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Structural complexity influences the ecosystem engineering effects of instream large wood

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ABSTRACT

Large wood (LW) is an ecosystem engineer and keystone structure in river ecosystems, influencing a range of hydromorphological and ecological processes and contributing to habitat heterogeneity and ecosystem condition. LW is increasingly being used in catchment restoration, but restored LW jams have been observed to differ in physical structure to naturally occurring jams, with potential implications for restoration outcomes. This paper examines the structural complexity and ecosystem engineering effects of LW jams at four sites with varying management intensity incorporating natural and restored wood. Our results reveal: (i) structural complexity and volume of jams was highest in the site with natural jams and low intensity riparian management, and lowest in the suburban site with simple restored jams; and (ii) that structural complexity influences the ecosystem engineering role of LW, with more complex jams generating the greatest effects on flow hydraulics (flow concentration, into bed flows) and sediment characteristics (D_{50}, organic content, fine sediment retention) and the simplest flow deflector-style restored jams having the least pronounced effects. We present a conceptual model describing a continuum of increasing jam structural complexity and associated hydromorphological effects that can be used as a basis for positioning and evaluating other sites along the management intensity spectrum to help inform restoration design and best practice.

***Keywords**:* Large wood, structural complexity, physical habitat diversity, river restoration, fluvial geomorphology

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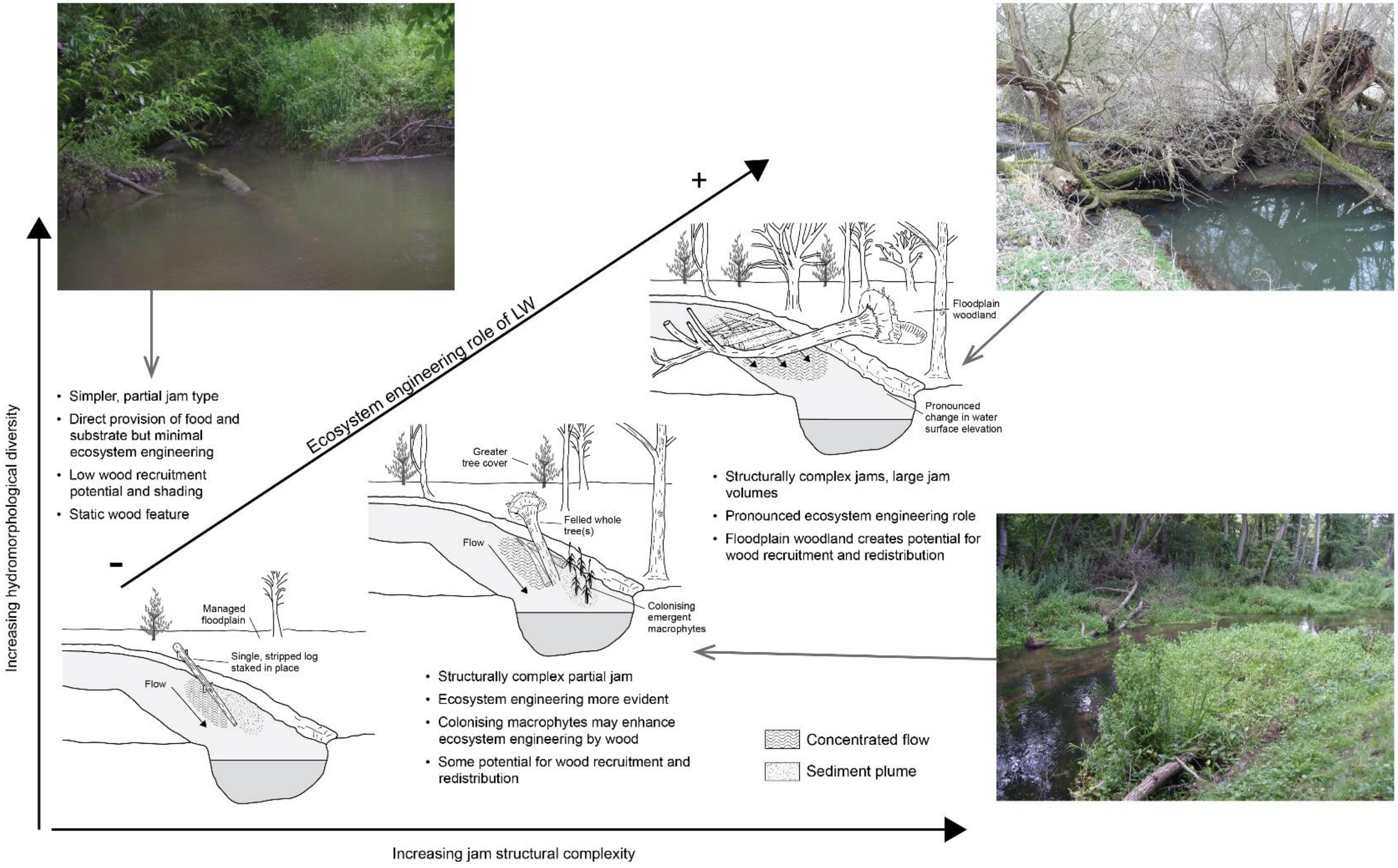
Graphical Abstract:



- Simpler, partial jam type
- Direct provision of food and substrate but minimal ecosystem engineering
- Low wood recruitment potential and shading
- Static wood feature

- Structurally complex partial jam
- Ecosystem engineering more evident
- Colonising macrophytes may enhance ecosystem engineering by wood
- Some potential for wood recruitment and redistribution

- Structurally complex jams, large jam volumes
- Pronounced ecosystem engineering role
- Floodplain woodland creates potential for wood recruitment and redistribution

1. INTRODUCTION

Historical river management, through river channelization, flow regime alteration, and vegetation clearance has had profound effects on rivers across the world (Brookes, 1988; Petts, 1984), with a general trend towards reduced diversity of geomorphic features and hence homogenisation of physical habitat (Gregory and Davis, 1992; Gregory et al., 1992; Brookes and Shields Jr, 1996; Moyle and Mount, 2007; Walter and Merritts, 2008; Wohl, 2014, 2019). In recognition of the negative effects of reduced habitat heterogeneity on ecosystem structure and function, a primary goal of many river restoration efforts has been to increase the diversity of physical habitat conditions (i.e. flow velocity and depth, substrate characteristics, water temperature) to restore functional processes (Harper and Everard, 1998; Clarke et al., 2003; Darby and Sear, 2008; Wohl et al., 2015; Cashman et al., 2018). Among these efforts is the recognition that plants and animals can act as 'ecosystem engineers' in river systems, actively or passively modifying habitats and resource flows (Jones et al., 2006) and potentially increasing restoration success and reducing costs and effort (Bailey et al., 2018). A key example is Large Wood (LW), also known as Large Woody Debris (or LWD), which is increasingly being reintroduced to rivers after a long history of removal (Watts, 2006; Wohl et al., 2015) to re-establish geomorphic diversity and habitat heterogeneity (Abbe et al., 2003; Roni et al., 2014; Harvey et al., 2018), and to restore biodiversity and enhance food webs (Thompson et al., 2018).

LW is commonly defined as pieces of wood larger than 10 cm in diameter and 1 m in length (Gippel et al., 1996) and has been recognized as a keystone ecosystem structure (Tews et al., 2004) for its role in initiating a series of hydromorphological and ecological processes that contribute to habitat quality and ecological condition (Gurnell et al., 2002; Wondzell and Bisson, 2003).

LW has been shown to diversify flow patterns (Kreutzweiser et al., 2005), trap organic matter (Bilby, 1981), and increase sediment storage, stability, and sorting in the channel (Bilby, 1984). The resulting heterogeneous habitat conditions have been associated with a range of ecological benefits including an enhanced seed bank (Osei et al., 2015), increased resource availability and nutritional quality for consumers (Cashman et al., 2016; Cashman et al., 2017), increased benthic invertebrate diversity (Pilotto et al., 2014), and increased fish abundance and diversity (Nagayama et al., 2012). However, the function of naturally occurring LW has previously been shown to diminish with increasing management of riparian conditions (e.g. clear cut and secondary growth compared to old-growth forests), as reduced instream wood abundance and complexity results in diminished geomorphic effects (Bilby and Ward, 1991).

LW has been used in a number of ways in river restoration design, but there has been a general tendency for projects to favour simpler flow deflector-style wood jams (e.g. single logs, stripped of branches and often fixed in place), over more structurally complex wood jams (Kail and Hering, 2005; Cashman et al., 2018). This largely reflects a response to concerns over flood risk and potential for wood mobilisation and damage to instream infrastructure (Gippel et al., 1996; Erskine and Webb, 2003; Roni et al., 2014). More recently, however, there has also been increased recognition of the potential flood risk management benefits of LW for example as a “slow the flow” measure. In the UK, this has led to the inclusion of LW reintroduction as a flood risk mitigation measure within government guidance, part of a series of ‘Natural Flood Management’ approaches that work with natural hydrogeomorphological processes to reduce flood risk (Environment Agency, 2017). Furthermore, the reintroduction of more structurally complex wood jams that aim to mimic natural wood recruitment to the active channel, such as felling whole trees from the riparian zone (River Restoration Centre, 2013), has been linked to modified sediment dynamics at multiple scales (Parker et al., 2017), channel recovery from over-widening (Harvey et al., 2018), and increased biodiversity through alterations to abundance and biomass of food web consumers and resources (Thompson et al., 2018). A full understanding of the spectrum of LW structural characteristics and associated physical microhabitats across a range of natural and restored conditions is currently lacking but is crucial to the development of best practice in river restoration, the improvement of restoration outcomes and improved modelling of hydraulic and hydrological effects of LW (Addy and Wilkinson, 2019; Pinto et al., 2019).

This paper examines the structural characteristics of LW jams and their associated habitat conditions, such as flow depth, flow velocity, and bed sediment properties at four sites with differing riparian management intensity and natural and restored wood: natural jams in low and moderate management intensity settings, and restored jams in moderate and high management intensity settings. In particular, in this study we examine: (1) variation in structural complexity of wood jams among the four sites, and (2) relationships between wood jam complexity and various metrics of habitat heterogeneity (flow and sediment conditions and variability).”

2. MATERIALS AND METHODS

2.1 Field sites

Four field sites (river reaches) in England were selected to represent differing levels of riparian and instream wood management and human intervention: (1) an unmanaged channel and riparian zone with naturally occurring LW jams in an agricultural catchment (i.e. natural LW jams with low levels of floodplain management; hereafter referred to as ‘NL’); (2) natural LW jams in a forested catchment but with a grazed riparian zone (i.e. natural LW, moderate floodplain management; ‘NM’); (3) a wooded river corridor in an agricultural catchment, with restored LW jams that incorporate whole felled trees (restored LW, moderate floodplain management; ‘RM’); and (4) a river with a heavily managed corridor in a predominantly urban catchment that has been restored using wood in the form of single log deflectors (restored LW, high floodplain management; ‘RH’) (Supplementary Data Table 1). Sites were chosen to represent a range of management and intervention conditions, and restored sites were selected to capture distinct styles of wood restorations occurring in the United Kingdom in the National River Restoration Inventory (Cashman et al. 2018). Site conditions are typical of lowland rivers in England. The reaches are situated in laterally unconfined valley settings, have catchment areas < 150 km^2 and channel gradients between 0.0009 and 0.0027 m/m (see Supplementary Data Table 1 for site details). Channel widths ranged between 3 - 9 m, smaller than or similar to the average length of key pieces in wood jams (RH average channel width was 2 m greater than LW key piece length). All sampling was conducted in July and August 2012.

The NL site was located on the River Dene which flows through predominantly agricultural land in Warwickshire. This reach provides a rare example, within the UK and Europe, of natural LW in an unmanaged setting. The study reach is set in mixed-deciduous woodland adjacent to a butterfly meadow designated as a Site of Special Scientific Interest, and the channel and riparian zone have remained unmodified for over 60 years. The study reach was 500 m long with average channel width of 6 m, mean LW key piece length 6.3 m and grain size D_{50} = 3.9 mm. The riparian zone is characterised by deciduous woodland extending approximately 30-100 m on either side of the river channel.

The NM site was located on the Highland Water, which flows through the New Forest National Park in Hampshire. The site has experienced minimal management of in-channel LW over the past 60 years although, until recently, some large LW accumulations have been removed for flood mitigation. Catchment land cover is a combination of mixed-deciduous forest and heathland and, while the majority of the riparian zone is forested, there is heavy understory grazing by free-roaming and privately-owned pigs, deer, and horses. This river has been the subject of a number of studies of LW in lowland river systems (Gregory et al., 1994; Gurnell et al., 2002; Gurnell et al., 2005; Millington and Sear, 2007; Osei et al., 2015). The study reach was 700 m long with average channel width of 3 m, mean LW key piece length 8.8 m and grain size D_{50} = 14.8 mm. The riparian zone is characterised by deciduous woodland extending a minimum of 80 - 100 m either side of the channel.

The RM site is located on the River Bure which drains a predominantly agricultural catchment in Norfolk. The study reach is located within the National Trust's Blickling Hall estate and has a history of mill development resulting in channel realignment, LW removal, and widening to increase conveyance and holding capacity. In 2008 and 2010, a restoration scheme based on the reintroduction of LW jams was undertaken in response to excess surficial fine sediment (predominantly silt and clays) in the over-widened channels. Riparian trees were felled into the river using a chainsaw and where possible were left to self-anchor, although in a few cases the trees were fixed to the bed using wooden stakes in order to prevent downstream mobility (see River Restoration Centre, 2013 for full details of the approach). The study reach was 400 m long with average channel width of 9 m, mean LW key piece length 11.9 m and grain size D_{50} = 1.9 mm. The riparian zone is characterised by deciduous woodland that extends 40 – 60 m either side of the channel.

The RH site is located on the River Blackwater, a small river draining a predominantly urban catchment in Hampshire/Berkshire. The reach has a history of gravel extraction works and channel diversion associated with construction of the A31 motorway in the 1980s, and as a result, much of this section has been historically straightened and deepened. In 2007, the Environment Agency implemented a LW restoration in response to fine sediment concerns (predominantly silts and clays) using single tree trunks fixed in position and depth in the water column with metal stakes (Martyn, Pers. Comm). The study reach was 400 m long with average channel width of 8 m, mean LW key piece length 5.9 m and grain size D_{50} = 7.7 mm. The riparian zone includes deciduous trees either as isolated trees or small groups.

2.2 Wood jam structural survey

All wood jams were surveyed within each study reach, ranging from 5 jams in the RH site to 10-13 at the other sites. A structural wood survey (Table 1) was conducted on these jams based on key survey metrics outlined in Wohl et al. (2010) and previous research on LW (Gurnell, Pers. Comm). The metrics used in this study are summarized in Table 1, but included: reach-scale jam density, jam volume, the number of structurally integral key wood pieces and their dimensions, the decay status of the wood, submergence and orientation of the jam, and the number of mesohabitats. An additional characteristic, the jam interstitial complexity, was computed as the percentage of the jam volume that comprises wood interstices accessible to water (see Table 1). In addition, each jam was assigned a ‘jam class’ after the categories identified by Gregory et al. (1985): “partial jams” which only partially span the channel; “complete jams” which span the channel but do not cause a pronounced change in water level; and “active jams” which completely span the channel and are sufficiently impermeable to induce pronounced upstream/downstream differences in water level under base-flow conditions (Figure 1). Touching wood pieces were considered to be part of the same functional jam unit.

2.3 Jam hydraulics and sediment properties

In and around each jam, distinct flow types and patches of flow concentration/convergence were identified visually on the basis of surface flow conditions (e.g. smooth flow, rippled flow, unbroken standing waves, broken standing waves; Kemp et al., 2000; Newson et al., 1998). At each jam, a survey of water depth and flow conditions was conducted across the range of surface flow types, within and surrounding each jam; flow velocity was captured in three dimensions for a 30s sampling period using a three-dimensional FlowTracker Handheld-ADVM (Sontek, San Diego, California, USA). The exact number of depth and velocity sampling locations varied by jam and river according to variation in depth and surface flow types, and ranged between 4-12 sampling locations per jam (mean = 8). At each sampling location, velocity measurements were captured at 60% of the flow depth from water surface (‘mid-depth’) and 80% of the flow depth from the water surface (‘near-bed’). Measurements of surficial fine sediment depth (all sediments finer than gravel with grain sizes < 2 mm, but predominantly silts and clays at our study locations) were also captured at each water depth and flow measurement location by inserting a 1 m long, 5 mm wide metal pin into the bed using consistent force until increased resistance due to underlying substrate (gravel/cobbles) was encountered (Lisle and Hilton, 1992). Flow velocity, water depth, and fine sediment depth measurements were taken at cross-sections ~ 5 – 10 m upstream and downstream of each measured jam to examine the range of flow and sediment properties outside the direct impact of the jams. The exact number of non-jam cross sections sampled ranged between 6 and 12 across the sites, according to differences in jam spacing, extent of jam influence, and availability of non-jam influenced sections.

Four main patch types were identified across the different jams: upstream; jam-created concentrated flow; within-jam; and downstream sediment plume. Within each patch type, the top 5-cm of sediment, which included coarse and fine fractions, were collected using a 47-mm diameter

Perspex corer. Due to the low jam orientation angle and close spacing of jams at the RM site (River Bure), the upstream and jam-created concentrated flow patches could not be distinguished so three locations (*i.e.,* concentrated flow, within-jam, and downstream sediment plume) were sampled. Sediment samples were transported in cold storage, stored at -20°C in the laboratory, and analysed within 30 days. After thawing, all samples were dried at 100˚C overnight and sieved to separate the fraction finer than gravel (< 2 mm). A sub-sample of the fine fraction was analysed to estimate organic content through loss on ignition at 550°C for 4 h. A second sub-sample, with no organic matter removed, was analysed using an LS100 Beckman Coulter Counter (Beckman Coulter, Inc., High Wycombe, United Kingdom) to determine the particle size distribution of the fine fraction. Particle size distribution $\geq$ 2 mm and total fine sediment size categories were combined and analysed using Gradistat v. 8.0 software for grain size analysis in order to determine D_{50} and the proportions of gravel (> 2 mm), sand (2 mm - 63 μm), silt (63 - 4 μm), and clay (<2 μm) in each sample by weight (Blott and Pye, 2001).

2.4 Statistical analysis

A Principal Components Analysis (PCA) was conducted for all jam structural variables across the four studied rivers to explore the key gradients in the data, with all variables scaled and centred to allow for comparison of variables with different ranges and variances. The PCA was conducted using the *prcomp* function in R (R Core Team 2019, Vienna, Austria). Univariate differences in wood and mesohabitat variables were analysed using Kruskal-Wallis tests in R due to heteroscedasticity in variances, and post-hoc tests were performed using pairwise Dunn's-test with Bonferonni-adjusted P values for multiple comparisons in the R package *PMCMR* (Pohlert, 2014). Multivariate differences in structural attributes between reaches and jam classes were analysed using

PerMANOVAs with the function *adonis* and Bray-Curtis distances with 9999 permutations in the package *vegan* in R (Oksanen *et al.*, 2013). PerMANOVA, frequently used in assessments of biological community compositions, is a permutational version of a Multiple ANOVA that allows for multiple factor comparison across multiple dependant variables, and with permutation testing to avoid issues resulting from requirements to meet the assumptions of normality and heteroscedasticity.

Multiple linear regression with stepwise model selection was used to explore statistically significant relationships between the structural attributes of wood jams for flow concentration and bed sediment organic content and bed sediment size (D_{50}) within flow concentration patches around jams. All models also used river identity/management type as a grouping variable to control for background catchment conditions and allow examination of the effects only related to structural variables. Multiple regression was conducted in R using *lm* and stepwise pruning procedures comprising both forward and backward searches using the Bayesian Information Criterion (BIC) and the *step* function. BIC was used, rather than P-values (see discussion by Burnham and Anderson et al., 2014), due to the improved performance for model comparison and selection and improved fit for potential future observations (Aho et al. 2014; Brewer et al., 2016). All variables were centred and scaled using the *preProcess* function from the *caret* package (Kuhn et al. 2008) prior to modelling to facilitate comparison among coefficients for variables of different raw scales and variances (e.g. Jam Volume vs Max Piece Diameter). Partial jams were considered the default contrast for jam class within the regression model.

3. RESULTS

3.1 Structural characteristics

Jam density$_{\text{Reach}}$ greatly varied across the four rivers (Table 2; Figure 2) with the highest values at the NL site (1098 m^3 ha^{-1}) and the lowest values in the most heavily managed RH site (43 m^3 ha^{-1}). Average volume for each individual jam was also greatest at NL (16.20 m^3), and lowest at RH (1.65 m^3), while the NM and RM were intermediate between the two (2.76 and 3.93 m^3 respectively). Jams spanned 80% of the channel on average for the naturally-formed jams (NL and NM sites), but under 50% at RM and under 40% at RH (Table 2). Across all sites, jams were typically supported by two structurally-important pieces, except for the RH jams which were primarily formed of a single log stripped of branches (Table 2). While the median diameter of the key wood pieces in each jam were relatively similar across the sites (range 0.4 – 0.7 m), the maximum wood diameter in each jam was greatest in the natural jams at NL (1.29 ± 0.25 m) and NM (1.13 ± 0.22 m; Table 2).

These characteristics largely reflect the frequency of occurrence of jam classes (i.e. partial, complete, and active) which varied among the sites. All three jam types were present in both natural jam sites (NL and NM) while in the restored LW sites (RM, RH) partial jams accounted for all wood accumulations (Figure 2). When present, active jams accounted for a disproportionate amount of the total jam volume present in the channel relative to their frequency. For example, active jams at the NL site accounted for 30% of all jams present but >80% of the total jam volume, and at the NM site, active jams accounted for ~20% of all jams but 65% of total jam volume (Figure 2).

Wood decay prevented the identification of wood species for most jams (~60%) but, where identifiable, jams predominantly comprised alder (*Alnus glutinosa* (L.)). Average wood decay class again reflected the management gradient, with greatest levels of decay noted for the natural jams at NL and NM, intermediate levels of decay at RM, and little noticeable decay at RH (Table 2).

Results from the PCA are presented in Figure 3, showing the position of the reaches and the jam types along the two derived gradients (PCs). The first four PCs had eigenvalues greater than 1, but PCs 1 and 2 cumulatively accounted for 43% of the variability in the data and showed clearer physical meaning, so analysis focused on these first two PCs. Variable loadings indicated that PC1 represents a gradient of channel obstruction, structural complexity, and potential for flow deflection as represented by jam volume, percentage of the channel spanned, and interstitial complexity, and largely captures increasing structural complexity from partial to complete to active jams (Figure 3B). PC2 represents a gradient of wood decay and submergence, and mainly represents variation found within partial jams (Figure 3B). Jam properties were most structurally diverse at NL and homogeneous at RH (Figure 3A). There is considerable overlap in PC scores between the two natural wood sites NL and NM, which span the range of values on PC1. At RM, variability primarily occurred along PC2, while at RH, there was limited variability in PC1 and PC2, as the deflector style jams of RH mostly occupied a distinct area of higher submergence, low decay, and large median wood piece size. Overall, multivariate structural metrics were significantly different in the deflector style jams at RH compared to the other three sites (Figure 3A; Pairwise PERMANOVA; df = 1, all Pr(>F) < 0.05). The differences observed across rivers were largely driven by the varying occurrence of the jam structural types (Figure 3B) since jam classes, regardless of site, occupied broadly different positions on the biplot. Thus, increasing PC1 scores were associated with increasing jam complexity (partial < complete < active jams), and PC2 scores were largely associated with structural variations within partial jams. Overall, the active jams, regardless of site, were significantly different from both partial and complete jams in terms of their structural properties (Pairwise PERMANOVA; df = 1, all Pr(>F) < 0.05).

3.2 Jam hydraulics and sediment properties

Overall, baseflow water depths within the jams (median and maximum) were more variable among the natural jams at the NL and NM sites relative to the restored jams at RM and RH sites (Figure 4 A/B). The relationship between water depths within the jam relative to the water depths in the surrounding channel did, however, vary inconsistently by site: maximum depths within the jam were greater than the surrounding channel at NM and RH sites, shallower than surrounding channel areas at the NL site, and indistinct from surrounding areas for the RM site. Overall, differences between jam-associated water depths and non-jam water depths were greater in the NL and NM sites compared to the RM and RH sites The largest increases in flow velocities were in the NL site, and median increases were much smaller in the remaining sites. In addition, NL and NM contained the largest variability (range) and highest maximum and upper quartile values for flow concentration among jams. These trends were observed for both the streamwise velocity flows at mid-depths (60% from water surface) and for vertical velocities in the near-bed region (80% of depth from water surface; Figures 4C/D).

Fine sediment conditions were highly variable across all sites in both jam-associated areas and in channel areas without jams. Areas of minimal surficial fine sediments existed in jam-associated areas at NL compared to channel areas without jams (Figure 5A), as well as overall lower average accumulation depths (Figure 5B), although this pattern was not consistent across sites. All sites contained jam-associated surficial fine sediment deposits in excess of 0.5 m, with accumulations greater than 1 m recorded at NL, NM, and RM sites (Figure 5C). At the natural wood sites, maximum fine sediment depths were generally greater within the jams than in other surrounding channel areas, while at the restored wood sites, within-jam fine sediment depths were not distinct in relation to the surrounding channel areas (Figure 5C). The variability in the fine sediment depths in- and around the jams (Figure 5D) was greatest at the NL site, and this variability declined along the gradient of increasing management.

Bed sediment characteristics sampled in different parts of the jam (within the wood itself, in the concentrated flow patch, and upstream and downstream of the wood) showed variable responses at each site (Figure 6). Jam sediment sorting by mesohabitat location was not always clear, although concentrated-flow zones generally had larger bed sediment particle size. D_{50} in downstream areas was comparable to adjacent concentrated flow patches for the NL and NM sites, due to plunge-pools in active jams causing scouring flows, while downstream locations in the RM and RH sites had generally lower D_{50} since they functioned as slow-flow depositional areas. Organic content was predictably higher within the wood relative to the other jam areas for NL, NM and RM sites. Organic matter was lower in concentrated flow patches relative to other nearby mesohabitat locations for NL, NM and RM sites, but organic matter was higher in concentrated flow patches around the simple jams in the RH site (Figure 6D).

3.3 Relationships between jam structural properties and mesohabitat characteristics

Multiple regression using stepwise model selection relating structural attributes to flow variables had relatively low explanatory power but were both significant (Into-bed flows: $R^2 = 0.36$, $P < 0.01$; mid-depth flows; $R^2 = 0.30$, $P < 0.05$; Figure 7). Jam volume had the largest effect in both models, with increased jam volume associated with increased flow concentration for the mid-channel and into-bed. Perpendicular jam orientations against the centreline of flow were associated with reductions for into-bed flow changes (Figure 7). Jam interstitial complexity, maximum piece diameter, and wood decay were also retained by the stepwise model selection according to the BIC, although these terms were not significant at $p < 0.05$.

Sediment models (Figure 8) were both significant, with low explanatory power for D_{50} ($R^2 = 0.43$, $p < 0.01$) but improved for organic content ($R^2 = 0.60$, $p < 0.001$). Active and complete jams were significantly associated with lower organic content compared to partial jams, and increased jam volume was associated with reduced sediment D_{50} within concentrated flows. Interestingly, while increased jam interstitial complexity was related to increased sediment D_{50}, it also was associated with increased sediment organic content. While active and complete jams contained lower organic content on average, greater jam interstitial complexity, when controlling for other factors, resulted in greater organic content and greater sediment D_{50}. Jam orientation and flow deflection away from centreline, median piece size, and percentage of the channel spanned by the jam were retained by the BIC selection for one or both of the models, but were not significant at $P< 0.05$ (Figure 8).

4. DISCUSSION

This paper examined variability in the structural characteristics of LW jams and associated physical habitat for natural and restored jams at four sites in different management settings. The most structurally complex jam types (‘active’ and ‘complete’ jams) only occurred within the natural jam sites, while all restored wood jams were classed as ‘partial’ jams with a comparatively simpler structure. The simplest flow-deflector style jams, consisting of a single key piece with branches removed, were found at the most heavily managed site (RH) located in a suburban setting, and these jams were structurally distinct from the jams occurring in other settings. This style of jam is representative of lowland river restoration projects which tend to preferentially favour simpler deflector-style wood structures over more complex jams (Cashman et al., 2018), often as a result of flood risk and wood mobility concerns (Gippel et al., 1996; Erskine and Webb, 2003). In contrast, the restored partial jams at the less managed RM site were more structurally complex, reflecting a more ambitious restoration design that favoured self-anchoring, incorporated several key pieces (River Restoration Centre, 2013), and generated greater jam volumes. The structural complexity of the jams resulted in increased jam interstitial complexity and sediment trapping capacity.

Whilst simple LW structures can still promote physical habitat heterogeneity in rivers and provide important elements of stability, particularly for fine sediment dominated rivers (see Pilotto et al., 2016), our results suggest that greater wood jam complexity led to more pronounced effects on key habitat variables (e.g. D_{50}, organic matter, flow velocity, into-bed flows) and jam-associated habitat heterogeneity (e.g. sediment sorting and variability, water depth and hydraulic variability) compared to the simpler restored jams. The more complex jams generated a more heterogeneous physical environment, enhancing variability in water depths by creating plunge-pools (RH site), which can function as drought refugia (Kalogianni et al. 2020), and in the NL site, trapping substantial amounts of sediment upstream of active jams and lowering water depths. In addition, jams with greater structural complexity created more pronounced areas of flow concentration adjacent to the wood, enhanced sediment variability and sorting, and reduced the amount of fine sediment and organic matter within the river bed, lessening the detrimental impacts of colmation (Wharton et al., 2017). Although complex jam structures can cause flow concentration and scour in some locations, the physical complexity of the jam structure itself traps additional coarse particulate organic matter, provides cover and refugia from predators (McMahon and Hartman, 1989), and supplies jam interstitial habitat space. As a result, these effects alter the spatial organisation and hydromorphological characteristics of mesohabitats throughout a reach.

Our findings indicate a greater ‘ecosystem engineering’ effect of more complex LW jams compared to the simpler structures that have been widely installed in restoration projects to date (Cashman et al., 2018). This is particularly important, as the creation of habitat diversity at various scales, particularly by increasing habitat composition and habitat variability, has been shown to influence ecological recovery post-restoration (Verdonschot et al., 2016). Components of the aquatic ecosystem respond differently to various scales of hydromorphic complexity and thus restoration of habitat complexity must occur at the scale relevant to the intended ecological target (Hasselquist et al. 2018). We suggest that the structural complexity of LW jams should be given particular attention in the design of restoration schemes. The more ambitious restoration approach taken on the River Bure (RM site) illustrates that more complex restored partial jams can have a more pronounced ecosystem engineering effect than the simpler flow-deflector style jams. The jams at the RM site have been shown to influence sediment transfer and storage at the patch and reach scales (Parker et al., 2017), promote channel and habitat recovery from over-widening (Harvey et al., 2018), and drive changes across river food webs, increasing the abundance and diversity of invertebrates and increasing brown trout (*Salmo trutta*) populations (Thompson et al., 2018). Understanding variations in structural properties of LW and associated hydromorphological effects in natural and restored settings is also crucial to improved modelling of the hydraulic and hydrological impacts of LW, for example within the context of Natural Flood Management (Addy and Wilkinson, 2019).

Identifying geomorphologically similar sites in which to study LW is inherently challenging as a result of long-term impacts on natural jams through channel maintenance and riparian zone management, as well as the sometimes *ad hoc* nature of river restoration projects. We selected lowland reaches in unconfined valley settings with similar catchment size and channel dimensions. Within this, the four sites had differing levels of instream and riparian LW management, from natural wood with no floodplain management to heavily managed riparian zone and restored simple LW jams. The designs of restored sites were cross-referenced against the range of wood-restoration schemes in the National River Restoration Inventory (Cashman et al 2019). All sites had low gradient channels, but there was some variation among the reaches, with higher slopes and smaller channel widths at the natural LW sites relative to the restored LW sites. While we recognise that this may influence the ecosystem engineering effect of the LW jams, jam structural properties did not align with the channel gradient. For instance, the most structurally complex reach (NL) does not have the highest gradient (NM), and RM and RH sites had similar gradients but distinct jam structural properties and physical habitat. Indeed, jam complexity at the RM site showed greater similarity with the natural wood sites than the RH site despite exhibiting a lower channel gradient than the natural sites. In addition, our regression models demonstrated that jam attributes and structural complexity remained significant predictors of in-channel flows and sediment characteristics even after controlling for unaccounted-for site-specific variations, such as gradient.

An additional factor not considered explicitly here is jam age. The restored jams were between 1 and 4 years old at the time of survey and showed minimal decay, while the natural jam ages were unknown but likely to be considerably older as indicated by more advanced states of decay. This will also influence the processes the structures have been exposed to through time, but we observed greater ecosystem engineering effects at the most recently installed but more complex restored jams (RM site) compared to the older but simpler structures at the RH site. It is therefore possible that restored jam complexity and associated engineering effects may increase through time, but for simple jams this would likely require the integration of further LW pieces, sediments, and aquatic plants into the jam. For the simpler structures at the RH site, this integration is unlikely given the stripped trunk and absence of protrusions to snag additional wood pieces. Furthermore, adequate supply of LW from upstream may be less likely in settings with more managed riparian zones and hence the original jam design may be more important.

Our results show that structurally complex wood jams have the potential to provide a wider range of habitat functions at various scales and may offer greater potential for river recovery from degradation through a more pronounced ‘ecosystem engineering’ effect on the physical environment. Structural differences between restored and natural LW jams may therefore help to explain some previous research that has identified limited effects of large wood on the hydraulic environment (Matheson et al., 2017) or minimal ecological responses (Verdonschot et al., 2016). In particular, this study further explores the relationship between design decisions in restoration and habitat composition and diversity, which have been shown to be critical in understanding ecological responses (Verdonschot et al., 2016). Of course, hydromorphology and habitat heterogeneity may not always be the limiting factors of ecological system health even before habitat enhancement (Bernhardt and Palmer 2011), and viable source communities for re-colonization after restoration remain an important factor in recovery (Sunderman et al. 2011). However, when LW is used in restoration projects, our findings suggest that trade-offs between the structural attributes of the jams and other goals or constraints should be carefully considered. Figure 9 provides a conceptual diagram illustrating a continuum of increasing jam structural complexity which is associated with increasing effects on the physical environment, for example flow hydraulics and sediment characteristics, and its heterogeneity. It is important to note that in a number of contexts, the installation of simpler wood jams may be the most appropriate restoration design, particularly in heavily impacted or managed areas where flood risk, erosion, and wood mobility concerns may be significant. The use of simpler jam types, however, may mean that the ecosystem engineering effects on the wider river environment may be minimal, and in these cases the role of wood may relate primarily to the individual wood piece providing a direct substrate for attachment, shelter, or a food source particularly when the availability of other hard substrates is limited (Cashman et al., 2016; Pilotto et al., 2016).

For more complex jam structures, with multiple wood pieces but not necessarily spanning the channel width, wider ecosystem engineering effects may be more evident. This may include the trapping and retention of organic-rich fine sediment in sheltered lee areas combined with flow deflection and scour in areas of flow concentration around or in between jams, reducing sediment colmation (Wood and Armitage, 1999; Wharton et al., 2017). The retention of organic-rich fine sediment by complex large wood jams may provide a rich growth substrate for emergent macrophytes, and these may become a prominent feature in locations where the channel is not fully shaded by riparian woodland. Macrophytes can then further act as ecosystem engineers by creating areas of deposition within their stands and helping to stabilize the bed (Cotton et al., 2006; Parker et al., 2017; Wharton et al., 2006) and maintaining hydrodynamic conditions that support high biodiversity (Cornacchia et al., 2020). These processes may encourage wider ecosystem engineering effects including channel recovery from historic overwidening promoted by the combination of restored LW and emergent macrophytes (Harvey et al., 2018). These jams may be anchored to the bank by the root boles of key pieces which may generate some stability, but redistribution of smaller pieces may introduce some spatio-temporal variability. The most complex jam structures have a more pronounced effect on the sediment and hydraulic environment, generating distinct habitat patches of flow concentration and scour and fine sediment accumulation. Where floodplain woodland remains intact, new LW recruitment through tree fall may contribute to a more dynamic system with higher levels of LW structural complexity, mobility, and redistribution. To test this model further, research is required to both extend the number of sites along the management intensity continuum and explore potential for changes in structural properties and ecosystem engineering effects through time at restored LW sites.

Conclusion

This paper identifies structural differences in naturally occurring and restored LW jams that influence the 'ecosystem engineering' role of LW in modifying flow hydraulics and sediment characteristics. These findings are relevant to river management as restoration approaches seek to balance conservation and habitat improvement goals with the management of flood and erosion risk, as well as other concerns such as water quality. Our results suggest that restoration design should seek to maximise structural complexity of restored wood jams where possible within the context of other goals and appropriate levels of risk. This will help to increase the wider geomorphic and ecosystem effects of the wood jams, working with natural processes to restore channel morphology and physical habitat heterogeneity. Furthermore, our results show that naturally occurring jams were the most complex in structure, supporting more holistic catchment management strategies for LW that combine preservation of intact riparian zones and natural jams and the restoration of riparian zones as well as instream reintroduction of LW. We describe a continuum of increasing jam structural complexity that is associated with increasing diversity of the physical river environment. With further testing, this model can be used to evaluate other river sites with different instream and riparian management intensities and to help inform restoration design considerations and best practice.

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6. TABLES

Table 1: Jam survey variables used in this study

Variable	Unit	Definition
Jam $\text{Density}_{\text{Reach}}$	$\text{meters}^3\ \text{hectare}^{-1}$	Sum of all jam volumes (see below) across the reach, standardized by wetted channel area.
Jam Volume	meters^3	Volume of the smallest rectangular box into which a multi-piece wood jam would fit, multiplied by the percentage of the box containing wood, also called interstitial complexity (See Jam Interstitial Complexity below). Single piece jams volumes were estimated directly through measuring length and diameter. See Gurnell et al. (2000) for more detail.
% Channel Spanned	Percent	Percent of the channel width spanned by an individual jam.
No of Key Pieces	Count	Number of wood pieces integral to jam stability.
Median/Max Piece Diameter	Meters	Median and max of diameter and length measurements of all key pieces collected at each jam.
Jam Class	Categorical (Partial/ Complete/ Active)	Partial: Jam only spans part of the channel. Complete: Jam completely spans channel and is sufficiently permeable to not cause a step in the water surface under baseflow. Active: Jam completely spans channel and is sufficiently impermeable to cause a step in the water surface under baseflow. See Gregory et al. (1985) and Figure 1 for more detail.
Decay Status	Ordinal (1-5)	Visual decay status from 1-5 in order of increasing decay, for example: 1: intact bark, small twigs present, original colour; 3: Trace bark, absent small twigs, some surface abrasion, beginning to darken; 5: Absent bark, absent twigs, vesicular texture with many openings, dark colour. See Schuett-Hames et al. (1999) for more detail.
Jam Interstitial Complexity	Percent	Visual estimate of the percentage of the jam box used to estimate jam volume that contained wood and provided wood-water interfaces. Single jams with non-branching trunks were given 0% interstitial complexity.
Submergence	Percent	Percent of the total jam volume submerged at baseflow.
Jam Orientation	Degree	Central axis of jam orientation compared to centre-line of river flow.
Flow Deflection	Degree	Direction of jam-deflected flow from central line of channel.
Root Wad	Binary	Presence of root wad.
Sum Jam-associated mesohabitats	Count	Number of substrate types, flow types, channel features and vegetation types surrounding jam. Unique types adapted from Raven et al., 1996.

Table 2: Table of selected jam structural variables for each of the four sites. Values are mean ± 1 standard error derived from all jams in a site. Letters represent significant differences by group according to a Kruskal-Wallace post-hoc pairwise Dunn's test for multiple comparisons with Bonferroni corrections.

Management Type	# of Jams (n)	Jam Density$_{Reach}$ (m^3 ha^{-1})	Jam Volume (m^3)	Channel Spanned (%)	# of Key Pieces	Max Key Piece Diameter (m)	Median Key Piece Diameter (m)	Decay Status (1-5)	Jam Interstitial Complexity (%)	Submerged (%)	Orientation (°)	Flow Deflection (°)	Root Wad Present (%)	Sum Meso-habitats (n)
NL	10	1098	16.20 ± 6.50	84 ± 10^{b}	2.2 ± 0.4	1.26 ± 0.22	0.63 ± 0.15	2.9 ± 0.3^{b}	60 ± 11^{b}	37 ± 3^{ab}	54 ± 12^{ab}	25 ± 10	10	5.1 ± 0.9
NM	12	246	2.76 ± 1.71	88 ± 5^{bc}	1.8 ± 0.3	1.13 ± 0.22	0.45 ± 0.08	2.8 ± 0.2^{b}	52 ± 9^{ab}	30 ± 4^{a}	68 ± 8^{b}	33 ± 8	16	4.8 ± 0.4
RM	13	227	3.93 ± 0.63	46 ± 6^{a}	2.3 ± 0.3	0.62 ± 0.10	0.40 ± 0.08	2.1 ± 0.3^{ab}	48 ± 6^{b}	39 ± 6^{ab}	28 ± 8^{a}	21 ± 4	0	3.5 ± 0.6
RH	5	43	1.65 ± 0.78	38 ± 7^{ab}	1.2 ± 0.2	0.73 ± 0.12	0.70 ± 0.14	1.4 ± 0.3^{ab}	4 ± 2^{a}	81 ± 11^{b}	78 ± 6^{ab}	9 ± 9	0	3.8 ± 0.7

7. FIGURES

Figure 1: Examples of partial jams (A), complete jams (B), and active jams (C) from the River Dene, Warwickshire, England. Partial jams are single pieces of large wood (LW) that do not obstruct the whole channel. Complete jams span the channel width, but do not obstruct the flow of water to an extent that will cause damming and a step in the water level. Active jams span the entire channel width and have a damming effect on flow, causing a noticeable step in the water level. Pictures are looking downriver from centre of the channel (A,C) and from the bank (B). (Photos A&B taken by M. Cashman 15 July, 2011; Photo C taken by G. Harvey 28 Feb, 2012)

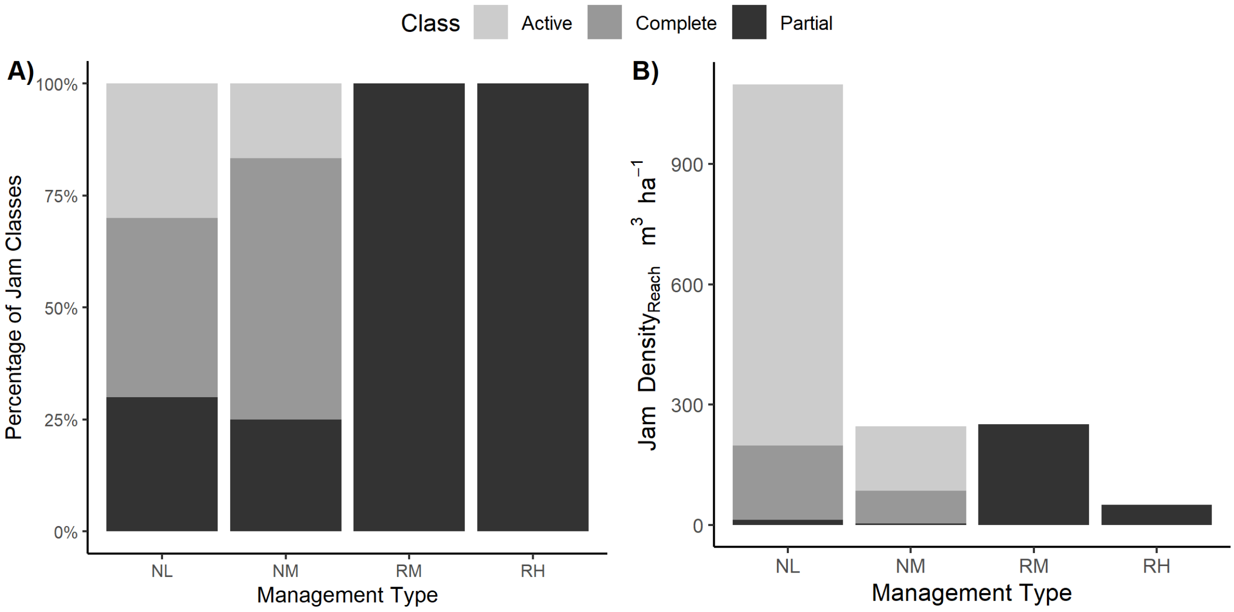

Figure 2: The variation in jam classes within the four study rivers (A) and jam density within the reach, standardized per hectare of river area (B), with bar plots shaded by jam class type

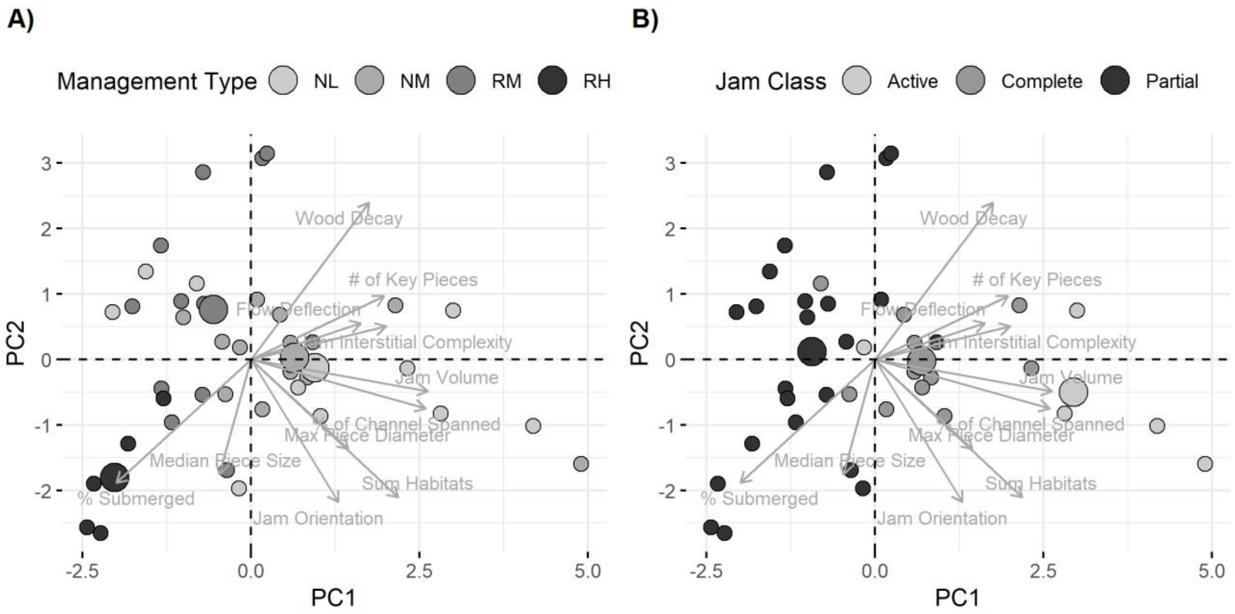

Figure 3: A PCA of all jam structural variables in the study, with symbols coloured by Management Type (A; left) and jam class type (B; right). Group means are indicated by larger circles, while smaller circles indicate individual jams. Arrows and variable names indicate eigenvectors of contributing variables, with larger arrows associated with larger contribution of that variable along that vector in a positive relationship.

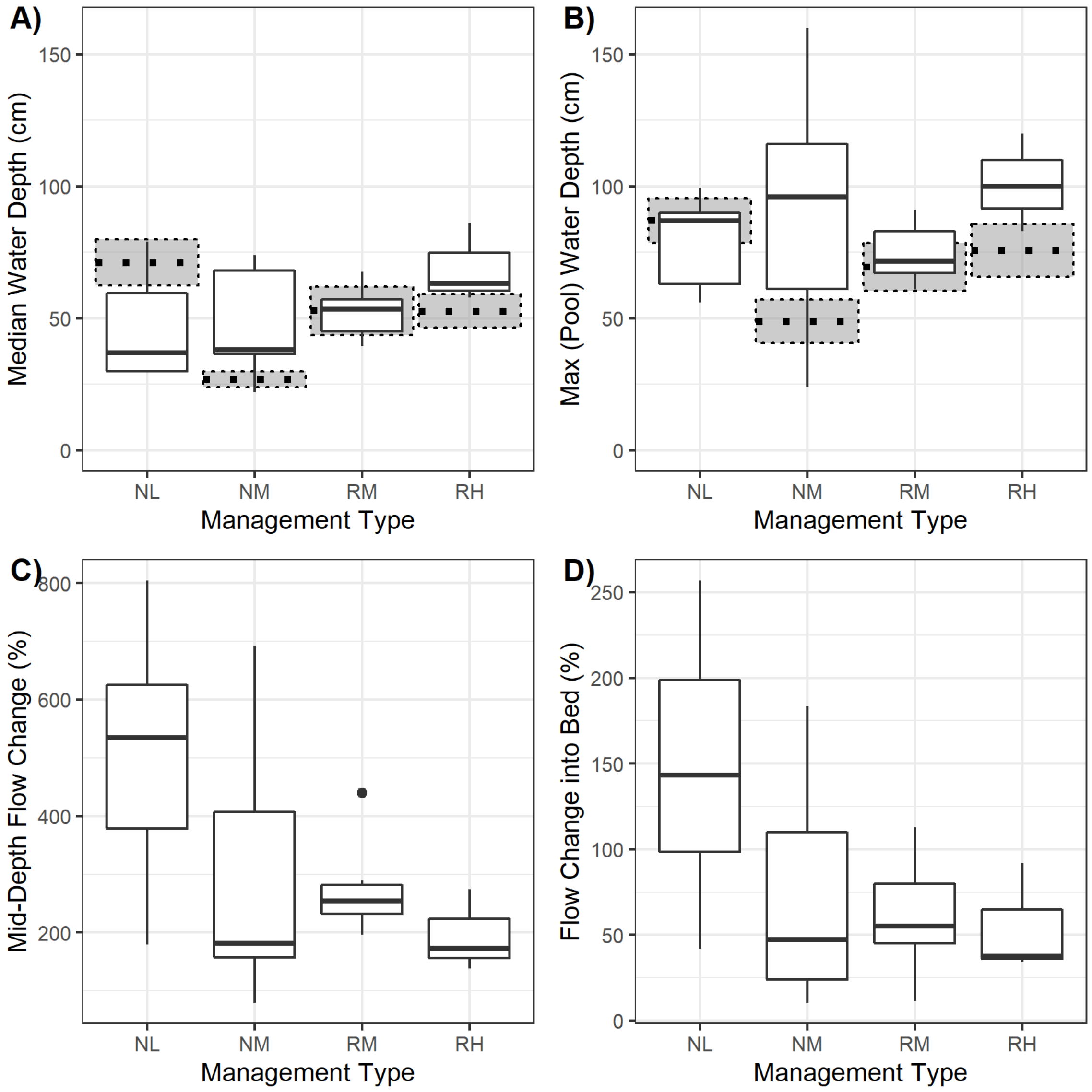

Figure 4: A) Median jam water depth ± 1 standard error in each of the study rivers. B) Maximum jam water depth ± 1 standard error in each of the study rivers. C) Percent change in flow from average non-jam affected river flows to the concentrated flows around the jam for both the mid-depth and D) near-bed flows directed into the bed (Z-axis) (right). Grey boxes indicate the non-jam affected river conditions based on measurements taken at cross-sections outside of the jam-affected areas (average +/- 1 standard error), NL = 12, NM = 9, RM = 6, RH = 8. LW jam sample sizes are NL = 10, NM = 12, RM = 13, RH = 5.

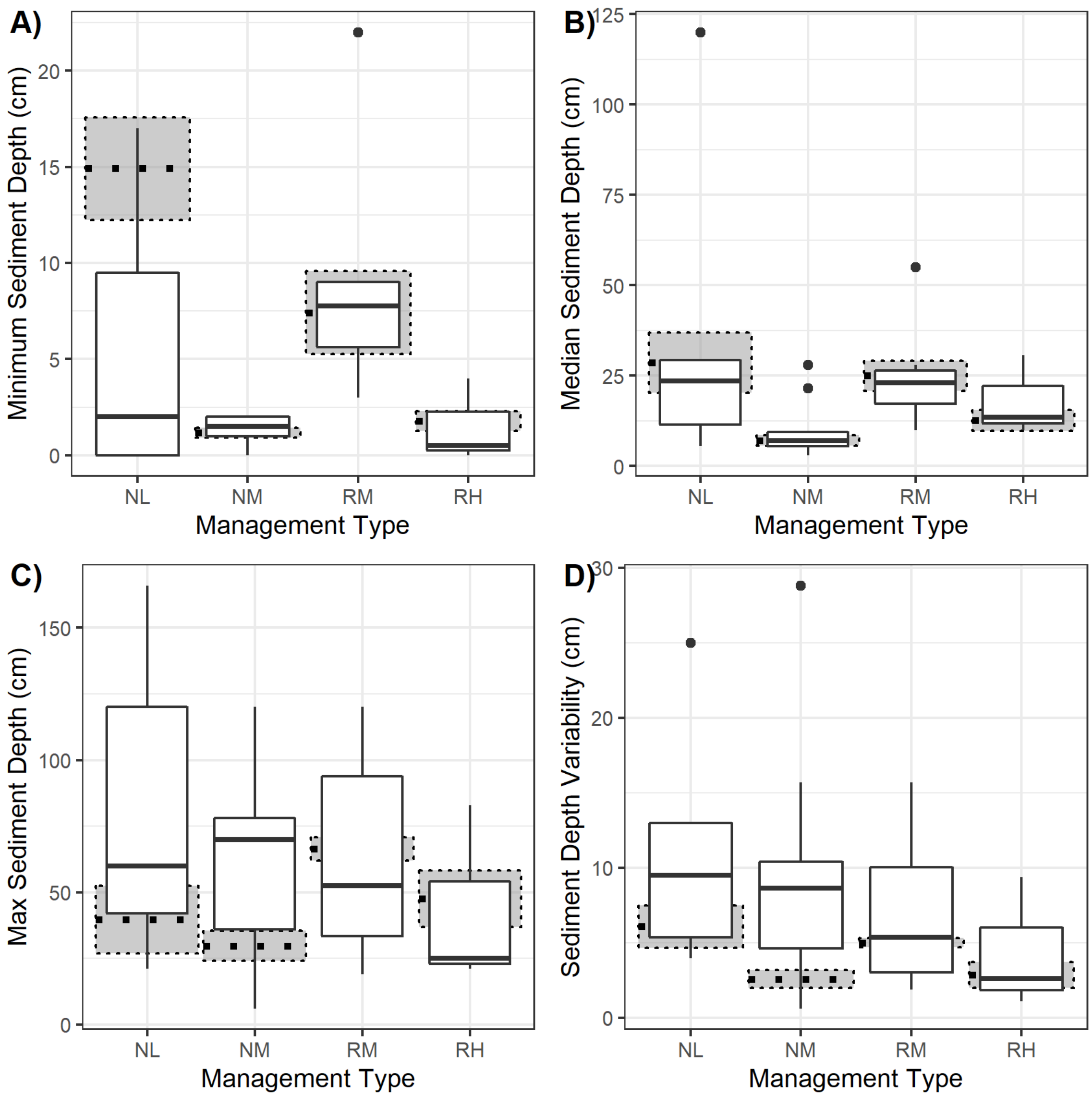

Figure 5: Minimum (A), Median (B), Maximum (C), and sediment depth variability (1 SE; D) in each of the study rivers). Grey boxes indicate the non-jam affected river conditions based on measurements taken at cross-sections outside of the jam-affected areas (average +/- 1 standard error), NL = 12, NM = 9, RM = 6, RH = 8. LW jam sample sizes are NL = 10, NM = 12, RM = 13, RH = 5.

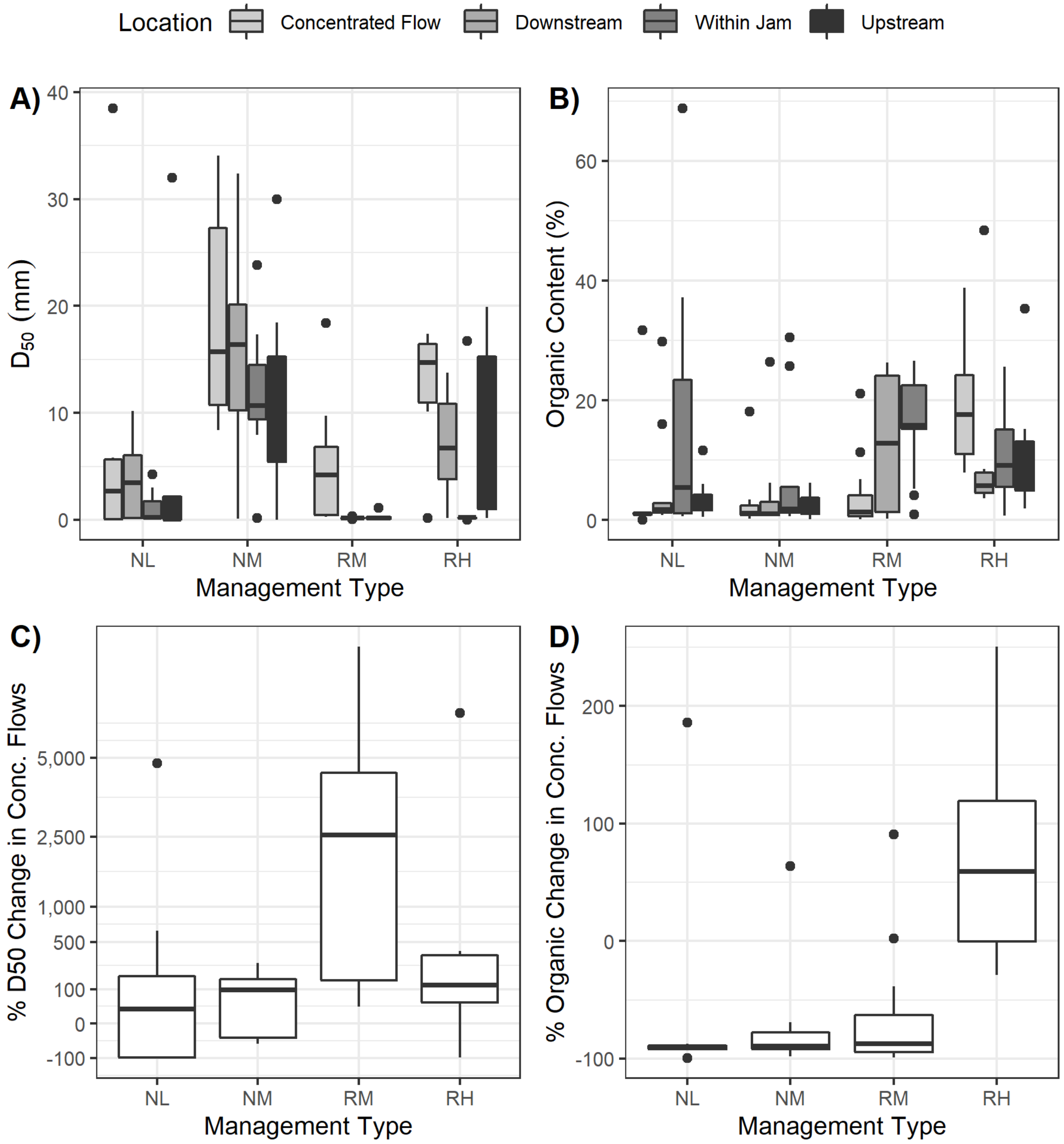

Figure 6: D_{50} (A,C), as well as organic content (B, D) by location around the jam across the sampled within-jam locations (A,B) and shown by pairwise percent differences for concentrated flows versus other habitats in each jam sample (C,D). LW jam sample sizes are NL = 10, NM = 12, RM = 13, RH = 5.

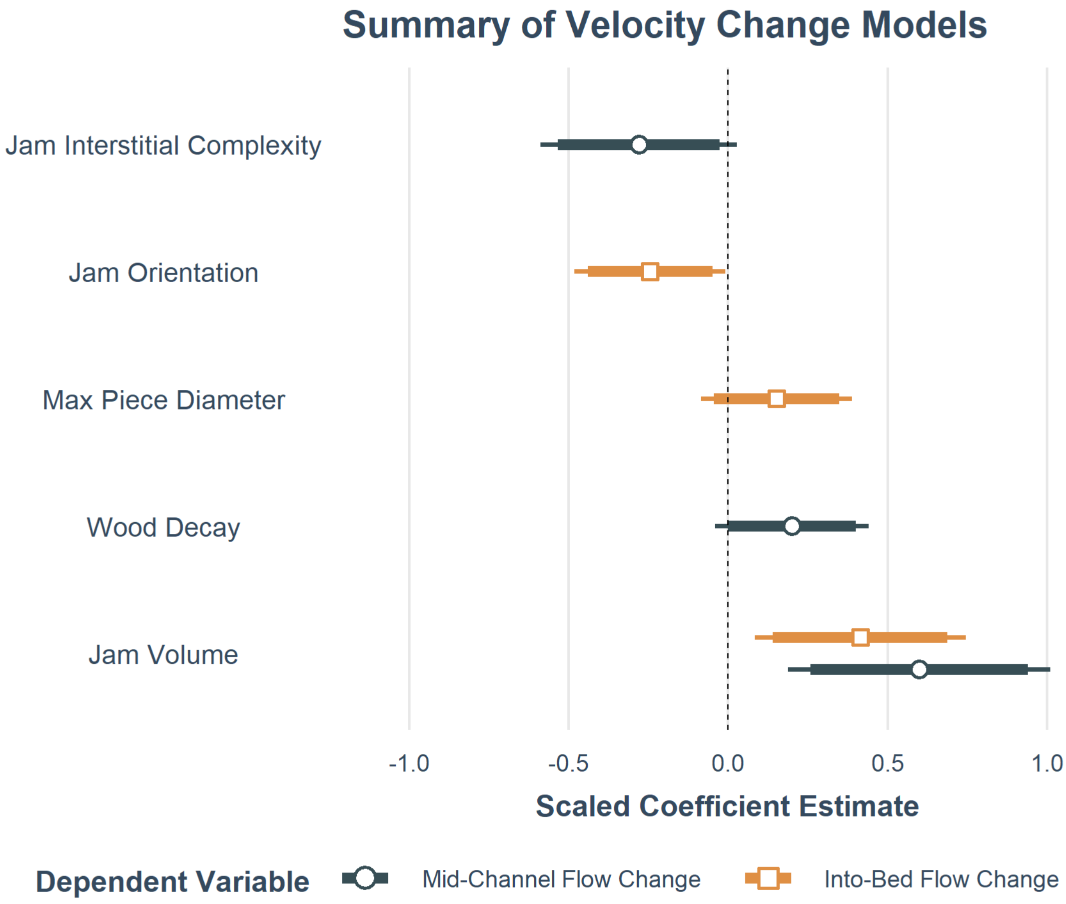

Figure 7: Regression coefficient summary plots for velocity change models: the mid-channel flow change model (black/circle) and into-bed flow change (yellow/square). The position of the symbol on the x axis indicates coefficient estimate, and the bars represent confidence intervals at P = 0.1 (thick inner bars) and P = 0.05 (thin outer bars). Bars that do not overlap 0 indicate significance at that confidence level. Variables on the Y axis are those retained by the stepwise model selection for one or both flow models.

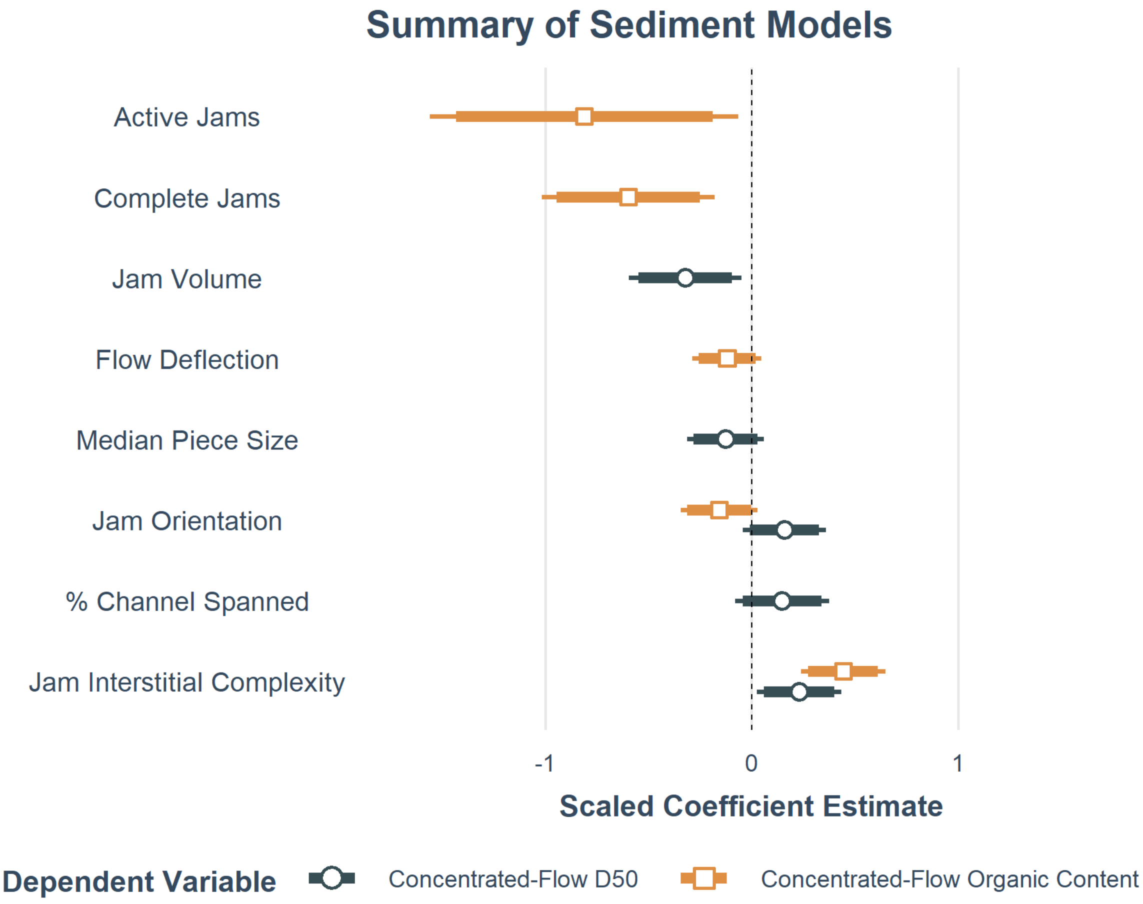

Figure 8: Regression coefficient summary plots for sediment models for both sediment D_{50} in concentrated-flows (black/circle) and sediment organic content in concentrated-flows (yellow/square). The position of the symbol on the x axis indicates coefficient estimate, and the bars represent confidence intervals at P = 0.1 (thick inner bars) and P = 0.05 (thin outer bars). Bars that do not overlap 0 indicate significance at that confidence level. Variables on the Y axis are those retained by the stepwise model selection for one or both flow change models. Management type was also identified as a significant variable in the final regression model for organic content at P < 0.01 but was omitted from the figure for clarity.

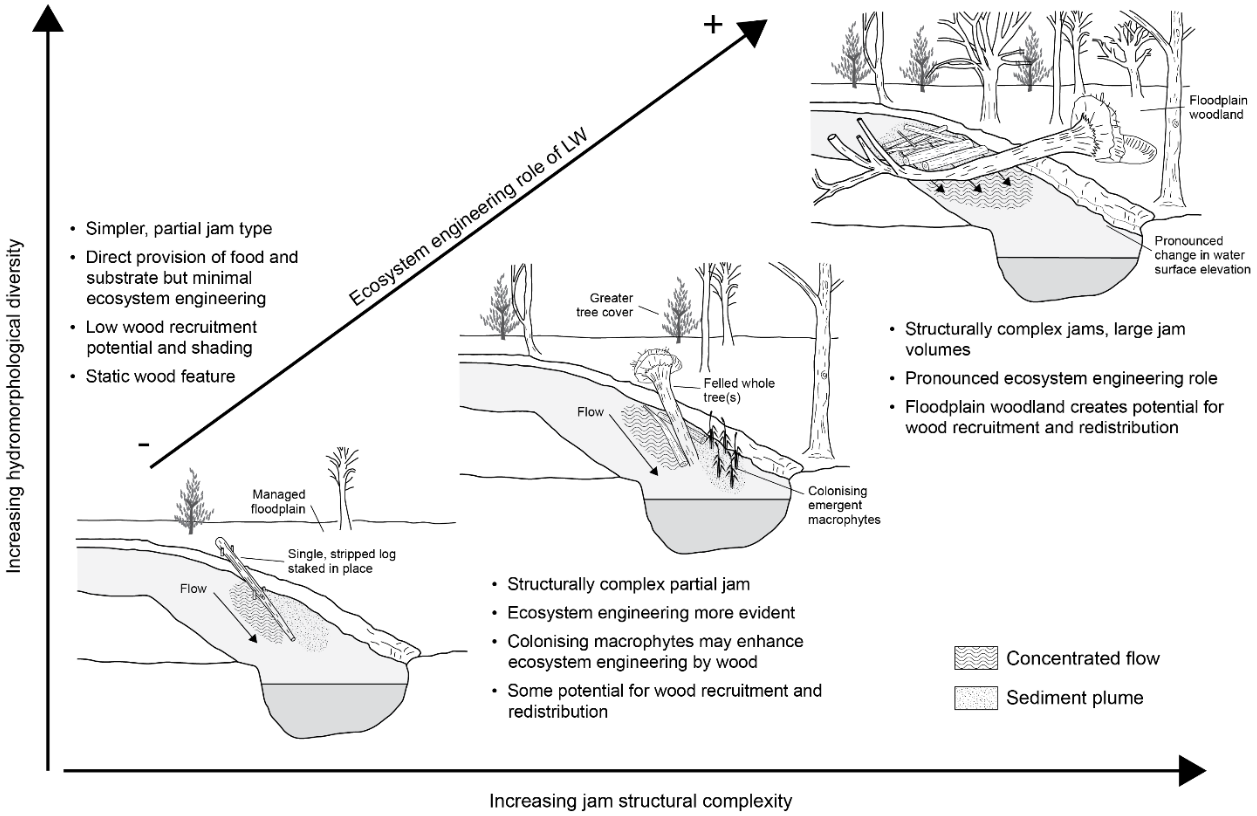

Figure 9: Conceptual model showing how increasing jam structural complexity results in increasing hydromorphological diversity. There is potential for a temporal dimension as well as a spatial dimension to this model if sufficient wood supply and/or aquatic vegetation development enables restored jams to increase in structural complexity through time.

8. APPENDIX

Supplementary Table 1: Field location study sites, UK Grid Reference, and other site information of the four rivers selected for examination of LW jams. Channel width measurements are means ± 1 standard error. Geology data obtained from UK Geological Survey online viewer (1:50,000; www.bgs.ac.uk/discoveringGeology/geologyOfBritain/viewer.html).Q50 was based on annual flow data from the previous 10 years, obtained from the National Flow Archive, and flow exceedance was determined based on flow data from the sampling date (averaged over entire sampling week). Catchment and wood management characteristics were determined by visual surveys and personal communication with land managers.

	Location	Channel Width (m)	Geology	Q50 (m^3 s^{-1})	Flow Exceedance at Sampling	Catchment Land-Use	Wood Management	Channel gradient (m/m)
Dene (NL)	Warwickshire, UK GR: SP 3068 5059	5.9 ± 0.2	Mudstone/ Limestone	0.264	31.67%	Rural (arable/ pasture)	Natural wood. Unmanaged, minimal grazing	0.0021
Highland Water (NH)	New Forest NP, UK GR: SU 2706 0731	3.0 ± 0.4	Bracklesham and Barton: sand, silt, and clay	0.425	32.44%	Rural (forest)	Natural wood. Minimal management, heavy grazing	0.0027
Bure (RL)	Norfolk, UK GR: TG 1613 2995	9.2 ± 0.7	Wroxham Crag: sand and gravel	1.01	81.71%	Rural (arable)	Restored wood. Felled riparian trees, minimal fixing	0.0017
Blackwater (RH)	Surrey, UK GR: SU 8629 5861	8.6 ± 0.4/	Bracklesham and Barton: sand, silt, and clay	0.407	89.09%	Urban (mixed-use)	Restored wood. Imported wood, clean trunks, uniform fixing	0.0009