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Floodplain connectivity, disturbance and change: a palaeoentomological investigation of floodplain ecology from south-west England

S. R. DAVIS, A. G. BROWN* and M. H. DINNIN
Department of Archaeology, University College Dublin, Newman Building, Belfield, Dublin 4, Republic of Ireland; and
**Department of Geography, University of Exeter, Amory Building, Rennes Drive, Exeter, UK. EX4 4RJ, UK*

Summary

1. Floodplain environments are increasingly subject to enhancement and restoration, with the purpose of increasing their biodiversity and returning them to a more 'natural' state. Defining such a state based solely upon neoecological data is problematic and has led several authors to suggest the use of a palaeoecological approach.
2. Fossil Coleopteran assemblages recovered from multiple palaeochannel fills in south-west England were used to investigate past floodplain and channel characteristics during the mid- to late-Holocene. Ordination of coleopteran data was performed using Detrended Correspondence Analysis (DCA) and produced clear and discrete clustering. This clustering pattern is related to the nature of the environment in which assemblages were deposited and hence channel configuration and dynamics.
3. The DCA clustering pattern is strongly related to measures of ecological evenness, and a strong relationship between these indices and the composition of the water beetle assemblage within samples was revealed. Repeating the ordination with presence–absence data results in a similar pattern of clustering, implying that assemblage composition is crucial in determining cluster placement.
4. As assemblage composition is primarily a function of floodplain topography and hence disturbance regime, we attempt to relate these data to the Intermediate Disturbance Hypothesis (IDH). A significant positive correlation was found between ecological diversity (Shannon's H') and Axis 1 of all ordinations in predominantly aquatic assemblages.

Key-words: Coleoptera, Detrended Correspondence Analysis, ecological baselines, floodplain ecology, floodplain restoration, palaeoecology.

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Introduction

Floodplains are ecologically rich and complex environments that are frequently subject to change, both natural and artificial. This is reflected in their coleopteran communities (Sheldon, Boulton & Puckridge 2002; Sadler, Bell & Fowles 2004; Ballinger, MacNally & Lake 2005). These communities and their stability over time should reflect the lateral connectivity (the degree to which the river channel and the floodplain are interlinked) and disturbance regime of the floodplain–river system (Smith & Howard 2004). The analysis of Coleoptera from fluvial and riparian environments has been increasingly used to characterize, describe and assess rivers and floodplains, providing valuable ecological information for river and floodplain enhancement, restoration and management (e.g. Gerken *et al.* 1991; Greenwood *et al.* 1991; Petts, Armitage & Castella 1993; Bell, Petts & Sadler 1999; Aakra 2000). Many of these studies examine contemporary communities in order to identify relict habitats and communities as a baseline for restoration. However, studies of contemporary assemblages are unable to provide information regarding the ecological status of an unmodified system against which to assess habitat or community change. Consequently, previous studies have suggested the application of

Correspondence: S. R. Davis, Department of Archaeology, University College Dublin, Newman Building, Belfield, Dublin 4, Republic of Ireland. E-mail: s.r.davis@ex.ac.uk

palaeoecological methods as a means of establishing a baseline for restoration (e.g. Thoms, Ogden & Reid 1999; Andersen, Conley & Hedal 2004). The analysis of palaeo-coleopteran assemblages from floodplain sites has the advantage of providing not only such baseline information, but also a temporal perspective on changes in communities, habitats and conditions at specific points (both temporal and spatial) in floodplain–landscape development (Amoros & van Urk 1989; Brayshay & Dinnin 1999). This information can be used to make better-informed decisions about floodplain restoration and management. Fossil insect analysis may provide detailed information on past conditions relating to water quality (i.e. trophic status, turbidity, oxygenation), flow regime (i.e. stagnant, sluggish, fast-flowing), bedload characteristics (i.e. coarse/fine sediments) and the character of floodplain surfaces, including both insect and plant species composition, diversity and structure (Dinnin 1997; Brayshay & Dinnin 1999; Brown *et al.* 2001; Smith & Howard 2004; Smith *et al.* 2005). This paper employs a palaeoentomological approach to investigate past river conditions, disturbance and heterogeneity in a relatively unimproved rural floodplain, and to test general ecological principles that are thought to govern ecosystem stability and sensitivity. In particular this study tests the following hypotheses:

1. Coleoptera, connectivity and channel change: lateral connectivity has been suggested to directly influence patterns of diversity within a variety of taxonomic groups (Bornette, Amoros & Chessel 1994; Tockner, Malard & Ward 2000; Amoros 2001; Sheldon, Boulton & Puckridge 2002) including invertebrates. Given the 'four-dimensional' diversity of floodplain habitat patches (Ward 1989; Tockner *et al.* 2000; Robinson, Tockner & Ward 2002; Andersen *et al.* 2004) substantial subdivision of invertebrate assemblages should be possible, given a range of degrees of connectivity (e.g. assemblages characteristic of fast waters, slow waters, disconnected waterbodies, backwaters, etc.). As sample sediment composition is a direct function of the degree of connectivity to the active channel, sediment type is likely to be the primary factor in determining both the composition and diversity of coleopteran assemblages within each sample. Furthermore, conventional theories of floodplain evolution (Makaske 2001; Brown 2002) suggest that within the Holocene, a progression from forested anastomosing (multichannel) systems to single incised channels has taken place in many cases. This may be evident within the fossil record as a shift from predominantly low-energy assemblages characteristic of multiple small channels, to fast water assemblages characteristic of large-scale overbank deposition, potentially indicating extreme flood events.

2. Taphonomy as a complicating factor: the interpretation of insect death assemblages from fluvial sediments is particularly complicated owing to taphonomic issues (i.e. processes occurring between organism death and recovery). In particular, high allochthonous diversity may result from increased inwash. While it has been suggested that high diversity of terrestrial taxa (particularly those of open ground, grassland and meadow environments) within predominantly fluvial samples is likely to arise as a result of external inputs (Kenward 1978; Greenwood & Smith 2005), this hypothesis is untested. In addition, Smith & Howard (2004) assert that a consistently higher ratio of individuals to taxa (i.e. lower ecological evenness) is characteristic of fast-water deposition. We address this by comparing measures of diversity and evenness between samples categorized by sediment type, which is related to depositional environment, and age.

3. Disturbance regime: as the floodplain invertebrate community is closely linked to disturbance regime and palaeoentomological diversity is to some extent quantifiable, it may be possible to relate fossil coleopteran diversity to the Intermediate Disturbance Hypothesis (IDH – Grime 1973; Connell 1978), previously discussed for floodplains in relation to the Flood Pulse Concept (FPC – Junk, Bayley & Sparks 1989; Junk & Wantzen 2004). The two extremes of high and low disturbance may be defined, respectively, as (1) frequent or permanent changes in the physical habitat structure caused by flooding, and (2) few or infrequent hydrological changes leading to a 'climax community' (Junk & Wantzen 2004). Island-braided and anastomosing floodplains, comprising a network of channels and islands, fall between these two extremes, and are accordingly expected to possess the highest ecological diversity (Tockner *et al.* 2000). It has been hypothesized that the high coleopteran diversity found in studies of mid-Holocene floodplains (e.g. Dinnin 1997; Brayshay & Dinnin 1999) reflects the existence of such multichannel systems (Brown 2002; Greenwood & Smith 2005).

The study area

The data set comprises 38 samples distributed over four study reaches of the River Culm (Fig. 1) with two additional sites; Cutton Alders (on the floodplain of a tributary River Clyst, Devon) and Lower Chitterley (on the floodplain of the River Exe, Devon). The Culm floodplain is characterized by a residual multichannel or anastomosing channel pattern with secondary and tertiary channels in direct contact with the main river channel. There also exists a large network of palaeochannels of approximately 3·75 × the main contemporary channel length and many of these channels act as flood channels during overbank events. Some of these channels have infilled with organic sediments, silts and clays. The river has a rural catchment unimpacted by urban or industrial developments and only moderately impacted by arable agriculture and river engineering. Radiocarbon dating, optically stimulated luminescence dating (OSL) and ^{137}Cs/^{210}Pb dating suggests that at least one reach was actively braiding around 6000 BP and that the anastomosing pattern was established by *c.* 3500 BP with accelerated overbank deposition occurring in the last 300 years. It is believed that the anastomosing pattern did in this case evolve from a braided pattern under conditions of reduced flow variability and probably

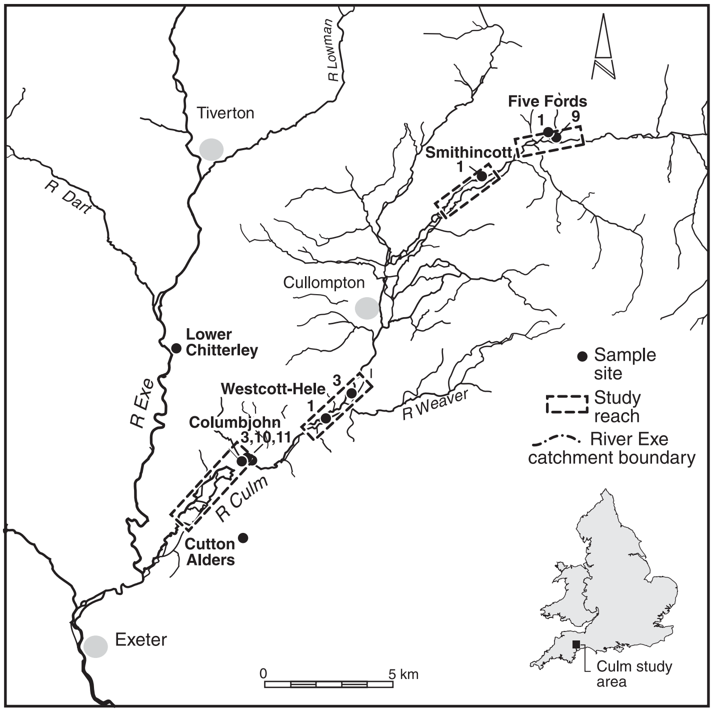

Fig. 1. Map showing study sites and designated reaches of the River Culm, Devon.

increasing vegetation on the floodplain (Brown *et al.* in prep.). Today the floodplain is covered by grassland (both improved and unimproved) with small wet woodlands, riparian alders *Alnus glutinosa* L., hedges and standard trees (*Quercus* and *Fraxinus*). The sampling locations are described in detail in Table 3.

Materials and methods

Bulk samples of 7–10 L sediment were collected either by excavation of a pit or from cut-back river bank sections where the present channels intersected palaeochannel fills. Where possible, multiple sediment samples for beetle analysis were collected in 10–15 cm spits. Sample preparation followed a standard paraffin flotation technique (Kenward, Hall & Jones 1980). The resulting 'flot' was decanted and washed with warm water and detergent to remove the excess paraffin. These flots were then sorted for insect remains under a low power stereomicroscope and the resulting remains stored in denatured ethanol. Coleoptera were identified with reference to the collections housed in the Royal Albert Memorial Museum, Exeter with the aid of standard entomological keys. Taxonomy follows that of Lucht (1987).

Twenty-eight samples of identified plant remains were submitted for AMS radiocarbon dating (25 to the SUERC AMS Radiocarbon Facility, Strathclyde, UK) using standard methods. Where possible, these dates constituted a basal date for each palaeochannel sequence and a date from the centre of each beetle sampling interval. Between radiocarbon dates and upper and lower sedimentary unit boundaries were dated using linear interpolation. Radiocarbon dates (Table 1) were calibrated to 2σ (95% confidence) using CALIB 5·0 (Stuiver, Reimer & Reimer 2005).

Coleopteran data were analysed using Detrended Correspondence Analysis (DCA) in the form of both raw count and binary (presence–absence) data using the CANOCO 4·5 computer package (ter Braak & Šmilauer 2002). Detrending was performed by segments, rare taxa downweighted and raw count data were square-root transformed. Ordination employed environmental categories based upon the ecological groupings devised by Robinson (1981, 1993), which were treated as supplemental variables (Table 2). These were supplied as a percentage of individuals belonging to each ecological category. Analysis was also performed using supplemental variables supplied as percentage taxa per ecological category. This resulted in a similar overall configuration, so is not illustrated. Coleopteran taxa were assigned to ecological categories using detailed modern ecological information derived from the BUGS Coleopteran Ecology package (Buckland *et al.* 2002), which incorporates a comprehensive survey of literature pertaining to modern coleopteran ecology.

Samples were classified into four groups based upon sediment characteristics; predominantly sandy sediments, silty sediments and two types of peaty sediments; wood peat and herbaceous peat. In addition samples were divided into three groups based upon radiocarbon age; samples less then 1500 years old, those between 1500 and 3500 years in age and greater than 3500 years. The length of these age divisions was based upon the distribution of radiocarbon dates among the samples analysed. Further subdivision of this last category exhibited

Table 1. Calibrated AMS radiocarbon dates (2σ, 95% confidence range) of material included in study. Calibration using CALIB 5·0 (Stuiver *et al.* 2005)

Sample ID	Sample depth (cm)	Laboratory no.	Conventional radiocarbon age	Radiocarbon age (Cal BP) 95% limits
CA 70–80	75	SUERC-2819	3516 ± 28	3880–3680
CA 80–90	85	SUERC-2820	4759 ± 30	5620–5420
CA 90–100	95	SUERC-2821	4801 ± 30	5640–5440
CA 100–110	105	SUERC-2822	4629 ± 27	5510–5270
CA 110–120	115	SUERC-2823	6262 ± 35	7310–7030
CA 120–130	125	SUERC-3103	7030 ± 42	7980–7740
OH 40–50	45	SUERC-2831	1538 ± 25	1550–1350
OH 50–60	55	SUERC-3096	2549 ± 23	2830–2470
OH 60–70	65	SUERC-3097	2770 ± 20	2910–2790
OH 70–80	75	SUERC-2831	2963 ± 35	3250–3010
FF9 60–80	70	SUERC-3107	2501 ± 23	2730–2450
WH3 170–185	177	SUERC-3108	4580 ± 29	5530–5010
WH3 185–200	192	SUERC-3109	4627 ± 27	5510–5270
CJ3 150–160	155	SUERC-2825	990 ± 22	1000–800
CJ3 160–170	165	SUERC-2826	936 ± 22	960–760
CJ3 170–180	175	SUERC-2829	939 ± 25	960–760
CJ11 135–150	142	SUERC-2835	794 ± 20	780–660
SM1 110–125	117	SUERC-2830	933 ± 25	794–916
SM1 125–140	132	SUERC-3102	1011 ± 25	1000–880
SM1 140–155	147	SUERC-2836	970 ± 25	980–780
SM1 155–170	162	SUERC-2839	953 ± 25	970–770
CJ10 150–160	155	SUERC-3098	713 ± 24	730–610
CJ10 160–170	165	SUERC-3099	4641 ± 31	5490–5290
WH1 140–160	150	SUERC-3100	1135 ± 24	1120–960
WH1 190–205	197	SUERC-3101	1098 ± 29	1100–940
LC 61–62	61	UtC-8502	4720 ± 40	5323–5583
LC 117–118	117	UtC-9609	9520 ± 50	10 608–11 088
LC 150	150	UtC-8622	12 590 ± 120	14 216–15 157

no systematic grouping, so was not subjected to further analysis.

Diversity was assessed using Shannon's *H′* (Shannon 1948), which despite criticisms (e.g. Routledge 1979; Magurran 1988; Mouillot & Lepretre 1999; Buckland *et al.* 2005) is still the most widely used index of biological diversity (Spellerberg & Fedor 2003). Evenness was assessed using three measures; Pielou's (1966) *J′*, defined as $H'/\ln s$, where *H′* is Shannon's Index and s = number of species, and two variations on Hill's (1973) numbers, $E_{1\cdot 0}$ (N_1/N_0) and $F_{2\cdot 1}$ (defined as $(N_2 - 1)/(N_1 - 1)$). Hill's (1973) numbers are defined as follows:

$$N_0 = \text{species richness; } N_1 = e^{H'/s} \text{ and } N_2 = 1\Big/\sum_{i=1}^{s} p_i^2$$

Although Pielou's *J′* is the most commonly employed measure of evenness, Alatalo (1981) concludes that it is inappropriate for comparisons of samples where species richness varies considerably due to the mathematical relationship between species richness and *J′* (DeBenedictis 1973; Stirling & Wilsey 2001; Ma 2005). Both Hill's ratios have been recommended as superior alternatives in that they satisfy the fundamental requirement that an evenness index is entirely independent of species richness (Alatalo 1981; Smith & Wilson 1996; Ricotta & Avena 2003) and therefore an independent measure of community evenness (Alatalo 1981).

Results

SAMPLE ORDINATION BY SEDIMENT TYPE AND RADIOCARBON AGE

Using square-root transformed counts this analysis resulted in clear separation between the four sediment categories (Fig. 2a). 'Sandy' sediments plot negatively on Axis 1 and relate to the fast water, meadow, mould, arable/disturbed and pasture/dung variables while samples of the 'wood peat' category plot positively on Axis 1 and relate to grassland, woodland, refuse and running water variables. 'Nonwood peat samples' plot strongly positively on Axis 1 but also (along with 'silty' samples) negatively on Axis 2, their location primarily related to the slow water, aquatic/marsh, pasture/dung and arable/disturbed variables. Analysis of presence–absence data (Fig. 2b) resulted in a comparable pattern, although samples of the 'silty' group do not separate clearly from those of the 'sandy' cluster in this ordination.

Classification of samples by radiocarbon age resulted in three clear clusters in all ordinations (Fig. 3), which correspond closely with the clusters observed in the sediment type ordinations. Samples that plot most negatively on Axis 1 are almost all of the youngest group (< 1500 BP) while the reverse situation is evident for those samples plotting positively on Axis 1, which almost

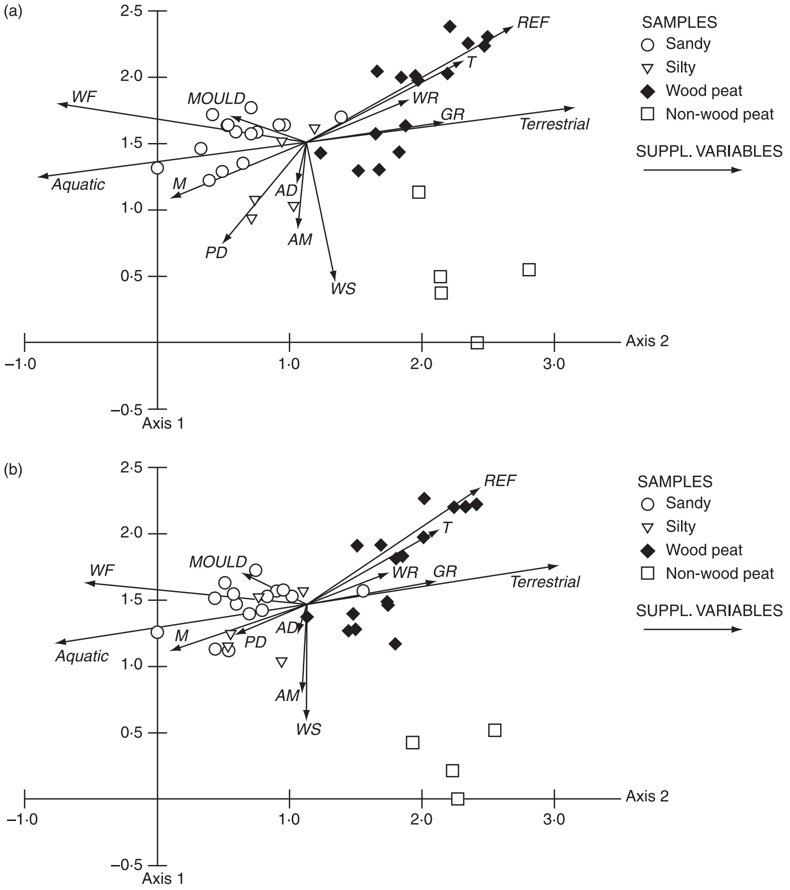

Fig. 2. (a) DCA square-root transformed raw data categorized by sediment type, incorporating percentage individuals per ecological category as supplementary variables; (b) as 2(a) using presence/absence data.

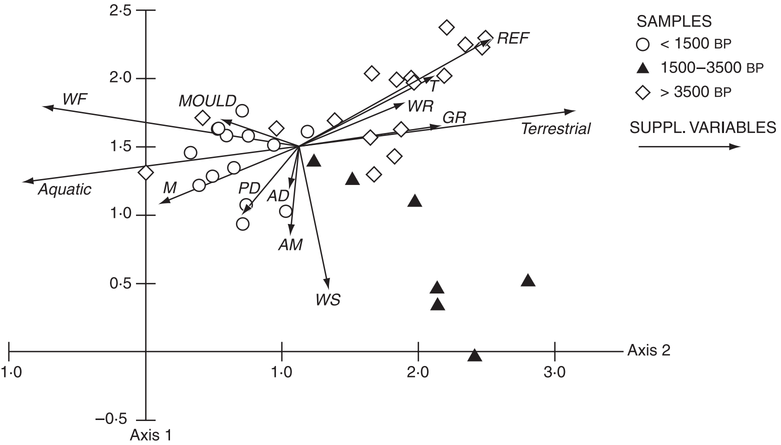

Fig. 3. DCA square-root transformed raw data categorized by radiocarbon age, incorporating percentage individuals per ecological category as supplementary variables.

exclusively belong to the > 3500 BP age group. The samples of the 'nonwood peat' sediment classification are all of intermediate age (1500–3500 BP). As previously, differences arising in configuration between presence–absence data and square-root transformed raw data are minimal.

DEPOSITIONAL ENVIRONMENT AND EVENNESS

All three evenness indices perform in a similar fashion, and result in statistically significant differences between classifications; in sediment groupings these arise between sandy and peaty assemblages and between those of silty and peaty sediments (no significant difference occurs between sandy and silty sediments). In age groupings, these differences occur between the youngest samples and the other two groupings but not between the intermediate age group and the oldest samples (Table 4). A strong relationship also exists between DCA Axis 1 scores (DCA performed on binary data to remove any effects of species abundance) and all evenness measures (Fig. 4) by virtue of the strong relationship

Table 2. Modified ecological groups after Robinson (1981, 1993)

	Species group	Only include:
AD	Arable/disturbed ground	Carabids of open weedy, bare disturbed or arable ground
AM	Aquatic and marsh plants	Members of the Chrysomelidae and Curculionidae that feed exclusively on marsh and aquatic plants
GR	Grassland	Taxa associated with grassland environments (e.g. Elateridae of the genera *Agriotes* and *Athous*)
MOULD	Mould beetles	Mould beetles of the family Lathridiidae
M	Meadowland	Weevils of genera *Apion* and *Sitona*: generally feed on meadow plants: vetches, clovers etc. (excluding those found on mallow, nettle, willow or shrubs/trees)
M	Meadow	Meadow taxa, particularly weevils of the genera *Sitona* and *Apion*
PD	Pasture and dung	Members of the genera *Geotrupes*, *Colobopterus*, *Aphodius* and *Onthophagus* that feed on dung in fields, rather than in manure or compost
REF	Plant refuse/foul organic matter	Members of the genera *Cercyon*, *Megasternum*, *Cryptopleurum*, *Anotylus* and *Platystethus arenarius* (Fourc.) group that live in accumulations of foul organic matter
T	Trees, shrubs	Wood and tree-dependent species (i.e. strictly associated with wood and wood fungi)
WF	Aquatic species of fast waters	Beetles which spend much of their adult life in fast-moving water bodies (e.g. Elmids, *Hydraena gracilis* Germ.)
WR	Aquatic species of running waters	Beetles which spend much of their adult life in running water of indeterminate velocity (e.g. *Limnebius truncatellus* (Thun.), *Ochthebius* spp.)
WS	Aquatic species of slow waters	Beetles that spend much of their adult life in slow-moving water bodies (e.g. *Helophorus* spp., *Hydraena testacea* Curt.)

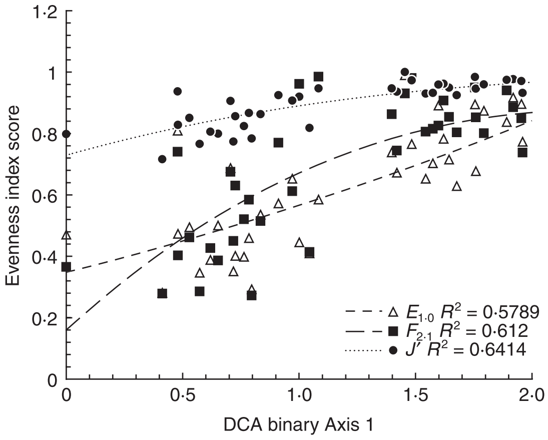

Fig. 4. Evenness indices (Pielou's J' and Hill's $F_{2\cdot1}$ and $E_{1\cdot0}$) against binary DCA axis 1(presence absence data).

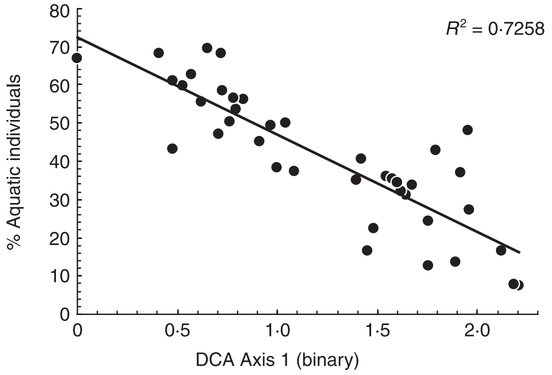

Fig. 5. DCA axis 1 for presence/absence data vs. percentage aquatic individuals (R^2 = 0·7258, P < 0·000).

evident between DCA Axis 1 and percentage aquatic individuals per sample (r = –0·845, P < 0·000, Fig. 5).

Discussion

SAMPLE ORDINATION BY SEDIMENT TYPE AND RADIOCARBON AGE

Inclusion of percentage aquatic and terrestrial supplemental variables in the ordination establishes this as the primary gradient evident on Axis 1. Axis 2 of both raw data and presence–absence ordinations are of similar configuration, the most influential negative factor being the proportion of slow water individuals. Using supplementary variables derived from percentage taxa per ecological grouping within the ordination, woodland taxa are more influential on Axis 2, demonstrating that while present at high diversity these are not numerically well represented.

The positioning of the 'silty' samples close to the origin on Axis 1 in addition to their plotting positively on Axis 2 is consistent with these being semiterrestrial in nature. This is borne out by the presence of semiterrestrial chironomid taxa within these samples (Z. Ruiz pers. comm.). Samples plotting most negatively on Axis 2 are consistent with having been deposited in a treeless environment. This is suggested not only by these samples plotting in the opposite direction to the woodland vector but also as they are dominated by slow water taxa, it is likely that the majority of coleopteran remains recovered from these sites result from autochthonous rather than allochthonous deposition.

Table 3. Description of sampling locations, including calibrated radiocarbon dates

Reach	Site name + code	NGR	Site description	Channel size (width × depth)	No. of samples
Five Fords	Five Fords 1 (FF1)	ST 0883 1386	Palaeochannel, located at floodplain edge > 250 m from the main channel, measuring *c*. 25 m in width but only 1 m in depth. Large size suggests it carried most of the flow. Pollen evidence shows channel-fill post-dates regional dry-land clearance but spans the clearance of local wet woodland and the transformation of floodplain to open pasture. Five samples of herbaceous (nonwood) peat recovered by excavation.	25 × 1 m	5
	Five Fords 9 (FF9)	ST 0915 1370	Small palaeochannel towards middle of floodplain, *c*. 120 m from the active channel. Situated in area of complex topographic variation that incorporates a network of terrace fragments. OSL date on one of these is comparatively early (6560 BP). Small size suggests limited flow as part of a multichannel system. Pollen evidence shows that fill post-dates regional dryland deforestation, but pre-dates local wet woodland clearance. One sample of wood peat recovered by excavation.	3 × 0·8 m	1
Smithicott	Smithincott 1 (SM1)	ST 0618 1210	At northern edge of floodplain, *c*. 200 m from active channel. Large palaeochannel, believed to be the apex of a meander bend. Size suggests it carried most of the flow through the reach. Pollen evidence shows site post-dates both regional slope deforestation and deforestation of the floodplain; cereals represented throughout pollen diagram. Five samples of organic silts recovered by excavation.	10 × 2 m	5
Westcott-Hele	Westcott-Hele 1 (WH1)	ST 0015 0289	Large palaeochannel of similar dimensions to the active channel. Visible as a bank exposure. Situated towards south of floodplain, within a multichannel region. Size suggests channel carried majority of flow through reach. Organics in two sections with *c*. 30 cm gravel separating them. Pollen evidence suggests open canopy woodland/ parkland environment, with dry land taxa (e.g. *Quercus*) higher than those of wet woodland (e.g. *Alnus*). Two samples of organic-rich sands recovered from bank section.	10 × 2 m	2
	Westcott-Hele 3 (WH1)	ST 0120 0390	Mid-floodplain site, visible as bank section. Mid-sized palaeochannel, > 150 m from the floodplain edge. Dimensions suggest part of a multichannel system. Pollen evidence shows sequence post-dates much regional dryland deforestation (though some *Tilia* and *Quercus* present) and pre-dates local deforestation of wet woodland. Three samples of organic-rich sands recovered from bank section.	7 × 1·5 m	3

Table 3 *Continued*

Reach	Site name + code	NGR	Site description	Channel size (width × depth)	No. of samples
Columbjohn	Columbjohn 3 (CJ3)	SS 9732 0142	Evident as bank section in active channel. Smaller than active channel, even with current bi-channel form in this reach. Suggesting part of a multichannel system. Pollen shows site post-dates deforestation of dryland valley slopes and clearance of most local wet woodland. OSL provided an historical date for the overlying sands (AD 1730 at a depth of 110 cm). Five samples of organic-rich sands recovered from bank section.	5 × 1·7 m	5
	Columbjohn 10 (CJ10)	SS 9721 0141	*c*. 50 m from floodplain edge where floodplain narrows to 250 m. Expressed as a bank exposure in active channel. Small dimensions suggest part of multichannel system. Pollen shows site post-dates the regional dry woodland clearance but predates clearance of some alder-dominated wet woodland. Two samples of organic-rich sands recovered from bank section.	4 × 1·7	2
	Columbjohn 11 (CJ11)	SS 9697 0130	Located < 100 m from edge of floodplain. Expressed as a bank exposure in active channel. Dimensions similar to present channel, suggesting the system was single channel. Pollen evidence post-dates clearance of regional dry woodland and local wet woodland, suggesting a relatively late date. This is corroborated by an OSL date from the overlying sands of AD 1080. One sample of organic-rich sands recovered from bank section.	12 × 2	1
Other	Cutton Alders (CA)	SX 9700 9830	Relict area of 18·7 ha floodplain broadleaved woodland at a distance of *c*. 1·8 km from River Culm at Columbjohn and 1·4 km from the River Clyst at Broadclyst. Pollen evidence demonstrates that site has been wooded without complete clearance since Early Holocene (radiocarbon date of 7980–7740 cal BP has obtained from depth of 120 cm). Some signs of clearance at *c*. 3500 BP (some decline in *Alnus*, increase in Poaceae). Five samples of wood peat recovered by excavation.	Large horizontal area, 1·5 m depth	8
	Lower Chitterley (LC)	SS 9440 5375	The site comprises and infilled terrace palaeochannel, situated on an extensive late-glacial terrace at 30 m OD. Deposits of over 2 m have been recovered, including some of late-glacial interstadial date. The top metre of sequence of which proved to be organic rich (wood peat), from which six samples were removed for analysis by excavation.	10 × > 2 m (1·0 m Holocene)	6

Table 4. Tukey's HSD values for one-way ANOVA of three evenness indices, Hill's $E_{1\cdot0}$ and $F_{2\cdot1}$ and Pielou's J', grouped either by sediment type or radiocarbon age. Nonwood and wood peat are grouped together for the purpose of this analysis

	Sediment group (a)	Sediment group (b)	Mean difference (a–b)
$E_{1\cdot0}$	Sandy	Silty	–0·034
		Peaty	–0·118**
	Silty	Peaty	–0·839**
$F_{2\cdot1}$	Sandy	Silty	–0·166*
		Peaty	–0·371**
	Silty	Peaty	–0·205**
J'	Sandy	Silty	–0·344
		Peaty	–0·118**
	Silty	Peaty	–0·084**

Evenness Index	Age group (a)	Age group (b)	Mean difference (a–b)
$E_{1\cdot0}$	< 1500 BP	1500–3500 BP	–0·373**
		> 3500 BP	–0·265**
	1500–3500 BP	> 3500 BP	0·109
$F_{2\cdot1}$	< 1500 BP	1500–3500 BP	–0·355**
		> 3500 BP	–0·276**
	1500–3500 BP	> 3500 BP	0·078
J'	< 1500 BP	1500–3500 BP	–0·128**
		> 3500 BP	–0·098**
	1500–3500 BP	> 3500 BP	–0·030

**P < 0·005; *P = 0·063.

Table 5. Tukey's HSD values for one-way ANOVA of three Shannon's H' and species richness, grouped either by sediment type or radiocarbon age. Nonwood and wood peat are grouped together for the purpose of this analysis

	Sediment group (a)	Sediment group (b)	Mean difference (a–b)
Shannon's H'	Sandy	Silty	–0·394
		Peaty	–0·088
	Silty	Peaty	0·306
Species richness	Sandy	Silty	23·73
		Peaty	22·117*
	Silty	Peaty	45·85**

Evenness Index	Age group (a)	Age group (b)	Mean difference (a–b)
Shannon's H'	< 1500 BP	1500–3500 BP	0·33
		> 3500 BP	0·071
	1500–3500 BP	> 3500 BP	–0·259
Species richness	< 1500 BP	1500–3500 BP	43·36**
		> 3500 BP	33·48**
	1500–3500 BP	> 3500 BP	–9·87

**P < 0·005; *P < 0·05.

The lack of separation between 'silty' and 'sandy' clusters in the presence–absence ordination is expected as these samples although semiterrestrial possess the highest proportion of aquatic taxa of all samples analysed (mean = 74%). This is because these samples include not only slow water taxa but those from the fast water group. Such samples, which include mixed fast and slow water assemblages, may have been deposited either in flood events or downstream of a pool-riffle sequence. When converted to presence–absence data these mixed assemblage samples appear statistically more like their predominantly aquatic counterparts, hence cluster with aquatic rather than terrestrial samples.

As regards ecological evenness, samples of fast and slow water environments (sandy and silty, respectively) are numerically dominated by few taxa (e.g. elmids for fast water or *Helophorus* spp. for slow water). This contrasts with predominantly terrestrial environments (wood-peat), which include many taxa with few individuals. This results in lower evenness scores for aquatic samples in comparison with terrestrial samples. A similar pattern is observed when samples are classified by radiocarbon age (i.e. younger sites, being predominantly fast-water are of lower evenness).

Comparison of the age-related pattern of clustering with pollen data (Fyfe, Brown & Coles 2003; Fletcher, unpub.) shows that samples in the > 3500 BP age category pre-date local clearance of wet woodland while those of the youngest category are from sites where local woodland was largely absent. This is in keeping with models of floodplain development that predict the progression from forested anastomosing systems to single incised channels in post-clearance floodplain environments (Makaske 2001; Brown 2002). Four elmid-dominated samples are present in the oldest age category; three samples from WH3 and one from CJ10. Given the late date of CJ10 150–160 cm (713 ± 24 BP) in comparison with CJ10 160–170 (4641 ± 31 BP), the latter may represent reworking of older material. However, the two dates from WH3 appear stratigraphically constrained (WH3185–200 dates to 4627 ± 27 BP and WH3170–185 to 4580 ± 29 BP) and may relate either to an intense flood event within an anastomosing system or overbanking from an older section of single channel form. Pollen evidence suggests the channel existed in an environment with abundant local wet-woodland (up to 60% *Alnus* pollen) and appreciable presence of regional dryland tree taxa (10% *Quercus*, 5% *Tilia*; Fletcher unpub). The presence of occasional grains of cereal pollen may indicate early agricultural impact, which is suggested by Macklin & Lewin (2003) as contributing to increased run-off and sediment supply from *c.* 4500 BP, and this may have been responsible for maintaining and even expanding the anastomosing channel network.

DETERMINATION OF PAST FLOODPLAIN CONDITIONS AND DEPOSITONAL ENVIRONMENTS

With regard to the determination of specific flood events as attempted by Smith & Howard (2004), none of the sequences analysed presented a varied enough stratigraphy to interpret in such a fashion. However, a ranked plot of radiocarbon age shows a clearly

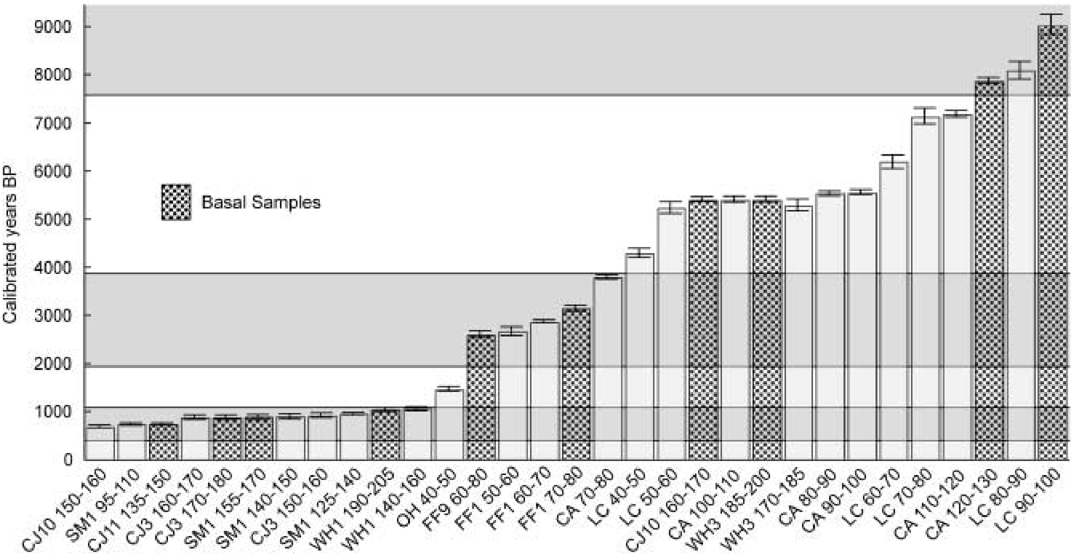

Fig. 6. Calibrated radiocarbon age distribution of samples included in analysis. Shaded bands denote Macklin & Lewin's (2003) periods of increased flood frequency.

discontinuous distribution, with at least three plateaux evident (Fig. 6). These may relate to periods of increased flooding within the Holocene. Such periods have been discussed by several authors (e.g. Passmore & Macklin 2000; Macklin & Lewin 2003), with the latter describing three periods of increased major flood episodes, corresponding reasonably well with those on the Culm; 400–1070 BP, 1940–3940 BP and 7570–10 420 BP. The lack of fast-water dominated samples in the oldest age category is striking and is a key factor in the clustering pattern as it largely accounts for variation in ecological evenness, driven by a proportion of aquatic individuals. The clear division between young, fast-water and old, slow-water deposits must relate to the effect of taphonomic bias, to a fundamental change in channel form, or to a change in available depositional environments occurring some time after local deforestation. The paucity of older fluvial deposits has previously been recognized by Lewin & Macklin (2003), who conclude that 'the skewed and censored distributions of preserved units do not necessarily reflect the frequencies/sizes of units originally formed' (Lewin & Macklin 2003, p. 117). As such, the lack of older, fast-water sediments may reflect the dichotomy between deposits arising as a result of differences in the process of channel abandonment. Lateral channel migration, when not combined with a high rate of aggradation, has the effect of eliminating older units and skewing preservation towards younger deposits (Lewin & Macklin 2003; Lewin, Macklin & Johnstone 2005). However, there is very limited evidence of active meander migration present on the Culm. An alternative explanation is that avulsion (defined as the process by which flow is diverted out of an established river channel and into a new course on the adjacent floodplain – Slingerland & Smith 2004) may result in a similar pattern of preservation. Although avulsion, particularly in anastomosing systems is often regarded as a very slow process, resulting in older, vertically infilling channels such as those at Cutton Alders and Lower Chitterley (Makaske 2001), a systematic reduction in the number of channels, restricting flow to an active part of the floodplain may result in increased deposition of more recent material relative to older material.

INTERMEDIATE DISTURBANCE AND DIVERSITY

The IDH (cf. Grime 1973; Connell 1978; Wilkinson 1999) has been discussed in detail with relation to floodplain environments in a number of articles (e.g. Ward 1998; Ward & Tockner 2001; Amoros & Bornette 2002). In the current study Axis 1 of all ordinations is strongly related to water velocity and in turn therefore connectivity and flood pulse frequency and magnitude. Fast-water-dominated sites, subject to a greater degree of flood disturbance plot most negatively, terrestrial-dominated sites subject to low-level flood disturbance plot most positively and slow-water-dominated sites subject to moderate frequency/magnitude flooding plot centrally. In order for the data to fit the IDH, it would be expected that those sites with intermediate Axis 1 scores would possess the highest diversity, in a 'hump-backed' form of distribution (Fig. 7).

Taking $x = 1{\cdot}044$ as the cut-off point includes all but one such sample and, with two samples (CA 50–60 cm and WH3 170–185 cm, both with the lowest overall species richness) removed as outliers, significant positive and negative correlations with Shannon's H' are observed. These results support the IDH and suggest a gradient in species richness, lowest in sites of high and low energy deposition, and highest in intermediate samples. It would be hoped that the inclusion of further samples in the analysis would enhance the strength of this relationship.

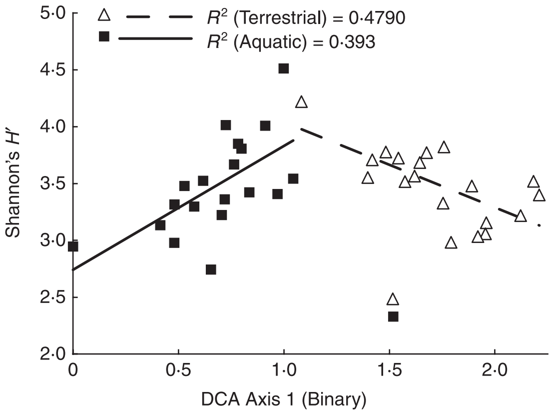

Fig. 7. DCA axis 1 scores (presence/absence data) vs. Shannon's H', divided into aquatic and terrestrial categories (two outliers removed). Positive correlation evident in aquatic samples ($R^2 = 0{\cdot}398$, $P < 0{\cdot}005$) and between terrestrial samples and DCA Axis 1 ($R^2 = -0{\cdot}4790$, $P < 0{\cdot}005$).

IMPLICATIONS FOR FLOODPLAIN RESTORATION

This study has highlighted the apparent progression from a mid-Holocene anastomosing system, characterized by low-energy flow, widely distributed over a network of channels and well-connected to the floodplain to a single incised channel subject to catastrophic flooding resulting in coarse-grained deposition. This reduction in spatial and temporal variation, while most apparent in constrained catchments such as the Culm, is believed to have led to a reduction in habitat diversity at the floodplain scale (Brown 1997). Despite no significant difference being observed between Shannon's H' and either sediment type or radiocarbon age category, significant differences in species richness occur between age and sediment categories, with younger samples having the highest overall species richness, as well as higher aquatic and terrestrial species richness (Table 5). This contrasts with the higher diversity predicted in samples of mid-Holocene age and illustrates how diversity is a complex state variable and should not be the sole target measure of restoration schemes. Instead decisions should be made on the particular assemblages desired and that are possible and may have existed before as shown by studies such as this. Also important is the overall ecological state as measured by a variety of ecological indices. The palaeoecological data here could be used to provide a variety or combination of baselines to which more impacted river–floodplain systems could be restored through the creation or reconnection of secondary channels and appropriate land use.

Conclusions

This study has recognized four clear site clusters through the ordination of coleopteran data. These are most readily related to sediment characteristics. Of these clusters, two are analogous to those of Smith & Howard (2004) – a fast water assemblage, dominated by riffle beetles and possessing low ecological evenness, and a slow water assemblage, lacking these taxa but including *Donacia*/*Plateumaris* spp. and the weevil *Notaris acridulus* (L.), both taxa characteristic of emergent vegetation. A further two categories are also recognized, one a slow-water assemblage of silty sediments dominated by *Helophorus* spp. and *Hydraena testacea*, suggesting a semipermanent but disconnected floodplain water body such as a ditch fill or abandoned channel (e.g. Jaques *et al.* 2002), the other, characteristic of wood peats, and related to the slow water assemblage of Smith & Howard (2004) and including taxa such as *Stenichnus collaris* (Müll.) and *Cerylon histeroides* (F.), with a conspicuous lack of water beetles. This leaves scope for substantial further subdivision of floodplain coleopteran assemblage types given the analysis of more samples. It is recommended that the hypotheses put forward here be investigated further with reference to a wider variety of catchment types (including larger systems such as the Trent or the Thames) and sediment composition and sample age.

Furthermore, the numbers of both individuals and taxa are elevated in predominantly fast-water-dominated aquatic samples. This is in agreement with Kenward (1978) and also the findings of Smith & Howard (2004) in that these presumably include greater diversity of autochthonous and allochthonous taxa. Measures of evenness have proved to be strongly related to the sediment composition of the samples investigated, and so to the conditions under which these samples were deposited. Samples with the lowest evenness are of the fast water category while those of slow waters are of significantly higher evenness. This is due to the extreme numerical dominance of few fast-water taxa within the former group (as observed by Smith & Howard 2004). However, the presence of a strong relationship between the DCA Axis 1 scores (on binary data) and three separate measures of evenness (J', $E_{1{\cdot}0}$ and $F_{2{\cdot}1}$) was not predicted and is an important factor in the placement of samples by such ordination. This confirms that not only are species abundances important but also that samples are also defined by particular 'fingerprint' assemblages of taxa, retaining their position within ordinations irrespective of numerical abundance.

Finally, this study has revealed evidence in support of the IDH in floodplain beetle assemblages. A positive correlation exists between DCA axis 1 (a proxy for percentage aquatic individuals vs. percentage terrestrial individuals, low evenness vs. high evenness and so high disturbance vs. low disturbance) and diversity for predominantly aquatic assemblages, and a corresponding negative correlation (necessary for a 'hump-back' distribution) was found in predominantly terrestrial assemblages. The inclusion in the ordination of further samples from more diverse contexts is likely to provide a stronger relationship than is currently evident.

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