Reconstructing riverine paleo-flow regimes using subfossil insects (Coleoptera and Trichoptera): the application of the LIFE methodology to paleochannel sediments.

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Abstract

Sub-fossil insect remains have the potential to characterise changing environmental conditions in both lentic and lotic water systems however, relatively few studies have been undertaken in riverine environments. This paper uses sub-fossil caddisfly larvae (Trichoptera) and aquatic beetles (Coleoptera) to reconstruct river flow conditions for a large paleochannel (from multiple monoliths) using the Lotic invertebrate Index for Flow Evaluation (LIFE). Examination of the larval Trichoptera and Coleoptera remains indicated a marked change in the community and flow environment, as suggested by paleoLIFE scores within the profile of 3 of the monoliths examined. At the base of the channel the community was characterised by taxa indicative of high-energy lotic habitats with predominantly mineral substrates (e.g. Trichoptera: *Hydropsyche contubernalis* and *Brachycentrus subnubilis,* Coleoptera: *Elmis aenea* and *Esolus parallelepipedus*). Within three of the monoliths there was a change in community composition to one indicative of a low-energy backwater/ lentic environment with abundant submerged and emergent vegetation (e.g. Trichoptera: *Phryganea bipunctata* and *Limnephilus flavicornis,* Coleoptera: *Colymbetes fuscus* and *Hydrobius fuscipes*). Detrended Correspondence Analysis (DCA) and loss of mass on ignition (LOI) indicated the presence of a strong environmental gradient within the data, associated with river flow. The utilisation of two aquatic insect orders provides clear evidence of temporal changes within the instream community and when combined with knowledge of ecological and habitat associations, allows differences between the two groups to be interpreted more clearly.

Keywords: Aquatic beetles, Caddisfly larvae, Lotic invertebrate Index for Flow Evaluation, Paleohydrology, River flow variability.

Introduction

Floodplains and the sedimentary archive they contain constitute important repositories for paleolimnological, environmental and archaeological research (Brown 1996; Howard 2005). The sedimentary sequences present include those in abandoned channels and cut off water bodies (Brown et al 2001; Lewin et al 2005). The potential of such sequences to record changing environmental conditions has been largely ignored within paleolimnology in comparison to lentic sequences, due to the comparatively short time periods they cover. However, such sequences can provide valuable evidence of changes in river flow and wider floodplain characteristics over the time-period during which the channel evolved (Greenwood and Smith 2005). The subfossil remains of riverine flora and fauna (e.g. pollen, plant macrofossils and insect sclerites) are frequently preserved within the lateral and vertical accretion deposits of the river and floodplain, and they provide valuable evidence of the prevailing environmental conditions under which they were laid down (Greenwood et al. 2006).

The use of adult Coleoptera as paleoecological indicators is well established in both terrestrial and aquatic environments (Coope, 1986; Smith et al. 2005; Elias 1994). Most Coleoptera have well known ecological and habitat associations and many are stenothermic, making them ideal for establishing the range of environmental conditions present within a paleochannel during its evolution (Buckland and Buckland 2006). In the field of paleohydrology, aquatic beetle faunas were first used in an archaeological context, as indicators of riverbed hydraulic conditions, for example, within the Bronze-Age River Avon (Osborne 1988). Subsequently, Coleoptera fauna have been associated with river discharge within low-gradient alluvial systems (Smith and Howard 2004), and they have been used to investigate floodplain connectivity and disturbance events (e.g. floods) within riverine sedimentary sequences (Davis et al. 2007).

Trichoptera larvae have also been recognised as potential indicators of environmental and paleoflow conditions (Williams 1988), but in marked contrast to Coleoptera, only limited use has been made of them until recently (Solem and Birks 2002; Greenwood et al. 2003; 2006). Trichoptera larvae are found in a wide variety of aquatic environments from fast flowing open channels to lentic bodies and ephemeral pools (Bacher and Waringer 1996; Wiberg-Larsen et al. 2000). In order to interpret the past environmental history, it is necessary to employ an analogue approach through direct comparison with the modern fauna, an approach that is generally considered valid for the latter half of the Holocene (Lowe and Walker 1997).

The Lotic invertebrate Index for Flow Evaluation (LIFE methodology) was devised to assess the contemporary aquatic macroinvertebrate communities associated with river-flow variability (Extence et al. 1999; Monk et al. 2006). The LIFE methodology assigns a score to each macroinvertebrate taxon that is related to their known flow-velocity preferences (Flow groups I to VI, fast flow to semi permanent aquatic habitats). The LIFE score is calculated from the sum of the individual scores and a measure of their overall abundance at a site. The LIFE methodology and index provides a succinct analytical tool for relating the flow requirements of contemporary macroinvertebrate communities to the historic populations represented by the preserved subfossil remains within paleochannel sediments.

The application of the LIFE methodology in a paleoenvironmental context was tested using the remains of subfossil Trichoptera larvae from 17 paleochannels located in the middle reaches of the River Trent floodplain U.K.

(Greenwood et al. 2006). The current paper provides the first test of the PaleoLIFE methodology outlined by Greenwood et al. (2006), and extends its development by (i) employing a multiproxy approach through the use of both Trichoptera and Coleoptera sub-fossil remains; and (ii) testing the cross-channel (within channel) replicability of the approach, via the use of multiple monoliths from a single large paleochannel.

Study site

The River Trent has been the focus for several sedimentological (Brown et al. 1994, Brown et al. 2001, Howard 2005) archaeological (Salisbury 1992, Howard et al. 2007) and paleoecological (Greenwood et al. 2003, Smith et al. 2005) investigations. The River Trent has a catchment area of 7486 km^2, a length of approximately 149 km and is one of the UK's most active rivers.

The study site was located at Aston-on-Trent, Derbyshire, (52°51'10" N: 1°21'40" W), in the middle reaches of the River Trent where a number of palaeochannels have been studied historically (Greenwood et al. 2006). The paleochannel used in the current study was a large freshly exposed channel (80-90 m wide) not utilised in previous research. The channel was exposed during commercial gravel extraction and its large size provided an ideal opportunity to examine both spatial (cross-channel) and temporal variations in sub-fossil lotic faunal remains.

Methodology

Field sampling, Laboratory processing and taxonomic identification

Four monolith profiles varying from 0.9 to 1.8 m in depth were collected from the exposed paleochannel. Two monoliths were collected to characterise the margin (A and D) and two to characterise the centre (B and C). A total of 49 samples of approximately 5 kg were extracted at 10-cm intervals from top to bottom of each monolith. Field sampling and processing followed Greenwood et al. (2003). Approximately 1 kg of each sample (0.5-1.0 l) was processed for aquatic insect remains following standard paraffin floatation methodology of Coope (1986) as modified by Greenwood et al. (2003), and with the introduction of a 90-µm-mesh sieve to retain smaller insect sclerites. A small fraction of the unprocessed sediment from each of the 49 samples was retained for determination of organic matter content by loss of mass on ignition (LOI) (Dean 1974).

Identification of fauna was achieved by comparison with standard taxonomic texts (Trichoptera: Hickin 1967; Hiley 1973; 1976; Wallace 1980; Edington and Hildrew 1995; Greenwood et al. 2003; Wallace et al. 2003; Coleoptera: Hansen 1987; Holmen 1987; Nilsson and Holmen 1995; Harde 1998; Friday 1988). Taxonomy followed Barnard (1985) for Trichoptera and Duff (2008) for Coleoptera.

Dating control and statistical analysis

Seven calibrated radiocarbon dates for the paleochannel sediments were obtained from plant macrofossil material (6 from seeds of *Schoenoplectus* and *Rubus* spp. with 1 from a wood sample, see Table 1). These established the basal dates for each monolith, together with three additional dates for the longest monolith (B) where samples were collected either side of the gravel horizon and the channel surface. Dating indicated the basal section to be Neolithic in age (5470-4960 cal

BP: Table 1). The upper levels, which were situated approximately 30 cm below the present land surface, were c. 1500 cal. BP.

For each sample the LIFE score was calculated following the original methodology of Extence et al. (1999) as modified by Greenwood et al. (2006), for application in paleolimnological research. The original Trichoptera and aquatic Coleoptera LIFE scores were used throughout, with the exception of some difficult taxa that can only be identified to a generic or species group, based on subfossil material (e.g. *Hygrotus* spp. (Coleoptera: Dytiscidae) and *Limnephilus rhombicus/marmoratus* (Trichoptera: Limnephilidae)). In some instances this resulted in taxa that could be designated to two different LIFE flow groups (Table 1). When this occurred, taxa were assigned a hybrid score (IV/V) so the potential effect of taxonomic resolution could also be examined. To examine the utility of using more than one taxonomic group, the combined paleoLIFE score was calculated, as well as the scores for the individual orders (Trichoptera and Coleoptera). The difference in the paleoLIFE score derived from the combined and individual orders was then directly compared.

Detrended Correspondence Analysis within the program CANOCO 4.5 (ter Braak and Šmilauer 2002) was undertaken to examine/identify any underlying biotic or environmental gradients within the data. All data were transformed ($\log_{10}$+1) prior to analysis to reduce any clustering effects associated with common and/or abundant taxa. Following preliminary analysis, rare taxa that occurred in single samples or as individual specimens were down weighted, due to the overriding effect their presence had on the ordination output.

Results

Stratigraphy

The majority of the samples consisted of organic-rich silty sediment with varying amounts of fine-to-medium grained sand. Notable in the profile of two monoliths was a 10-cm-thick matrix supported gravel horizon (Monolith A – 90-80 cm and Monolith B - 100-90 cm) with clasts up to 3.2 cm in diameter. There was an increase in organic matter across the profile from D to A and from base to top of Monolith A. Stratigraphic correlation of monoliths was achieved with reference to specific horizons (a reed layer, bone material and gravel horizons), differential GPS measurements and the AMS dates established (Fig. 1).

Faunal variation

A total of 44 Trichoptera taxa representing 15 families was found within the four monoliths. Taxa not recorded in Greenwood et al. (2006) are presented in Table 2. Abundance varied across the section from 29 to 63 frontoclypeal fragments l^{-1}. A clear zonation was apparent in three of the monoliths; characterised by the fauna recorded above and below the gravel horizon in monolith A and B (Fig. 1a) and above 60 cm in monolith C. The base of the channel (Zone 1) was dominated by taxa from LIFE flow group II, primarily from the families Hydropsychidae (*Hydropsyche contubernalis, H. pellucidula, Cheumatopsyche lepida*) and Brachycentridae (*Brachycentrus subnubilis*).

Above the gravel horizon (Zone 2), the faunal assemblage in Monolith A, B and C was characterised by the presence of the families Limnephilidae, Polycentropodidae and Phryganeidae from LIFE flow groups IV-VI and an absence of taxa from the families Hydropsychidae, Rhyacophilidae or Lepidostomatidae.

The stratigraphy of monolith D did not display any clear zonation (Fig. 1b) and was dominated by taxa associated with LIFE flow group II throughout the profile (Hydropsychidae and Brachycentridae). The low abundance of taxa from the families Limnephilidae and Polycentropodidae and absence of Phryganeidae also indicates a high-energy environment throughout the profile.

A total of 58 aquatic Coleoptera taxa, representing 6 families, was present in the paleochannel (Table 2). The abundance of individuals varied between 22 and 44 minimum number of individuals (MNI) l^{-1}. Distinct faunal differences between the upper and lower zones in Monoliths A, B and C were recorded. Taxa from the families Elmidae (*Elmis aenea, Limnius volkmari, Esolus parallelepipedus*, *Riolus subviolaceus* and *Normandia nitens*) and Hydraenidae (*Hydraena* spp.) dominated the lower levels (Zone 1), with only three members of the family Dytiscidae from LIFE groups II and III (*Potamonectes depressus elegans*, *Platambus maculatus* and *Stictotarsus duodecimpustulatus*).

The upper levels of Monoliths A - C (Zone 2) were dominated by members of the families Dytiscidae from LIFE flow groups IV and V (e.g. *Colymbetes fuscus*, *Hygrotus quinquelineatus*, *H. versicolor*, *Porhydrus lineatus*, *Agabus* spp. and *Rhantus* spp.) and Hydrophilidae (e.g. *Hydrobius fuscipes*, *Dicyrtocercyon ustulatus* and *Cercyon tristis*). In addition, areas of open water were indicated by the presence of *Gyrinus* sp. The aquatic coleopteran fauna from Monolith D displayed little evidence of a change in faunal composition throughout the profile. Taxa from the family Elmidae were present throughout the sequence (*Oulimnius sp*., *Riolus subviolaceus*, *Esolus parallelepipedus*), although their abundance was significantly reduced at the top of the profile.

LIFE score variability

The paleoLIFE score for individual levels varied across the paleochannel profile from 5.4 to 7.3 with a mean value of 6.5, indicating a range of flow velocity regimes from fast (greater than 1 m s^{-1}) to slow flow velocities (less the 0.2 m s^{-1}) and even lentic conditions. Distinct temporal variability was identified within some sections (Monolith B, Fig. 1a) with marked differences in the paleoLIFE score above and below the gravel horizon (100-90 cm); scores in the lower section ranging between 7.1 - 7.3 and from 5.4 - 5.9 above it. This pattern was similar within three of the monoliths examined (A, B and C) and reflects the observed differences in the stratigraphy and the community composition noted above. In contrast to the other profiles, Monolith D had a consistently higher paleoLIFE score throughout (range 6.5 - 7.3), with all paleoLIFE scores equal or above the average (6.5) for the entire channel (Table 3).

Examination of the paleoLIFE scores from all four monoliths indicates that there were two distinct/dominant flow regimes represented within the paleochannel section: i) a high energy regime, with average paleoLIFE scores between 6.5 - 7.3, mostly represented by fauna from LIFE flow groups I and II, suggesting flow velocities within the range, 0.2 – >1.0 m s^{-1}; and ii) a lower energy regime, with paleoLIFE scores between 5.2 - 6.5, mostly represented by fauna from LIFE flow groups IV - VI, suggesting slowly flowing, still water or even temporary water bodies. The boundary for these changes occurred at the gravel horizon in Monoliths A and B and at 70-60 cm in Monolith C. Monolith D was characterised by high flow (0.2->1.0 m s^{-1}) throughout its evolution.

Examination of the difference in the paleoLIFE score, derived by using the Trichoptera and Coleoptera independently, indicated that the former yielded consistently higher scores than the latter (Table 3). Trichoptera paleoLIFE scores ranged from 5.0-8.0 (mean 6.9) compared to 5.3-7.7 (mean 6.2) for Coleoptera (Table 3). Differences between the two groups were greatest below the gravel horizon (Zone 1) within Monolith A, B and C and throughout Monolith D (mean difference of 0.9) and least above it (Zone 2, mean difference of 0.2) (Table 3).

Detrended Correspondence Analysis

To examine for the presence of any underlying biological or environmental gradients within the data, DCA of the combined Trichoptera and Coleoptera data (115 taxa) was undertaken. The first DCA axis accounted for 21.6% of the variance within the faunal data (Axis 2 - 5.2%; Axis 3 - 4.1% and Axis 4 - 2.6%). Examination of the distribution of the samples from the four monoliths indicated that they were distributed along the first axis, with the exception of Monolith D, which was clustered at the left side of Axis 1 (Fig. 2a). Examination of the individual samples and faunal associations (Fig. 2b and Fig. 2c) demonstrated that the distribution reflected the zonation of samples observed for Monolith A-C and the relatively clustered distribution for Monolith D.

Examination of the species biplot suggested the presence of an environmental gradient within the Trichoptera and Coleoptera data reflecting flow conditions. Trichoptera and Coleoptera data were analysed in combination, but for presentation purposes, they are presented separately in Fig. 2b and Fig. 2c. Trichoptera fauna from LIFE flow groups I and II (*Glossosoma boltoni*, *Psychomyia pusilla* and *Rhyacophila dorsalis* - Fig. 2c) and Coleoptera (*Elmis* *aenea*, *Riolus subviolaceus*, *Limnius volkmari* - Fig. 2b) formed a cluster on the right side of the ordination biplot (Axis 1 - Fig. 2d). In addition, a small number of taxa from LIFE flow groups III-IV were also recorded in this region of the biplot (*Macronychus quadrituberculatus*, *Helichus substriatus*, *Cyrnus trimaculatus*). Fauna from LIFE flow groups V-VI were predominately located on the left of Axis 1 (Fig. 2d), represented by a number of Coleoptera from the families Dytiscidae (*Colymbetes fuscus*, *Agabus bipustulatus* and several species of *Hygrotus*). Also present here were Hydrochidae and Hydrophilidae (*Hydrobius fuscipes*, *Hydrochus crenatus* and *Cercyon tristis*) which are characteristic of lentic or very slow flowing habitats (Fig. 2b). A limited number of Trichoptera taxa from LIFE flow groups IV and V, *Holocentropus picicornis* (Polycentropodidae), *Agrypnia pagetana* (Phryganeidae) *Limnephilus flavicornis* (Limnephilidae) and *Triaenodes bicolor* (Leptoceridae), also plotted in this region (Fig. 2c).

The distribution of samples on axis 2 indicated that samples from Zone 1 and from Monolith D were not widely distributed when compared to samples from Zone 2 (Fig. 2a). (I apologize, I can't succeed at improving the following sentence. It is a run-on sentence that should be separted into 2 clear statements) The distribution of sites on axis 2 almost certainly reflects a difference in the range of habitats represented by the Zone 1 and Zone 2 communities. Zone 1 taxa are distinctive and closely spaced, indicating high energy and high flow velocities. The Zone 2 community is widely spaced, indicating a diversity of lentic habitats,ranging from open water with silt substrate through to dense emergent and/or floating leaved macrophyte communities.

In order to further investigate whether an environmental gradient associated with flow variability exists within the data, the organic carbon values, as determined by loss of weight on ignition (LOI %) were examined in association with the sample scores on the first DCA axis. This indicated the presence of a significant inverse relationship ($r = 0.632$, $p<0.005$).

Discussion

River flow variability is widely acknowledged as a fundamental control on the distribution of macroinvertebrates within riverine environments (Lytle and Poff 2004; Monk et al. 2006). Trichoptera have been used widely in contemporary investigations to characterise instream flow and hydraulic characteristics (Olden et al. 2004; Wiberg-Larsen et al. 2000), and larval remains have been demonstrated to be strong indicators of past flow regimes through the analysis of subfossil material from a variety of paleochannels of differing age (Greenwood et al. 2006). The results of this research provide further evidence of the utility of Trichoptera in the study of river flow variability previously outlined in Greenwood et al (2006), and so discussion herein is centred on the aquatic Coleoptera and comparisons between the two faunal groups. Aquatic Coleoptera have also been used to characterise lotic habitats (Osborne 1988; Ponel et al. 2005). However, with the exception of the family Elmidae and a limited number of taxa from the family Dytiscidae (e.g. *Potamonectes depressus elegans* and *Platambus maculatus*), they are usually associated with slow flowing and lentic conditions (Lemdahl 2000; Smith et al. 2001). Despite this limitation, their value as indicators of riverine landscape evolution and disturbance events associated with flooding has been increasingly acknowledged (Davis et al. 2007; Smith and Howard 2004).

The LIFE methodology was developed to assess changes in the aquatic faunal communities in relation to temporal hydrological variability (Extence et al. 1999). It has been used successfully to evaluate the influence of river flow regime variability on benthic macroinvertebrates at a range of sites in England and Wales spatially and temporally (Monk et al. 2006; Monk et al. 2008) and in association with other macroinvertebrate community metrics (Clewe and Ormerod in press). As part of the methodology, macroinvertebrate taxa have been assigned species and family level scores, with the exception of aquatic Diptera larvae such as Chironomidae and Simuliidae. When combined, this index provides an indication of river flow, or regime, variability over time, anthropogenic impacts such as water abstraction pressures, or natural stresses such as flood and drought (Extence et al., 1999 Monk et al. 2006; 2008).

In its current form the LIFE methodology does not provide a quantitative measure of flow velocity or river discharge. Lentic and lotic taxa from LIFE flow groups I and IV are frequently recorded co-existing in contemporary river channels, some inhabiting areas of bare gravel substratum experiencing flow velocities in excess of 1 m s^{-1} while others inhabit macrophytes stands where flow velocity may be less that 0.05 m s^{-1}. The LIFE methodology was never intended to provide quantitative measure of river flow (velocity or discharge) since the flow groups span wide ranges of flow velocity. The methodology, therefore, should be considered as a tool to provide information on the nature of the flow regime and the range of flow velocities present at particular points in time, especially where flow histories may be punctuated by drought, flood or other instream disturbances. Using the metric in isolation only provides partial information, and there is a fundamental need to understand the ecology of the organisms contributing to the score.

Trichoptera and aquatic Coleoptera have a number of distinct advantages for use in paleohydrological and paleoecological investigations: i) both are species rich compared to other aquatic invertebrate groups and represent almost 60% of the taxa currently assigned LIFE flow groups; ii) subfossil remains of both groups are relatively abundant, durable and can be relatively easily identified to specific or generic level from riverine and lentic sediments; iii) the ecology and habitat associations of both groups have been widely studied; and iv) both groups comprise fauna which inhabit a wide range of lotic and lentic habitats; although Trichoptera are particularly well represented in fast flowing environments and Coleoptera are well represented at low flow and lentic conditions. As a result, the use of both groups is complementary and potentially provides more accurate indication of instream macroinvertebrate community response to changes in the flow regime and aquatic habitat characteristics associated with paleochannel and floodplain evolution, than either order independently.

Examination of the paleoLIFE scores at the Aston-on-Trent site clearly indicated that those derived using Trichoptera were consistently higher (mean value 6.9) than those of the aquatic Coleoptera (mean value 6.2) (Table 3), although the overall range for Coleoptera paleoLIFE scores is lower (2.2) than for Trichoptera (3.0). However, if the individual zones are considered, the paleoLIFE scores within zone 2 display a lower mean difference (0.5) than samples within zone 1 (mean difference of 1.0). The difference between the paleoLIFE scores derived from the two taxonomic groups may reflect life history characteristics, habitat preferences and the distributions of the two aquatic insect groups within riverine ecosystems. The majority of Trichoptera in the UK are benthic, except some free swimming taxa within the family Leptoceridae. In contrast, the majority of Coleoptera, except for Dryopidae and Elmidae, require atmospheric oxygen at regular intervals, and as a result, either swim within the water column to obtain air, or are confined to marginal areas of the channel where they can easily swim or crawl to the surface.

The large paleochannel cross-section at Aston-on–Trent allowed examination of the spatial variability in the flow regime record based on the subfossil Trichoptera and Coleoptera from replicate sections/monoliths. This demonstrated that three of the monoliths provided strikingly similar records of change (A-C) within the time span studied (c. 5000 cal BP – 1500 cal. BP). These three monoliths (A, B and C) indicated a change in faunal community composition, reflecting a higher mean flow velocity to a lower velocity regime as one moves up the profile. The remaining monolith indicated a relatively stable community and that this part of the channel experienced relatively high flow velocities throughout its evolution.

The record of change in river flow regime from Aston-on-Trent can therefore be divided into two distinct faunal zones. The fauna recorded within Zone 1 was dominated by Trichoptera and Coleoptera and was predominantly from LIFE flow group II, e.g., *Hydropsyche contubernalis, Brachycentrus subnubilis, Elmis aenea* and *Esolus parallelepipedus*, representing an average paleoflow velocity of 0.2-1.0 m s^{-1}

The fauna within Zone 2 was dominated by Trichoptera and Coleoptera from LIFE flow groups IV-VI from the families Limnephilidae, Polycentropodidae and Phryganeidae, all of which represent very slowly flowing (less than 0.2 m s^{-1}) to lentic conditions (Wallace et al. 2003). The Coleoptera within Zone 2 were dominated by members of the families Dytiscidae and Hydrophilidae (e.g., *Hydrobius fuscipes* and *Colymbetes fuscus*), both of which are primarily found in stagnant water, drains and ditches, frequently amongst vegetation near the waters edge (Balfour-Browne 1950; Hansen 1987). This is also reinforced by evidence of an abundance of plant macrofossils and high organic carbon (LOI) values.

The zonation of the fauna within the records from Aston-on-Trent suggests little taphonomic mixing had occurred during the process of deposition. In addition, the well-preserved nature of the remains also indicates that little transport of material had occurred since the Trichoptera frontoclypeal apotome in particular, would be subject to degradation under such conditions (Williams 1988). However, a number of the taxa recorded in Zone 1 and within Monolith D, and clearly indicated on the DCA axis 1 (Fig. 2c), are from LIFE flow groups III-V. These include a number of Trichoptera from the family Limnephilidae (*Limnephilus lunatus/incisus, Glyphotaelius pellucidus, Anabolia nervosa* and *Limnephilus flavicornis*), indicating some slower-flowing, well-vegetated, marginal environments (Urbanič et al. 2005; Wallace et al. 2003). In addition, a number of Coleoptera taxa common in muddy and vegetated streams, such as the Hydraenidae (*Hydraena testacea Ochthebius cf. minimus*) and Helophoridae (*Helophorus* spp.: Friday 1988; Hansen 1987; Merritt 2006) were recorded alongside taxa indicative of high energy/flow environments (Fig. 2b). It should therefore be clearly recognised that even within river channels characterised by high energy/flow velocity regimes, marginal habitats and backwaters exist and these would almost certainly provide appropriate conditions for taxa usually associated with lower energy environments. It is notable that although elements representing low energy/flow habitats may appear alongside taxa indicative of higher energy/flows, the converse is not the case. The paleochannel in the current study therefore reflects the evolution of one channel section with a period of active flow and a second representing isolation and eventual terrestrialisation. The temporal pattern reflected in the sequences is characteristic of the spatial pattern recorded on contemporary floodplain water bodies (Castella et al. 1984; Paillex et al. 2007), where active channels, cut-offs and isolated backwaters may all exist in close proximity, and highlights the biological value of diverse floodplain water bodies, and paleochannels in the study of river channel evolution.

Conclusions

The use of two aquatic insect orders (Trichoptera and Coleoptera) and the paleoLIFE methodology provided strong evidence of changing flow regime and habitat characteristics within a large paleochannel deposit of the River Trent. The collection of multiple monoliths from this large channel clearly demonstrates the replicability of the paleoLIFE methodology. Utilisation of two aquatic insect orders clearly provides further information regarding the temporal changes in community composition associated with flow variability. Further research is required to extend the paleoLIFE methodology incorporating other insect groups that are common within riverine sediments, such as Chironomidae (non-biting midges) and Simuliidae (Blackfly) larval remains. However, these aquatic insect families are currently not included at the generic/specific level within the contemporary LIFE methodology and require further consideration. The paleoLIFE methodology/index is a potentially powerful paleolimnological tool providing valuable paleohydrological and ecological information. Its use may enhance traditional paleohydrological and environmental archaeological investigations through a greater awareness of prevailing instream conditions, such as flow, habitat structure and faunal community composition, which may ultimately be related to natural or anthropogenic change to the channel or to the river flow regime.

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Table 1 Calibrated radiocarbon dates (C^{14} - AMS) from the Aston-on-Trent paleochannel (LU = Loughborough University, BA = Birmingham Archaeology)

Sample location	**Date (BP) Uncal.**	**Date (Cal BP)**	**Calibration**	**Source**	**Material**	**Code**
Base of Monolith B	4470 +/-40	5300-4960	IntCal 04	LU	Schoenoplectus seeds	Beta-216487
Base of Monolith C	4240 +/-50	4870-4640	IntCal 04	LU	Schoenoplectus /Rubus seeds	Beta-225751
Base of Monolith D	4220 +/-40	4850-4640	IntCal 04	LU	Schoenoplectus /Rubus seeds	Beta-225752
Base of Monolith A	3240 +/-40	3560-3380	IntCal 04	LU	Schoenoplectus /Rubus seeds	Beta-225750
B110-100 (below gravel horizon)	3530 +/-40	3900-3700	IntCal 04	LU	Schoenoplectus seeds	Beta-216488
B90-80 (above gravel horizon)	2520 +/-40	2750-2460	IntCal 04	LU	Schoenoplectus seeds	Beta-216489
Ground surface level (close to B)	1555 +/-35	1530-1350	OxCal 3.8	BA	Wood (Salix)	SUERC-4834

Table 2 Coleoptera taxa and Trichoptera (not previously included in Greenwood et al 2006) recorded in this study indicating LIFE group affiliation and channel Zone position.

Family	Taxon	Main channel Zone	LIFE Group[a]
COLEOPTERA			
Gyrinidae	*Gyrinus* spp.	2	IV/V[b]
Haliplidae	*Haliplus* spp.	2	IV[b]
Dytiscidae	*Agabus bipustulatus* (L.)	2	IV
	Ilybius sp.	2	IV/V[b]
	Platambus maculatus (L.)	1	II
	Colymbetes fuscus (L.)	2	V
	Rhantus exsoletus (Forst.)	2	V
	Acilius sp.	Eu	V
	Hydaticus transversalis (Pont.)	2	V
	Graptodytes pictus (F.)	2	IV
	Graptodytes sp.	2	IV/V[b]
	Hydroporus palustris (L.)	2	IV
	Hydroporus sp.	2	IV[b]
	Potamonectes depressus elegans (F.)	Eu	IV
	Porhydrus lineatus (F.)	2	V
	Stictotarsus duodecimpustulatus (F.)	2	II
	Hygrotus decoratus (Gyll.)	2	V
	Hygrotus inequalis (F.)	2	IV
	Hygrotus quinquelineatus (Zett.)	2	V
	Hygrotus versicolor (Sch.)	2	IV
	Hygrotus spp.	2	IV/V[b]
Hydrochidae	*Hydrochus brevis*	2	V
	Hydrochus crenatus Germ.	2	V
	Hydrochus elongatus (Schall.)	2	V
	Hydrochus spp.	Eu	V
Helophoridae	*Helophorus* spp.	2	IV/V[b]
Hydrophilidae	*Cymbiodyta marginellus* (F.)	Eu	V
	Enochrus sp.	2	IV/V[b]
	Hydrobius fuscipes (L.)	2	V
	Hydrophilus piceus (L.)	2	V
	Laccobius spp.	2	IV/V[b]
	Coelostoma orbiculare (F.)	2	VI
	Cercyon bifenestratus Küster	2	VI
	Cercyon marinus Thoms.	2	VI
	Cercyon melanocephalus (L.)	2	VI
	(Cercyon pygmaeus (Ill.))	1	N/A
	Cercyon terminatus (Marsham)	2	VI
	Cercyon cf. tristis (Ill.)	2	VI
	Dicyrtocercyon ustulatus (Preys.)	2	VI
	Cercyon spp.	Eu	VI
	(Megasternum concinnum (Marhsam))	2	N/A
	(Cryptopleurum minutum (F.))	2	N/A
	(Sphaeridium scarabaeoides (L.))	2	N/A
Hydraenidae	*Hydraena gracilis* Germ.	Eu	II
	Hydraena nigrita Germ.	1	II
	Hydraena palustris Er.	2	V
	Hydraena riparia Kug.	Eu	IV
	Hydraena testacea Curtis.	1	IV
	Hydraena spp.	Eu	IV[b]
	Limnebius spp.	2	IV[b]
	Ochthebius cf. minimus (F.)	2	V
Dryopidae	*Helichus substriatus* Muller	1	IV
	Dryops sp. Olivier	Eu	N/A
Elmidae	*Elmis aenea* (Muller)	1	II
	Esolus parallelepipedus (Muller)	1	II
	Limnius volkmari (Panz.)	1	II
	Macronychus quadrituberculatus Muller	1	III
	Normandia nitens (Muller)	1	II

	Oulimnius spp.	Eu	IV
	Riolus cupreus (Muller)	1	II
	Riolus subviolaceus (Muller)	1	II
	Stenelmis canaliculata (Gyll)	1	III
TRICHOPTERA			
Polycentropodidae	*Cyrnus trimaculatus* (Curtis)	1	IV
	Holocentropus dubius (Rambur)	2	V
Lepidostomatidae	*Lasiocephala basalis* (Kol)	1	II
Limnephilidae	*Chaetopteryx villosa* (F.)	1	II
	Glyphotaelius pellucidus (Retzius)	1	IV
	Limnephilus fusicornis (Rambur)	1	II
	L. cf. lunatus/incisus Curtis	2	IV
	L. stigma Curtis	Eu	V
	L. vittatus type (F.)	2	V
Beraeidae	*Beraea cf pullata* (Curtis)	1	III
Molannidae	*Molanna angustata* Curtis	1	IV
Lepidostomatidae	*Oecetis lacustris* (Pictet)	1	IV
Hydroptilidae	*Ithytrichia* sp. Eaton	1	II

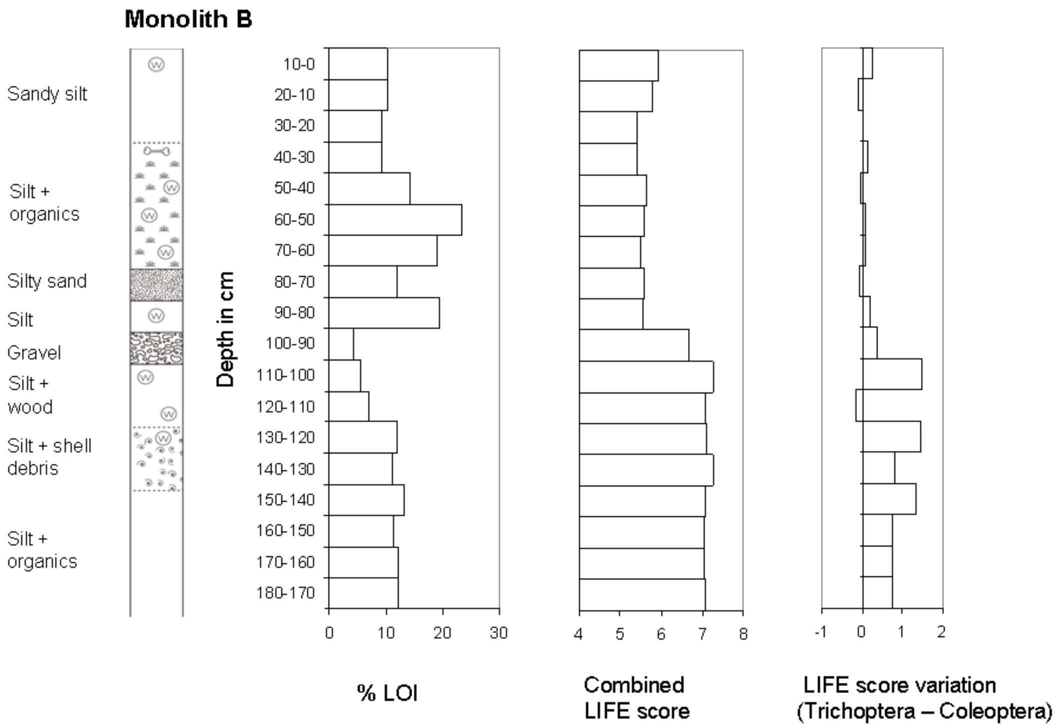
Footnotes: Order and nomenclature follows Barnard (1985), Duff (2008).
Notes: [a] LIFE flow groups are as follows Group I – Taxa primarily associated with rapid flows (typically > 1 m s^{-1}); Group II - Taxa primarily associated with moderate to fast flows (typically 0.2-1.0 m s^{-1}); Group III – Taxa typically associated with slow or sluggish flows (typically <0.2 m s^{-1}); Group IV – Taxa primarily associated with slow flowing and standing waters; Group V – Taxa primarily associated with standing waters and Group VI – Taxa associated with drying or drought impacted sites.
[b] Taxa with variable flow requirements.
N/A Non aquatic taxa not included in the LIFE classification.
Eu - Taxa found equally in both faunal Zones.
Taxon names within brackets () are riparian/semi-aquatic and have not been assigned LIFE flow groups.

Table 3 Summary of mean LIFE scores based on Trichoptera, Coleoptera, combined community and difference between the two orders (Trichoptera minus Coleoptera) for individual monoliths (A-D), for zones based on stratigraphy and community composition (note Zone 2 type community absent from Monolith D and so all samples included with Zone 1), and for all monoliths

LIFE score	**A**	**B**	**C**	**D**	**Z1 (A-D)**	**Z2 (A-C)**	**All Monoliths**
Trichoptera							
Mean	6.3	6.6	7.0	7.6	7.6	6.4	6.9
Range	3.0	2.6	1.9	1.3	1.0	1.8	3.0
Max	8.0	8.0	7.9	8.0	8.0	6.8	8.0
Min	5.0	5.4	6.0	6.7	7.0	5.0	5.0
Coleoptera							
Mean	5.9	6.1	6.2	6.4	6.7	5.9	6.2
Range	2.2	1.8	1.1	0.4	1.1	0.8	2.2
Max	7.5	7.2	6.9	6.6	7.5	6.1	7.5
Min	5.3	5.4	5.8	6.2	6.4	5.3	5.3
Combined							
Mean	6.1	6.3	6.6	7.0	7.2	6.1	6.5
Range	2.5	1.9	1.3	0.8	1.0	1.2	2.5
Max	7.7	7.3	7.2	7.3	7.7	6.4	7.7
Min	5.2	5.4	5.9	6.5	6.7	5.2	5.2
Difference (Tr – Co)	0.4	0.5	0.2	1.2	0.9	0.2	0.7

Figure 1 Stratigraphy of monoliths, loss on ignition (LOI), combined Trichoptera and Coleoptera LIFE scores and the difference in the LIFE score based on the individual orders (Trichoptera minus Coleoptera score) for (a) Monolith B and (b) Monolith D

a)



b)

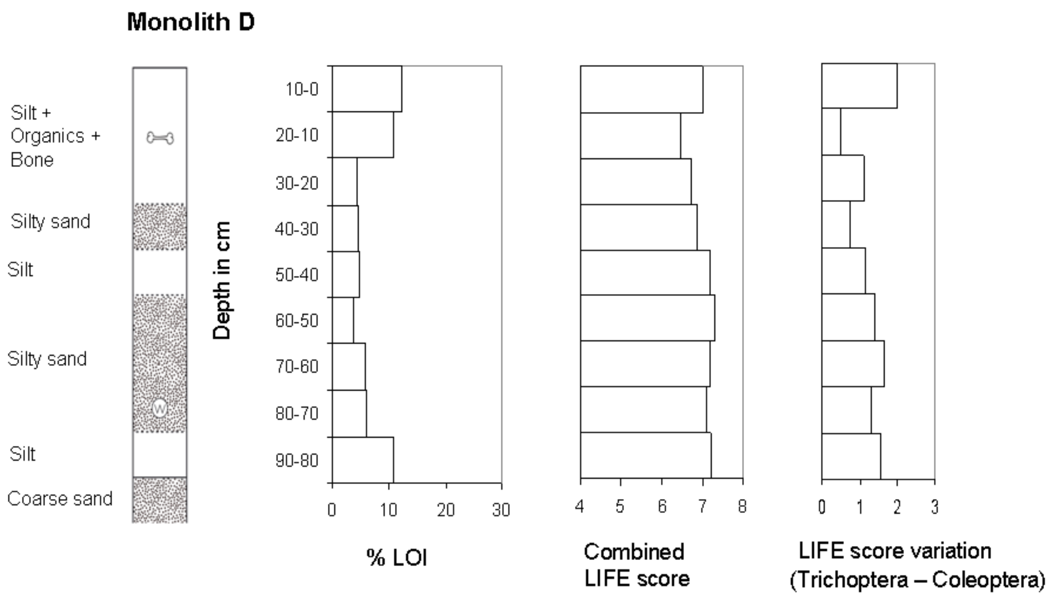


Figure 2 Detrended correspondence analysis (DCA) of sub-fossil Trichoptera and aquatic Coleoptera from 4 monoliths at Aston-on-Trent: (a) sample-biplot indicating samples from individual monoliths; (b) taxon biplot highlighting Coleoptera; (c) taxon biplot highlighting Trichoptera; and (d) taxon biplot indicating LIFE flow group affiliations
Notes: Limnephilid group C = Limnephilini in (b), Esolus p. = Esolus parallelepipedus in (c)

Fig. 2a

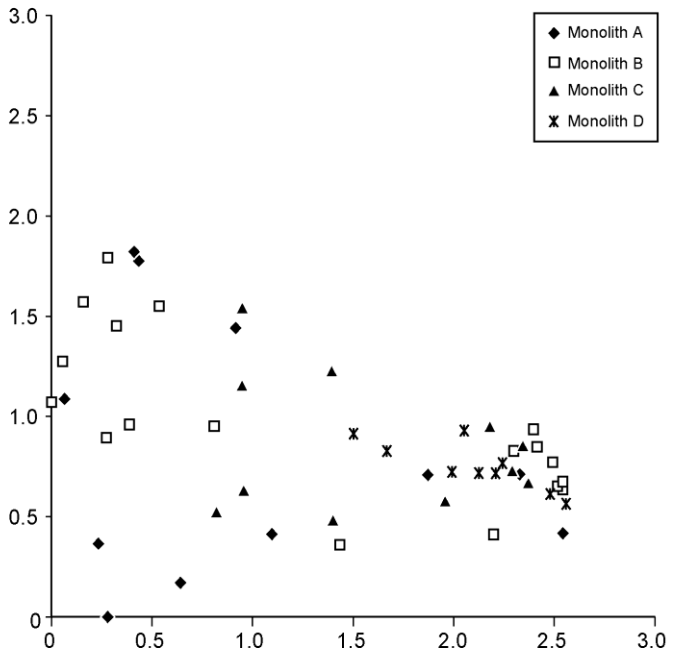


Fig. 2b

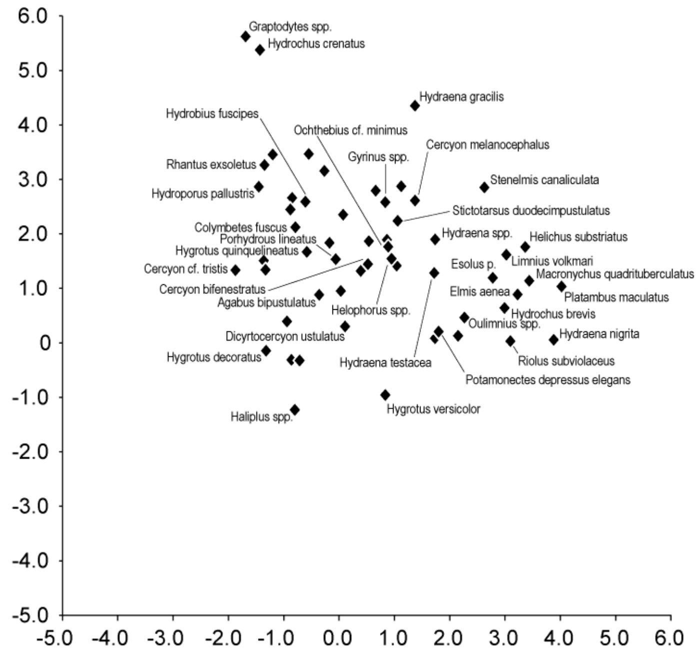


Fig. 2c

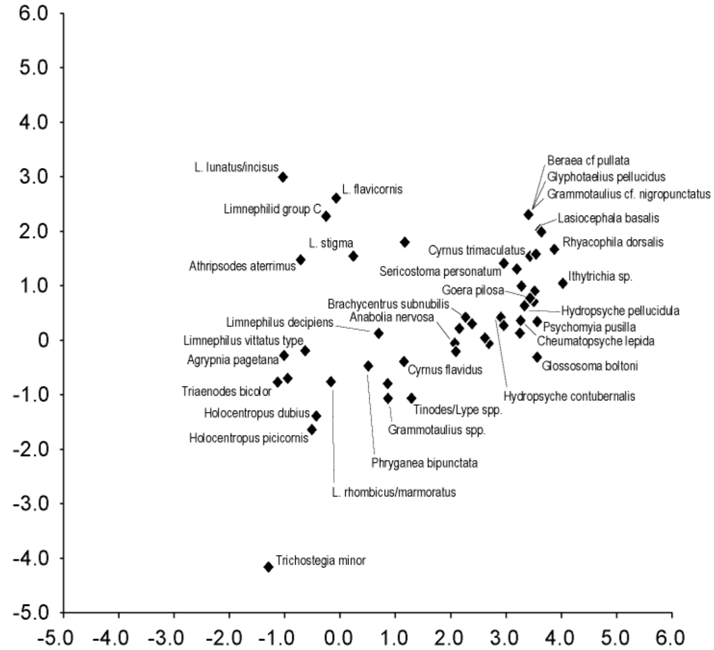
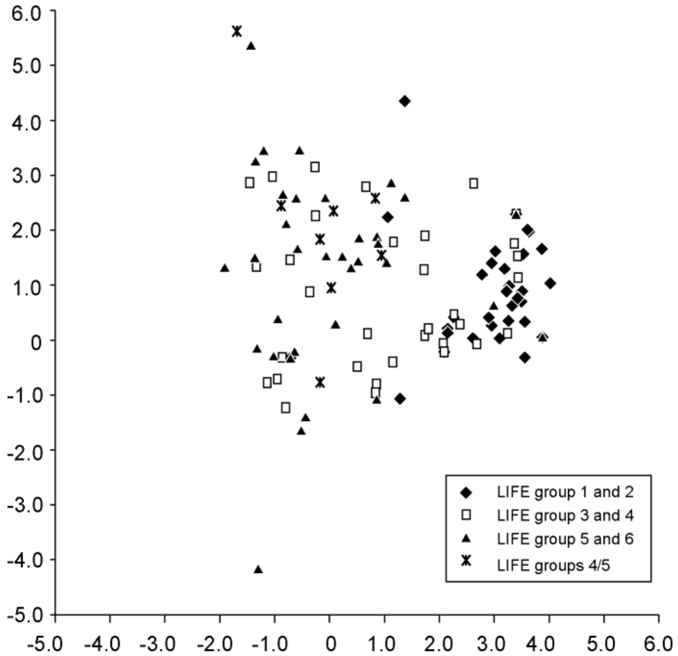

L. lunatus/incisus
L. flavicornis
Limnephilid group C
L. stigma
Athripsodes aterrimus
Beraea cf pullata
Glyphotaelius pellucidus
Grammotaulius cf. nigropunctatus
Lasiocephala basalis
Rhyacophila dorsalis
Cyrnus trimaculatus
Sericostoma personatum
Ithytrichia sp.
Goera pilosa
Brachycentrus subnubilis
Anabolia nervosa
Hydropsyche pellucidula
Limnephilus decipiens
Psychomyia pusilla
Limnephilus vittatus type
Cheumatopsyche lepida
Agrypnia pagetana
Glossosoma boltoni
Cyrnus flavidus
Triaenodes bicolor
Hydropsyche contubernalis
Tinodes/Lype spp.
Holocentropus dubius
Grammotaulius spp.
Holocentropus picicornis
Phryganea bipunctata
L. rhombicus/marmoratus
Trichostegia minor

Fig. 2d


LIFE group 1 and 2
LIFE group 3 and 4
LIFE group 5 and 6
LIFE groups 4/5