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RESEARCH ARTICLE

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Signal crayfish burrowing, bank retreat and sediment supply to rivers: A biophysical sediment budget

H. Sanders[1,2] | S.P. Rice[1] | P.J. Wood[1]

[1]Geography and Environment, Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK

[2]Geography, School of Human and Life Sciences, Canterbury Christ Church University, Canterbury, Kent, CT1 1QU, UK

Correspondence
H. Sanders, Geography, School of Human and Life Sciences, Canterbury Christ Church University, Canterbury. Kent, CT1 1QU, UK.
Email: harry.sanders@canterbury.ac.uk

Abstract

Burrowing into riverbanks by animals transfers sediment directly into river channels and has been hypothesised to accelerate bank erosion and promote mass failure. A field monitoring study on two UK rivers invaded by signal crayfish (Pacifastacus leniusculus) assessed the impact of burrowing on bank erosion processes. Erosion pins were installed in 17 riverbanks across a gradient of crayfish burrow densities and monitored for 22 months. Bank retreat increased significantly with crayfish burrow density. At the bank scale (<6 m river length), high crayfish burrow densities were associated with accelerated bank retreat of up to 253% and more than a doubling of the area of bank collapse compared with banks without burrows. Direct sediment supply by burrowing activity contributed 0.2% and 0.6% of total sediment at the reach (1.1 km) and local bank (<6 m) scales. However, accelerated bank retreat caused by burrows contributed 12.2% and 29.8% of the total sediment supply at the reach and bank scales. Together, burrowing and the associated acceleration of retreat and collapse supplied an additional 25.4 t km^{-1} a^{-1} of floodplain sediments at one site, demonstrating the substantial impact that signal crayfish can have on fine sediment supply. For the first time, an empirical relation linking animal burrow characteristics to riverbank retreat is presented. The study adds to a small number of sediment budget studies that compare sediment fluxes driven by biotic and abiotic energy but is unique in isolating and measuring the substantial interactive effect of the acceleration of abiotic bank erosion facilitated by biotic activity. Biotic energy expended through burrowing represents an energy surcharge to the river system that can augment sediment erosion by geophysical mechanisms.

KEYWORDS
biogeomorphology, burrow, crayfish, riverbank erosion, sediment budget, zoogeomorphology

1 | INTRODUCTION

The active role of animals in geomorphological processes is increasingly acknowledged, particularly in aquatic environments (Albertson & Allen, 2015; Butler, 1995; Fei et al., 2014; Moore, 2006; Rice et al., 2012; Statzner, 2012; Viles et al., 2008; Wilkes et al., 2019). Of the various ways that animals affect sediment dynamics and river geomorphology, burrowing by animals in riverbanks is a relatively understudied fluvial process (Harvey et al., 2019). Burrowing can directly supply sediment to rivers (Faller et al., 2016; Guan, 1994; Harvey et al., 2011, 2014; Haussmann, 2017; Rice et al., 2014, 2016) and is also hypothesised to accelerate bank erosion processes, leading to additional sediment supply and geomorphic change.

Evidence that burrowing can accelerate bank erosion comes from ex situ experiments (Onda & Itakura, 1997; Vu et al., 2017), and physical (Saghaee et al., 2017; Viero et al., 2013) and numerical modelling (Borgatti et al., 2017; Camici et al., 2014; Orlandini et al., 2015). Reviewing this and other research, Harvey et al. (2019) suggest that animal burrowing may alter bank erosion processes via several mechanisms. Burrows may have (i) geotechnical and hydrological effects by modifying the spatial distribution of pore water pressure and reducing the length of failure planes, (ii) hydraulic effects by modifying near bank flow structures and increasing bank surface roughness, and (iii) geochemical and biological effects by removing stabilising agents such as vegetation and altering biofilm and fungal networks through changing bank moisture parameters.

Bank erosion processes are widely understood to be a key control of river behaviour with important implications for the nature of channel migration, meandering and avulsion (Darby et al., 2002; Iwasaki et al., 2018; Nagata et al., 2000). In addition, bank retreat can threaten valuable floodplain assets and generate substantial risks to society, including flooding if levees are damaged (Mutton & Haque, 2004; Orlandini et al., 2015; Viero et al., 2013). Accelerated supply of predominantly fine riverbank sediment into river systems can also be problematic for channel stability and flood risk (Lane et al., 2007; Lisle & Church, 2002; Marston et al., 1995; Sidorchuk & Golosov, 2003), water chemistry (Bai & Lung, 2005) and aquatic ecology (Bilotta & Brazier, 2008; Jones et al., 2012; Kemp et al., 2011; Wood & Armitage, 1997).

Establishing the nature, extent and magnitude of the contribution made by burrowing animals is therefore important (Harvey et al., 2019). This study investigates the role of burrowing signal crayfish (Pacifastacus leniusculus) as drivers of sediment supply, bank erosion and geomorphic change in two UK rivers. In the first in situ field investigation we are aware of, we quantify the magnitude of direct (burrowing) and indirect (augmented bank erosion) crayfish effects on sediment supply, relative to bank erosion in the absence of burrowing. In this way, we can develop zoogeomorphic sediment budgets that quantify the contributions of purely biotic and abiotic processes but also their interactive effects.

Signal crayfish are invasive in the UK, following their introduction in the 1970s for aquaculture (Holdich, 2000). Signal crayfish are present in at least 60% of English catchments (Chadwick 2019), where they often burrow into riverbanks (Faller et al., 2016; Guan, 1994; Guan & Wiles, 1997; Harvey et al., 2014; Stanton, 2004). The mass of sediment directly excavated into rivers via crayfish burrowing has been measured at a small number of sites in the UK (Faller et al., 2016; Rice et al., 2016), anglers and others have reported increased bank erosion rates associated with high crayfish population densities (e.g. West, 2010), and burrowing by red swamp crayfish (Procambarus clarkii) has been associated with bank erosion and collapse in Northern Spain (Arce & Dieguez-Uribeondo, 2015; Barbaresi et al., 2004). However, the impact of crayfish burrowing on volumes of riverbank erosion has not previously been measured. Indeed, Harvey et al. (2019) highlight the lack of quantitative research into the physical damage to riverbanks caused by burrowing.

A field-based monitoring study was undertaken to address four key questions:

1. Do signal crayfish burrows accelerate bank retreat?
2. How do crayfish burrows affect bank retreat? Specifically, how do crayfish burrows affect:
   a. Diffuse erosion (erosion in the absence of obvious collapse events)
   b. Bank collapse (erosion attributed to obvious collapse events; Figure 1b)
   c. Bank morphology
3. How much sediment does accelerated bank retreat associated with crayfish burrows supply to river systems?
4. What are the relative roles of direct sediment input from crayfish burrows, the accelerated bank erosion caused by crayfish burrows, and bank erosion in the absence of crayfish burrows in supplying sediment to river channels?

2 | METHODS

Erosion pins were installed into 17 banks on two UK rivers infested by signal crayfish. The 17 banks had varying densities of crayfish burrows, including no burrows (Figure 1a). The rate and nature of riverbank retreat was monitored for 22 months.

2.1 | Field site selection

Two rivers with established signal crayfish populations and reported burrowing (Johnson et al., 2014; Peay, 2001; Sibley, 2000; Stanton, 2004) were used in this study (Figure 2): the River Bain, Lincolnshire (TF 2457 7947), and Gaddesby Brook, Leicestershire (SK 7312 1016). Overnight trapping using Swedish 'trappy traps' confirmed high signal crayfish populations in both study reaches (catch per unit effort = 7.7 and 9.3, respectively). The two rivers were selected to capture between-catchment variability across two morphologically and geographically similar lowland streams; the types of stream where signal crayfish are most common and abundant in the UK (e.g. Cooper et al., 2016; Guan & Wiles, 1997, 1999; Harvey et al., 2014; Rice et al., 2014, 2016). In each river, a homogeneous reach without tributaries was identified, in which broadly consistent bed materials, riparian vegetation, slope, land use, hydrology and channel geometry, which were qualitatively consistent throughout the study, isolated variations in burrow density as the primary within-reach variable that could potentially affect bank erosion.

On Gaddesby Brook, the study reach was approximately 100 m long, the mean channel width was 2.7 m, and the mean bankfull height was 0.88 m [± 0.15 m (1 SD) at the study banks]. It is estimated that crayfish first invaded the reach in 1992 (Belchier et al., 1998; National Biodiversity Network, 2020; Sibley, 2000). The River Bain is also a small, lowland river, and the study reach was approximately 1.1 km long, the mean channel width was 3.4 m, and the mean bankfull height was 1.03 m [± 0.14 m (1 SD) at the study banks]. Discharge quantiles at the River Bain are Q_{95} = 0.092 m^3 s^{-1}, Q_{50} = 0.247 m^3 s^{-1} and Q_5 = 0.855 m^3 s^{-1} (Bain at Goulceby Bridge gauging station, 1971–2019). No discharge data are available for Gaddesby Brook, but bankfull discharge was estimated using Manning's equation as 2.8 m^3 s^{-1}. It is estimated that crayfish first colonised this reach in 1997. The substrate in both reaches was dominated by gravel (Gaddesby Brook D_{50} = 13.2 mm; Bain D_{50}~15 mm, but unquantified due to deep overlaying fines), but overlain by up to 0.4 m of fine sediments (D_{50} < 2 mm).

Samples of bank face material (approximately 500 g) were collected from four banks on each reach and wet sieved to establish the average grain size distribution of the banks in each channel. Banks were composed of homogeneous, cohesive fine sediments (41% silt

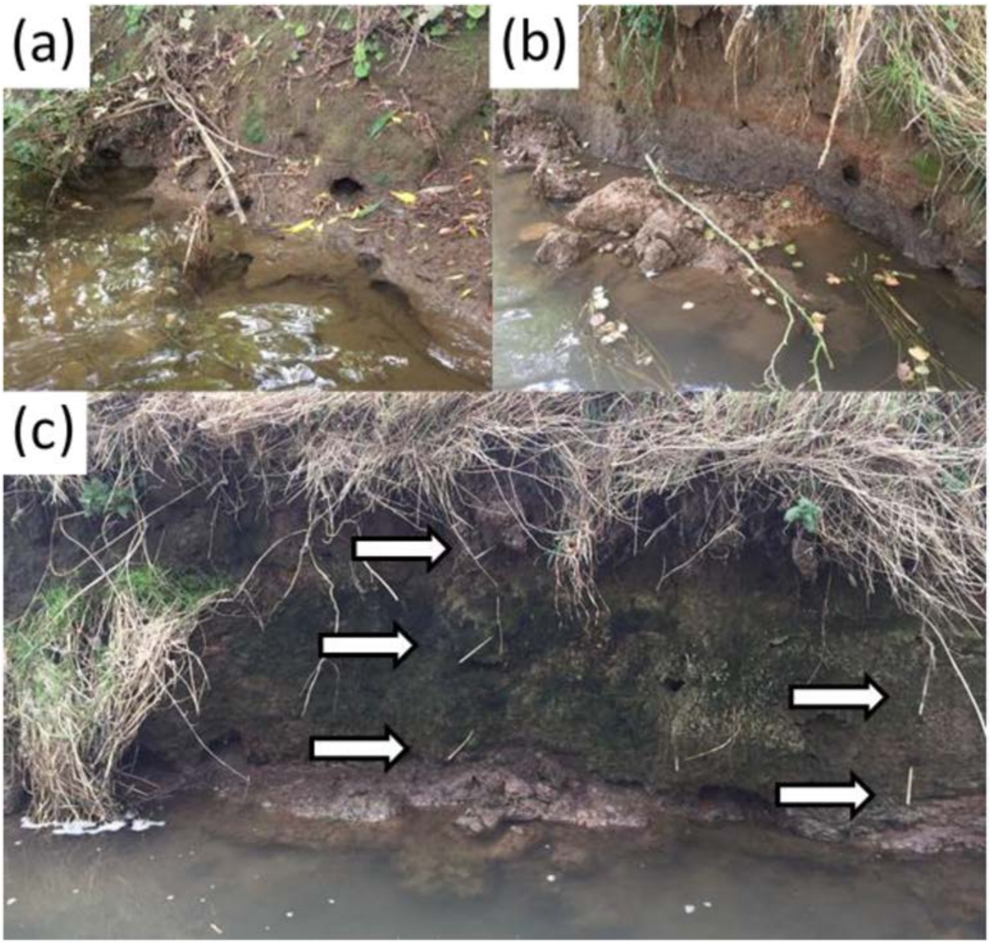

FIGURE 1 (a) Signal crayfish burrows in a bank on Gaddesby Brook, (b) a mass failure event on the River Bain; and (c) erosion pins in a bank on the River Bain. (NB: Pins are visually exposed following a collapse event, and were installed with 30–50 mm of pin exposure for ease of relocation.) Photograph locations are shown on Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

and clay with 59% sand on Gaddesby Brook, and 35% silt and clay with 64% sand at the River Bain). Whilst wet sieving did not allow for the clay-silt fraction to be separately reported, qualitatively there was no apparent difference in bank material characteristics within each reach. In each case, the bank materials were homogeneous, contained no structural elements and had no significant stratigraphic variations. Within each reach, the study banks were selected to be similar in geometry, without vegetation cover and on straight channel sections to minimise between-site differences that might otherwise affect bank erosion processes. However, the selected banks captured a large range of burrow densities, from 0 burrows m^{-2} to a maximum density of 4.8 burrows m^{-2} on Gaddesby Brook, and 6.15 burrows m^{-2} on the River Bain.

2.2 | The use and installation of erosion pins

Erosion pins are metal rods inserted horizontally into riverbanks at an angle perpendicular to the channel to allow lateral erosion to be quantified. If the pin remains in a known and stable location, incremental changes in exposure over time record bank retreat. Erosion pins can detect small amounts of recession at very local scales (Thorne, 1981), are considered a valuable technique for short- to medium-term monitoring studies (Foucher et al., 2017) and have widely been used to calculate fluvial sediment budgets (e.g. Foucher et al., 2017; Henshaw et al., 2013; Kronvang et al., 2013; Palmer et al., 2014). Erosion pins do present some limitations (Couper et al., 2002), including lack of contiguous spatial coverage. The application of digital photogrammetry, terrestrial laser scanning (TLS) and structure from motion (SfM) can overcome this limitation, but the presence of overhanging riparian vegetation and variable water depths suggested these would be problematic techniques to apply (Bird et al., 2010; Jugie et al., 2018; Micheletti, et al., 2014). In addition, erosion pins allowed bank retreat measurements to be recorded below the water surface, which would not have been possible using standard TLS or SfM. This was important because burrowing occurs below the water surface and, in a nationwide survey of 23 burrowed sites, 45% of burrows were underwater during low flow conditions (Sanders, 2020).

Welding rods 350 mm in length and 2.5 mm in diameter were used as erosion pins (Couper et al., 2002; Lawler et al., 1999). Pins were installed leaving 30–50 mm exposed for ease of relocation in a grid formation (0.3 m vertically and 0.5 m horizontally: Figure 1c). The lowest row of pins was installed along the low water mark, and rows were added to the top of the bank. A total of 317 pins were installed into 11 banks on the River Bain, and 164 pins were installed into 6 banks at Gaddesby Brook (Table 1).

2.3 | Burrow characteristics

Total burrow numbers are likely to be a crude measure of how burrow presence affects erosional processes, so a suite of six burrow metrics was determined for each bank. Burrow depths and the width and height of burrow entrances were measured using a meter rule to the

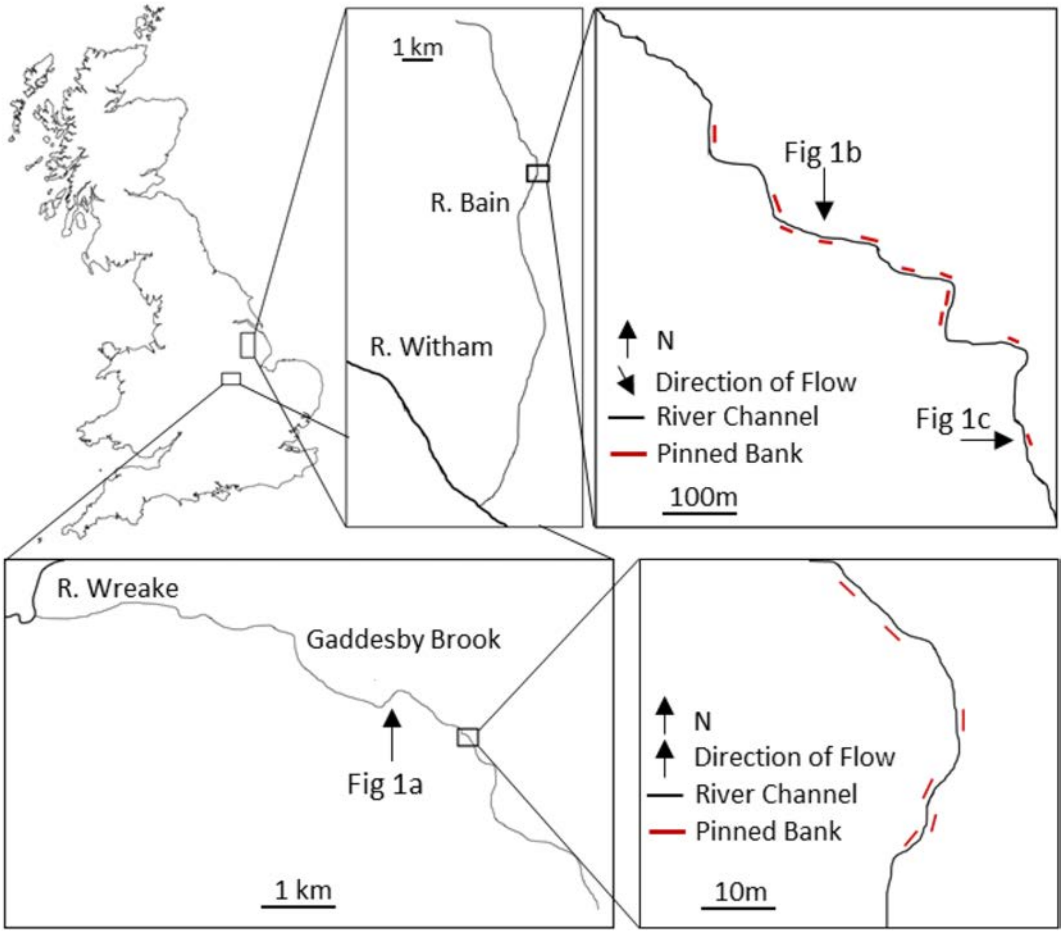

FIGURE 2 The location of the River Bain and Gaddesby Brook, UK, the studied banks throughout the reaches, and the locations of photographs presented in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Bank characteristics including deployment of erosion pins and burrow details on the River Bain and Gaddesby Brook

River	Bank number	Bank length (m)	Bank area (m^2)	Number of pins	Number of burrows	Burrow volume ($m^3 \times 10^{-3}$)	Burrow entrance area ($m^2 \times 10^{-3}$)
River Bain	1	5.5	5.1	34	0	0.00	0.00
	2	3.0	3.6	24	0	0.00	0.00
	3	3.5	3.6	24	2	0.95	4.71
	4	4.5	4.2	28	4	2.27	12.72
	5	3.0	3.3	22	4	4.74	13.19
	6	3.0	3.5	23	6	2.54	12.56
	7	3.5	3.5	23	6	3.25	11.82
	8	3.5	3.0	20	7	1.77	9.26
	9	3.5	4.5	30	7	2.85	13.27
	10	3.5	3.2	21	12	3.73	20.96
	11	3.5	3.9	26	24	15.91	51.26
Gaddesby Brook	1	5.0	3.9	26	0	0.00	0.00
	2	4.5	4.8	32	5	5.74	85.33
	3	4.5	3.6	24	7	6.37	86.74
	4	4.0	3.0	20	14	8.35	123.60
	5	4.0	3.2	21	17	19.15	62.80
	6	4.5	4.8	32	18	14.48	58.80

nearest 5 mm. Burrow depths were measured at the centre of the opening, to account for a sloping bank face. Volume of sediment excavated was calculated by treating the burrow shape as an elliptical cylinder, as in Faller et al. (2016):

$$A_E = \pi (W/2\,H/2) \tag{1}$$

where A_E is burrow entrance area, W is the burrow entrance width, and H is the entrance height.

$$V_B = A_E\,L_B \tag{2}$$

where V_B is burrow volume, and L_B is the length of the burrow.

At the River Bain, burrows had, on average, a length of 17.4 cm (± 8.2 cm; 1 SD), an entrance area of 21.3 cm^2 (± 11.9 cm^2) and a volume of 516.1 cm^3 (± 440.0 cm^3). At Gaddesby Brook, burrows had an average length of 14.2 cm (± 10.3 cm), an entrance area of 886.7 cm^2 (± 697.6 cm^2) and a volume of 68.4 cm^3 (± 67.1 cm^3).

Burrow characteristics were measured at the start of the study, and the number of burrows (n_B), total entrance area (ΣA_E) and total volume of sediment excavated from burrows (ΣV_B) were calculated for each bank and normalised by respective bank area (A) and bank length (L), yielding six burrow metrics (Table 2):

i. Burrow density per unit bank area ($B_A = n_B/A$; burrows m^{-2}).
ii. Burrow density per unit length ($B_L = n_B/L$; burrows m^{-1}).
iii. Burrow entrance area per unit bank area ($E_A = \Sigma A_E/A$; % cover).
iv. Burrow entrance area per unit bank length ($E_L = \Sigma A_E/L$; $m^2\ m^{-1}$).
v. Burrow volume per unit bank area ($V_A = \Sigma V_B/A$; $m^3\ m^{-2}$).
vi. Burrow volume per unit bank length ($V_L = \Sigma V_B/L$; $m^3\ m^{-1}$).

Burrow volume was considered because of its potential impact on bank geotechnical and hydrological properties, and burrow entrance area was considered because this may affect turbulence generation at the bank face, and thus directly amplify the entrainment of sediment (Harvey et al., 2019). Bank area, as well as bank length, were used to normalise these values to include bank height given its role in determining the weight of material above the burrows, and so propensity to fail (Fredlund & Rahardjo, 1993; Fredlund et al., 1978).

2.4 | Data collection

Pins were installed into the River Bain in September 2017 and Gaddesby Brook in October 2017. Data were collected over a 22-month period (647 days at Gaddesby Brook and 677 days at the River Bain). A total of five repeat sets of readings were obtained from the River Bain and four sets of readings at Gaddesby Brook; all pins were measured to 1 mm accuracy.

2.5 | Data analysis

There has been much debate over the treatment of the recording of negative values in erosion pin datasets (reviewed in Couper et al., 2002). Negative pin values can indicate deposition and were recorded on all but one bank on both rivers. We retained these readings in the analysis because field observations confirmed that they corresponded to deposition. Positive and negative readings were combined to report morphodynamic activity (as in Couper et al., 2002;

TABLE 2 Calculated metrics of burrow density standardised for bank area (B_A; burrows m^{-2}) and bank length (B_L; burrows m^{-1}), burrow volume density standardised for bank area (V_A; $m^3\ m^{-2}$) and bank length (V_L; $m^3\ m^{-1}$), and burrow entrance area density standardised for bank area (E_A; $m^2\ m^{-2}$) and bank length (E_L; $m^2\ m^{-1}$) for all surveyed banks

River	Bank number	B_A (burrows m^{-2})	B_L (burrows m^{-1})	V_A ($m^3\ m^{-2} \times 10^{-4}$)	V_L ($m^3\ m^{-1} \times 10^{-4}$)	E_A (%)	E_L ($m^2\ m^{-1} \times 10^{-3}$)
River Bain	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.00	0.00	0.00	0.00	0.00
	3	0.56	0.57	2.63	2.71	0.13	1.35
	4	0.95	0.89	5.40	5.04	0.30	2.83
	5	1.21	1.33	14.36	15.80	0.40	4.40
	6	1.74	2.00	7.36	8.47	0.36	4.19
	7	1.74	1.71	9.42	9.28	0.34	3.38
	8	2.33	2.00	5.91	5.07	0.31	2.65
	9	1.56	2.00	5.91	5.07	0.31	2.65
	10	3.81	3.43	11.84	10.66	0.67	5.99
	11	6.15	6.86	40.81	45.47	1.31	14.65
Gaddesby Brook	1	0.00	0.00	0.00	0.00	0.00	0.00
	2	1.04	1.11	11.96	12.76	1.78	18.96
	3	1.94	4.56	17.69	14.15	2.41	19.28
	4	4.67	3.5	27.85	20.89	4.12	30.89
	5	5.40	4.25	60.80	47.88	1.99	15.70
	6	3.75	4.00	30.16	32.17	1.22	13.07

Kronvang et al., 2013), to allow for true volumetric changes to be calculated.

Mass movements in the form of bank collapses were apparent on the banks of both rivers. Collapses were identified in the field by obvious shear planes, and the deposition of coherent blocks or piles of bank material at the bottom of the bank (Figure 1b). Pins affected by bank collapses were noted to monitor the extent and nature of bank collapse at each site.

From the erosion pin data, five metrics were calculated for each bank covering the full 22-month period:

i. *Total retreat (m a^{-1})*: mean retreat of the bank per year when all pins were considered;
ii. *Diffuse erosion retreat (m a^{-1})*: mean retreat per year considering only pins that had not been identified as recording collapse;
iii. *Only collapse retreat (m a^{-1})*: mean retreat per year considering only pins that had been identified as recording a collapse (although diffuse erosion likely occurred as well as collapse during the monitoring period, and so these probably represent overestimates);
iv. *Area of bank collapsed (% a^{-1})*: the percentage of pins from the bank that recorded at least one collapse per year, which represents the sum extent of one or more collapses (the number of collapses could not be quantified);
v. *Relative change in riverbank morphology (m a^{-1})*: the difference in total retreat recorded between the top and the bottom of the bank, calculated as the mean retreat of the lowest row of pins minus the mean retreat for the highest row of pins. A positive value represents bank steepening, and a negative value represents a reduction in vertical slope.

Erosion estimates for each bank, time step and site were normally distributed (Shapiro–Wilk test; $p > 0.10$ in all cases), and so parametric tests [Pearson's r (r) for association and one-tailed Student's t-test (t) for significance at $a = 0.1$ significance level] were used for analysis. No statistical assumptions considering repeated measurements were violated. To evaluate questions 1 and 2, the six burrow metrics (Table 2) were tested for association with 'total retreat' (Q1), 'diffuse erosion' (Q2a), 'only collapse' and 'area of bank collapsed' (Q2b) and 'change in riverbank morphology' (Q2c).

2.6 | Data modelling

To address question 3, least-squares linear regression modelling was undertaken to develop a means of estimating the annual rate of bank retreat R (m a^{-1}) as a function of the burrow metric most strongly and consistently associated with it. Burrow volume per unit bank length V_L (m^3 m^{-1}) was the most strongly correlated burrow metric with measured bank retreat R (m a^{-1}) across the full study period and was the only burrow metric significantly correlated with bank retreat on both rivers. Linear regression models for each river were therefore of the form

$$R = \alpha + \beta V_L \quad (3)$$

where β is the retreat constant (acceleration of retreat due to burrows), V_L is the burrow volume (m^3 m^{-1}) and α is the baseline retreat rate (the rate of erosion in the absence of burrows, $V_L = 0$; m a^{-1}). For the purposes of estimating total reach scale sediment supply, Equation 3 was used to estimate an average retreat rate $\bar{R}$, in the presence of burrows using average burrow volume $\bar{V_L}$ equal to the sum of all burrow volumes divided by the sum of all affected bank lengths. The flux of sediment supplied per meter of riverbank with burrows (S_R, kg m^{-1} a^{-1}) was then estimated as:

$$S_R = \gamma \bar{R} h \quad (4)$$

where γ is riverbank bulk density (kg m^{-3}) and h is mean riverbank height (m). This rate includes sediment directly excavated by burrowing S_B (kg m^{-1} a^{-1}), sediment delivered by erosion in the absence of burrows S_0 (kg m^{-1} a^{-1}) and an additional bank erosion surcharge facilitated by burrowing effects S' (kg m^{-1} a^{-1}):

$$S_R = S_B + S_0 + S' \quad (5)$$

Considering question 4, the constituent fluxes of Equation 5 can be independently considered to estimate the masses of sediment supplied to the whole study reach from burrowed banks: (a) from bank erosion in the absence of burrows, (b) directly from crayfish burrow excavation and (c) from bank erosion facilitated by burrow presence:

$$S_B = \gamma \bar{V_L} q \quad (6)$$

$$S_0 = \gamma \alpha h \quad (7)$$

$$S' = S_R - S_0 - S_B \quad (8)$$

where q in Equation 6 is the proportion of observed burrows produced, on average, in a single year. This is not the total number of burrows observed because burrows have a lifespan which exceeds a single year, nor is it number of burrows observed divided by the duration of crayfish occupation because some burrows are lost to erosion. A separate piece of research, in which we monitored >1,500 individual burrows on five rivers for 4 years, suggests that the average number of new burrows per year is 56% of the number of burrows present (Sanders, 2020). Here, q is therefore equal 0.56.

These rates can then be converted to mass of sediment supplied per year M (kg a^{-1}) along the entire study reach considering the length L (m) of the reach, the proportion of the reach that exhibits burrowing p_B and assuming that both sides of the channel behave similarly:

$$M_B = 2 S_B L p_B \quad (9)$$

$$M_0 = 2 S_0 L \quad (10)$$

$$M' = 2 S' L p_B \quad (11)$$

$$M_R = M_B + M_0 + M' \quad (12)$$

from which proportional contributions to the total sediment supply estimates can also be determined.

Whilst this method provides a means of estimating reach-scale sediment supply, it hides substantial within-reach variability in sediment delivery driven by differences in burrow density. R and V_L have been measured for each bank along both rivers (Tables 1 and 2) and can be utilised in bank-scale equivalents of Equations 4 to 12 (with L set to the bank length and $p_B = 1.0$) to obtain estimates of the mass of sediment M_B, M_0 and M' at the bank scale.

3 | RESULTS

Erosion rates and patterns varied between banks, and across the same bank in both space and in time. Bank retreat was different between the two rivers, with mean bank retreat at the River Bain occurring more than ten times faster than at Gaddesby Brook (0.086 m a^{-1} and 0.008 m a^{-1}, respectively). For bank-averaged values, banks with no crayfish burrows retreated at 0.056 m a^{-1} at the River Bain and accreted by 0.005 m a^{-1} at Gaddesby Brook. Riverbank collapse was the dominant mechanism of erosion on the River Bain, with 21.1% of pins recording at least one collapse per year, which contributed 57.5% of the total erosion recorded. At Gaddesby Brook, only 3.2% of pins recorded at least one collapse per year, which contributed 0.6% of total recorded erosion.

3.1 | Do signal crayfish burrows accelerate bank retreat?

Retreat rates varied between individual banks at each river and ranged from 0.049 m a^{-1} (0 burrows m^{-1}) to 0.174 m a^{-1} (6.9 burrows m^{-1}) on the River Bain, a difference of 253%, and from accreting by 0.005 m a^{-1} (0 burrows m^{-1}) to retreating 0.025 m a^{-1} (4 burrows m^{-1}) at Gaddesby Brook (Table 3).

All burrow metrics were significantly positively associated with bank retreat on the River Bain ($p < 0.01$; Table 4), and V_L was positively associated with bank retreat at Gaddesby Brook ($r = 0.618$, $p = 0.096$; Figure 3a). At the River Bain, each additional burrow per metre of riverbank resulted in a significant increase in retreat of 0.017 m a^{-1} ($r = 0.701$, $p = 0.008$), so that a single burrow represents a 30.3% increase in retreat from banks without any burrows (Figure 3a). At Gaddesby Brook, an increase of one burrow per metre of riverbank increased bank retreat by 0.004 m a^{-1}.

3.2 | How do crayfish burrows affect bank retreat?

3.2.1 | Diffuse erosion

Diffuse erosion ranged from 0.016 m a^{-1} (0.6 burrows m^{-1}) to 0.057 m a^{-1} (2.0 burrows m^{-1}) at the River Bain, and from –0.004 m a^{-1} (0 burrows m^{-1}) to 0.025 m a^{-1} (4.0 burrows m^{-1}) at Gaddesby Brook (Table 3). V_L was significantly positively correlated with diffuse erosion at both rivers (River Bain $r = 0.709$, $p = 0.011$; Gaddesby Brook $r = 0.616$, $p = 0.097$; Figure 3b), and V_A was significantly correlated with diffuse erosion at the River Bain ($r = 0.647$, $p = 0.022$). Bain bank 11 was not included in the analysis because all pins recorded collapse in the final study period and so information about diffuse erosion was lost. Retaining bank 11 data but excluding the final period would have meant including diffuse erosion measured over a different time period to the other banks, but more importantly for a period with different hydrological drivers.

3.2.2 | Bank collapse

At the River Bain, bank collapse varied between sites, from no instances of collapse (2.0 burrows m^{-1}) to every pin recording collapse (6.86 burrows m^{-1}). Due to the low number ($n = 5$) of collapses recorded at Gaddesby Brook, only data from the River Bain were considered for quantitative analysis.

All burrow metrics had a strong positive association with the area of bank that exhibited collapse ($p < 0.05$; Table 4). All associations were significant, but B_L and B_A had the strongest associations ($r = 0.686$, $p = 0.010$; and $r = 0.688$, $p = 0.010$ respectively; Figure 3c). At the bank with the greatest density of burrows (bank 11), 100% of pins recorded collapse in the final stage of monitoring, following a high flow event. The bank that recorded collapse at Gaddesby Brook was also the bank with the greatest density of burrows.

3.2.3 | Bank morphology

During the full period of the study, E_A and E_L were significantly associated with change in riverbank morphology at Gaddesby Brook ($r = 0.840$, $p = 0.018$; and $r = 0.898$, $p = 0.008$, respectively; Figure 3d). There was no association between any change in morphology and any burrow metric at the River Bain (Table 4). Two-dimensional (2D) cross-sectional bank profiles revealed that the differences in retreat were the result of undercutting at Gaddesby Brook (Figure 4). Undercutting was associated with all banks where crayfish burrows were present, and greater undercutting was associated with banks characterised by high burrow volume densities (V_A and V_L). Undercutting also occurred on the River Bain, but no consistent patterns or associations were observed in relation to crayfish burrow volume density.

3.3 | Sediment supply modelling from accelerated bank retreat

V_L was the most strongly correlated burrow metric with total retreat across the entire study period and was the only burrow metric significantly correlated with bank retreat on both rivers. Linear regression models of the dependence of total retreat on V_L were therefore developed for each river. The reach-scale regression model was significant for the River Bain ($y = 27.3\ V_L + 0.058$; $r^2 = 0.545$, $F = 10.769$, $p < 0.01$) but not for Gaddesby Brook ($y = 4.67\ V_L - 0.003$; $r^2 = 0.382$, $F = 2.472$, $p = 0.191$).

At the reach scale, accelerated erosion facilitated by burrows was estimated to supply 24.9 t km^{-1} a^{-1} of sediment into the River Bain. At the bank scale, this crayfish surcharge to bank erosion supplied an average of 48.7 kg m^{-1} a^{-1}, ranging up to 189.1 kg m^{-1} a^{-1} of sediment at the River Bain, and an average of 18.2 kg m^{-1}, ranging up to 44.6 kg m^{-1} a^{-1} of sediment at Gaddesby Brook (Table 5).

TABLE 3 Retreat metrics, considering total retreat (m a^{-1}), diffuse erosion (m a^{-1}), collapse erosion (m a^{-1}), area of bank collapsed (% a^{-1}) and relative change in bank morphology (m a^{-1}), for all banks considering the full study period, considering mean and SEM (standard error) values

River	Bank number	Total retreat (m a^{-1})		Diffuse erosion (m a^{-1})		Collapse erosion (m a^{-1})		Pins collapsed (% a^{-1})	Relative change in Bank morphology (m a^{-1})
		Mean	SEM	Mean	SEM	Mean	SEM		
River Bain	1	0.063	0.01	0.020	0.00	0.162	0.01	17.4	0.056
	2	0.049	0.01	0.040	0.01	0.287	0.07	11.2	–0.097
	3	0.037	0.01	0.016	0.00	0.139	0.02	11.2	–0.079
	4	0.040	0.01	0.029	0.01	0.064	0.02	5.8	0.025
	5	0.108	0.01	0.069	0.01	0.144	0.02	19.6	0.062
	6	0.146	0.01	0.057	0.02	0.209	0.06	44.5	–0.074
	7	0.118	0.05	0.046	0.01	0.242	0.10	21.1	–0.151
	8	0.093	0.02	0.040	0.01	0.135	0.02	35.0	–0.002
	9	0.035	0.01	0.035	0.01	0.000	0.00	0.0	0.070
	10	0.079	0.02	0.031	0.01	0.131	0.01	20.5	–0.075
	11	0.174	0.00	-	-	0.191	0.01	53.9	0.023
Gaddesby Brook	1	–0.005	0.00	–0.004	0.00	-	-	-	–0.071
	2	–0.002	0.00	–0.002	0.00	-	-	-	0.006
	3	0.016	0.00	0.016	0.00	-	-	-	–0.003
	4	–0.004	0.00	0.004	0.00	-	-	-	0.008
	5	0.014	0.00	0.014	0.00	-	-	-	–0.005
	6	0.025	0.00	0.025	0.00	-	-	-	–0.040

TABLE 4 Associations (Pearson's r) between burrow density standardised for bank area (B_A; burrows m^{-2}) and bank length (B_L; burrows m^{-1}), burrow volume density standardised for bank area (V_A; m^3 m^{-2}) and bank length (V_L; m^3 m^{-1}), and burrow entrance area density standardised for bank area (E_A; %) and bank length (E_L; m^2 m^{-1}), with the rate of total bank retreat (m a^{-1}), diffuse erosion (m a^{-1}), bank collapse (m a^{-1}), area of bank collapse (% a^{-1}), and relative change in bank morphology (m a^{-1}), for Gaddesby Brook (GB) and the River Bain (RB) considering the full study period. Starred (*) values are significant at the *0.1, **0.05 and ***0.01 level

	Total retreat (m a^{-1})		Diffuse erosion (m a^{-1})		Bank collapse retreat (m a^{-1})		Area of Bank collapse (% a^{-1})		Change in morphology (m a^{-1})	
	GB	RB	GB	RB	GB	RB	GB	RB	GB	RB
B_A	0.415	0.682***	0.412	0.200	-	–0.014	-	0.686***	0.465	0.044
B_L	0.560	0.701***	0.557	0.276	-	–0.020	-	0.688***	0.371	0.098
V_A	0.507	0.744***	0.504	0.647**	-	0.069	-	0.669***	0.410	0.187
V_L	0.618*	0.738***	0.616*	0.709**	-	0.061	-	0.659**	0.349	0.218
E_A	–0.093	0.701***	–0.908	0.371	-	–0.016	-	0.663**	0.840**	0.122
E_L	–0.047	0.719***	–0.053	0.468*	-	–0.019	-	0.663**	0.898***	0.168

3.4 | Relative importance of biotic, abiotic and interactive sediment supply

Accelerated bank erosion caused by crayfish burrows was modelled to be an important driver of sediment dynamics on both rivers. At the reach scale, accelerated erosion supplied 49 times more sediment than burrows alone, and considering sediment supplied from all banks, including banks where burrows were absent, supplied 12.2% of all sediment at the River Bain. Considering the measured banks, accelerated retreat supplied 29.8% of all sediment, compared with 0.6% directly from burrows. This represents an increase of 43.7% of sediment supplied compared with riverbanks without burrows. At Gaddesby Brook, where the reach-scale regression model was not significant, bank-scale observations can be applied to Equations 4 to 12, with α being the observed erosion rate at the only bank without burrows (bank 1). At Gaddesby Brook, sediment deposition occurred in the absence of burrows, but erosion occurred in the presence of burrows. Therefore, burrows (10.4%) and accelerated retreat due to the presence of burrows (89.6%) jointly supplied 100% of sediment from the studied banks.

4 | DISCUSSION

Riverbank erosion caused by animal burrowing has previously been assessed qualitatively (Arce & Dieguez-Uribeondo, 2015; Faller et al., 2016; Sibley, 2000; West, 2010). Harvey et al. (2019) highlighted the need for quantitative data to assess both the direct input of sediment

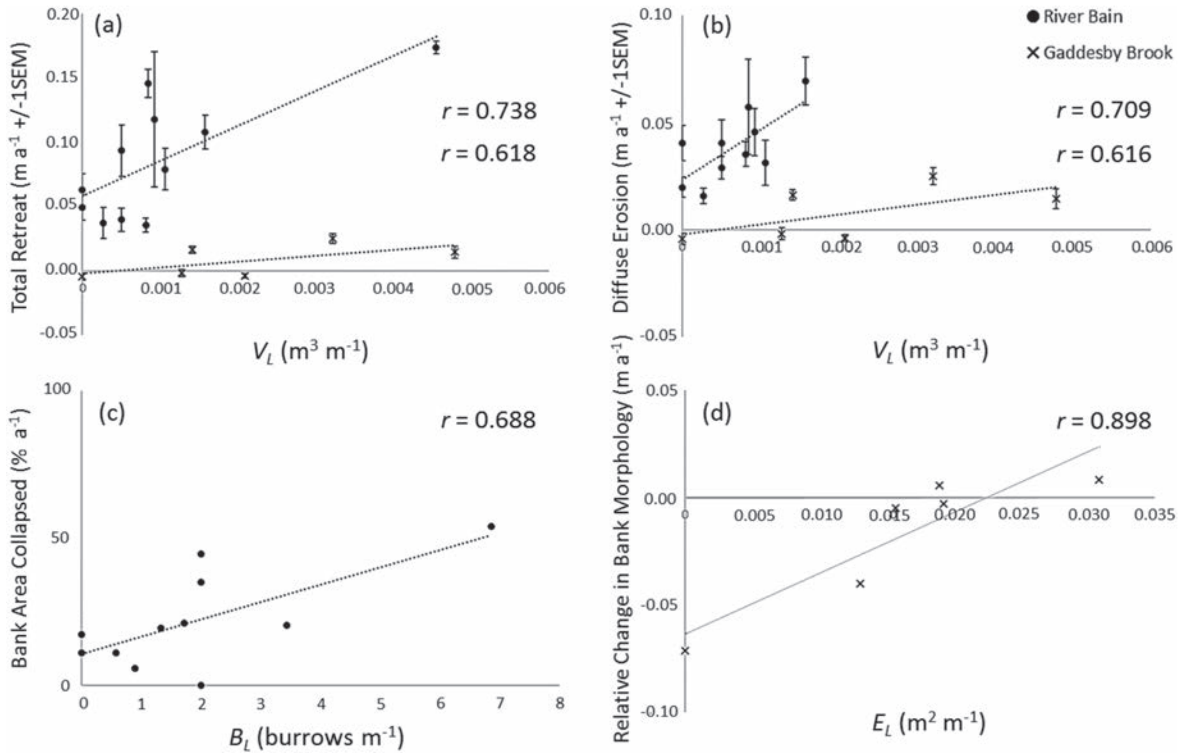

FIGURE 3 The associations between (a) total bank retreat (m a^{-1}) and burrow volume density (V_L; m^3 m^{-1}), (b) diffuse erosion (m a^{-1}) and burrow volume density (V_L; m^3 m^{-1}), (c) the area of bank collapsed (% a^{-1}) and burrow density (B_L; burrows m^{-1}) and (d) relative change in bank morphology (m a^{-1}) and burrow entrance size density (E_L; m^2 m^{-1}) at Gaddesby Brook and the River Bain for the full study period

produced by burrowing and indirect, burrowing-induced sediment supply; for example via accelerated bank erosion (e.g. Faller et al., 2016; Sofia et al., 2016). The results presented here provide the first quantitative association between animal burrows and riverbank retreat and describe the association between burrow characteristics and the nature of retreat over a 22-month study period. Harvey et al. (2019) hypothesised that animal burrows may alter bank erosion processes through (i) geotechnical and hydrological effects, and (ii) hydraulic effects. Significant associations between burrow volume and the prevalence of collapse events, and burrow entrance area and diffuse erosion recorded in this study provide supporting evidence for both suggestions.

The rate and nature of erosion was different between the two rivers, with higher rates dominated by collapse on the River Bain and lower rates driven by diffuse erosion on Gaddesby Brook. The grain size of materials collected from exposed river banks was similar on both rivers (41% silt and clay with 59% sand on Gaddesby Brook, and 35% silt and clay with 64% sand at the River Bain), which suggests that the difference in erosion rate is not caused by material properties. However, British Geological Survey borehole data from the floodplains, which may be more representative of general floodplain materials, indicate a predominance of clays at Gaddesby Brook and sandy silts at the River Bain (British Geological Survey, 2020), which is consistent with greater erosion rates and more collapse on the Bain. It is also notable that banks were considerably steeper on the Bain (74° versus 49° on Gaddesby Brook). These factors were not investigated in this study but may be important for explaining the differences in rates and mechanisms of retreat between the two sites. Despite the difference in retreat rates and mechanisms, crayfish burrow metrics were significantly associated with retreat metrics on both rivers, strongly suggesting that burrows play an important role in the geomorphology of rivers that exhibit different rates of retreat.

4.1 | Total retreat

Increased crayfish burrow density was associated with greater total retreat at both study sites, with the presence of each additional burrow per metre increasing retreat by 0.017 m a^{-1} on the River Bain. Compared with erosion of banks without burrows this represents an average increase of 30.3%, and the bank with the highest burrow density (6.15 burrows m^{-2}) recorded retreat that was 253% greater than the erosion of banks without burrows. This supports observations that signal crayfish accelerate bank erosion (Sibley, 2000; West, 2010) and Harvey et al.'s (2019) assertion that burrowing affects riverbank processes.

The number of burrows, the burrow volume and the burrow entrance area at bank 11 on the River Bain were at least twice that of the next most burrowed bank, and 4.26 times larger considering burrow volume. Whilst the burrow metrics of this bank are statistical outliers (3.83 × IQR > third quartile B_L and 5.82 × IQR > third quartile V_L), the dependent variables were not. Data from this bank were therefore retained in the analyses because crayfish burrows are typically highly clustered, so high densities are not uncommon. Faller et al. (2016) reported that burrows occupied just 3% of the total surveyed bank length, with infested reaches characterised by small areas of high burrow density. The burrow density of bank 11 (6.9 burrows m^{-1}) is consistent with previous burrow density recordings [5.6 burrows m^{-1} (Guan, 1994), 21.0 burrows m^{-1} (Guan & Wiles, 1997); 6.5 and 14.0 burrows m^{-1} (Stanton, 2004); 6.0 burrows m^{-1} (Faller et al.,

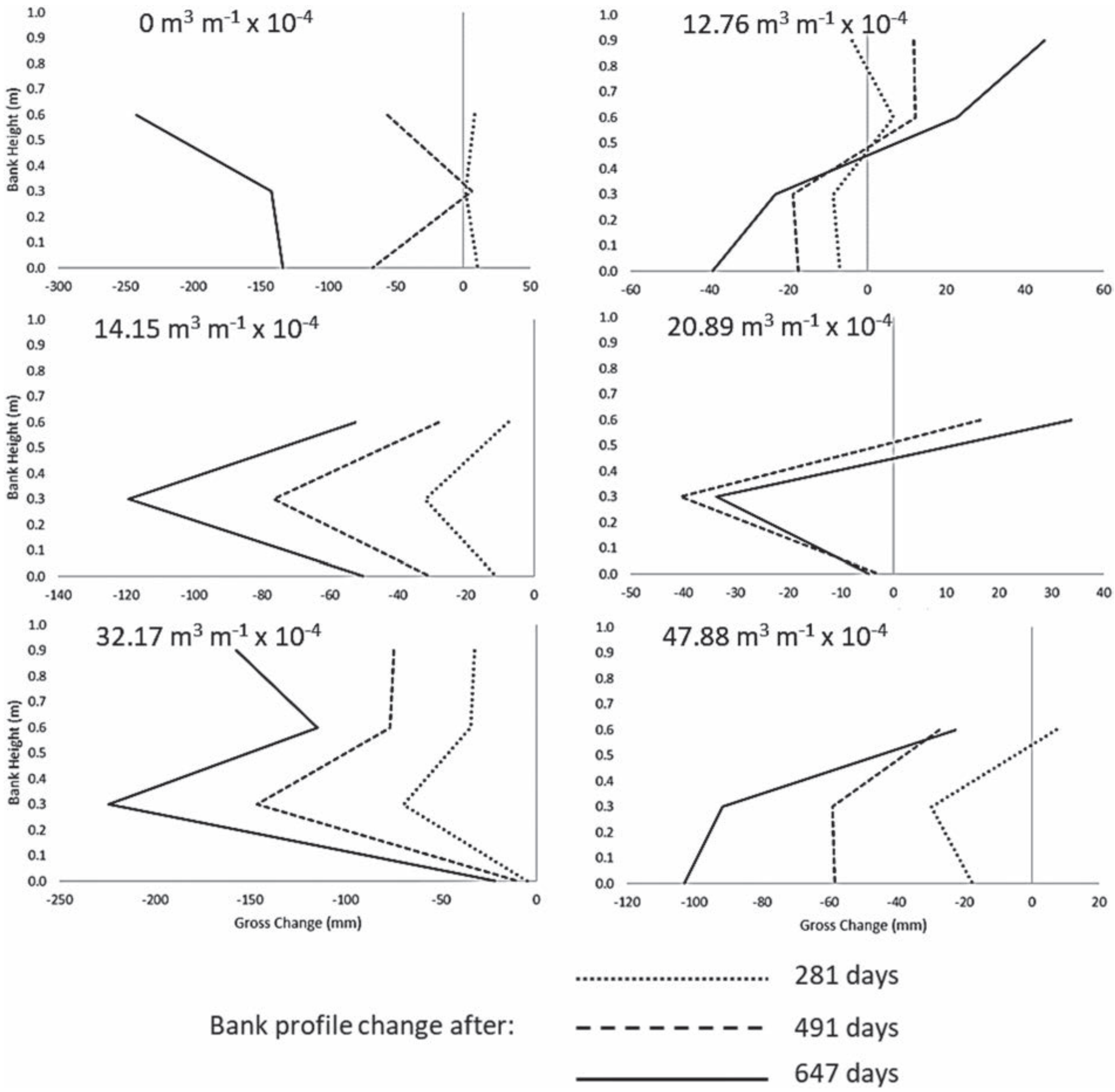

FIGURE 4 Changes in bank profile over time at Gaddesby Brook, in relation to initial conditions (represented as the zero line). Values in the top left corner are burrow volume density ($m^3\ m^{-1}$), as these had the strongest association of all metrics with change in bank morphology. Very little undercutting can be seen at the bank without crayfish burrows (top left), whereas consistent undercutting between 0.0 and 0.6 m in height can be seen on all burrowed banks

2016)], and so the range of densities observed on the River Bain and Gaddesby Brook are typical of distribution patterns of burrows on UK rivers. In this case, the responses observed here should not be regarded as extreme.

A large range of bank retreat values were recorded at the density of 2 burrows m^{-1} on the River Bain (Figure 3a). This variability may be a result of the collapse dominated nature of retreat on the Bain. Collapses, and thus recorded retreat, are sporadic events, and so occurred across the study period resulting in greater variance within the dataset. Longer monitoring periods would likely result in reduced variance among the datapoints, and thus a better understanding of the association between the measured variables.

Patterns of variability were also observed in diffuse erosion, suggesting that it was not just bank collapse driving the variability recorded between banks. It is likely that this scatter reflects the uncontrolled factors observed throughout bank retreat studies yielding typically large variability in measured rates (Table 6). Further, burrow characteristics used for analysis were only measured at the start of the study. Burrow densities can change over time through the construction of new burrows and the loss of burrows to erosion (Sanders, 2020), and so a proportion of the observed variation may reflect this. Despite this scatter, significant associations between bank retreat and crayfish burrowing were observed, which demonstrates the strength of effect that burrowing exerted and its importance as a driver of erosion.

4.2 | Diffuse erosion

Crayfish burrow volume density was associated with higher rates of diffuse erosion on both rivers. At Gaddesby Brook, the presence of burrows was associated with net erosion whereas banks without

TABLE 5 The relative inputs of bank erosion as a result of direct sediment input from crayfish burrows, the accelerated bank erosion caused by crayfish burrows, and bank erosion in the absence of crayfish burrows. Percentages are estimated as a proportion of total sediment supplied; negative values represent deposition, expressed as a proportion of sediment supplied

		Only erosion in the absence of crayfish burrows		Only crayfish burrows		Accelerated Bank retreat caused by crayfish burrows	
River	Bank number	kg a^{-1}	%	kg a^{-1}	%	kg a^{-1}	%
River Bain	1	482.5	100.0	0.0	0.0	0.0	0.0
	2	265.9	100.0	0.0	0.0	0.0	0.0
	3	313.6	99.7	0.8	0.3	−114.7	−36.5
	4	364.1	99.5	1.9	0.5	−117.2	−32.0
	5	287.1	53.7	4.0	0.7	243.5	45.6
	6	300.2	39.8	2.1	0.3	451.5	59.9
	7	301.5	49.2	2.7	0.4	308.9	50.4
	8	261.9	62.1	1.5	0.4	158.4	37.6
	9	392.8	99.4	2.4	0.6	−155.7	−39.4
	10	274.1	73.3	3.1	0.8	96.5	25.8
	11	338.0	33.4	13.4	1.3	661.8	65.3
	Total burrowed banks	3581.6	69.6	31.9	0.6	1532.0	29.8
	Total reach	179220.0	87.6	506.8	0.2	24942.9	12.2
Gaddesby Brook	1	−26.7	−100.0	0.0	0.0	0.0	0.0
	2	−32.9	−216.6	4.8	31.7	14.2	68.3
	3	−24.6	−22.7	5.3	4.9	107.1	95.1
	4	−20.5	−292.4	7.0	100.0	−4.3	−61.3
	5	−21.6	−28.0	16.1	20.8	73.7	79.2
	6	−32.9	−16.2	12.2	6.0	200.8	94.0
	Total burrowed banks	−159.3	−36.5	45.4	10.4	391.5	89.6
	Total reach	-	-	-	-	-	-

TABLE 6 Observed variability (± SD) in riverbank retreat along rivers where crayfish burrows were not present in comparison with this study

Study	Observed variability	River	Catchment area (km^2)	Bank sediments
This study	35 (± 30.9) to 174 (± 24.6) mm a^{-1}	Bain	66.0	Predominantly silt and clay
	−5 (± 14) to 25 (± 22) mm a^{-1}	Gaddesby brook	29.0	Predominantly silt and clay
Lawler et al., 1999	77.7 (± 105.6) to 440.1 (± 181.7) mm a^{-1}	Swale–Ouse system	3315.0	Predominantly sandy loam
Kronvang et al., 2013	22 (± 3) to 109 (± 43) t km^{-1}	River Odense	486.0	Predominantly sandy loam
Henshaw et al., 2013	7 (± 4) to 299 (± 321) mm a^{-1}	Pontbren catchment	12.5	Silt to boulder sized material
Palmer et al., 2014	16 (± 5.3) to 220 (± 227) mm a^{-1}	Walnut Creek	52.2	Predominantly sandy loam
Foucher et al., 2017	−275 to 100 m a^{-1}	Louroux pond catchment	24.0	-

crayfish burrows recorded deposition. This suggests that the presence of burrows caused erosion but also inhibited deposition, which was otherwise prevalent on Gaddesby Brook. This deposition appears to have been caused by the settling of loose material from along the bank tops onto lower parts of bank faces, which was possible because banks at Gaddesby Brook were not steep (39.7° to 64.2°; mean = 49.0°). It was demonstrated that burrowing was associated with steepening of the banks at Gaddesby Brook (Figure 3d), which may have rendered burrowed slopes too steep to retain sediment settling from above. Further, burrow entrance area (E_A and E_L) was significantly associated with bank erosion, which may be caused by increases in turbulence at the bank face (Harvey et al., 2019), which amplifies the entrainment of particles by diffuse erosion.

4.3 | Bank collapses

Area of bank collapse was significantly associated with all burrow metrics on the River Bain. Burrows and burrow features and structures partially remained and were clearly visible after collapse events had occurred, supporting hypotheses that single burrows can affect multiple collapse events (Faller et al., 2016). The presence of crayfish burrows constructed by red swamp crayfish (Procambarus clarkii) has been linked to the destabilisation and collapse of banks in rice paddies in the Iberian Peninsula (Arce & Dieguez-Uribeondo, 2015), with 73% of recorded burrows collapsing within 9 days of excavation (Barbaresi et al., 2004). Our results demonstrate a link between burrowing and riverbank mass failure through in situ monitoring for the first time, supporting the suggestions of Harvey et al. (2019) that burrows can drive riverbank mass failure.

Physical (Saghaee et al., 2017; Viero et al., 2013) and numerical (Borgatti et al., 2017; Camici et al., 2014; Orlandini et al., 2015) modelling has also indicated that the presence of animal burrowing increases the probability of riverbank collapse, particularly from burrows constructed on the waterside of levees (Saghaee et al., 2017). This occurs as a result of animal burrows increasing the hydraulic gradient across a levee, making the structure more liable to collapse and increasing flood risk. On the Foenna Stream (Camici et al., 2014) and the Secchia River (Orlandini et al., 2015) in Italy, crested porcupine (Hystrix cristata) burrows led to levee failures, resulting in over $500 m of damage in the latter case (Orlandini et al., 2015).

4.4 | Bank morphology

Over the entire study period, burrow entrance area (E_A and E_L) was strongly positively correlated with the steepening of riverbanks at Gaddesby Brook. Undercutting was associated with all banks where crayfish burrows were present (Figure 4), and greater undercutting was associated with banks with high burrow volume densities (V_A and V_L). Undercutting was not recorded at erosion pin sites on the River Bain but was observed in the field, and it was clear that erosion pins under-recorded undercutting because of low spatial resolution (Figure 5). This style of undercutting, with the creation of a roofed cavity at low level (Figure 5), is most easily explained by the interaction and collapse of multiple crayfish burrows rather than hydraulic erosion because the height and depth of these features correspond with crayfish burrow dimensions and were qualitatively similar to erosive features observed by the lead author in other rivers where crayfish burrows are prevalent. Given the propensity of undercutting to weaken the structural integrity of the bank and promote collapse, it is therefore likely that undercutting by crayfish contributed to the high incidence of mass failure on the River Bain.

More erosion was recorded at the toe of banks than at the top of banks, which is consistent with previous studies (Kronvang et al., 2013; Laubel et al., 2003; Veihe et al., 2010). Whilst these previous studies have attributed this to hydraulic action, erosion at the bank toe may have been exacerbated by a preference for crayfish excavating burrows just below the water line at the time of construction (Sanders, 2020). However, this effect was accentuated with increasing crayfish burrow densities (Figure 3d). At the start of the surveying period, the banks on the River Bain were almost vertical, whereas the average slope of banks at Gaddesby Brook were surveyed to be 49° across the full bank height, and 54.7° at the toe where crayfish burrows were present. It has previously been suggested that crayfish construct burrows in reaches with steep banks (Faller et al., 2016), but Figure 4 suggests that burrowing actively steepens banks over time, which may have further implications for the accelerated erosion of banks through modifying geotechnical and hydrological processes (Fox et al., 2007; Simon & Collison, 2001).

4.5 | Modelling sediment supply

In the study reach of the River Bain, accelerated retreat facilitated by crayfish burrows was estimated to supply 24.9 t km^{-1} a^{-1} of sediment, which represents a 14.2% and 43.7% increase of erosion in the absence of burrows at the reach and bank scale, respectively (Table 5). This is an order of magnitude greater than previous estimates of sediment production due to by burrow excavation alone: 0.25–0.5 t km^{-1} a^{-1} (Rice et al., 2016) and 3.0 t km^{-1} (Faller et al., 2016).

The distribution of crayfish burrows in invaded catchments is patchy (Faller et al., 2016), and only 25% of bank length along the River Bain study reach was affected by crayfish burrows. Distributed field surveys across rivers in the UK (n = 69 and 23) have found maximum impacted bank lengths at the reach scale of 23.5% and 27.1% (Faller et al., 2016; Sanders, 2020, respectively), and so the proportions at our study sites indicate that these are severely impacted reaches. However, crayfish invasion is progressive, with the proportion of impacted reach significantly positively associated with length of crayfish occupancy since invasion (Sanders, 2020). The proportion of impacted banks may therefore increase over time, with implications for sediment loading. Should burrows occupy 50% of riverbank length, accelerated erosion from burrows at the River Bain would be responsible for supplying 49.9 t km^{-1} a^{-1} into the system, 21.7% of total sediment contribution, and an increase of 28.4% over bank erosion in the absence of crayfish burrows.

This modelling provides estimates of the relative contribution of crayfish burrows to the supply of riverbank sediment along the River Bain. It is difficult to extrapolate these observations to other rivers, not least because of the significant variability between these two lowland streams. Further, the estimated baseline erosion rates are dependent on just two banks at the River Bain, and a larger sample of banks with no burrows would allow for greater confidence in these baseline values. Nevertheless, these data provide an insight into the magnitude of sediment being supplied to rivers as a direct and indirect result of crayfish burrowing relative to bank recession in the absence of burrows. The direct effect of burrowing contributes small amounts of sediment relative to the additional bank erosion facilitated by burrow presence: 49.2 times more on the River Bain, and 10 times more at Gaddesby Brook. Table 5 shows that bank erosion processes augmented by burrow presence account for an estimated 12.2% of sediment supply at the River Bain at the reach scale (accounting for unburrowed stretches), and that equivalent values at individual banks where burrows are present can be substantially higher.

Whilst V_L had the strongest association with riverbank retreat, and thus sediment supply, of all measured variables (Table 4), significant associations between bank retreat and the number of burrows (B_L and B_A) were also observed. This is important for future river management and suggests that non-intrusive surveys of burrow numbers could be used for estimating augmented sediment yields.

Now that associations between burrows and accelerated riverbank retreat have been established, understanding the spatial and

FIGURE 5 An undercut bank on the River Bain. The spacing of the erosion pins (denoted by circles) was often too coarse to detect these local processes which lead to large-scale collapses. (NB: Photograph taken during low flow conditions for clarity of bank morphology) [Colour figure can be viewed at wileyonlinelibrary.com]

temporal dynamics of these events is an important avenue of future research. The application of TLS or SfM would provide information at finer spatial scales and potentially over larger areas, which would help in understanding failure mechanisms and testing specific hypotheses about the processes at work but would require application beneath the water surface as well as on the exposed bank face. Greater temporal resolution would also help to identify links between erosional events and hydrological extremes. Preliminary evidence suggests possible associations between high magnitude flow events and increased retreat rates at burrowed banks, but the data on this are limited (Sanders, 2020). Alongside these data improvements, numerical modelling of riverbanks (e.g. Luppi et al., 2009; Rinaldi & Nardi, 2013) adapted to contain simulated burrows could be a primary means of identifying key mechanisms and their sensitivity to burrow characteristics.

This research quantifies the significant effect that crayfish can have on fine sediment supply via bank erosion, with implications for, amongst other things, ecosystem health. In particular, excessive fine sediment can smother riverbed gravels, which can degrade the quality of fish spawning habitat (Kemp et al., 2011; Sear et al., 2016; Soulsby et al., 2001), and reduce egg and juvenile survival (Jensen et al., 2009; Kemp et al., 2011; Suttle et al., 2004). Significant declines in fish populations have been observed since 1985 following the introduction of signal crayfish the River Bain in 1992 ($r = -0.161$, $p < 0.001$), particularly of dace (Leuciscus leuciscus; $r = -0.445$, $p < 0.001$) and chub (Leuciscus cephalus; $r = -0.403$, $p < 0.001$), for which clean gravels are important for feeding and spawning activities (Environment Agency, 2020; Pledger et al., 2016; Rice et al., 2019). A significant decrease in dace populations has also occurred at Gaddesby Brook following crayfish invasion over the same time period ($r = -0.722$, $p = 0.004$; Environment Agency, 2020). At both the River Bain and Gaddesby Brook, fine sediment accumulation over the riverbed has increased over the last 20 years, coinciding with crayfish invasion. Landowners and Environment Agency staff report clean gravel substrates and an absence of fine sediment accumulations 20 years ago, but we measured accumulations of 0.4 m depth of fine sediment at locations within both reaches. Other factors could be involved in accelerating fine sediment deposition and impoverishing fish habitat, although our sediment budgeting demonstrates that crayfish can be an effective cause of fine sediment loading that contributes to degradation of benthic habitat.

5 | CONCLUSIONS

This study has quantified the direct and indirect influence of animal burrows on riverbank erosion and shown that the presence of signal crayfish burrows significantly increases rates of bank retreat for the first time. Burrowing steepened banks, significantly increased the rate of diffuse erosion and increased the spatial extent of mass collapses. These results support the suggestions of Harvey et al. (2019) that animal burrows can alter riverbank erosion processes by promoting geotechnical failures and altering hydraulics at the bank face.

Sediment budgeting estimates that accelerated bank erosion caused by the presence of burrows supplied 49.2 times the mass of sediment from burrowing alone at the River Bain and contributed 12.2% and 29.8% of the total supplied sediment at reach and bank scales, respectively. This demonstrates the importance of burrowing in priming riverbanks to catalyse more substantial, secondary erosion that would otherwise be absent. This is consistent with the zoogeomorphic effects of other animals in rivers, including many benthic feeding fish, which impact sediment dynamics primarily by altering the propensity of sediment to move, rather than by directly moving it (Rice et al., 2019).

More generally, this research supports the suggestion that biological processes can be a substantial driver of geomorphological change, supplementing the geophysical processes that geomorphologists focus on. River biosecurity from invasive species, and signal crayfish in particular, is therefore a key geomorphological, as well as ecological, management consideration. The budgeting of sediment supply into biotic (direct burrowing), abiotic (erosion in the absence of burrowing) and interactive (abiotic erosion facilitated by burrowing) components is novel and adds to a small body of work comparing biotic and abiotic contributions to sediment dynamics. Our modelling enables the first comparative estimates of the relative importance of biotic, abiotic and interactive processes in driving fine sediment supply to river systems and confirm that signal crayfish burrowing can contribute a significant proportion of the fines delivered to infested streams.

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DATA AVAILABILITY STATEMENT

Data are available from the lead author upon reasonable request.

ORCID

H. Sanders https://orcid.org/0000-0003-3031-2227
S.P. Rice https://orcid.org/0000-0003-0737-9845

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