a permutational analysis of variance (PERMANOVA) using the *adonis* function in the Vegan package (Oksanen et al., 2017). Pairwise PERMANOVAs were used to test how communities differed between each paired combination of HGs. Principal coordinate analysis (PCoA) plots were constructed using a Bray–Curtis dissimilarity index to visualise community differences between HGs. PCoA was performed using the *cmdscale* function and displayed using the *ordispider* function (both in Vegan).

To examine whether each univariate community response metric differed between HGs, linear mixed-effect models (LMMs) were constructed using the *lmer* function in the lme4 package (Bates et al., 2016). For this, HG was examined as a fixed-effect and

the following procedures were adopted (and applied to all LMMs used throughout the study herein): (1) river and season were used as random effects to account for a potential lack of spatial and temporal independence between samples; (2) random intercept models were fitted using a maximum-likelihood approximation; (3) Quantile-Quantile plots were inspected to ensure that model residuals were normally distributed, while fitted values were plotted against Pearson residuals to examine the homogeneity of variances and identify outliers (Bolker et al., 2009; a maximum of six data points were removed from each LMM); (4) community abundance was $\log(x)$ transformed to satisfy model assumptions when used as a dependent variable within LMMs; (5) the significance of all LMMs were obtained via likelihood-ratio tests; and (f) the statistical variation explained by the fixed-effects within each LMM was examined through marginal pseudo r -squared values (r_m^2 ; see Nakagawa & Schielzeth, 2013) obtained from the *r2beta* function in the *r2glmm* package (Jaeger, 2017). Differences in the community response metric values between HGs were graphically presented using the *ggplot2* package (Wickham & Chang, 2016).

3.3.2 | Community responses to different sets of flow-related characteristics

Linear mixed-effect models were used to quantify the influence of each flow-related characteristic (i.e. the separate influence of Q, AF indices and the Froude number—see Figure 2) on each of the seven community response metrics. For this, Q and AF indices were scaled (i.e. z-scores calculated) to facilitate model convergence (Bolker et al., 2009). In total, six sets of statistical models were prepared, each consisting of seven LMMs testing the response of each community response metric (dependent variable). These six sets of LMMs comprised three statistical pairs corresponding to each flow-related characteristic (see Figure 2). The first set of LMMs modelled the additive influences of Q indices (flow–ecology relationships) as fixed effects (independent variables), with the second set of LMMs incorporating an interaction term between Q indices and HG (HG.flow–ecology)—these two sets represented the first statistical pair. This process was repeated by replacing the Q indices with AF indices (pair 2—flow alteration–ecology and HG.flow alteration–ecology) and the Froude number (pair 3). As such, the inclusion of a HG interaction term represented the only difference between each set of LMMs comprising each statistical pair. Comparisons between LMMs testing the same community response metric within each statistical pair were performed to test whether community responses to each flow-related characteristic differed between HGs. Comparisons were conducted through multiple lines of statistical evidence: (1) likelihood ratio tests were performed to test if LMMs differed significantly; (2) the amount of statistical variation explained by LMMs were derived from r_m^2 values; and (3) the statistical likelihood of the model was determined by comparing Akaike information criterion (AIC) values. For this, $\Delta AIC \geq 2$ indicated a difference in the statistical likelihood of the two LMMs, which provides a greater understanding of whether

the inclusion of a HG interaction term improved the model fit (specifically given its penalising function associated with a greater number of explanatory variables).

3.3.3 | Community responses to the most statistically influential flow-related indices

To examine community responses to the most statistically influential flow-related indices (Q, AF and Froude number), seven LMMs were constructed that tested each community response metric (dependent variable) against the additive influences of all flow-related characteristics selected following PCA and VIF analyses (these were used as fixed-effects, whereby z-scores were calculated to facilitate model convergence). Subsequently, a backwards stepwise procedure was performed via the *step* function in the *ImerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017) to identify the significant fixed-effects comprising each LMM. For this, the significant α level (0.05) was adjusted via the Bonferroni correction to prevent overfitting models. Optimal LMMs were constructed that comprised the additive influences of statistically significant indices (identified from the stepwise procedure) as fixed-effects. Subsequently, HG.optimal LMMs were constructed that examined the interaction between HG and the flow-related indices comprising each optimal LMM. The statistical significance (likelihood ratio tests), explanatory power (r_m^2) and statistical likelihood (AIC) of all optimal and HG.optimal LMMs was quantified and compared. These statistical summaries were also calculated for each individual fixed-effect, with the statistical variation explained by each variable being quantified by semi-partial r_m^2 values using the *r2beta* function and the significance of each individual fixed-effect being obtained from the *anova* function in *ImerTest*. Graphics displaying the responses of the most sensitive community response metrics to flow-related indices within the HG.optimal LMMs were prepared using the *effects* package (Fox et al., 2017).

4 | RESULTS

4.1 | Hydrological variability and anthropogenic flow alterations

All rivers examined displayed seasonally consistent changes in hydrological variability, with peak discharges occurring between late winter and early spring, before declining across the summer and autumn months (Figure 3; although this was least evident for Nadder 1—see Figure 3c). On average, naturalised discharges were reduced by 3.88% across the eight sampling sites over the study period. The rivers Ebble (Figure 3a,b) and Bourne (Figure 3g,h) displayed the most buffered hydrographs. Anthropogenic flow alterations within the Ebble deviated marginally from 0 (−2.89% to 3.89%), but the Bourne exhibited greater reductions in discharge (−13.14% to −0.43%). The Nadder displayed a more variable flow regime, with sharp rises and falls in discharge occurring (Figure 3c,d).

Flow alterations fluctuated marginally around 0 (−0.59% to 0.83%) at Nadder 1, while Nadder 2 exhibited small net reductions in discharge (−4.35% to 0%). The Wylde displayed some short-term (daily to weekly) spikes in discharges (Figure 3e,f), although not to the same degree as the River Nadder. Anthropogenic flow alterations in the Wylde were greater (−48.33% to 9.16%) compared to the other rivers studied.

The PCA of hydrological (Q—historic discharge) indices was used to select the 25 Q indices used in subsequent analyses, which were derived from PCA axes 1–6; all of which were significant (as indicated by the broken-stick procedure) and explained 97.40% of the total statistical variation. The 25 AF indices were derived from PCA axes 1–7 (all of which were significant) and accounted for 98.15% of the statistical variation. After VIFs were calculated to check for collinearity, 11 indices (5 Q and AF indices, in addition to the Froude number) were utilised in subsequent analyses (Table 3).

4.2 | Invertebrate community responses

The following results are divided into three sub-sections, which correspond directly to the three study aims (see Section 3.3 and Figure 2).

4.2.1 | Structural and functional community differences between habitat groups

PERMANOVAs indicated that invertebrate taxonomic ($F = 11.14$, $p \leq 0.001$) and functional trait compositions ($F = 8.82$, $p \leq 0.001$) differed significantly between HGs, which accounted for 23% ($r^2 = 0.23$) and 16% ($r^2 = 0.16$) of the total statistical variation, respectively. Pairwise PERMANOVAs indicated that taxonomic and functional trait compositions differed significantly between all HG pairs ($p \leq 0.001$ – 0.007). Greater amounts of statistical variation were explained when comparing taxonomic compositions supported by *Ranunculus* sp. versus coarse substrate ($r^2 = 0.19$; $F = 11.02$) and fine sediment ($r^2 = 0.24$; $F = 14.57$) HGs, compared to coarse substrates versus fine sediments ($r^2 = 0.12$; $F = 8.44$). Pairwise PERMANOVAs examining differences in functional trait compositions between HGs explained the lowest amount of statistical variation when testing coarse substrates versus *Ranunculus* sp. ($r^2 = 0.07$; $F = 3.23$), compared to fine sediments versus coarse substrates ($r^2 = 0.12$; $F = 8.33$) and *Ranunculus* sp. ($r^2 = 0.15$; $F = 8.43$). A PCoA plot indicated that each HG supported distinct invertebrate taxonomic compositions (Figure 4a). There was a greater overlap in the functional trait compositions supported by each HG, although communities inhabiting fine sediments were slightly more functionally distinct (Figure 4b).

Linear mixed-effect models highlighted that Abundance ($r^2 = 0.39$, $\chi^2 = 122.72$), TaxRic ($r^2 = 0.36$, $\chi^2 = 116.05$), TaxDiv ($r^2 = 0.15$, $\chi^2 = 39.53$), Berger–Parker ($r^2 = 0.12$, $\chi^2 = 28.72$), %EPT ($r^2 = 0.14$, $\chi^2 = 38.23$), FRic ($r^2 = 0.38$, $\chi^2 = 101.34$), and FEve ($r^2 = 0.20$, $\chi^2 = 50.12$) all differed significantly (all $p \leq 0.001$) between HGs. *Ranunculus* sp. supported greater Abundance (Figure 5a), TaxRic (Figure 5b), %EPT (Figure 5e) and FRic (Figure 5f) values.

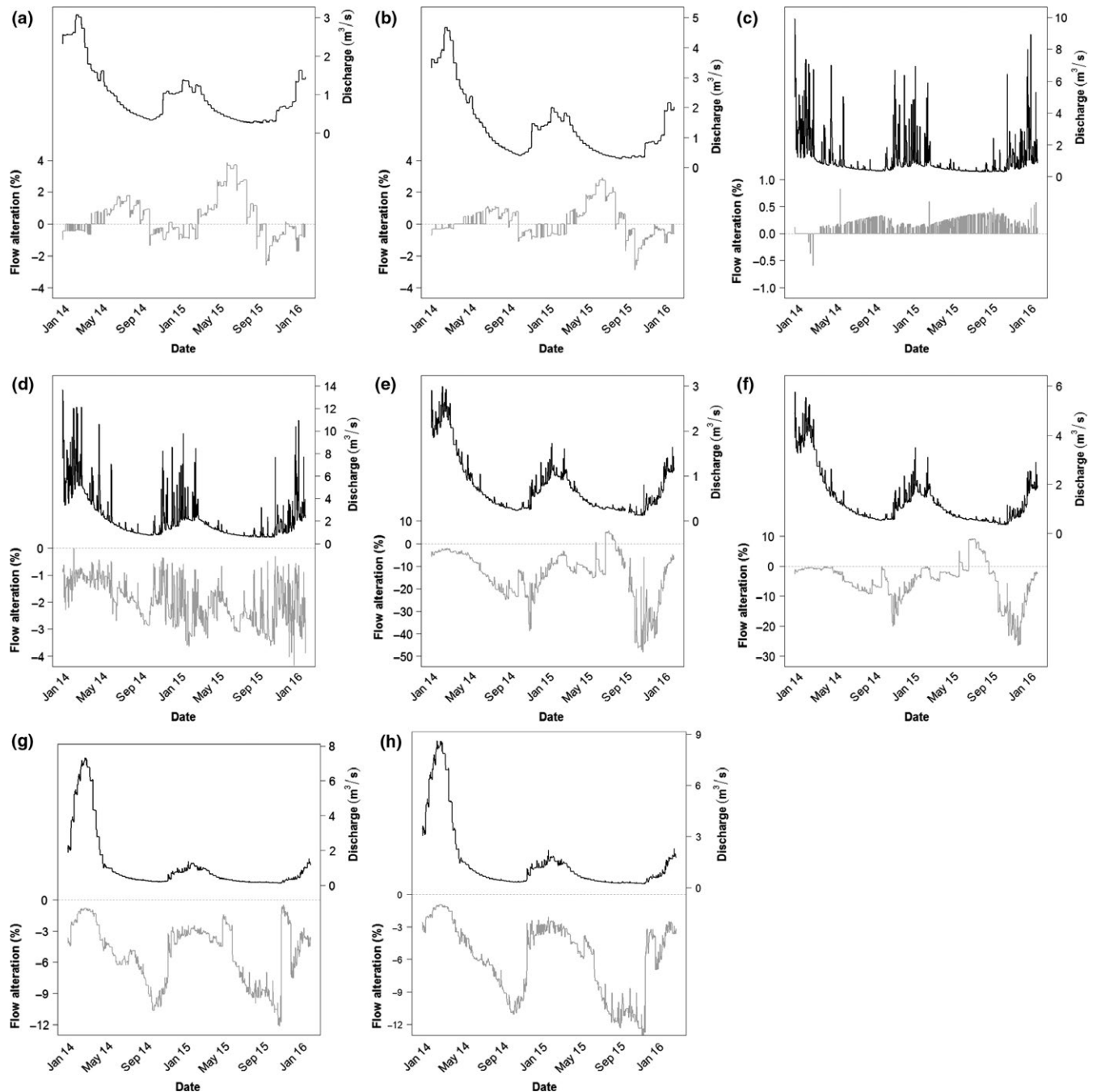


FIGURE 3 A daily time series of historical discharges (black) and anthropogenic flow alterations (grey) occurring at each study site: (a) Ebble 1; (b) Ebble 2; (c) Nadder 1; (d) Nadder 2; (e) Wylfe 1; (f) Wylfe 2; (g) Bourne 1; and (h) Bourne 2

TaxDiv was highest within coarse substrates (Figure 5c), while fine sediments supported communities characterised by a higher structural dominance (Berger-Parker index—Figure 5d), but a greater functional evenness (FEve—Figure 5g).

4.2.2 | Community responses to hydrological variability and anthropogenic flow alterations

Community response metrics typically displayed limited responses to the additive influences of hydrological (Q) and anthropogenic

flow alteration (AF) indices, respectively termed flow–ecology and flow alteration–ecology relationships (see Figure 2). LMMs detected 2 significant flow–ecology relationships and only one flow alteration–ecology relationship (see Table 4). Significant flow–ecology ($r_m^2 = 0.19$, $\chi^2 = 12.87$, $p = 0.025$) and flow alteration–ecology relationships ($r_m^2 = 0.10$, $\chi^2 = 14.71$, $p = 0.012$) were observed for FEve. Incorporating a HG interaction with Q indices (i.e. HG.flow–ecology relationships) significantly improved model fits for four community response metrics (Abundance, TaxDiv, FRic and FEve—but ΔAICc for TaxDiv >-2 , see Table 4) and accounted

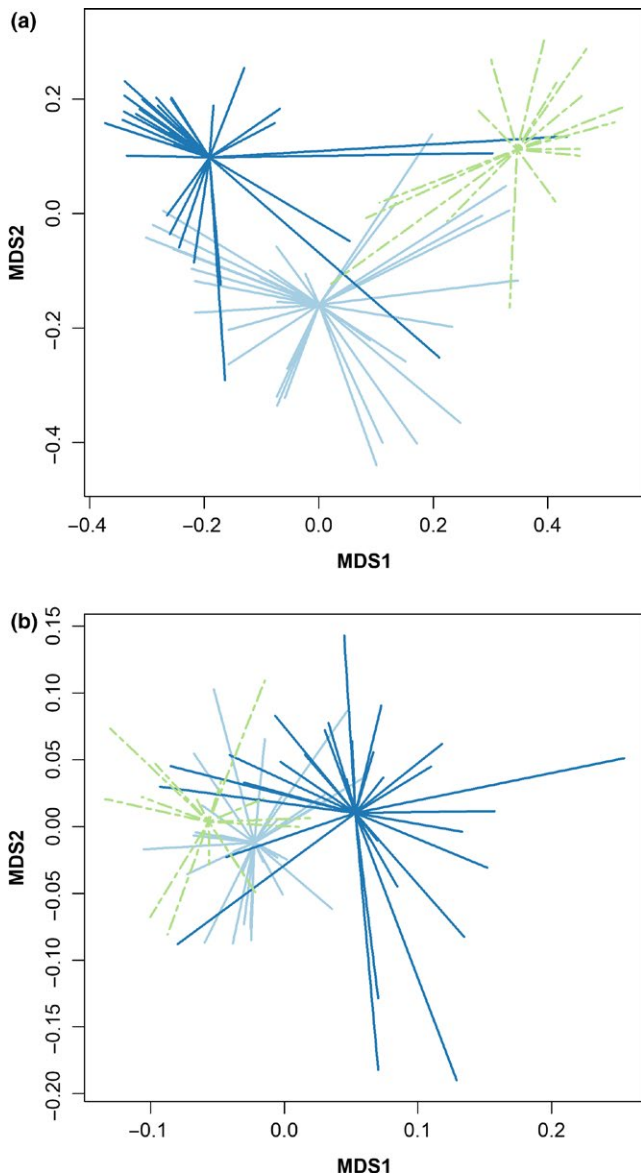


FIGURE 4 PCoA plot of invertebrate communities between habitat groups for (a) taxonomic and (b) functional trait compositions. Dark blue = fine sediments; light blue = coarse substrates and green = *Ranunculus* sp. (these lines are dashed to aid visual interpretation)

for a higher amount of statistical variation compared to all respective flow–ecology relationships (up to 23%— $\Delta r_m^2 = 0.23$ for FRic; see Table 4). HG.flow alteration–ecology relationships significantly improved model fits for three response metrics (Abundance, TaxRic and %EPT—but $\Delta AICc$ for %EPT > -2 , see Table 4) and explained a greater amount of statistical variation compared to all respective flow alteration–ecology relationships (up to 34%— $\Delta r_m^2 = 0.34$ for Abundance). The Froude number had a significant influence on all invertebrate community response metrics and these results are presented in the subsequent sub-section to avoid repetition (these findings were congruent with the outputs of the alternative analytical framework considered and outlined in Supporting Information Appendix S4: Table S5).

4.2.3 | Community responses to the most statistically influential flow-related indices

The backwards stepwise selection procedure performed on LMMs testing the additive influence of all flow-related indices (Q, AF, and Froude number) demonstrated that all invertebrate response metrics were most significantly modelled using 1–4 variables as fixed-effects. The *optimal* model testing TaxRic incorporated various flow-related indices (Froude number, AFJulianMin, QMax30, and QJulianMin) and accounted for 50% of the total statistical variation ($r_m^2 = 0.50$), which increased by 4% within the *HG.optimal* model (Table 5). Froude number was included within all optimal models and its individual effect explained a greater amount of statistical variation (6%–38%— $r_m^2 = 0.06$ –0.38) within each respective LMM compared to all other significant flow-related indices (Table 5). Abundance and TaxRic both exhibited a positive relationship with Froude number across coarse and *Ranunculus* sp. HGs, but this was less evident within fine sediment habitats (Figure 6a,b). TaxDiv responded positively with Froude number within coarse substrates and fine sediments but displayed a strong negative relationship within *Ranunculus* sp. (Figure 6c). FRic also exhibited a positive relationship with Froude number within mineralogical HGs but did not display a clear directional change within *Ranunculus* sp. (Figure 6d). In total, four Q indices were incorporated within three optimal models, although these individually explained up to 9% of the statistical variation ($r_m^2 = 0.09$ —Table 5). AF indices were included within two optimal LMMs when TaxRic and FEeve were modelled against AFJulianMin (the Julian day number when the minimum flow alteration occurred) and AFMay (the average flow alteration value in May), respectively; these statistical relationships accounted for 9%–20% ($r_m^2 = 0.09$ –0.20) of the statistical variation (Table 5). HG.optimal models exhibited a higher statistical power and differed significantly from each respective optimal model in all instances (Table 5). The Froude number exhibited a significantly greater statistical influence when its interaction with HG was considered in all instances, but this was not observed for Q and AF indices incorporated within optimal models (Table 5).

5 | DISCUSSION

5.1 | Invertebrate community differences between habitat groups

This study aimed to quantify how invertebrate communities inhabiting distinct lotic habitats responded to three sets of flow-related characteristics: antecedent hydrological variability; antecedent anthropogenic flow alterations (daily percentage of discharge removed or added to the river) and proximal hydraulic conditions (characterised by the Froude number). HGs supported distinct taxonomic compositions, supporting the findings of many studies reporting structural differences in invertebrate communities between mineralogical and organic habitat patches (e.g. Li, Chung, Bae, Kwon, & Park, 2012; Robson & Chester, 1999). Functional trait compositions

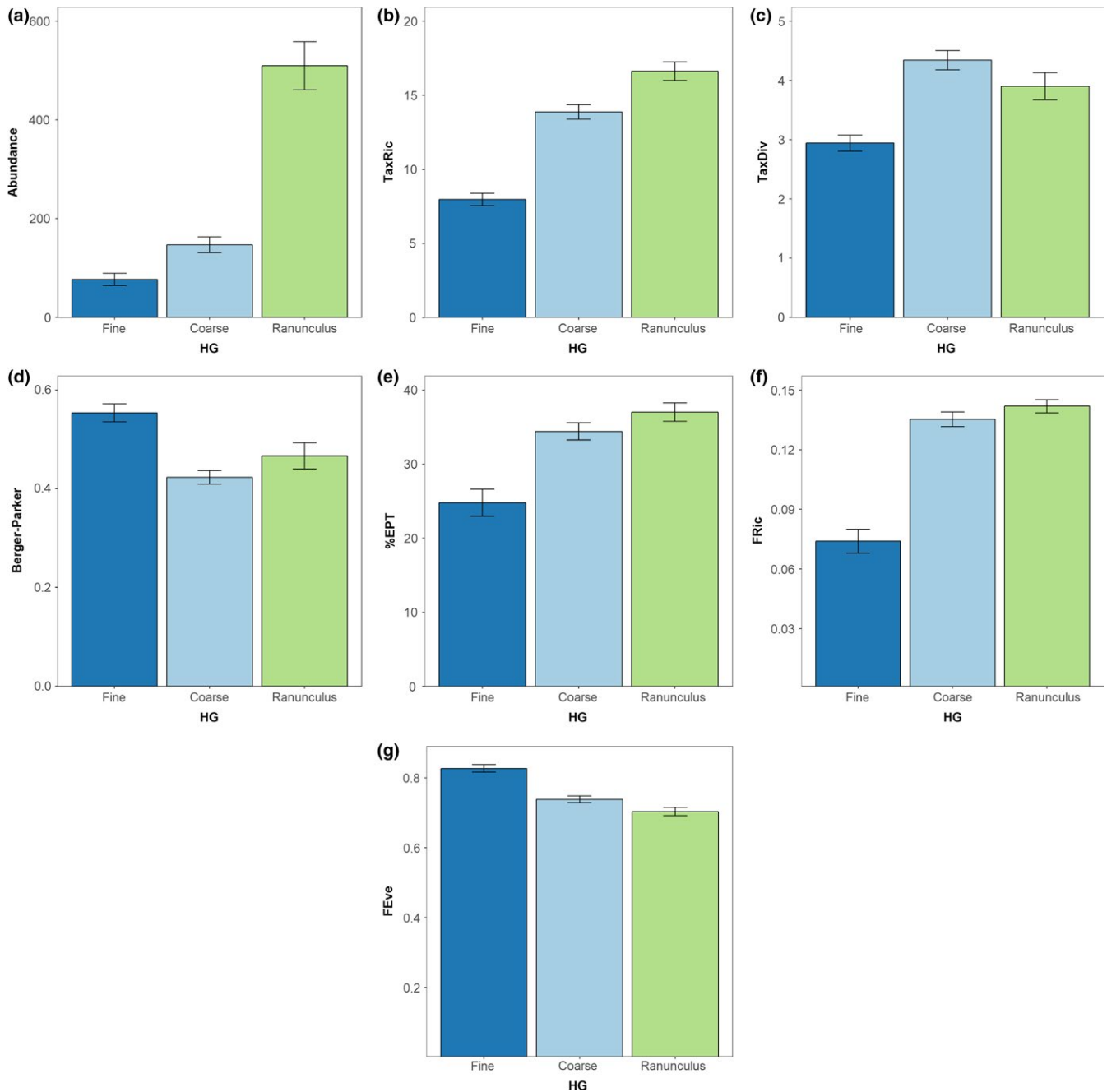


FIGURE 5 Average (± 1 standard error) values for invertebrate response metrics between different habitat groups (HGs). (a) Abundance; (b) TaxRic; (c) TaxDiv; (d) Berger-Parker index; (e) %EPT; (f) FRic and (g) FEve. Dark blue = Fine sediments; light blue = coarse substrates and green = *Ranunculus* sp

also differed between HGs, but there was a greater degree of overlap than for taxonomic compositions, particularly between *Ranunculus* sp. and coarse substrates. This contradicts the limited evidence reporting that the functional properties of invertebrate communities are more distinct between mineralogical and organic habitat patches than for taxonomic compositions (Demars et al., 2012; White, Hill, Bickerton, & Wood, 2017).

Ranunculus sp. supported the highest community abundances (Abundance), taxonomic and functional richness (TaxRic and FRic, respectively) and %EPT in each sample compared to other HGs. This

reflects the suite of ecological functions that *Ranunculus* sp. provides, including the provision of cover from predators, a habitat to lay eggs and attach egg sacks to, or a platform from which fauna can consume food resources (Gunn, 1985; Ladle, Bass, & Jenkins, 1972). Invertebrate communities inhabiting fine sediments displayed a high structural dominance (Berger-Parker), but a high degree of functional evenness (FEve). Greater FEve values occur when there is a high degree of taxonomic evenness or when functional distances among species are more regularly distributed (Villéger et al., 2008). As such, the latter must be true for invertebrate communities sampled from fine sediments given that

TABLE 4 Invertebrate community responses to the influences of hydrological variability and anthropogenic flow alterations (flow-ecology and flow alteration-ecology relationships, respectively) and their interaction with habitat groups (HG: HG.flow-ecology and HG.flow alteration-ecology relationships, respectively)

Response	Statistic	Hydrological variability			Anthropogenic flow alterations		
		Flow-ecology	HG.Flow-ecology	Difference	Flow alteration-ecology	HG.Flow alteration-ecology	Difference
Abundance	AIC	322.70	312.44	-	325.39	269.13	-
	r_m^2	0.06	0.15	-	0.03	0.37	-
	χ^2	4.36	34.63	30.26	1.67	77.93	76.26
	p-value	0.499(NS)	0.003**	<0.001***	0.893(NS)	<0.001***	<0.001***
TaxRic	AIC	1457.50	1465.00	-	1462.30	1458.90	-
	r_m^2	0.10	0.15	-	0.08	0.37	-
	χ^2	13.56	26.07	12.51	8.75	32.18	23.43
	p-value	0.019*	0.037*	0.252(NS)	0.119(NS)	0.006**	0.009**
TaxDiv	AIC	880.47	881.01	-	904.35	913.56	-
	r_m^2	0.04	0.12	-	0.01	0.05	-
	χ^2	9.10	28.56	19.46	1.36	12.15	10.79
	p-value	0.105(NS)	0.018*	0.035*	0.929(NS)	0.668(NS)	0.374(NS)
Berger-Parker index	AIC	-165.05	-155.67	-	-143.17	-129.85	-
	r_m^2	0.03	0.08	-	0.01	0.04	-
	χ^2	7.48	18.10	10.63	1.99	8.67	6.68
	p-value	0.188(NS)	0.257(NS)	0.387(NS)	0.851(NS)	0.894(NS)	0.755(NS)
%EPT	AIC	1863.50	1871.00	-	1857.60	1857.10	-
	r_m^2	0.08	0.13	-	0.06	0.22	-
	χ^2	6.22	18.80	12.57	7.48	28.04	20.56
	p-value	0.285(NS)	0.223(NS)	0.249(NS)	0.187(NS)	0.021*	0.024*
FRic	AIC	-668.30	-703.85	-	-678.33	-667.80	-
	r_m^2	0.03	0.26	-	0.03	0.08	-
	χ^2	6.68	62.23	55.56	6.98	16.45	9.47
	p-value	0.246(NS)	<0.001***	<0.001***	0.222(NS)	0.353(NS)	0.488(NS)
FEve	AIC	-393.45	-425.47	-	-391.86	-386.52	-
	r_m^2	0.10	0.25	-	0.19	0.27	-
	χ^2	12.87	54.88	42.02	14.71	29.37	14.66
	p-value	0.025*	<0.001***	<0.001***	0.012*	0.014*	0.145(NS)

Shaded boxes highlight significant differences whereby each statistical "pair" differs significantly and possesses higher r_m^2 and $\Delta AICc$ values ≤ -2 when a HG interaction is incorporated. Stars denote the degree of significance: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS = non-significant. See Section 3.3.2 and Figure 2 for statistical model descriptions and nomenclature.

greater FEve values occurred (relative to other HGs) despite exhibiting high Berger-Parker values (indicating a lower taxonomic evenness). The more even distribution of taxa across functional trait space (indicated by higher FEve values) within fine sediments suggests that the loss of taxa (TaxRic) occurred randomly, rather than clusters of taxa exhibiting comparable functional niches being extirpated (Barnum, Weller, & Williams, 2017). Larsen and Ormerod (2014) highlighted that fine sediment deposition led to random co-occurrences of species as biotic interactions weakened. Such ecological and community demographical processes could explain the higher FEve values occurring within fine sediments in the present study. Given that fine sediments are regularly disturbed and entrained in lotic environments (e.g. Gibbins, Vericat, &

Batalla, 2007), higher FEve values within fine sediments indirectly contradicts previous findings highlighting that FEve decreases with higher disturbance frequencies (e.g. Barnum et al., 2017; Schriever et al., 2015).

5.2 | Invertebrate community responses to hydrological variability and anthropogenic flow alterations

Two invertebrate community response metrics (TaxRic and FEve) were significantly influenced by antecedent hydrological conditions (derived from historic discharge time series—flow-ecology

TABLE 5 Invertebrate community responses to statistically *optimal* (derived from a backwards stepwise selection procedure) flow-related indices (Hydrological [Q], anthropogenic flow alteration [AF], and hydraulic [Froude]), as well as their interaction to habitat groups (HG)

Response	Optimal and HG.optimal model summaries					Difference	
	Covariates	r_m^2	AIC	F/χ^2	p-value	χ^2	p-value
Abundance	Froude	0.30	238.57	100.80/80.66	<0.001***	25.60	<0.001***
	HG × Froude	0.34	216.73	45.52/106.26	<0.001***		
TaxRic	Froude	0.38	1344.50	148.07	<0.001***	23.66	<0.001***
	HG × Froude	0.44	1324.80	61.47	<0.001***		
	AFJulianMin	0.20	1423.70	17.58	<0.001***	1.55	0.460(NS)
	HG × AFJulianMin	0.19	1426.10	8.35	<0.001***		
	QMax30	0.08	1428.00	20.52	<0.001***	6.67	0.036*
	HG × QMax30	0.07	1425.30	6.16	<0.001***		
	QJulianMin	0.04	1423.50	8.28	0.004**	2.81	0.246(NS)
	HG × QJulianMin	0.06	1424.70	5.09	0.002**		
	Froude + AFJulianMin + QMax30 + QJulianMin	0.50	1310.80	123.45	<0.001***	32.70	<0.001***
	HG × (Froude + AFJulianMin + QMax30 + QJulianMin)	0.54	1294.10	156.16	<0.001***		
TaxDiv	Froude	0.11	850.23	26.86/25.38	<0.001***	18.29	<0.001***
	HG × Froude	0.17	835.93	16.03/43.68	<0.001***		
Berger-Parker	Froude	0.06	-172.03	14.39/13.83	<0.001***	16.30	<0.001***
	HG × Froude	0.12	-184.33	10.73/30.12	<0.001***		
%EPT	Froude	0.11	1893.00	28.28/24.23	<0.001***	15.83	<0.001***
	HG × Froude	0.15	1881.20	15.22/40.07	<0.001***		
FRic	Froude	0.24	-718.49	66.94	<0.001***	54.83	<0.001***
	HG × Froude	0.39	-769.32	45.64	<0.001***		
	QMax30	0.05	-671.13	10.41	0.001**	0.74	0.692(NS)
	HG × QMax30	0.02	-667.86	1.32	0.270(NS)		
FEve	Froude + QMax30	0.24	-726.65	57.64	<0.001***	48.58	<0.001***
	HG × (Froude + QMax30)	0.39	-767.23	106.22	<0.001***		
	Froude	0.10	-413.37	25.65	<0.001***	20.39	<0.001***
	HG × Froude	0.15	-429.76	14.73	<0.001***		
	QMax30	0.09	-405.16	18.25	<0.001***	1.59	0.453(NS)
	HG × QMax30	0.07	-402.75	5.01	0.003**		
	AFMay	0.09	-405.46	10.81	0.001**	0.94	0.625(NS)
	HG × AFMay	0.10	-402.40	4.06	0.008**		
	Froude + QMax30 + AFMay	0.20	-433.18	39.81	<0.001***	19.51	0.003**
	HG × (Froude + QMax30 + AFMay)	0.25	-440.69	59.32	<0.001***		

F = F-value obtained from *anova* for each individual covariate (italicized), χ^2 derived from likelihood ratio tests for each full model (highlighted in bold). Shaded boxes highlight significant differences between optimal and HG.optimal (likelihood ratio test) and when the latter possesses a higher r_m^2 and $\Delta AICc$ values ≤ -2 . Stars denote the degree of significance: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS = non-significant. See Section 3.3.2 and Figure 2 for statistical model descriptions and nomenclature.

relationships). Such significant flow–ecology relationships support the plethora of evidence reported globally demonstrating the importance of river flow regimes in shaping the structure (e.g. Kennen, Riva-Murray, & Beaulieu, 2010; Steel, Peek, Lusardi, & Yarnell, 2018; Warfe, Hardie, Uytendaal, Bobbi, & Barmuta, 2014) and function of instream communities (e.g. Mims & Olden, 2013; Schriever et al., 2015; White, Hill, et al., 2017), although the latter

has been comparatively understudied worldwide (Arthington et al., 2018; Poff, 2018). However, statistical models in this study did not detect a significant influence of hydrological characteristics for some community response metrics and flow–ecology relationships explained relatively low ($\leq 10\%$) amounts of statistical variation, which potentially reflects the following five factors. First, samples were collected across a single catchment (eight sites) over

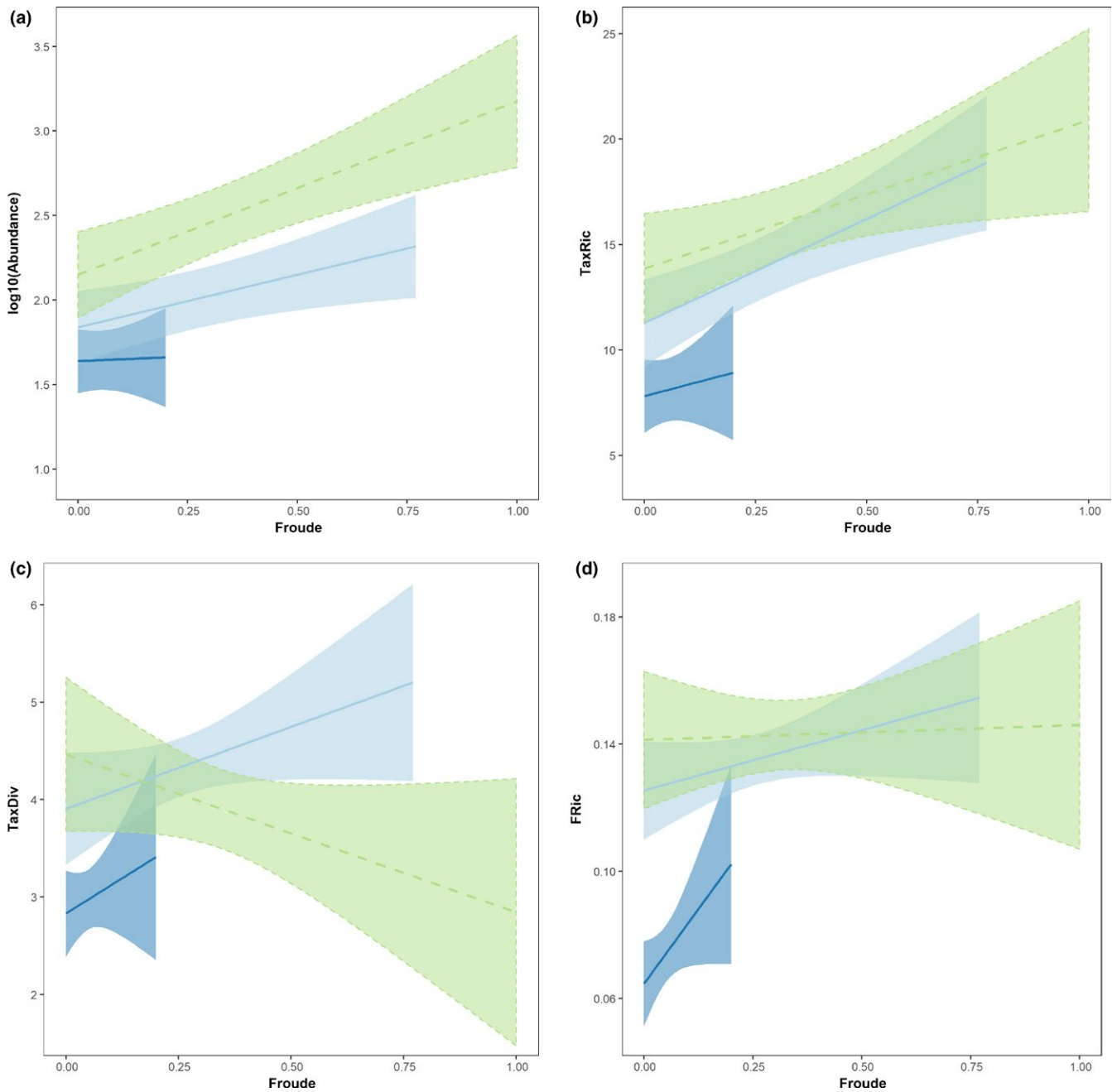


FIGURE 6 Statistical relationships between invertebrate community responses to Froude across different HGs, with 95% confidence intervals obtained from LMMs. (a) Abundance; (b) TaxRic; (c) TaxDiv and (d) FRic. Dark blue = Fine sediments; light blue = coarse substrates and green = *Ranunculus* sp. (these lines are dashed to aid visual interpretation)

1 year and specifically during a time when intermediate discharges occurred (i.e. no extreme flow events were recorded—Barker et al., 2016; White, 2018). As such, communities were exposed to a relatively limited range of hydrological conditions compared to studies undertaken across greater spatial and temporal scales (e.g. Chen & Olden, 2018; Monk et al., 2006). Second, river flow regimes are widely recognised as a strong environmental filter (*sensu* Poff, 1997) operating across large (catchment to regional) spatial scales (see Biggs, Nikora, & Snelder, 2005; Lytle & Poff, 2004). As such, riverine invertebrate species pools are confined

to taxa adapted to region-wide hydrological variations, which are then subjected to smaller scale environmental filters (e.g. habitat conditions—Poff, 1997). This helps explain the findings of this study given that statistical models did not consistently detect significant flow–ecology relationships and instream communities were more responsive to habitat-scale controls (HG and hydraulic conditions, see below). This suggests that the filtering effect of river flow regimes at the regional scale could not be statistically detected within this study conducted across a single catchment. Third, habitat replicates within the same reach used in this study

shared the same discharge-related (i.e. hydrological variability and anthropogenic flow alteration) values, which may have resulted in weaker statistical associations and highlights the difficulty in integrating flow-related characteristics across different spatial scales (see Biggs et al., 2005). Fourth, river flow regimes may act in concert with other environmental variables (e.g. water quality and morphological alterations) to exert a synergistic effect on instream ecological processes (see Booker, Snelder, Greenwood, & Crow, 2015). As such, flow–ecology relationships testing the individual effect of hydrological characteristics may overlook significant interactive effects with alternative environmental variables, as demonstrated with HGs in this study. Fifth, the nature and strength of flow–ecology relationships are artefacts of the underpinning ecological (Cuffney and Kennen, 2018) and hydrological (Wilby et al., 2017) information and the data used within this study may have had a key influence on the results. For example, within the family Chironomidae (Order: Diptera), species-specific flow–ecology relationships are likely to have occurred (e.g. Cañedo-Argüelles, Bogan, Lytle, & Prat, 2016), which would not have been detected in this study due to their consideration at the family level. However, it should be noted that invertebrate taxa were identified consistently and to the lowest practical resolution within this study, which has been demonstrated to provide the basis for developing consistent and robust flow–ecology relationships (see Monk et al., 2012).

Functional evenness (FEve) responded significantly to anthropogenic flow alterations, highlighting its potential use as a tool for underpinning significant flow–ecology (see above) and flow alteration–ecology relationships. This provides additional evidence supporting recent calls for the functional properties of biota to be incorporated into environmental flow (e-flow) science (e.g. Arthington et al., 2018; Poff, 2018). Non-significant flow alteration–ecology relationships observed in this study may be an artefact of the five factors discussed above. However, it is also likely that flow alterations across the rivers studied were not of sufficient magnitude to yield consistent, statistically detectable ecological responses. Long-term improvements in water management operations have occurred across the study region to limit extreme flow alterations (Bowles & Henderson, 2012). Discharges were reduced on average by just 3.88% across all sampling sites over the study period, which is much lower than extreme flow alterations being reported elsewhere globally (e.g. c. 100% reduction in discharge due to groundwater abstraction reported by Bradley et al., 2014, 2017). Moreover, although the daily reductions in historic discharges of up to 48.33% occurred at a single site in this study, in a UK study Bradley et al. (2017) only detected negative ecological effects of groundwater abstraction when river discharges were reduced by at least 50%. Such findings may explain the absence of significant flow alteration–ecology relationships observed in this study. Notwithstanding, this study represents the first of its kind to test ecological responses to a suite of indices characterising anthropogenic flow alterations (centred on the five facets of the flow regime—see Poff et al., 1997) that incorporates both subsurface (groundwater abstraction) and surface (e.g. effluent water

returns) hydrological changes. There is a paucity of information on how groundwater abstraction influences riverine ecosystems globally (Gleeson & Richter, 2018; Poff & Zimmerman, 2010). Given that groundwater abstraction practices are increasingly and severely depleting subsurface water resources (Gleeson, Wada, Bierkens, & van Beek, 2012) and substantially reducing river discharges globally (De Graaf et al., 2014), studies such as this are vital for guiding e-flow science and sustainable groundwater management operations.

Community responses to hydrological indices were stronger when incorporating their interaction with HGs (i.e. HG.flow–ecology relationships), which significantly improved the statistical fit of Abundance, FRic and FEve models. This highlights that hydrological controls on the total abundance and functional diversity of communities differs between HGs, which may have significant implications for the wider food web (Greenwood & Booker, 2015; Ledger, Brown, Edwards, Milner, & Woodward, 2013; Power, Parker, & Dietrich, 2008). Similarly, various community responses (most notably Abundance and TaxRic) to anthropogenic flow alterations were stronger when a HG interaction term was incorporated (HG.flow alteration–ecology relationships). Other studies have also reported habitat-specific invertebrate responses to flow alterations, including marginal habitats (which become regularly disconnected from the channel—Storey & Lynas, 2007) and riffles (due to the loss of rheophilic taxa—Brooks, Chessman, & Haeusler, 2011). In contrast, Bradley et al. (2017) reported that instream community responses to groundwater abstraction did not differ between substrate size classes. Variable ecological responses to flow alterations have been reported at global (e.g. Poff & Zimmerman, 2010), national (e.g. Mims & Olden, 2013), regional (e.g. Chen & Olden, 2018), and even system-specific scales (Thompson et al., 2018). The results of the present study provide evidence that ecological responses to anthropogenic flow alterations vary at the habitat-scale and specifically between distinct mineralogical and organic habitat patches, which have seldom been incorporated within e-flow research thus far (but see Bradley et al., 2017; Finn, Boulton, & Chessman, 2009; Lind et al., 2006).

5.3 | Statistically optimal flow-related characteristics driving ecological responses

The Froude number exerted a significant influence on all structural and functional community response metrics examined within this study. Froude number has been demonstrated to have a significant influence on the structural (Rempel, Richardson, & Healey, 2000) and functional (Lamouroux, Dolédec, & Gayraud, 2004) properties of river invertebrate communities as it characterises the hydraulic conditions experienced by biotic communities (Turner & Stewardson, 2014). Previous research has highlighted that the morphological properties of invertebrate species govern community responses to Froude number, such as organisms with streamlined body forms responding positively to higher flow velocities (Lamouroux et al., 2004; Rempel et al., 2000). In addition, the behavioural responses of invertebrates to hydraulic conditions shapes community responses

to Froude number, such as species migrating to different surface (Lancaster, Buffin-Bélanger, Reid, & Rice, 2006) or subsurface refuges (Holomuzki & Biggs, 2000) during adverse hydraulic conditions.

Examining changes in optimal hydraulic conditions (based on the preference of target organisms) over a range of river discharges has been a core part of habitat simulation e-flow methodologies (Lamouroux & Jowett, 2005). Various authors have demonstrated the application of such techniques within e-flow frameworks (e.g. Nikghalb, Shokoohi, Singh, & Yu, 2016; Strevens, 1999). For example, Lamouroux and Olivier (2015) used a hydraulic habitat model to reliably predict changes in fish populations in response to a restored flow regime. Findings from the present study reinforce the benefits of incorporating hydraulic observations within e-flow studies. Hydraulic observations provide an improved characterisation of the forces to which biota are exposed to at the time of sampling compared to the use of discharge-related statistics alone (e.g. Malcolm, Gibbins, Soulsby, Tetzlaff, & Moir, 2012; Monk et al., 2018). Given the crucial importance of hydraulic forces in shaping the structural and functional properties of communities, further observational and experimental studies are required to elucidate the causal mechanisms underpinning ecological responses to hydraulic characteristics to guide the practical application of future e-flow science (Arthington et al., 2018).

Froude number was utilised in this study due to its comparability between habitats, rivers and seasons (Jowett, 1993; Wadeson & Rowntree, 1998). Unsurprisingly, Froude number was highly correlated with flow velocities and is therefore intrinsically linked to the entrainment threshold of riverbed sediments, a widely recognised disturbance affecting instream communities (e.g. Gibbins et al., 2007). Froude number has also been demonstrated to reliably characterise the average shear stresses occurring between submerged plant strands within lotic environments (Folkard, 2011). However, differences in ecological responses to hydraulic conditions between different mineralogical and organic habitat patches (HGs in this study) has not been widely explored, in part due to the difficulties obtaining reliable hydraulic observations between macrophyte strands (see Marjoribanks, Hardy, & Lane, 2014).

This study demonstrated that invertebrate community responses to Froude number differed between HGs, highlighting how mineralogical and organic habitat patches mediate the structural and functional responses of biota to hydraulic conditions. This potentially reflects HGs supporting distinct communities which respond differently to Froude, such as various rheophilic taxa (e.g. *Rhyacophila dorsalis*, *Limnius volckmari* and *Elmis aenea*; see Supporting Information Appendix S5: Table S6 and Extence, Balbi, & Chadd, 1999) inhabiting coarse substrates and *Ranunculus* sp. patches and benefit from higher flow velocities. Alternatively, the significant interactive effects of Froude number and HGs on the structure and function of invertebrate communities could be attributed to mineralogical and organic habitat patches providing unique ecological functions which alter how instream communities respond to hydraulic conditions. For example, *Ranunculus* sp.

is typically located in channel areas exhibiting high flow velocities, which deliver high quantities of detritus between the porous plant stands. Many filter-feeding invertebrates (e.g. *Brachycentrus subnubilus*, *Hydropsyche* sp., and various Simuliidae species—see Supporting Information Appendix S5: Table S6) occupy *Ranunculus* sp. patches in order to consume food resources by attaching themselves to plant stems suspended in water column (Ladle et al., 1972; Wharton et al., 2006).

5.4 | Incorporating small-scale habitat features into environmental flow frameworks

The need to conserve and/or create ecologically favorable habitat conditions in order to enhance the effectiveness of river management strategies has received considerable research attention (see Palmer, Menninger, & Bernhardt, 2010). This has been most widely considered within the context of morphological river restoration efforts applied at the reach-scale (e.g. Kemp et al., 1999; White, Hill, et al., 2017). However, incorporating habitat-scale features within regional environmental flow (e-flow) strategies may be hindered by limited resources restricting the ability of scientists and practitioners to collect such fine-scale data across larger geographical scales (see Chen & Olden, 2018). Notwithstanding, a limited body of research has highlighted how flow regimes could be managed to indirectly benefit instream communities by modifying the composition of small-scale lotic habitats (e.g. Armitage & Pardo, 1995; Storey & Lynas, 2007). This study further emphasises how hydrological and hydraulic controls on habitat compositions could be incorporated into e-flow research. Moreover, the findings from this study provides rare evidence that the ecological benefits of e-flow frameworks and river restoration practices could be further improved by considering the hydraulic conditions occurring within distinct small-scale habitat patches. Further research is required to understand how flow characteristics shape riverine communities at the habitat-scale in order to provide a causal basis for guiding the development of regional e-flow strategies.

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