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Accounting for the power of nature: Using flume and field studies to compare the capacities of bio-energy and fluvial energy to move surficial gravels

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Abstract

River channels, riparian and floodplain forms and dynamics are all influenced strongly by biological processes. However, the influence of macroinvertebrates on entrainment and transport of river sediments remains poorly understood. We use an energy-based approach to explore the capacity of benthic animals to move surficial, gravel-bed particles in field and laboratory settings and use the results to assess the relative significance of biological and physical benthic processes. Our results showed that in 11 British gravel-bed rivers, the maximum energy content (i.e., calorific content) of macroinvertebrate communities generally matched the flow energy associated with median discharges and, at multiple sites, exceeded that of the 10-year return interval flood. A series of laboratory experiments used to estimate the minimum energy expended by signal crayfish (*Pacifastacus leniusculus*) when performing geomorphic work established that crayfish move gravel particles at energy levels below that expected of the flow, complicating direct comparisons of the capacity for macroinvertebrates and fluvial flows to influence bed mobility. Our findings suggest that the influence of macroinvertebrate communities in either promoting or suppressing, the mobilisation of the bed may be large compared to equivalent values of fluvial energy. Based on these findings, we conclude that in the gravel-bed rivers studied, the macroinvertebrate community's potential to perform geomorphic work matches or exceeds the stream power during most of the year. Although our study examined biological and fluvial energy systems separately, it is important to recognise that in nature, these systems are highly interactive. It follows that utilising the energy framework presented in this paper could lead to rapid advances in both fluvial bio-geomorphology and river management and restoration.

KEYWORDS
bedload, biogeomorphology, Ecohydraulics, ecosystem engineering, gravel-bed Rivers, sediment transport, stream power, Zoogeomorphology

1 | INTRODUCTION

Aquatic, riparian and floodplain animals can influence the dynamics of sediments and organic matter in rivers, with profound geomorphological implications (Mason & Sanders, 2021; Rice, Johnson, & Reid, 2012). Well-known examples include beaver, by building dams (Brazier et al., 2021), riverine fish by disturbing bed sediments during spawning and foraging (DeVries, 2012; Fremier, Yanites, &

Yager, 2018; Hassan et al., 2008; Pledger, Rice, & Millet, 2017) and crayfish and other large crustaceans, by burrowing (Albertson & Daniels, 2018; Harvey et al., 2014; Johnson et al., 2010; Statzner et al., 2000).

Insect larvae and other macroinvertebrates can also influence bed mobility and sediment loads through, for example, winnowing fine sediments from between larger grains (Pringle & Blake, 1994; Statzner et al., 1996; Zanetell & Peckarsky, 1996), binding and adhering grains together with silk threads and other sticky substances (Albertson et al., 2019; Cardinale, Gelmann, & Palmer, 2004; Johnson et al., 2009), building fixed and mobile assemblages of grains that alter threshold conditions for the entrainment of bed sediment (Mason & Sanders, 2021) and moving sediments vertically when moving through, and burrowing in, the bed (Mermillod-Blondin, 2011; Shrivastava, Stewardson, & Arora, 2021).

Typically, the zoogemorphological impact on river forms and processes made by individual organisms is small-scale (≤ 10 m^2), time-limited and difficult to detect. However, the impacts attributable to beaver (*Castor canadensis* and *Castor fiber*) are a notable exception (Brazier et al., 2021), while very large colonies of very small animals may change river behaviours at larger space and time scales, through their cumulative effects. For example, Rice et al. (2016) found invasive crayfish (*Pacifastacus leniusculus*) increased fine sediment transport at base flow in a 233 km^2 sub-catchment of the River Nene, UK, by 20% to 40%.

While there are numerous examples of invertebrate animals altering geomorphological processes in rivers (Mason & Sanders, 2021), zoogeomorphology is rarely considered in river science and is typically viewed as a phenomenon that is peculiar or novel (Rice, 2021); i.e., important in some narrow, specific contexts, but of secondary or even tertiary importance compared to the physical processes deemed responsible for forming and adjusting the channel geometry (Johnson et al., 2019). In contrast, the channel-forming impacts of plants are more widely acknowledged and better understood (e.g. Bertoldi, Gurnell, & Drake, 2011; Harvey et al., 2018), and vegetation impacts are accepted as significant at the largest temporal and spatial scales. For example, it was established over a decade ago that, globally, river planforms broadly adjusted towards meandering and multi-channel planforms in response to the evolution and spread of terrestrial vegetation during the Carboniferous (Davies & Gibling, 2010; Ward et al., 2000). Similarly, the contemporary impacts on channel planforms of vegetation destruction due to over-grazing by cattle (*Bovinae*), bison (*Bison bison*) and elk (*Cervus canadensis*) to river processes are well documented (Beschta et al., 2020; Trimble & Mendel, 1995).

Despite the long-known importance of plants to river forms and processes, and notwithstanding growing recognition of the influence of animals, studies and predictions of sediment transport and its interaction with channel morphology rarely incorporate animal activities. This is despite the fact that much of the research regarded as foundational in linking sediment transport to channel form is now known to have characterised processes and forms in anthropogenically altered streams (Walter & Merritts, 2008; Cluer & Thorne, 2014, Brown et al., 2018), which likely minimised or entirely eschewed the role of life in influencing stream forms, processes and functions and, by extension, our acknowledgement of these processes in the development of river science a (Johnson et al., 2019).

Research in biogeomorphology has quantified some of the myriad interactions between living organisms and geomorphic processes (Viles, 2019). However, without better consideration of the ways animals influence and interact with fluvial processes and landforms, progress in better understanding how rivers work will remain limited, especially in comparison to that in non-fluvial environments, where it is now fully appreciated that animal actors play fundamental roles in driving geomorphological processes. For example, animals are known to be significant at the largest temporal and spatial scales in the oceans, where invertebrate burrowing oxygenates sediments (Teal et al., 2008) in ways that were at least partially responsible for significant evolutionary diversifications in life during the Cambrian and Ordovician Periods (Herringshaw, Callow, & McIlory, 2017; van der Velde et al., 2018), and burrowing invertebrates mix soils, a process shown to be critical for the survival for all terrestrial life on Earth by Charles Darwin (Darwin, 1881; Wilkinson, Richards, & Humphreys, 2009).

Lack of appreciation of the capacity of animals to influence rivers stems from the untested assumption that river flows are too powerful for the actions of animals to be significant. In most gravel-bed rivers, stream power per unit width usually exceeds the threshold value for bed material entrainment and transport only during high, in-bank flows (Leopold, 1992). However, the frequency of such events is relatively low, and the bed sediment is in transport for only a fraction of the time (Blom et al., 2017; Wolman & Miller, 1960). In essence, while most rivers can reasonably be regarded as powerful geomorphic agents, they can also be characterised as being lazy, and, as a result, there are long periods when their channels, riparian corridors and floodplains are not significantly altered by the flow. During these periods, the activities of animals could be cumulatively significant either by moving bed sediment directly or altering bed surface grain size distributions and structures in ways that may increase or decrease threshold shear stresses required for entrainment during subsequent, high flows (e.g. Brown et al., 2022; Rice et al., 2016).

A metric for representing the potential contribution of biological processes in modulating geomorphological processes was explored in relation to plants by Phillips (2009). His energy-based approach revealed that the energy associated with terrestrial plant primary productivity on the Cumberland Plateau, USA, is six orders of magnitude higher than the energy associated with all the processes of tectonics and denudation, combined. However, no equivalent comparison has yet been made for fluvial processes and riverine animals.

To address this research gap, for the first time, we quantify the power of macroinvertebrates living in rivers. This only represents an initial attempt to compare bio- and fluvial processes in rivers, but it establishes a theoretical framework for integrating invertebrate life into models of riverscape change based on energy auditing. Our premise is that biogeomorphic processes result from inputs of energy from the biological to the physical energy system. Specifically, biological energy is expended in ways that alter the physical environment such that the magnitude of physical energy required to do a given amount of geomorphic work is altered. In the remainder of this paper, we quantify the energy potentially available to power such transfers, using macroinvertebrates as a study group and a range of locations along British gravel-bed rivers as our study sites. We then assess the relative significance of their bio-power by comparing it to the fluvial stream power at those study sites. We paired our field study with a
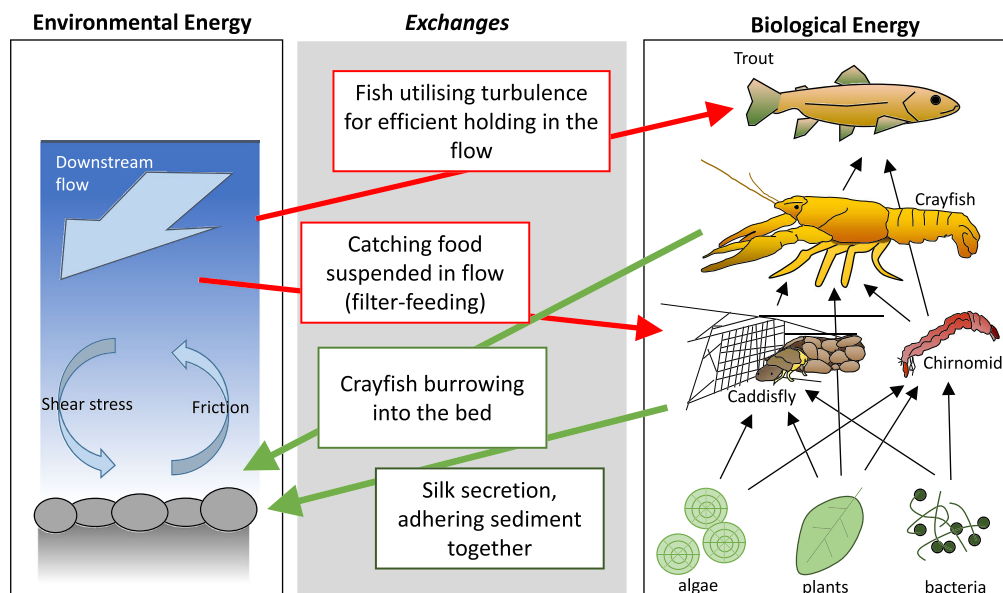
FIGURE 1 Conceptual diagram showing links between the fluvial and bio-energy systems. In this simple schematic, the fluvial energy system is depicted in terms of downstream flow and bed shear stress, which is balanced by friction. Bio-energy is represented by arrows indicating trophic links in the food web. Example exchanges between systems are shown by black and blue arrows indicating transfers from the fluvial to the bio-system, and from the bio-system to the fluvial system, respectively. Transfers may either increase or decrease the fluvial energy required to do a given amount of geomorphic work.

laboratory-based investigation under controlled conditions that allowed us to quantify the energy expended by individual crayfish in moving gravel-sized spheres and upscaled the results to a typical population level. As explicitly stated, our objectives were to:

1. calculate the total amount of biological energy in the macroinvertebrate community, representing the absolute maximum amount of bio-energy that could be available to zoogeomorphic work;
2. compare this to the stream power, representing the maximum amount of energy that could be available to do fluvial geomorphic work;
3. establish how relative amounts of bio-energy and fluvial energy vary through time and space;
4. quantify the bio-energy expended in doing zoogeomorphic work by an individual benthic animal, and use the results to gauge the capacity of a population of such animals to influence the benthic environment.

2 | METHODOLOGY AND METHODS

2.1 | Theoretical framework

As water flows downhill, potential energy is converted to kinetic energy, with some being lost to friction. The time rate of this energy conversion is defined by the river's stream power per unit channel length (w/m). Stream power per unit width (w/m^2), customarily referred to as 'specific stream power', has proven to be a reliable indicator of river's capacity to entrain and transport bed material at the reach scale (Bagnold, 1986; Bizzi & Lerner, 2013; Candell et al., 2021; Jain, Fryirs, & Brierley, 2008). The biosystem is likewise solar powered, and energy acquired from solar radiation flows through the

ecosystem via the trophic web, which is driven by how biota interact with each other and with the wider biome, of which they are part.

Energy is transferred between these two systems in both directions (Figure 1). The energy supplied by the physical system can alter behaviours and energy expenditure in the ecosystem. For example, filter-feeding invertebrates take advantage of fluvial energy to deliver phytoplankton to them, and fish seeking to avoid being flushed downstream during floods exploit the turbulent wakes behind large wood pieces and jams to reduce the amount of bio-energy they need to expend while holding station (black arrows in Figure 1). In the other direction, bio-energy can be transferred to the physical system in ways that alter the expenditure of physical energy required to alter the riverscape. Examples include crayfish disturbing the surface armour in a gravel-bed river (which alters bed friction), or caddisfly larvae binding gravel particles together using silk webs, which increases the critical stream power for entrainment (blue arrows in Figure 1).

In our studies, two metrics were employed to quantify the bio-energy aquatic macroinvertebrate communities available for geomorphic work. First, in the field study, the total amount of energy in the sampled macroinvertebrate community was calculated as the calorific content of that community. This is similar to the measure of primary productivity used by Phillips (2009) to represent bio-energy in plants. It is also comparable to using stream power to represent the total amount of physical energy available to a river to do geomorphic work because both systems are characterised by the low efficiency with which the energy available is applied to moving sediment. In other words, the fact that animals expend energy on living costs with only a small proportion used in geomorphic work is broadly similar in our framework to the river expending energy on overcoming frictional resistance.

Second, in the laboratory study, the minimum bio-energy expenditure involved in doing a typical geomorphic task was directly quantified for an indicator zoogeomorphic agent, the decapod crustacean

P. leniusculus or signal crayfish. In the experiment, bio-energy expenditure was measured in an aquarium with a bed formed of gravel-sized, spherical grains of uniform size and weight. Grain uniformity made it straightforward to calculate the minimum energy required to move a single grain a set distance (and therefore calculate energy applied to geomorphic work). Over 2 hours, the total number of grains moved and the distance each of the grains was moved were recorded using videography.

The signal crayfish was selected for this study as there was already a body of published work detailing its zoogeomorphic activities (e.g. Albertson & Daniels, 2018; Harvey et al., 2011; Johnson et al., 2011; Sanders et al., 2021; Statzner et al., 1996). We drew on this body of knowledge not only to design the laboratory study but also to provide the field data needed to upscale, extrapolate and compare our results at the population scale.

Most academic studies report the density of adult (i.e., large) crayfish from trapping data while acknowledging the much higher densities of small juveniles, which are not included because they are small enough to evade crayfish traps. Specifically, we used the density of adult crayfish recorded in Brampton Branch (a tributary to the River Nene) by Rice et al. (2016) to make indicative estimates of the calorific content of the population in a typical watercourse and to compare the bio-energy that a signal crayfish population could expend to the river's fluvial energy.

2.2 | Field data for determining macroinvertebrate bio-energy and river fluvial energy

To compare the bio-energy associated with macroinvertebrate communities with the fluvial energy in the host river, we cross-referenced the WildFish RiverFly Census (https://wildfish.org/project/riverfly-census/) with the National River Flow Archive (https://nrfa.ceh.ac.uk/) to identify 10 British rivers with both species-level macroinvertebrate abundance data (2015, 2016, 2021 survey dates) and a daily discharge record from a gauge located within 1 km of the macroinvertebrate sampling site and with no intervening tributaries (Figure 2).

Macroinvertebrate communities were kick-sampled by the same operator (Everall), following the EA standard sampling protocol (HMSO, 1985, Environment Agency, 2009), preserved and identified to the highest taxonomic level possible, which was typically species-level with the exception of worms (*Oligochaeta*), which were identified to family-level. The total abundance of animals within each taxonomic group was counted. For our analysis, taxonomic resolution was coarsened to genus level.

Further data were also obtained from the EA for 11 sites along the River Trent that were sampled in 2015 and for sites in Brampton Branch that were sampled in the same years as WildFish Census data. The additional data from the River Trent allowed us to investigate downstream trends in bio- and fluvial energies in a single river. The data from Brampton Branch allowed upscaling, extrapolation and comparison of the laboratory crayfish data because, as noted above, it has a well-documented signal crayfish population (Rice et al., 2016). Kick sampling in both the Trent and Brampton branches used the standard protocol described above. The EA identifies mixed taxonomic resolution; mostly species-level with the exception of flies
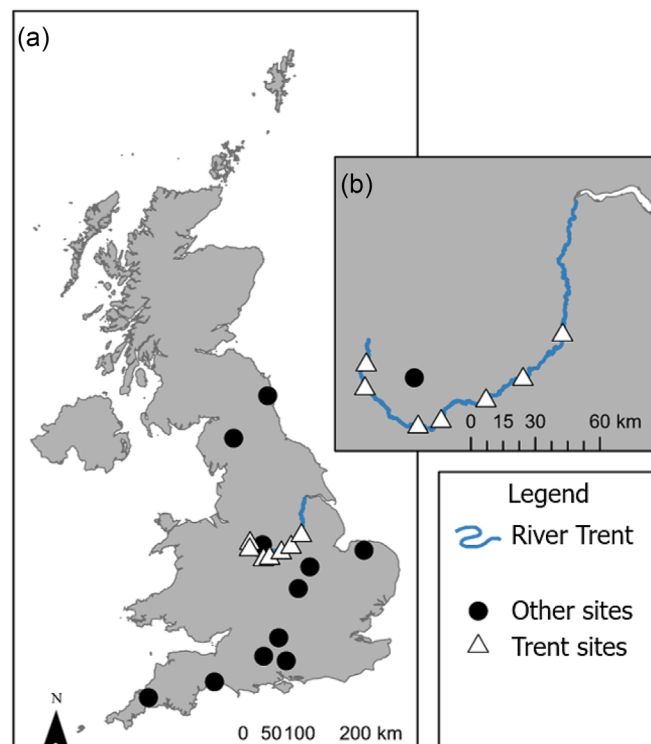

FIGURE 2 Locations of the 10 study sites sampled in this investigation, and the 11 sites along the river Trent for which data were obtained from the EA. At each site, bio-energy in the macroinvertebrate community was compared to fluvial energy in the river.

(*Diptera*) and worms (*Oligochaete*), which are resolved to family and subclass levels, respectively. In all cases, EA and WildFish invertebrate sampling took place in Spring and Autumn.

The rivers used in our field study represent a range of river types and geographical locations yet they are broadly similar in character: 10–21 m wide, wadable, with bed sediments dominated by gravel details in Supp. Table A).

2.3 | Quantifying macroinvertebrate bio-energy

The macroinvertebrate community data for each site were used to make a quantitative estimate of the bio-energy metric (energy per unit bed area) using a three-step process. The first step was to estimate the total mass of each sampled genus. This was necessary because it was infeasible to weigh every individual while identifying them. Instead, biomass was estimated based on the trait database compiled by Usseglio-Polatera et al. (2000), which is commonly referred to as the 'Tachet database'. We assigned the mid-point of the relevant Tachet body-length category to each genus. For animals included in multiple length categories, we used the dominant category and for animals in multiple size categories with equal trait weightings (in two cases), the smaller body length was used to provide a conservative estimate of body length.

The dry weight (biomass) of macroinvertebrates was then calculated from their body lengths, based on strong positive regression relationships ($R^2 = 0.70$ to 0.99) between body length and biomass across multiple macroinvertebrate taxa reported by Benke et al.

(1999). Unfortunately, no such relationships could be found for either flatworms (Phylum Platyhelminthes) or leeches (subclass Hirudinea), but since at all sites they represented less than ~2% of the sample population we excluded them from biomass estimates.

In the second step, biomass was converted to energy using calorie-per-gram relationships for a range of macroinvertebrate taxa compiled by Cummins & Wuycheck (1971), which are commonly used to study energy transfers between trophic levels in the food web due to predation. The calorific content of each taxon was then converted to Joules to give an estimate of total bio-energy (Joules).

The final step was to convert the total amount of bio-energy in the invertebrate community into energy per unit bed area; a metric that is directly comparable to the amount of fluvial energy applied to the bed by the river. This required one further approximation because the standard kick sample method used in data collection is not spatially standardised. Past work has compared spatially-standardised Surber sampling at a scale of 1 m² with the results obtained using the standard kick sampling approach used herein and shows that though the latter provides a good estimate of macroinvertebrate biodiversity, it underestimates abundance (Everall et al., 2017). Consequently, our kick sample-based estimates of bio-energy per unit bed area (J/m²) in the sampled macroinvertebrate communities are conservative.

Given the approximations made at each step in this process, the results are best regarded as being indicative. Accepting this, we believe they are suitable for comparison with our estimates of energy in the fluvial system and provide the basis for assessing the relative magnitudes of bio-energy and fluvial energy at the study sites.

2.4 | Quantifying fluvial energy

As mentioned above, the capacity of rivers to do geomorphic work by moving bed sediments is often estimated based on the stream power per unit width (W/m²), which is defined as:

$$\omega = \frac{QSg\rho}{w} \qquad (eq1)$$

where, Q = discharge (m³/s), S = slope (−), g = gravitational acceleration (9.81 m/s²), ρ = water density (1,000 kg/m³), w = channel width (m) and ω = specific stream power (W/m²). Note that when a river does geomorphic work at a rate of 1 joule per second, the rate of power expenditure is 1 watt.

For each study river, Q_{10} (high), Q_{50} (median) and Q_{95} (low) flows were calculated from average daily discharge data for the available periods of record, which ranged from 41 years for the River Trent, to 82 years for the Brampton Branch of the Nene (Supp. Table A). We used ArcGIS Professional and a 2 m spatial resolution Digital Elevation Model (DEM) to estimate channel slope at each study site, based on the fall in top-bank elevation measured over a 10 km reach of river centred on the gauging station. River width was measured at a point approximately 20 m downstream of the gauging station using 2022 aerial imagery in Google Earth.

The measure of stream power per unit area was converted to a measure of energy per unit area (J/m²) by multiplying it by the duration for which the stream power was maintained (using one day as an indicative time period) (s). This was necessary to generate a fluvial energy metric directly comparable to the calorific content of macroinvertebrates per unit bed area (J/m²). As the discharge data are daily averages, the time rate of energy expenditure per unit bed area (W/m²) was multiplied by the number of seconds in a day (84,600) to yield the fluvial energy per unit bed area, in J/m², which is directly comparable to our metric of bio-energy estimated for the invertebrate community at each study site. Hence, we compare bio- and fluvial energies on a daily basis. While the duration of a given high flow-related sediment transport event may be longer (or shorter) than a single day, daily values for the energy associated with high, median and low flows provide a suitable basis for comparing fluvial energy to similarly gross estimates of energy in the macroinvertebrate community.

2.5 | Laboratory study of bio-energy expended by a signal crayfish

Crayfish with carapace lengths of 50 to 70 mm and no obvious injuries were recruited for the laboratory study, from Gaddesby Brook, Leicestershire and acclimated for one week in aquaria. Experiments were conducted in a mesocosm consisting of a 0.5 × 0.5 m aquarium with a level bed formed by an 8 cm thick layer of spherical, glass marbles. The marbles were uniform in both size (11 mm) and weight (2.47 g), with further details provided in the supplementary materials and an illustration of the marble bed in Figure 3. While signal crayfish live on a variety of substrate sizes in the UK, from clays to gravel and cobble-bed rivers, a grain diameter of 11 mm is similar to the median substrate grain size occupied by a well-established crayfish population in the River Bain, Lincolnshire (Johnson et al., 2010).

To establish how much energy signal crayfish expend when they move gravel-sized bed grains, in each experiment a single crayfish was recorded on video while actively moving the idealised grains during a

FIGURE 3 Study crayfish moving grains on the bed of the mesocosm.

2-hour period. The video cameras were mounted orthogonally and laterally, making it possible to both observe how crayfish interacted with the bed grains and measure the distance each grain was moved. A single operator (Johnson) analysed the videos and recorded the number of grains moved, the initial accelerations and the distances the grains were moved, to the nearest grain diameter (i.e., 1 cm).

Although grain movements were primarily horizontal there were also small, vertical movements. Grains moved vertically up and down as they were rolled over static grains, but when averaged over a few centimetres of horizontal travel, these motions cancelled each other out. More significantly, later in the experiments, grains travelled upwards 10 to 20 millimetres when moved upslope, out of the hollows in the surface that were purposefully created by the crayfish (Johnson et al., 2010). These vertical movements could not be quantified, and the bio-energy estimates reported are based solely on the horizontal distances grains were moved. As vertical movements were predominantly upwards, the bio-energy measurements are therefore conservative. Similarly, crayfish may have expended energy attempting to move grains that they were unable to dislodge and that consequently remained stable.

Bearing in mind the way that measurements were made and approximated, they are indicative rather than absolute. However, we are confident that they are of the correct order of magnitude, which is sufficient for them to be compared to the estimated magnitudes of daily fluvial energy based on our calculated values of specific stream power. The experiment was repeated 10 times, with 10 different crayfish, to generate 10 replicate measures of minimum bio-energy expenditure by crayfish in performing zoogeomorphic work, under controlled conditions and during a 2 hour period.

The force required to move a single grain was calculated as:

$$F = M \times A \qquad (eq2)$$

where F = the force required to move a single grain (N), M = mass of a single grain (0.025 kg) and A = acceleration when mobilised by a crayfish (m/s^2). Frame-by-frame differencing of the videos recorded during the experiments yielded a mean acceleration of 0.01 m/s^2. Hence, the force required to dislodge a grain was 2.5×10^{-4} N.

The work done moving grain through a distance of 1 cm (or about one-grain diameter) was calculated as:

$$Work = F \times d \qquad (eq3)$$

Work done is equivalent to energy expended, and the rate of energy expenditure was 2×10^{-6} J/m. To calculate the minimum amount of bio-energy expended by each crayfish in performing all the zoogeomorphic work recorded during each experiment:

$$Minimum\ bio-energy\ expended\ in\ moving\ grains = n \times \overline{d} \qquad (eq4)$$

where n = number of grains moved and $\overline{d}$ = average distance the grains were moved. Results were then multiplied by four to upscale the 0.25 m^2 enclosure area to a standard measure of bio-energy in J/m^2.

Because the minimum bio-energy was expended over a 2 hour period, bio-power (W/m^2) could also be calculated as:

$$Bio-power = specific\ bio-energy/t \qquad (eq5)$$

where t = time (seconds).

This enabled mesocosm results to be extrapolated to a well-studied crayfish population in Brampton Branch, where crayfish density was estimated from trapping as 4 m^{-2} and activity lasted approximately 10 hours between dusk and dawn (Rice et al., 2016). As noted above, crayfish densities derived from trapping data typically represent only large adults, with the much higher density of small juveniles missing because they can evade crayfish traps. Consequently, using an average density of four crayfish per square metre again makes our estimates of specific bio-energy conservative.

3 | RESULTS

3.1 | Specific bio- and fluvial energies at the field study sites

Figure 4 compares the specific bio-energies of the macroinvertebrate communities in 2015, 2016 and 2012, to the specific fluvial energy for the Q$_{95}$, Q$_{50}$ and Q$_{10}$ daily flows at our field study sites on 11, British, gravel-bed rivers. At the study sites, specific bio-energies of the macroinvertebrate communities were comparable to the specific fluvial energy, typically approximating the specific fluvial energy for the median flow (Q$_{50}$) but exceeding it at 73% of the sites in at least one of the study years.

Comparable magnitudes of specific bio- and fluvial energies are attributable to the high specific abundance of macroinvertebrates at the study sites, which varied between 723 and 3,229 individuals of the 16 to 33 taxa, sampled. However, the total bio-energies of invertebrate communities varied substantially, both between rivers and between years. This was mostly due to differences in taxonomic composition rather than abundance, reflecting the dramatically different biomasses of different taxa (Figure 5). In particular, molluscs tend to be present in low numbers, but their large body size has a substantial impact on the calorific content within communities. In contrast, mayfly (Ephemeroptera) and cased caddisfly (Trichoptera) are numerous at most sites but contribute little to overall calorific content due to their small size (Figure 5).

Downstream variations in specific bio- and fluvial energies were explored using EA data for the River Trent (Figure 6). The downstream distribution of specific fluvial energy displays a 'hump-shaped' pattern that becomes progressively more pronounced as discharge increases, which aligns with previous findings (e.g., Barker et al., 2009).

Bio-energy consistently exceeded fluvial energy at low flow (Q$_{95}$) at all eleven stations and exceeded median (Q$_{50}$) fluvial energy at five. Furthermore, as the fluvial energy at the high flow (Q$_{10}$) declines downstream of river kilometre 75, a threshold is crossed in that specific bio-energy approximates and in one case exceeds, specific fluvial energy.

Figure 7 compares daily average values of specific fluvial energy during the calendar year 2015 to seasonally-averaged, spring and autumn values of the specific bio-energy of the macroinvertebrate populations. Variation in daily average values of specific fluvial energy was due to changes in discharge. At four stations there were lengthy periods during which specific bio-energy exceeded specific fluvial
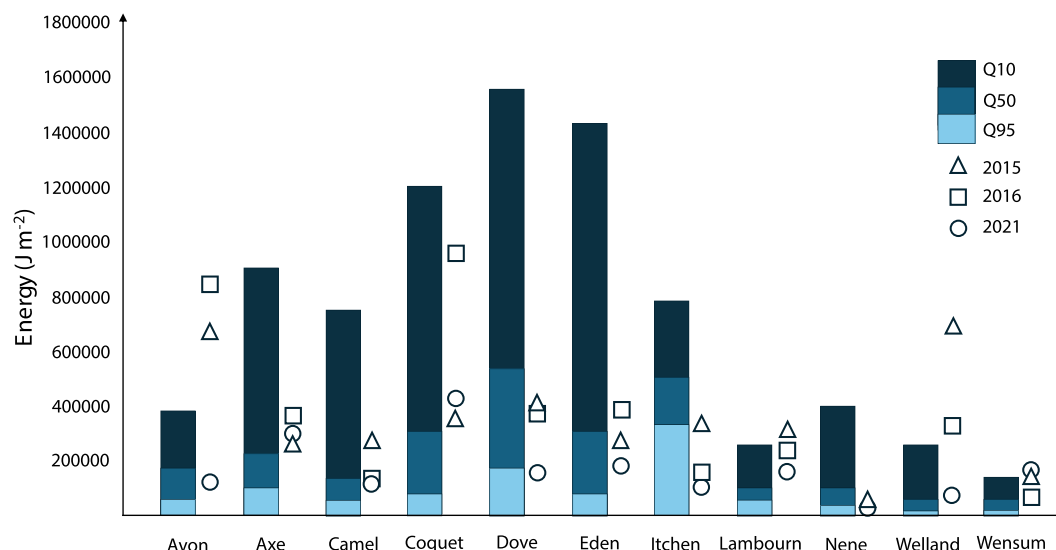
FIGURE 4 Comparison between the bio-energy of the macroinvertebrate community averaged over spring and autumn in 2015, 2016 and 2021 (symbols), and the fluvial energy at the study site at low (Q_{95}), median (Q_{50}) and high (Q_{10}) flows (blue bars). Note that at some sites, bio-energy varied widely between years.

energy, especially at the stations furthest up and downstream. Typically, these periods occurred in summer and autumn, when the flows (and hence specific fluvial energies) tended to be lower.

Variation in specific bio-energy was associated with community composition and, specifically, the presence of 'Demon shrimp' (*Dikerogammarus haemobaphes*) an invasive crustacean, which dominated the biomass at some stations (Figure 8). For example, >1,000 individuals were recorded at Drakelow, and this explains the unusually high value of specific bio-energy at that location.

3.2 | Specific bio-energy and bio-power of signal crayfish

In summary, the results of the 10 × 2-hour, mesocosm experiments are that, on average, an individual signal crayfish moved 150 marbles at least one grain diameter, and the average distance a grain was moved was 4 grain diameters (Table 1).

The numbers of grains moved by crayfish in the mesocosm varied widely (33 to 308) between animals, but the volumes of 'bed material' are broadly similar to those observed in previous studies of crayfish burrowing activities (e.g., Rodrigues Valido et al., 2020). The average specific bio-energy expended by a crayfish during the 2 hour experiments was 6.1×10^{-3} J/m², which equates to a specific bio-power of 8.5×10^{-7} W/m².

To extrapolate these values to the Brampton Branch, we multiplied by the observed crayfish density (4 per m²) and allowed for 10 hours of nocturnal activity. This indicates that the crayfish community would on average expend a minimum of ∼0.12 J/m² of bio-energy and perform at least 1.7×10^{-5} W/m² of zoogeomorphic work each night. However, the specific fluvial energy at a low (Q_{95}) flow in this stream is 86,400 J/m², which equates to a specific stream power of 1 W/m². This indicates that, in Brampton Branch, the minimum specific bio-power of the crayfish community is several orders of magnitude smaller than the specific stream power of a low flow, although it should be noted that only a small proportion of

the stream power would actually be used to drive geomorphic changes.

Applying the approach used above to estimate the total calorific content of an invertebrate community, the specific calorific content associated with the biomass of adult crayfish in Brampton Branch is 1,900,800 J/m². This is higher than that for the entire community of invertebrates sampled at several of the study rivers, reflecting the far larger body sizes of crayfish compared with animals usually caught by kick sampling. The biomass energy of the crayfish community equates to a specific bio-power of 22 W/m². These maximum specific bio-energy and bio-power values would exceed those of specific fluvial energy and power 99% of the time between 2010 and 2020. Hence, the minimum and maximum estimates of crayfish bio-power reported here bracket those of low flow stream power in Brampton Branch.

One other significant finding of the mesocosm study is that crayfish move sediments much more efficiently than fluvial processes. Specifically, in the laboratory, under controlled conditions, crayfish were observed to be easily capable of moving grains ∼11 mm in diameter. This is not surprising because in previous studies, crayfish have been shown to be able to move gravel particles up to 40 mm in diameter (Johnson et al., 2010).

Based on multiple prior studies, the critical specific stream power required to entrain an 11 mm bed grain is in the range of 7 to 15 W/m² (Figure 9). This is orders of magnitude higher than the minimum specific bio-power exerted by the study crayfish in the microcosm experiments (see column 5 in Table 1, above), but of the same order as the maximum possible bio-power associated with crayfish biomass in Brampton Branch (i.e., the calorific content of 22 W/m²).

4 | DISCUSSION

4.1 | Bio-power and geomorphic effectiveness

The theoretical framework that we developed for quantifying bio-energy and applied to field and laboratory data at individual and
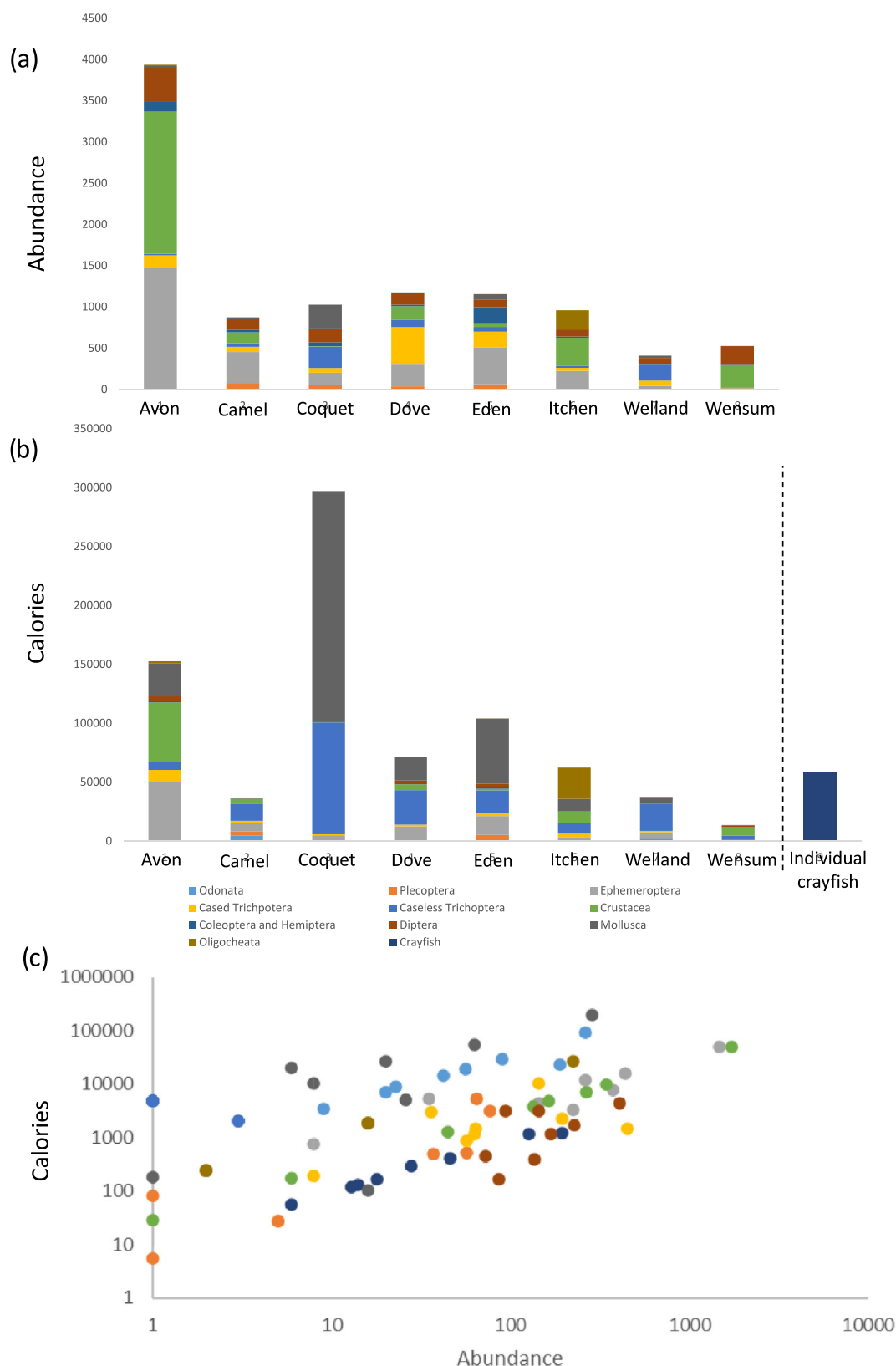
FIGURE 5 (a) Relative abundance of taxonomic groups of macroinvertebrates in a subset of eight of the study rivers. (b) Calorific content for each group (note: 1 cal = 4.2 joules). The calorific content of a single signal crayfish with a length of 8 cm is also plotted for comparison (c) the relationship between calorific content and abundance of different taxonomic groups, demonstrating the markedly different taxa-specific increments in bio-energy associated with increased abundance.

community scales provides a proof-of-concept basis for further discussion and research concerning the capacity of animals to influence stream forms and processes through their zoogeomorphic activities.

In formulating and applying this framework, our intention was not to conduct a comprehensive investigation of bio-energetics but to assemble the indicative data needed to establish if one community of
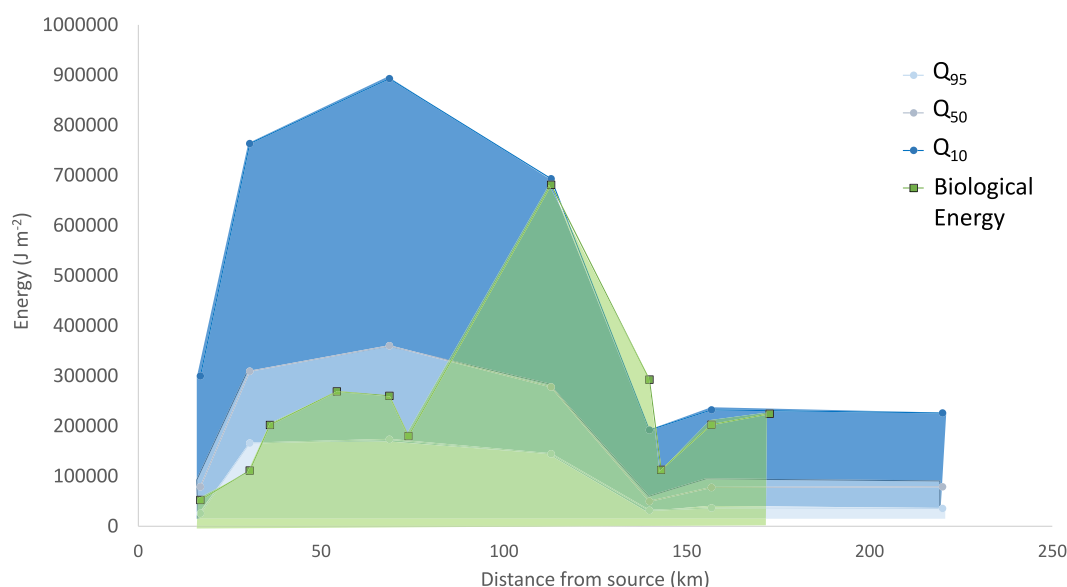
FIGURE 6 Comparison between downstream distributions of the specific bio-energy of the macroinvertebrate community in 2015 (J/m^2, green data points and shaded area), and specific fluvial energy for low (Q_{95}), median (Q_{50}), and high (Q_{10}) flows (J/m^2; blue data points and shaded areas) sampled near gauging stations along the river Trent. Study reach extends from near the river's source to near its tidal limit (Colwick, Nottinghamshire).

benthic animals, namely macroinvertebrates, represents an energy source equivalent to the median discharge in the gravel-bed rivers studied. Our finding that the bio-energy of the invertebrate communities in 11 British gravel-bed rivers equals or exceeds the energy available to drive fluvial processes at the median (Q_{50}) flow does just that. It is expected that only a small percentage of this bio-energy is actually available to move bed grains. However, the same is true of stream power, most of which is consumed in overcoming boundary friction and turbulent viscosity.

Further, as demonstrated in the mesocosm experiments, the energy expenditures that animals make in moving bed grains are orders of magnitude lower than those expended by the river in achieving the same geomorphic outcomes. Given that macroinvertebrate communities are ubiquitous in British gravel-bed rivers and the activities that disturb sediments are necessary for their survival (e.g. feeding, nesting, sheltering; Mason & Sanders, 2021), it is reasonable to propose that in British gravel-bed rivers, during typical summer and autumn flows, the influences of zoogeomorphic and fluvial geomorphic processes may be comparable.

We accept that gravel-bed rivers are powerful geomorphic agents. Nonetheless, fluvial processes alter the bed and bank morphologies infrequently and, most effectively, during high in-bank flows (Wolman & Miller, 1960). Our results indicate that during the long pauses between the geomorphologically effective flows, invertebrate bio-power regularly exceeded fluvial energy in most of the gravel-bed rivers sampled. During each fluvial interregnum, invertebrates can change bed material properties by, for example, secreting sticky substances on bed particles to catch phytoplankton, which retards fluvial entrainment (Albertson & Allen, 2015; Johnson et al., 2009) or loosening and moving grains during foraging, reproduction and burrowing activities, which disturbs the surface armour and make it easier for flow to mobilise the bed (Hassan et al., 2015; Johnson et al., 2011).

As the fabric, packing and protrusion of gravel bed grains are known to influence their entrainment, the long periods where bio-power exceeds stream power may result in significant changes to threshold values for bed material entrainment and motion. Such effects have been documented in the field for fish; for example, Pledger, Rice, & Millet (2017) found cyprinid fish reworked gravel substrates at low flows through their feeding activity, and Brown et al. (2022) found spawning Chinook salmon (*Oncorhynchus tshawytscha*) reworked recently restored gravels, which could cause topographic changes to substrates that exceed those associated with the flow under drought if populations meet their post-restoration target.

Upscaling the results of mesocosm experiments suggests that the minimum threshold power for crayfish to move 10 mm particles (estimated between 0.12 and 22 W/m^2) is tiny relative to specific stream power in British gravel-bed rivers, even at low flows. This is because the mesocosm specifically measures the energy required to move sediment, whereas stream power – as discussed above – is an estimate of the maximum available power. It also demonstrates the high efficiency with which crayfish could mobilise bed grains in the laboratory.

Crayfish are known to play a significant role in fluvial transport of both coarse and fine sediment (Harvey et al., 2014; Rice et al., 2016). With respect to coarse sediment, they have been observed to be capable of moving gravel with intermediate (b) axes of up to 40 mm (Johnson et al., 2010), which would typically require stream powers between 20 and 40 W/m^2 (Petit et al., 2005). This allows crayfish to de-structure surface sediments using a tiny fraction of the energy required for the flow to achieve the same result. This is partially because of the low mean velocities operating near the substrate surface due to logarithmic velocity profiles and no-slip conditions and the interlocking and organised geometry of grains that offer stability against entrainment by uni-directional flows (e.g. Hassan et al., 2020; Perret et al., 2019; Vázquez-Tarrío et al., 2020).
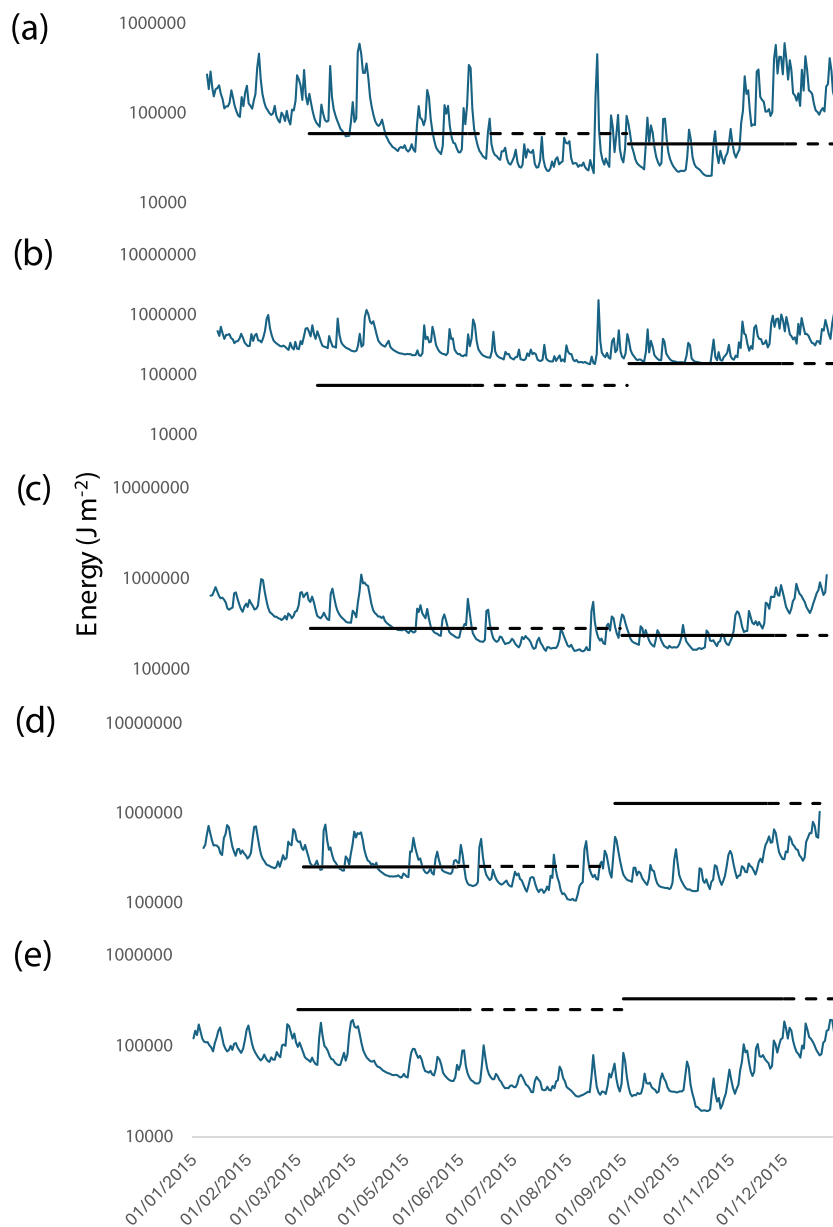
FIGURE 7 Daily average values of specific fluvial energy (J/m^2) in the river Trent during 2015 (blue lines) for gauging stations located at (a) Stoke (river kilometre 17), (b) Darlaston (RK 31), (c) Yoxall (RK 69), (d) Drakelow (RK 113) and (e) Shardlow (RK 140). Horizontal black lines represent specific bio-energy (J/m^2) at those sites, averaged for spring and autumn, and extended across summer and winter (dashed lines) for comparative purposes.

Additionally, it should be recognised that the crayfish moving grains in the mesocosm were operating in still water. Consequently, crayfish had to do all the work entailed in moving bed grains. In perennial rivers like those we studied, the flow is perpetually exerting forces of streamwise drag force and vertical lift on bed particles. When seeking to move a grain, a crayfish can leverage those hydraulic forces, further reducing the expenditure of bio-power necessary to mobilise a bed particle. Again, this hints at how animals can achieve their zoogeomorphic goals while contributing a relatively small amount of bio-energy to the fluvial energy system.

A limitation of our investigations is the lack of field measurements of the energy expended by invertebrates and crayfish during their zoogeomorphic activities. Future research could usefully attempt to record the energy expenditure of animals during their geomorphological activities to demonstrate metabolic cost, adding detail to the minimum and maximum estimates we have provided. However, such work will be challenging, requiring novel combinations of expertise and overcoming logistical challenges associated with the fact that zoogeomorphic work, such as burrowing, can take place in short

bursts (seconds) of activity that are intermittent over longer periods of time (hours). This is in contrast to past bioenergetics work in flowing respirators that has focused more on the holding and swimming behaviours of fish and crayfish, where the time duration of a given behaviour can be controlled and is relatively consistent over periods of minutes to hours (e.g., Rubio-Gracia et al., 2022). However, if bio-energy can be measured in the field, then comparisons could also be made to more accurate estimates of flow energy, as opposed to the simplified, daily metrics used here.

4.2 | The power of biological communities

In our investigation, we summed the calorific contents of individuals and taxa to estimate community totals, but assemblages of animals are likely to have contrasting zoogeomorphic effects. For example, in the rivers we sampled, taxa known to de-structure bed surface layers co-habit with others known to stabilise them. The 'net' effects of animals in promoting or inhibiting entrainment and sediment transport
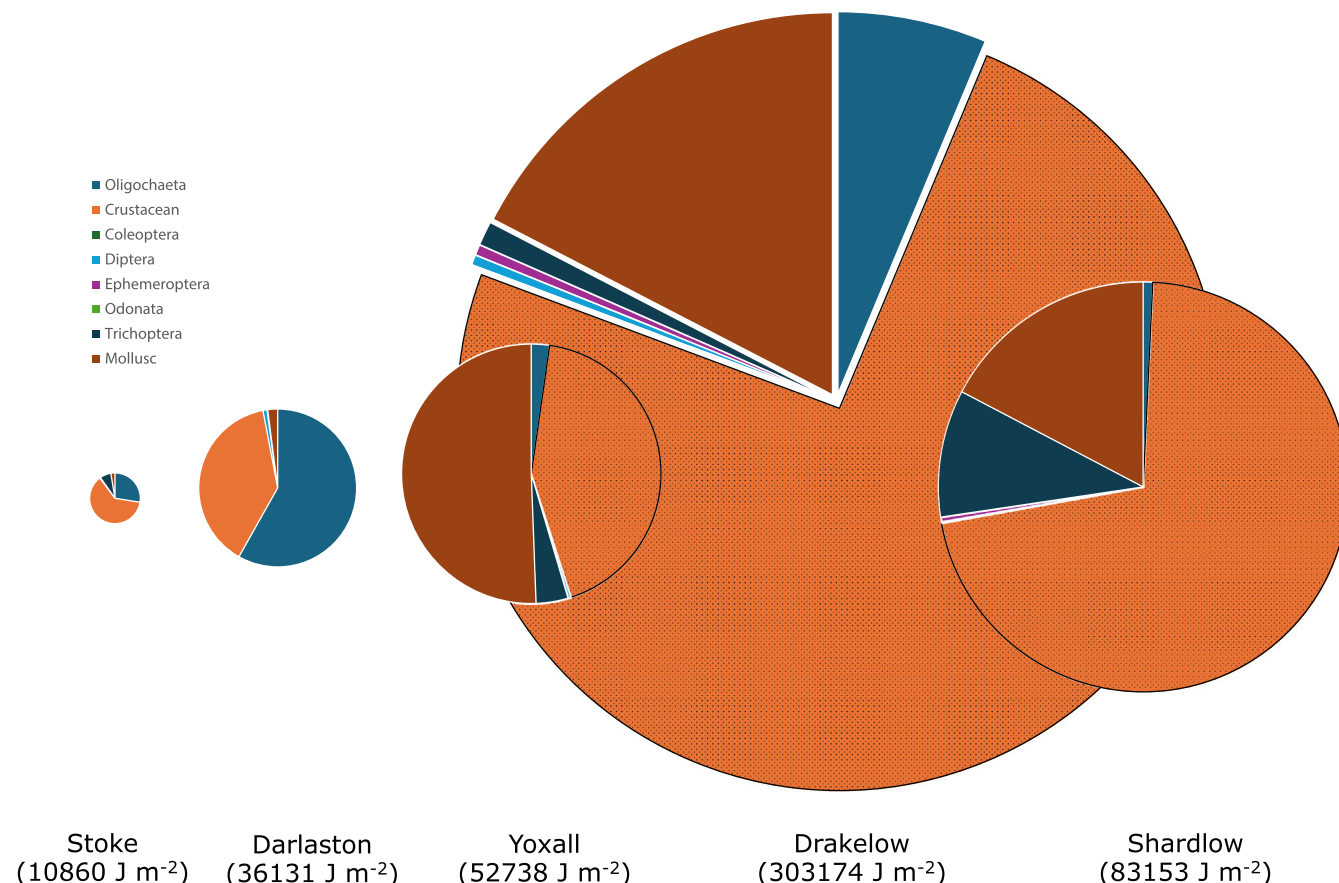
FIGURE 8 Contributions of the different taxonomic groups making up the invertebrate communities sampled in the river Trent at, from left to right: Stoke (RK 17), Darlaston (RK 31), Yoxall (RK 69), Drakelow (RK 113) and Shardlow (RK 140). The pie chart size is proportional to the specific bio-energy of the sampled invertebrate community (i.e., the total calorific content of its biomass). Dot shading represents the proportion of invasive species in each group. At the upstream stations (Stoke and Darlaston) the community is entirely native, but at other stations, the crustaceans that dominate the community are composed entirely of invasive species.

therefore depend on community composition. While we show that taxa composition dominates variability in a macroinvertebrate community's total calorific content, it remains to be found how it influences net geomorphic impact.

Animals also interact in complex ways through processes of predation, competition and facilitation (e.g., Figure 1), and so the relationship between biogeomorphic effectiveness and population density is unlikely to be linear. For example, Rice, Johnson, & Reid (2012) found that two crayfish did not have twice the geomorphic impact of a single crayfish. Instead, the two crayfish cumulatively did the same work as one crayfish because the crayfish typically fought and the 'winner' continued geomorphic work, while the 'loser' hid from the victor and was indolent, (Rice, Johnson, & Reid, 2012). Recognising this, it is important that future zoogeomorphic research builds on laboratory experiments with single individuals and species exploring the impacts of communities and ecosystems.

Our research focused on macroinvertebrates. We did not, for example, study micro or meio-fauna (i.e., < 1 mm^2) which readily evade being trapped during kick sampling. Our results show that in an energy framework based on calorific content, bigger animals dominate, and at several sampling sites a single crayfish was found to have a calorific content similar in magnitude to that of the entire macroinvertebrate community. Whilst this is consistent with other

theoretical work that suggests that body size is an important determinant of biogeomorphic significance (Moore, 2006), it takes into account neither the different efficiencies of energy use possessed by larger and smaller animals nor the potential discrepancy in their energy exchanges (i.e., a tiny amount of zoogeomorphic work by some very small organisms like caddisfly larvae can result in disproportionately large increases in the specific stream power required to move bed sediments that are 'cabled' together by their nets of underwater silk).

The presence of invasive species also skews estimates of biological energy. At downstream stations, invasive species made up a large proportion of the macroinvertebrate populations sampled in the River Trent (up to 75% by biomass), particularly, shrimp and bivalves. Where invasives were present, native communities were poorer in both diversity and abundance. On the River Nene, where there is a well-established population of invasive signal crayfish, the macroinvertebrate community was limited to low abundances of organisms mostly specialised to live in fine, mobile sediments (Figure 5; Mathers et al., 2016). Therefore, anthropogenically altering ecological communities in ways that lead to native species loss and introducing alien species could both have important zoogeomorphic implications, as has been demonstrated for the invasive signal crayfish (Harvey et al., 2011).

TABLE 1 Results of the mesocosm experiments.

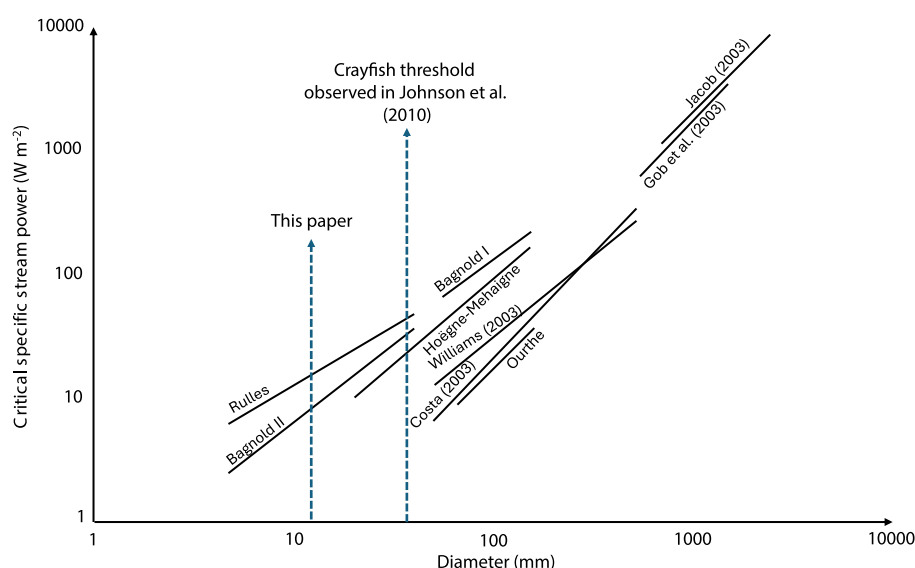| Crayfish number	Number of grains moved	Average distance (grain diameters)	Minimum specific bio-energy (J/m^2)	Minimum specific bio-power (W/m^2)
1	140	3	4.2×10^{-3}	5.8×10^{-7}
2	260	4	1.0×10^{-2}	1.4×10^{-6}
3	33	3	9.9×10^{-4}	1.4×10^{-7}
4	79	5	3.6×10^{-3}	5.5×10^{-7}
5	181	5	9.1×10^{-3}	1.3×10^{-6}
6	224	3	6.7×10^{-3}	9.3×10^{-7}
7	308	4	1.2×10^{-2}	1.7×10^{-6}
8	103	5	5.2×10^{-3}	7.2×10^{-7}
9	61	2	1.2×10^{-3}	1.7×10^{-7}
10	106	7	7.4×10^{-3}	1.0×10^{-6}

FIGURE 9 Critical specific stream power for entrainment of gravel particles over a range of sizes according to multiple bedload transport equations. Critical stream powers for grain sizes of 12 and 40 mm due to fluid shear flows in rivers are orders of magnitude greater than those exerted by crayfish when directly observed to move grains with those diameters. Graph modified from Petit et al. (2005).

Zoogeomorphology is also likely to be of greater significance in some reaches rather than others along gravel-bed rivers, and different types of zoogeomorphic activities are likely to occur preferentially in some river reaches, due to differing community compositions and downstream trends in stream power and channel form (Mason & Sanders, 2021). For example, in headwater streams with coarse beds, winnowing of fine sediment from the matrix between larger frame-work grains is likely to be the dominant zoogeomorphic function of invertebrate animals (Parkyn et al., 1997; Zanetell & Peckarsky, 1996). In contrast, in downstream reaches with low stream power and fine bed sediments, bioturbation by burrowing organisms is likely to domi-nate zoogeomorphic activities (Mermillod-Blondin, 2011). As such, it is not only the relative power of biology that is important but also the catchment, environmental and community contexts.

In the River Trent, the downstream distributions of stream and bio-powers were similar, with peaks in the middle reaches of the river. However, the downstream rate of decline in bio-power was lower than that of stream power, so that in the lower course of the Trent bio-power often matched stream power during summer and autumn, even at high discharges. Consequently, it is in the lower reaches of alluvial rivers that animals are likely to be the most influential in altering the structure and erosion resistance of bed sediments during the long periods (weeks to months) between fluvial events that mobilise the bed. In the middle reaches, the interregnums during which animals can alter bed mobility are shorter, and when they do occur, high flows are more powerful. However, it is not only the bed that is subject to zoogeomorphic actions. For example, burrowing into cohesive bank materials is known to alter bank erodibility and mass stability at both low and high flows (Sanders et al., 2021), and so animals may influence bank retreat and planform change throughout the fluvial system.

4.3 | The power of biology in anthropogenic streams

We found that, at high flow (e.g., Q_{95}), stream power was greater than bio-power in most of the British study rivers. However, these anthro-pogenically modified rivers may not represent the pre-disturbance state of British rivers. Rivers throughout the UK have centuries-long histories of management and engineering for land drainage and flood control. As a result, their planforms are commonly single-threaded, their cross-sections are usually overly large and simplified, and their channels are disconnected from their floodplains (Brown et al., 2022; Gurnell & Downs, 2021).

When an anthropogenic, incised, single-thread channel replaces the multi-thread, anastomosed river-wetland corridor that predated it, this concentrates flow and increases specific stream power at all in-bank discharges, but especially during intermediate and high flows that would naturally spread across floodplain (Brown et al., 2018; Cluer & Thorne, 2014; Walsh et al., 2005). It is therefore probable that an unintended consequence of channelising the middle courses of British gravel-bed rivers has been to reduce the *relative* power of biology.

Furthermore, it is likely that the zoogeomorphic contexts of the rivers we study today are different to those of the past because they are incapable of supporting former diversities and abundances of organisms, also reducing the *absolute* power of biology. Impacts of anthropogenic disturbance are expected to include a reduced total abundance of aquatic biota, changes to their traits and zoogeomorphic impacts and changes in body size frequency distributions. As such, the significance of zoogeomorphology indicated in our study is likely to be, in part, related to the level of human impact on the studied rivers, with implications for channel form, stability and functions (Albertson & Daniels, 2018). More broadly, it seems likely that conventional perceptions of the relative importance of biota to geomorphological processes have been distorted by a shifting understanding of what constitutes the "natural" baseline.

Increasingly, river restoration aims to promote lateral reconnection, floodplain rehydration, and recovery of lost levels of morpho-diversity and habitat patchiness, through reinstating anastomosed planforms (Flitcroft et al., 2022) and reintroducing key zoogeomorphic species, such as beaver (Pollock et al., 2014). Restoration of this sort is specifically intended to re-empower aquatic, riparian, wetland and floodplain species and so enhance both the *absolute* power of biology (by increasing species richness, diversity and abundance) and the *relative* biological power (by altering channel forms in ways that disperse flows and reduce specific stream powers).

These approaches should be highly beneficial in the context of climate change, as they benefit from (a) an increase in the adaptive capacity of the river (because the healthier riverscape ecosystem helps the river respond to and accommodate future conditions) and (b) an increase in the capacity of the river to recover from disturbance (because the healthier ecosystem gives the river a recuperative capacity that physics-dominated rivers cannot match). In short, increasing the power of biology is key to building river resilience in an uncertain future (Johnson et al., 2019).

5 | CONCLUSIONS

Animal activity is known to alter geomorphic conditions in rivers, but it is understudied and underappreciated. The power present in the invertebrate community is large, broadly equivalent to the specific stream power at the median flow in most of the rivers we studied. Consideration of the energy that communities of riverine animals hold and can exchange with the fluvial system offers a novel framework within which to identify biogeomorphological linkages and feedbacks, enabling future work to better consider the asymmetrical and bi-directional exchanges of energy between biological (trophic) and fluvial (physical) systems.

However, comparisons are complicated, not least because there are likely different efficiencies in energy expended in the movement of sediment between fluvial and biological energy. Only a small proportion of the stream power will be used in sediment movement, and similarly, only a small proportion of the calorific content of the invertebrate community can be used in zoogeomorphic activities.

It follows that estimating the fraction of bio-power directly involved in modifying sediments could significantly advance the research we report here, and better inform where and how living organisms influence river forms and processes. The impacts of organisms will depend on both position within the river network and the environmental context (particularly with respect to sediment grain size), as well as levels of anthropogenic alteration to river channels and aquatic communities.

It is reasonable to assume that past human alterations to rivers have diminished the influence of aquatic life on channel-forming processes, and restoration activities that lower stream power per unit width through spreading high flows across wide floodplains or and/or altering channel forms and dimensions could have important benefits through revitalising ecosystems and empowering animals by facilitating their work in influencing sediment stability and transport in rivers.

DATA AVAILABILITY STATEMENT
Data associated with this manuscript is shared as online-only supplementary material to this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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