The Semi-Aquatic Habitats of Terrestrial Coleoptera in a Lowland River Floodplain

by

Derek A. Lott

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Abstract

281 species of terrestrial ground-living beetles were recorded from 69 riparian and wetland sites in the floodplain of the lowland River Soar, England. Differences in species composition between pitfall trapped and timed hand-collected samples were smaller than those attributable to environmental and seasonal factors. Detrended Correspondence Analysis consistently ranked all sites against seasonal variations between April and June and floodplain sites against annual variations. DCA axis 1 scores were slightly better correlated with important environmental variables at the ecohabitat (<50m) scale rather than the microhabitat scale. Canonical Correspondence Analysis detected assemblage responses to flooding disturbance and grazing pressure along the main channel, as well as to water level stability in the floodplain. A conceptual model of floodplain land-use and river management postulated a dynamic equilibrium between flooding disturbances and vegetational succession, producing geomorphic and vegetational structures which serve as semi-aquatic habitats for terrestrial beetle assemblages with appropriate species traits. Impoundment for navigation affects assemblages by modifying the severity of flooding disturbance. The effects of grazing pressure resemble flooding disturbance. The short-term (<5yr) impact of bank regrading was explained by differences in severity, predictability and frequency compared to the beetles' generation length.

Evenness and species richness were affected only by flooding and grazing disturbance. This response was not predicted by the intermediate disturbance hypothesis because the frequencies of flooding and grazing disturbances in the Soar valley are not appropriate to the hypothesis, which more closely relates to disturbance by bank regrading. In comparison to diversity indices, a rarity index was much less sensitive to environmental factors than species diversity indices and more robust against seasonal and yearly fluctuations. Consequently, it has more potential for use in site quality assessment.

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1 Introduction

Rivers have long occupied an important position in the human perception of the natural world. In Britain, rivers and their sources were venerated in Celtic cultures (Ross 1967) and similar practices continue today in modern India. Today, river corridors attract more frequent visits and draw visitors from a wider area than parks and other open spaces (Green & Tunstall 1992). Surveys of modern public attitudes toward rivers in Britain reveal that people appreciate their landscape value and the associated variety of wildlife (Green & Tunstall 1992).

Rivers are often recognised as important features of landscape protection areas and a set of methods for river landscape assessment (NRA 1993a) has recently been published. Conservation of the variety of wildlife along a river is more problematic and requires a detailed understanding of floral and faunal diversity and its interactions with fluvial and ecological processes (Boon 1992). This study is a contribution toward the conservation of a particular section of that faunal diversity which until very recently has been severely neglected. Aquatic and terrestrial systems are two of the major divisions of animal habitats suggested by Elton & Miller (1954), but a further class, the aquatic - terrestrial transition zone has received much less attention. However semi-aquatic habitats occur at all boundaries between aquatic and terrestrial systems and occupy wide areas in wetlands. The diversity and interest of beetles in semi-aquatic environments in the riparian and floodplain zones of river systems, especially lowland rivers, are largely unappreciated outside specialist entomological circles.

Petts *et al.* (1995) described how in the past scientists failed to communicate the results of their research to managers and decision makers with detrimental consequences for the riverine natural environment. Since then the upsurge of concern regarding environmental issues has led to more co-operation between hydrologists, ecologists and river authorities and the implementation of schemes to benefit the aquatic environment in rivers. It is intended that the results of this study on the semi-aquatic environment will be of value to river authorities in extending their nature conservation initiatives to terrestrial margins and floodplain wetlands.

The following introduction reviews what is known about the diversity of terrestrial beetles in riverine semi-aquatic habitats and how this relates to

1) the riverine environment

2) the environmental requirements of the organism

3) their conservation.

It finishes with a set of aims and objectives for the study.

1.1 Ecological perspectives

A large amount has been published on fluvial processes and their manifestations in channel morphology, floodplain sedimentology and water quality (e.g. Gregory & Walling 1973, Gregory 1977, Lewin 1981). Literature on the ecological aspects of these processes has concentrated overwhelmingly on aquatic organisms (e.g. Hynes 1970, Allan 1995). The River Continuum Concept recognises the importance of riparian vegetation but only in respect of its importance to the aquatic ecosystem (Vannote *et al.* 1980). Similarly work on land / water ecotones has dealt with the transport of material from land to water and its effect on aquatic organisms (Naiman & Decamps 1990, Bretschko 1995). Ecological studies of the riparian zone *per se* have concentrated on plant communities (e.g. Halsam 1978, Holmes 1983, Pautou & Decamps 1985) or vertebrates (e.g. Decamps *et al.* 1987, Carter 1989, Strachan & Jefferies 1993). Much of the work that has been done on riparian beetles has been carried out in central Europe or Scandinavia and published in German and these are possible contributory reasons for their neglect in anglophone countries. Many of the older studies are mainly faunistic (e.g. Palmen & Platanoff 1943, Kless 1961) and more recent papers are often preoccupied with interspecific competition, scattered in specialist journals and mainly confined to one family, the ground beetles.

Studies of the human impact on river systems have mostly been confined to geomorphological changes (e.g. Park 1977, Brookes 1985) and their effect on aquatic invertebrates, fish, riparian vegetation and vertebrates (e.g. Cadbury 1984, Petts 1984, Brooker 1985, Brookes 1988, Smith *et al.* 1990, Petts et al. 1993, Nilsson & Dynesius 1994, Mason 1995). Similar studies dealing with riparian beetles (e.g. Plachter 1986) are very rare.

However, although such information specific to riparian invertebrates is scarce, much of the above work provides a useful framework for considering which environmental factors are likely to be important for beetles with semi-aquatic habitats. The following section considers the physical environment in terms of natural processes and the influences of human land use and river management.

1.2 The riparian and floodplain environment

Gregory *et al.* (1991) put forward a model of rivers and their riparian zones to show how geomorphic and hydrologic processes such as erosion and sediment transport combine with terrestrial plant-successional processes to provide physical habitat and nutritional resources in aquatic ecosystems (see fig. 1.1). Naiman *et al.* (1992) considered that climatic and geomorphic processes affect habitat features and biota at five different scales, namely at the levels of catchment, segment (length of river between major confluences), reach (length of river with similar gradient), pool/riffle system and microhabitat (see fig 1.2). Each scale has a spatial and temporal dimension with small scale structures such as microhabitats lasting for around a year and larger scale units lasting for progressively longer time scales. When these time scales are matched with the time scales of the life histories and community processes of beetles, they may indicate a useful spatial scale for investigations into their habitat and conservation requirements .

Amoros *et al.* (1987) viewed a river system as a continuum which changes longitudinally from source to mouth, laterally into the floodplain and vertically into groundwater aquifers. The longitudinal geomorphological continuum involves changes from small steep channels to large flat channels and is connected to an ecological continuum involving transport of organic matter. However these upstream - downstream gradients combine with confluence effects to give discontinuities in the continuum and divide the river up into *functional sectors.* For example, The River Rhone between Geneva and Lyons passes through a gorge section, a braided section, a meander section, an anastomosed section and then at the confluence of the River Ain another braided section. The boundaries between these *functional sectors* are set by geological disjunctions and confluences with major tributaries. Within each sector discrete landforms such as sedimentary bars serve as *functional units,* whose attributes such as sediment type and biotic character are termed *functional describers.*

All these approaches link fluvial processes to geomorphic and vegetational structures. Variation in these structures occurs at different scales and derives from environmental factors

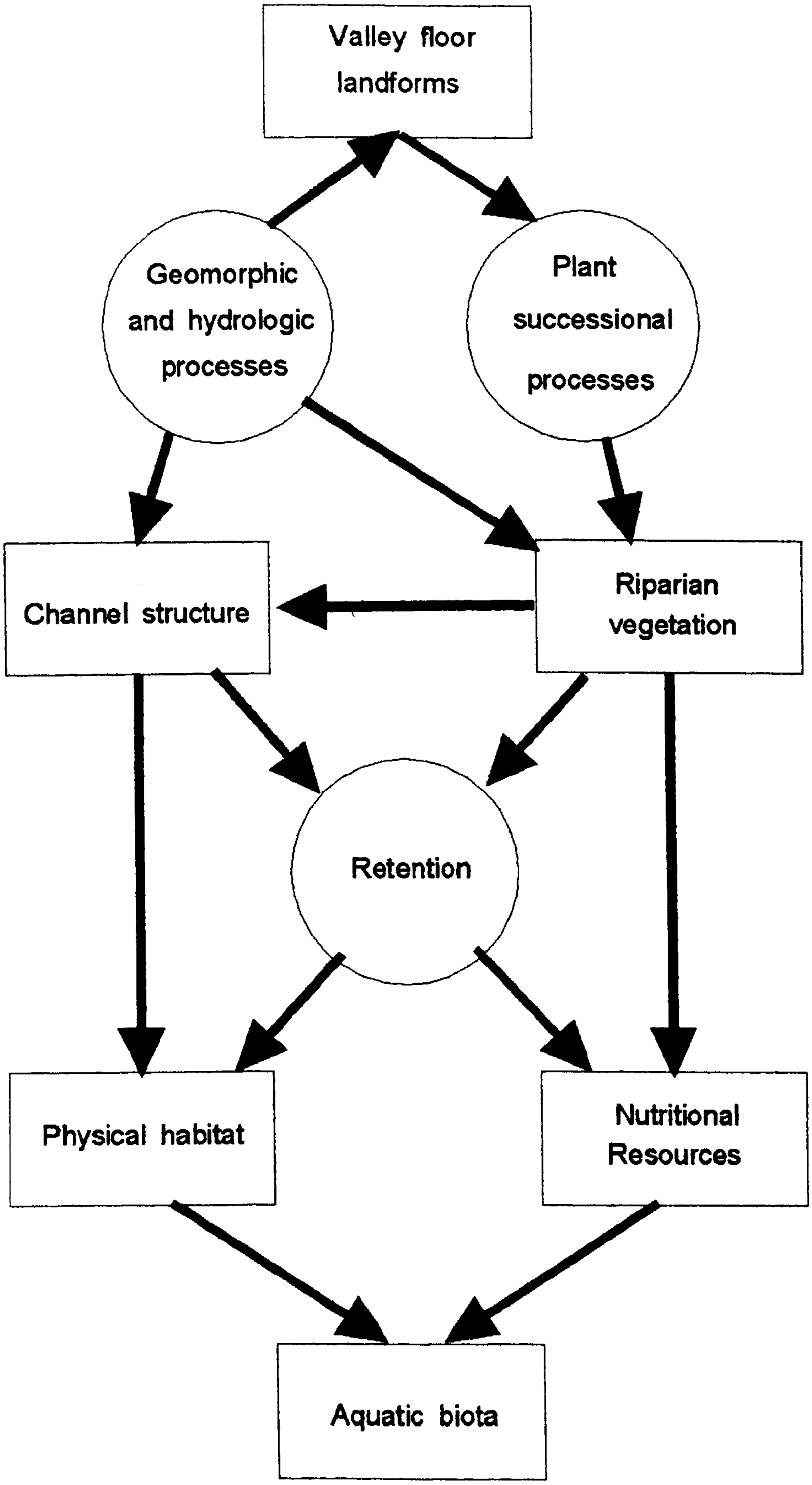

Figure 1.1 : Interaction of floodplain structures and processes (after Gregory *et al* 1991). Arrows represent predominant influences of physical and ecological processes (circles) on geomorphic and biotic components (rectangles).

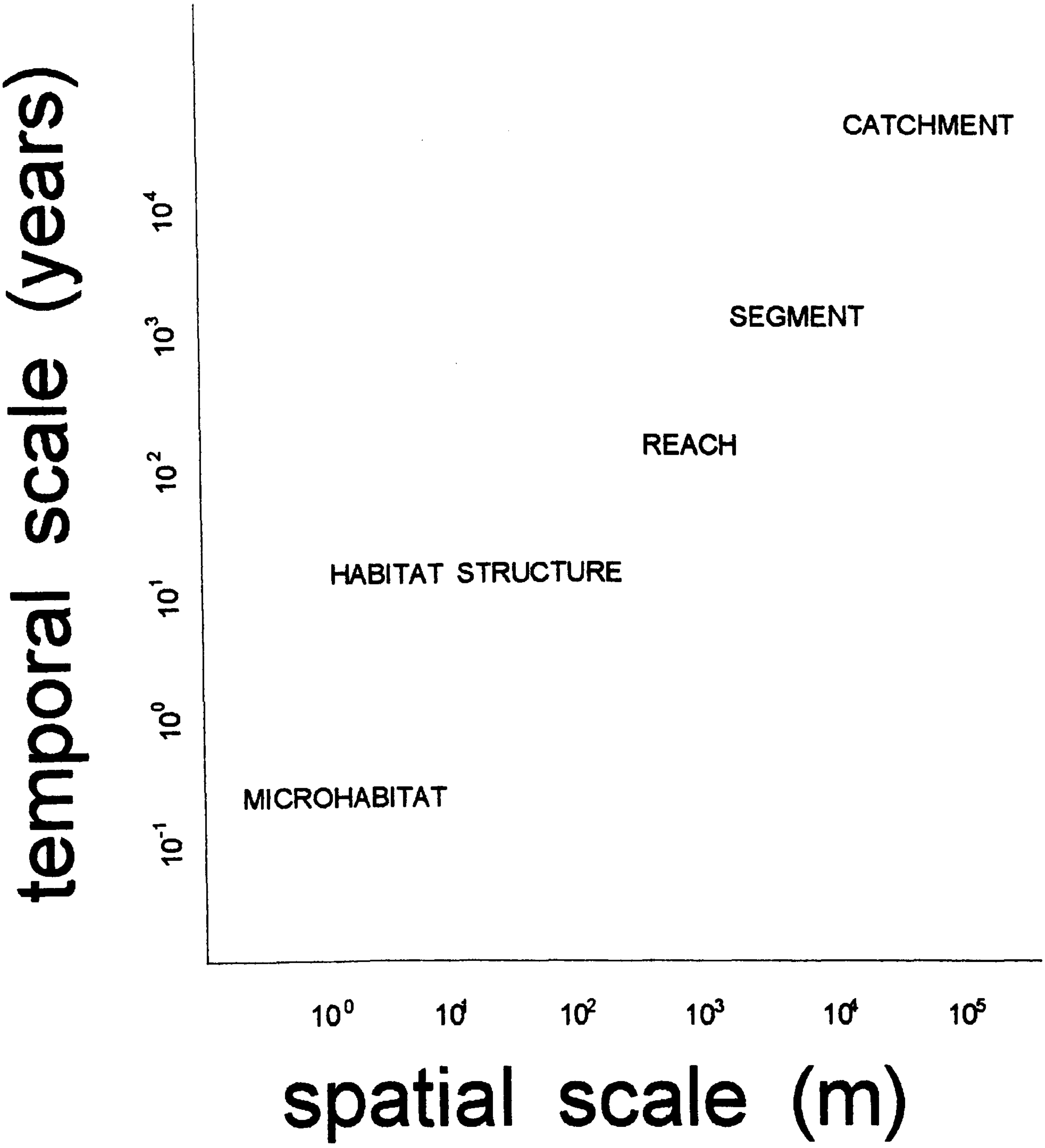

Fig. 1.2. Spatial and temporal scales of riverine habitats (adapted from a table in Naiman *et al* 1992)

such as climate and geology. A number of distinct types of semi-aquatic geomorphic and vegetation structures can be identified along river floodplains. They are here termed *habitat structures* or *biotopes* in concordance with the terminology of Samways (1994) who reserved the term *habitat* for the requirements of individual species from their environment.

1.2.1 The main channel - fluvial processes and geomorphic structures

Probably the most obvious feature of the riparian zone along the main channels of rivers is the variability in topography and nature of the substrate. This variability is both spatial and temporal (Gregory *et al.* 1991). It is related to the manner in which rivers transport particles which either roll along the river bed as bed load or are carried in suspension as sediment load. Flow rate and particle size are two important factors in this process. For any particle size there is a critical flow rate at which the particle will be moved (Petts 1983). Above this flow rate the particle will be picked up by the flow. Below this flow rate the particle will be deposited on the river bed. Larger particle sizes require faster flow rates to pick them up. However because of cohesive properties of fine sediments such as clay the critical flow rate required to pick them up is greater than the flow rate required to deposit them (Allan 1995). Therefore clay banks are more resistant to erosion than sand banks even though they are composed of smaller individual particles.

Flow rate along a river channel varies with changes of gradient and the sinuosity of the channel. Consequently along the river channel there are sites where banks are being eroded over a period of time and sites of net sedimentary deposition. Zones of erosion and deposition exist on the bends in active meanders (Ferguson 1981). On the outside of bends the flow rate is relatively high and typically the banks are sites of active erosion. Eroding banks composed of cohesive clay and silt on the outside of bends are usually steep and often undercut. Shallower slopes or slumped banks can be caused by the collapse of an undercut bank especially where cohesive fine sediments overlay uncohesive coarse sediments.

On the inside of bends the flow rate is relatively slow and the bank downstream of a bend is often a site of active deposition of sediment which when exposed become suitable for colonisation by riparian invertebrates. The sedimentary structure formed by this process is called a point bar.

In steep stretches of river, erosion can take place by incision into the bed to form gullies. Where the channel cuts down to the bedrock it can create a relatively stable riparian environment despite the high scouring power of the water flow. Moss growing on rock walls and large boulders provides shelter for a characteristic community of invertebrates. When the gradient decreases material is often deposited in mid-channel shoals in straight stretches of river which may fan out into a braided stream.

Lewin (1981) described the large variety of channel bars and shoals which can form in areas of coarse sediments. Mid-channel shoals termed medial bars can be longitudinal or lobate (transverse). When they migrate downstream they can evolve into diagonal or lateral bars attached to the bank. Lateral bars also occur at confluences where sediment is brought in by a tributary (Brookes 1988).

Different bar forms have different characteristics (Lewin 1981) and some of these differences are of potential importance to riparian beetles. Point bars are often formed from material derived from nearby eroding banks associated with long-lasting meanders. Consequently they tend to be relatively stable with regard to position. On the other hand mid-channel shoals may be derived from material whose origin is relatively remote. They are often mobile and can change form as they migrate down the channel. This variability in stability has implications for the range of life cycles that can be accommodated at a site.

Brookes (1995) considered that channel morphology is adapted to high flows which occur on average around once every two or three years. In many rivers in England and Wales this corresponds to bankfull discharge when the water level rises to the top of the banks. This means that the forms of many riparian geomorphic structures are determined by floods which happen at this frequency. However where rivers flow through easily erodable material such as sand, riparian structures can be altered more frequently (Ferguson 1981). By contrast in upland areas structures made of boulders are only affected by flood intensities which happen very infrequently. The stability of an erosional or depositional structure is therefore dependant on both the nature of the substrate and the flow regime of the river.

The amount of exposed sediment available for riparian invertebrates will partly depend on the extent of erosional activity within the catchment area. Many lowland rivers in England lack sufficient stream power to erode their banks even where their course is sinuous and in such cases well developed point bars are rare (Ferguson 1981). Exceptions include large rivers such as the Trent which has migrated over large areas of its floodplain in historical times (Petts *et al.* 1992, Salisbury 1995). Apart from the main channel Lewin (1981) recognised two other natural erosion domains which acted as sources for riverine sediments. Firstly hillslopes provide sediment through creep, wash, solution processes and localised mass movement. Secondly streamheads provide sediment through seepage and overland flow. Clearly the extent and nature of exposed sediment at any one site depends on a range of factors connected with entire catchment area upstream. These factors include topography, type of bedrock and drift and the extent to which vegetation interferes with erosional processes.

In Britain water levels are highest during winter months and lowest during the summer, although some Scottish rivers have a secondary peak in spring as a result of snow-melt (Ward 1981). Consequently, in most British rivers exposed sediment is available for use by riparian invertebrates from spring to autumn. The amplitude between mean winter levels and mean summer levels varies considerably from river to river and this is another factor leading to variation in the amount of exposed sediment between catchments. Daily fluctuations also vary considerably between catchments and this leads to differences between river segments in the frequency of disturbance of exposed sediments by high flows associated with spates.

Within catchments the nature of sedimentary bars changes longitudinally along the river. In upland areas where the channel gradient is high, finer sediments tend to be washed out to leave bars which are mainly composed of coarse sediments (Lewin 1981). By contrast in lowland areas there is a higher proportion of finer sediment in deposited material.

Segregation of sediments by particle size can be observed in most point bars. In its simplest form this involves deposits of coarser sediments at the head of the bar grading into finer sediments at the tail where the current is slower. Successive high flows may partially rework this material to give localised series of graded particles within the overall pattern. The situation is further complicated by the complex topographies of some point bars which are composed of several different lobes arising from successive depositions. Inner depressions may form within compound bars as a result of dissection by chutes or the blocking of former channels. These depressions often retain remnant pools and deposits of finer sediments.

Mixing of particle sizes can occur when smaller particles are trapped in the interstices between larger particles. Vertical stratification can occur when successive deposits of sediments occur under different flow conditions or when the nature of the sediment load changes. It is common in Britain for fine sediments to be protected against erosion by a superficial layer of coarse sediments. This is called armouring.

Substrates are generally classified by their particle size (Allan 1995). Particle size can be measured by sieving, but it is also easy to estimate broad classes of particle size in the field. Other attributes of potential importance to riparian beetles such as packing and surface texture are more difficult to measure.

Apart from their mineral content substrates also contain varying amounts of organic matter. Aquatic organic detritus is often classified by particle size into coarse particulate organic matter (CPOM, > 1mm), fine particulate organic matter (FPOM, > 0.45 um < 1mm) and dissolved organic matter (DOM, < 0.45um) (Maltby 1992). All of these size classes can be incorporated into exposed sediments. The source of the detritus may be upstream or vegetation and animals living on site. Consequently the quantity and type of detritus depends on both local and catchment-wide factors. Typically a large amount of CPOM enters the system through headwaters and is converted to FPOM through physical and biological processes as it is carried downstream.

1.2.2 The main channel - vegetation

Haslam (1978) describes both aquatic and riparian vegetation along rivers in Britain and North America and discusses the influences of flow, substrate type, nutrients, channel width and slope. Coarse sediments are characterised by communities of fringing herbs described as semi-emergent, somewhat bushy, short dicotyledons. However the shallow rooting systems of fringing herbs makes them susceptible to scouring by spates. Coarse sediments subject to scouring are therefore often free of vegetation and provide areas of bare substrate when exposed during low flows. Fine sediments are colonised by communities of tall monocotyledonous plants with deep rooting systems which are resistant to scouring. Even when the above-ground part of the plant is destroyed or damaged, regeneration can take place from the roots. Their resistance to scouring coupled with the binding properties of their roots retard bank erosion and provide relatively stable microhabitats (Wade 1995).

Species of tall monocotyledons often dominate species-poor communities both along the margins of slow-flowing river channels and floodplain wetlands where they create a reedswamp habitat (Rodwell 1995). Characteristically they produce a high weight of leaves and litter (Day *et al.* 1988, Hills *et al.* 1994).

Lateral zonation of riparian vegetation is noticeable along many rivers. Church (1992) described a well defined boundary at the lower limit of continuous terrestrial vegetation and suggested that the duration, depth and periodicity of flooding at various bank heights may play a significant role in the distribution of plant communities in the active channel below this boundary.

1.2.3 Floodplain wetlands

Floodplain biotopes receive water, sediment and organic matter from several sources. During peak flow conditions a large amount of fine sediment is deposited across large areas of the floodplain when floods overtop the bank. Floodwater also imports organic matter, mainly FPOM and DOM, and dissolved minerals. CPOM is produced on site and this may either be retained by the habitat structure or partially removed by floodwater. Groundwater sources may either maintain water levels between flooding or even provide the only source of surface water via springs. A further source of water is rainwater.

Several types of semi-aquatic habitat structure can be recognised from the literature. Crevasse splays are fans of sediment deposited onto the floodplain by high flows breaking through levees on the bank (Gregory & Walling 1973). They have received little attention from ecologists. There is more information available on backswamps and abandoned channels.

In braided rivers mid-channel deposition causes the channel to split up into distributaries. When more permanent islands are formed the channel is said to be anastomosed. In small side-channels, flows and stream power are considerably reduced leading to deposition of finer sediments than in the main channel. These side channels can eventually become filled with sediment so that flow above ground becomes seasonal or even restricted to rare floods. Abandoned river courses can also arise from sudden changes in course (avulsions) and cut off events following the formation of chutes across point bars or the necks of meanders (Lewin 1992).

Remnant marshes, pools and lakes are potentially important, semi-aquatic features in abandoned channels. When they occur in old meanders they are called oxbow lakes. A more general term employed here is *backwater*. The term *cut-off* is avoided because it has been applied to several different features. The ecology of backwaters has not attracted much attention in Britain, although they are known to be of importance as spawning grounds and refuges for fish (Petts 1984). Research into floodplain sedimentology suggests that they must have been a common feature of the Holocene landscape (Lewin 1992). Work on the floodplain of the River Rhone has revealed two different types of vegetational succession in backwaters depending on the nature of the abandoned channel (Bravard *et al.* 1992). In abandoned meanders and anastomosed channels the succession proceeds slowly from open water communities through reedswamp, *Salix cinerea* fen to *Alnus glutinosa* carr. In former braided channels the succession proceeds more quickly through a stage dominated by *Phalaris arundinacea* to *Ulmus minor* woodland. Chemical analysis of sediments in these old channels also revealed two patterns of development (Rostan *et al.* 1987). Sediments with a high organic content were found in large sites in meanders which were abandoned before 1880 - 1890 and are termed paleopotamon. Lower organic contents were found at smaller sites more closely connected with the main channel and derived from braided channels abandoned after 1880 - 1890. This type of site is termed plesiopotamon, or parapotamon if there is still a permanent connection with the main channel.

Floodplain wetlands also occur where levees along the riverbank prevent the return of floodwater to the main channel. When the water ponds in low lying areas backswamps can form. Gilman (1994) classifies these along with other types of wetland according to their stage of vegetational and hydrological succession from marsh, through fen to carr or bog.

The succession in both backwaters and backswamps is similar in both broad vegetational and hydrological terms to the classic hydrosere (Tansley 1939). Marsh develops on a mainly mineral substrate either along the margins of open water or in frequently flooded sites, but as organic matter builds up the substrate becomes peaty and a fen community develops. As the peat builds up the ground surface becomes isolated from the groundwater and the fen community is replaced by carr or in areas of high rainfall, ombrogenous bog.

This succession from aquatic to terrestrial systems is driven by organic matter produced within the site. Hydrological connection to the main channel can either retard this succession or send it in a different direction (Bravard *et al.* 1992). Flood flows through abandoned channels can remove organic matter and retard peat formation. The duration, frequency, season and depth of flooding, termed the hydroperiod (Lugo *et al.* 1990) has a direct influence on the composition of the vegetational community. Many trees in their early stages cannot tolerate prolonged submersion. Consequently sites which are subject to more frequent and prolonged flooding have their succession retarded unless submersion is avoided by the formation of floating mats of vegetation (Kangas 1990). Deposition of silt by floodwaters maintains the mineral content of the substrate which is necessary for the maintenance of marsh communities. When the succession is driven by silt rather than by organic matter produced on site, the marsh stage proceeds quickly to a terrestrial stage without any fen stage (Rostan *et al.* 1987).

Fluctuating water levels are a common type of disturbance which can result in reversals and perturbations of the succession (Kangas 1990). When hydroperiods increase, trees die and forest systems can revert to fen or marsh in a process termed paludification. Drought leads to aeration of the substrate, oxidation of peat and, when the water table rises again, a marsh community based on mineral substrates results.

Studies of the ecology of disturbance have concentrated on forest, arid grasslands and marine littoral ecosystems (Pickett & White 1985). However, flooding is clearly an important disturbance factor in both floodplains and along main channels. Sousa (1984) listed five descriptors of disturbance regimes (see table 1.1), all of which can be applied to disturbance by flooding. The spatial scale of disturbance by flooding is highly characteristic, being much larger in the longitudinal dimension than the lateral dimension.

Succession can also be regulated by alluvial aquifers which maintain a high water table; variations in the chemical properties of the groundwater can result in the development of either an oligotrophic or a minerotrophic vegetation community (Bravard *et al.* 1992). Connectivity between groundwater and the main channel is affected by the geology and topography of the

Descriptor	How measured
spatial scale	size of disturbed area
magnitude	*intensity* measured as the strength of the disturbing force (e.g power of current), *severity* measured as the damage caused by the disturbance (e.g. mortality, habitat change)
frequency	number of disturbances per unit time
predictability	variance in the mean time between disturbances
turnover rate	the mean time required to disturb the entire area in question

Table 1.1. Descriptors of disturbance regimes (adapted from Sousa 1984).

floodplain (Brinson 1990). Thick clay strata and clay plugs in abandoned channels restrict groundwater movement between the main channel and its floodplain.

Figure 1.3 summarises the successional processes operating in river floodplains.

1.2.4 Impact of river management

Engineering works on river channels can be divided into two main categories. Firstly channelisation involving embankments and direct modifications to the channel are carried out to alleviate flooding, to assist drainage schemes in the adjacent floodplain, to control erosion and to aid navigation. Secondly rivers are impounded by weirs and dams for a variety of purposes: fishing, navigation, flood control, water mills, hydroelectric schemes, water supply and irrigation.

Channelisation is the method used in most flood alleviation schemes in Britain. It has severe effects, both direct and indirect, on semi-aquatic habitat structures. Direct effects include the removal of physical structures, bankside vegetation and especially trees (Brooker 1985). Brookes (1985, 1988) lists the main operations involved in modern channelisation works. Resectioning involves widening or deepening the main channel to achieve a trapezoidal section sufficient to take the desired peak discharge. Sedimentary bars may be totally removed. Banks are regraded to a 45° slope which replaces existing steep eroding banks and lateral bars. Sometimes banks are revetted. This involves lining the banks with materials ranging from willow piling to concrete. In urban areas the channel may be completely lined with concrete or steel sheets.

Realignment involves the shortening of river channels by artificial cut-off channels to by-pass meanders. The abandoned meanders, if not filled in, then become floodplain structures while the number of structures within the main channel decreases. Realignment also increases the slope and thus the flow within the main channel resulting in greater bed scouring. In some cases a nick point develops in the channel bed and progresses upstream. The increase in sediment load leads to greater deposition downstream of the realignment. Consequently realignment can change channel morphology both upstream and downstream. Both resectioning and realignment can also have large short term effects during the construction phase when downstream sediment loads can reach forty times their natural level.

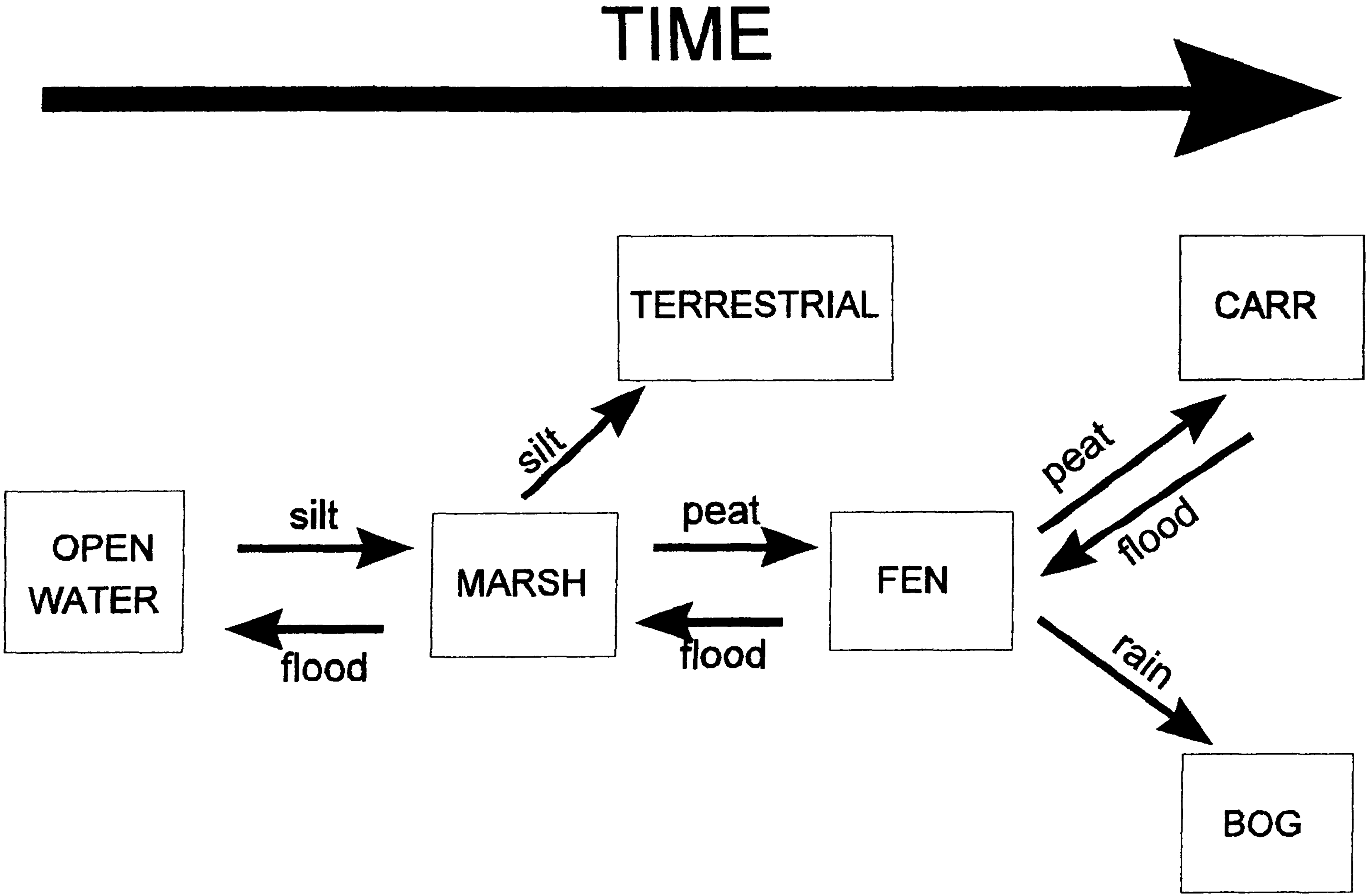

Fig 1.3 Succession in floodplain wetlands

Bank protection in the form of groynes is used to protect banks from erosion in large rivers flowing through easy erodable materials such as sand. This measure encourages the deposition of sediment and so increases the area of exposed bars.

Embankment involves the construction of a flood bank to a height designed to cut down the frequency of floods reaching the floodplain. Petts (1987) points out that this reduces connectivity between the main channel and the floodplain. This would have a significant effect on floodplain biotopes whose ecological succession is regulated by flooding. Bravard *et al.* (1986) studied the effects of the construction of a submersible embankment which imposed a single navigation channel onto braided and anastomosed stretches of the Rhone. Slow accumulation of silt and organic matter occurred in formerly active channels but aggradation in the main channel raised the water table in old channels nearby maintaining open water conditions and retarding the succession. Consequently the embankment created a new generation of floodplain habitat structures whose rate of succession varied with distance from the main channel. However these new structures were gained at the expense of diversity of main channel habitat structures. Elsewhere on the Rhone, Bornette & Heiler (1994) found that deepening of the channel led to some abandoned channels becoming more oligotrophic due to the increased influence of hillslope aquifers, whereas other old channels dried out because of the lowering of the water table.

Petts (1984) gives a comprehensive account of the effects of dam construction on channel morphology, vegetation and aquatic fauna due to changes in hydrology, water quality and sediment transport. Of particular relevance to sedimentary structures is the interception of sediment and organic matter by reservoirs. Grimshaw & Lewin (1980) found that the Afon Rheidol below a dam which cut off 84% of its catchment, had sediments 16 to 17 times lower than a neighbouring unregulated river. Large amounts of fine sediment are deposited in the impounded reservoir and the build of nutrients encourages algal blooms. Changes in downstream patterns of erosion and sedimentation take place throughout a significant length of river and may take several decades to be completed. Outflows of clear sediment-free water rapidly erode the channel causing incision or bank erosion where the bed is protected by armouring. However, because peak flows are diminished in reservoir outflows, stream power is also reduced and increased deposition of sediment is often observed at the confluence of unaffected tributaries downstream. Reduction of peak flows also reduces the lateral flow of water to floodplain wetlands.

Much less information is available on the effects of smaller impoundments. Murphy *et al.* (1995) describe how rivers modified for navigation by locks and weirs have a low habitat diversity with a predominantly depositional regime with low seasonal variations in water level. Prolonged dry weather may result in low flows and almost lacustrine conditions.

Natural lakes act as sediment traps in a manner similar to artificial impoundments. However by the 1980s the effects of man-made lakes on stream flow exceeded that of natural lakes by a factor of three (Petts 1984). In small rivers natural impoundments can also result from debris jams such as fallen trees (Church 1992) or the activities of beavers which Naiman *et al.* (1986) found to have considerable effects on the hydrology, channel geomorphology and community productivity of river systems in Canada.

1.2.5 Effects of recreation

Liddle & Scorgie (1980) review the effects of recreational activities on both aquatic and riparian wildlife. Of water-based activities, boating is considered to have the greatest impact. Wash from boats not only erodes the bank but also affects vegetational composition because some plants are better able to withstand the eroding action of wash than others. Mooring and accidental collision can also erode areas of bank and completely remove areas of riparian vegetation.

A variety of shore-based activities can lead to trampling of riparian vegetation. Use of a stretch of the River Ouse near Huntingdon by anglers resulted in replacement of tall riparian vegetation by a short sward of grasses and plantains along 20% of the riverbank, rising to 30% near an access track (Liddle & Scorgie 1980) . This had the effect of breaking up a continuous habitat into small units. Anglers can also cause localised erosion of the bank where they fish. The impact of anglers on habitat structures varies according to the type of water body and associated vegetation. Lowland sites with soft margins and vegetation subject to trampling by a high density of anglers may be affected more than sparsely vegetated upland sites on coarse sediments with a low density of anglers (Murphy & Pearce 1987).

Clearly recreational activities have an impact on riparian vegetation. Disturbance also affects nesting birds (Liddle & Scorgie 1980), but the responses of riparian invertebrates to recreation along rivers are unknown.

1.2.6 Effects of discharge and abstraction

Under natural conditions British rivers show a wide variation in water quality because of differences in the nature of dissolved substances or solute load (Walling & Webb 1981). Upland catchments with high rainfalls tend to have a lower concentration of dissolved ions and a lower pH than lowland catchments containing basic bedrock and mineral-rich drift. However human activity has changed the water quality of rivers to the extent that at low flows the major proportion of many lowland rivers is made up of treated discharge from industrial and sewage outfalls (Mason 1991). The high concentration of pollutants in some lowland rivers is also connected to abstraction of water upstream.

Eutrophication of lowland rivers arises from agricultural run-off containing nitrates and sewage outfalls containing phosphates. In parts of Western Europe and North America levels of dissolved nitrogen and phosphorus have increased by a factor of 10 to 50 from natural levels (Allan 1995). In floodplains with established agriculture nitrates originate largely from fertilisers. However, the drainage of wetland areas in floodplains can also lead to long term increased nitrate loads through oxidation of drying organic matter in the soil (Harris & Parish 1992). Eutrophication affects the productivity, cover and species composition of vegetation communities.

Discharge of sewage into rivers has long been known to have a deleterious effect on most natural aquatic macroinvertebrates by removing oxygen from the water (Mason 1991). The effects on semi-aquatic macroinvertebrates are likely to be quite different. Green (1983) recorded species rich assemblages of 79 species of Coleoptera from both untreated and treated sewage sludge drying beds at three sites near Birmingham. The species recorded included many normally found on freshwater shores as well as those associated with decaying vegetation and dung. Hammond (1971) described differences in the habitats of the rove beetles, *Platystethus cornutus* and *P. degener* as being related to the content of organic matter in mud.

Heavy metals are potentially important pollutants in sediments. Persistent heavy metal contamination originating from 19th century mining was reported by Lewin *et al.* (1977) in reworked sediments in Wales. Transport of heavy metals which are adsorbed onto clay particles can result in concentrations of heavy metals in floodplain deposits and other fine sediments in lowland parts of the catchment far from their points of origin which can be mining operations or industrial discharges (Rang & Schouten 1989). Although heavy metals may affect benthic macroinvertebrates, their effects on semi-aquatic organisms are unclear. Fowles (1988) found that the distribution of beetles on coarse sediments in Wales was uncorrelated with heavy metal concentrations and Green (1983) recorded a rich assemblage of beetles from sewage sludge which contained increased levels of heavy metal concentration arising from trade waste.

1.2.7 Impact of catchment-wide land use

Lewin (1981) lists causes of increased soil erosion and consequent increased entry of fine sediments into river systems. These include agricultural tillage, ditching and field drainage, industrial activity and in uplands deep ditching as part of coniferous afforestation. Osborne (1988) investigated a late bronze age deposit from the River Avon in Worcestershire and found a sub-fossil assemblage of elmids associated with fast-flowing gravel rivers, conditions quite different from the modern nature of the river which is slow-flowing and silty. Many of these elmids have very restricted modern distributions although they are widely recorded in deposits up to the Roman period. It is suggested that the disappearance of these species at the Avon site and elsewhere was due to the influx of silt into the river following deforestation and the introduction of agriculture as reported by Shotton (1978). The siltation of British rivers which followed prehistoric landscape changes from forest to agriculture has probably affected some semi-aquatic shingle bank species in a similar fashion.

Park (1977) reviews some effects of urbanisation on river channels. Urbanisation in the catchment area removes vegetation and covers large areas of ground with impermeable surfaces. These changes together with the action of storm drainage systems lead to a large increase in run off with consequent faster build up of higher peak discharges. Urbanisation is regarded as the most important cause of man-made flooding (Brandon 1987) and leads to changes in channel size and geometry. Increased run off and ground disturbance during large-scale construction works can, like agricultural tillage, increase sediment load by a factor of five to ten (Walling & Gregory 1970). Consequently urbanisation upstream is likely to result in greater and more frequent disturbance of both main channel and floodplain habitat structures as well as larger volumes of sediment being deposited at least in the floodplain. Thoms (1987) reported less sediment than expected in the River Tame, an urban river in the British midlands, suggesting that excess sediment caused by construction works is quickly resorted by the increased flow velocities and frequency of flood discharge. Thoms also found that the sediment derived from urban sources was finer than in natural stretches. Urban sediments can include some exotic types of material such as plastic, glass, domestic refuse and supermarket trolleys (Park 1977)!

Floodplain wetlands have been directly affected by a variety of land uses and some biotopes such as floodplain forests are now very rare in Europe (Brinson 1990). Conversion to agriculture has considerably reduced floodplain wetland and most of what remains has been affected by drainage and eutrophication. Drainage not only has the direct effect of lowering water levels but also creates conditions which lead to increased stocking levels and the infilling of small dykes (Mountford & Sheail 1984). Grazing interferes with the natural succession of wetland vegetation resulting in the establishment of graminoid communities (Tallis 1983).

Floodplains are also important areas for gravel extraction. Although this can destroy large areas of floodplain wetland, the resulting gravel pits have been recognised as potentially valuable for birds and other forms of wildlife (Giles 1992). Koch (1977) found that some riparian beetles colonised gravel pits up to 7 km from the Rhine. Plachter (1986) found that at least two thirds of the ground beetles associated with natural gravel bars along the River Isar in Bavaria had colonised similar habitat structures in gravel pits.

1.2.8 Conclusions

Studies of the physical environment, aquatic biotic communities and riparian vegetation have resulted in advances in the understanding of hydrologic, geomorphic and successional processes. These advances also provide potentially valuable insights into how the same processes could affect the physical environment of invertebrates in semi-aquatic habitat structures. Figure 1.4 shows how Gregory *et al.*'s (1992) model of the riverine aquatic ecosystem (fig. 1.1) can be adapted for semi-aquatic ecosystems. The rectangles are components which vary spatially and the circles are components which give rise to temporal variations. Table 1.2 lists the environmental factors which influence the fluvial processes operating at scales corresponding to the levels of whole catchment and river segment (*sensu* Naimann *et al.* 1992) or functional sector (*sensu* Amoros *et al.* 1987). The different types of semi-aquatic habitat structure formed by these processes are listed in table 1.3.

In any one segment of floodplain between major confluences, the factors listed in table 1.2 tend not to vary very much. However other environmental factors vary at a smaller scale. The factors listed in table 1.4 vary within individual habitat structures. Consequently an individual habitat structure at a particular site contains microhabitat structures covering a range of values for each factor. Furthermore individual habitat structures at separate sites contain different ranges of values. For example a point bar associated with a riffle may be composed of sparsely vegetated shingle grading to coarse sand, while a point bar further downstream may be composed of sand and silt with patches of well developed vegetation.

Human activities have resulted in major modifications to the riverine environment starting probably in the Neolithic period and escalating from the 19th century onward. Understanding the natural processes operating in this environment leads to an understanding and prediction of the consequences of river and land management. Potentially important impacts of human activities for invertebrates of semi-aquatic habitat structures are listed in tables 1.5 and 1.6.

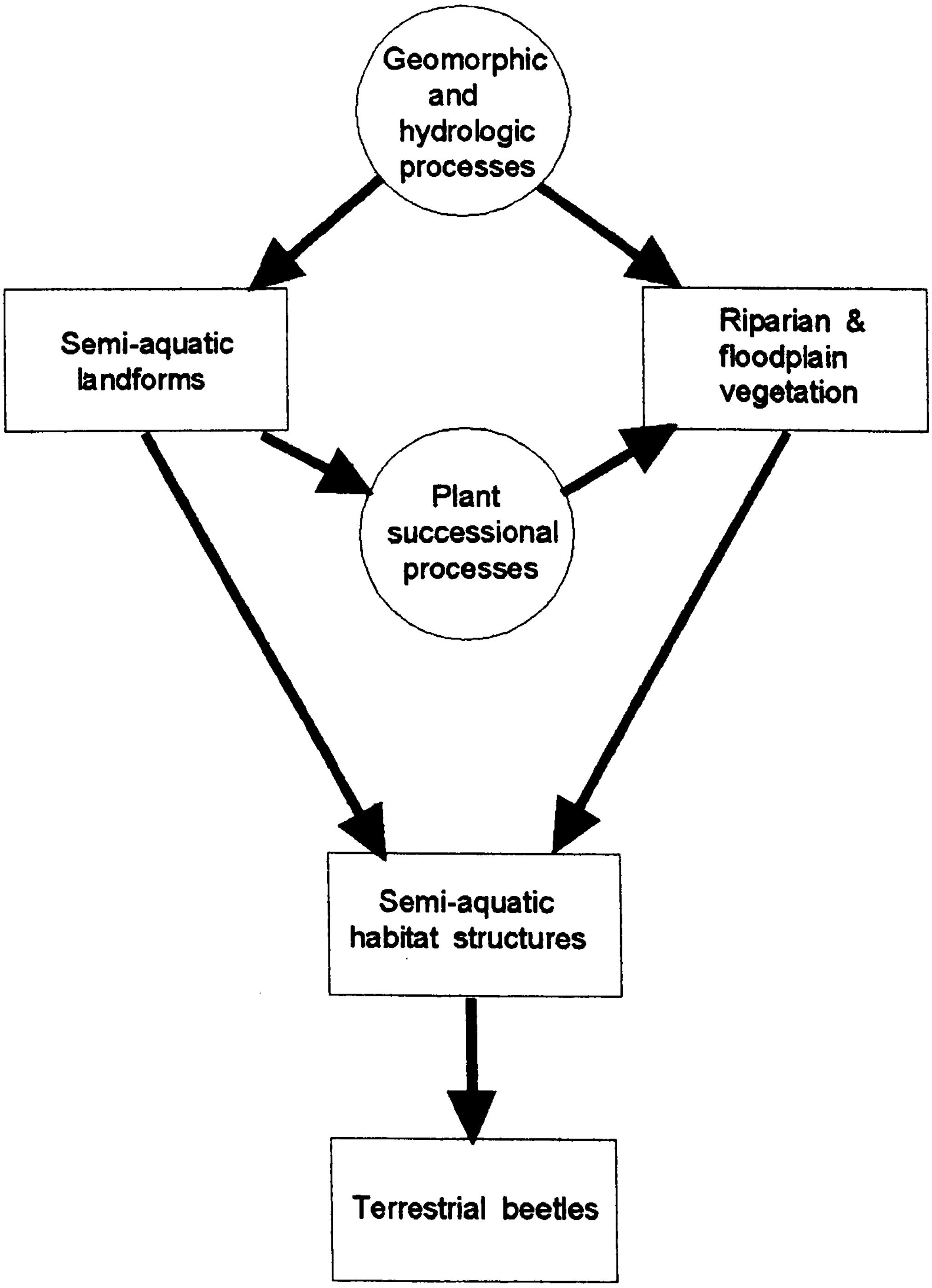

Fig. 1.4. Interaction of fluvial and ecological processes to produce semi-aquatic habitat structures for terrestrial beetles.

Process	**Potentially important attributes**	**Large scale environmental factors which influence attributes**
Hydrology (flow above ground)	Peak discharge / stream power Flow regime - seasonality Flow regime - daily variations or spatiness	Catchment area Rainfall - volume Rainfall - temporal variations Topography Solid geology Drift geology Land cover - evapotranspiration Land cover - ecological productivity Temperature - evapotranspiration Snowfall Glaciers
Hydrology (ground-water flow)	Seasonal fluctuations	
Sediment transport, erosion and deposition	Volume Particle size Mineral content	
Transport of organic matter	Volume Type	
Transport of solutes	Influence on riparian vegetation Toxicity	

Table 1.2. Fluvial processes of potential importance for beetles of semi-aquatic habitats.

Sediment transport status	Habitat structure	Classes of each structure described in literature	Factors varying between classes
Nett erosion	eroding bank	undercut bank or cliff	topography
		slumped bank	
	incised gully / ravine		
Nett deposition	sedimentary bar	medial bar (transverse, longitudinal, diagonal)	position in channel, shape, stability (Lewin 1981)
		point bar	
		lateral bar / berm	
	backwater	parapotamon	connectivity with main channel flow (Rostan et al 1987)
		plesiopotamon	
		paleopotamon	
		open water	stage of vegetational succession (Bravard et al 1992)
		reed-swamp	
		fen	
		carr	
	backswamp	marsh	stage of vegetational and hydrological succession (Gilman 1994)
		fen	
		bog	
		carr	
	crevasse splay		

Table 1.3. Habitat structures of potential importance for beetles of semi-aquatic environments.

Environmental variable	attribute
Hydrology (flow above ground)	peak flow rate
	connectivity with main channel
Hydrology (ground-water flow)	height of water table
	lateral flow rate
Substrate	particle size
	cohesiveness (resistance to erosion)
	proportion of organic matter
	type of organic matter
	packing
	surface texture
Vegetation	cover
	species composition / successional stage
	productivity (litter)
Topography	slope
	complexity (remnant pools etc)
	aspect

Table 1.4. Small scale environmental variables which are of potential importance for beetles of semi-aquatic habitat structures

	Sedimentary bars	Floodplain wetlands
Forest clearance and agricultural tillage	Increase in sediment Change from coarse sediments to silt and clay Eutrophication leading to changes in vegetation	Drainage and conversion to terrestrial habitat Eutrophication leading to changes in vegetation
Floodplain grazing		Interruption of vegetational succession and change to graminoid community
Urbanisation	Decrease in stability and change in particle size and vegetation	Increase in flooding leading either to retardation of succession or change in type of succession
Floodplain gravel extraction	Possible increase in sediment although this is subject to control in U.K.	New sites

Table 1.5. Possible effects of catchment land uses on some semi-aquatic habitat structures.

	Sedimentary bars	Floodplain wetlands
Resectioning	Removal	Lowering of water table
Realignment	Conversion to floodplain structure Increased scouring upstream and downstream leading to lack of stability and change in particle size and vegetation	New sites
Groyne construction	New sites	
Embankment		Reduction in flooding leading either to accelaration of succession or change in type of succession
Impoundment	Increased scouring downstream leading to lack of stability and change in particle size and vegetation Decrease in particle size and increase in organic matter upstream	Possible reduction in flooding downstream from reservoirs leading either to accelaration of succession or change in type of succession
Recreational use including boating and angling	Bank erosion Changes in vegetation community Localised reduction in vegetation cover	Bank erosion Changes in vegetation community Localised reduction in vegetation cover
Discharge of sewage etc and abstraction	Eutrophication leading to changes in vegetation	Eutrophication leading to changes in vegetation Heavy metal contamination of sediments

Table 1.6. Possible effects of river management practices on some semi-aquatic habitat structures.

1.3 The organisms

The geomorphic and vegetational structures which are the products of these processes can be viewed as habitat structures available for occupation by populations of beetles. These structures are often recorded as habitats in, for example, river corridor habitat surveys (NRA 1992), but they do not necessarily represent ecologically functional units (Harper *et al.* 1995). Harper *et al.* (1992) empirically analysed the functional relevance of habitat structures, defined in terms of geomorphic and vegetational structures in streams, by studying the distribution of aquatic invertebrate species between these structures.

Information on the autoecology of species and synecology of species assemblages may give insights into the functional relevance of various attributes of habitat structures. This section looks at how the species traits of riparian and floodplain beetles are expressed in environmental requirements which are constrained by the fluvial and successional processes described in the previous section.

1.3.1 Taxonomic groups with semi-aquatic habitats.

Table 1.7 shows the families of British beetles with semi-aquatic habitats except for those confined to coastal habitats. The numbers of relevant species in each family were identified from individual species accounts in Koch (1989 - 92), Hyman (1992, 1994) and from personal experience in Britain, France and Spain, supplemented by works on individual families (Clarke 1973, Lindroth 1977, Boyce *et al.* 1991, Majerus 1991, Johnson 1992, 1993). Species are categorised as riparian if they are predominantly associated with open shores. They are characterised as wetland if they are associated with more vegetated marshes and mires. Because of difficulties in defining boundaries between such broad habitat types, numbers must be regarded as approximate, but they do give some indication of the taxonomic distribution of the potential diversity of beetles along river floodplains. The riparian species are all liable to be found by main river channels, although they also occur by lakes and trickles on crumbling cliffs. The wetland species have the potential to occur in floodplain wetlands, but may also occur along the main channels of slow-flowing rivers.

76% of riparian species and 54% of wetland species belong to just two families: the Staphylinidae or rove beetles and the Carabidae or ground beetles. These and some of the

Family	**Approximate number of species associated with**		
	river margins	**wetlands**	**trees near water**
Carabidae	60	53	
Microsporidae	1		
Georissidae	1		
Hydrophilidae	3	4	
Ptiliidae	3	8	
Staphylinidae	128	159	
Pselaphidae	3	11	
Scarabaeidae	1		
Clambidae	3	1	
Scirtidae	2	17	
Byrrhidae	1	1	
Phesphenidae		1	
Heteroceridae	3		
Limnichidae	1		
Dryopidae	2	7	
Elateridae	5	2	
Cantharidae		4	2
Melyridae		2	
Nitidulidae		4	
Rhizophagidae	2		
Silvanidae		1	
Cryptophagidae	1	12	1
Phalacridae		2	
Corylophidae		3	
Coccinellidae	1	3	
Lathridiidae		1	
Anthicidae	1		
Chrysomelidae	1	50	15
Apionidae		2	
Curculionidae	24	46	18
total	*248*	*394*	*36*

Table 1.7. Families containing specialist semi-aquatic beetles associated with rivers and wetlands in Britain (not including species confined to coastal habitats).

other families represented in the table are normally considered to be predominantly ground-living predators (Good & Giller 1991, Thiele 1977), although some fossorial Staphylinidae feed on algae (Herman 1986) and Lindroth (1949) has pointed out that the majority of Carabidae are in fact omnivorous. Hering and Plachter (1997) reported that riparian ground beetles along the River Isar in Germany feed largely on aquatic insects and their *exuviae* which drift ashore on the water surface. Families such as the Cantharidae, Chrysomelidae and Curculionidae, whose adults tend to climb plants and trees, are less well represented, especially in the riparian category.

1.3.2 Morphological and behavioural adaptations

Adult ground beetles show a variety of morphological adaptations to different lifestyles (Forsythe 1987). Evans (1990) classified ground beetles into three groups according to the anatomy of their legs, which suited them to different locomotor lifestyles. *Rapid runners* have long thin legs and are able to sprint over the surface, but they are weak at pushing against a force. *Strong wedge-pushers* have thicker legs and are slower runners, but their large hind trochanters enable them to push horizontally into crevices. *Powerful burrowers* have shorter legs still and so are much less mobile above ground. However, their powerful leg muscles enable them to burrow into the ground. Often the front tibia are flattened and equipped with teeth to facilitate digging and their bodies are elongate and pedunculate. Evans (1990) found that most ground beetles were *strong wedge-pushers,* but noted the high numbers of *rapid runners* and *powerful burrowers* in riparian habitats where their adaptations are suited either to a cursorial or fossorial lifestyle in areas of bare sand. *Strong wedge-pushers* are suited to a compromise lifestyle and are equipped both for activity on the surface and also for pushing into hiding places at the end of activity periods. They are also well equipped for activity in deciduous litter which requires pushing against vegetative obstacles (Evans & Forsythe 1984). A remarkable morphological adaptation is exhibited by species of *Omophron* which have a leg structure similar to *rapid runners*, but the body shape of a dytiscid water beetle and this enables them to move through loose sand (Forsythe 1991). Andersen (1978) found that species of *Cicindela, Omophron* and *Bembidion* subgenus *Chrysobracteon,* which have long legs for running as well as the ability to burrow into sand, have similar modifications to the front tibiae.

A similar gradient in leg morphology seems to occur in the Staphylinidae. Several species of *Stenus* s. str. , *Paederidus* and *Tachyusa*) have long thin legs and are often encountered running over bare soils in riparian habitats. Coiffait (1972) mentioned two genera with tibiae adapted for a fossorial lifestyle. *Bledius* and, to a lesser extent, *Carpelimus* are two riparian genera with adaptations for burrowing. Remarkably few, if any, authors mention the long thin body shape of rove beetles which would appear to be an adaptation for moving through fissures in the ground and tangled vegetation in litter and tussocks. It is also useful for sheltering in hollow plant stems during hibernation (Palmen 1949).

Andersen (1985a) divided Norwegian species of *Bembidion* into three groups according to their hind body shape. He found that flat parallel-sided species are confined to gravel or stone shores and banks, whereas more convex species, which tend to have more rounded elytra, live in more or less vegetated sites on fine sand, silt or clay. Species of intermediate morphology tended to occur on a wider range of substrate types. These results were supported by Desender (1989) in a study of seven Belgian species of riverbank *Bembidion*, who found a similar relationship between the convexity of body type and particle size of the preferred substrate type. Andersen (1985a) proposed that a flattened body-form is an adaptation for moving in a restricted environment under stones to find food and breeding partners. He lists several further beetles which are confined to coarse substrates and which have flattened bodies. These include ground beetles in the genera *Perileptus* and *Nebria*, rove beetles in the genera *Thinobius*, *Hydrosmecta* and *Aloconota*, and the click beetle, *Fleutiauxellus maritimus*. However this group exhibit a wide range of leg morphology and fall into several groups according to Evans (1990). Beetles such as *Nebria*, *Aloconota* and *Fleutiauxellus maritimus* have long legs which are adapted to running fast over the surface and which would be disadvantageous when moving through gravel or under stones. Possibly their flattened body shape is adapted less for activity in this environmental and more for hiding during periods of inactivity.

Well vegetated habitat structures such as fens contain several species of ground beetles and rove beetles capable of climbing plants. *Demetrias* species and several fenland *Stenus* species have enlarged bilobed tarsal segments similar to Chrysomelidae and Coccinellidae which are habitual plant-climbers. Several species of *Quedius* and *Hygronoma* are adept at climbing the vertical walls of glass tubes (personal observation). Landry (1994) found that, out of four species of *Agonum* in a Canadian lakeside fen, *A. nigriceps* had the highest climbing ability and also the longest tarsi. He associated this climbing ability to a preference on the part of *A. nigriceps* for flooded areas with tall emergent vegetation. Other fenland beetles such as *A. thoreyi* and *Paederus riparius* survive flooding by clinging to submersed vegetation and becoming torpid (Palmen 1945). Palmen (1945, 1949) showed that many species can survive submersion in this way at least in cold water for long periods of time. However, Arens and Bauer (1987) observed that *Blethisa multipunctata* is quite active when it enters the water and suggested that it habitually enters water in order to escape predation and to hunt.

Joy (1910) studied the behaviour of beetles during flooding of main river channels. He identified four types of active locomotion over the water surface to escape from submersion. Firstly several species of rove beetles in the subfamily Steninae together with the ground beetle, *Agonum albipes*, can skim over the water surface. In order to do this they secrete a substance which lowers the surface tension behind them and propels them forward. Some species of *Stenus* together with several species of *Bembidion* swim with their legs, whereas other species of *Stenus* raise themselves above the water surface and walk. Joy also observed the rove beetle, *Gnypeta carbonaria*, raising itself above the surface with its abdomen held aloft like a sail to be propelled by the wind. This behaviour has also been observed in a species of *Myllaena* in Spain (G.N. Foster, pers. comm.). Andersen (1968) recorded two species of *Bembidion* flying from the water surface at temperatures above 25° C and suggested that species of *Bledius* and *Gnypeta* can fly from the water at lower temperatures. When on the water surface, beetles tend to orientate themselves toward the largest dark object on the horizon which is usually the bank (Jenkins 1959, Andersen 1968). Zulka (1994) reported that some ground beetles associated with floodplains were relatively fast at reaching the bank when stranded on water. However, Joy (1910) also notes that several species of *Quedius* and many smaller rove beetles are very poor at moving in the water and his observations of huge numbers of beetles in flood litter deposited on the bank suggests that many individuals escape submersion passively by clinging onto fragments of vegetation.

Andersen (1968) studied the response of riparian beetles to rising floodwater and suggested that fossorial adults and larvae tended to remain in the substrate. However, adults are often forced out of coarser substrates, where the current tends to be stronger. Cursorial species retreat up the bank as the flood advances.

Rehfeldt (1984) looked at the characteristics of ground beetles in several different habitats in a river valley in Lower Saxony and found that riverbanks contained a high proportion of both diurnal species and macropterous species. He suggested that macroptery in riparian ground beetles enabled them to colonise new habitat structures created by flooding. However, macroptery in ground beetles is not always associated with good dispersal ability. Dispersing ground beetles are often weak fliers which disperse passively using wind currents and often time their flights with optimal weather conditions, whereas species that use flight to hunt or migrate tend to be strong fliers in control of their flight direction and geographically conservative (den Boer 1990). Some full-winged beetles cannot fly at all. The flight muscles of many insects degenerate during periods of reproductive activity (Johnson 1969) and Nelemans (1987) found that most individuals of the full-winged ground beetle, *Nebria brevicollis*, in cultivated land in the Netherlands have undeveloped flight muscles and disperse by walking.

1.3.3 Life histories

Larsson (1939) listed details of the reproductive cycle in all Danish ground beetles and recognised three different types of cycle. All of them involve one generation per year. *Autumn-breeders* reproduce in the autumn and overwinter as larvae. *Spring-breeders with autumn activity* overwinter as adults and reproduce in the spring after which the adults die off. The new generation of adults emerges in the autumn but does not reproduce until after hibernation. *Spring-breeders without autumn activity* have a similar breeding season, but freshly emerged adults remain inactive in the autumn. Lindroth (1949) noted that some species showed regional variations in Fennoscandia and introduced an additional group which overwintered both as larvae and adults. He also relabelled *spring breeders* as *imaginal hibernators* and *autumn breeders* as *larval hibernators*. Thiele (1977) pointed out that in many regions Larsson's *autumn breeders* actually breed in the summer and gave examples of several variations to his life history types involving diapause and partial overwintering of adult *autumn-breeders*. Furthermore he reported that *spring-breeders* can exhibit different levels of autumn activity in different parts of their range and are best treated as a single group. Clearly there are wide variations from Larsson's original simple classification even within single species. Butterfield (1986) found that, at higher altitudes in northern England, *Carabus problematicus* females bred in their second year rather than their first. Den Boer & den Boer-Daanje (1990) rejected Larsson's classification into *spring breeders* and *autumn breeders* after reviewing the breeding periods of 68 species in the Netherlands. They discovered a continuous gradation of breeding seasons between spring and autumn. They also found evidence of winter breeding in several species. Due to partial overwintering of adults in some species, they also rejected Lindroth's classification into *larval hibernators* and *imaginal hibernators*. However, they did find that species could be classified into species with summer larvae and species with winter larvae and these roughly correspond to Larsson's *spring breeders* and *autumn breeders,* terms which are still widely quoted in the literature.

Kasule (1968) recognised four types of reproductive cycle in rove beetles based on field studies in Scotland. Species with summer larvae are equivalent to Larsson's *spring breeders* and species with winter larvae are equivalent to *autumn breeders. Stenus impressus* was categorised as a species with autumn and winter larvae. Eggs were laid between the end of July and the beginning of October. Some larvae matured in the autumn and overwinter as adults while some remained as larvae throughout the winter. The final group includes two species of *Othius* in which larvae were present for a greater part of or throughout the year. In fact *O. myrmecophilus* bred all year round, while *O. punctulatus* had a break from breeding in the autumn (Kasule 1970). Luff (1966) also found that *Stenus impressus* overwintered as larvae, but unlike Kasule did not find any adults overwintering. He also found that *Stenus clavicornis* bred in spring and summer and had summer larvae. Walker (1985) was able to allocate six species to the first two of Kasule's groups on the basis of fieldwork in woodland and pasture in Durham. Frank (1967, 1968) also labelled seven woodland species in Berkshire as either summer breeding (= *spring breeders*) or winter breeding (= *autumn breeders*), but found that some adult *Quedius picipes*, which is an *autumn breeder,* overwintered after breeding. Steel (1970) divided Omaliinae into those which lay eggs in the summer and those which lay eggs in the late autumn. However there are variations which include winter activity and periods of adult quiescence.

Although the reproductive cycles of rove beetles seem to fit into categories similar to those of ground beetles, they have received much less attention especially amongst the smaller species, It is possible that a wider range of cycles remains to be discovered. Bordoni (1982) mentioned that some Oxytelinae and Aleocharinae have three generations per year. Herman (1986) quoted reports of two or more breeding periods in Danish and Japanese species of *Bledius*, but it is unclear whether this is due to more than one generation per year or a prolonged breeding season of a single generation.

Lehmann (1965) found that in ground beetle assemblages along the Rhine, *autumn breeders* predominated in woods and meadows above the riverbank but in areas regularly inundated by the river they were almost entirely replaced by *spring breeders*. The only *autumn breeder* present on the bank was *Amara fulva*, which was confined to the topmost zone. Lehmann reviewed faunal lists of riverbank ground beetles from Scandinavia and found that they were composed almost entirely of *spring breeders*. He attributed the scarcity of *autumn breeders* to the difficulty of their larvae in escaping the effects of high winter flows. Wetland ground beetles show a similar pattern to riparian ground beetles. Murdoch studied the life histories of 21 wetland ground beetles in marshes in Britain and found that all but one are *spring breeders*. Furthermore he examined data on Scandinavian ground beetles and found that only 11 out of 124 hygrophilous species were *autumn breeders*. Like Lehmann he suggested that larvae are vulnerable to inundation during the winter, whereas adults can escape more easily into hibernation quarters. However, the proposed vulnerability of larvae to flooding does not explain the preponderance of *spring breeders* along the banks of the Rhine (Lehmann 1965) and rivers in Norway (Andersen 1969) whose seasonal high water levels occur in the spring or early summer when the larvae are present along the bank. Lehmann's suggestion that the majority of larvae along the Rhine are killed each summer and that populations are sustained by annual immigrations each spring implies that the banks of the Rhine act as a huge mortality sink for local riparian populations and seems implausible. Furthermore Andersen (1968) reported high survival rates of eggs, larvae and pupae during submersion and even recorded a higher survival rate for larvae than adults.

There are some riparian species which overwinter as larvae. *Nebria gyllenhali, Bembidion lunatum* and *Trechus secalis* are riparian or wetland specialists classified by Andersen (1969) as exclusively *larval hibernators*. In addition the reproductive cycles of riparian ground beetle species are not always constant. Meissner (1983) reported that a population of *Bembidion femoratum* by a German gravel pit was sexually active all year round and egg laying occurred over a long period from March to September. Andersen (1969) recorded teneral adults of several riparian species of *Bembidion* in early spring suggesting occasional larval or pupal overwintering. He also found that *Asaphidion pallipes* hibernates commonly as both larvae and adults.

It is not known whether the domination of *spring breeders* amongst riparian ground beetle assemblages is reflected amongst rove beetles. Methodically collected information on riparian rove beetles is lacking, although Horion (1963, 1965, 1967) gives records of many riparian and wetland species overwintering as adults. On the other hand Steel (1970) reported that riparian species of *Lesteva* breed in autumn and overwinter as larvae. He also found larvae of the riparian species *Psephidonus (= Geodromicus) nigrita* in September and October but suspected that it hibernated in the adult stage. Clarke (1973) gives breeding details of the heterocerid, *Heterocerus fenestratus,* which conform to the standard pattern of a *spring breeder.*

Usually evidence of breeding in riparian or wetland structures relies on examination of the female ovaries or the presence of teneral adults (e.g. Dawson 1965, Kurka 1975, 1976) However Krogerus (1948) included field observations of developmental stages when he studied the insect fauna of a Finnish lake margin whose seasonal water levels were affected by snow-melt. The ground beetles were nearly all *spring breeders* (except *Agonum obscurum & Amara brunnea*) but did not arrive at the breeding site until late May or June. Numbers built up very quickly with strong migrations from hibernation sites on the warm days. Some species arrived one week later than others. Many species showed an abundance peak in late summer as well as in June. However there was no breeding activity at this time. Krogerus suggested three explanations for the non-appearance of some species at this time:

1) They visit the lake margin in spring but do not breed there.

2) They overwinter at their pupation sites.

3) Adults do occur at the lake margin in late summer but in such low numbers that they are not sampled.

Young larvae first appeared in June close to the water margin. As the water level dropped, the adults moved with it and most died off several weeks later. The larvae lived deep within the soil and did not move from a zone which became progressively drier and more remote from the water margin. By July remaining adults were concentrated near the water's edge, young larvae were found higher up the bank and older larvae were found higher still. Pupation took place in flat depressions on mud under a thin layer of moss. Adults emerged from their pupation site in August. Mass emergences often followed heavy rain. The teneral adults hardened up in dry areas high up on the bank and then moved down to the water margin before migrating to hibernation sites in September. There were annual fluctuations in the timing of these events which were related to weather conditions.

Andersen (1978) observed *Bembidion argenteolum* in the laboratory ovipositing in burrows excavated in sand whereas *B. schueppeli* and *B. semipunctatum* oviposited in natural crevices. He found that the larvae of several species were able to burrow but that this depended on the nature of the substrate. Bauer (1974) found that larvae of *Elaphrus* species are active surface predators. They are nocturnal and so avoid the adults which are active by day on the same area of riverbank. Field records of wetland rove beetle larvae and pupae are very scarce. Welch (1965) reported finding two pupae of *Stenus canaliculatus* in soft rotten timber beneath the bark of a fallen willow on the muddy banks of a stream.

Interest in the hibernation sites of riparian beetles has been generated by observations of their absence from riparian habitats during the winter. For example, Palmen & Platanoff (1943) found that the summer fauna of Karelian riverbanks disappeared in mid September and returned suddenly in mid May. In Sweden Lindroth (1942) concluded that the ground beetle, *Oodes gracilis,* flies some distance from its summer habitat in order to hibernate. Krogerus (1948) reported that most species of a Finnish lake shore assemblage of ground beetles and rove beetles were found in large numbers above marginal areas in leaf litter in sallow scrub in the winter. Only a few species were found by the water's edge and these were often washed up into the sallow scrub by winter floods. Some species were never found in winter and must have overwintered at some distance from the lake. There were fewer species in this group but they included many of the larger species. Krogerus reported isolated instances from elsewhere in Finland of some of these species (*Blethisa multipunctata, Pterostichus minor. P. nigrita & Agonum versutum)* being found in leaf litter around 1km from the nearest wetland.

Palmen (1945) observed that some shore habitats such as extensive reedbeds growing in shallow water do not lose their summer fauna in the winter. He investigated overwintering in six beetle species which spent the summer in a reedbed growing in the shallow margins of an almost freshwater inlet of the Baltic and found that *Agonum fuliginosum* moved higher up the bank to an area dominated by sedge during the autumn. However, there was no sudden emigration as had been reported by Palmen & Platanoff (1943). There was also a partial migration of the rove beetle, *Paederus riparius,* to the sedge zone. The other species investigated together with some *Paederus riparius* stayed throughout the winter in the inundated reedbed. Several small species including many rove beetles were found sheltering in hollow reed stems in ice (Palmen 1949). Laboratory experiments suggested that the presence of litter is important in enabling many beetles to survive freezing conditions underwater (Palmen 1945, 1949). Species of marsh *Agonum* and *Pterostichus* in Oxfordshire were found hibernating in rotten logs and grass tussocks on site, although some individuals washed out by winter floods moved to grass tussocks in surrounding grassland (Murdoch 1966).

Andersen (1968) investigated hibernation sites on rivers in Norway where winter water levels are not the highest of the year. He found that many species (several species of *Bembidion, Hypnoidus* and many rove beetles including *Bledius* species) overwintered close to their breeding grounds, albeit slightly higher on the riverbank. There is evidence that some of these species may change their hibernation site in the event of flooding. He also found overwintering larvae of the ground beetles, *Nebria gyllenhali* and *Bembidion lunatum* on the riverbank. Andersen suggested that *Bembidion semipunctatum* and *B. quadrimaculatum* hibernate in areas adjacent to the riverbank and that other species of *Bembidion* together with many rove beetles that probably hibernate as adults (species of *Ochthephilus, Thinobius, Stenus, Tachyusa* and *Gnypeta*) fly to hibernation sites more distant from the river. Similar variations in hibernation strategies are reported from elsewhere. *Agonum albipes* was found to be absent from the banks of mountain streams in Bohemia between late October and mid March (Kurka 1976), whereas *Bembidion tibiale* was present on gravel deposits all year round (Kurka 1975). Dieterich (1996) captured four species of *Bembidion* (*B. ascendens, B. conforme, B. andreae* and *B. tricolor*) hibernating in traps filled with coarse sediment buried at depths of up to 75 depths of up to 75 cms in gravel bars by the River Isar in Germany. Meissner (1983) found that *Bembidion punctulatum* and, to a minor degree, *B. femoratum,* undertook seasonal migration flights over long distances between their breeding sites by a German gravel pit and their hibernation sites which were suspected to be hedges and woodland edges. Bauer (1974) found that in Austria *Elaphrus cupreus* and *E. riparius* moved away from the water to find dry ground into which they dug several centimetres in order to pass the winter. He found no evidence of long-distance flight to hibernation sites remote from the river as suggested by Krogerus (1948).

The available information on hibernation for wetland beetles including those of open shores suggests three hibernation strategies.

1) Beetles can stay at their breeding sites and cope with winter conditions.

2) Beetles can move to adjacent areas to escape winter inundations. This can be accomplished either actively or passively in flood debris (Joy 1910).

3) Beetles can migrate to hibernation sites well away from the river.

Individual populations may adopt more than one strategy (Palmen 1945).

There has been plenty of speculation that riparian beetles need to be good dispersers in order to recolonise riverbanks after flooding (Lindroth 1949, Lehmann 1965, Holeski 1984). On the basis of three decades of pitfall trapping and window trapping in the Netherlands, den Boer (1990) considered that a dispersal phase amongst ground beetles was the rule rather than the exception. He suggested that some species, especially the larger ones, disperse by walking, but that individuals from many macropterous and wing-dimorphic species disperse by flight to new breeding sites after emergence from the pupa. Lindroth (1949) reviewed flight records of Scandinavian ground beetles and found that for *spring breeders* there was a peak of activity in the spring suggesting that dispersal takes place between hibernation and breeding. Many rove beetles also disperse by flight. Bauer (1989b) found a high incidence of vagrant species in an upland site in northern England and Lindroth (1949) quotes a report that rove beetles were the most abundant beetle family in high altitude aerial plankton.

1.3.4 Habitat preferences

In any consideration of habitats it is necessary to be clear about definitions of terms. Firstly habitats can be considered at different scales. Secondly habitats of beetles can be defined as the requirements of species in terms of physical and chemical factors such as temperature, humidity, salinity, soil particle size etc. (Lindroth 1949) or in the more traditional terms of habitat structures such as woodland, riverbanks, mammal nests etc. (e.g. Koch 1989-1992).

The scale problem has been addressed for rivers by Naiman *et al.* (1992) (see section 1.2) who classified environmental processes according to the spatial and temporal scale on which they were operating. One habitat scale which has been defined in terms related to the requirements of beetles is microhabitat. Luff (1966) defined microhabitat as *the minimum part of the ecohabitat which supplies the requirements of the species in its particular physiological state at that time.* Information on the life histories of riparian and wetland ground beetles suggests that they could potentially have five different microhabitat requirements at different life stages, namely larva, pupa, teneral adult, hibernating adult and active adult. Furthermore breeding and feeding adults restrict their activities to different times of the day (Thiele & Weber 1968) and may use different microhabitats when resting and when active. By extending Luff's definition of microhabitat we can regard the habitat of an organism as the sum of all the microhabitats required to complete its life cycle.

This definition fits in the use of *habitat* as an autoecological term to describe the interaction of a species with its environment (Samways 1994). There is then a choice of description of habitats in terms of quantitative environmental factors which relate to the requirements of species and species assemblages, or in terms of traditional habitat structures reflecting land management categories and vegetation communities which are easy to identify and interpret as products of fluvial or successional processes. This choice will depend on the context in which habitat descriptions are to be used.

On the subcontinental scale the geographic distributions of beetles are often matched against macroclimatic influences portrayed as isotherms and isohyets or dispersal events following macroclimatic change (Lindroth 1949). At the landscape scale many works on beetles often characterise their habitats in terms of land management units or vegetation community type. For example Buse (1988) described the habitats occupied by beetles in Wales as herb-rich grassland, wet flush and several other categories defined by their dominant plant species. However, in a series of laboratory experiments Lindroth (1949) showed that several Fennoscandian ground beetles traditionally regarded as limestone grassland species should more accurately be described as thermophilic and xerophilic. Lindroth concluded that the decisive influences on the local distribution of ground beetles are local climatic factors and soil factors, both physical and chemical.

Lindroth's analysis has implications for the concept of a riparian species. Riparian ground beetles may not be obligate riverbank-dwellers. They may be species whose physical and chemical requirements are matched by the combination of local climatic and edaphic factors found in the riparian environment. This hypothesis is supported by the fact that many species characteristic of open exposed riverine sediments are also found on similar artificial structures such as gravel pit margins (Plachter 1986, Gerken *et al.* 1991) or on similar natural structures such as lake margins and sea shores (Andersen 1969, 1983). Superficial differences in occupied habitat structures may sometimes mask a similarity of environmental conditions. Furthermore the same environmental conditions may be provided by superficially different habitat structures in different regions. Table 1.8 shows the variation in habitat structures occupied by three species of ground beetle in Britain, Holland, Scandinavia and Central Europe. Similar variations are found in the rove beetles. For example, *Scopaeus laevigatus* is characteristic of riverbanks and associated wetlands in Central Europe (Koch 1989-1992) and Spain (Lott, personal observation) but is one of a group of such species which have only been recorded in Britain from beside trickles on collapsing sea cliffs along the south coast (Hyman 1994). In northern Norway, Andersen (1983) found a wide variation in the degree to which species of *Bembidion* were restricted to riverbanks. Some species were mainly confined to one type of river, whereas four species occurred in a wide range of sites including those away from water. He also reported that, although *Bembidion lunatum* was confined to sites by flowing water in northern Norway, it occurred in a wider range of sites including gravel pits and roadsides in central Norway.

Species	Britain	Holland (Turin et al. 1991)	Central Europe (Koch 1989-1992)	Scandinavia (Lindroth 1985)
Elaphrus riparius	barren sand or clay by freshwater (Lindroth 1974)	young moist habitats in polders and other colonisation sites	sunny sand and mud banks, brickpits	banks of standing or slow-running waters in open country
Clivina collaris		open localities, predominantly riparian	open sand and gravel banks	cultivated areas with humus-rich soil
Bembidion schuppeli	on damp fine sand and silt or fine shingle with 50-100% cover of low herbage on riverbanks (Reid & Eyre 1985)		shaded muddy banks of woodland pools	on moist silty vegetated riverbanks

Table 1.8. Regional variations in the occupation of habitat structures by three species of ground beetles

Palmen & Platanoff (1943) characterised beetle species along riverbanks in southern Karelia according to their habitat preferences within the region. 63 species were mostly confined to riverbanks and were described as stenotopic species. Eurytopic species were defined as those found in other damp habitats such as lake margins and woodland pools. However, Lindroth (1949) found that their list of eurytopic ground beetle species contained several which are regarded as stenotopic riverbank species in Sweden and other parts of Finland and suggested that a species is often more stenotopic at the edge of its range. Turin *et al.* (1991) calculated values of ecological amplitude for Dutch species of ground beetles based on the range of habitat structures recorded for each species. Species with a large ecological amplitude were regarded as eurytopic. However their values were based on *a priori* selected habitat structures which may be unevenly distributed along the natural environmental gradients which are important to ground beetles. Therefore these values are not necessarily related to their true ecological amplitude which would reflect their degree of adaptability to a range of environmental conditions. Moreover their values were based on pitfall samples from a set of sites in which riparian habitat structures were poorly represented and in which floodplain wetland habitat structures were not differentiated. Consequently species with strong associations with riverine semi-aquatic habitat structures emerged with high values for their ecological amplitude.

These arguments show that the designation of a species as stenotopic or eurytopic has only local validity because a species' occupancy of habitat structure types may vary between regions. Furthermore these terms are subjective in that they are relative to the range and classification of habitat structures selected for analysis. However, although the characterisation of species as stenotopic riparian or wetland may lack ecological validity, it could have some use in conservation work because it reflects the way that the landscape is divided up for land management.

Relatively little work has been done on the preferences of species for different types of semi-aquatic habitats at the scale of river segment or catchment, termed *macrohabitat* by some authors (Spence 1977, Andersen 1983). Andersen (1983) found that some species were mainly found by rivers of a certain size category. Fowles (1989) found that some species of ground beetles had an uneven longitudinal distribution on shingle banks along the River Ystwyth in Wales. *Bembidion punctulatum* was confined to the lower mature stretches whereas *Bembidion tibiale* was mostly restricted to the higher stretches and smaller tributaries lower down. Similarly in a study of ground beetles on gravel banks along the River Isar in Bavaria Plachter (1986) found that alpine and subalpine species were concentrated in the upper stretches although they were present in smaller numbers on gravel banks as far as 110 km north of the mountains. He reported that species confined to lower levels tended to be more eurytopic.

In Karelia, Palmen and Platanoff (1943) studied the distribution of beetle species between steep banks which were not covered by floods and sloping banks which were more frequently inundated. They reported that species confined to structures subject to inundation tended to be hygrophiles whereas species confined to steep banks tended to prefer dry habitats. They also found that many species preferred banks composed of substrates with a particular particle size and these were characterised as shingle, sand, fine sand/clay and clay. Many authors have stressed the importance of substrate particle size in determining the presence of particular species of ground beetles (e.g. Lindroth 1945, Andersen 1969, Reid & Eyre 1985, Desender 1989, Koch 1989-92, Gerken *et al.* 1991), but unfortunately they are often imprecise with regard to scale and usually employ a rather simple classification of substrate particle size which does not take account of the local heterogeneity that usually occurs along rivers. Most work on substrate type has been carried out at the microhabitat scale.

The vast majority of work on microhabitat preferences for riparian beetles has been done on ground beetles, especially active adults, although Andersen (1969) noted that larvae of *Bembidion* species had stricter microhabitat preferences than adults. Andersen (1969, 1983) described a number of different microhabitats using a wide range of environmental factors including height on bank, substrate particle size and organic content, vegetation cover, shade and presence of litter. He found that many species of Norwegian *Bembidion* were present in high numbers at only one or a few microhabitats, although a few species seem to change their microhabitat preferences from site to site. Similarly in Bavaria Plachter (1986) found that a large proportion of shingle bank ground beetle species were collected mainly in one of four microhabitats classified by distance from water and vegetation cover. Along the Weser, Gerken *et al.* (1991) found that the activity of *Bembidion decorum* and *B. punctulatum* was mainly confined to sparsely vegetated, coarse substrates, whereas *Bembidion articulatum* was active over a wide range of substrate particle sizes and percentage vegetation cover. Lehmann

(1965) found that ground beetle species abundances varied between lateral zones on the banks of the Rhine. Bauer (1974) regarded shade as an important factor in separating the microhabitats of *Elaphrus cupreus* and *E. riparius.*

In laboratory experiments Andersen (1978) and Meissner (1984) found that several species of *Bembidion* preferred substrates of a certain particle size, but that their preferences were often affected or overridden by differences in moisture. Substrate preferences can also be affected by the presence of other species (Sowig 1986). Species vary in the range of substrate particle sizes that they prefer (Andersen 1978, Meissner 1984). Laboratory experiments also show that temperature and humidity responses vary with time and the physiological state of the beetle (Andersen 1985b, 1986). Evans (1988) found that riparian ground beetles are attracted to volatile chemicals collected from microflora associated with their habitats in the field and suggested that they use them to locate suitable microhabitats.

Clearly a number of environmental factors are important in determining the microhabitat preferences of riparian ground beetles and that these vary from species to species. Other than descriptive accounts very little information is available on the microhabitats of riparian rove beetles.

In wetland sites the distribution of species of ground beetles between different vegetation communities has been studied by Dawson (1965) and Landry (1994). At a microhabitat scale Dawson (1965) found variations between species of ground beetle in their occupation of different layers, ranging from the soil through litter to low vegetation. Landry (1994) found that some species of *Agonum* in Canadian marshes were strongly associated with particular microhabitats such as emergent tussocks and concentrations of dead vegetation.

1.3.5 Habitat templets

In recent decades major progress in ecological theory has arisen from attempts to find a predictive relationship between habitat and species traits such as life history strategies. Southwood (1977) proposed that habitat acted as a templet which selected certain species traits. Southwood (1988) attempted to unify four major theories linking habitat and species traits and identified a habitat type in which growth potential or productivity is high, disturbance is low and interactions with other organisms (e.g. competition) is high as a common feature to all theories. Habitats deviate from this condition along three main axes related to disturbance, adversity or environmental stress and degree of biotic interaction (fig. 1.5). The adversity axis is often interpreted environmentally as productivity (Hildrew & Townsend 1987, Eyre 1994). Inclusion of the third axis could be somewhat contentious. For example, Begon *et al.* (1990) regard predation as a type of disturbance.

However, the disturbance axis is a feature common to all theories and its importance in the selection of life history strategies has been the subject of a large amount of literature. Highly disturbed environments favour r-selected organisms which invest a large proportion of their resources in fecundity, whereas stable environments favour K-selected organisms which invest a large proportion of their resources in survivorship. There has been a wide range of interpretation of r- and K-selection (Parry 1981) and the original concept has been broadened to take in a variety of perspectives (e.g. Southwood 1977). In simple life-history terms r-selected organisms tend to have earlier maturity, more offspring and breed only once. Most riparian ground beetles appear to be univoltine (Larsson 1939) suggesting little scope for variation between r- and K-selection in this respect, although some wetland species of *Agonum* and *Pterostichus* live for two years and breed twice (Dawson 1965, Murdoch 1966, Wasner 1979), a possible tendency toward a K-strategy. In addition Wasner (1979) found that *Agonum thoreyi* had a higher egg production than related species of *Agonum* suggesting that fecundity may be a more effective descriptor of r- and K-selection among ground beetles than generation time.

Because they are associated with temporary habitat structures, r-selected insects also show a high rate of dispersal in order to be able to colonise newly disturbed sites (Schowalter 1985). Aukema (1987) found that in wing-dimorphic populations of the ground beetle, *Calathus erythroderus,* full-winged females tend to have higher fecundity and a longer egg-laying period than short-winged females. Den Boer (1977) characterised 64 common species of ground beetle in a cultivated region of the Netherlands as either good dispersers or poor dispersers according to the ratio of wing length to length of elytron and their frequency of capture in window traps. He found that poor dispersers tended to exist in populations with an even spread of abundances, whereas good dispersers are also found in populations of low abundances which could represent unsuccessful or nascent colonies (den Boer 1977). Poor dispersers also tend to have lower population turn-overs (frequency of extinction and

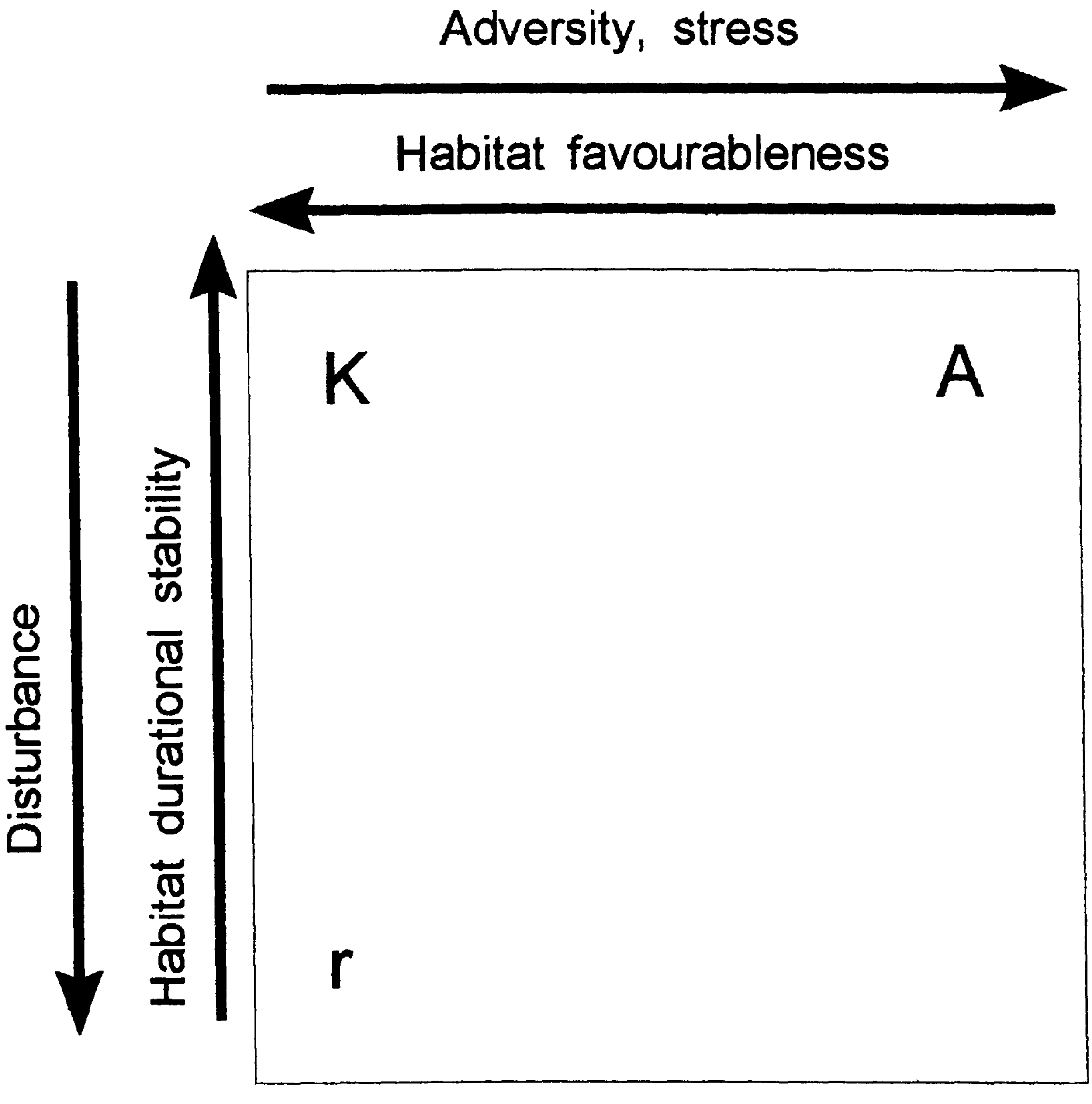

Fig 1.5: Habitat templet (from Southwood 1988)

recolonisation) and within a population it is suggested that genes associated with poor dispersal are positively selected in a stable environment (den Boer 1987). Den Boer (1990) suggested that ground beetle species of old stable habitats are threatened with extinction in a fragmented landscape because they have lost the ability to disperse across unsuitable disturbed areas between habitat islands.

Eyre (1994) analysed the distribution of ground beetles in 160 sites in northern England in terms of their response to a two dimensional disturbance - productivity matrix. Most species were found to have significant responses to these indices and were classified into ten strategy groups. Eyre argued that it should be possible to describe the distribution of ground beetles in terms of environmental stresses (in which he includes disturbance), but pointed out that this is most easily achieved in limited situations where environmental stresses can be identified more confidently.

Townsend & Hildrew (1994) devised a habitat templet for predicting the habitat distribution of species traits in aquatic systems within the upper Rhone valley. Their first axis was related to temporal scale of disturbance and their second axis was spatial heterogeneity which interacted with the first axis, in that heterogeneous habitats were more likely to ameliorate the effects of disturbance through the provision of refuges. A large amount of data from thirteen taxonomic groups was used to test the predictions of Townsend & Hildrew (1994), but although there was a significant relationship between species traits and habitat utilisation and although species traits were significantly arranged along the axes of spatial and temporal heterogeneity for most groups, the species traits did not follow the predicted pattern (Resh *et al.* 1994). Resh *et al.* (1994) suggested that, despite the failure of habitat templet theory to predict the precise species traits present along a disturbance gradient, two important lessons for ecologically sound river management emerged from the study. Firstly habitat does act as a templet for species traits. Secondly species traits are relatively uniformly distributed within each taxonomic group. It could be added that habitat templets can be used to interpret correlation between environmental factors and species traits in a functional context and that if the functional relationship between natural habitat characteristics and species traits is understood for a certain group, then we may be able to predict the species traits favoured by human activity.

Habitat templet theory is based on the premise that habitats provide the templet on which evolution forges characteristic species traits (Southwood 1977). Evans (1990) suggested that morphological traits present in one habitat may have been pre-adaptations which were selected in an ancestral habitat. Traits found in species occupying modern habitat structures created by human activity have probably evolved in natural habitats if we accept that they have existed for a short period in the timescale of evolutionary processes. However, we can still use the predictive methodology outlined above if we also consider selection of species traits in a habitat structure as an ecological process governing occupancy of that structure.

1.3.6 Species assemblages

An ecological community is defined as a group of organisms from all taxonomic groups within an ecosystem in order to include relationships between different trophic groups (Putman 1994). Therefore the term *species assemblage* will be used to cover the collection of taxonomically related species found in one place. A species assemblage has several attributes. One of the most obvious is species composition. There have been many studies comparing assemblages from different samples to investigate how differences in various environmental factors are related to differences in species composition, either using direct gradient analysis to study variation along a single environmental gradient (Gauch 1982) or multivariate analysis to consider variation along several axes related to more than one environmental factor (ter Braak & Prentice 1988). Multivariate analyses of ground beetle assemblages have been carried out at several different scales. At a regional scale these have included TWINSPAN classifications of assemblages according to species composition and relating the resultant end groups to habitat structures or environmental gradients (Eyre & Luff 1990a, 1990b, Luff *et al.* 1989, Turin *et al.* 1991). Most of these studies recognised soil humidity and altitude as important façtors affecting species composition. At a more local scale an ordination technique, DECORANA or detrended correspondence analysis (Hill & Gauch 1980), has been widely used to interpret variations in species composition as being influenced by a number of factors including moorland vegetation type and wetness (Gardner 1991), meadow vegetation structure (Foster *et al.* 1995), botanical diversity of hedgerow margins (Asteraki 1994), forest fragmentation (Halme & Niemela 1993) and grassland management (Eyre *et al.* 1989, 1990, Rushton *et al.* 1990). Assemblages of rove beetles have received less attention. Ordinations of assemblages on arable land and pasture in south-west Ireland were used to investigate the effects of different management operations (Good & Giller 1991). The importance of a variety of edaphic factors as well as afforestation, altitude and habitat size was suggested by studies involving ordination of rove beetle assemblages in northern England (Bauer 1989a, Buse & Good 1993).

Similar studies of riparian or floodplain assemblages are very rare. Desender *et al.* (1994) used ordination to compare 25 samples of ground beetles from seven sites beside a Belgian river and found that samples were distributed along the main axis of variation according to substrate particle size and vegetation cover at the sample site. Sustek (1994) analysed terrestrial and wetland assemblages from 26 sites in floodplains in Moravia and Slovakia. Correspondence analysis revealed important variations in species composition between assemblages from dry sites and damp sites subject to flooding and also between assemblages from oligotrophic sites flooded by fast-flowing water and eutrophic sites flooded by stagnant water. Sustek also found significant differences between assemblages in sites flooded only in early spring and those in sites flooded more frequently. Other comparisons of species composition between assemblages have relied on the use of similarity indices between a small number of sample sites. Zulka (1994) argued that flooding was the major factor determining species assemblages in the floodplain of the Morava river in Austria, but his conclusions were based on a comparison of only five sites.

A species assemblage can also be described by the species traits exhibited by its members. Relationships between such assemblage attributes and their distribution along environmental gradients have been explored for grassland ground beetles and body length (Blake *et al.* 1994), water beetles and morphology (Ribera & Isert 1992) and floodplain water beetles and a variety of species traits (Richoux 1994).

Perhaps because computerised multivariate analysis packages have only become widely available relatively recently, species diversity indices have been used more often than species composition in quantitative comparisons between beetle assemblages from the riparian and floodplain environment. Many different diversity indices have been formulated, but in general they are composed of two elements, one relating to species richness or number of species, which is dependent on sampling effort (Southwood 1978), the other relating to equitability, often termed evenness, which relates to the distribution of abundances between species (Putman 1994). Hill (1973) reviewed several versions of diversity index and concluded that they differed in the weighting that they gave to rare species. He showed that evenness could be quantified as the quotient of two similarly formatted diversity indices. Evenness is also related to the slope of a graph drawn between log abundance and rank (Begon *et al.* 1990). Consequently it can be related theoretically to different models of niche occupancy (Putman 1994). In ecological communities with high levels of interspecific competition, a geometric relationship between abundance and rank is predicted with low values for evenness. In stochastic community models involving chance colonisations a *broken stick* relationship is predicted with high values for evenness. Southwood's habitat templet would predict that K-selecting environments with high levels of biotic interactions should support assemblages with lower values for evenness than r-selecting disturbed environments. However, Magurran (1988) gave examples of studies which found reductions in species diversity following pollution of freshwater systems. Several studies found an increase in dominance, which is inversely related to evenness.

Huston (1979) modelled the population changes of six species with different life history strategies and varied the frequency of periodic disturbance which he defined as a density-independent event causing mortality. His model predicted that species richness should peak at intermediate frequencies of disturbance. As disturbances become less frequent competitive interactions leads to extinctions of less K-selected species. As disturbances become more frequent K-selected species become extinct as they are unable to recover between disturbance events. His model also predicts at constant frequency of disturbance a similar response curve of species richness to ecosystem productivity which operates by affecting growth rate. In effect these predictions are similar to the intermediate disturbance hypothesis (White & Pickett 1985) which predicts maximum species diversity at intermediate levels of disturbance, i.e. magnitude rather than frequency.

The lateral floodplain gradient in frequency of disturbance led Townsend and Hildrew (1994) to predict maximum species diversity within the upper Rhone valley at intermediate levels of spatial and temporal variability. However, Resh *et al.* (1994) reported that such a pattern was found only in water beetles (Richoux 1994) out of thirteen taxonomic groups.

Shmida and Wilson (1985) described four determinants of species richness which operated at different scales the within community scale (alpha diversity), the between community scale (beta diversity) and the regional scale (gamma diversity). They suggested that *niche relationships* are most important at the community scale, whereas *habitat diversity* is important at all scales, although it is difficult to appreciate the separation of niche relationships and microhabitat diversity at community level. Their third determinant is *mass effects*, which relates to the presence of vagrant individuals from adjacent habitats. This determinant becomes unimportant at regional level. Their fourth determinant is *ecological equivalency* which only becomes important at regional level. Application of Shmida and Wilson's analysis to the intermediate disturbance hypothesis shows that it is based primarily on *niche relationships* as a determinant and takes no account of *mass effects*. Combining Shmida and Wilson's analysis with the work of den Boer (1990) on dispersal of ground beetles suggests that *mass effects* will have an important impact on alpha diversity in disturbed landscapes.

In a study of beetles at a site in North Wales, Buse (1988) found that their species richness at different sampling stations was correlated with the species richness of plants and suggested that this relationship is due to the greater variety of microhabitats available for the beetle species when more plant species are present. A number of studies of floodplain ground beetles have compared the species diversities of different assemblages (Holeski & Graves 1978, Jarosik 1983, Rehfeldt 1984, Vitner & Vitner 1986). Unfortunately, the results have rarely been placed in any theoretical or functional context.

1.3.7 Summary

- Ground beetles and rove beetles are the most species-rich beetle families likely to be found in semi-aquatic biotopes in the riparian and floodplain zones of river systems.

- These beetles show a variety of morphological and behavioural adaptations to disturbance by flooding, but little is known about their variations in life history strategies.

- Assemblages of these beetles show variations in species composition and other attributes along environmental gradients.

1.4 Nature Conservation and rivers - the riparian and floodplain environments

An ecological framework for conserving diversity in riparian and floodplain beetles is now apparent. A knowledge of fluvial and successional processes allows prediction of the effects of human activity on geomorphic and vegetational structures. A deeper knowledge of the environmental requirements of beetles occupying these structures will allow prediction of the effects of human activity directly on beetle assemblages. This present section examines the conservation practices currently being employed on rivers and other ecosystems which might be relevant to riparian and floodplain beetles.

1.4.1 Recognition of conservation value in rivers

Reviews of plant and animal groups associated with rivers normally include vertebrates, aquatic macro-invertebrates, higher plants, bryophytes and, more rarely, phytoplankton (e.g. Whitton 1975, Calow & Petts 1992, RSPB *et al.* 1994). Possibly because there is no well defined dividing line between aquatic and terrestrial plants, botanists have tended to include riparian species in their studies more than zoologists (e.g. Haslam 1978, Holmes 1983). Although the use of the riparian zone by certain mammals and birds is well known (Newbold *et al.* 1983), riparian invertebrates have received very little attention. Williams & Feltmate (1992) are unusual in listing several families in the insect orders Collembola, Hemiptera, Coleoptera and Diptera which are normally considered to be terrestrial but which contain specialist species associated with the margins of aquatic habitats.

Conservationists have therefore generally regarded river biodiversity as being concentrated in aquatic organisms especially fish and macro-invertebrates. Riparian communities of plants do not receive the same degree of attention in Britain as more species-rich communities such as those found in semi-natural grassland. Conservation efforts targeted at inland wetland birds have relied heavily on nature reserves created on reservoirs and other man-made habitats rather than more natural habitats along rivers. Only initiatives toward the conservation of otters (NRA 1993b) and more recently water voles (Strachan & Jefferies 1993) have viewed terrestrial river margins as being of major conservation importance.

In Britain rivers considered important for nature conservation have been given statutory protection by being designated as Sites of Special Scientific Interest or SSSIs. Rivers have been selected as SSSIs firstly by classifying them according to abiotic factors and then by evaluating them on the basis of their plants, amphibia, mammals, birds and some aquatic invertebrate groups (Newbold *et al.* 1983).

The bias toward aquatic organisms ignores important semi-aquatic invertebrate communities in the riparian zone. Table 1.9 shows the numbers of species in various groups found in faunal surveys conducted along various riverbanks in Europe. It is probable that the number of riparian invertebrate species along rivers is of a similar magnitude to the number of aquatic species as enumerated by RSPB *et al.* (1994).

Among the rich assemblages of species in the riparian zone are invertebrates whose populations are believed to be under threat. In Britain the conservation profile of shingle bank beetles has recently been raised by a study of the River Ystwyth in Wales which discovered a number of rare species including the endemic rove beetle, *Thinobius newberyi*, which had not been recorded for fifty years (Fowles 1989). Shirt (1987) listed insects which are rare or threatened in Britain and included 23 beetle species with well-established associations with riverbanks (see table 1.10). Many more nationally scarce riverbank beetles are listed by Hyman (1992, 1994). Mawdsley & Stork (1995) analysed the habitats of both rare and threatened beetles in Britain and found that riparian habitats were included in the top five habitats in each category. Consequently upland shingle banks are now becoming recognised as of conservation value for semi-aquatic beetles (Stubbs & Whelan 1991, Kirby 1992, RSPB *et al.* 1994) even if there is not yet any coherent strategy for their conservation. However recent studies in Belgium have found several rare ground beetles along lowland rivers (Desender *et al.* 1994). There is an urgent need to investigate British lowland riverbanks whose neglected beetle fauna contribute eleven (48%) of the rare and threatened species listed in table 1.10.

Modern approaches to nature conservation along rivers emphasise the importance of the ecological connectivity between a river and its floodplain (Newson 1992). Studies of floodplain habitats in the floodplain of the River Rhone in France have highlighted the ecological value of floodplain communities and their hydrological interdependence with the main channel (Bravard *et al.* 1992). Several European studies of floodplain forest ground beetles (e.g. Lehmann 1965, Lienemann 1978, Vitner & Vitner 1987) have concentrated on relatively dry areas whose assemblages contained species present in a wider range of woodland habitats. However, other studies (Jarosik 1983, Sustek 1984, Zulka 1994) have revealed rich

Location	Major groups recorded together with no. species	Source
7 rivers in S. Karelia	Coleoptera (295)	Palmen & Platanoff (1943)
R. Wutach, SW Germany (4 types of bank)	Heteroptera (3-10), Coleoptera (52-148)	Kless (1961)
R. Rhein, Cologne (Germany)	Coleoptera - Carabidae (31+)	Lehmann (1965)
F. Arno & F. Serchio, Tuscany (Italy)	Coleoptera - Carabidae & Staphylinidae (88)	Bordoni (1967, 1969)
9 streams in Ohio (U.S.A.)	Coleoptera - Carabidae, Staphylinidae & Heteroceridae (90)	Holeski & Graves (1978)
R. Ourthe, Belgium	Diptera - Dolichopodidae (26)	Pollet et al. (1988)
R. Rheidol & R. Ystwyth, Wales	Orthoptera (2), Heteroptera (1), Diptera - Empididae (6), Hymenoptera - Formicidae (3), Coleoptera (70), Araneae (44)	Fowles (1988)
Upper Weser, Germany	Coleoptera - Carabidae (127)	Gerken et al. (1991)
Guadiato river basin, SW Spain (2 sites)	Coleoptera - Carabidae (46 & 33)	Cardenas & Bach (1993)
Grensmaas, Belgium	Coleoptera - Carabidae (81)	Desender *et al.* (1994)
8 streams in N Hesse	Araneae (77), Coleoptera (55)	Smit *et al.* (1996)

Table 1.9. Numbers of riparian invertebrate species recorded in some faunal studies along riverbanks

Species	Habitat	Sources
Bembidion virens	shingle by lakes and rivers	Lindroth (1985), Shirt (1987)
Lionychus quadrillum	fine gravel on shingle banks	Fowles (1989)
Polistichus connexus	coastal undercliffs, silt & clay riverbanks, saltmarshes	Shirt (1987), Hyman (1992)
Drypta dentata	trickles on cliffs, silt & clay riverbanks	Shirt (1987), Hyman (1992)
Bledius erraticus	sandy riverbanks & sandpits	Hyman (1994)
Carpelimus obesus	bare mud by streams & rivers	Hyman (1994)
Carpelimus subtilis	sandy margins of rivers, dykes & ponds	Hyman (1994)
Thinobius major	sand & fine shingle by rivers & lakes	Hyman (1994)
Thinobius newberyi	river shingle	Shirt (1987), Fowles (1989)
Stenus calcaratus	banks of large rivers	Horion (1963)
Stenus incanus	sand & shingle by rivers	Hyman (1994)
Lathrobium dilutum	sand & shingle by rivers & lakes	Hyman (1994)
Lathrobium pallidum	riversides & marshes	Hyman (1994)
Scopaeus gracilis	riverside shingle	Hyman (1994)
Scopaeus laevigatus	trickles on cliffs, sand, mud & detritus by streams and pits	Horion (1965), Hyman (1994)
Gabrius astutoides	undercliffs, streamside shingle	Horion (1965), Hyman (1994)
Quedius riparius	moss by fast-flowing streams	Kless (1961), Hyman (1994)
Ilyobates propinquus	sandy riverbanks & sandpits	Hyman (1994)
Calodera uliginosa	riverside debris	Hyman (1994)
Oxypoda riparia	sandpits & riverbanks	Hyman (1994)
Negastrius pulchellus	river shingle	Hyman (1992)
Negastrius sabulicola	river shingle	Hyman (1992)
Coccinella quinquepunctata	river shingle	Majerus & Fowles (1989)

Table 1.10. Riverbank beetles included in the British Red Data Book (Shirt 1987)

assemblages of hygrophilous species. In a flooded meadow in the floodplain of the River Morava in Austria, Zulka (1994) found that the dominant species included three rare wetland species of high conservation interest, *Agonum longiventre, Agonum dolens* and *Blethisa multipunctata.* For invertebrate groups other than ground beetles, faunal studies of floodplain wetlands are even scarcer. At a Moravian lake margin Obrtel (1972) recorded 36 species of rove beetles and 32 species of ground beetles amongst 116 species of beetles in a reedswamp, a habitat structure well represented in floodplains. In two wetland sites in the Trent floodplain in Britain, Greenwood *et al.* (1991) recorded respectively 21 and 23 rove beetle taxa. Floodplain wetlands are likely to support species-rich assemblages of rove beetles as well as ground beetles. By contrast the reedswamps and carr characteristic of floodplain wetlands in Britain are characterised by somewhat species-poor plant communities (Rodwell 1995) and as a consequence are not highly valued for conservation purposes. Floodplain habitats of Community interest that are listed in the European Community Habitats Directive (European Communities 1992) include lowland hay meadows and residual alluvial forests but none of the wetland categories are represented in lowland floodplains in Britain. Consequently, there is an urgent need to assess the value of floodplain wetland habitat structures for invertebrates in Britain.

1.4.2 River management and conservation

Petts (1989) summarises the early history of river management in Britain which stretches back at least to Roman times, when rivers were channelled for navigation. Impoundment of British rivers also has a long history. The Domesday Book of 1086 contains references to over 5,000 water mills. However the weirs constructed for fishing and water mills were generally small-scale. A major increase in the canal network in the 18th century saw several rivers impounded over long stretches by weirs and locks to make them navigable. The use of rivers for navigation also led to the clearance of riparian vegetation for towpaths. Larger dams were needed for the construction of reservoirs for storage of water supplies in the 19th century. In the latter half of the 19th century land drainage and river engineering became widespread so that by 1880 major works had been carried out on most rivers which were subsequently maintained by regular dredging. The number and scale of river engineering works increased rapidly after the second world war primarily to assist land drainage schemes for agriculture. Brookes *et al.* (1983) calculated that between 1930 and 1980 8,504 km of major and capital works were carried out along rivers in England and Wales. At the same time a further 35,500 km of river in England and Wales were regularly maintained

The environmental effects of such widespread and large scale activity became apparent as rivers lost their natural morphology and vegetation. This inevitably caused appreciable concern which was articulated by Purseglove (1988) in a television series and accompanying book. Purseglove acknowledged that river maintenance was necessary but suggested that different methods could not only reduce environmental damage but even enhance the environmental value of rivers. Brookes (1985, 1988) reviewed the unforeseen effects of engineering practices on channel morphology and suggested alternative practices which retained more of the river's natural features.

The formation of the National Rivers Authority in 1991 and its successor body, the Environment Agency, with a statutory duty "to further conservation in respect of proposals relating to its functions, to protect sites of conservation interest and to take account of the effects that any proposals would have" (NRA 1992) meant that these concerns are now taken into account in carrying out engineering and maintenance work. There is now a handbook for river management containing not only more environment-friendly methods of river engineering and maintenance but also suggestions for methods of habitat creation which could be included in schemes as mitigation exercises (RSPB *et al.* 1994). Further current river conservation initiatives include the alleviation of low flows (NRA 1993c) and river restoration projects which seek to reverse channel straightening and other unsympathetic operations carried out in previous engineering schemes (Brookes 1992). The changes in management practices are backed up by a programme of river corridor habitat surveys which seek to identify features of ecological value along river channels (NRA 1992). Maps compiled from these surveys enable the design of maintenance works to conserve identified features of interest and add new ones.

Concern over the ecological effects of river management on both in-stream and bankside organisms (Brooker 1985) was followed by a realisation that river regulation was also having a serious impact on floodplain ecology (Bravard *et al.* 1986). The hydrological and ecological interconnections between the main river channel and its terrestrial surrounds require a much broader perspective to be taken of the main channel and its relations with the river corridor, the floodplain, the valley floor and finally to the whole catchment (Newson 1992). Such a broad perspective also has advantages for meeting objectives in managing flooding, pollution, sewage discharge and low flows. The Environment Agency is now committed to developing a programme of catchment management plans which offer opportunities for environmental enhancement and seeking solutions through control of land use rather than main channel engineering works (Gardiner & Cole 1992).

These improved approaches have undoubtedly led to rivers which fit more attractively into the landscape. Also benefits have accrued to those sections of the flora and fauna whose requirements were considered in the formulation of the new practices. However, we have no idea whether this enlightened regime benefits or damages riparian invertebrate communities, because we do not know enough about their composition, their habitat requirements or their responses to river management.

1.4.3 Site classification and conservation evaluation criteria

When selecting sites for conservation action, Margules (1986) suggested a five stage procedure for site evaluation which has particular relevance to isolated homogeneous areas:

1) pre-evaluation classification or sorting;

2) allocation of sites according to which class they represent;

3) use of threshold criteria to select sites for detailed consideration (e.g. area, naturalness);

4) use of ranking criteria for prioritisation (e.g. rarity, diversity);

5) use of pragmatic criteria (e.g. threat, availability, accessibility).

Kirkpatrick (1983) used an iterative procedure to select sites for nature reserves in Tasmania. He ranked sites according to weighted attributes such as rare species or habitats and then after selecting the highest-scoring site reduced the weightings for attributes represented in the site before the next selection. This effectively removes the need for classification and the use of representativeness, but still requires the selection of criteria to rank sites. Pressey and Nicholls (1989) found that iterative procedures were more efficient at giving protection to attributes than the use of simple, static scoring systems, but their use is based on the premise that sites are ecologically independent, a premise which is not applicable to sites within river catchments.

Proposals for assessing the conservation potential for rivers and selecting them for protection (Boon 1992, Naiman *et al.* 1992) have suggested a river classification system and a set of evaluation criteria. Boon (1995) described two classification systems for British rivers, both of which are community classifications rather than environmental classifications. A classification based on aquatic and riparian plants was developed by Holmes (1983) who used TWINSPAN to classify 1,055 sites surveyed on over 200 rivers. The first two divisions into four major groups are related to altitude, geographical location and geology (Holmes 1989). This classification has been adapted to give ten river types which form have formed the basis of SSSI selection in Britain (Holmes 1989). Aquatic macroinvertebrate communities in unpolluted streams were classified by Wright *et al.* (1984) and linked to environmental variables so that the natural community could be predicted from a set of environmental measurements at any stream (Moss *et al.* 1987). The recorded community present could then indicate any impact of pollution. Naiman *et al.* (1992) pointed out that this predictive model is based on direct impact on water quality in-channel physical features and ignores impacts on a larger scale. It is not known how well either of these classifications match the variety of beetle assemblages found in British riparian and floodplain environments.

The much-quoted list of criteria used to assess and select sites representative of natural and semi-natural ecosystems in Britain includes size, diversity, naturalness, rarity, fragility, typicalness, recorded history, proximity to other sites of value, potential value and intrinsic appeal (Ratcliffe 1977). Diversity is one of the most popular criteria used to assess conservation value (Margules & Usher 1981). However, there are major problems in its application. There is no generally accepted method of measuring diversity for conservation value although Usher (1986) recommends species richness. Values of species richness increase with sampling effort (Southwood 1978). Rarefaction which reduces the samples of sites being compared to the same size is recommended by Usher (1986) to solve this problem, but this could inflate the values of samples with low species richness and high evenness relative to samples with high species richness and low evenness. For conservation purposes the inflation of species richness values by vagrant species is also undesirable (Shmida & Wilson 1985). A further problem arises from the sensitivity of species richness to disturbance (White & Pickett

1985). Niemela *et al.* (1993) found that the species richness of ground beetle assemblages in primary boreal forests was lower than regenerating secondary forests even though primary forest specialists had disappeared after cutting. The use of habitat diversity as an evaluation criterion as measured by Margules & Usher (1986) or implicit in the site management approach of Kirby (1992) is only applicable if the habitat requirements of the species present at the site are known, The habitat structures recognised by conservationists do not necessarily correspond with those that are important for all organisms (Harper *et al.* 1995).

Rarity is another popular evaluation criterion (Margules & Usher 1981), because it is tacitly believed to be a good measure of threat of extinction (Gaston 1994). However, its use has attracted some criticism, either because many threatened organisms are not perceived as rare (McIntyre 1992) or because it is unfeasible to collect enough data for the rarity status of many invertebrate species to be established (Disney 1986). Rabinowitz (1981) recognised seven categories of rarity based on different combinations of low abundance, restricted geographic range and narrow range of habitat occupancy. Gaston (1994) based the term *rarity* on both low abundance and small range size. He stressed the positive correlation generally found between abundance and range size and pointed out that at very small scales range size becomes equivalent to abundance. However, departures from this relationship are likely to be interesting. For plants, McIntyre (1992) argued that the use of small range size to establish rarity status will overlook widely distributed species with declining populations which may be under the greatest threat. On the other hand for ground beetles in disturbed landscapes, den Boer (1977) found that poor dispersers which are declining in Holland (Turin & den Boer 1988) tend to be found in relatively high abundances, whereas they have restricted ranges, because they are confined to isolated patches of stable biotopes. This contradiction may arise from the different scales used to measure geographic range. Gaston (1994) points out that the scale of precision in measuring the range size of a species will often affect its rarity status. This is one of several artefacts that cause problems in the determination of species rarity. Gaston described pseudo-rarity and non-apparent rarity as two forms of false rarity status. Amongst their causes he listed inappropriate sampling techniques and the possibility of under-recording cryptic species.

Site comparisons using the numbers of rare species recorded will be affected by inconsistent sampling effort in the same way as species richness. Eyre & Rushton (1989) developed a system for scoring beetle assemblages by weighting all of their constituent species according to their recorded range sizes and this aims to be independent of sampling effort. The values of rarity scores for sites will, like species richness, be affected by vagrant species (Gaston 1994), though if these are common species, rarity scores may be depressed rather than inflated. In a study of rare plants in the Sheffield area, Hodgson (1986a) found that the ranges of rare species are usually affected by scarcity of suitable habitat and that this scarcity is connected to changing land use (Hodgson 1986b). Rare species tend to be adapted to environmental stress (Grime 1979) and occur most frequently in species-rich, *ancient* biotopes on less fertile soils. In results similar to those found by Turin & den Boer (1988) for Dutch ground beetles, disturbed sites contain a high proportion of common species and Hodgson suggested that in the Sheffield area plants adapted to environmental stress are being replaced by species adapted to disturbance.

Naturalness is also a popular evaluation criterion, but has proved both difficult to define and to quantify (Margules & Usher 1981, Usher 1986). Descriptive terms such as *semi-natural* are often used to cover uncertainties with regard to definitions and characterisation of sites. Usher (1986) suggested that the amount of disturbance at a site may provide a reasonable basis for quantification of naturalness, though presumably disturbance due to natural processes would need to be distinguished from disturbance of human origin. Attempts at quantification of typicalness have centred on the distance of a site in ordination space from the mean scores of its habitat group (Eyre *et al.* 1986, Eyre & Rushton 1989). Obviously the applicability of this criterion is closely connected with the validity of the habitat classification. It is difficult to appreciate the relevance of a habitat classification with boundaries derived from an arbitrary number of divisions along environmental gradients whose importance may be dependent on the selection of sites for analysis. Typicalness of *a priori* selected habitat structures may be relevant to site evaluation in that it may relate the site to a particular natural or management process.

In a conservation evaluation of sites along four Welsh rivers species richness and rarity of plants were used by Slater *et al.* (1987) along with a more unusual criterion, uniqueness, which is high for sites which are most different from other sites. Unique sites may contain locally rare habitats in which case uniqueness is the opposite of representativeness or typicalness. Uniqueness is a special type of rarity score in that it is based on species rarity scores calculated from distributions within the study area, rather than from wider regional distributions. Values of uniqueness will be markedly affected by any sampling bias operating in site selection.

A more comprehensive evaluation system currently being developed for evaluating rivers on the catchment segment scale and above is SERCON (System for Evaluating Rivers for Conservation) (Boon *et al.* 1994). SERCON is a computerised expert system which uses a variety of weighted evaluation criteria including physical and species diversity, rarity and levels of threat and human impact. It has the capacity to process information on riparian invertebrate assemblages, were they to become available (Boon, pers. comm.)

1.4.4 Use of beetles in site quality evaluation and monitoring environmental change

Refseth (1980) stressed the value of ground beetles as ecological indicators because they are widely distributed, easily identified and their species are restricted to specific habitats, yet responsive to environmental changes. It has been suggested that the diverse rove beetle fauna in floodplain biotopes makes them useful candidates for assessing the conservation value of floodplain functional units (Greenwood *et al.* 1991, Petts *et al.* 1992). Luff & Woiwod (1995) listed desirable properties of taxonomic groups for use as environmental indicators.

1) They should have enough species to represent, and be characteristic of, a wide range of habitats.

2) They should be readily identifiable and taxonomically stable.

3) There should be a suitable sampling method available which should not be too restricted by seasonality.

Foster (1987) proposed that a group containing 300 to 500 species would meet both criteria 1 and 2. If restricted to the riparian and floodplain wetland environments, ground beetles and rove beetles together would constitute this number of species (see table 1.7). Taxonomic uncertainty within British rove beetles can be found within the *Atheta fungi* species group (Bruge 1994), but this group does not form an important component of riparian or wetland assemblages. However, there appear to be seasonal variations in riparian and wetland beetle assemblages (Palmen & Platanoff 1943, Krogerus 1948) and these sampling constraints require further investigation.

Several studies have demonstrated the sensitivity of riparian ground beetles to site management. Lehmann (1965) investigated the ground beetle assemblage on a bank of the Rhine which was reinforced with stones to create a series of steep steps and found its species composition to be more similar to nearby grassland assemblages than nearby assemblages on natural riverbanks. Plachter (1986) attributed incongruities in the distribution of ground beetles along a 196 km stretch of the River Isar in Bavaria to human channel modifications. Further upstream, Manderbach and Reich (1995) found that the construction of a reservoir dam had reduced the species richness of the ground beetle fauna by altering the flow characteristics of the river, although a smaller dam on the same river had quite different effects. Friden (1984) investigated riparian ground beetle assemblages of regulated lakes in Scandinavia and found that species associated with natural lake shores were less abundant whereas species associated with high altitude benefited from the colder water and eurytopic species benefited from increased quantities of organic detritus. More indirect evidence of ground beetle sensitivity to management comes from the work of Andersen (1969, 1983) who found that several species of Norwegian *Bembidion* have strict habitat preferences. Within floodplains there seems to be a distinct wetland beetle fauna which not only depends on flooding but is sensitive to different flood regimes (Sustek 1994, Zulka 1994). Management operations which affect flooding should also affect these assemblages (Greenwood *et al.* 1991).

Mawdsley & Stork (1995) found that drainage and river engineering were the sixth most numerous threat to all rare and endangered beetle species listed by Shirt (1987) and Hyman (1992) and the fourth most numerous threat to ground beetles. The information available indicates that both ground beetles and rove beetles should make excellent subjects for both conservation evaluation and measuring the environmental impact of human activity in riparian and floodplain environments.

1.4.5 Summary

- It is known that there is an important reservoir of biodiversity among beetles in semi-aquatic habitat structures along rivers in Europe. These habitat structures are not generally considered to be of major importance for higher-profile groups such as birds and plants.

- Amongst riparian beetles only the conservation value of upland shingle bank beetles is recognised in Britain.

- In populated regions modern rivers are highly managed systems which are subject to both large scale engineering projects and frequent small scale maintenance.

- Recent moves to make river management practices more attuned to environmental protection have concentrated on benefiting within-channel organisms and paid little attention to the requirements of riparian invertebrates.

- Assemblages of beetles with semi-aquatic habitats in the riparian and floodplain environments are sensitive to river management practices and have sufficient diversity to be good candidates for measuring the impact of human activities.

- Research is urgently needed on the diversity, habitat requirements and responses to site management of terrestrial beetles along river margins and in floodplain wetlands.

1.5 Objectives of this study

The broad aims of this project are twofold:

1) to evaluate the conservation interest of terrestrial beetles with semi-aquatic habitats along a lowland river floodplain.

2) to investigate the effects on these beetles of human activity, especially river management practices.

In order to achieve these aims this study attempts to answer the following questions.

1) Are there robust, measurable attributes that we can use to describe beetle assemblages found on semi-aquatic habitat structures in a typical lowland river floodplain segment?

2) How are these descriptors affected by natural fluvial and successional processes?

3) Are these descriptors sensitive to management operations along the river and on adjacent land?

4) Can we predict the impact of management operations from the response patterns of assemblages to natural processes?

The lower course of the River Soar in Leicestershire was chosen for study as a typical medium-sized lowland river with a wide range of main channel and floodplain habitat structures. The lower Soar also affords opportunities to study the impacts of several management activities, because large stretches have been impounded for navigation and there have been extensive recent engineering works as part of a flood alleviation scheme.

2 Study site

The River Soar is a tributary of the River Trent with a catchment area of 1388 sq. km and a length of 67.5 km. There is no maritime influence and the catchment is almost completely lowland in character. Only a small area in the Charnwood Forest rising to just 278 metres altitude on acidic, siliceous rocks can be considered to be vaguely upland in character. Most of the catchment surface geology is dominated by neutral clays and siltstones to the west and more basic clays and limestone to the east (Martin 1988). However, much of the solid geology is overlain by glacial boulder clay. Consequently, although the average rainfall at around 600 mm per year over much of the catchment is lower than most of England and Wales (Wildig 1988), high levels of surface run-off lead to spates within the river system. Surface run-off is also increased by the large conurbation centred on Leicester and drainage systems associated with agriculture.

Outside of population centres, land use is dominated by agriculture which has changed markedly in character in recent decades. A predominantly pastoral landscape with hedges has been converted to larger fields used for arable cultivation and grass ley. The intensification of agriculture has almost certainly resulted in increased levels of fine sediment coming into the river system. Certainly nitrate concentrations in the River Soar are very high and rising. Jose (1989) reported that mean nitrate concentrations measured from 1982 to 1986 at Red Hill Lock near the confluence with the Trent were at 11.44 mg l^{-1} the highest of eight sample points in the Trent catchment and the rate of increase was the second highest value. However, the water quality of the lower Soar is not regarded as poor. It is designated as belonging to chemical class 2, which is defined as *suitable for potable supply after advanced treatment and capable of supporting reasonably good coarse fisheries* (NRA 1989). The major discharge of effluents into the river occurs at Wanlip, where sewage from Leicester is treated. Approximately three quarters of the summer flow below Wanlip originates as sewage effluent. Biological indices of water quality indicate a decrease in organic pollution away from Wanlip toward the Trent confluence, but even near Wanlip these indices have improved considerably following improvements to sewage treatment in the 1960s and 1970s (Harding 1986). The sewage outfall from Loughborough, a large town within the lower Soar study area, appears to have little effect on the biological indices (Harding 1986).

The length of the Soar investigated during this project was 30 km between its confluence with the Trent and a point upstream from Barrow upon Soar which constitutes most of a natural segment between two major confluences, but excludes an upstream stretch of about 7 km below the outfall at Wanlip. For most of this length the Soar forms the boundary between Leicestershire and Nottinghamshire. The gradient along this stretch is very shallow and the river drops a mere 15 metres. Consequently, it is very slow-flowing and main channel sediments are primarily composed of silt and fine sand. Further reductions in flow rate result from the impoundment of long stretches for navigation. Shingle deposits are very limited and confined to just two stretches of unimpounded river at Cotes and Ratcliffe on Soar, although accumulations of bricks and other debris from artificial structures sometimes occur elsewhere. Steep bare banks are also confined to unimpounded stretches. Although these banks are undoubtedly scoured by the river, erosion of bank material is probably not very severe. Old maps provide no evidence that major natural changes in channel position have occurred for three hundred years. Personal observation over twenty years suggests that bank erosion and channel movement is limited to areas immediately downstream of weirs. Nevertheless, large deposits of silt and fine sand, in some cases covering up to half a hectare, are not uncommon below the towpath and these have presumably accumulated since navigation was introduced to the river.

In areas of the floodplain not protected by flood alleviation schemes, flooding occurs regularly two or three times a year and inundation can last for up to four days (NRA 1990). From personal observation, flooding is more frequent in winter months, even though August tends to have the highest monthly rainfall (Wildig 1988). Numerous secondary channels can be seen in the form of long winding depressions in floodplain meadows. Many of these channels flood regularly in the winter and retain water to varying degrees into the spring and summer. In grazed meadows, these remnant pools tend to have a largely mineral substrate, but in unmanaged areas, wet woodland has formed and the substrate is composed of layers of undecayed organic matter (CPOM) interspersed with silt deposited by winter floods. When large amounts of CPOM are incorporated into fine sediment they change the physical properties of the substrate radically. The irregular shapes of CPOM create a much less closely packed matrix containing interstitial spaces which are often exploited by invertebrates. Organic detritus also acts as a food source for organisms such as Collembola which are important prey items for many ground-living beetles. The origins of these secondary channels are largely unknown, but several are possibly related to the sites of old mill races.

Under the vegetation classification scheme devised by Holmes (1983), most of the lower Soar would be placed in the A2iv group of clay rivers, whose characteristic plants include *Nuphar lutea, Scirpus lacustris, Sagittaria sagittaria, Rorippa amphibia, Polygonum amphibium* and *Glyceria maxima*. This vegetation type is associated with an almost pure clay catchment and a spatey flow regime.

In the late eighteenth century, well over half the main channel was impounded for navigation by a system of locks and weirs. In these sections, flow rates are now slower, water levels are maintained higher and adjacent land is more frequently affected by flooding. By means of a canal, the navigation avoided three stretches. These were the Quorn loop, the Ratcliffe loop and a long stretch between Pillings Lock, Quorn and Bishops Meadow near Dishley. However, even in these stretches there are additional impoundments connected with old mills. A large weir at Cotes Mill affected a long stretch of unnavigable river, but when this collapsed in the late 1980s an older rubble weir was exposed two kilometres upstream. Other types of impoundment include the base of the road bridge at Cotes and a ford at Ratcliffe.

Following widespread flooding of property in 1977, engineering works commenced in 1983 as part of a flood alleviation scheme. These works were designed to reduce flooding to a frequency of once every ten years over most of the floodplain and once every hundred years adjacent to villages (NRA 1990). The engineering works consisted of three main types of operation. Firstly the channel was dredged to achieve a cross-section whose width and depth gave the minimum necessary area required to remove a quantity of water calculated according to a mathematical model. Secondly, an embankment was constructed above the natural bank in order to hold back floods which overtopped the natural bank. Thirdly, where necessary, the natural bank was regraded to an angle of 45° and cleared of obstructions, such as trees, which might impede flow. Near Normanton, there is a stretch of riverbank which has been faced with vertical steel piling. However, bank regrading was not necessary on all stretches and only one bank was regraded along many stretches.

Apart from engineering operations, many banks are affected by adjacent land use. Where cattle have access to the banks, they have a big impact on its structure and vegetation.

Trampling causes steep banks to collapse and breaks up the surface of sedimentary deposits. Trampling and grazing reduce vegetation cover. These conditions are found on approximately half the length of river bank and are only absent where the river runs beside arable fields or plantations such as old osier beds. Some navigable stretches which are higher than adjacent land are protected from grazing stock by a ditch system. Along river banks unaffected by cattle, anglers can affect small localised areas by cutting back vegetation for fishing platforms.

2.1 Environmental variables available for investigation

There are a range of habitat structures in the lower Soar floodplain including main channel sedimentary deposits and floodplain wetlands. These structures contain a number of microhabitat types. In terms of mineral sediment particle size, the range from clay to coarse sand is well represented, but shingle is found at only a few sites. A particular feature of many floodplain wetland sediments and some main channel sediments is the incorporation of Coarse Particulate Organic Material (CPOM) into the matrix. There is also wide variation in vegetation cover, vegetation type, shade and quantity of surface litter.

At a larger scale, there is variation in the severity of disturbance by flooding and, in floodplains, in the frequency of flooding. The levels of severity of disturbance by flooding along the lower Soar occupy an intermediate position between those on its headwaters and those on the larger River Trent downstream. All stages of vegetational succession are represented in floodplain wetlands, although fen and marsh are less common than carr and shallow grassland depressions which dry out early in the year. These successional stages are characterised by different levels of hydrological stability.

Different stretches of the riverbank have been regraded at different times between 1984 and 1991. Other stretches have been directly unaffected by engineering. Similarly different stretches have been impounded for navigation since the end of the 18th century. Other human pressures which vary between stretches include grazing and use by anglers. Larger scale catchment land use factors, such as urbanisation will not be expressed in differences within the study area and require a comparison of sub-catchments.

3 Methods

3.1 Sequence of investigation and site selection

In 1991, thirty sites were sampled to investigate the relative importance of environmental variables across all habitat structures and to select an appropriate scale for further investigation. Only samples collected in April and May were used in the analysis, although additional samples were collected in other months in order to investigate seasonal variations. It was considered that thirty sites would allow all environmental variables with an important influence on species assemblages to be detected. The sites were selected to represent the complete range of habitat structures present in the lower Soar floodplain from a stretch of 5 km between Loughborough and Barrow whose short length minimised unwanted large scale variations. They are mapped in figure 1 and their habitat structures summarised in table 3.1. A more detailed breakdown of environmental variables is given in appendices 3.1 and 3.2.

The influence of environmental variables specific to floodplain wetland assemblages was investigated using a set of 27 samples collected between 1991 and 1994. Twelve of these samples were from additional sites outside the stretch studied in 1991. The influence of river management on main channel assemblages was investigated using samples collected from 30 sites in 1992. Eight of these sites had also been represented in the 1991 data set.

Concurrently with these investigations, 15 reference sites originally sampled in 1991, were repeatedly sampled up to 1994 in order to evaluate seasonal and annual variations and sampling methods as detailed in chapter 4. After 1991, it was recognised that some large floodplain wetland sites contained areas managed in different ways and covered too large a range of environmental variables. From 1992, large sites were split into separate sampling units as detailed in table 4.26.

3.2 Sampling methodology

3.2.1 Target groups

Because of the variety of beetle habitats and life histories, a suite of sampling methods is often required in order to study the full faunal diversity in any one habitat. For the present study, it was cost-effective to define certain target families and so limit the number of sampling methods. Table 1.7 shows the number of species in each beetle family which occur in British

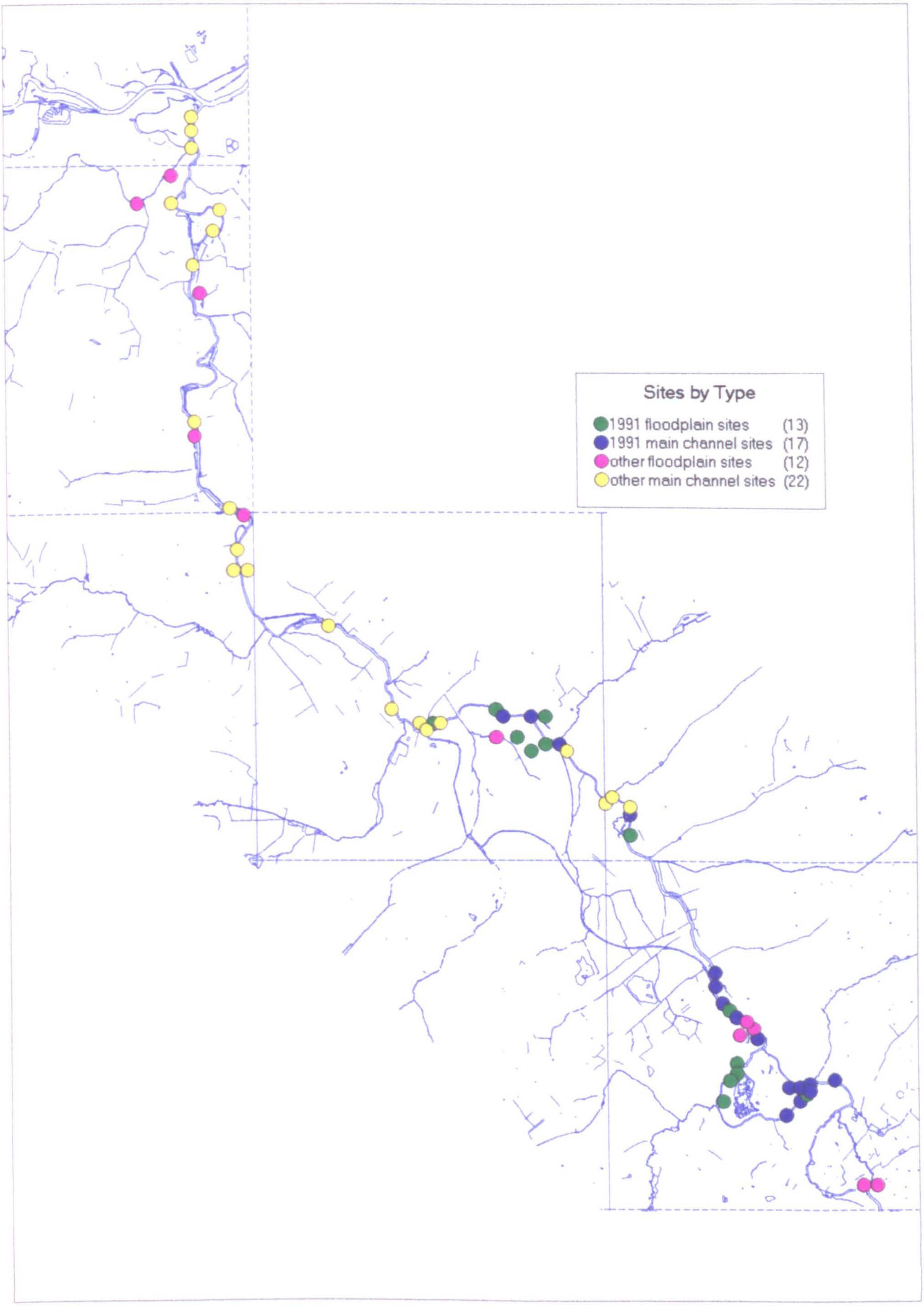

Figure 3.1: Map of lower Soar showing locations of sampling sites.

Main channel structures (17 sites)		Floodplain wetland structures (13 sites)	
shingle banks	1	marsh	2
sand banks	4	fen	2
silt banks	10	carr	7
slumped eroding banks	2	grassland depression	3
		spring-fed flush	1

Table 3.1: Number of sites investigated in 1991 representing different types of habitat structure. Note that some large floodplain wetlands contained more than one vegetation type.

wetland and riparian sites. The two most species-rich families are Staphylinidae and Carabidae and so it is these families that constitute the main target groups. These are predominantly ground-living species and there are a number of appropriate sampling methods which have been successfully employed for their study.

Adults of species in the families Scirtidae, Phesphenidae, Cantharidae, Melyridae, Nitidulidae, Phalacridae, Coccinellidae and Chrysomelidae tend to climb vegetation. This is also true to a lesser extent for Apionidae and Curculionidae. Collecting methods designed for ground-living species would not yield representative samples of these families which were, therefore, not included in the analyses.

Many species in the families Hydrophilidae and Dryopidae are aquatic. Some species of the genus *Cercyon* appear to be exclusive to terrestrial margins, but adults of other genera appear in terrestrial habitats either intermittently or under special circumstances such as the drying out of ponds. Sampling of the terrestrial margins of water bodies would not yield representative samples of these groups which were also excluded from the analyses.

Species of Rhizophagidae have specialised habitats such as the bark of driftwood which would not be adequately sampled except by techniques peculiar to that group. There are identification problems with *Acrotrichis,* the main genus of Ptiliidae. Although specialist riparian and wetland species of Cryptophagidae and Lathridiidae do occur in Leicestershire, they are very rare compared with ubiquitous species in the same family which would dominate the samples and which would not furnish very useful information. All of these families were also removed from the list of target groups and were not used in the analysis of results.

Of the remaining families, only Pselaphidae, Heteroceridae, Elateridae and Silvanidae have wetland or riparian species occurring in Leicestershire. Consequently, these families were added to Carabidae and Staphylinidae and together they constitute the target groups for sampling in this study.

3.2.2 Hand collecting

Within each site, six sampling stations were chosen so as to maximise environmental variation according to the following priority:

a) substrate particle size,

b) percentage of bare substrate,

c) vegetation type,

d) depth of litter,

e) shade.

Based on the number of pitfall traps required to give a representative sample (Obrtel 1971), six sampling stations were considered sufficient to yield a representative hand-collected sample. Sampling stations were always damp either on or just below the surface and generally within two metres of open water where this was present. Most sites along the River Soar are fairly narrow and under-representation of species confined to dryer areas further away from the water was assumed to be unimportant.

This protocol leads to sampling stratified by environmental variables rather than by spatial position and was designed to suit the mosaics of microhabitat structures present at most sites. Random selection of sampling stations would have required a much larger number of stations to have covered the variation in species composition and environmental variables present at each site. In 1992 the sampling protocol was modified slightly in order to suit regraded sites which were more homogeneous in nature. Stations were selected from separate, contiguous ten metre lengths at each site. Within each ten metre length, environmental variation was maximised according to the priority listed above.

Collecting for unit time was adopted to standardise sampling effort. At each station beetles were collected with the aid of a pooter for five minutes. Thus, during each site visit, beetles were collected for a total of thirty minutes. Collecting was carried out when the air temperature was 14° C or above. The following techniques were used.

Bare ground was splashed with water and soft sediments were lightly trampled. On vegetated ground, the basal parts of plants were examined or pulled apart. Litter and dense mats of fallen vegetation were sieved over a plastic sheet. The time taken to sieve vegetable matter was not included in the five minutes, only the time taken to search and collect the beetles on the plastic sheet. Floating vegetation mats were trampled underwater and beetles scooped up with a tea-strainer.

Specimens were killed with ethyl acetate. Specimens from each sampling station within the site were pooled for the purposes of analysis at site level.

3.2.3 Pitfall trapping

At each site, six stations were chosen adjacent to those used for hand-collecting and with similar environmental conditions. At each station, a polypropylene beaker with a 8.5 mm. opening was sunk into the substrate so that its mouth was flush with the surface. Commercial anti-freeze containing ethylene glycol was poured into the bottom of the beaker as preservative. The catch from all six traps was pooled, sorted in a white tray and beetles extracted into 70% alcohol.

3.2.4 Species identification

Prior to commencing these investigations, taxonomic expertise had been acquired through contact with specialists in each of the target groups. Specimens in these families were identified down to species level, where possible, using published keys and a reference collection. In 1991, females belonging to the rove beetle genus, *Gabrius,* and the subgenus, *Philhygra,* of the genus, *Atheta,* could not be identified. However from 1992 onwards it proved possible to identify *Philhygra* females by examining their genital segments. Most specimens were stored in 70% IMS and lodged in the care of Leicestershire Museums Service. However, some critical specimens were mounted dry on card and remain in the reference collection maintained by the author. A copy of all records is held by the Leicestershire Biological Records Centre.

3.3 Ordination of samples using species assemblage parameters

For each sample, various indices were calculated mostly using weighted averages, where the weights were derived from scores given to the species forming the assemblage. Two versions of each weighted average index were calculated. The *species* version was based on the presence or absence of species and is simply the mean of all the scores of each individual species. The *abundance-weighted* version used the untransformed abundances of each species.

3.3.1 Species richness and evenness

Two measures of species diversity were used. The Species Richness, S, was calculated as the number of species recorded in a sample. The Evenness, E, was calculated from the regression coefficient of log species abundance plotted against species rank abundance using the equation:

$$E = -1 / r \qquad (3.1)$$

where r is the regression coefficient.

3.3.2 Species composition

For several sample sets, an objective ordination based on species composition was performed using Detrended Correspondence Analysis, (Hill 1979). DCA is a version of correspondence analysis, also called reciprocal averaging, which removes unwanted mathematical artefacts (Hill & Gauch 1980). Using this method, species scores are derived iteratively from the average scores of the samples in which they occur, in contrast to the subjective ordinations described below, where species scores were derived from attributes such as rarity and wing-length which are independent of the samples in which they occur. Several orthogonal axes of variation can be derived using DCA. Axis 1 accounts for the largest variation between samples. Axis 2 is the next most important. Two axes plotted together constitute an ordination plot. For the purposes of this study, axis 1 and, to a lesser extent, other axes were treated as approximations to combinations of important environmental gradients, to which individual species abundances exhibited a unimodal response (Jongman *et al.* 1995).

3.3.3 Rarity

Various rarity indices were adapted from the Species Quality Score (SQS) used by Eyre & Rushton (1989). SQS is a summation of individual species rarity scores which are grouped into classes given values equal to geometric powers of two. This sum is then divided by the total number of species in order to correct for sampling effort. The SQS of an assemblage is therefore the arithmetic mean of all individual species rarity scores arrayed in classes on a geometric scale. It is a type of weighted average using rarity to weight the scores of individual species. Eyre & Rushton used only presence and absence data and calculated rarity scores on one scale. Four different rarity indices were calculated for this study.

The Local Species Rarity Index, R_{ls} , used individual species scores which were inversely related to the number of post-1979 1 kilometre square records held by the Leicestershire Biological Records Centre. This databank holds over 55,000 records of beetle species from within the vice-county of Leicestershire. Table 3.2 shows the relationship between individual species scores and the number of records held in the databank. R_{ls} can then be calculated as follows:

$$R_{ls} = \Sigma r_i / S \qquad (3.2)$$

where r_i is the score for an individual species.

In addition a Local Abundance-weighted Rarity Index, R_{ln}, was calculated from the same individual species scores:

$$R_{ln} = \Sigma n_i r_i / N \qquad (3.3)$$

where n_i is the abundance of an individual species and N is the total number of specimens present in the sample. Both of these indices range from 1 to a theoretical maximum of 64.

Similar calculations were used for the National Species Rarity Index, R_{ns}, and the National Abundance-weighted Rarity Index, R_{nn}, except that the individual species scores were based on national rarity rather than local rarity. Species were scored on the basis of their national conservation status which is based on the estimated number of 10 km squares occupied in Britain (Hyman 1992, 1994). These indices range from 1 to a theoretical maximum of 8 (see table 3.3).

3.3.4 Ability to disperse

Species of ground beetle were divided into four classes depending on their wing length in British specimens as described by Luff (1998). These groups were labelled B for constantly brachypterous (short-winged) species, C for brachypterous species with occasional macropterous (full-winged) specimens, D for constantly wing-dimorphic species and M for

Number of 1 km squares occupied in Leicestershire	Individual species rarity score
>63	1
32-63	2
16-31	4
8-15	8
4-7	16
2-3	32
1	64

Table 3.2: Derivation of individual species scores used to calculate local rarity indices.

National conservation status (Hyman 1992, 1994)	Estimated no. of 10 km squares occupied in Britain	Individual species rarity score
no status	>100	1
Nb or N-	<100	2
RK or Na	<30	4
R3 or RI	<15	8

Table 3.3: Derivation of individual species scores used to calculate national rarity indices.

constantly macropterous species. Indices were then based on either the proportion of species or the proportion of individual specimens in each class:

$$W_{bs} = S_b / S_c \qquad (3.4)$$

where W_{bs} is the Brachypter Species Index and S_b is the number of species of brachypterous Carabidae;

$$W_{bn} = N_b / N_c \qquad (3.5)$$

where W_{bn} is the Brachypter Abundance-weighted Index and N_b is the number of individual specimens of brachypterous species of Carabidae.

Similar calculations were used for W_{cs}, the Rarely Dimorphic Species Index; W_{ds}, the Constantly Dimorphic Species Index; W_{ms}, the Macropter Species Index and for W_{cn}, the Rarely Dimorphic Abundance-weighted Index; W_{dn}, the Constantly Dimorphic Abundance-weighted Index and W_{mn}, the Macropter Abundance-weighted Index. All of these indices range from 0 to 1.

Because dispersal ability is not always related to wing length (den Boer 1977), the possibility of calculating indices based on the dispersal ability of ground beetles in the Netherlands were investigated, but, unfortunately, the available data (den Boer 1977, Turin & den Boer 1988) does not include many of the riparian and wetland species that occur along the River Soar. Furthermore, there is a strong possibility that dispersal ability varies between regions and the idea was abandoned.

3.2.5 Land use association

Because riparian habitats occur in small patches, a proportion of specimens in any sample are likely to belong to non-riparian species. Species associated with adjacent habitats may not be easy to recognise if they occur regularly in samples. However, from a conservation perspective, it is important to give consideration to riparian specialist species rather than vagrants whose presence is unconnected to the environmental and management factors being studied.

In order to address this problem an index of association with other land uses was devised from records held at the Leicestershire Biological Records Centre. These records were collected in a variety of ways but most come from systematic surveys using either pitfall traps or hand collecting. Firstly, post 1979 records restricted to the target beetle families selected in section 3.1.1. were extracted and then those with habitat data were classified into four land use categories comprising of 1) riparian and wetland sites, 2) grassland, 3) recently disturbed sites with extensive areas of bare ground such as arable land, recently disused quarries and demolition sites and 4) other land use types. Flood refuse records were excluded because under such conditions specimens are removed from their natural habitat. Because some ground beetles and rove beetles hibernate in habitats completely different to their breeding habitats, records taken between October and March were also excluded. Records were then condensed to a set of one record per species per land use category per 100m national grid square. Individual species scores were then calculated for each land use category based on the proportion of records in each category. The Land use Association Species Index for Grassland, L_{gs}, was then calculated as follows:

$$L_{gs} = \Sigma\, g_i / S \qquad (3.6)$$

where g_i is the grassland association score for an individual species.

In addition, a Land use Association Abundance-weighted Index for Grassland, L_{gn}, was calculated from the same individual species scores:

$$L_{gn} = \Sigma\, n_i g_i / N \qquad (3.7)$$

Similar indices were calculated for riparian and wetland sites, L_{ws} and L_{wn}, and recently disturbed sites, L_{ds} and L_{dn}. All of these indices range from 0 to 1.

3.3 Measurement and quantification of environmental variables

At each sampling station a range of environmental measurements was taken. Substrate particle size was recorded by estimating the proportion of material near the surface belonging to five categories: 1) shingle and larger particles, 2) sand, 3) silt and clay, 4) coarse particulate organic matter incorporated into the substrate, 5) artificial material including dumped aggregate and rubble from collapsed weirs. Although coarse particulate organic matter is not normally included as a substrate category in this type of study, dead leaves, litter and peaty material were found to be a common and characteristic feature which had an important influence on the physical nature of the substrate at many sites. Proportions were estimated to the nearest tenth.

The proportion of the surface exposed at eye level and the proportion of the southern half of the sky shaded by trees and bushes were both estimated to the nearest tenth. The quantity of dead plant litter was scored according to table 3.4. Surface moisture was scored according to table 3.5.

Sites were then ordinated either by combining scores derived from their sampling stations or scoring further environmental and management attributes as follows.

3.4.1 Substrate

Four environmental indices were devised to describe the substrate characteristics of each site. SHINGLE was calculated by averaging the estimated proportions in tenths of shingle and larger particles at each sampling station. SAND, SILT and CPOM were calculated in the same way from the proportions of sand, silt and clay, and coarse particulate organic matter respectively. Each substrate index for a single sample was therefore derived from six values, one for each sampling stations, but for pooled samples from separate visits, multiples of six values were used. The four substrate indices were almost colinear because artificial material, the fifth category of substrate measured at each sampling station, was very rare.

3.4.2 Vegetation cover

Four environmental indices related to cover were used. BAREGRD was calculated by averaging the proportion of bare ground surface viewed from eye level at each sampling station. SHADE was calculated by averaging the proportion of shade at each sampling station. LITTER was calculated by averaging the scores derived from the quantity of dead plant litter on the surface at each sampling station. HIBSITES was scored as either 0 or 1 on the basis of the presence or absence on the bank above the site of suitable hibernation sites in the form of grass tussocks or dead wood. HIBSITES is therefore a nominal variable.

Description	Score
no surface litter	0
scattered accumulations of litter	1
thin layer of litter covering surface	2
surface litter layer more than 10cm thick	3

Table 3.4: Derivation of scores for surface litter at each sampling station

Description	Score
surface dry	0
surface damp, but with no free water	1
free water on surface	2

Table 3.5: Derivation of scores for surface moisture at each sampling station

3.4.3 Hydrology

Two hydrological indices were used. DWATER was devised to represent the amplitude of fluctuations in water level at each site, although it can also be related to the degree of permanence of open water which has been termed hydroperiod (Lugo *et al.* 1990). The whole site was scored according to table 3.6. CONNECT was devised to measure the connectivity of the site to the main channel. This is related to the frequency of flooding. The whole site was scored according to table 3.7.

3.4.4 Natural disturbance

NATDIST is an index devised to measure the severity of natural disturbance by flooding at each site. It was calculated from the substrate particles present at the site. Each sampling station was scored according to the predominant substrate category present (0 = coarse particulate organic matter, 1 = silt and clay, 2 = sand, 3 = shingle). NATDIST was then calculated as the average score for the whole site. It is essentially a measure of the flow rate of water running over the site during inundations since this is what determines particle size in the substrate and is a more useful overall measure of natural disturbance than the individual substrate indices SHINGLE, SAND, SILT and CPOM each of which covers only a narrow range of severity of disturbance.

3.4.5 Management

Three indices were devised to represent the intensity of management at each site. GRAZING is an score based on the degree to which sites had been trampled by stock within the last three years. Sites with no history of grazing were given a score of 0, whereas trampled sites were given a score of 2. Partially or infrequently grazed sites were given a score of 1. The animals present at all grazed sites were cattle except at one site where horses were present. At three sites both cattle and sheep were present. At some sites, information on stocking was available from tenants. At other sites, the history of access by grazing stock was deduced from adjacent land use. Even when stock was absent during the year of survey, it was often possible to find evidence of their recent presence in the form of hoof-marks. IMPOUND was scored as either 0 or 1 on the basis of impoundment for navigation of the stretch of river where the site was situated. RECR was scored as either 0 or 1 on the basis of presence or absence of small areas cleared of vegetation usually by anglers.

Description	Score
Low fluctuations - floating mats of vegetation are present at floodplain sites; high water levels are maintained by impoundment at main channel sites.	1
Large areas of substrate are exposed only in the summer, but open water is always present.	2
Open water disappears during the summer but moisture is always retained in the substrate close to the surface.	3
The substrate dries out completely near to the surface.	4

Table 3.6: Derivation of scores for DWATER, an index of water level fluctuations at each site.

Description	Score
no permanent connection to the main channel; only connected during major floods.	1
permanently connected at one end.	2
permanently connected at both ends, but only a secondary channel.	3
directly on the main channel.	4

Table 3.7: Derivation of scores for CONNECT, an index of connectivity to the main channel.

3.4 Relation of species assemblage parameters to environmental and management factors

Values derived from the ordination of species assemblage parameters were treated as response variables and compared with the values of environmental and management factors, but a number of problems were identified in using methods which assumed a normal distribution of values. Few of the species assemblage parameters could be assumed to be normally distributed between sites. For example, species richness is expressed in integers and is more likely to follow a Poisson distribution, while rarity indices are based on component species scores distributed along a geometric scale and so are likely to have a skewed distribution producing outliers with high values. Non-parametric methods which are free from assumptions about normal distribution and reduce the influence of outliers (Kendall & Gibbons 1990), were employed to relate species assemblage parameters to environmental factors.

In addition, ordination of species assemblages was obtained directly from linear combinations of the environmental variables using Canonical Correspondence Analysis (CCA). CCA is a method of multivariate analysis which is similar to DCA in assuming a unimodal response model. However, CCA uses environmental variables to constrain the ordination during iteration (ter Braak 1986, 1987-1992) and so avoids a separate interpretation of ordination axes in order to relate them to environmental variables. CCA was used mainly to detect which species were most sensitive to the chosen environmental factors.

4 Evaluation of sampling methods

4.1 Comparison of pitfall trapping and hand collecting

4.1.1 Introduction

Beetles in riparian and wetland biotopes have been sampled using pitfall traps (Lehmann 1965, Murdoch 1966, Meissner 1983, Fowles 1989, Greenwood *et al.* 1991, Desender *et al.* 1994, Sustek 1994, Zulka 1994) and a variety of hand-collecting methods (Murdoch 1966, Koch 1977, Kohler 1996). Methods of standardising hand-collected samples have involved searching a unit area or quadrat (Krogerus 1948, Murdoch 1966, Andersen 1969, Kurka 1975, Holeski & Graves 1978, Landry 1994) and collecting for a unit length of time (Andersen 1969, Plachter 1986). Sampling unit areas is the method best suited for estimating population densities, although Andersen (1969) devised a method for converting abundances, derived from timed catches, into estimated population densities using habitat correction factors. However, Andersen experienced difficulties with quadrat sampling due to the presence of bushes, high vegetation or uneven ground. He also found it unsuitable for small habitat mosaics. Active and less abundant species were under-represented in quadrat samples. Fowles (1988) obtained very low numbers of specimens when using quadrat sampling on shingle banks in Wales. Similarly, in pilot studies along the River Soar, population densities were found to vary enormously from site to site and many 1m^2 quadrats would have contained no beetles at all. For these reasons timed searching rather than quadrat sampling was used to standardise sampling effort when collecting by hand.

Andersen (1969) listed three causes of unwanted variation in hand-collected samples:

a) the subjective collecting error due to the varying efficiency of the collector;

b) the varying activity of the beetles depending upon weather conditions;

c) the fact that more time is used on the collecting itself in proportion to the time used for searching when the abundance is high.

The species composition of pitfall trap samples is sensitive to small changes in trap design (Luff 1975) and so is liable to variations in efficiency just like hand-collecting. However, pitfall trapping avoids variation arising from (c) and reduces problems connected with short-term variations in weather conditions by operating over an extended time period. When compared with pitfall trapping, hand-collecting has several further possible disadvantages. Nocturnal species may be under-represented in samples collected by hand during the day. Evidence for this comes from Andersen (1995), who found that nocturnal ground beetles were better represented in riverbank pitfall trap samples than quadrat samples. In addition, small species may escape detection during hand-collecting and be less well represented than larger species. However, there is also a bias toward larger species in pitfall trap samples of ground beetles, because they are more active and so more likely to meet with traps than smaller species (Andersen 1995).

An important feature of pitfall traps is that the numbers of a beetle species caught is dependent not only on population density, but also on behaviour. Interspecific variations in surface activity and ability to avoid or escape from traps may lead to unwanted bias in results, especially between habitat structures which differentially affect species' activity by impeding surface movement. Consequently, it might be expected that active, cursorial species would be better represented in pitfall trap samples than hand-collected samples, because their locomotory activity would lead to more encounters with traps, while ensuring a better chance of escaping from the pooter. Conversely, fossorial species which do not move so easily over the surface, might be expected to be better represented in hand-collected samples than pitfall trap samples.

In summary, it is predicted that hand-collected samples may contain a bias against nocturnal species and cursorial species. Pitfall trap samples may contain a bias against fossorial species and toward cursorial species. Both methods may favour large species.

Reported logistic problems, when using pitfall traps in riparian sites, include flooding (Plachter 1986, Fowles 1988) and interference from children, bathers and anglers (Koch 1977).

It was decided to investigate the practicality and bias of timed hand-collecting and pitfall trapping by direct comparison of samples taken by each method from the same set of sites. It was also decided to evaluate the importance of differences in species composition arising from different sampling methods in relation to between-site differences and seasonal variations.

4.1.2 Methods

In 1992, five sites listed in table 4.1 were selected to cover a range of habitat structures. Six pitfall traps, as described in section 3.1.3, were set within 10 metre lengths at each site, in positions chosen to cover variations in microhabitat. They were operated throughout May. Timed hand-collected samples, as described in section 3.1.2, were taken at the start and end of the trapping period. Specimens of the target groups, chosen in section 3.1.1, were identified to species.

In 1994, six pitfall traps were set at each of five main-channel sites (sites 4,9,11,13,18) and operated for five one-week periods in April, May, June, July and September. Hand-collected samples were taken from each site at the same time that the traps were either set or taken up.

The results from 1994 were ordinated using DCA. For both years the number of specimens and number of species in each sample were recorded. For each sample, the proportion of species and individual specimens in each family and major subfamily of Staphylinidae were calculated together with indices based on size and daily activity. For the calculation of size indices, species were grouped into classes based on a geometric scale of body length and scored as in table 4.2. The Species Size Index was then calculated as the average score of all species in the sample. The Specimen Size Index was calculated as the average score of all specimens in the sample. For the calculation of the Daily Activity Index, ground beetle species were scored from 0 to 3 according to the proportion of activity that takes place during the day as reported by Thiele & Weber (1968). For the 1994 results, the proportions of fossorial and cursorial individuals in each sample were calculated and termed Fossorial Index and Cursorial Index respectively. The species regarded as fossorial or cursorial were selected on the basis of their morphology and personal observation. They are listed in table 4.3.

The means of indices, calculated from pitfall trap samples, were compared with those from hand-collected samples by studying the distribution of values obtained by subtracting hand-collected sample values from the equivalent pitfall trap values. Wilcoxon's test for paired comparisons (Bailey 1995) was used to test the significance of the departure of these differential values from zero. This test was chosen because it is free from assumptions about the distribution of sample values which are probably not normally distributed between habitat structures for this data set.

Site	Brief description
4	Exposed, mixed sand and silt deposit by main channel, adjacent to ungrazed hay-meadow.
5c	Ungrazed backwater with stable water level and covered by flating mat of tall vegetation.
8w	Shaded, ungrazed backwater with fluctuating water levels.
13	Exposed, mixed sand and silt deposit by main channel, adjacent to disused osier bed.
23	Exposed, mixed sand and silt deposit by main channel, adjacent to grazed meadow and heavily trampled by cattle.

Table 4.1: Sites selected to compare hand-collected samples and pitfall trap samples in 1992.

Average Body Length (mm.)	Individual Species Score
< 1	0
1-2	1
2-4	2
4-8	3
8-16	4
>16	5

Table 4.2: Derivation of individual species scores used to calculate size indices. Average body lengths are taken from Lindroth (1974) and Freude, Harde & Lohse (1964, 1974).

Fossorial species	Cursorial species
Clivina spp. *Dyschirius* spp. *Bledius* spp. *Carpelimus* spp. *Lathrobium* spp. *Xantholinus* spp.	*Nebria* spp. *Elaphrus* spp. *Bembidion dentellum* *Bembidion genei* *Agonum marginatum* *Chlaenius vestitus* *Stenus* (subgenus *Stenus* s. str.) *Tachyusa* spp. *Chloporata longitarsis*

Table 4.3: Taxa selected to calculate proportion of fossorial and cursorial indices of each sample.

4.1.3 Results

The respective abundances of each species in pitfall trap samples and hand-collected samples are listed in tables 4.4 to 4.11. The full distribution of species between samples is given in appendices 1 and 2. Large variations in efficiency between the two sampling methods are apparent for individual species.

Heavy rain caused flooding of pitfall trap sites by main channels in 1992. Pitfall traps at site 4 were rescued and reset after water levels had subsided. There was insufficient time to rescue the traps at site 13 and the results were lost. The traps at site 23 were destroyed by the trampling of cattle and, again, the results were lost. In 1994 several traps at site 11 were affected by human interference in June and July. The traps at site 9 were destroyed by an influx of cattle in May and subsequently trapping was discontinued. The results for these sites were discarded and analysis was restricted to sites 4, 13 and 18.

Figure 4.1 shows the ordination diagram for the 1994 results. Hand-collected samples and pitfall trap samples from the same site and month are linked by a line. The overwhelming majority of lines are vertical indicating very little difference in species composition along axis 1, the major axis of variation. Even along axis 2, the differences between pitfall trap samples and hand-collected samples are smaller than those between sites and months. Consequently it can be concluded that differences in species composition due to these sampling methods are small compared to those caused by other factors.

The values of indices for samples collected in 1992 are shown in table 4.12. The Daily Activity Index, which is based exclusively on ground beetle attributes, was not calculated for the 1992 samples because of the small number of ground beetle species recorded at site 5c. Values of the differences between hand-collected and pitfall trap samples at each site are shown in table 4.13, together with the mean difference for each index. Positive values indicate a higher value for pitfall trap samples and negative values indicate a higher value for hand-collected samples. Species richness, mean species size and mean specimen size were all significantly higher in pitfall trap samples. No significant differences were found for the proportions of species from different families. When abundances were used in the analysis, it was found that ground beetles were caught in higher numbers in most pitfall traps, while rove beetles were recorded in higher numbers by hand-collecting. However, the level of significance was just outside the normally accepted confidence limits of 95%.

The results from April to July, 1994 are similar to those for 1992. Table 4.15 shows that a significantly larger number of species was recorded by pitfall trapping, although table 4.14 shows that higher number of individual specimens usually caught in pitfall traps was not significant. There was no significant difference between the proportions of species belonging to the two main families but ground beetles were recorded in significantly higher abundances in pitfall traps (see tables 4.16 to 4.19). Rove beetles belonging to the subfamily, Steninae, were recorded in lower numbers in pitfall traps (see tables 4.20 and 4.21). Tables 4.22 and 4.23 show the values of various indices derived from the two sampling methods. Significantly larger species and larger specimens were recorded in pitfall traps. However, the expected higher numbers of nocturnal species in pitfall traps were not significant. Furthermore the distribution of the most abundant nocturnal species, *Agonum albipes,* was not significantly biased toward pitfall trap samples (see table 4.24). Similarly, the expected poorer representation of fossorial species in pitfall traps was not significant. Cursorial species tended to be slightly more abundant in hand-collected samples, a result contrary to expectations.

Table 4.25 shows the numbers of specimens and species recorded in September, 1994. In contrast to the results from other months, pitfall trap samples were very poor in numbers. This is probably due to the low levels of activity at this season of spring breeders which constitute the major proportion of species assemblages in these biotopes.

4.1.4 Discussion

Despite the large differences in sampling efficiency for individual species, many of the expected differences in assemblage parameters between pitfall trap samples and hand-collected samples were found to be of no or lesser significance. Both sampling methods give equivalent species compositions when comparing samples from different sites and different seasons. Expected biases of hand-collecting away from nocturnal species and cursorial species were not confirmed, despite the finding of Andersen (1995) that nocturnal species were better represented in pitfall trap samples. Any bias toward larger species in hand-collected samples was masked by an even larger bias toward larger species in pitfall trap samples.

The higher number of specimens recorded in pitfall traps is not an inherent property of pitfall traps, but reflects the relative sampling efforts represented by the sampling protocols employed in this project. The catch numbers could easily be adjusted by either aggregating repeated hand-collected samples or changing the pitfall trap design to reduce its efficiency. However the raw figures for numbers of specimens and numbers of species in 1992 show huge variations for pitfall trap samples compared to hand-collected samples (see table 4.4). There are two factors which could lead to such a result. Firstly, because the hand-collecting method is standardised by time rather than area, samples from a sparsely populated site will cover a wider area leading to a reduction in variation of numbers of individuals between densely and sparsely populated sites. Quadrat sampling would presumably show much wider variations in catch totals. Secondly, the relatively low numbers of specimens and species traps at site 5c may be due to the lower trapping efficiency of pitfall traps in this biotope. Site 5c contains a floating mat of tall marsh vegetation with a permanently high water level. Beetles present at the site are adapted for climbing plants and coping with floods. They should be able to avoid entrapment by the preservative and climb up the sides of the trap. Beetles in other biotopes may be able to avoid entrapment by the preservative, but are less likely to be able to climb the sides of the trap. Therefore, it should be expected that beetles at site 5c will have a higher escape rate from traps than beetles at sites in other biotopes.

The results from the River Soar support the findings of Andersen (1995) that pitfall traps yield higher values of species richness and higher numbers of larger species. They also differ from hand-collected samples in the relative abundances of some families and subfamilies. However, whatever their merits or drawbacks, the use of pitfall traps for this project was found to be impractical because of problems connected with flooding, human interference and trampling by cattle. In contrast, the expected deficiencies of hand-collecting with regard to nocturnal species and cursorial species were not detected.

Species	Abundance in hand-collected samples	Abundance in pitfall trap samples	Species	Abundance in hand-collected samples	Abundance in pitfall trap samples
Agonum albipes	3	54	*B. tetracolum*	4	19
A. fuliginosum	6	14	*Clivina collaris*	1	
A. livens	2	171	*C. fossor*		1
A. marginatum	1		*Dyschirius aeneus*	1	
A. micans	2	18	*D. luedersi*	3	
A. moestum		2	*Elaphrus cupreus*	8	3
A. thoreyi	13	10	*E. riparius*	4	13
Amara communis		1	*Loricera pilicornis*	1	15
A. familiaris		8	*Nebria brevicollis*		6
Badister bipustulatus		2	*Notiophilus biguttatus*	4	5
Bembidion aeneum		1	*Pterostichus cupreus*		1
B. articulatum	2	11	*P. macer*		1
B. biguttatum	49	92	*P. minor*	6	15
B. clarki	112	187	*P. nigrita*	6	177
B. dentellum	21	19	*P. strenuus*	1	11
B. genei		2	*P. vernalis*		1
B. gilvipes	2	19	*P. versicolor*		2
B. guttula	2	6	*Stenolophus mixtus*	1	9
B. harpaloides	1		*Stomis pumicatus*	1	3
B. lunulatum	2		*Tachys parvulus*		12
B. obtusum	11	28	*Trechus obtusus*		1
B. properans	1	1			

Table 4.4: Species of Carabidae recorded in samples collected in 1992 in order to compare sampling methods.

Species	Abundance in hand-collected samples	Abundance in pitfall trap samples	Species	Abundance in hand-collected samples	Abundance in pitfall trap samples
Anotylus insecatus	1	2	*P. laminatus*		8
A. rugosus	3	4	*P. sordidus*		1
A. sculpturatus		26	*P. varius*		1
A. tetracarinatus		5	*Platystethus cornutus*	3	6
Carpelimus bilineatus	3		*Proteinus ovalis*		1
C. corticinus	2		*Quedius curtipennis*		3
C. elongatulus		1	*Q. maurorufus*	3	1
C. gracilis		1	*Q. scintillans*		2
C. impressus	23	1	*Sepedophilus marshami*		1
C. rivularis	36	4	*Staphylinus melanarius*		2
C. subtilicornis		3	*S. olens*		4
Gabrius pennatus		3	*Stenus bimaculatus*	6	5
Lathrobium brunnipes	21	6	*S. boops*	8	9
L. fulvipenne	4	11	*S. juno*	23	10
L. geminum		1	*S. solutus*	2	
Lesteva heeri	6		*Tachinus corticinus*		4
L. longoelytrata	5	3	*T. laticollis*		1
L. pubescens		2	*T. signatus*		85
Neobisnius villosulus	3	1	*Tachyporus dispar*	1	1
Omalium caesum		21	*T. hypnorum*	1	10
O. rivulare		12	*T. nitidulus*		2
Othius laeviusculus	4		*T. obtusus*	3	3
O. punctulatum		1	*T. pallidus*	2	7
Oxytelus fulvipes	1		*Xantholinus linearis*	8	13
Philonthus cognatus		2	*X. longiventris*	3	29

Table 4.5: Species of Staphylinidae (subfamilies Proteininae to Tachyporinae) recorded in samples collected in 1992 in order to compare sampling methods.

Species	Abundance in hand-collected samples	Abundance in pitfall trap samples	Species	Abundance in hand-collected samples	Abundance in pitfall trap samples
Aleochara bipustulata		1	*Deinopsis erosa*	1	
A. lanuginosa	1		*Deubelia picina*	5	6
Aloconota gregaria	1	5	*Dinaraea angustula*		6
A. sulcifrons	1		*Dochmonota clancula*	4	
Amischa analis	3	2	*Geostiba circellaris*		5
A. decipiens		1	*Gnypeta carbonaria*	21	1
Atheta debilis	1		*G. velata*	6	
A. elongatula	11	2	*Hygronoma dimidiata*	1	3
A. fungi agg.	8	9	*Ilyobates propinquus*		1
A. graminicola	19	33	*Liogluta nitidula*	1	128
A. hygrobia	8		*Myllaena dubia*	30	2
A. luteipes		4	*M. infuscata*	2	
A. malleus	23	2	*Oxypoda brachyptera*		1
A. vilis	1	1	*O. elongatula*	11	
A. volans	1		*O. lentula*	19	2
Callicerus obscurus		9	*O. opaca*		1
C. rigidicornis		61	*O. umbrata*		3
Calodera aethiops	1	3	*Pachnida nigella*	15	1
C. riparia		1	*Tachyusa atra*		1
Chiloporata longitarsis	5	9	*T. coarctata*	1	

Table 4.6: Species of Staphylinidae (subfamily Aleocharinae) recorded in samples collected in 1992 in order to compare sampling methods.

Species	Abundance in hand-collected samples	Abundance in pitfall trap samples	Species	Abundance in hand-collected samples	Abundance in pitfall trap samples
Bryaxis bulbifer	1		*H. marginatus*	1	2
Rybaxis longicornis	1		*Agriotes obscurus*	1	
Heterocerus fenestratus	13	4			

Table 4.7: Species of Heteroceridae and Elateridae recorded in samples collected in 1992 in order to compare sampling methods.

Species	Abundance in hand-collected samples	Abundance in pitfall trap samples	Species	Abundance in hand-collected samples	Abundance in pitfall trap samples
Agonum albipes	114	190	*Carabus granulatus*	1	39
A. assimile	11	28	*Chlaenius nigricornis*		4
A. dorsale	1	4	*C. vestitus*	1	
A. fuliginosum	9	19	*Clivina collaris*	5	7
A. micans	64	107	*C. fossor*		5
A. moestum		4	*Elaphrus cupreus*		14
A. muelleri		1	*E. riparius*	10	32
A. obscurum		3	*Harpalus latus*		1
A. thoreyi	1	1	*H. rufipes*		1
Amara similata		1	*Loricera pilicornis*	7	168
Asaphidion stierlieni		2	*Nebria brevicollis*	2	1
Bembidion aeneum	3	2	*Notiophilus biguttatus*	1	
B. articulatum	1		*N. substriatus*	1	
B. biguttatum	42	32	*Patrobus atrorufus*		12
B. dentellum	59	60	*Pterostichus cupreus*		1
B. gilvipes	14	32	*P. melanarius*		3
B. guttula	50	40	*P. minor*		6
B. lunulatum	41	5	*P. nigrita*	3	29
B. obtusum	33	26	*P. strenuus*	2	11
B. properans	1		*P. vernalis*	12	30
B. quadrimaculatum		1	*Trechus discus*		4
B. tetracolum	30	52			

Table 4.8: Species of Carabidae recorded in samples collected from main channel sites in 1994 in order to compare sampling methods.

Species	Abundance in hand-collected samples	Abundance in pitfall trap samples	Species	Abundance in hand-collected samples	Abundance in pitfall trap samples
Anotylus insecatus		1	*P. varians*		1
A. rugosus	37	115	*P. varius*		1
A. sculpturatus	1	3	*Platystethus cornutus*	1	
Carpelimus bilineatus	9	1	*Proteinus macropterus*		45
C. corticinus	3		*Quedius curtipennis*		1
C. gracilis		2	*Q. maurorufus*	1	
C. impressus	5	4	*S. bifoveolatus*	1	
C. rivularis	128	40	*S. bimaculatus*		3
C. subtilicornis	131	176	*S. boops*	74	51
C. subtilis		2	*S. cicindeloides*	2	
Deleaster dichrous		1	*S. formicetorum*		2
Gabrius bishopi	4		*S. juno*	24	11
G. pennatus		1	*S. pubescens*	1	
Lathrobium brunnipes	2	4	*S. pusillus*		1
L. fulvipenne	1	19	*S. solutus*	1	
L. geminum	8	7	*S. tarsalis*	2	7
L. pallidum		1	*Sunius propinquus*	2	
L. quadratum	1	1	*Tachinus signatus*	7	111
Lesteva longoelytrata	12	2	*Tachyporus hypnorum*	1	1
Micropeplus porcatus		1	*T. obtusum*	17	15
Neobisnius villosulus	1	2	*T. pallidum*	3	
Philonthus cognatus	2		*T. solutus*	1	
P. laminatus		4	*Xantholinus linearis*		2
P. quisquiliarius	3	2	*X. longiventris*	1	6
P. umbratilis	2				

Table 4.9: Species of Staphylinidae (subfamilies Micropeplinae to Tachyporinae) recorded in samples collected from main channel sites in 1994 in order to compare sampling methods.

Species	Abundance in hand-collected samples	Abundance in pitfall trap samples	Species	Abundance in hand-collected samples	Abundance in pitfall trap samples
Alianta incana	1		*Chiloporata longitarsis*	52	16
Aloconota gregaria	4	5	*Dinaraea angustula*	1	5
Amischa analis		1	*Geostiba circellaris*	4	167
A. cavifrons	2	15	*Gnypeta carbonaria*	5	
Atheta crassicornis		2	*G. ripicola*	2	
A. elongatula	265	124	*G. velata*	2	
A. fungi agg.	20	79	*Gyrophaena angustata*		2
A. graminicola	120	108	*Hygronoma dimidiata*		1
A. hygrotopora	1	1	*Oxypoda brachyptera*		4
A. laticollis	10	52	*O. elongatula*		1
A. luteipes		3	*O. exoleta*		1
A. malleus	12		*O. umbrata*		1
A. obfuscata		1	*Tachyusa atra*	2	2
A. volans	3		*T. coarctata*	2	
Callicerus rigidicornis		1	*T. leucopus*	1	

Table 4.10: Species of Staphylinidae (subfamily Aleocharinae) recorded in samples collected from main channel sites in 1994 in order to compare sampling methods.

Species	Abundance in hand-collected samples	Abundance in pitfall trap samples	Species	Abundance in hand-collected samples	Abundance in pitfall trap samples
Rybaxis longicornis		1	*Adrastus pallens*	1	1
Tychus niger		1	*Hypnoides riparius*		9
Heterocerus fenestratus	1		*Selatosomus incanus*		1

Table 4.11: Species of Pselaphidae, Heteroceridae and Elateridae recorded in samples collected from main channel sites in 1994 in order to compare sampling methods.

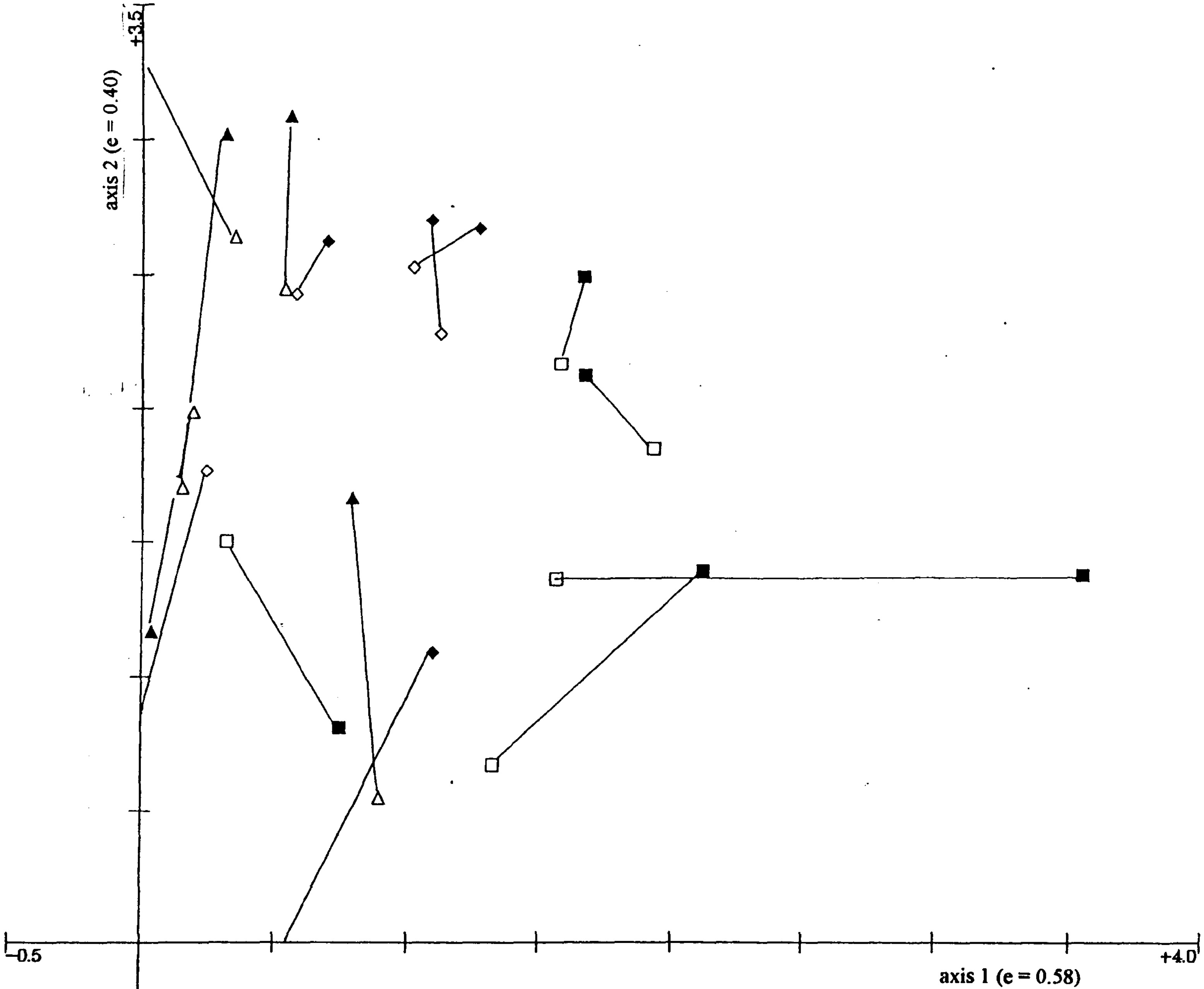

Figure 4.1: DECORANA ordination plot of paired pitfall trap and hand-collected samples taken in 1994. (filled symbols = pitfall trap samples, unfilled symbols = hand-collected samples; square = site 4, diamond = site 13, triangle = site 18).

Sample	No. specimens	No. species	Species Size Index	Specimen Size Index	Proportion of species		Proportion of specimens	
					Carabidae	Staphylinidae	Carabidae	Staphylinidae
SH04(1)	110	29	2.55	2.38	0.38	0.55	0.29	0.66
SH04(2)	87	27	2.37	2.18	0.41	0.56	0.24	0.66
SH5c(1)	100	21	2.33	2.41	0.1	0.9	0.1	0.89
SH5c(2)	56	21	2.67	2.63	0.33	0.67	0.3	0.7
SH8w(1)	179	25	2.64	2.43	0.44	0.52	0.76	0.23
SH8w(2)	133	32	2.56	2.5	0.28	0.72	0.42	0.57
SP04	258	64	2.64	2.8	0.39	0.58	0.59	0.38
SP5c	61	22	2.77	2.84	0.32	0.68	0.41	0.59
SP8w	1239	75	2.71	3	0.31	0.69	0.61	0.39

Table 4.12: Values of various indices for pitfall trap samples and corresponding hand-collected samples taken in 1992.

Sample	No. specimens	No. species	Species Size Index	Specimen Size Index	Proportion of species		Proportion of specimens	
					Carabidae	Staphylinidae	Carabidae	Staphylinidae
SH04(1)	148	35	0.09	0.42	0.01	0.03	0.3	-0.28
SH04(2)	171	37	0.27	0.62	-0.02	0.02	0.35	-0.27
SH5c(1)	-39	1	0.44	0.43	0.22	-0.22	0.31	-0.3
SH5c(2)	5	1	0.11	0.21	-0.02	0.02	0.11	-0.11
SH8w(1)	1060	50	0.07	0.57	-0.13	0.17	-0.15	0.16
SH8w(2)	1106	43	0.14	0.5	0.03	-0.03	0.19	-0.18
mean difference	408.5	27.83	0.19	0.46	0.02	0	0.18	-0.16
P	ns (< 0.1)	< 0.05	< 0.05	< 0.05	ns	ns	ns (< 0.1)	ns (< 0.1)

Table 4.13: Differences in index values between pitfall trap and hand-collected samples in 1992 and significance of departure from zero for mean difference according to Wilcoxon's test for paired comparisons.

Month	Site	pitfall trap samples	hand-collected samples	difference
4	4	110	63	47
4	13	141	27	114
4	18	65	55	10
5	4	107	127	-20
5	13	113	120	-7
5	18	71	176	-105
6	4	166	64	102
6	13	112	72	40
6	18	186	71	115
7	4	387	139	248
7	13	220	232	-12
7	18	506	188	318
mean		182	111.17	70.83
			P	ns (< 0.1)

Table 4.14: Numbers of specimens taken in samples collected in 1994.

Month	Site	hand-collected samples	pitfall trap samples	difference
4	4	14	24	10
4	13	14	32	18
4	18	20	20	0
5	4	20	25	5
5	13	25	29	4
5	18	24	26	2
6	4	22	17	-5
6	13	17	30	13
6	18	18	40	22
7	4	19	39	20
7	13	20	29	9
7	18	21	44	23
mean		19.5	29.58	10.08
			P	< 0.01

Table 4.15: Numbers of species taken in samples collected in 1994.

Sample	Carabidae	Staphylinidae (inc. Pselaphidae)	Heteroceridae	Elateridae
SH0404	0.57	0.43	0.00	0.00
SH0413	0.57	0.43	0.00	0.00
SH0418	0.65	0.35	0.00	0.00
SH0504	0.30	0.65	0.05	0.00
SH0513	0.40	0.60	0.00	0.00
SH0518	0.54	0.46	0.00	0.00
SH0604	0.45	0.55	0.00	0.00
SH0613	0.47	0.53	0.00	0.00
SH0618	0.33	0.67	0.00	0.00
SH0704	0.37	0.58	0.00	0.05
SH0713	0.30	0.70	0.00	0.00
SH0718	0.24	0.76	0.00	0.00
SP0404	0.46	0.50	0.00	0.04
SP0413	0.53	0.47	0.00	0.00
SP0418	0.65	0.35	0.00	0.00
SP0504	0.44	0.56	0.00	0.00
SP0513	0.66	0.34	0.00	0.00
SP0518	0.62	0.38	0.00	0.00
SP0604	0.35	0.65	0.00	0.00
SP0613	0.47	0.53	0.00	0.00
SP0618	0.60	0.40	0.00	0.00
SP0704	0.44	0.51	0.00	0.05
SP0713	0.41	0.59	0.00	0.00
SP0718	0.41	0.57	0.00	0.02

Table 4.16: Proportion of species belonging to different families in 1994 samples.

Sample	Carabidae	Staphylinidae
SP0404	-0.11	0.07
SP0413	-0.04	0.04
SP0418	0.00	0.00
SP0504	0.14	-0.09
SP0513	0.26	-0.26
SP0518	0.07	-0.07
SP0604	-0.10	0.10
SP0613	0.00	0.00
SP0618	0.27	-0.27
SP0704	0.07	-0.07
SP0713	0.11	-0.11
SP0718	0.17	-0.19
mean diff.	0.07	-0.07
P	ns	ns

Table 4.17: Differences in proportions of species belonging to different families between pitfall trap and hand-collected samples in 1994 and significance of departure from zero for mean difference according to Wilcoxon's test for paired comparisons.

Sample	Carabidae	Staphylinidae (inc. Pselaphidae)	Heteroceridae	Elateridae
SH0404	0.70	0.30	0.00	0.00
SH0413	0.67	0.33	0.00	0.00
SH0418	0.65	0.35	0.00	0.00
SH0504	0.20	0.80	0.01	0.00
SH0513	0.38	0.62	0.00	0.00
SH0518	0.49	0.51	0.00	0.00
SH0604	0.28	0.72	0.00	0.00
SH0613	0.61	0.39	0.00	0.00
SH0618	0.31	0.69	0.00	0.00
SH0704	0.29	0.70	0.00	0.01
SH0713	0.05	0.95	0.00	0.00
SH0718	0.20	0.80	0.00	0.00
SP0404	0.73	0.20	0.00	0.07
SP0413	0.62	0.38	0.00	0.00
SP0418	0.72	0.28	0.00	0.00
SP0504	0.64	0.36	0.00	0.00
SP0513	0.69	0.31	0.00	0.00
SP0518	0.72	0.28	0.00	0.00
SP0604	0.08	0.92	0.00	0.00
SP0613	0.69	0.31	0.00	0.00
SP0618	0.77	0.23	0.00	0.00
SP0704	0.26	0.73	0.00	0.01
SP0713	0.19	0.81	0.00	0.00
SP0718	0.35	0.65	0.00	0.00

Table 4.18: Proportion of specimens belonging to different families in 1994 samples.

Sample	Carabidae	Staphylinidae
SP0404	0.03	-0.10
SP0413	-0.05	0.05
SP0418	0.07	-0.07
SP0504	0.45	-0.44
SP0513	0.31	-0.31
SP0518	0.23	-0.23
SP0604	-0.20	0.20
SP0613	0.08	-0.08
SP0618	0.46	-0.46
SP0704	-0.03	0.04
SP0713	0.13	-0.13
SP0718	0.15	-0.15
mean diff.	0.14	-0.14
P	< 0.05	< 0.05

Table 4.19: Differences in proportions of specimens belonging to different families between pitfall trap and hand-collected samples in 1994 and significance of departure from zero for mean difference according to Wilcoxon's test for paired comparisons.

Sample	Oxytelinae	Steninae	Aleocharinae
SH0404	0.13	0.08	0.03
SH0413	0.11	0.07	0.07
SH0418	0.05	0.16	0.13
SH0504	0.39	0.02	0.35
SH0513	0.38	0.03	0.13
SH0518	0.15	0.20	0.10
SH0604	0.48	0.03	0.19
SH0613	0.03	0.08	0.17
SH0618	0.06	0.07	0.54
SH0704	0.31	0.04	0.30
SH0713	0.04	0.02	0.86
SH0718	0.44	0.07	0.28
SP0404	0.08	0.02	0.02
SP0413	0.27	0.01	0.06
SP0418	0.02	0.11	0.15
SP0504	0.04	0.03	0.18
SP0513	0.20	0.03	0.04
SP0518	0.10	0.08	0.04
SP0604	0.07	0.01	0.80
SP0613	0.06	0.06	0.13
SP0618	0.05	0.05	0.09
SP0704	0.27	0.03	0.21
SP0713	0.24	0.02	0.38
SP0718	0.15	0.04	0.37

Table 4.20: Proportion of specimens belonging to the main subfamilies of Staphylinidae in 1994 samples.

Sample	Oxytelinae	Steninae	Aleocharinae
SP0404	-0.05	-0.06	-0.01
SP0413	0.16	-0.06	-0.01
SP0418	-0.04	-0.06	0.03
SP0504	-0.35	0.01	-0.17
SP0513	-0.17	-0.01	-0.10
SP0518	-0.05	-0.12	-0.06
SP0604	-0.41	-0.03	0.61
SP0613	0.03	-0.02	-0.04
SP0618	-0.01	-0.02	-0.45
SP0704	-0.04	-0.01	-0.09
SP0713	0.20	0.00	-0.48
SP0718	-0.28	-0.04	0.09
mean diff.	-0.08	-0.03	-0.06
P	ns	< 0.01	ns

Table 4.21: Differences in proportions of specimens belonging to the main subfamilies of Staphylinidae between pitfall trap and hand-collected samples in 1994 and significance of departure from zero for mean difference according to Wilcoxon's test for paired comparisons.

Month	Site	pitfall trap samples	hand-collected samples	difference
4	4	0.4	0.13	0.27
4	13	0.23	0.22	0.01
4	18	0.08	0.05	0.02
5	4	0.25	0.03	0.22
5	13	0.12	0.16	-0.03
5	18	0.13	0.13	0
6	4	0.04	0.03	0
6	13	0.22	0.28	-0.05
6	18	0.07	0.11	-0.04
7	4	0.03	0.02	0.01
7	13	0	0.01	-0.01
7	18	0	0.01	0
	mean	0.13	0.1	0.03
			P	ns

Table 4.24: Numbers of *Agonum albipes* expressed as proportion of 1994 samples.

Site	No. specimens		No. species	
	Pitfall Trap Samples	Hand-collected Samples	Pitfall Trap Samples	Hand-collected Samples
4	11	58	6	19
13	27	39	5	12
18	8	88	4	28

Table 4.25: Numbers of specimens and species recorded in September, 1994.

	Carabid	Staph	Other
April	27	27	1
May	28	25	
June	26	31	
July	26	35	3
Sept	4	6	
April	18	12	
May	15	26	1
June	15	23	
July	11	23	1
Sept	15	25	

	N(Pt)	N(SH)	S(Pt)	S(SH)
4	316	145	18	76
5	291	423	69	80
6	464	207	57	87
7	1113	559	60	112
9	46	185	15	59
	2230	1519		

	Pt
Carabidae	38
Staphylinidae	60
Heteroceridae	~~5~~0
Elateridae	3
	101

Sample	Species Size Index	Specimen Size Index	Daily Activity Index	Fossorial Index	Cursorial Index
SH0404	2.50	2.43	1.33	0.17	0.02
SH0413	2.71	2.74	1.43	0.19	0.07
SH0418	2.75	2.84	1.00	0.02	0.13
SH0504	2.45	2.43	1.00	0.43	0.30
SH0513	2.64	2.48	1.41	0.40	0.16
SH0518	2.71	2.65	1.18	0.15	0.11
SH0604	2.36	2.27	1.75	0.47	0.16
SH0613	2.76	2.85	1.00	0.03	0.17
SH0618	2.72	2.85	1.00	0.06	0.13
SH0704	2.47	2.19	2.50	0.23	0.04
SH0713	2.70	2.14	1.00	0.03	0.02
SH0718	2.38	2.14	1.00	0.36	0.02
SP0404	2.75	2.85	1.14	0.12	0.01
SP0413	2.72	2.91	1.40	0.26	0.04
SP0418	3.05	3.46	1.38	0.03	0.09
SP0504	2.76	2.70	1.44	0.13	0.21
SP0513	2.97	2.81	1.58	0.22	0.09
SP0518	3.08	3.15	1.41	0.06	0.14
SP0604	2.59	2.14	1.55	0.09	0.02
SP0613	2.70	2.83	1.31	0.09	0.10
SP0618	2.98	3.00	1.40	0.04	0.12
SP0704	2.69	2.49	1.66	0.18	0.06
SP0713	2.62	2.30	1.20	0.11	0.02
SP0718	2.68	2.58	1.16	0.10	0.05

Table 4.22: Values of various indices for samples taken in 1994.

Sample	Species Size Index	Specimen Size Index	Daily Activity Index	Fossorial Index	Cursorial Index
SP0404	0.25	0.43	-0.19	-0.06	-0.01
SP0413	0.00	0.17	-0.03	0.08	-0.03
SP0418	0.30	0.63	0.38	0.01	-0.04
SP0504	0.31	0.28	0.44	-0.29	-0.09
SP0513	0.33	0.33	0.17	-0.18	-0.07
SP0518	0.37	0.51	0.23	-0.09	0.03
SP0604	0.22	-0.12	-0.20	-0.38	-0.14
SP0613	-0.06	-0.02	0.31	0.06	-0.07
SP0618	0.25	0.15	0.40	-0.01	-0.01
SP0704	0.22	0.30	-0.84	-0.05	0.02
SP0713	-0.08	0.16	0.20	0.08	0.01
SP0718	0.30	0.44	0.16	-0.25	0.03
mean diff.	0.20	0.27	0.08	-0.09	-0.03
P	< 0.01	< 0.01	ns	ns	ns (< 0.1)

Table 4.23: Differences in index values between pitfall trap and hand-collected samples in 1994 and significance of departure from zero for mean difference according to Wilcoxon's test for paired comparisons.

Month	Site	pitfall trap samples	hand-collected samples	difference
4	4	0.4	0.13	0.27
4	13	0.23	0.22	0.01
4	18	0.08	0.05	0.02
5	4	0.25	0.03	0.22
5	13	0.12	0.16	-0.03
5	18	0.13	0.13	0
6	4	0.04	0.03	0
6	13	0.22	0.28	-0.05
6	18	0.07	0.11	-0.04
7	4	0.03	0.02	0.01
7	13	0	0.01	-0.01
7	18	0	0.01	0
	mean	0.13	0.1	0.03
			P	ns

Table 4.24: Numbers of *Agonum albipes* expressed as proportion of 1994 samples.

Site	No. specimens		No. species	
	Pitfall Trap Samples	Hand-collected Samples	Pitfall Trap Samples	Hand-collected Samples
4	11	58	6	19
13	27	39	5	12
18	8	88	4	28

Table 4.25: Numbers of specimens and species recorded in September, 1994.

Seasonal and annual variations

4.2.1 Introduction

Before using the various species assemblage indices described in 3.2. to ordinate samples for comparison with ordinations based on environmental and management factors, it is necessary to investigate the robustness of these indices against unwanted variations. In particular, the seasonality of activity in riparian species has been highlighted by several authors (e.g. Krogerus 1948, Lehmann 1965) and the domination of all types of wetland ground beetle assemblages by spring breeders (Murdoch 1967) might be expected to lead to markedly different results between the spring breeding season and other times of the year. Furthermore, at any one site, annual fluctuations in weather and community dynamics might be expected to lead both to gross annual variations and to annual variations in seasonal effects.

4.2.2 Methods

30 sites were selected for sampling by hand-collection during 1991 in each of the following seasons: late March to April, May, June, July and September to October. The abundances of species in target families were recorded for each monthly sample. Samples from fifteen sites with full data sets were then ordinated using DCA. Eight main channel sites and seven floodplain wetland sites were selected as reference sites and resampled in April, May and June, 1994. They were also sampled at least once in 1992 and 1993. However, because of changes in site selection procedures, the seven floodplain wetland sites sampled from 1992 onwards were not equivalent to those used for analysis in 1991. All the samples used in the analysis are listed in table 4.26.

In order to investigate the seasonal robustness of various parameters, April, May and June samples from reference sites were divided into four sets defined by year and whether they were from main channel or floodplain wetland sites. Each set was then ordinated using DCA. The indices described in section 3.2. were calculated for each sample. Within each sample set, sites were ranked for each month and W, Kendall's coefficient of concordance (Kendall & Gibbons 1990), was calculated in order to measure the consistency of rankings. This procedure was then repeated for rankings of monthly samples from each site. Rankings of sites obtained from DCA ordinations of separate monthly sample sets were also compared.

Sites		1991			1992	1993	1994		
main channel	4		13.5		13.6	21.6		31.5	
	9	11.4	9.5	30.6	22.6	24.6	24.4	30.5	14.6
	11		10.5		6.5	24.6			12.6
	13	26.4	15.5	8.6	14.6	24.6	26.4	1.5	12.6
	17	29.3	9.5	30.6	28.5	23.6	26.4	27.5	14.6
	18	28.3	9.5	30.6	26.5	23.6	26.4	27.5	14.6
	23	28.4	12.5	29.6	12.6	24.6	29.4	31.5	13.6
	30	27.4	19.5	29.6	28.5	27.6	29.4	29.5	13.6
flood-plain	1	11.4	7.5	14.6					
	1c				3.5	28.6	28.4	30.5	28.6
	1e				3.5	28.6	28.4	30.5	28.6
	1w				3.5	29.6	28.4	31.5	28.6
	5	3.4	8.5	10.6					
	5c				11.4	8.5	20.4	30.5	30.6
	5w				11.4	8.5	20.4	30.5	30.6
	8	3.4	8.5	10.6					
	8e				9.4	4.5	22.4	28.5	30.6
	8w				9.4	4.5	21.4	28.5	28.6
	16	29.3	8.5	8.6					
	21	10.4	19.5	26.6					
	25	28.4	18.5	8.6					

Table 4.26: Sampling dates of reference sites used for evaluation of seasonal and annual variations.

In order to measure the robustness of parameters against purely annual fluctuations, sets of one sample per site from each year were analysed in a similar fashion for main channel and floodplain wetland sites separately. The samples chosen for analysis from each year were those collected at the date closest to May 31st. It was possible to analyse main channel sites over four years between 1991 and 1994 and floodplain wetland sites over three years between 1992 and 1994.

4.2.3 Results

For various reasons it was not possible to obtain a full set of monthly samples for every site in 1991. In June, site 10 was destroyed by unscheduled engineering works. In the same month, heavy flooding severely disrupted sampling and no sample was taken from site 4, because it was under water on each occasion that it was visited. Sites 6, 7 and 22 are shallow floodplain sites which dried out during the summer and became impossible to sample using standard hand-collecting techniques. Floodplain sites 8, 16, 20, 21 and 25 also lost all their open water, but retained sufficient moisture in their peaty substrates to remain viable for sampling throughout the year. Heavy flooding returned toward the end of September and main channel sites 23 and 29 which were visited after that date yielded samples containing species characteristic of flood refuse rather than of riparian sites.

Full lists of species recorded at each site are included in appendix 2. Table 4.27 gives the seasonal abundances of ground beetles recorded in 1991. Nearly all the most abundant species reach peak numbers in April or, more usually, May as would be expected for spring breeders. *Clivina collaris* and *Bembidion gilvipes* decreased in numbers relatively early in the season, while *Elaphrus riparius* peaked in June which was late compared with other spring breeders. These results were repeated in 1994 as shown by table 4.28. The main difference in 1994 was that, with the exception of two species associated with intensive agriculture, namely *Bembidion guttula* and *B. lunulatum*, numbers of spring breeders dropped off rapidly before July. The other big difference in 1994, was that no summer breeders were recorded. This may be due to the smaller number of sites sampled in 1994, because summer breeders are much less abundant in the study sites than spring breeders. Of the summer breeders recorded in 1991, *Patrobus atrorufus* and *Trechus discus* reached peaked numbers in June, while *Trechus secalis* was present in equal numbers in June and July. These peaks overlapped with late spring breeders and were slightly earlier than expected. The flooding in June 1991 may have caused these species to become more easily caught and led to the other observed differences between the two years.

Tables 4.29 and 4.30 show the seasonal abundances of rove beetles in 1991 and 1994 respectively. The dominance of species with peak abundances in the spring is not as evident as in the ground beetles, although *Aloconota gregaria, Lathrobium fulvipenne, Oxypoda lentula, Pachnida nigella* and to a lesser extent, *Carpelimus bilineatus* and *C. impressus* were all captured more frequently in the spring. Caution should be exercised in labelling these species as spring breeders, because *Lesteva longoelytrata,* which shows a marked peak of abundance in May in both years, was categorised by Steel (1970) as an autumn breeder with overwintering larvae. Other species peaked in either summer or autumn. In 1991, a few species exhibited two peaks of abundance separated by a marked drop in numbers in June. For *Stenus boops* and *S. juno,* this may have been connected with the June floods of that year, because they showed a unimodal peak of abundance in spring 1994. However, for *Carpelimus rivularis* and *C. subtilicornis,* the low June abundances were repeated in 1994. Tables 4.31 and 4.32 show seasonal abundances for other target families, but these are too poor in numbers of species to exhibit any patterns.

Annual fluctuations in spring abundances are shown in tables 4.33 to 4.40. There appear to be larger fluctuations at main-channel sites than floodplain sites. Similarly, there appear to be larger fluctuations for rove beetles than ground beetles.

Figure 4.2 shows the ordination diagram of monthly samples from fifteen sites sampled in 1991. Sampling date dominates axis 2 with late season samples scoring highly, but it also has an influence on axis 1, with late season samples tending to score higher. Clearly, there are difficulties in comparing the species compositions of samples collected in July or September with those from spring unless seasonal variations are removed using partial correlation. This is especially true when looking at variation along axis 2.

Figures 4.3 to 4.5 show the ordination plots for each of the seasonal sample sets from reference sites. Figures 4.3 and 4.4 show main channel and floodplain samples from April to June 1991 ordinated separately. Figure 4.5 shows main channel and floodplain samples from 1994 ordinated together in order to show the greater variation between floodplain sites (1,5,8) than main channel sites (9,13,17,18,23,30). Two main channel sites had to be removed from the analysis. Site 4 lacked a sample for June 1991 because of flooding. The numbers of specimens taken in early 1994 at site 11 were so low that they could not be meaningfully interpreted. When restricted to samples taken in spring, seasonal variation became much less important than differences between sites except for two samples taken at sites 9 and 18 in June 1991 which were probably affected by previous flooding. Figures 4.6 and 4.7 show the ordination diagrams for the yearly sample sets from reference sites. For the seven floodplain sites, annual variations were much less important than between-site differences. However, annual fluctuations in species composition at the eight main channel sites were more important and annual variation may lead to difficulties when comparing samples taken from similar main channel sites in different years.

Tables 4.41 and 4.42 list the coefficients of concordance for rankings of various indices between months and different years. The high figures for DCA axis 1 scores indicate a highly significant consistency of rankings of sites between months and demonstrate the robustness of coupling DCA to the hand collecting methods used in this project. The concordance of rankings based on species richness, S, and evenness, E, was more variable. Seasonal concordance of rankings was higher in 1991 than 1994. Concordance of rankings based on species richness between different years was significant at the 5% level for main channel sites. However, whenever a high concordance of rankings of sites was achieved, this was coupled with high variability between months or years. Consequently, if a meaningful ranking of sites based on species richness can be achieved, it can only be done from samples taken during the same month and in the same year. Evenness produced slightly less consistent site rankings than species richness, but tended to be less affected by seasonal and annual variations.

Rankings of sites based on local rarity, R_l showed significant levels of concordance for floodplain sites, but not for main channel sites. However, rankings of main channel sites showed higher levels of concordance than rankings of months or years. Consequently, approximate rankings of main-channel sites can be achieved which are relatively independent of the month or year in which they were sampled. The abundance-weighted index did not perform consistently better than the raw index and, if anything, tended to suffer from higher seasonal and annual fluctuations. National rarity indices, R_n also gave consistent rankings, but the small proportions of species with national scores tended to yield many tied rankings, leading to difficulties in discriminating between sites below the top echelon.

A surprisingly good concordance of site rankings was achieved from some indices based on ground beetle wing length. Very low numbers of brachypterous species were caught and an index based on brachypterous species, W_b, was unworkable in the present study. Indices based on rarely dimorphic species, W_c, (i.e. species which are normally brachypterous) produced significantly consistent rankings of floodplain sites between different months. However, the low proportion of these species in main channel sites led to many tied rankings and poor discrimination. Furthermore, low numbers of these species in 1992 and 1993 meant that the robustness of this index against annual fluctuations could not be tested. Indices based on constantly dimorphic species, W_d, were more useful for main channel sites, although, as in rarity indices, the concordance of rankings was not significantly high. Moreover, because of the low numbers of ground beetles recorded in 1993, these samples had to be omitted from the analysis in order to investigate the concordance of rankings between different years. Indices based on macropterous species, W_m, were more generally applicable, because they were based on a larger number of species. However, they tended to have a lower degree of seasonal robustness than indices based on dimorphic species. Abundance-weighted wing-length indices did not give a consistently better performance in terms of robustness, but were more widely applicable, because they led to fewer tied rankings and, thus, better discrimination.

The performance of land use indices was highly variable. In 1994, river and wetland indices, L_w, gave consistent monthly rankings of floodplain sites, whereas grassland indices, L_g, gave consistent monthly rankings of main channel sites. However, this was not reflected in the 1991 results. In general, these indices were not very robust against annual fluctuations, although the disturbed ground indices, L_d, gave consistent rankings of floodplain sites. Abundance-weighted land use indices performed only marginally better in terms of site ranking concordance and tended to be more affected by seasonal and annual variations.

An evaluation of the performance of the various indices is given in table 4.43. Indices which perform well in terms of robustness will yield representative site rankings. Indices, where the relative importance of seasonal and annual variations are low, can be used to compare samples from different months and years.

4.2.4 Discussion

The variations in species composition between samples taken later in the season in July and September and those taken in the spring are not surprising. The seasonal pattern of riparian and wetland beetle life histories dictates that comparable results can best be achieved by concentrating sampling during the spring months of April, May and June. This period coincides with the main activity periods of spring-breeding adults (Krogerus 1948). Exclusion of later samples will lead to under-representation of late summer and autumn breeders. However, these constitute a small minority of species along the River Soar. Among the ground beetles, *Patrobus atrorufus, Trechus discus* and *T. secalis* are the only autumn breeders with a particular association with riparian and wetland sites. Late season samples contain many wetland and riparian rove beetles belonging to the subfamily Aleocharinae, but a high proportion of these species are also found in samples taken in the spring.

Results from samples taken in April were generally comparable with those taken in May, even though some species would not have arrived on site from their hibernation sites. However, in 1994, the dominant ground beetle at site 11, *Bembidion punctulatum,* did not arrive on site until well into May and this contributed to the very low numbers of beetles recorded there in April.

The DCA axis 1 score proved to be the most powerful discriminant of both main channel and wetland sites. The only sample set which did not yield significantly consistent rankings of axis 1 scores was the yearly set from main channel sites. All other indices exhibited properties which could lead to difficulties when used to compare sites. In particular, it was difficult to achieve consistent rankings of main channel sites. There are a number of possible causes. The main channel sites exhibited less between-site variation in the species composition of their beetle assemblages (see figure 4.5) and so any temporal variations will be relatively large. Indeed large variations between years are to be expected at main channel sites because of the severe disturbance effects of winter flooding or the fast rate of vegetational succession in their absence. Consequently, the annual variations in site rankings may reflect fluid population dynamics in a variable environment, rather than an inherent lack of robustness in the indices used. Temporal variations can also be caused by unseasonal flooding such as occurred during June, 1991. Some temporal variations may be artefacts caused by varying weather conditions during the sampling programme. Unwanted temporal variations may be reduced by aggregating samples taken at different times.

Despite these problems with main channel sites, R_{ls} , the Local Species Rarity Index has potential for use with floodplain sites and its applicability to main channel sites might be improved by aggregating repeated samples. As a measure of conservation value, it proved to be more robust at ranking sites than species richness, especially when applied to samples collected in different months and years. National rarity, as defined in chapter 3, cannot be used along the River Soar, because of the low proportion of nationally rare species.

Although the indices based on wing length appear to have potential in relating dispersal ability to environmental factors, they suffer from a lack of discrimination power, because of the low numbers of ground beetles apportioned to the various categories. In order to maximise their discrimination power, it is necessary to use the abundance-weighted indices, W_{en}, W_{dn} and W_{mn}. For all other indices there is little to be gained by using abundance-weighted versions.

The above evaluation of the performances of various indices used site rankings and so is highly dependent on the level of real between-site variation. Indices which failed to achieve a statistically significant concordance of site rankings using the reference sample sets might perform better on samples from a different set of sites, especially if these sites covered a wider range of environmental variables.

Species	Abundance					Species	Abundance				
	Apr	May	Jun	Jul	Sep		Apr	May	Jun	Jul	Sep
Acupalpus consputus		1				*B. punctulatum*	5	5	5	14	1
Agonum albipes	106	118	101	75	66	*B. quadrimaculatum*	7	3		1	
A. assimile	2	2	4	1	2	*B. tetracolum*	104	72	23	11	13
A. dorsale	2	1	11	1		*B. varium*					1
A. fuliginosum	20	50	12	12	4	*Carabus granulatus*		2	2		
A. livens		3	1		9	*Chlaenius nigricornis*			1		
A. marginatum	6	9	8	5		*Clivina collaris*	8	10			
A. micans	55	105	53	34	22	*C. fossor*	4	24	11	3	
A. moestum	2	2		1		*Demetrias atricapillus*	8	3	2		5
A. obscurum	2	8	8	3	1	*Dromius linearis*	2	3	1		1
A. thoreyi	27	18	4	1	3	*D. melanocephalus*		4			
A. viduum	7	4	1	1	1	*Dyschirius aeneus*		1			
Amara aenea	1	1	2			*D. luedersi*		2	1		
A. communis		2				*Elaphrus cupreus*	6	14	6	5	14
A. familiaris	3	14	1			*E. riparius*	2	9	10	8	1
A. plebeja	1	4	2	2		*Harpalus rufipes*		3			
A. similata	2	5	2			*Loricera pilicornis*	6	2		6	14
Asaphidion curtum	4	2	2	1	1	*Microlestes maurus*		1			
A. stierlieni	1		1		1	*Nebria brevicollis*	1	15	4		3
Badister bipustulatus		1				*Notiophilus biguttatus*	5		5	1	
Bembidion aeneum	275	204	47	51	14	*Patrobus atrorufus*	1		15		2
B. articulatum		2	3	1	3	*Pterostichus cupreus*	5	5	1		
B. biguttatum	276	222	99	56	63	*P. melanarius*	1		1		
B. bruxellense	1					*P. minor*	6	20	10	2	
B. clarki	66	49	24	6	4	*Pterostichus nigrita*	10	31	18	7	6
B. dentellum	38	112	51	42	36	*P. strenuus*	70	49	21	11	7
B. fumigatum			1			*P. vernalis*	20	25	10	3	4
B. genei		1				*P. versicolor*	1	9			
B. gilvipes	85	93	9	4	5	*Stenolophus mixtus*		1		3	
B. guttula	84	53	9	22	105	*Stomis pumicatus*		5			
B. harpaloides	7	3			1	*Trechus discus*			10		2
B. lampros	2	8	5	2		*T. micros*				1	
B. lunulatum	73	88	23	51	42	*T. quadristriatus*	2	4	7	1	3
B. obliquum				1		*T. secalis*			5	5	
B. obtusum	7	8	7		1	*Trichocellus placidus*		3	1	1	
B. properans	12	5	1	1							

Table 4.27: Total abundances of Carabidae per monthly sample recorded in 1991.

Species	Abundance				Species	Abundance			
	Apr	May	Jun	Jul		Apr	May	Jun	Jul
Acupalpus meridianus			1		*B. obtusum*	3	1		
Agonum albipes	40	100	60	4	*B. properans*	1	2		
A. assimile	3	8	1		*B. tetracolum*	9	7	10	1
A. dorsale	1	1	1		*Chlaenius vestitus*		1		
A. fuliginosum	7	24	9		*Clivina collaris*	1	4		
A. livens	7	5	4		*C. fossor*	1			
A. marginatum	5	1	4		*Dyschirius luedersi*	2			
A. micans	18	56	10	1	*Elaphrus cupreus*	5	5	2	
A. thoreyi	47	55	11		*E. riparius*	4	14	5	
A. viduum		1			*Harpalus rufipes*		1		
Asaphidion stierlieni		2			*Loricera pilicornis*	3	2	1	
Bembidion aeneum	6	4	10		*Nebria brevicollis*		2	3	
Bembidion assimile			1		*Notiophilus biguttatus*	1			
B. biguttatum	58	51	48	3	*Patrobus atrorufus*			3	
B. clarki	29	24	20		*Pterostichus anthracinus*			1	
B. dentellum	11	37	19	3	*P. minor*		17	5	
B. genei			1		*Pterostichus nigrita*	3	3	3	
B. gilvipes	21	8	2		*P. strenuus*	4	3	2	
B. guttula	5	5	4	15	*P. vernalis*	4	5	2	
B. harpaloides	1				*Stenolophus mixtus*		2		
B. lampros	1	1			*Tachys parvulus*		2		
B. lunulatum	7	5	25	23					

Table 4.28: Total abundances of Carabidae per monthly sample recorded in 1994.

Species	Abundance					Species	Abundance				
	Apr	May	Jun	Jul	Sep		Apr	May	Jun	Jul	Sep
Aleochara lanuginosa		1				*C. corticinus*	3	15	2	2	1
Aloconota gregaria	22	13	4	2		*C. elongatulus*	4				
A. insecta		1				*C. impressus*	14	126	109	51	39
A. sulcifrons				1		*C. obesus*	1	1			
Amischa analis	14	21	2	3	2	*C. rivularis*	65	90	40	62	47
A. cavifrons		2				*C. similis*		13	1		
A. decipiens	1	1	1	1	1	*C. subtilicornis*	57	91	8	52	19
A. forcipata	1	2				*Chiloporata longitarsis*			24	9	1
A. soror		4				*Deinopsis erosa*	4	2	4	1	3
Anotylus rugosus	18	9	1	8	15	*Deubelia picina*	14	10	6	9	7
A. sculpturatus			3		2	*Dochmonota clancula*		1	1	1	
A. tetracarinatus	1	1				*Gabrius bishopi*	1	5			15
Atheta celata	1					*G. pennatus*		5	2		3
A. elongatula	13	12	6	155	36	*G. trossulus*		1			1
A. fungi	10	19	10	85	46	*Geostiba circellaris*	1	1			
A. graminicola	86	116	62	77	230	*Gnypeta carbonaria*	12	1	4	9	8
A. gyllenhali				1	1	*G. ripicola*		6	5	41	32
A. hygrobia	1	1	1	2	1	*G. rubrior*	1	19	7	15	24
A. hygrotopora				2	17	*G. velata*		1		1	11
A. indubia				1		*Hygronoma dimidiata*	2	4	3		7
A. laticollis					27	*Lathrobium brunnipes*	10	17	18	14	9
A. luridipennis		1		1		*L. elongatum*	1		1	2	
A. luteipes	1		2	2		*L. fulvipenne*	21	37	4	5	
A. malleus	12	11	4	19	18	*L. geminum*		3	1		1
A. melanocera				1	1	*L. impressum*		1			
A. nigra			1		2	*L. longulum*	1	1			
A. obfuscata		1				*L. quadratum*			2	2	
A. parvulus					1	*L. terminatum*				1	
A. volans	5	3	3	5	4	*Lesteva heeri*	7	8	8	1	10
Brachyusa concolor	2	1		2	3	*L. longoelytrata*	9	98	6		
Callicerus rigidicornis		1				*Megarthrus sinuaticollis*					1
Calodera aethiops		3				*Mycetoporus splendidus*					1
C. uliginosa	6	5				*Myllaena dubia*	2	7	2	22	21
Carpelimus bilineatus	16	13	4	2	11	*M. elongata*	1			1	

Table 4.29: Total abundances of Staphylinidae per monthly sample recorded in 1991.

Species	Abundance				
	Apr	May	Jun	Jul	Sep
M. intermedia			1		
Neobisnius villosulus	2	3		2	1
Omalium caesum					2
O. excavatum					1
O. oxyacanthae			1		
O. rivulare		3			
Oxypoda brachyptera	1	1	1		
Oxypoda elongatula	4	5		2	6
O. exoleta	9	1		1	
O. lentula	3	43	17	4	1
O. umbrata		1			2
Oxytelus laqueatus					1
Pachnida nigella	3	16	19	4	3
Philonthus cognatus		1			
P. fimetarius			1		10
P. laminatus		2	1	1	1
P. marginatus			1		1
P. micantoides	2	1			
P. quisquilianus	1		4	4	9
P. umbratilis				1	4
P. varius	1	1		1	
Platystethus cornutus	5	8	16	3	4
P. nitens		2	1		1
P. nodifrons		3	1	1	3
Proteinus ovalis	2				
Quedius fuliginosus					1
Q. maurorufus	4	2	3	2	4
Q. molochinus			2		
Q. nitipennis					1
Q. schatzmayri			1		
Q. tristis				1	
Rugilus orbiculatus	1	1	1	1	
R. rufipes	1				
Sepedophilus marshami		3		1	1
Staphylinus melanarius			1		
Stenus argus			2		1
S. bifoveolatus				4	
S. bimaculatus	2	6	2	12	10
S. boops	29	47	19	29	42
S. canaliculatus				2	
S. cicindeloides	1		1	2	1
S. clavicornis		1			
S. fulvicornis			1		
S. juno	29	49	15	47	69
S. melanopus		3	6	6	1
S. nanus			1		
S. nitidiusculus	2	1	2	4	1
S. pallitarsis		1			
S. picipes			1		
S. pubescens	1				11
S. pusillus	2	1	2		
S. solutus	1	2	1	1	2
S. tarsalis	9	7	6	6	22
Tachinus laticollis					1
T. signatus	2	3	1	6	6
Tachyporus atriceps				1	
T. chrysomelinus		1	6	3	1
T. dispar	9	8	15	1	8
T. hypnorum	17	8	17	9	17
T. nitidulus	4	7	2	1	3
T. obtusus	2	3	14	35	56
T. pallidus	3	19	9	23	22
T. pusillus	6	2			1
T. solutus		9	8	10	4
Tachyusa atra	5	2	1	13	8
T. coarctatus			1		
Xantholinus linearis		4	6		
X. longiventris	10	10	7	2	4

Table 4.29 (cont.): Total abundances of Staphylinidae per monthly sample recorded in 1991.

Species	Abundance			
	Apr	May	Jun	Jul
Alianta incana		4	1	
Aloconota gregaria	13	5		
Amischa analis	2			
Anotylus rugosus	9	4	10	20
A. sculpturatus			1	
A. tetracarinatus		4	1	
Atheta elongatula	2	2	237	224
A. fungi	7	11	17	8
A. graminicola	63	73	98	15
A. hygrobia	1		26	
A. hygrotopora	1	3	3	
A. indubia			4	
A. laticollis		4	1	
A. luteipes		1		
A. malleus	27	6	15	3
A. vilis	2	21	5	
A. volans	3			1
Brachyusa concolor			6	
Carpelimus bilineatus	10	4	2	5
C. corticinus	2		1	1
C. elongatulus		1	1	
C. gracilis			1	
C. impressus	15	30	16	4
C. rivularis	64	69	11	55
C. subtilicornis	5	42	4	7
Chiloporata longitarsis	1	13	14	2
Deinopsis erosa		3		
Dinaraea angustula	17	17	12	
Deubelia picina	1			
Dochmonota clancula		5	1	
Gabrius bishopi		1	2	1
G. pennatus	4			
Gnypeta carbonaria	60	11	37	
G. ripicola	4	2	1	
G. rubrior			13	
G. velata	1			
Gyrohypnus fracticornis	1			
Lathrobium brunnipes	1	11	1	1
L. fulvipenne				1
L. geminum	1	2	4	
L. quadratum		1		
Lesteva heeri	2	27	1	
L. longoelytrata	3	75	2	
Myllaena dubia	17	11	7	
Nehemitropia sordida		1		
Omalium caesum		1		
O. rivulare		1		
Oxypoda elongatula	8	5	1	
O. lentula		1		
O. opaca			2	
O. umbrata		1	13	
Oxytelus fulvipes		2		
O. laqueatus	1			
Pachnida nigella	5	13	7	
Philonthus cognatus			1	
P. quisquiliarius	1	4	4	
P. umbratilis		2	1	
P. varians			1	
P. varius			1	
Platystethus cornutus			8	
Quedius maurorufus	3	4	4	
Q. schatzmayri			9	
Stenus bifoveolatus	11	9	9	1
S. bimaculatus	3	4	1	
S. boops	68	73	33	15
S. cicindeloides	7	6	3	
S. formicetorum	7	5	7	
S. juno	47	56	30	2

Table 4.30: Total abundances of Staphylinidae per monthly sample recorded in 1994.

Species	Abundance				Species	Abundance			
	Apr	May	Jun	Jul		Apr	May	Jun	Jul
S. melanopus	4	2			*T. hypnorum*	2	2		
S. picipes			1		*T. nitidulus*		1		
S. pubescens	26	2	13		*T. obtusus*		2	6	1
S. solutus	9	12	1		*T. pallidus*		2	4	
S. tarsalis	2	1		1	*Tachyusa atra*	1	1	2	
Tachinus signatus	2	3	1	2	*Thinodromus arcuatus*	1			
Tachyporus dispar		1			*Xantholinus longiventris*	1	1	1	

Table 4.30 (cont.): Total abundances of Staphylinidae per monthly sample recorded in 1994.

Species	Abundance					Species	Abundance				
	Apr	May	Jun	Jul	Sep		Apr	May	Jun	Jul	Sep
Rybaxis longicornis					2	*Agriotes lineatus*		1			
Heterocerus fenestratus		2	4	3	7	*A. obscurus*		1	1		
H. marginatus		2	1	2	2	*Selatosomus nigricornis*			1		

Table 4.31: Total abundances of Pselaphidae, Heteroceridae and Elateridae per monthly sample recorded in 1991.

Species	Abundance				Species	Abundance			
	Apr	May	Jun	Jul		Apr	May	Jun	Jul
Rybaxis longicornis		1	1		*Heterocerus marginatus*	1	1		

Table 4.32: Total abundances of Pselaphidae, Heteroceridae and Elateridae per monthly sample recorded in 1994.

Species	Abundance			Species	Abundance		
	1992	1993	1994		1992	1993	1994
Acupalpus consputus		1		*B. lampros*			1
Agonum albipes	13	6	6	*B. lunulatum*	3	4	
A. dorsale		1	1	*B. obtusum*	6	2	1
A. fuliginosum	10	6	20	*B. properans*		1	1
A. livens	4	2	5	*B. tetracolum*	1	1	
A. micans	7	8	6	*Demetrias atricapillus*	1	2	
A. moestum		1		*Dromius linearis*		1	
A. thoreyi	26	41	55	*Dyschirius luedersi*		2	
A. viduum			1	*Elaphrus cupreus*	5	6	5
A. obscurum	1			*E. riparius*	14	3	5
Bembidion aenum	1	4	1	*Loricera pilicornis*		1	
B. articulatum	5			*Notiophilus biguttatus*	5	2	
B. assimile		3		*Patrobus atrorufus*		1	
B. biguttatum	91	33	21	*Pterostichus minor*	9	3	17
B. clarki	148	108	24	*P. nigrita*	4	3	1
B. dentellum	5	3	8	*P. strenuus*	4	1	
B. gilvipes	7	5		*P. vernalis*		1	
B. guttula	2	1		*Stenolophus mixtus*		4	
B. harpaloides		1					

Table 4.33: Annual abundances of species of Carabidae recorded in samples collected from floodplain reference sites in May.

Species	Abundance		
	1992	1993	1994
Anotylus rugosus	5		2
A. tetracarinatus	1		4
Anthobium atrocephalum	2		
Carpelimus bilineatus	1	1	1
C. corticinus	3	1	
C. elongatulus	2	1	1
C. impressus	7	46	30
C. rivularis	6	9	37
C. subtilicornis			1
Gabrius pennatus		1	
Habrocerus capillaricornis	1		
Lathrobium brunnipes	18	4	7
L. fulvipenne	2	3	
L. geminum	1		
L. longulum	1		
L. heeri		11	11
L. longoelytrata	22	18	34
Omalium caesum		1	1
O. rivulare	2		1
O. laeviusculus		1	
Oxytelus fulvipes	2		2
Philonthus quisquiliarius		7	1
P. umbratilis		2	
Platystethus cornutus		3	
P. nitens		1	
Proteinus ovalis	1		
Quedius maurorufus	3	1	4
Stenus bifoveolatus	5	4	9
S. bimaculatus	3	2	4
S. boops	25	36	35
S. canaliculatus		1	
S. cicindeloides	1	3	6
S. formicetorum	1		5
S. fulvicornis		1	
S. juno	80	27	45
S. melanopus		3	2
S. pubescens			2
S. solutus	4	6	12
Tachyporus chrysomelinus	2		
T. dispar	4		1
T. hypnorum	1		1
T. nitidulum	1		1
T. obtusum	1		2
T. pallidum			2
Tachinus signatus			2
Xantholinus linearis	2		
X. longiventris		3	

Table 4.34: Annual abundances in May of species of Staphylinidae (subfamilies Micropeplinae to Tachyporinae) recorded in samples collected from floodplain reference sites.

Species	Abundance			Species	Abundance		
	1992	1993	1994		1992	1993	1994
Aleochara lanuginosa	1			*Deinopsis erosa*		1	1
Alianta incana			4	*Deubelia picina*	13	25	17
Aloconota gregaria	1			*Dochmonota clancula*		9	5
Amischa analis	4	1		*Geostiba circellaris*	4		
A. decipiens	1			*Gnypeta carbonaria*	2	4	10
Atheta elongatula		5	2	*G. rubrior*	1		
A. fungi agg.	10	6	11	*Hygronoma dimidiata*	3	5	
A. graminicola	54	23	47	*Liogluta nitidula*	8	4	
A. gyllenhali	1	1		*Myllaena dubia*	29	20	11
A. hygrobia	14	2		*M. infuscata*	2	2	
A. hygrotopora		1	3	*Nehemitropia sordida*			1
A. laticollis	1			*Oxypoda elongatula*	15	11	5
A. luteipes		1	1	*O. exoleta*	1	1	
A. malleus	9	8	2	*O. lentula*	19	3	1
A. vilis		39	21	*O. umbrata*	4		1
A. volans	2	1		*Pachnida nigella*	9	14	13
Chiloporata longitarsis		1	9	*Tachyusa atra*		2	

Table 4.35: Annual abundances in May of species of Staphylinidae (subfamily Aleocharinae) recorded in samples collected from floodplain reference sites.

Species	Abundance			Species	Abundance		
	1992	1993	1994		1992	1993	1994
Bryaxis bulbifer	1			*Heterocerus fenestratus*	1	1	
Rybaxis longicornis			1	*H. marginatus*			1

Table 4.36: Annual abundances of species of Pselaphidae and Heteroceridae recorded in samples collected from floodplain reference sites in May.

Species	Abundance				Species	Abundance			
	1991	1992	1993	1994		1991	1992	1993	1994
Acupalpus meridianus			1		*B. lunulatum*	43	20	3	7
Agonum albipes	26	13	30	103	*B. obliquum*		1		
A. assimile			3	8	*B. obtusum*	3	3	4	13
A. dorsale			1		*B. properans*		1		1
A. fuliginosum	3	1		4	*B. punctulatum*	5	10	5	3
A. marginatum	6	4	2	1	*B. quadrimaculatum*			1	1
A. micans	32	13	7	52	*B. tetracolum*	12	7	5	10
A. moestum			1		*Carabus granulatus*	1			
A. obscurum	1	1			*Clivina collaris*	7	2	2	2
A. viduum	1				*C. fossor*	2			
Amara aenea	1	1			*Dromius melanocephalus*	1		1	
A. communis	2				*Dyschirius aeneus*		3		
A. plebeja	1				*D. luedersi*	2	7		
A. similata		1			*Elaphrus cupreus*	1	4		
Asaphidion curtum	1				*E. riparius*	7	18	4	6
A. stierlieni				2	*Harpalus rufibarbis*				1
Bembidion aeneum	110	6		5	*H. rufipes*	2			
B. articulatum		6	1		*Loricera pilicornis*	2	1	1	4
B. assimile		1			*Nebria brevicollis*		2		4
B. biguttatum	41	22	6	34	*Notiophilus biguttatus*				1
B. clarki		1			*Pterostichus minor*		1		
B. dentellum	38	21	9	29	*P. nigrita*	9	5		2
B. fumigatum		1			*P. strenuus*	8	2		3
B. genei		8			*P. vernalis*	11	3		5
B. gilvipes	18	14	1	6	*Stenolophus mixtus*	1	12		2
B. guttula	23	14	1	8	*Stomis pumicatus*	1			
B. lampros		1	1		*Tachys parvulus*		1		2

Table 4.37: Annual abundances of species of Carabidae recorded in samples collected from main-channel reference sites in May.

Species	Abundance				Species	Abundance			
	1991	1992	1993	1994		1991	1992	1993	1994
Anotylus rugosus	3	3		2	*P. laminatus*	1			
A. sculpturatus		1			*P. quisquiliarius*		12	1	2
Bledius gallicus		2			*P. umbratilis*		1		2
Carpelimus bilineatus	6	5	3	3	*P. varians*		1		
C. corticinus	5	6			*Platystethus cornutus*	5	12	2	
C. impressus	2	1			*P. nitens*	1			
C. obesus	1				*P. nodifrons*	2			
C. rivularis	49	65	13	25	*Stenus bimaculatus*	2	4	1	
C. similis	1				*S. boops*	25	19	5	40
C. subtilicornis	30	11		57	*S. cicindeloides*		1		
Gabrius bishopi	4	6			*S. juno*	15	14	3	13
G. pennatus	1	13			*S. melanopus*	1	5		
Lathrobium brunnipes	3	11		4	*S. pusillus*		1		
L. fulvipenne	1	3	4		*S. solutus*			1	
L. geminum	2	2		6	*S. tarsalis*	4	4		1
L. pallidum		1			*Tachinus signatus*		4		1
L. quadratum		1			*Tachyporus dispar*	1	3		
L. terminatum		1			*T. hypnorum*		1		1
Lesteva heeri	8	3		16	*T. nitidulus*	4			
L. longoelytrata	40	2		35	*T. obtusus*	1	3	3	7
Mycetoporus splendidus			1		*T. pallidus*	3	3	1	2
Neobisnius villosulus	3	4	1	1	*T. solutus*	1			
Omalium rivulare	1				*Xantholinus linearis*	1			
Oxytelus laqueatus		1			*X. longiventris*	3	2		2
Philonthus fimetarius		1							

Table 4.38: Annual abundances of species of Staphylinidae (subfamilies Omaliinae to Tachyporinae) recorded in samples collected from main-channel reference sites in May.

Species	Abundance				Species	Abundance			
	1991	1992	1993	1994		1991	1992	1993	1994
Alianta incana		1			*Callicerus rigidicornis*	1			
Aloconota gregaria	4	1		2	*Chiloporata longitarsis*		133	1	42
A. insecta	1				*Deinopsis erosa*	1	8		2
Amischa cavifrons	1			2	*Geostiba circellaris*				1
Atheta elongatula	4	41	15	3	*Gnypeta carbonaria*		8		4
A. fungi agg.	3	4	9	1	*G. ripicola*	1	1	2	
A. graminicola	26	2		28	*G. rubrior*	16	1	1	
A. hygrotopora			12	1	*G. velata*		8		
A. indubia			1		*Hygronoma dimidiata*	1	2		
A. laticollis			2	4	*Myllaena intermedia*		3		
A. luridipennis	1				*Oxypoda brachyptera*	1			
A. luteipes		7			*O. exoleta*	1			
A. malleus	4	15	3	2	*Tachyusa atra*	1	9		1
A. obfuscata	1				*T. coarctata*		1	1	1
A. volans	2	1			*T. leucopus*				1

Table 4.39: Annual abundances of species of Staphylinidae (subfamily Aleocharinae) recorded in samples collected from main-channel reference sites in May.

Species	Abundance				Species	Abundance			
	1991	1992	1993	1994		1991	1992	1993	1994
Heterocerus fenestratus	2	18		1	*H. marginatus*	2			

Table 4.40: Annual abundances of species of Heteroceridae recorded in samples collected from main-channel reference sites in May.

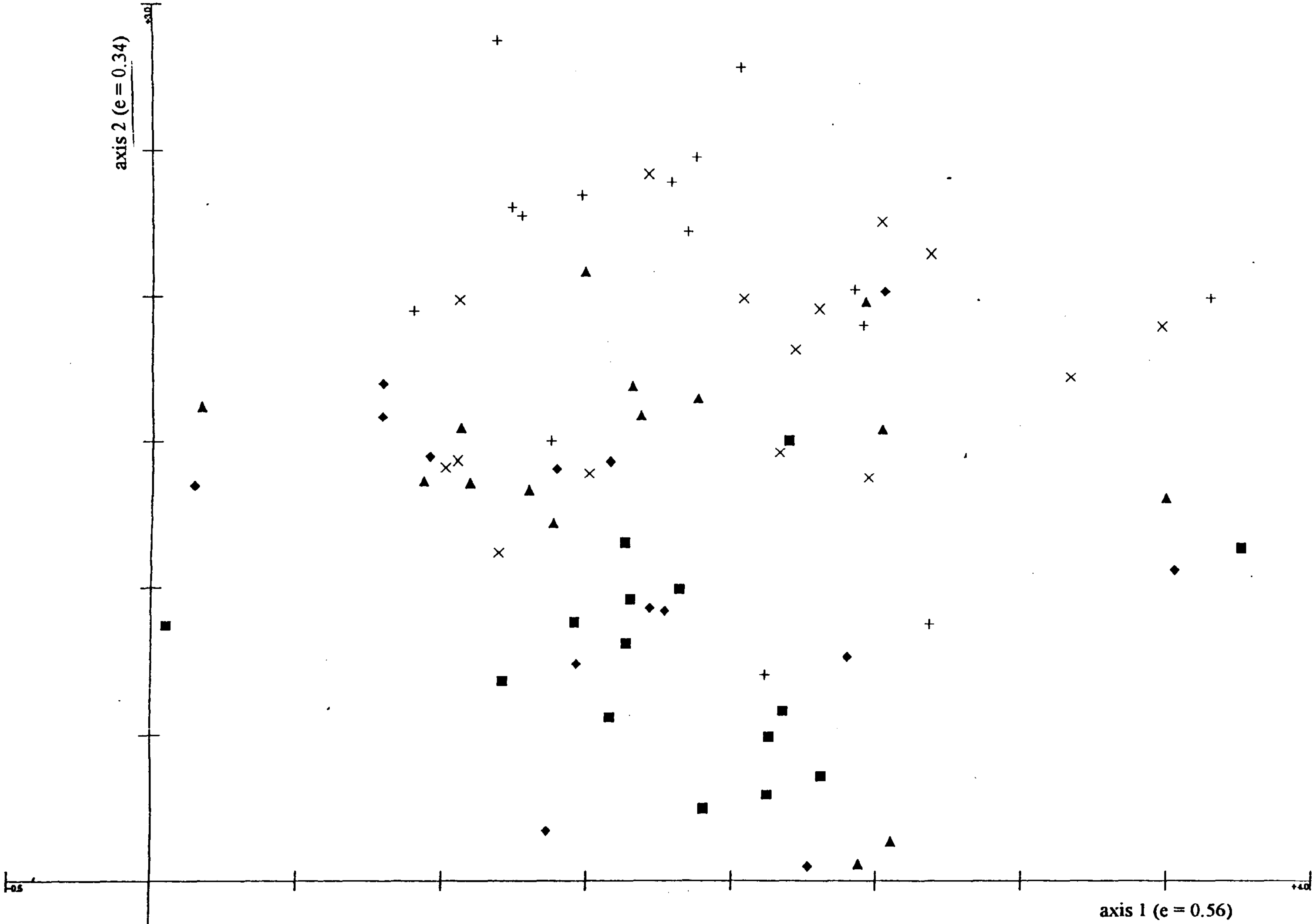

Figure 4.2: DCA ordination plot of monthly samples taken from 15 sites during 1994 (square = April, diamond = May, triangle = June, + = July, X = September).

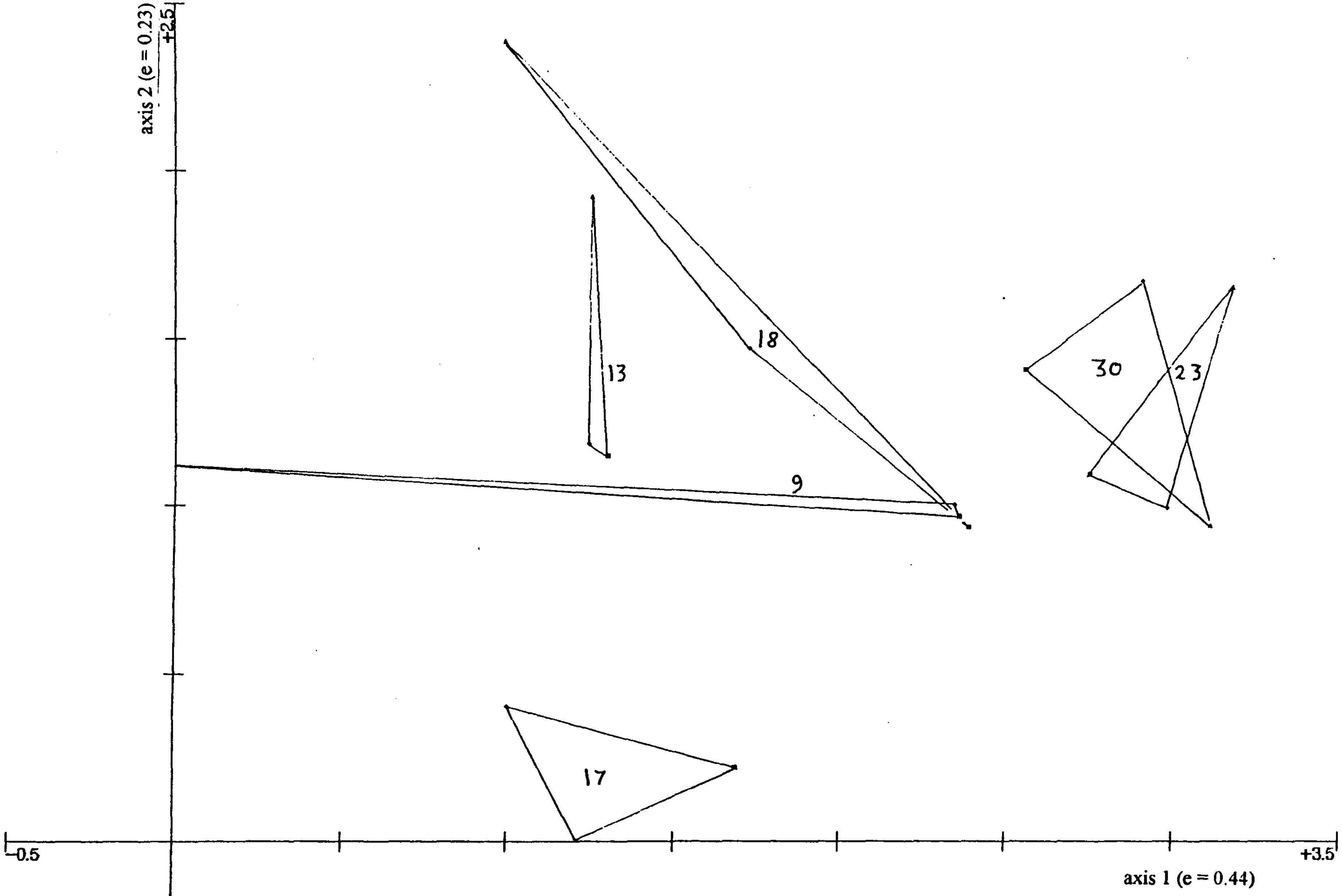

Figure 4.3: DCA ordination plot of monthly samples taken from main-channel reference sites in spring, 1991. Points from each site are enclosed within polygons and labelled by site number.

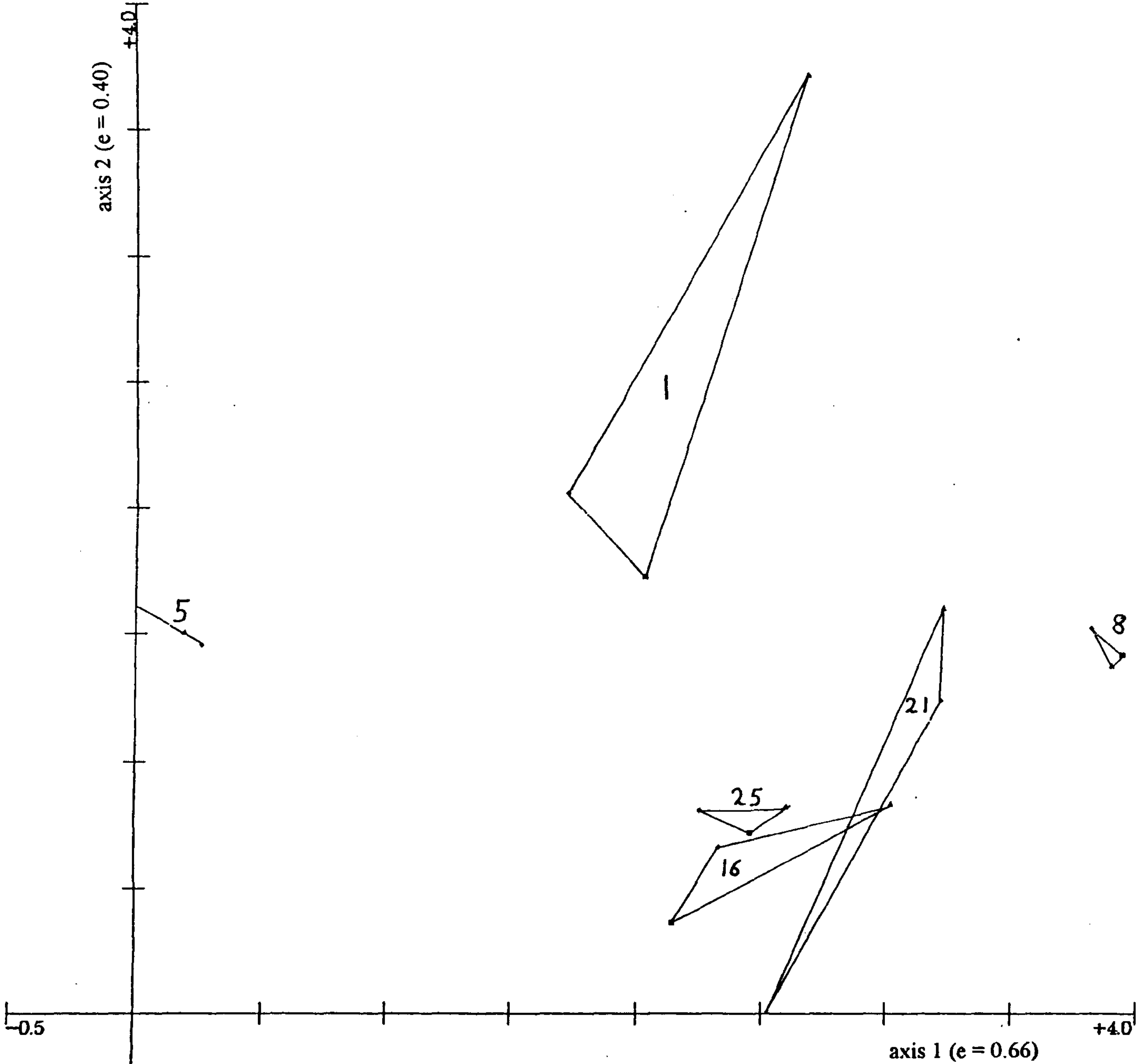

Figure 4.4: DCA ordination plot of monthly samples taken from floodplain reference sites in spring, 1991. Points from each site are enclosed within polygons and labelled by site number.

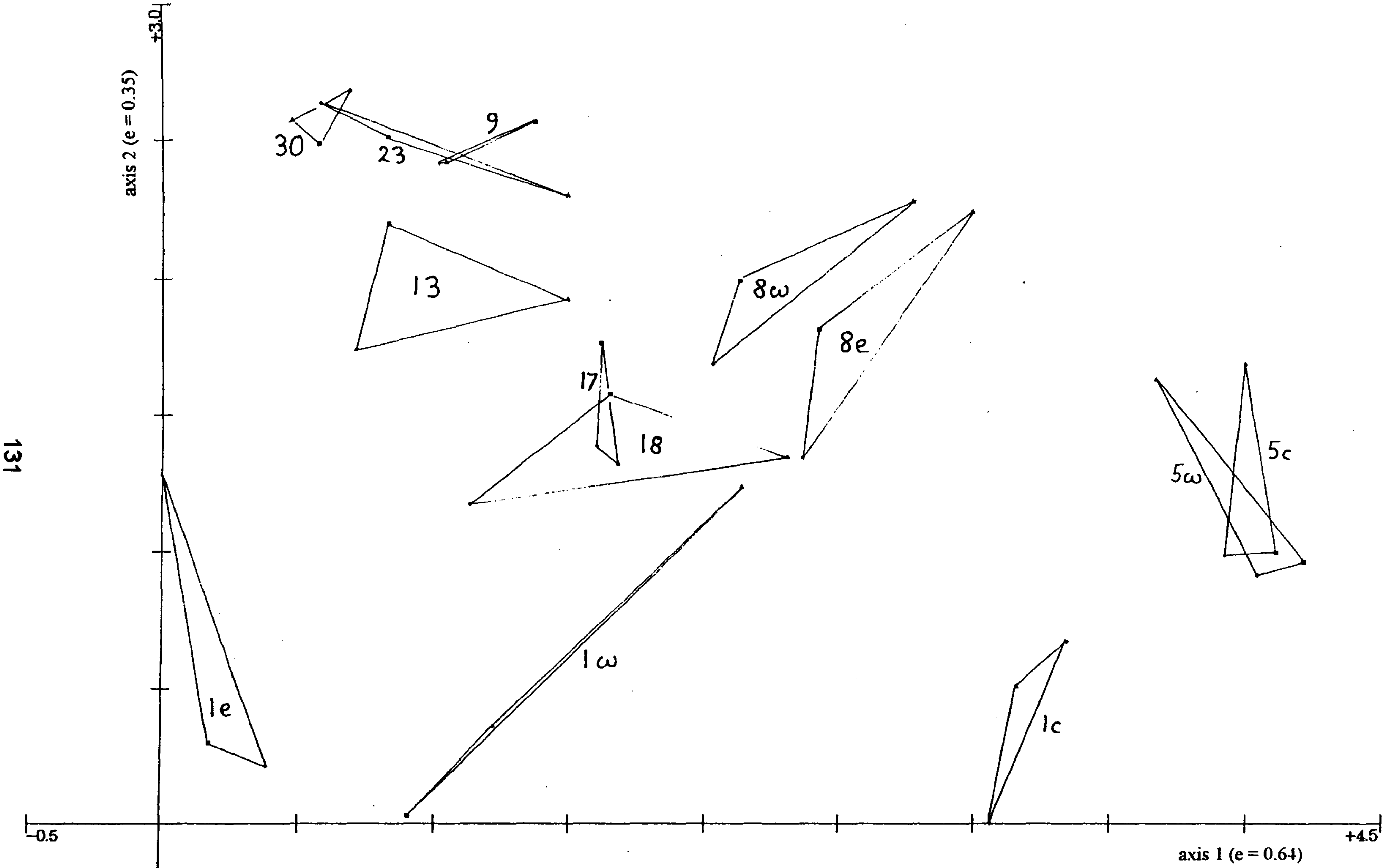

Figure 4.5: DCA ordination plot of monthly samples taken from main-channel and floodplain reference sites in spring, 1994. Points from each site are enclosed within polygons and labelled by site number.

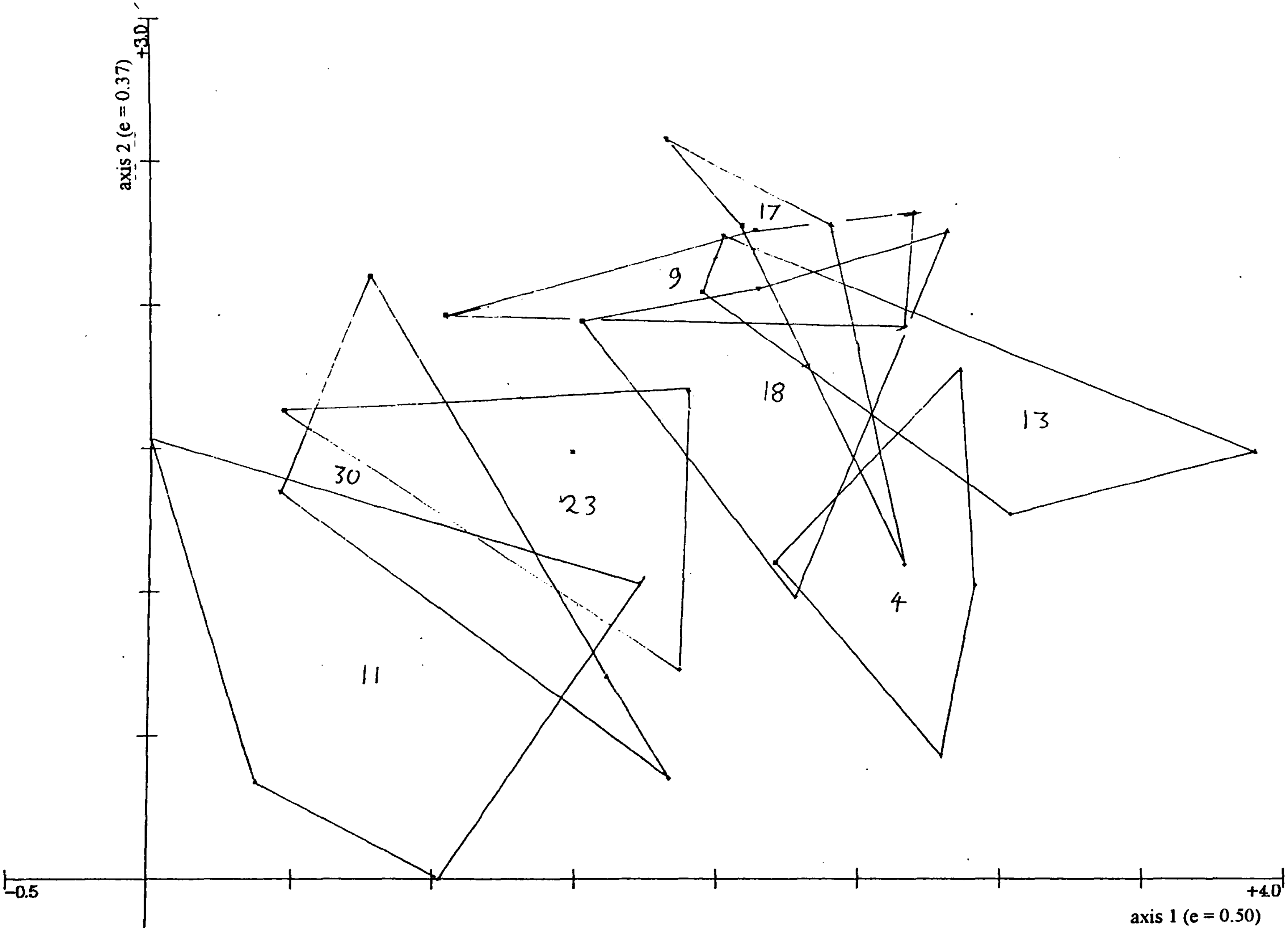

Figure 4.6: DCA ordination plot of yearly samples taken from main-channel reference sites from 1991 to 1994. Points from each site are enclosed within polygons and labelled by site number.

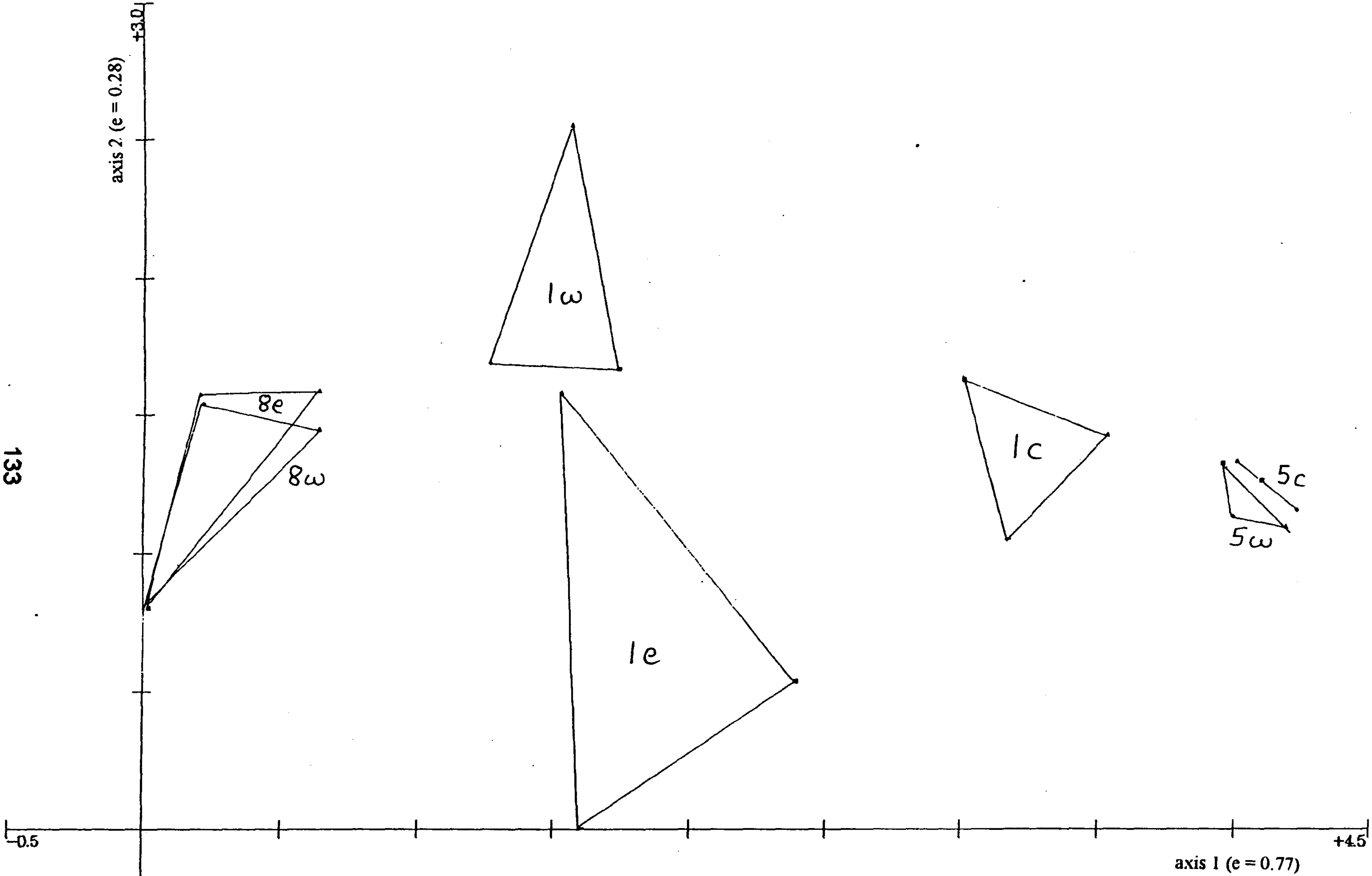

Figure 4.7: DCA ordination plot of yearly samples taken from floodplain reference sites from 1992 to 1994. Points from each site are enclosed within polygons and labelled by site number.

	-1991-						-1994-					
	Main Channel			Floodplain			Main Channel			Floodplain		
Index	W_{Sites}	W_{Season}	Sig.	W_{Sites}	W_{Season}	Sig.	W_{Sites}	W_{Season}	Sig.	W_{Sites}	W_{Season}	Sig.
Ax.1	0.71		<0.05	0.82		<0.01	0.93		<0.01	0.98		<0.01
S	0.64	0.69	-	0.51	0.55	-	0.34	0.03	-	0.13	0.19	-
E	0.57	0.11	-	0.24	0.08	-	0.49	0.11	-	0.21	0.06	-
R_{ls}	0.42	0.19	-	0.58	0.03	-	0.42	0.03	-	0.94	0.06	<0.01
R_{ln}	0.49	0.11	-	0.77	0.19	<0.05	0.21	0.03	-	0.87	0.18	<0.01
R_{ms}	NA			0.66	0.26	<0.05	NA			NA		
R_{mn}	NA			0.84	0.63	<0.01	NA			NA		
W_{bs}	NA			NA			NA			NA		
W_{bn}	NA			NA			NA			NA		
W_{cs}	NA			NA			NA			0.83	0.04	<0.01
W_{cn}	NA			0.85	0.27	<0.01	NA			0.79	0.60	<0.01
W_{ds}	0.63	0.36	-	0.45	0.40	-	0.52	0.27	-	NA		
W_{dn}	0.61	0.53	-	0.21	0.11	-	0.58	0.25	-	NA		
W_{ms}	0.50	0.33	-	0.46	0.51	-	0.43	0.33	-	0.51	0.01	-
W_{mn}	0.63	0.11	-	0.59	0.53	-	0.57	0.53	-	0.48	0.01	-
L_{ws}	0.30	0.03	-	0.47	0.19	-	0.61	0.19	-	0.72	0.20	<0.05
L_{wn}	0.42	0.11	-	0.44	0.11	-	0.77	0.36	<0.05	0.78	0.24	<0.01
L_{gs}	0.30	0.19	-	0.59	0.53	-	0.73	0.11	<0.05	0.55	0.14	-
L_{gn}	0.53	0.36	-	0.57	0.19	-	0.90	0.36	<0.01	0.52	0.14	-
L_{ds}	0.09	0.00	-	0.35	0.19	-	0.34	0.02	-	0.53	0.06	-
L_{dn}	0.42	0.08	-	0.29	0.33	-	0.57	0.53	-	0.25	0.06	-

Table 4.41: Values of Kendall's coefficient of concordance for samples ranked according to various indices, where W_{Sites} is based on rankings of sites in each month between April and June and W_{Season} is based on rankings of monthly samples for each site. Sig. = level of significance of W_{Sites} based on the sum of squares of average ranking minus the mean ranking. Ax. 1 = axis 1 score derived from DCA ordination of sites within each monthly set. NA denotes more than three tied rankings.

	Main Channel			Floodplain		
Index	W_{Sites}	W_{Year}	Sig.	W_{Sites}	W_{Year}	Sig.
Ax.1	0.49		-	0.66		< 0.05
S	0.72	0.78	< 0.05	0.52	0.01	-
E	0.53	0.53	-	0.59	0.02	-
R_{ls}	0.63	0.14	-	0.84	0.02	< 0.01
R_{ln}	0.62	0.19	-	0.71	0.24	< 0.05
R_{bs}	NA			NA		
R_{mi}	NA			NA		
W_{bs}	NA			NA		
W_{bn}	NA			NA		
W_{cs}	NA			NA		
W_{cn}	NA			NA		
W_{ds}	NA			NA		
W_{dn}	(0.45)	(0.27)	-	NA		
W_{ms}	NA			NA		
W_{mn}	(0.52)	(0.28)	-	0.76	0.29	< 0.05
L_{ws}	0.35	0.14	-	0.40	0.16	-
L_{wn}	0.27	0.13	-	0.10	0.65	-
L_{gs}	0.39	0.17	-	0.21	0.13	-
L_{gn}	0.30	0.31	-	0.21	0.16	-
L_{ds}	0.38	0.21	-	0.84	0.05	< 0.01
L_{dn}	0.35	0.02	-	0.79	0.29	< 0.05

Table 4.42: Values of Kendall's coefficient of concordance for samples ranked according to various indices, where W_{Sites} is based on rankings of sites in each year and W_{Year} is based on rankings of annual samples for each site. Sig. = level of significance of W_{Sites} based on the sum of squares of average ranking minus the mean ranking. NA denotes more than three tied rankings. Values in brackets were calculated after exclusion of samples taken in 1993.

Index	Seasonal robustness of site ranking	Annual robustness of site ranking	Relative importance of seasonal variation	Relative importance of annual variation	Relative performance of abundance-weighted index
Ax.1	very good	moderate for main channel sites; good for floodplain sites	low	low except for similar main channel sites	
S	variable	moderate	high	high for main channel sites; low for floodplain sites	
E	variable	moderate	low	high for main channel sites; low for floodplain sites	
R_{ls}	moderate for main channel sites; good for floodplain sites	moderate for main channel sites; good for floodplain sites	low	low	similar
R_{ns}	good for floodplain sites but poor discrimination	unknown due to poor discrimination	low for floodplain sites	unknown	similar
W_{bs}	poor discrimination	poor discrimination			
W_{cs}	good for floodplain sites; discrimination poor for main channel sites	unknown due to poor discrimination	low?	unknown	more affected by seasonal variation but better discrimination
W_{ds}	moderate for main channel sites	moderate? for main channel sites	high	high?	better discrimination
W_{ms}	moderate	moderate to good	high	moderate	better discrimination
L_{ws}	variable	poor	low	low	similar
L_{gs}	moderate to high	poor	mostly low	low	similar
L_{ds}	poor	good for floodplain sites	low	low	similar

Table 4.43: Evaluation of performance of various indices against seasonal and annual variations. For details of indices and their codes, see section 3.2.

5 Relation of variation in species composition to environmental and management factors

5.1 Variation in species composition at different scales

5.1.1 Introduction

Despite the recognition that environmental factors in river systems operate at a particular spatial scale (Naiman et al. 1992), there have been few attempts to compare the distributions of riparian and wetland beetles at different spatial scales. Landry (1994) found that some species of *Agonum* in Canadian marshes were restricted to a particular habitat structure which he termed macrohabitat, but fairly catholic in their microhabitat occupancy, whereas other species specialised in a particular microhabitat (e.g. tussocks) but were found over a wider range of habitat structures. On the basis of quadrat and time-catch samples, Andersen (1983) reported that Norwegian species of riparian *Bembidion* species often had a restricted microhabitat distribution, especially among egg-laying females. However, the habitat requirements of a riparian or wetland beetle may include several different microhabitats over its complete life cycle (see section 1.3.4). The presence of species at a microsite may reflect the preference of active adults for that microhabitat, but the nearby availability of a microhabitat connected with a different stage in the life history may be more important. If so, we might expect that species composition at any one microsite would be more dependent on the characteristics of the whole site rather than the microsite.

It was decided to investigate the relative importance of factors operating at microhabitat and macrohabitat scales along the River Soar by comparing the distribution of species between whole sites with the distribution of species between sampling stations within sites.

5.1.2 Methods

The investigation was carried out on samples from 180 sampling stations in 30 sites studied in May 1991. Samples were collected by hand using methods described in section 3.1. Environmental measurements were made as described in section 3.3. The DCA plot, obtained by ordinating 180 sub-samples was compared with the plot, obtained by ordinating aggregated samples from each of the 30 sites.

The axis 1 sample scores from the ordination of 180 sub-samples were compared with values for the following environmental measurements at each sampling station: the proportion of sand, silt and undecayed organic matter in the substrate, the proportion of bare ground, the amount of dead vegetable matter on the surface and the surface moisture. Interset correlations of these environmental variables with axes 1 and 2, were calculated using the computer programme, CANOCO (ter Braak 1987-1992). They were also similarly compared with two environmental measurements calculated for the site as a whole, namely the amount of bare ground (BAREGRD) and the amount of dead vegetable matter (LITTER). Interset correlation coefficients cannot be used to derive the statistical significance of any correlations, because they are clearly not based on values with normal distributions (Bailey 1995), However, they can be used in an exploratory sense to investigate the relative importance of the relationship between measured environmental variables and the latent environmental variables represented by the ordination axes (Jongman *et al.* 1995). Furthermore, they have the advantage over multiple regression coefficients that they are unaffected by multicolinearity in the environmental variables (ter Braak 1986).

5.1.3 Results

The species recorded in May 1991, are listed in appendix 2B. Values for environmental variables at each sampling site are given in appendix 3A.

Figure 5.1 shows the ordination plot for 180 sub-samples. As is often necessary in data sets with species-poor samples (Jongman *et al.* 1995), it was necessary to use downweighting of rare species in order to reduce the influence of outliers. It was found that this gave better correlations with environmental variables along axis 1. As well as using downweighting of rare species, it was necessary to render three sub-samples passive to reduce their influence on the ordination. Two of these subsamples contained only one species. The third was dominated by a species which did not occur in any other sample. The eigenvalues of the first three axes at 0.59, 0.46 and 0.38 indicate a large amount of variation. The arrangement of sub-samples from microsites is very similar to that in the ordination plot of aggregated samples from sites, shown in figure 5.2. The eigenvalues of the first three axes of the ordination plot of aggregated samples are lower at 0.43, 0.34 and 0.15, but this is to be expected because of the larger number of species in each sample and the consequent increase of overlap in species composition.

In figure 5.1 the sub-samples from four sites are represented by symbols designated for those sites, in order to illustrate their separation in ordination space. Although there is overlap between sites, sub-samples from any one site are localised in a relatively small area of ordination space. If one outlying subsample containing a single species is excluded, the average range of scores along axis 1 from one site is 1.4 compared to a total axis length of 4.47. Only four sites have a range greater than 2, the highest range being 2.63, whereas the lowest range is 0.82.

Table 5.1 contains the interset correlations of environmental variables with axes 1 and 2. The small scale factors which most closely affected species composition at microhabitat scale appeared to be the amount of dead vegetation, which is negatively correlated with axis 1, and the proportion of bare ground which is positively correlated with axis 1. However, both of these factors were slightly less important than the equivalent factors operating at site scale, LITTER and BAREGRD. There was less correlation with axis 2 for all environmental variables except surface moisture, but even here the correlation coefficient was relatively small.

5.1.4 Discussion

The similarity of sample distributions along axis 1 in the two ordination plots indicate that the most important environmental factors affecting species composition operate at both microhabitat and site scale. The grouping of subsamples in figure 5.1 and the slightly higher correlation coefficients for environmental variables measured over the whole site, suggest that the total microhabitat resource at a site is at least as important and possibly more important for most species in the Soar Valley than the microhabitat from which the species is sampled.

This result is expected from a consideration of the different microhabitats that are required by a species throughout its life history. An alternative explanation is suggested by the temporal instability of microhabitats along the River Soar. Fluctuating water levels and the rapid growth of vegetation on fertile sediments lead to marked seasonal changes in many of the environmental variables at any one microsite. Any species which require a particular microhabitat over an extended period would need to move about over the site as conditions change.

Results indicate that analysis at the whole-site scale is preferred for the interpretation of the effect of environmental factors. Analysis at this scale also allows the collection of larger samples with a consequent increase in robustness of assemblage parameters.

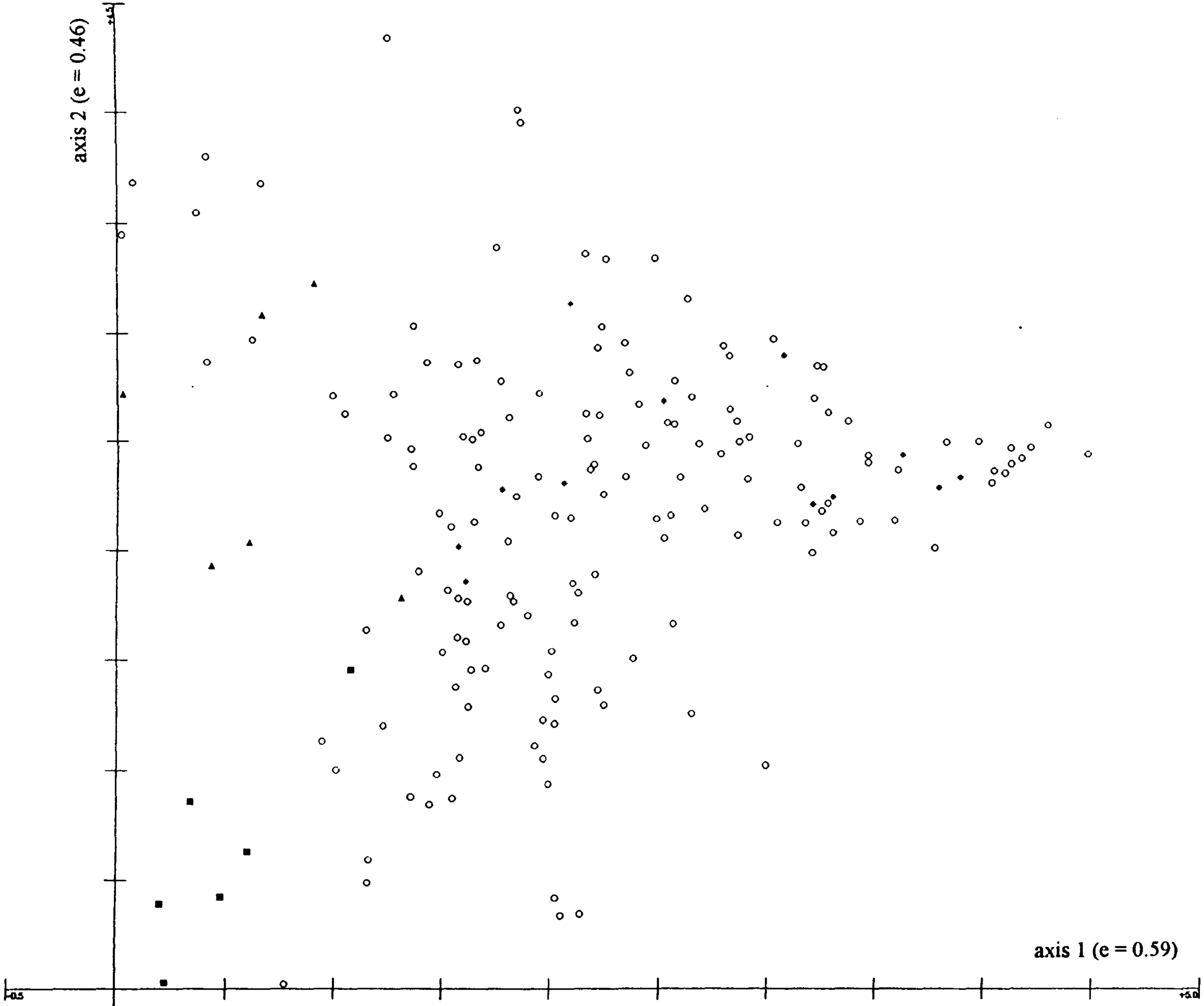

Figure 5.1: DCA ordination plot of 180 sub-samples collected in May 1991 (square = site 5, triangle = site 8, asterisk = site 13, diamond = site 23).

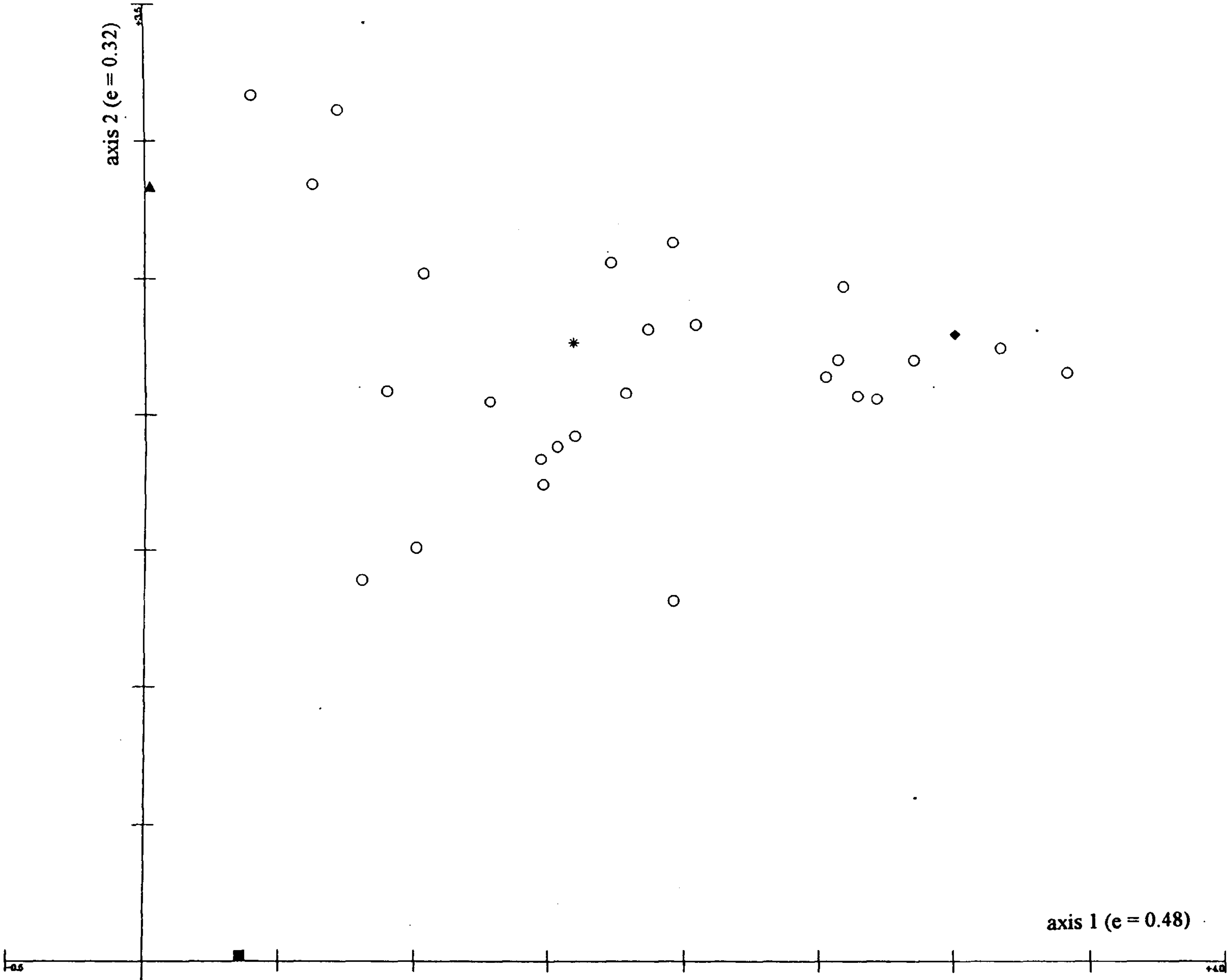

Figure 5.2: DCA ordination plot of 30 aggregated samples collected in May 1991 (square = site 5, triangle = site 8, asterisk = site 13, diamond = site 23).

Environmental variable	Axis 1 (eigenvalue = 0.59)	Axis 2 (e = 0.46)	Axis 3 (e = 0.38)
Surface moisture	-0.22	0.25	0.34
Sand	0.16	0.14	0.15
Silt	0.36	0.22	-0.28
Litter in substrate	-0.49	-0.27	0.05
Surface litter (microsite)	-0.58	-0.2	0.14
Surface litter (whole site)	-0.6	-0.29	0.09
Bare ground (microsite)	0.53	0.48	0.00
Bare ground (whole site)	0.56	0.47	0.15

Table 5.1: Interset correlation coefficients between environmental variables and sample scores on the first three axes of variation produced by a DCA ordination of 180 subsamples taken in May, 1991.

5.2 Variation in species composition across all habitat structures

5.2.1 Introduction

Having established an appropriate spatial scale of investigation, it is now feasible to investigate associations between the species composition of assemblages and environmental factors. This can be carried out at a range of functional levels. At one level, species composition is often directly related to the physical resources present at a site (see section 1.3.4). These resources include substrate, moisture, undecayed organic matter etc. Section 1.3.2. reported several interpretations of species' adaptations for using these resources. At another level, species composition is indirectly related to wider scale processes which regulate these resources. It is these indirect associations that are of use to conservationists in understanding the effects of land use and management on species assemblages.

This section attempts to associate trends in species composition to environmental and management factors operating within the study area at different functional levels. It attempts to use associations with physical resources to interpret the relationship of species composition to more indirect factors. A general theory linking these factors to species composition could then be formulated for the Soar valley.

5.2.2 Methods

Samples collected from 30 sites in April and May 1991, were pooled and ordinated using DCA. Pooling of samples was carried out in order to reduce the problems with seasonal robustness of species parameters that were identified in chapter 4. Sites from June, 1991, were not included because of problems associated with missing samples and suspected distortion of the results due to flooding. In order to achieve a more general interpretation of the DCA ordination, it was necessary to reduce the influence of sites 5 and 8 by downweighting rare species. Both these sites contained a high proportion of species unrecorded elsewhere in 1991. Coefficients were calculated for interset correlations between sample scores on the first three axes of ordination and the following environmental variables: SHINGLE, SAND, SILT, CPOM, LITTER, SHADE, BAREGRD, HIBSITES, DWATER, CONNECT, NATDIST, GRAZING, RECR, IMPOUND.

The same sample set was then subjected to Canonical Correspondence Analysis (CCA) using NATDIST, CONNECT and GRAZING as constraining environmental variables. These variables are considered to be larger scale causative factors for the other smaller scale variables which were measured. Monte Carlo permutation routines were used to test the significance of variation along the resulting ordination axes by comparing their eigenvalues with those from 99 random permutations of samples. This gives a resolution down to p = 0.01. Tests were carried out on both axis 1 and the trace which is the sum of the eigenvalues of all constrained axes.

5.2.3 Results

4,681 specimens belonging to 167 species were collected. The species are listed in tables 5.2 to 5.5 together with the number of sites from which they were recorded and the total number of specimens for each species. A complete table of abundances of each species at each site is given in appendices 2A and 2B. Values of environmental variables at each site are given in appendix 3B.

Figure 5.3 shows the ordination plot for the 1991 samples from 30 sites. Also included are the centroids of samples belonging to classes of the following variables: SHINGLE, SAND, HIBSITES and CONNECT. The co-ordinates of the HIBSITES and CONNECT centroids are calculated from the average scores along the species axes of all the samples from sites in class zero of each variable. The co-ordinates of the other centroids are weighted averages of sample scores along the species axes. The use of centroids in ordination diagrams is recommended for nominal variables (ter Braak 1986). Ter Braak (1987-1992) also notes the potential utility of centroids for quantitative variables that can be absent. This is certainly the case for variables such as SHINGLE, which score zero for most sites and, so correlate poorly with species axes over the whole sample set.

The position of the centroids in the ordination plot show that samples from sites with shingle and, to a lesser extent, sand score highly on axis 1. Sites with no hibernation sites also score highly on axis 1, whereas sites with little connection to the main channel have low scores on this axis.

Table 5.6 contains the interset correlation coefficients between environmental variables and sample scores along the species axes. As in section 5.1, these coefficients have an exploratory value. They indicate that several physical features at a site may have an important effect on its species composition. Axis 1 in the ordination plot is negatively correlated with surface litter, the presence of hibernation sites, substrate litter and shade, and positively correlated with the presence of bare ground. These physical features often occur together at sites. Sites containing large quantities of surface litter are usually shaded and the litter is often incorporated into the substrate. Hibernation sites are provided by rotten wood. Litter is rarely present in quantity at sites containing large areas of bare ground and shingle. Correlations between all these physical features are probably due to their similar dependence on disturbance. Disturbance from flooding reduces the amount of litter at a site and produces bare ground. The strong correlations of the natural disturbance factor, NATDIST, and the connectivity of a site to the main channel, CONNECT, with axis 1 are, therefore, probably connected with their effects on these physical features. Grazing pressure is another important type of disturbance. It also produces bare ground through trampling and feeding and the removal of vegetation prevents the build up of litter. Hibernation sites are reduced through the removal of grass tussocks. GRAZING is also strongly correlated with axis 1 and its influence is indistinguishable from the influence of flooding within the DCA ordination.

The only environmental variable which is even moderately correlated with axis 2 is DWATER, a measure of fluctuations in water levels. Variation along axis 2 is mainly confined to samples with low scores on axis 1. Consequently DWATER is probably a more important factor in undisturbed sites than in disturbed sites.

Figures 5.4 and 5.5 show the species - environmental biplots obtained from performing CCA. The relationship between species composition and linear combinations of CONNECT, NATDIST and GRAZING was found to be significant at $p = 0.01$ both for axis 1 and the sum of the three constrained axes. Like the DCA ordination, axis 1 is related to disturbance and all three environmental variables are positively correlated with it. Unlike the DCA ordination, the gradients associated with GRAZING and CONNECT are well separated along axis 2. GRAZING and NATDIST are separated along axis 3. However, the eigenvalues of axes 2 and 3 are only 0.14 and 0.13 respectively. Variation along these axes is much less important than along axis 1 (eigenvalue = 0.38). Figure 5.4 indicates that species scoring low on axis 1 such as *Bembidion clarki* and *Carpelimus impressus* are sensitive to at least two of the environmental factors, whereas species scoring high on axis 1, such as *Bembidion tetracolum* and *B. lunulatum* are tolerant of these factors. Species scoring high on axis 2, such as *Agonum viduum* and *Elaphrus cupreus* appear to be relatively sensitive to connectivity with the main channel and tolerant of grazing, whereas species scoring low on axis 2, such as *Neobisnius* *villosulus,* are sensitive to grazing, but tolerant of connectivity to the main channel. Species responses to the different environmental variables, as opposed to the general disturbance factor, are best seen in a plot of axis 2 against axis 3 (figure 5.5). Several species appear to be more intolerant of grazing than other forms of disturbance. These include *Agonum obscurum, Clivina collaris* and *Carpelimus similis.* Species which are intolerant of CONNECT, relative to other variables, tend to be grassland species such as *Bembidion lunulatum, Clivina fossor* and *Amischa analis.* However, some wetland species, such as *Agonum viduum* and *Elaphrus cupreus* fall into this category. Fewer species, such as *Agonum marginatum,* are more sensitive to NATDIST.

5.2.4 Discussion

Meaningful environmental interpretations of the ordinations were possible despite the rather coarse, ordinal quantification of many of the environmental variables. In both ordinations, the main variation in species composition can be related to a general disturbance factor. Two types of disturbance appeared to have similar effects. Trampling and grazing by cattle (GRAZING) and flooding (CONNECT + NATDIST) both result in bare ground. They also reverse vegetational succession (Bravard *et al.* 1992) which gives rise to litter and shade. However, some species appear to be more sensitive to one type of disturbance than others. The strong association of some species with NATDIST is probably connected with their requirement for coarse substrates, which are found on sites with high values for NATDIST, but not necessarily high values for GRAZING. These species include *Bembidion punctulatum* which requires shingle (Meissner 1984) and *Oxypoda exoleta* which requires sand (Hyman 1994).

Flooding has long been known to have an important influence on semi-aquatic beetle species both in the riparian zone (e.g. Andersen 1968, Lehmann 1965) and in floodplain wetlands (e.g. Zulka 1994). The importance of grazing have been less well recognised, although Drake (1995) found differences in the species composition of two-winged fly assemblages along the banks of a lowland river between sites that were fenced off against grazing stock and unfenced sites.

Discerning differences between the effects of the two types of disturbance along the River Soar required examination of the second and third species axes of CCA ordination. There was much less variation in species composition between grazed sites and flood-disturbed sites than between undisturbed sites and sites subject to either form of disturbance. However, several species with asymmetric responses were identified including *Bembidion punctulatum, Agonum viduum, Gnypeta carbonaria, Neobisnius villosulus* and other species which are found away from the origin in figure 5.5. The two types of disturbance are therefore not entirely equivalent. Intensive grazing will tend to remove hibernation sites and refuges from flooding on the adjacent bank. Consequently, we can expect species which have strict requirements for these resources to be more sensitive to grazing pressure than to flooding. Many species which require bare ground benefit from both grazing and flooding disturbances, but species which require coarse substrates are found exclusively at sites with high severity of flooding.

The two variables used to describe disturbance by flooding are CONNECT, an ordinal measure of connectivity with the main channel, and NATDIST, an estimate of flow during floods. These can be approximated to two of the descriptors which Sousa (1984) recommended for characterising disturbances. NATDIST can be approximated to the severity of the disturbance. CONNECT can be approximated to the frequency of disturbance, if we assume that sites with a closer connectivity to the main channel flood more frequently. During flooding in June, 1991, many of the sites in CONNECT class 1 were unaffected. It is possible that they are very rarely disturbed by flooding during the main breeding season. Some grassland and wetland species which appeared to be sensitive to high values of CONNECT may well be vulnerable to flooding during the breeding season. However, although some asymmetric species responses to NATDIST and CONNECT were detected, the high correlation in nature between severity of flooding and frequency of flooding will always make separation difficult in field studies. Furthermore, the coarse ordinal measure used for CONNECT is difficult to relate to both flooding frequency and the time scale of species life cycles and so of limited use in testing theories of life history strategies.

The small variation in species responses between these different types of disturbance is reflected in their lack of influence on axis 2 of the DCA ordination. Variation between samples along axis 2 was concentrated in those from less disturbed sites with low scores on axis 1. Further investigation of species - environment relationships in undisturbed sites is described in section 5.4 using a sample set taken from floodplain sites only.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Acupalpus consputus	1	1	*B. obtusum*	7	15
Agonum albipes	26	224	*B. properans*	8	17
A. assimile	2	4	*B. punctulatum*	1	10
A. dorsale	3	3	*B. quadrimaculatum*	7	10
A. fuliginosum	16	70	*B. tetracolum*	17	176
A. livens	2	3	*Carabus granulatus*	2	2
A. marginatum	10	15	*Clivina collaris*	8	18
A. micans	18	160	*C. fossor*	10	28
A. moestum	2	4	*Demetrias atricapillus*	4	11
A. obscurum	5	10	*Dromius linearis*	4	5
A. thoreyi	2	45	*D. melanocephalus*	4	4
A. viduum	4	11	*Dyschirius aeneus*	1	1
Amara aenea	2	2	*D. luedersi*	2	2
A. communis	1	2	*Elaphrus cupreus*	8	20
A. familiaris	4	17	*E. riparius*	6	11
A. plebeja	4	5	*Harpalus rufipes*	2	3
A. similata	4	7	*Loricera pilicornis*	6	8
Asaphidion curtum	5	6	*Microlestes maurus*	1	1
A. stierlieni	1	1	*Nebria brevicollis*	2	16
Badister bipustulatus	1	1	*Notiophilus biguttatus*	3	5
Bembidion aeneum	26	479	*Patrobus atrorufus*	1	1
B. articulatum	2	2	*Pterostichus cupreus*	6	10
B. biguttatum	29	498	*P. melanarius*	1	1
B. bruxellense	1	1	*P. minor*	5	26
B. clarki	6	115	*P. nigrita*	19	41
B. dentellum	22	150	*P. strenuus*	22	119
B. genei	1	1	*P. vernalis*	15	45
B. gilvipes	25	178	*P. versicolor*	2	10
B. guttula	27	137	*Stenolophus mixtus*	1	1
B. harpaloides	4	10	*Stomis pumicatus*	3	5
B. lampros	5	10	*Trechus quadristriatus*	6	6
B. lunulatum	21	161	*Trichocellus placidus*	1	3

Table 5.2: Species of Carabidae recorded in pooled samples from 30 sites visited in April and May, 1991.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Anotylus rugosus	15	27	*P. nodifrons*	2	3
A. tetracarinatus	2	2	*Proteinus ovalis*	2	2
Carpelimus bilineatus	8	29	*Quedius maurorufus*	2	6
C. corticinus	6	18	*Rugilus orbiculatus*	2	2
C. elongatulus	3	4	*R. rufipes*	1	1
C. impressus	8	140	*Sepedophilus marshami*	3	3
C. obesus	2	2	*Stenus bimaculatus*	8	8
C. rivularis	19	155	*S. boops*	18	76
C. similis	4	13	*S. cicindeloides*	1	1
C. subtilicornis	15	148	*S. clavicornis*	1	1
Gabrius bishopi	5	6	*S. juno*	20	78
G. pennatus	3	5	*S. melanopus*	2	3
G. trossulus	1	1	*S. nitidiusculus*	1	3
Lathrobium brunnipes	10	27	*S. pallitarsis*	1	1
L. elongatum	1	1	*S. pubescens*	1	1
L. fulvipenne	11	58	*S. pusillus*	3	3
L. geminum	2	3	*S. solutus*	1	3
L. impressum	1	1	*S. tarsalis*	7	16
L. longulum	2	2	*Tachinus signatus*	4	5
Lesteva heeri	5	15	*Tachyporus chrysomelinus*	1	1
L. longoelytrata	22	107	*T. dispar*	10	17
Neobisnius villosulus	2	5	*T. hypnorum*	12	25
Omalium rivulare	3	3	*T. nitidiusculus*	6	11
Philonthus cognatus	1	1	*T. obscurus*	5	5
P. laminatus	2	2	*T. pallidus*	10	22
P. micantoides	2	3	*T. pusillus*	5	8
P. quisquiliarius	1	1	*T. solutus*	4	9
P. varius	2	2	*Xantholinus linearis*	2	4
Platystethus cornutus	7	13	*X. longiventris*	12	20
P. nitens	2	2			

Table 5.3: Species of Staphylinidae (subfamilies Proteininae to Tachyporinae) recorded in pooled samples from 30 sites visited in April and May, 1991.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Aleochara lanuginosa	1	1	*Calodera aethiops*	1	3
Aloconota gregaria	16	35	*C. uliginosa*	2	11
A. insecta	1	1	*Deinopsis erosa*	3	6
Amischa analis	13	35	*Deubelia picina*	1	24
A. cavifrons	2	2	*Dochmonota clancula*	1	1
A. decipiens	2	2	*Geostibus circellaris*	2	2
A. forcipata	2	3	*Gnypeta carbonaria*	7	13
A. soror	1	4	*G. ripicola*	3	6
Atheta celata	1	1	*G. rubrior*	5	20
A. elongatula	12	25	*G. velata*	1	1
A. fungi agg.	13	29	*Hygronoma dimidiata*	5	6
A. graminicola	26	202	*Myllaena dubia*	1	9
A. hygrobia	1	2	*M. elongata*	1	1
A. luridipennis	1	1	*Oxypoda brachyptera*	2	2
A. luteipes	1	1	*O. elongatula*	4	9
A. malleus	14	23	*O. exoleta*	2	10
A. obfuscata	1	1	*O. lentula*	3	46
A. volans	5	8	*O. umbrata*	1	1
Brachyusa concolor	3	3	*Pachnida nigella*	1	19
Callicerus rigidicornis	1	1	*Tachyusa atra*	5	7

Table 5.4: Species of Staphylinidae (subfamily Aleocharinae) recorded in pooled samples from 30 sites visited in April and May, 1991.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Heterocerus fenestratus	2	2	*Agriotes lineatus*	1	1
Heterocerus marginatus	2	2	*Agriotes obscurus*	1	1

Table 5.5: Species of Heteroceridae and Elateridae recorded in pooled samples from 30 sites visited in April and May, 1991.

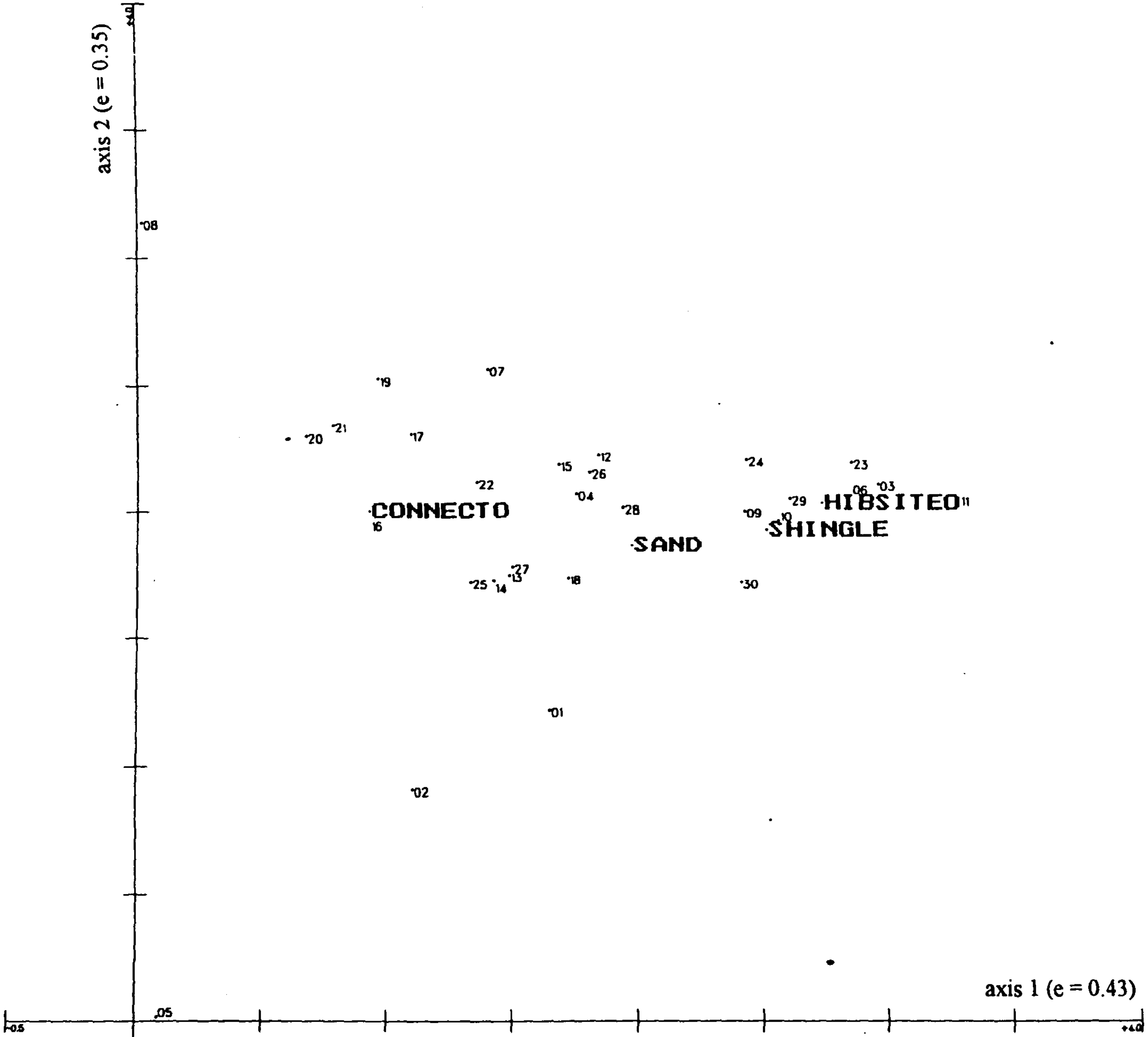

Figure 5.3: DCA ordination plot of pooled samples collected in April and May 1991 (numerals refer to site numbers).

Environmental variable	Axis 1 (eigenvalue = 0.43)	Axis 2 (e = 0.34)	Axis 3 (e = 0.15)
SHINGLE	0.34	-0.04	0.07
SAND	0.37	-0.19	-0.4
SILT	0.35	0.29	0.01
CPOM	-0.7	-0.01	0.32
LITTER	-0.78	-0.18	0.07
SHADE	-0.62	0.25	-0.06
BAREGRD	0.64	0.06	-0.63
HIBSITES	-0.72	-0.03	-0.17
DWATER	-0.14	0.50	0.36
CONNECT	0.63	-0.01	-0.32
NATDIST	0.63	-0.04	-0.39
GRAZING	0.59	-0.09	0.02
RECR	0.1	0.01	-0.14
IMPOUND	-0.06	-0.1	0.28

Table 5.6: Interset correlation coefficients between environmental varaiables and sample scores on the first three axes of variation produced by a DCA ordination of pooled samples from 30 sites visited in April and May, 1991.

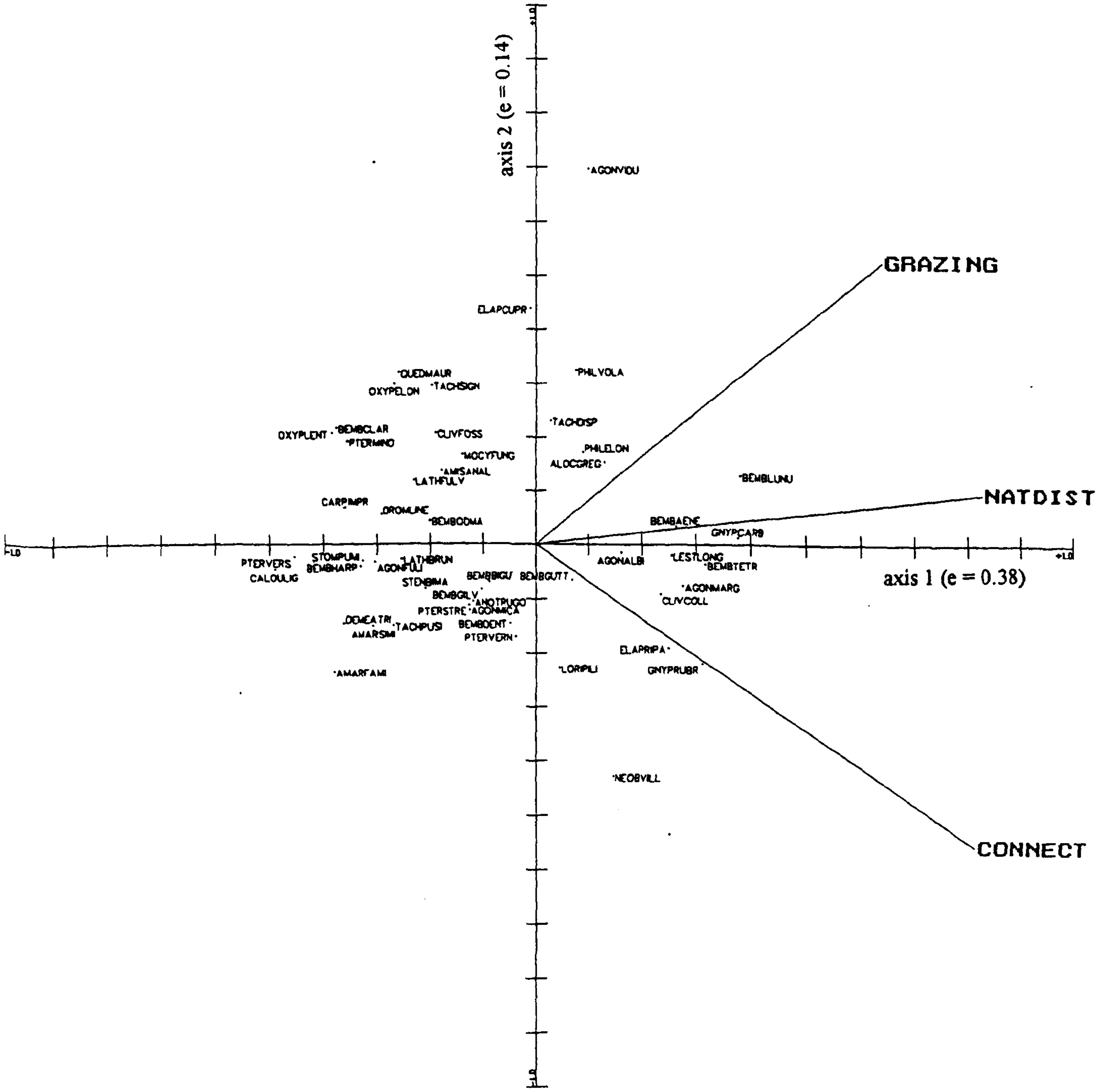

Figure 5.4: CCA axis 1 / axis 2 biplot of species and environmental variables derived from pooled samples collected in April and May 1991.

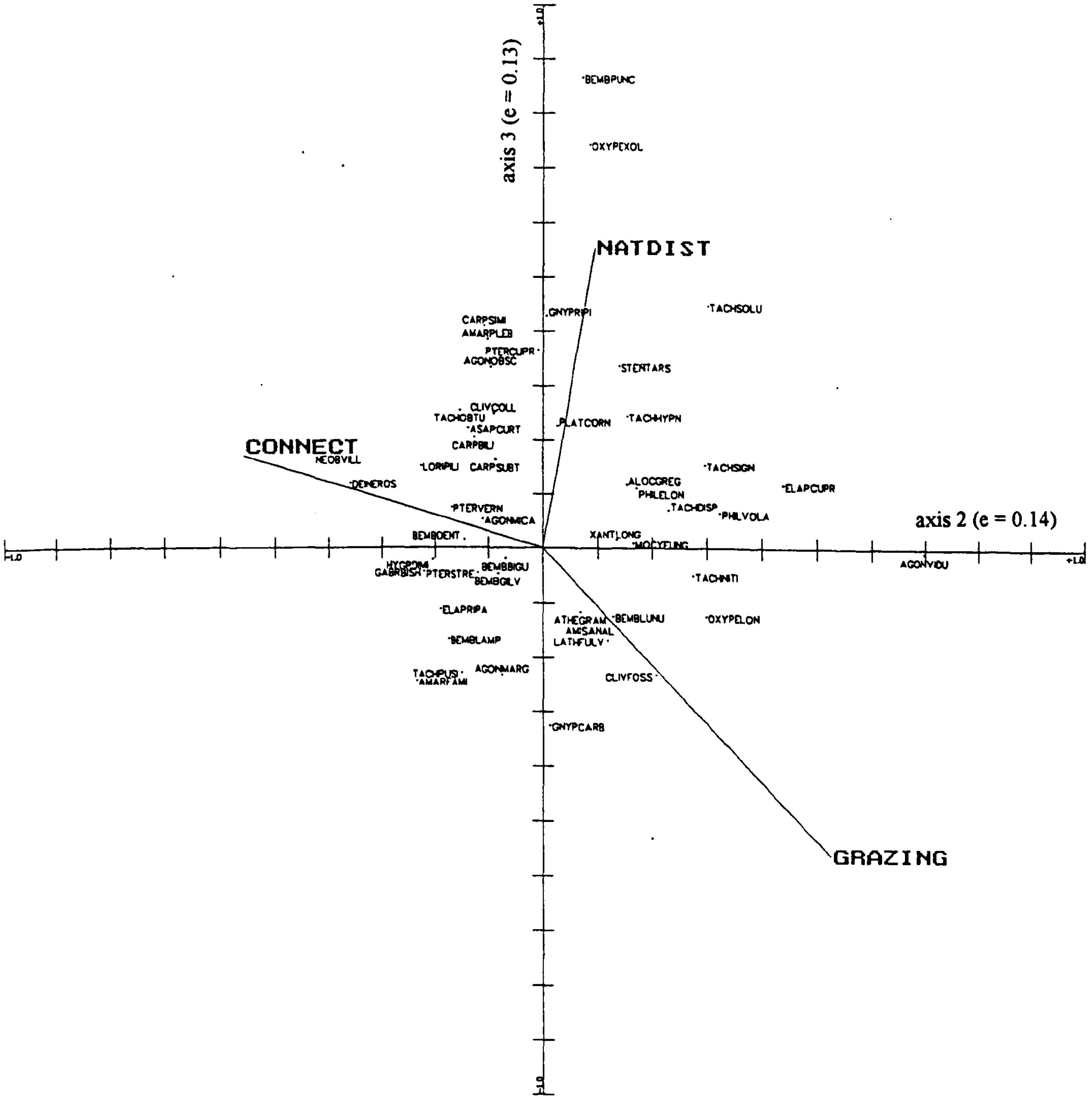

Figure 5.5: CCA axis 2 / axis 3 biplot of species and environmental variables derived from pooled samples collected in April and May 1991.

Site	Group	Wb	Wc	Wd	Wm
S1	G	0	0.02	0.4	0.57
S2	G	0	0.02	0.2	0.77
S3	CG	0	0.03	0.33	0.65
S4	C	0.01	0.1	0.27	0.62
S5	0	0	0.26	0.08	0.66
S6	G	0.02	0.07	0.18	0.73
S7	0	0.01	0.01	0.75	0.22
S8	0	0	0.13	0.57	0.31
S9	-	0	0	0.28	0.73
S10	CG	0	0.08	0.23	0.69
S11	C	0.01	0.13	0.14	0.73
S12	G	0	0	0.53	0.47
S13	C	0.01	0.12	0.28	0.59
S14	-	0	0.08	0.14	0.78
S15	C	0	0.13	0.48	0.38
S16	0	0	0.54	0.16	0.3
S17	C	0.05	0.07	0.37	0.5
S18	C	0	0.02	0.13	0.85
S19	0	0	0.12	0.44	0.44
S20	0	0	0.43	0.17	0.4
S21	0	0	0	0.65	0.35
S22	G	0	0	0.48	0.52
S23	CG	0	0.13	0.43	0.44
S24	CG	0	0.36	0.21	0.43
S25	G	0	0.14	0.27	0.59
S26	-	0.01	0.22	0.56	0.21
S27	-	0.02	0.07	0.39	0.53
S28	C	0	0.05	0.53	0.42
S29	CG	0	0.02	0.55	0.43
S30	CG	0	0	0.66	0.34

Table 5.7: Values of species indices based on wing length for sites sampled in April and May, 1991.

5.3 Variation in Species Composition according to Wing-length

5.3.1 Introduction

In section 5.2, variation in species composition was used to identify important environmental and management factors operating within the study area and concluded that disturbance from two distinct sources had a major influence. In order to understand how environmental factors affect species composition, it would be useful to investigate how species characteristics vary between sites subject to different levels of disturbance. Dispersal has often been assumed to be an important mechanism for ground beetles in recolonising areas after flooding (Holeski 1984). In particular, dispersal by flight onto riparian breeding grounds can occur in the spring (Lindroth 1949, Lehmann 1965). Consequently, we might expect the proportion of macropterous species in assemblages to increase with the frequency of flooding disturbance, though not necessarily grazing disturbance.

5.3.2 Methods

The abundance-weighted indices, W_b, W_e, W_d and W_m, were calculated according to the method described in section 3.2.4, for the 30 pooled samples collected in April and May, 1991. These indices are based on the proportion of ground beetle species with particular wing-length characteristics. 26 of these samples were divided into four groups on the basis of grazing pressure and connectivity with the main channel. Seven samples from sites in CONNECT classes 1 and 2 and GRAZING class 0 were placed in the group 0. Six samples in CONNECT classes 1 and 2 and GRAZING classes 1 and 2 were placed in the group G. Seven samples in CONNECT class 4 and GRAZING class 0 were placed in the group C and six samples from CONNECT class 4 and GRAZING class 2 were placed in the group CG. Four samples from the intermediate CONNECT class 3 were excluded from the analysis. The mean of each wing-length index was calculated for each group. The significance of the differences in means was tested using a two-sample rank test, the Mann-Whitney test, available on the MINITAB computer programme.

5.3.3 Results

The values of wing-length indices for each sample are shown in table 5.7. Very few exclusively brachypterous species were recorded and the index, W_b, was not investigated further. Figure 5.6 shows the means of each index for each sample group. Also shown for comparison are the means of the axis 1 DCA score, calculated in section 5.2. This score can be interpreted as a latent environmental variable related to a general disturbance factor. No significant differences were found between the means of W_e from different sample groups, nor between the means of W_d. However, values of W_m, the proportion of macropterous species, was significantly lower at sites with both low connectivity to the main channel and no access to grazing stock.

The results for ungrazed sites seem to fit the prediction that the proportion of exclusively macropterous species increases with frequency of flooding, but the results for grazed backwaters also suggest that the proportion of macropterous species is similarly affected by grazing pressure. No significant increase was found between grazed backwaters and grazed main channel sites. Indeed the mean value of grazed main channel sites was slightly lower.

Because of the low abundances of exclusively brachypterous species, variations in W_m are closely linked with variations in the abundances of wing-dimorphic species. A suite of widespread permanently wing-dimorphic species including *Clivina fossor*, *Bembidion aeneum*, *B. gilvipes*, *B. guttula*, *Pterostichus strenuus* and *P. vernalis*, occurred in a wide range of samples and gave rise to increases in W_d and reductions in W_m across all site groups. Luff (1998) lists grassland as a habitat for all of these species except *B. gilvipes*. All of them have been recorded from grassland in Leicestershire including *B. gilvipes* which has been recorded from alluvial meadows. The presence of these species in sites subject to flooding could be due to vagrancy or recruitment from adjacent biotopes. However, three wing-dimorphic species were found almost exclusively in backwater sites with no access to grazing stock. *Pterostichus minor* is permanently dimorphic while *Bembidion clarki* and *Agonum fuliginosum* are usually brachypterous and only rarely macropterous. These species are rarely recorded away from wetlands in Leicestershire and are regarded as marsh or freshwater margin species by Luff (1998). It is possible that their restricted distribution between samples is connected with a sensitivity to disturbance by flooding or grazing. *Bembidion tetracolum* is also a wing-dimorphic species with a restricted distribution between samples. Luff (1998) includes arable land amongst its habitats, but it has rarely been recorded away from riverbanks in Leicestershire. In contrast to the other wing-dimorphic species, mentioned above, it was restricted to samples from sites with higher levels of disturbance. and would seem to contradict any argument that exclusively macropterous populations are a necessary adaptation for coping with disturbance by flooding.

5.3.4 Discussion

A significantly higher proportion of exclusively macropterous species occurred at sites away from undisturbed backwaters, but it should not be assumed that species occurring in more disturbed sites are better at dispersing. Den Boer (1977) found that not all specimens with apparently full wing lengths are capable of flight. Also, full-winged morphs of dimorphic species can be very effective dispersers, as demonstrated by den Boer (1977) for *Agonum fuliginosum*. However, populations of permanently dimorphic species cannot rely on an annual winged recolonisation of sites which have been disturbed by flooding without large-scale mortality to flightless morphs. Flightless morphs of *Bembidion tetracolum* and grassland species probably colonise breeding grounds on the main channel sites by walking from neighbouring hibernation sites. It is possible that dimorphic species that are restricted to ungrazed backwaters, are unable to breed regularly in sites which are subject to grazing, because of a lack of suitable hibernation sites near to the breeding habitat.

Despite the observed differences between undisturbed backwaters and other types of site, the apparent relationship between the proportion of dimorphic species and levels of disturbance depends on just three wetland species. Furthermore, the observed distribution of another species, *Bembidion tetracolum,* conflicts with this relationship. The possibility of a relationship between the proportion of wing-dimorphic species and levels of disturbance remains tenuous. However, the virtual absence of exclusively brachypterous species suggests that at least occasional dispersal by flight is probably a necessary mechanism for long-term survival of populations in the floodplain wetland environment of the Soar Valley.

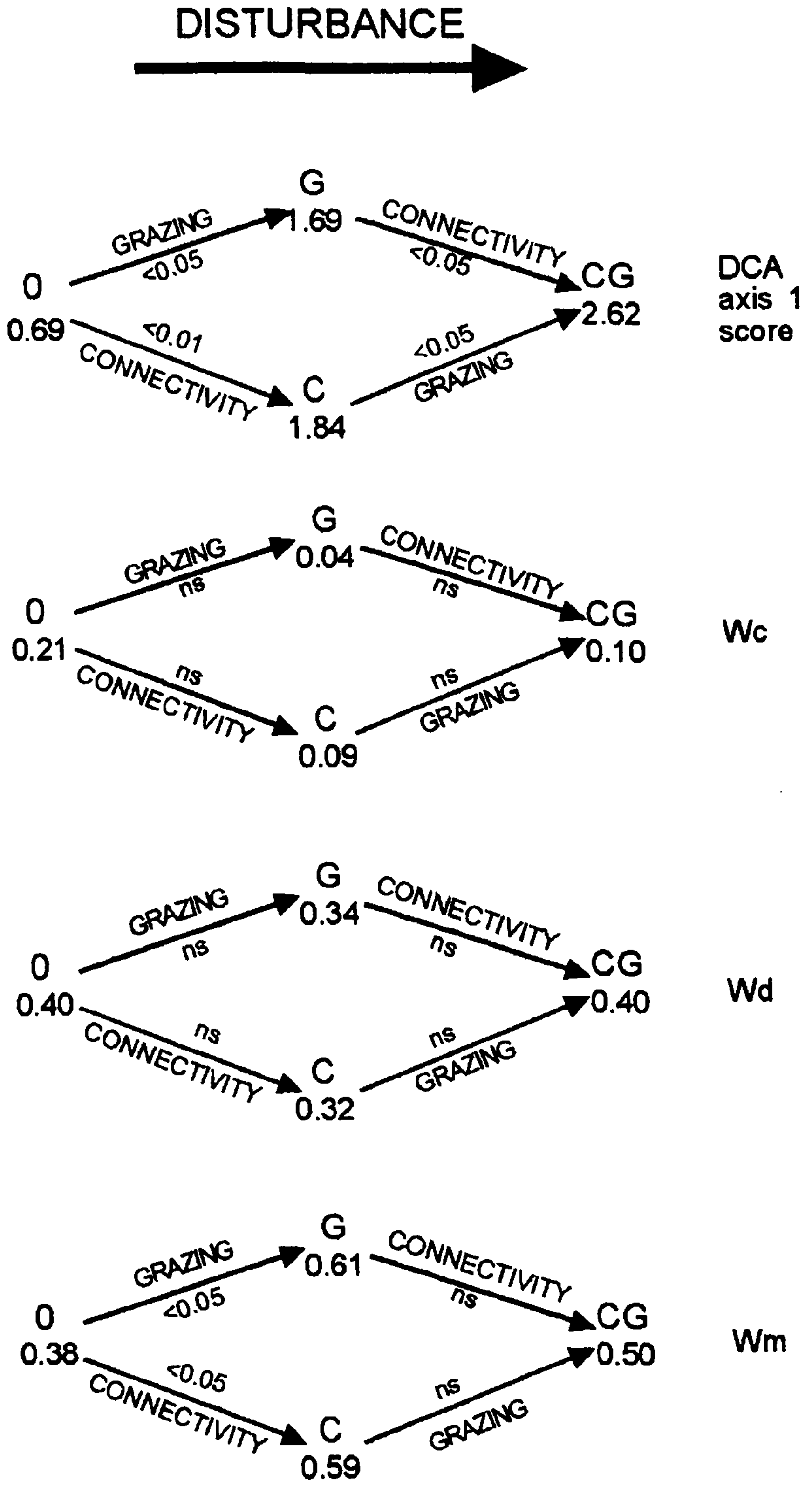

Figure 5.6: The means of DCA axis 1 scores and species indices based on wing length for groups of sites classified by grazing pressure and connectivity to the main channel (Wc = Rarely Dimorphic Species Index, Wd = Dimorphic Species Index, Wm = Macropter Species Index). Also given are the significances of differences in mean according to a Mann-Whitney test.

5.4 Variation in species composition at floodplain sites

5.4.1 Introduction

The DCA ordination of species assemblages described in section 5.2, identified various disturbance factors as having an important effect on species composition. However, the second axis of variation was more difficult to interpret. Fluctuations in water levels, quantified as DWATER, produced the most significant correlations with axis 2 scores, but interpretation was handicapped by the fact that variation along axis 2 was concentrated in samples from undisturbed sites which scored low on axis 1. It was decided to carry out an investigation confined to floodplain sites with low levels of natural disturbance by flooding, in order to clarify any relationship between species composition and water level fluctuations or other environmental factors.

Section 1.2.3 described how floodplain habitat structures can be produced by an equilibrium between vegetational succession and periodic disturbance by flooding similar to that found in the Rhone valley by Bravard *et al.* (1992) (see figure 1.5). Section 1.2.4 includes descriptions of changes in floodplain habitat structures arising from hydrological changes following river management operations (Bravard *et al.* 1986, Bornette & Heiler 1994). The equilibrium model has some potential in predicting the effects of river management on habitat structures through shifts in the equilibrium position. Investigation of environmental factors such as DWATER may yield some insight into how such changes in habitat structures may affect species assemblages.

5.4.2 Methods

From 1991 to 1994, 27 floodplain sites were sampled by hand for beetles using the methods described in section 3.1. Six of the samples were collected in 1991 and formed part of the data set used for the analysis in sections 5.2 and 5.3, although, unlike in that investigation, samples were not pooled from more than one visit. The sites chosen consisted of pools in abandoned channels and old ditches and drains. They were mostly well-established with no known recent, major disturbances. Recently excavated sites were avoided. The most recently disturbed site was site 45, a fishpond dug in a former marsh about six years previously. Sites 5e and 8e contained materials such as hard core which had obviously been tipped there at some time in the past, but they were at least partially covered by vegetation and litter.

The resulting species lists were subjected to CCA using DWATER, GRAZING, SHADE and IMPOUND as constraining environmental variables. IMPOUND, the nominal variable describing the presence or absence of weirs, was derived from the status of the main channel close to the floodplain site. Monte Carlo permutation routines were used to test the significance of variation along the resulting ordination axes.

5.4.3 Results

3,263 specimens belonging to 147 species were collected. The species are listed in tables 5.8 to 5.11 together with the number of sites from which they were recorded and the total abundance of each species across all sites. A complete table of abundances of each species at each site is included in appendix 2. Appendix 3C contains the management scores for each site.

Figure 5.7 shows the CCA species - environmental biplot. The relationship between species composition and linear combinations of the chosen environmental variables was found to be significant at p = 0.01 both for axis 1 and the sum of the four constrained axes. DWATER is strongly correlated with the main axis of variation, axis 1 which has a high eigenvalue (0.53). Axis 2 also has a high eigenvalue (0.41) and is correlated positively with GRAZING and negatively with SHADE. IMPOUND is of lesser importance on the two main axes of variation. Axis 3 and axis 4 have much lower eigenvalues (0.26 and 0.25) and are not considered further.

Only species with a minimum weight of 7% and a minimum fit of 10% are included in the biplot. Species which were confined to sites with stable water levels included *Agonum thoreyi, Stenus solutus, Myllaena dubia, Pachnida nigella* and *Deubelia picina.* Species associated with sites with the largest fluctuations in water level, included *Clivina fossor, Bembidion aeneum, B. guttula, B. lunulatum and Lathrobium fulvipenne,* all species widely collected in pitfall traps in grassland in Leicestershire. Species associated with grazed, unshaded sites included *Bembidion aeneum, B. guttula, B. lunulatum* and *Gnypeta carbonaria.* A characteristic assemblage including several rarer species such as *Bembidion clarki, Carpelimus impressus* and *Dilacra vilis,* were found in undisturbed, shaded sites with moderate fluctuations in water level.

5.4.4 Discussion

The results show that DWATER is an important factor affecting species distribution between floodplain sites. In ordination plots (see table 5.6 and figure 5.7), it is associated with axes that are orthogonal to those associated with a general disturbance factor and so its effects on the composition of species assemblages are quite different to those of disturbance. DWATER was designed to represent the amplitude in seasonal fluctuations in surface water levels which is inversely related to hydroperiod. However, it is an ordinal classification rather than a direct numerical measurement and so requires some further scrutiny.

Sites allocated to DWATER class 1 include floating mats of *Glyceria maxima* and *Typha latifolia* at 1c, 5c and 5w. 1c has formed on a recently abandoned oxbow close to the main channel and is probably regularly flooded. 5c and 5w are separated from the main channel by a railway embankment. The high water levels at these two sites have resulted from the blockage of a culvert by silt and the consequent ponding of water. It is likely that these sites are rarely flooded by surface water and they are probably at a transitional fen stage and succeeding to carr. Sites allocated to DWATER class 2 include sites 1w, 40, 43 and 45 which are often close to the main channel and regularly flooded by high water. Sites 57, 95 and 96 permanently receive water from drainage of areas elsewhere on the floodplain. All of these class 2 sites normally retain surface water all year round and are characterised by a lush growth of tall monocotyledonous plants such as *Glyceria maxima.* Persistent high water at these sites probably plays an important role in retarding the influx of trees and succession to carr. DWATER class 2 also includes sites at 1e and 96 whose vegetational cover is severely reduced by the activities of grazing cattle. DWATER classes 3 and 4 include sites that are regularly flooded by overtopping of the main channel. However, they dry out to varying extents in the summer, because they are either shallow, dominated by trees which take up a lot of surface moisture, or subject to greater fluctuations in ground water levels.

The qualitative, ordinal nature of DWATER makes it a rather imprecise measurement of water level fluctuation, but it can be related to the successional processes operating in the floodplain, at least for ungrazed sites. Figure 5.8 shows the expected variation of DWATER with vegetational succession. This diagram could be used as a model to predict how a change in the equilibrium between vegetational succession and natural disturbance due to flooding would affect seasonal fluctuations in water levels and hence the species composition of beetle assemblages.

The estimated current equilibrium position of ungrazed sites in the study area are shown in figure 5.8. It is noticeable that habitat structures characteristic of early stages of succession are rare in the Soar floodplain. Although, historically, the Soar has frequently flooded, it probably has insufficient power to maintain an equilibrium at the marsh stage in the floodplain. Indeed, site 95 which is at the earliest stage of succession, is close to the confluence with the River Trent and may be influenced by the larger discharge in that river. However, main channel sites could be considered to be at the marsh stage, because they are characterised by mineral substrates and more frequent and severe flooding. Section 5.2 showed that DWATER would not make a good predictor of species assemblages for main channel sites and that disturbance factors would be more appropriate to use in this area.

The almost opposite correlations of GRAZING and SHADE with axis 2 might be thought to reflect colinearity in the data set, in that grazed sites are likely to be less shaded than ungrazed sites. Table 5.12 shows the weighted correlation matrix (weight = sample total) and this is clearly not the case. In fact, SHADE is more closely correlated in the data set with DWATER, although these environmental factors are well separated by the ordination. The opposite response of species to SHADE and GRAZING is independent of any bias in site selection and may be connected to the response to a general disturbance factor identified in section 5.2. SHADE can be related to the successional model in figure 5.8, because the tree cover will increase during the later successional stages as fen succeeds to carr. GRAZING is likely to affect vegetational succession through the reduction of litter, but its effects are difficult to interpret using the model in figure 5.8, because it does not reverse sites to an earlier natural stage of succession. It is best considered as a disturbance factor which affects species assemblages along a disturbance gradient.

The samples were collected in four different years, but annual fluctuations in populations and weather conditions were assumed to be unimportant. In section 4.2, it was found that DCA ordination scores in a set of reference floodplain sites were both robust and comparable between different years during the period of study.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Agonum albipes	13	81	*B. lampros*	2	2
A. assimile	2	4	*B. lunulatum*	3	13
A. dorsale	1	1	*B. obtusum*	4	5
A. fuliginosum	16	59	*B. properans*	1	1
A. livens	3	5	*B. quadrimaculatum*	1	1
A. marginatum	2	7	*B. tetracolum*	4	4
A. micans	16	56	*Clivina collaris*	1	1
A. moestum	2	3	*C. fossor*	6	29
A. obscurum	4	5	*Demetrias atricapillus*	2	3
A. thoreyi	12	68	*Dromius linearis*	1	1
A. viduum	2	2	*Elaphrus cupreus*	11	19
Amara communis	1	1	*E. riparius*	3	10
A. familiaris	1	2	*Loricera pilicornis*	2	2
A. similata	1	2	*Nebria brevicollis*	1	1
Asaphidion curtum	1	1	*Patrobus atrorufus*	1	1
Bembidion aeneum	8	30	*Pterostichus anthracinus*	2	2
B. articulatum	1	2	*P. gracilis*	3	5
B. assimile	4	10	*P. minor*	8	18
B. biguttatum	20	177	*P. nigrita*	10	19
B. clarki	7	117	*P. strenuus*	11	33
B. dentellum	13	61	*P. vernalis*	8	12
B. fumigatum	1	1	*Stenolophus mixtus*	1	4
B. gilvipes	12	34	*Stomis pumicatus*	1	2
B. guttula	5	16	*Trichocellus placidus*	1	7
B. harpaloides	2	2			

Table 5.8: Species of Carabidae recorded in samples from 27 floodplain sites.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Anotylus rugosus	7	10	*Q. maurorufus*	1	1
A. sculpturatus	2	3	*Q. molochinus*	1	1
A. tetracarinatus	1	1	*Q. nemoralis*	1	1
Carpelimus bilineatus	5	11	*Q. nitipennis*	1	1
C. corticinus	3	8	*Rugilus orbiculatus*	1	1
C. elongatulus	2	6	*Stenus bifoveolatus*	2	4
C. impressus	14	165	*S. bimaculatus*	9	15
C. rivulare	14	63	*S. boops*	17	76
C. similis	1	1	*S. canaliculatus*	1	1
C. subtilicornis	3	7	*S. cicindeloides*	3	4
Gabrius pennatus	9	22	*S. clavicornis*	1	1
Lathrobium brunnipes	12	47	*S. formicetorum*	2	6
L. elongatum	1	2	*S. fulvicornis*	1	1
L. fulvipenne	6	27	*S. juno*	24	118
L. geminum	2	4	*S. melanopus*	2	2
L. longulum	1	1	*S. pallitarsis*	3	3
L. quadratum	1	1	*S. pubescens*	2	3
L. terminatum	1	2	*S. pusillus*	1	2
Lesteva heeri	10	40	*S. solutus*	4	14
L. longoelytrata	15	57	*S. tarsalis*	1	2
Mycetoporus splendidus	1	1	*Tachinus signatus*	1	1
Omalium caesum	2	2	*Tachyporus chrysomelinus*	2	3
Philonthus micans	1	1	*T. dispar*	2	2
P. micantoides	1	1	*T. hypnorum*	2	2
P. quisquiliarius	3	5	*T. nitidulus*	3	4
P. umbratilis	2	2	*T. obtusus*	8	16
P. varius	1	1	*T. pallidus*	4	5
Platystethus cornutus	4	7	*Thinodromus arcuatus*	1	2
P. nitens	2	2	*Xantholinus longiventris*	6	11
Quedius curtipennis	1	1			

Table 5.9: Species of Staphylinidae (subfamilies Omaliinae to Tachyporinae) recorded in samples from 27 floodplain sites.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Aloconota gregaria	2	2	*Dochmonota clancula*	4	12
Amischa analis	6	14	*Geostiba circellaris*	2	3
A. cavifrons	1	1	*Gnypeta carbonaria*	3	15
Atheta elongatula	6	7	*G. ripicola*	2	2
A. fungi agg.	15	24	*G. velata*	1	1
A. graminicola	22	146	*Hygronoma dimidiata*	6	9
A. hygrobia	1	2	*Liogluta nitidula*	2	4
A. hygrotopora	2	3	*Myllaena dubia*	6	33
A. luteipes	2	2	*M. infuscata*	2	2
A. malleus	13	25	*M. intermedia*	1	1
A. vilis	2	39	*Oxypoda elongatula*	2	12
A. volans	3	3	*O. exoleta*	1	1
Calodera uliginosa	1	3	*O. lentula*	5	12
Chiloporata longitarsis	7	22	*O. umbrata*	1	1
Deinopsis erosa	5	8	*Pachnida nigella*	2	14
Deubelia picina	2	25	*Tachyusa atra*	1	1
Dinaraea angustula	1	1	*T. leucopus*	1	1

Table 5.10: Species of Staphylinidae (subfamily Aleocharinae) recorded in samples from 27 floodplain sites.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Rybaxis longicornis	1	1	*Agriotes lineatus*	1	1
Heterocerus fenestratus	1	1	*Agriotes obscurus*	2	2
H. marginatus	1	1			

Table 5.11: Species of Pselaphidae, Heteroceridae and Elateridae recorded in samples from 27 floodplain sites.

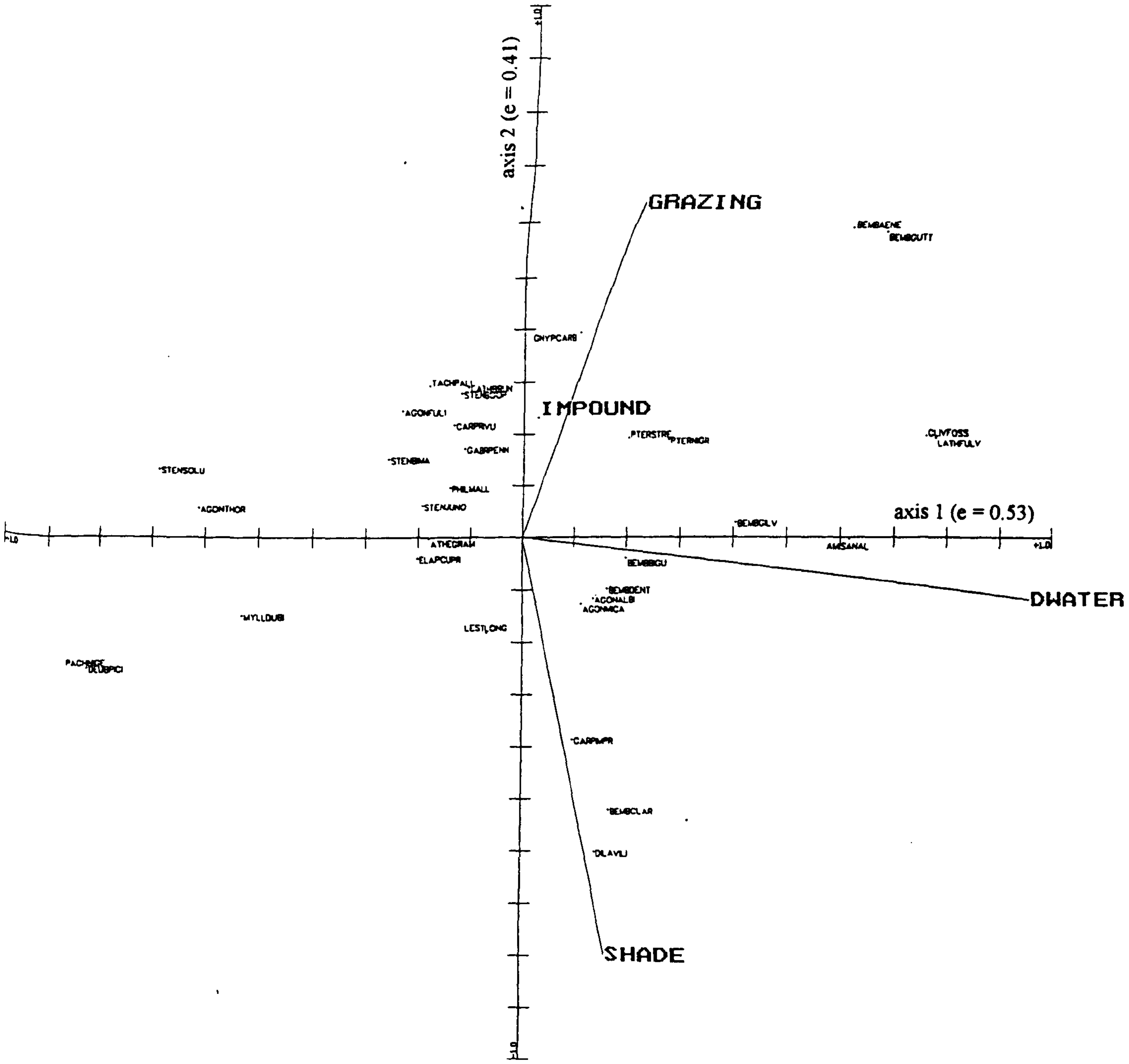

Figure 5.7: CCA axis 1 / axis 2 biplot of species and environmental variables derived from samples collected from 27 floodplain sites.

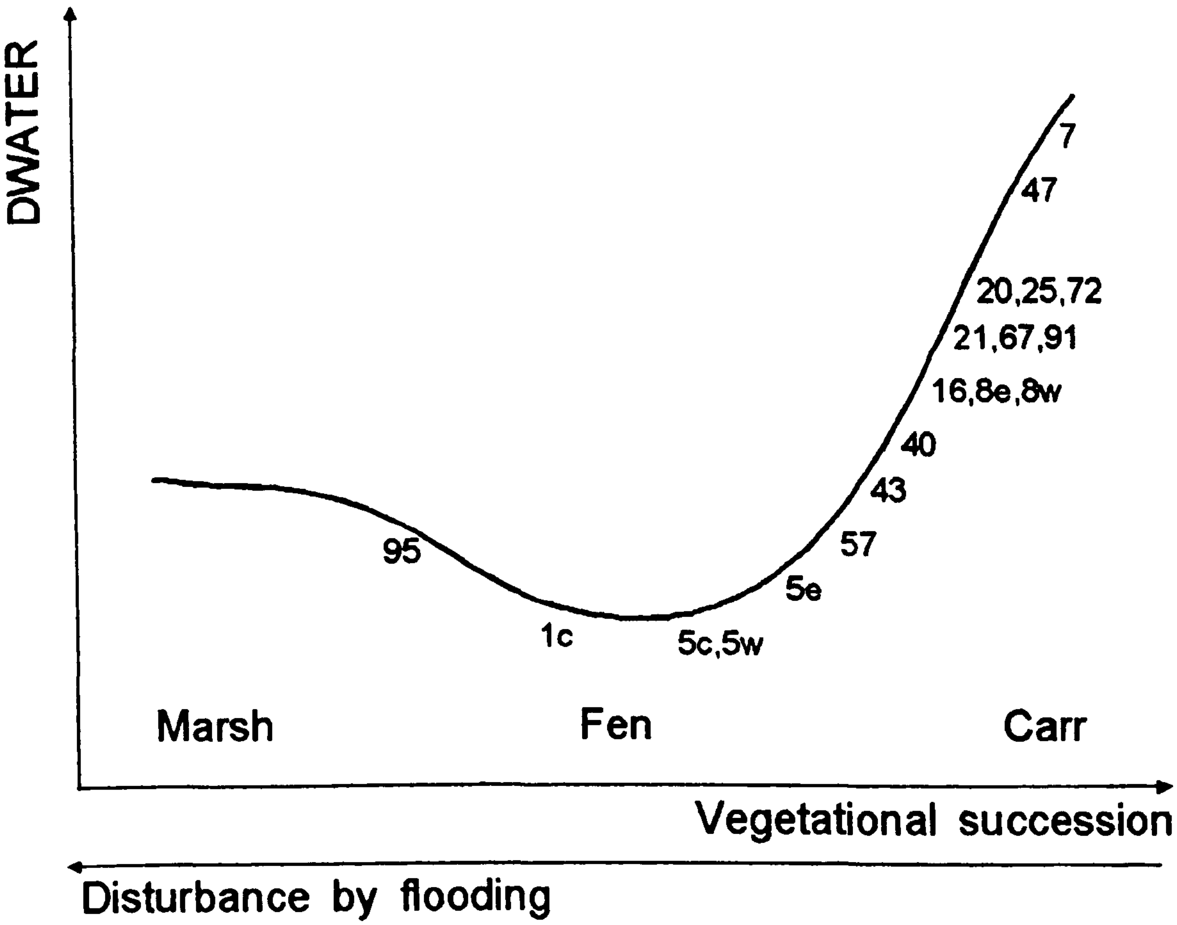

Figure 5.8: Relation of DWATER to the position of the equilibrium between vegetational succession and disturbance by flooding together with estimates of the position of ungrazed sites in the Soar floodplain.

SHADE	1			
GRAZING	-0.26	1		
IMPOUND	0.03	-0.02	1	
DWATER	0.4	0.09	0.2	1
	SHADE	GRAZING	IMPOUND	DWATER

Table 5.12: Weighted correlation matrix (weight =sample total) of environmental factors used in CCA ordination of floodplain wetland sites.

5.5 Variation in species composition at main channel sites

5.5.1 Introduction

River engineering and other management operations produce modifications of river morphology which have considerable ecological impact on the riparian zone (Brooker 1985, Brookes 1988). Lehmann (1965) found differences in ground beetle species assemblages between artificial and natural banks along the Rhine. However, no other detailed investigations on this theme have been published, although it has been implied that river management has had an impact on the riparian ground-beetle fauna (Plachter 1986).

The investigation described in section 5.2, indicated that types of disturbance due to flooding and grazing pressure were the major environmental factors affecting the composition of species assemblages in main-channel sites along the River Soar. Consequently, it may be possible to predict the effect of river management operations on riparian beetle assemblages from a consideration of the amount of disturbance that they cause.

Over half of the River Soar flowing through the study area, is impounded for navigation. This has had the effect of reducing flows at both normal and flood flows and so has reduced the severity of disturbance due to flooding over long stretches of river. We might, therefore expect to find assemblages more characteristic of less disturbed sites along navigable stretches than along unimpounded stretches. However, it should be noted that, although impoundment reduces the severity of disturbance by flooding, it should not reduce the frequency of flooding and may even slightly increase it. Therefore, the effects of impoundment should be more evident at main channel sites rather than at floodplain sites where the severity of disturbance by flooding is already low.

As part of the flood alleviation scheme described in section 2, many banks have been regraded. This has had a more direct impact on riparian habitat structures through removal of exposed sedimentary deposits and replacement of natural banks by a 45^0 slope cut out of the predominantly clay bank material. The initial impact of this work is likely to represent a major disturbance event, but the longer-term effects are more difficult to predict.

5.5.2 Methods

30 main channel sites were sampled by hand using the methods described in section 3.1. The sites selected included banks which had been regraded as part of the River Soar flood

alleviation scheme. Using information supplied by engineers in the National Rivers Authority, regraded and untouched banks were identified and the year in which their stretch of river had been engineered was established. One section between Cotes Bridge and Zouch had been engineered one year before fieldwork. The section between Zouch and the confluence with the Trent had been engineered at various times between five and eight years previous to fieldwork. The section upstream from Cotes Bridge had been unaffected by recent works.

The resulting species lists were subjected to CCA using five nominal variables as constraining environmental variables. IMPOUND and GRAZING are management factors described in section 3. REGRAD0, REGRAD1 and REGRAD5 scored 1 respectively for sites that had never been regraded, sites regraded the previous year and sites regraded more than four years previously. NATDIST was not measured, because the substrate particle size on which it is based is a product of engineering works rather than natural deposition during floods and so does not describe the severity of disturbance by flooding. All sites were situated on the main channel and so had equal scores for CONNECT, the environmental variable devised to describe periodicity of flooding.

Monte Carlo permutation routines were used to test the significance of variation along the CCA ordination axes.

5.5.3 Results

2,128 specimens belonging to 126 species were collected. The species are listed in tables 5.13 to 5.15 together with the number of sites from which they were recorded and the total abundance of each species across all sites. A complete table of abundances of each species at each site is given in appendix 2F. Appendix 3D contains the management scores for each site.

Figures 5.9 and 5.10 show the CCA species - environmental biplots for the three most important axes of variation. The relationship between species composition and linear combinations of the chosen environmental variables was found to be significant at $p = 0.01$ both for axis 1 and the sum of the four constrained axes. However, the eigenvalues for the three main axes at 0.33, 0.22 and 0.16 are much lower than those for CCA ordination of floodplain sites. The constrained axes only account for 20% of the total variance in the data set and the variation in species assemblages between main channel sites may be heavily influenced by stochastic factors. Certainly, variation along the second axis of the DCA ordination of the whole range of sites sampled in 1991 (see section 5.2) was largely confined to floodplain sites.

Axis 1 separates recently regraded sites and, to a lesser extent, impounded and grazed sites from sites with no recent impact from management. This axis seems to be equivalent to a gradient related to naturalness. Axis 2 separates impounded sites from recently regraded sites and seems to be equivalent to a disturbance gradient, similar to that identified in section 5.2. Ordination of species along this axis separates *Elaphrus riparius, Bembidion tetracolum* and *B. punctulatum* which are characteristic of open sites subject to disturbance, from *Lathrobium brunnipes* and *Gabrius pennatus* which are characteristic of more vegetated sites and which are often found on the floodplain. Axis 3 separates sites regraded more than five years previously.

Several species were recorded from a large number of sites and showed no marked sensitivity to regrading. These included *Elaphrus riparius, Bembidion tetracolum, Agonum albipes* and *Stenus juno.* However, other species were more uneven in their distribution between sites of different regrading classes. Figure 5.10 shows axis 1 plotted against axis 3 and identifies associations between individual species and site management history. Several species were found to favour recently regraded sites. They include *Bembidion aeneum, B. lunulatum* and *Nebria brevicollis* which are characteristic of intensively managed grassland in Leicestershire. In 1991, the first two species were found to be associated with sites trampled by grazing stock. They also include a contingent of riparian specialists such as *Bembidion articulatum, Stenus comma* and *Heterocerus marginatus* which are often found in gravel pits. *Tachyporus hypnorum* is a ubiquitous aphid predator whose recorded abundance at some recently regraded sites may be related to swarming behaviour. Similar aggregations of this species have also been observed at local quarries.

By contrast, a larger number of species tended to avoid recently regraded sites. *Bembidion punctulatum, Carpelimus subtilicornis, Neobisnius villosulus* and *Gnypeta carbonaria* were found to favour sites which had never been regraded. Many species, including *Atheta malleus, Agonum micans, Clivina collaris, Carpelimus rivularis, Bembidion biguttatum, Philonthus quisquiliarius, Bembidion dentellum, Carpelimus bilineatus* and *Pterostichus nigrita* were found not only on ungraded sites, but also to varying degrees on sites which had been regraded more than four years previously. *Hypnoidus riparius, Dyschirius aeneus, Bembidion obtusum* and *Xantholinus longiventris* exhibited a preference for sites which had been regraded more than five years previously.

5.5.4 Discussion

The results indicate that along the River Soar, bank regrading has had an immediate impact on the riparian beetle fauna which outweighs the effects of grazing and impoundment. Assemblages on sites which had been regraded in the previous year were well separated from other sites on the two most important axes of variation. Although many of the species on recently regraded sites were found to be associated with disturbed sites in 1991, other species characteristic of sites disturbed by grazing and flooding, such as *Bembidion punctulatum* and *Agonum marginatum,* were found to be absent or rare. The immediate impact of regrading appears to be different in character to the impact of other disturbance factors.

The lack of separation along axes 1 and 2 of ungraded sites and sites regraded more than four years previously, suggests that the initial impact of bank regrading is only temporary and does not last beyond five years. Many old regraded sites were found to have acquired a vegetation cover which at some sites included plants such as sedges and this may account for the observed rarity of species strongly associated with recently regraded sites. However, these species were also rare at sites where bare ground was maintained by erosion or fresh sedimentary deposition.

Separation of old regraded sites along axis 3 suggests that there has been a long-term impact of regrading along the Soar. However, this has been less important than the initial impact and quite different in character. Although the variation along axis 3 was not very large, some interesting patterns of distribution could be observed. Sites on regraded banks which were similar to ungraded banks in terms of slope and substrate also tended to be similar in the beetle assemblages that they supported. Species such as *Agonum micans, Clivina collaris* and *Atheta malleus* which were found in both ungraded and old regraded sites, were, in fact, confined to or most abundant at sites 31, 32 and 39 amongst old regraded sites. Sites 31 and 32 were characterised by exposed deposits of fresh sediment which produced a much shallower slope than other regraded sites. They could have been taken for natural, ungraded riverbanks were it not for the engineering records. Site 39 was the remains of a huge silt-bank, whose width had been approximately halved during engineering works. Consequently, it had never been converted to the standard 45^0 profile. On the other hand, banks which retained their steep profile shared fewer species with ungraded sites. Therefore, the long-term effects of bank regrading may be related to the steepness of slope. Unfortunately, this hypothesis is impossible to test along the Soar, where natural 45^0 banks are very rare and associated with sloughing due to springs or, more frequently, trampling by cattle. Natural riverbanks are either shallow or more or less perpendicular, in which case they do not support beetle assemblages. However, along steep river banks on Karelian rivers, Palmen & Platanoff (1943) reported that the riparian fauna contained more xerophilic species.

The predominantly clay substrate in regraded banks along the Soar may also be an important factor affecting species composition. *Bembidion punctulatum* appears to favour sand and shingle substrates and was not found on the regraded banks along the Soar. However, it has been recorded on the Trent on regraded banks composed of shingle.

If changes of slope and substrate are responsible for the long term impact of regrading on riparian beetle assemblages, then this has implications for minimising the ecological effects of river engineering schemes. The construction of new banks with more natural profiles and substrates may lessen the long-term effects of bank regrading.

The separation of impounded sites along axis 2 supports the prediction that they will support assemblages more sensitive to disturbance. As predicted, the effects of impoundment are more important than those found in the investigation on floodplain sites in section 5.4. This result also implies that the severity of disturbance by flooding can affect species assemblages independently of its periodicity. The mechanism for the relationship between severity of flooding and species composition is probably connected to substrate particle size which is a product of flooding severity.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Acupalpus consputus	1	1	*B. properans*	7	14
A. meridianus	2	2	*B. punctulatum*	4	26
Agonum albipes	27	155	*B. quadrimaculatum*	1	1
A. fuliginosum	1	2	*B. tetracolum*	23	88
A. marginatum	7	10	*Clivina collaris*	6	6
A. micans	8	28	*C. fossor*	2	2
A. muelleri	1	1	*Demetrias atricapillus*	2	2
A. obscurum	1	1	*Dromius linearis*	3	4
Amara similata	2	3	*Dyschirius aeneus*	6	16
Badister bipustulatus	1	1	*D. luedersi*	4	8
Bembidion aeneum	15	44	*Elaphrus cupreus*	4	4
B. articulatum	10	38	*E. riparius*	18	62
B. assimile	2	3	*Loricera pilicornis*	1	1
B. biguttatum	17	58	*Nebria brevicornis*	5	13
B. clarki	1	1	*N. salina*	1	1
B. dentellum	19	81	*Notiophilus biguttatus*	2	6
B. femoratum	3	3	*Pterostichus cupreus*	1	1
B. genei	5	18	*P. gracilis*	1	1
B. gilvipes	12	28	*P. minor*	1	1
B. guttula	17	33	*P. nigrita*	12	22
B. harpaloides	1	1	*P. strenuus*	7	9
B. lampros	6	6	*P. vernalis*	6	8
B. lunulatum	17	48	*Stenolophus mixtus*	6	14
B. obliquum	1	1	*Trechus quadristriatus*	2	3
B. obtusum	5	11			

Table 5.13: Species of Carabidae recorded in 1992 in samples from 30 main channel sites.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Heterocerus fenestratus	9	18	*Hypnoidus riparius*	2	6
H. marginatus	4	11			

Table 5.14: Species of Heteroceridae and Elateridae recorded in 1992 in samples from 30 main channel sites.

Species	No. sites	Total abundance	Species	No. sites	Total abundance
Aloconota cambrica	2	2	*L. terminatum*	1	1
A. gregaria	4	5	*Lesteva heeri*	5	10
A. sulcifrons	1	1	*L. longoelytrata*	18	47
Amischa cavifrons	1	1	*Myllaena elongata*	3	7
Anotylus insecatus	1	1	*M. intermedia*	3	5
A. rugosus	7	11	*Neobisnius villosulus*	4	7
A. sculpturatus	2	2	*Oxypoda brachyptera*	1	1
Atheta debilis	1	1	*O. exoleta*	2	2
A. fungi agg.	3	4	*O. longipes*	1	1
A. graminicola	7	24	*Oxytelus laqueatus*	1	1
A. elongatula	5	7	*Philonthus quisquiliarius*	9	29
A. hygrotopora	1	1	*P. umbratilis*	2	2
A. luteipes	5	12	*P. varians*	1	1
A. malleus	14	68	*Platystethus cornutus*	10	36
A. volans	4	4	*Rugilus rufipes*	2	2
Bledius gallicus	1	2	*Stenus bimaculatus*	3	7
Carpelimus bilineatus	14	27	*S. boops*	18	70
C. corticinus	2	4	*S. canaliculatus*	1	2
C. impressus	1	1	*S. cicindeloides*	1	1
C. rivularis	20	150	*S. comma*	6	11
C. similis	5	11	*S. juno*	12	36
C. subtilicornis	11	62	*S. melanopus*	1	5
Chiloporata longitarsis	13	259	*S. pubescens*	1	1
Deinopsis erosa	8	18	*S. pusillus*	3	3
Dochmonota clancula	1	1	*S. tarsalis*	3	5
Drusilla canaliculata	1	1	*Tachinus signatus*	4	5
Gabrius bishopi	1	5	*Tachyporus chrysomelinus*	1	1
G. pennatus	3	9	*T. dispar*	1	1
Geostiba circellaris	1	1	*T. hypnorum*	10	24
Gnypeta carbonaria	11	41	*T. nitidulus*	1	1
G. ripicola	1	2	*T. obtusus*	3	7
G. velata	3	6	*T. pallidus*	9	13
Hygronoma dimidiata	2	3	*T. solutus*	1	1
Lathrobium brunnipes	4	13	*Tachyusa atra*	4	14
L. fulvipenne	13	33	*Thinodromus arcuatus*	1	2
L. geminum	3	4	*Xantholinus linearis*	4	4
L. pallidum	1	1	*X. longiventris*	15	38

Table 5.15: Species of Staphylinidae recorded in 1992 in samples from 30 main channel sites.

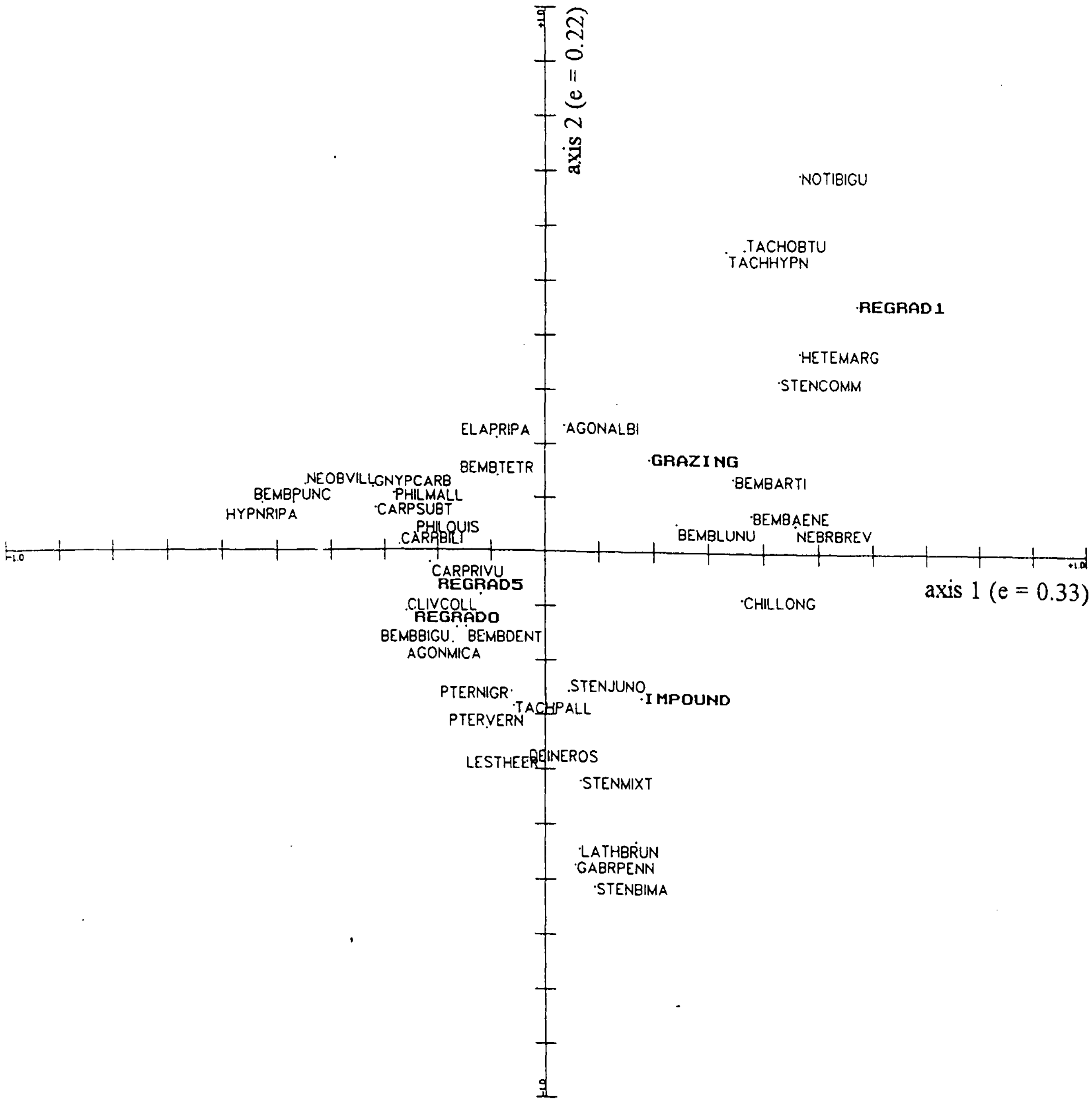

Figure 5.9: CCA axis 1 / axis 2 biplot of species and environmental variables derived from samples collected from main channel sites studied in 1992.

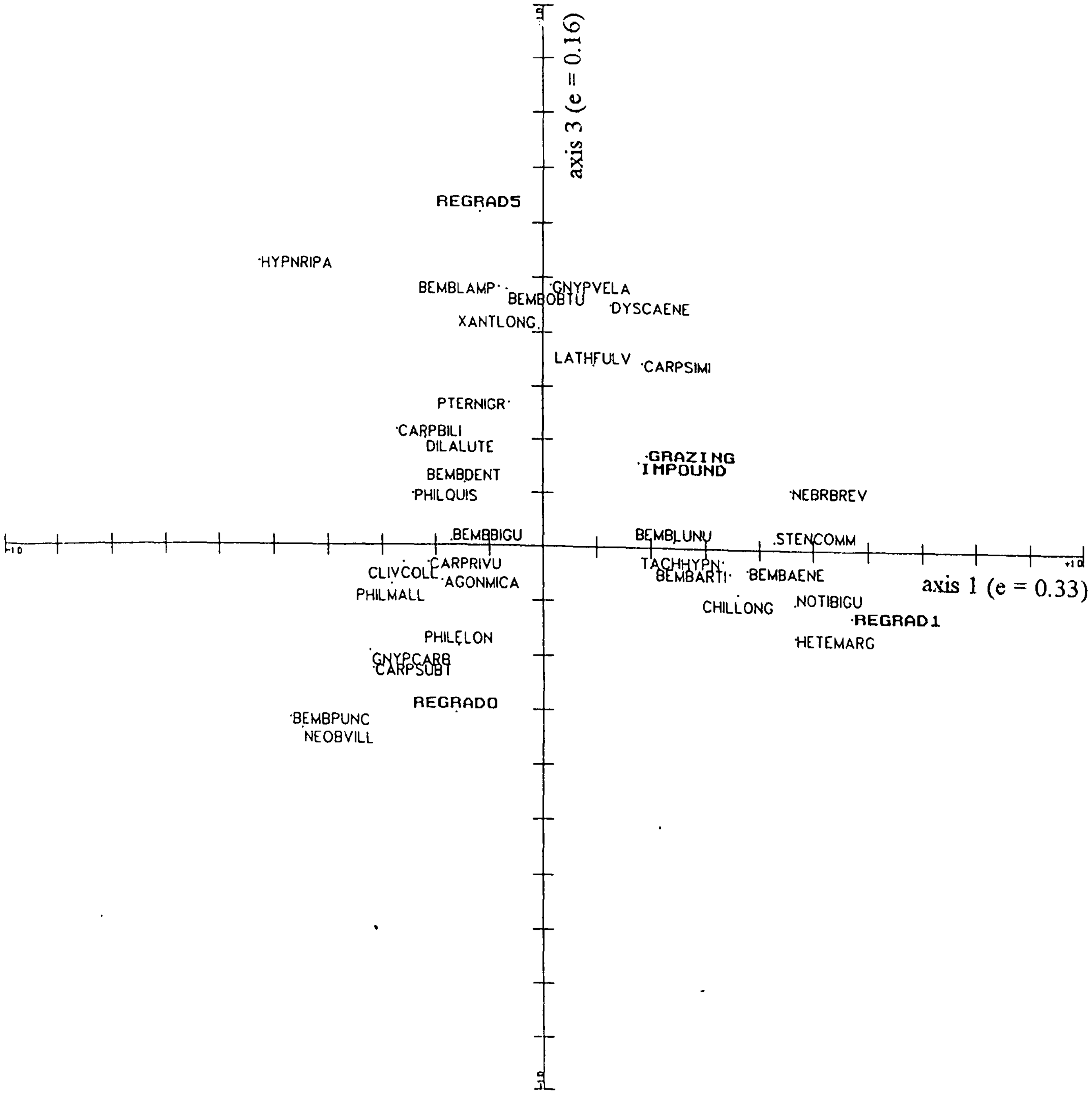

Figure 5.10: CCA axis 1 / axis 3 biplot of species and environmental variables derived from samples collected from main channel sites studied in 1992.

6 Relation of nature conservation evaluation criteria to environmental and management factors

6.1 Variation of nature conservation evaluation criteria with levels of disturbance

6.1.1 Introduction

Diversity indices and rarity scores are widely used for conservation evaluation (see section 1.4.3), but they can only be applied appropriately, if their responses to environmental variables are understood. Magurran (1988) pointed out that naturally species-poor assemblages would be undervalued by comparison with naturally species-rich assemblages, if a diversity index were used as the sole criterion. Similar arguments could be used against the exclusive use of rarity indices.

The intermediate disturbance hypothesis predicts changes of species diversity with different levels of disturbance (see section 1.3.6). Therefore, we might expect to see species richness and evenness varying both with frequency and severity of flooding and with grazing pressure. Although there are theories on the relationship between diversity and disturbance, little work has been done on rarity. However, if the species adapted to disturbance were more widespread than average, as suggested by Turin & den Boer (1988), we might expect to see significant variations in rarity indices. Furthermore, the proportion of specialist riverine and wetland species should be lower in more highly disturbed sites, where they should be replaced by more eurytopic species.

6.1.2 Methods

The species richness (S), evenness (E), local rarity index (R_l) and land use association indices for wetland (L_w), grassland (L_g) and highly disturbed sites (L_d) were calculated for the 30 pooled samples collected in April and May, 1991. Two methods were used to relate these indices to levels of disturbance.

Firstly, the axis 1 scores of the CCA ordination performed in section 5.2 were used to represent a general disturbance gradient for comparison with species assemblage parameters. Spearman's rank correlation coefficient (r_s) between each axis score and each species assemblage parameter was calculated using MINITAB.

Secondly, 26 of the samples were divided into four groups (labelled 0, C, G and CG) on the basis of grazing pressure and connectivity with the main channel as detailed in section 5.3.2. The mean of each species index was calculated for each group. The significance of the differences in means was tested using the Mann-Whitney test.

6.1.3 Results

The values of species indices for each site are shown in table 6.1. Table 6.2 shows values of the rank correlation coefficients. Highly significant negative correlations were found between disturbance and the two diversity indices. Figure 6.1 shows the means of diversity and rarity indices for each sample group. Significant differences in the means of diversity indices (species richness and evenness) were confined to those between sites subject to disturbance by both grazing and frequent flooding (group CG) and all other sites. No significant differences were detected between other sample groups. This would suggest that the relationship between site disturbance and species diversity is most marked at higher levels of disturbance.

Table 6.2 shows no significant relationship between disturbance and rarity index. By contrast, figure 6.1 shows that the mean rarity index in samples from sites subject to disturbance by both grazing and frequent flooding (group CG) was significantly less than the mean rarity indices of all other sample groups. As with diversity indices, there were no significant differences between other sample groups.

No significant differences were found between sample groups for any mean land use indices. However, table 6.2 shows a positive correlation between disturbance and L_w, the proportion of species associated with wetlands. This result is contrary to what was predicted and is due to large values of L_g, the proportion of grassland species, in samples from undisturbed sites. Unexpectedly, L_d, the proportion of species associated with highly disturbed sites, did not vary consistently along the disturbance gradient represented in this sample set.

6.1.4 Discussion

The two methods of relating species indices to levels of disturbance gave slightly different results. Correlation with a general disturbance factor yielded relationships for diversity and land-use indices with higher levels of confidence. However, additional information was gained by comparing the means of diversity indices in sample groups from sites subject to different types of disturbance. Comparison of means also detected a relationship for the rarity index which was not identified using correlation over the whole disturbance gradient.

The low diversity indices measured at grazed main channel sites are consistent with the decrease of diversity at high levels of disturbance predicted by the intermediate disturbance hypothesis (Huston 1979). However, sites with low levels of disturbance and low diversity were not detected. If the model behind the intermediate disturbance hypothesis is applied to this data set, sites with low levels of disturbance would be lacking. They are unrepresented in the data set. Most sites would be categorised as having intermediate levels of disturbance. This is consistent with their position in the floodplain and vulnerability to flooding, even if this is relatively infrequent. Sites with high levels of disturbance would be represented by main channel sites with access to grazing stock. In France and Sweden, variations in riparian plant species richness have also been interpreted as a product of intermediate disturbance (Nilsson *et al.* 1991, Decamps & Tabacchi 1992), together with habitat heterogeneity and other factors related to their larger scale of study.

In practical conservation terms, the species diversity of main channel sites along the Soar is reduced by grazing, but there is no significant difference in species diversity between floodplain sites which are grazed and ungrazed. Although as many rare species occur at grazed sites as at ungrazed sites on the floodplain, species which occur at grazed main channel sites tend to be less rare in Leicestershire than species occurring at ungrazed main channel sites or floodplain sites. These results are in broad agreement with the findings of Hodgson (1986b) for plants and Turin and den Boer (1988) for beetles that disturbed sites contain a high proportion of common species.

Application of these conservation measures to species assemblages along the Soar suggests that access of grazing stock to main channel sites reduces their conservation value both in terms of diversity and the presence of rare species. However, they do not reflect the changes in species composition between grazed and ungrazed floodplain sites which were identified by direct ordination.

The lack of any relationship between levels of disturbance and the proportion of species associated with highly disturbed sites away from river floodplains suggests that the forms of disturbance due to flooding and grazing along the River Soar require different adaptations from forms of disturbance operating in quarries and urban sites. Consequently, they attract different species assemblages. The higher proportion of grassland species in less disturbed sites means that assemblages in disturbed sites contain a higher proportion of specialist wetland and riverine species.

Site	Group	S	E	R	L_w	L_g	L_d
S1	G	26	7.31	2.04	81.22	10.19	4.01
S2	G	43	17.88	2.14	75.05	14.07	4.48
S3	CG	21	5.86	1.76	79.44	11.01	6.76
S4	C	44	13.13	3.16	79.25	11.32	4.91
S5	0	39	9.46	2.54	73.01	14.18	5.57
S6	G	23	6.49	3.04	71.02	17.79	5.32
S7	0	29	7.71	3.24	67.42	19.67	5.71
S8	0	41	11.74	4.15	77.96	12.54	4.26
S9	-	26	7.51	2.08	80.58	13.29	2.57
S10	CG	23	5.66	1.74	72.59	17.16	5.19
S11	C	20	4.83	3.05	80.19	11.39	3.5
S12	G	45	11.17	1.98	79.24	12.58	3.53
S13	C	42	11.55	2.93	81.98	10.22	2.27
S14	-	45	13.72	2	77.74	13	3.87
S15	C	32	8.17	1.66	78.8	11.82	4.51
S16	0	44	12.64	2.75	71.84	17.1	4.45
S17	C	42	13.43	2.45	86.8	8.27	1.58
S18	C	41	11.33	1.93	77.09	14.28	4.36
S19	0	34	9.78	1.68	81.07	11.54	2.3
S20	0	34	9.34	2.5	79.37	13.28	2.6
S21	0	43	12.27	2.07	76.64	12.7	4.65
S22	G	25	9.58	2.36	69.78	18.54	3.65
S23	CG	23	6.66	1.61	81.15	11.79	3.38
S24	CG	14	3.93	2.64	80.08	11.47	3.69
S25	G	35	11.16	1.8	78.02	13.89	3.09
S26	-	22	6.14	1.45	72.97	16.71	5.12
S27	-	34	10.18	1.91	75.46	14.88	4.31
S28	C	27	7.44	2.78	77.22	12.81	4.47
S29	CG	16	3.39	1.31	83.99	9.96	2.61
S30	CG	22	5.76	1.77	80.72	11.7	3.4

Table 6.1: Values of species indices for sites sampled in April and May, 1991.

Species index	r_s	P
S	-0.63	<0.001
E	-0.65	<0.001
R	-0.27	ns
L_w	0.34	<0.05
L_g	-0.31	<0.05
L_d	0	ns

Table 6.2: Spearman's Rank Correlation Coefficients for associations between species indices and axis 1 scores derived from the CCA ordination of sites sampled in April and May, 1991.

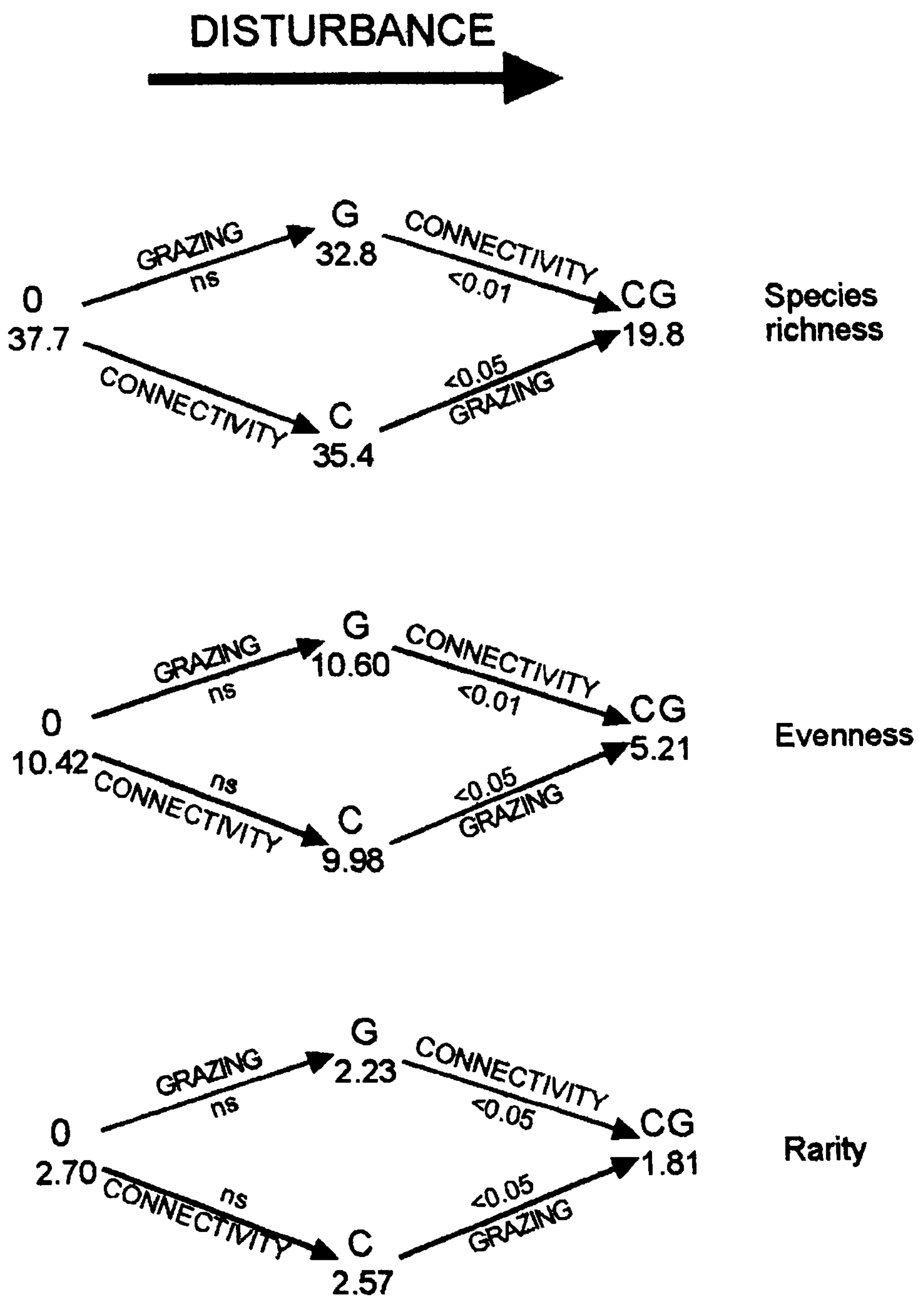

Figure 6.1: The means of evaluation criteria for nature conservation for sites classified by grazing pressure and connectivity to the main channel. Also given are the significances of differences in mean according to the Mann-Whitney test.

6.2 Variation in nature conservation evaluation criteria at floodplain sites

6.2.1 Introduction

The above findings predict little variation in species diversity for the floodplain data set used in section 5.4. All floodplain sites in the 1991 data set were thought to receive intermediate levels of disturbance with no identifiable trends in species diversity. Similarly, no significant variation in rarity was found between floodplain sites in section 5.4. However, the removal of main-channel sites from the analysis and concentration on a larger number of floodplain sites may allow more subtle trends within floodplain sites to be detected. The higher proportion of common ground beetle species in disturbed Dutch sites (Turin & den Boer 1988) may be mirrored in a lower rarity index for grazed sites in the Soar floodplain. If so, these more widespread species should be eurytopic species with lower associations with wetland and higher associations with grassland or highly disturbed sites.

6.2.2 Methods

The species richness (S), evenness (E), local rarity index (R) and land use association indices for wetland (L_w), grassland (L_g) and highly disturbed sites (L_d) were calculated for samples from all 27 sites investigated in section 5.4.

The axis scores of the CCA ordination performed in section 5.4 were used to represent environmental variables for comparison with species assemblage parameters in the same way as they were used to represent a general disturbance gradient in section 6.1. These axis scores can be viewed as linear combinations of environmental variables constrained to give maximum variation in species composition along two independent axes. They are more difficult to interpret than the pure values of environmental variables, but are more likely to uncover relationships between environment and species traits because they are related to maximal variations in composition of species assemblages. Also, the coarse ordinal values of DWATER and GRAZING are unsuitable for rank correlation because of tied rankings. Spearman's rank correlation coefficient (r_s) between each axis score and each species assemblage parameter was calculated using MINITAB.

6.2.3 Results

The values of all species assemblage parameters are shown in table 6.3. Values of the rank correlation coefficients are shown in table 6.4. Highly significant correlations were found between all the land use association indices and axis 1, which is closely related to DWATER (see figure 5.7). The lower proportion of specialist wetland species and the higher proportion of grassland species at sites which score highly on axis 1, may reflect environmental conditions which are closer to grassland. The higher proportion of species associated with high levels of disturbance at sites with high axis 1 scores, is more difficult to explain. Such a relationship would be more expected for axis 2, which can be more easily related to disturbance. However there are no significant relationships between any of the land use association indices and axis 2. These results reinforce the suggestion made in section 6.1 that there is little equivalence between the forms of disturbance operating in the Soar floodplain and those operating on industrial and urban sites.

No significant correlations were found for either species richness or evenness, as expected. Rarity was negatively correlated with axis 2. However, because there was no correlation between axis 2 and land use association indices, low rarity scores for sites which score highly on axis 2, were not caused by high numbers of eurytopic species as might have been expected.

6.2.4 Discussion

The apparent association of low rarity scores with grazing disturbance is unconnected with the similar relationship with agricultural disturbance observed in the Netherlands (Turin & den Boer 1988), because no significant increase in eurytopic species was observed in samples from grazed sites. Instead, the correlation observed in the Soar floodplain, appears to have been caused by rare species recorded at shady, ungrazed sites with moderate fluctuations in water levels. One possible explanation for the concentration of rare species at shady, ungrazed sites is provided by an inherent weakness in rarity indices. Gaston (1994) suggested that inappropriate sampling techniques can result in species appearing to be rarer than they actually are. It may be that the Leicestershire data base upon which species rarity scores are based, is biased against species occurring in certain habitat structures which have not been frequently sampled. However, sites in wet woodland and undisturbed floodplain wetland are well represented in the Leicestershire database and species associated with such habitat structures are unlikely to suffer from spurious designations of rarity. It appears that there is a genuinely high proportion of rare species in shady, undisturbed floodplain wetlands in the Soar Valley, either connected to a high beta-diversity or low population levels. The high rarity indices for these sites indicates that they are important for nature conservation in the Soar valley.

Unfortunately, their value is apt to be overlooked, because they are often shaded, temporary water bodies. This type of habitat structure is poorly regarded by many conservationists, despite the fact that Biggs *et al.* (1994) pointed out that both shaded and temporary ponds can contain rare aquatic plants and animals.

The observed variation in rarity scores is difficult to put into any functional context, although it is of value in formulating conservation priorities within the Soar valley when combined with the floodplain equilibrium model. Assemblages associated with ungrazed sites at the *carr* stage are likely to contain a higher than average proportion of rarer species. Sites which dry out completely on the surface in the summer have assemblages containing fewer specialist wetland species. Access by grazing stock disturbs succession and alters the species composition of assemblages.

Site	S	E	R	L_w	L_g	L_d
S1c	21	5.63	2.9	84.91	7.87	1.4
S1e	13	3.28	1.85	87.1	7.22	3.04
S1w	23	6.45	2	91.19	5.27	1.35
S5c	21	5.79	3.1	90.07	5.38	1.59
S5e	21	6.54	2.57	90.72	5.02	1.87
S5w	23	6.75	2.91	87.45	6.72	1.44
S6	13	6.49	3.15	61.68	23.48	7.16
S7	21	7.71	4.05	68.05	19.96	5.67
S8e	23	5.9	5.7	88.01	6.84	1.48
S8w	22	5.7	5.73	82.14	6.47	2.34
S16	23	8.6	2.78	87.64	6.78	1.53
S20	22	9.34	2.77	80.12	12.83	2.09
S21	34	12.27	2.09	80.41	10.97	3.36
S22	15	9.58	2.73	65.11	22.53	3.89
S25	23	11.16	1.57	81.18	12.38	2.15
S40	31	11.48	2.13	84.46	9.64	1.55
S43	32	11.51	2.5	91.31	5.61	0.74
S45	21	9.13	2	87.49	8.26	1.59
S47	23	5.81	2.52	88.79	7.58	1.67
S57	21	6.56	2.43	90.22	6.35	0.89
S66	25	9.98	2.64	79.28	9.72	2.41
S67	16	4.79	2.19	71.7	14.09	3.24
S72	26	10.98	3.81	86.67	7.77	1.54
S73	20	7.65	1.55	80.73	10.85	3.1
S91	26	6.13	2.23	83.28	7.66	1.78
S95	22	6.83	2.91	89.97	6.81	0.68
S96	31	13.77	2	76.25	11.44	2.87

Table 6.3: Values of species indices for floodplain sites.

Species index	Axis 1		Axis 2	
	r_s	P	r_s	P
S	-0.25	n.s.	-0.3	n.s.
E	0.08	n.s.	-0.06	n.s.
R	-0.08	n.s.	-0.36	< 0.05
L_w	-0.73	< 0.001	0	n.s.
L_g	0.76	< 0.001	0.12	n.s.
L_d	0.76	< 0.001	0.01	n.s.

Table 6.4: Spearman's Rank Correlation Coefficients for associations between species indices and axis scores derived from CCA ordination of floodplain sites.

6.3 Variation in nature conservation evaluation criteria at main channel sites

6.3.1 Introduction

The investigations described in section 5.5 found that there was much less variation in species composition between main-channel sites than floodplain sites, but that management operations still had a significant effect on species assemblages at main-channel sites. Management operations which alter or resemble the natural disturbance of flooding could be expected to affect diversity indices in a fashion similar to that found in section 6.1. However, the management operation with the biggest impact on species composition was bank regrading and this type of disturbance was expressed differently to the general disturbance gradient identified in earlier investigations. Some species which preferred recently regraded sites are characteristic of intensively managed grassland. In contrast to naturally disturbed sites, it is possible that recently regraded sites support assemblages of eurytopic species similar to those which Turin and den Boer (1988) found to be associated with disturbed sites in the Netherlands. Consequently, we might expect to find that recently regraded sites have relatively low rarity scores and scores for L_w, the index of association with wetlands and relatively high scores for L_g and L_d, the indices of association with grassland and disturbed sites respectively. We might also expect that according to the intermediate disturbance hypothesis, these sites have a lower species diversity, because of the disturbance involved in regrading.

In section 5.5 the long term effects of bank regrading were found to be smaller and different in character from the short term effects and it was suggested that differences in slope and substrate of regraded banks may be responsible for long term changes in species composition. Lehmann (1965) found that artificial banks along the Rhine contained species more characteristic of adjacent land than the natural riverbank. Palmen & Platanoff (1943) found that steeper banks on Karelian rivers tended to support a higher proportion of xerophilic species. Because regraded banks tend to be steeper and therefore drier than natural banks, we might expect them to support species assemblages which contain a smaller proportion of wetland specialists.

6.3.2 Methods

The species richness (S), evenness (E), local rarity index (R) and land use association indices for wetland (L_w), grassland (L_g) and highly disturbed sites (L_d) were calculated for samples from all 30 sites investigated in section 5.5.

The axis scores of the CCA ordination performed in section 5.5 were used to represent environmental variables for comparison with species assemblage parameters as in sections 6.1 and 6.2. Spearman's rank correlation coefficient (r_s) between each axis score and each species assemblage parameter was calculated using MINITAB.

In addition, the means of each parameter were calculated for the sets of samples from each regrading class (REGRAD0, REGRAD1 and REGRAD5). The significance of the differences in means was tested using the Mann-Whitney test.

6.3.3 Results

The values of all species assemblage parameters are shown in table 6.5. Values of the rank correlation coefficients are shown in table 6.6. In section 5.5, axis 1 was related to management and, in particular, the immediate impact of regrading. No significant correlations were found with species diversity or rarity index, but highly managed sites had a lower proportion of wetland species and a higher proportion of grassland and post-industrial species. Axis 2 was related to the general disturbance factor associated with flooding and grazing. Highly significant decreases in both measures of species diversity were found in more highly disturbed sites, but no correlations were found for indices of rarity or association with land use. Axis 3 was related to the long term effects of bank regrading. Correlations with species indices were very similar to axis 1 with a lower proportion of wetland species being found at regraded sites. Thus the observed differences in species composition between old and recently regraded sites were not reflected in conservation evaluation criteria. Although there tended to be fewer rare species at older regraded sites, the results were not significant at the 95% level of confidence.

The mean values of species indices in each regrading class are shown in table 6.7. The significance of any differences according to the Mann-Whitney test are shown in table 6.8. The two diversity indices behaved differently. Species richness separated recently regraded sites from ungraded sites whereas evenness separated recently regraded sites from old regraded sites. The most significant differences found were for land use association indices between recently regraded sites and ungraded sites. A lower proportion of wetland species and a higher proportion of grassland and post-industrial species were found in recently regraded sites. However, no significant difference was found for old regraded sites, presumably because of the influence of the three sites which were mentioned in section 5.5 and which had acquired the physical characteristics of natural sites.

6.3.4 Discussion

These results combined with those from section 5.5 indicate that the disturbance caused by bank regrading has completely separate effects on riparian beetle assemblages from those caused by flooding. Correlation of the two species indices with scores on each CCA axis clearly shows that they respond to disturbance by flooding and grazing, but that they are affected neither in the short nor the long term by bank regrading. This would seem to contradict predictions made according to the intermediate disturbance hypothesis that highly disturbed sites should have a lower species diversity. The lack of response of species diversity indices to bank regrading contrasts with the findings of Nilsson *et al.* (1991), who found that riparian plant species richness in Sweden was lower along a regulated river than a natural river.

By contrast, the land use association indices responded as expected to bank regrading and remained unaffected by other forms of disturbance. The higher proportion of grassland species associated with undisturbed sites which was found in section 6.1, was not detected in this data set confined to main-channel sites.

The higher proportion of post-industrial species on recently regraded sites is not unexpected given the similarity of the massive artificial disturbance of bank regrading to post-industrial demolition. However, their presence at old regraded sites is less easy to explain than the high proportion of grassland species at all regraded sites which is probably connected to steeper slopes, drier conditions and less vulnerability to flooding. These non-wetland species may be equivalent to the eurytopic species identified by Turin and den Boer (1988), but this was not reflected in significantly lower rarity scores, possibly because the higher recording effort expended on wetland sites in Leicestershire has resulted in low rarity scores for wetland species and, in consequence, relatively high rarity scores for eurytopic species.

Site	S	E	R	L_w	L_g	L_d
4	29	8.14	4.17	85.71	8.7	3
9	18	5.95	1.33	85.7	9.3	1.64
11	11	3.01	4.91	89.13	5.1	2.72
13	31	9.04	2.81	89.62	6.86	1.19
17	36	12.1	2.67	87.63	8.19	1.25
18	39	12.88	4.46	87.42	8.76	1.38
23	24	9.88	1.88	87.3	7.41	2.56
30	28	8.7	2.21	83.96	9.81	2.15
31	25	8.36	2.4	89.55	6.67	1.42
32	36	13.15	2.92	91.38	5.53	1.29
33	14	5.34	1.29	87.49	7.03	1.97
35	18	5.38	2.33	70.28	15.74	7.23
36	23	8.92	2.3	83.71	10.42	2.88
38	16	4.59	3.13	88.87	7.43	1.46
39	32	12.08	2.5	82.08	10.4	3.93
42	19	7.08	1.47	78.49	13.51	5.06
44	11	7.93	3.27	89.63	6.62	1.41
46	26	9.73	1.5	81.75	10.5	2.93
48	18	7.26	1.61	69.48	18.78	6.98
49	27	12.56	2.11	83.69	8.85	2.61
50	23	10.93	3.39	78.55	11.62	4.41
51	15	4.82	2	76.74	11.99	6.17
52	14	4.01	2.5	68.64	13.91	10.39
53	27	10.26	4.81	81.15	10.64	3.48
54	25	8.13	2.04	88.84	7.47	1.02
55	18	6.17	5.83	86.13	8.53	2.64
58	24	7.38	2.04	83.82	7.68	4.21
60	17	5.33	2.18	86.96	7.43	3.18
62	14	4.87	1.93	84.18	10.95	1.94
63	8	2.5	1.13	82.62	9.85	3.46

Table 6.5: Values of species indices for main-channel sites sampled in 1992.

Species index	Axis 1		Axis 2		Axis 3	
	r_s	P	r_s	P	r_s	P
S	-0.2	n.s.	-0.47	<0.01	-0.12	n.s.
E	-0.21	n.s.	-0.58	<0.001	0.08	n.s.
R	-0.1	n.s.	-0.1	n.s.	-0.26	n.s.
L_w	-0.42	<0.05	0	n.s.	-0.39	<0.05
L_g	0.4	<0.05	-0.05	n.s.	0.42	<0.05
L_d	0.33	<0.05	0.14	n.s.	0.36	<0.05

Table 6.6: Spearman's Rank Correlation Coefficients for associations between species indices and axis scores derived from CCA ordination of main-channel sites sampled in 1992.

Species index	REGRAD class		
	0	1	5
S	25.08	17.14	22.27
E	8.36	5.72	8.74
R	2.83	2.89	2.27
L_w	87.07	80.47	82.03
L_g	7.94	10.51	10.62
L_d	2.01	4.61	3.59

Table 6.7: Mean values of species indices for samples within each class of site defined by history of bank regrading where 0 = never regraded, 1 = regraded the previous year, 5 = regraded between five and eight years previously.

Species index	null hypothesis		
	$x_0 = x_1$	$x_0 = x_5$	$x_1 = x_5$
S	<0.05	n.s.	n.s.
E	n.s.	n.s.	<0.05
R	n.s.	n.s.	n.s.
L_w	<0.01	n.s.	n.s.
L_g	<0.01	n.s.	n.s.
L_d	<0.01	n.s.	n.s.

Table 6.8: Significances of differences in mean values of species indices between class of site defined by history of bank regrading, according to the Mann-Whitney test, where x_0 = mean value of samples from sites which have never been regraded, x_1 = mean value of samples from sites which were regraded in the previous year, x_5 = mean value of samples from sites which were regraded between five and eight years previously.

7 General Discussion

The introduction to this thesis concluded with four questions concerning the measurement of the conservation interest of semi-aquatic beetle assemblages and the influence of river management practices. The following discussion now seeks to address these questions.

7.1 Are there robust measurable attributes that we can use to describe beetle assemblages found on semi-aquatic habitat structures in a typical lowland river floodplain segment?

7.1.1 Species composition

As expected, a large number of species within the target families were recorded along the River Soar. The total of 281 species falls below the 300 to 500 species suggested by Foster (1987) for groups of value for site quality assessment, but Foster's recommendation was for use at a national scale rather than the landscape scale adopted by this investigation.

Table 7.1 shows that 96% of the species belonged to two families, the Carabidae (ground beetles) and the Staphylinidae (rove beetles) with the Pselaphidae, Heteroceridae and Elateridae providing only a few species, most of which were not taken in large numbers. Even though the largest contingent of species are rove beetles, ground beetles form a comparatively large proportion of the most abundant species. Table 7.2 lists the twenty most abundant species. Over half are ground beetles. It can be argued that abundant, well-established species are most likely to be of practical use in the investigation of the effects of changes in environment, because they are more easily sampled, a criterion listed by Luff & Woiwod (1995) for selecting indicators of land use change. Also their presence is more likely to be linked to real environmental factors rather than stochastic factors such as vagrancy. Consequently, although more rove beetle species were recorded in the investigation, ground beetles are probably of equal value in interpreting the influence of environmental and management factors. Neither family could be said to be redundant, because ground beetles tended to be more diverse at disturbed main-channel sites and rove beetles more diverse at undisturbed floodplain sites.

Small numbers of species from non-target families were collected during sampling. The largest contingent of specimens from non-target species belonged to the Hydrophilidae. The species most often encountered were *Helophorus aequalis, H. brevipalpis, H. grandis, H. obscurus, Cercyon convexiusculus, C. marinus, C. tristis* and *C. ustulatus*. A single specimen of the

Family	No. of species in each abundance class					Total no. of species
	1	2 -10	11-100	101-1000	>1000	
Carabidae	11	22	33	18	2	86
Staphylinidae	32	67	59	25	1	184
Pselaphidae	2	1				3
Heteroceridae			2			2
Elateridae	3	2	1			6
Total	48	92	95	43	3	281

Table 7.1: Numbers of species recorded in the investigation.

Family	Species	Total abundance
Carabidae	*Bembidion biguttatum*	1,279
Carabidae	*Agonum albipes*	1,207
Staphylinidae	*Atheta graminicola*	1,147
Staphylinidae	*Atheta elongatula*	887
Staphylinidae	*Carpelimus rivularis*	780
Carabidae	*Bembidion aeneum*	681
Carabidae	*Bembidion clarki*	671
Staphylinidae	*Carpelimus subtilicornis*	609
Staphylinidae	*Stenus boops*	601
Staphylinidae	*Stenus juno*	591
Carabidae	*Bembidion dentellum*	566
Carabidae	*Agonum micans*	563
Staphylinidae	*Carpelimus impressus*	507
Carabidae	*Bembidion tetracolum*	434
Carabidae	*Bembidion guttula*	426
Carabidae	*Bembidion lunulatum*	419
Staphylinidae	*Chiloporata longitarsis*	405
Staphylinidae	*Atheta fungi* agg.	345
Carabidae	*Bembidion gilvipes*	339
Carabidae	*Pterostichus nigrita*	327

Table 7.2: The twenty most abundant species in samples collected during the investigation.

riparian specialist, *Cercyon bifenestratus* was also collected. Specimens of Ptiliidae were also present in many samples and included two wetland species, *Acrotrichis henrici and A. sitkaensis* which were identified by Mr Colin Johnson from a small number of specimens sent to him. Samples also contained other wetland species in non-target families including the ladybirds, *Anisostictus novemdecimpunctatus, Coccidula rufa* and *C. scutellata,* the weevils, *Notaris aethiops, N. bimaculatus* and *N. scirpi* and a variety of leaf beetles which feed on riparian plants. Samples from sites with large quantities of litter sometimes contained several ubiquitous species of Cryptophagidae and Lathridiidae. However, in all samples, both the numbers of specimens and the numbers of species from non-target families were small compared with ground beetles and rove beetles.

The precise ranking of the most abundant target species listed in table 7.2 is affected by the selection of sites for sampling and the availability of habitat within those sites. However, all the species in the list can be said to be well established and thriving in semi-aquatic environments in the Soar Valley. Some such as *Bembidion aeneum, B. lunulatum* and *Pterostichus nigrita,* are also widespread in grassland, but others, such as *Bembidion clarki, Agonum micans, Carpelimus impressus* and *C. subtilicornis* appear to have more restrictive riverine or wetland habitats, at least within Leicestershire.

48 species were represented in the samples by only one specimen. Many of these are not normally associated with semi-aquatic habitats and their occurrence in samples may be due to vagrancy. The list also includes *Bembidion varium, Chlaenius vestitus, Deleaster dichrous, Stenus picipennis, Lathrobium impressum, Philonthus micans* and *Aloconota insecta,* all of which are usually associated with riparian or wetland environments. They are unlikely to have maintained viable breeding populations at the sampling sites during the period of investigation, because these species are easily caught by the sampling methods used. The single specimens collected may well have been vagrants. However, other species recorded as single specimens may have been under-recorded because they are difficult to sample. Records held by the Leicestershire Biological Records Centre (LBRC) show that *Trechus micros* was recorded several times during the 1980s in flood refuse in the area of investigation. The subterranean habits of this species (Lindroth 1985) may have led to its absence from hand-collected samples. The single specimen of *Selatosomus nigricornis* was recorded from site 7 within the Loughborough Big Meadow SSSI, where, according to LBRC records, further specimens have

been collected from drier areas using pitfall traps. This suggests that there is an established population in the area. *Selatosomus nigricornis* has either been under-recorded in this investigation, possibly because of a short adult emergence period, or it has a drier habitat at Loughborough Big Meadow than would be expected from Hyman (1992) who reported that the larvae of this species develop in waterlogged soil.

In addition to the 48 species represented by a single specimen, 92 species were represented by 10 or fewer specimens. This class includes probable vagrants unassociated with semi-aquatic habitats. It also includes riparian and wetland species such as *Lesteva pubescens, Bledius gallicus* and *Tachyusa leucopus* which are probably genuinely rare or ephemeral in the Soar Valley and further species which are possibly under-recorded. *Carpelimus subtilis, Lathrobium pallidum* and *Atheta debilis* are all species whose partly subterranean habits may have affected their recorded abundance.

Good separation of samples using species composition was achieved by DCA ordination as has been done by Desender *et al.* (1994) for ground beetles on Belgian riverbank sites and by numerous other workers for ground beetles in other habitats. The investigations described here, however, are the first to use multivariate analysis on both ground beetles and rove beetles together in a riverine environment. The inclusion of rove beetles in the analysis has undoubtedly enhanced the analyses of undisturbed floodplain habitat structures, which tended to yield samples with a relatively low diversity of ground beetles.

Significant relationships were found between species composition and environmental and management factors measured at the sampling site. Both indirect gradient analysis using DCA coupled with inter set correlation and direct gradient analysis using CCA appeared to be successful. However, any conclusions on relationships between environmental factors and species composition make assumptions about lack of sampling bias and these assumptions need some examination.

The suspicion that the observed rarity of some species is due to sampling bias implies that there is a wider problem of variation in sampling efficiency between species. The dependence of observed species abundances on their *catchability* as well as real population levels is demonstrated by the differences in results gained by pitfall-trapping and hand-collecting (see section 4.1). However, as long as the sampling bias remains constant along an environmental gradient, then it will not affect any correlation between that gradient and an axis of variation in species composition. Sampling bias influences observations of changes in species composition along an environmental gradient, only if the *catchability* of a species varies along that gradient. Therefore the observed relationships between species composition and environmental or management factors hold true if we assume that variation in sampling bias between sites is unimportant for any species. This assumption can probably be made with more justification for hand-collecting than for pitfall-trapping which relies on the activity of target species. The activity patterns of any one species can clearly be affected by environmental gradients such as vegetation structure (Refseth 1980). Nevertheless, even for hand-collecting, this assumption cannot hold perfectly. The same species might occupy different microhabitats on different substrates and so vary in the ease with which it can be seen and captured along gradients related to substrate particle size and quantity of litter.

A further bias may arise from site selection. The importance of random sampling for ecological investigation is stressed in many texts (Southwood 1978, Jongman *et al.* 1995). However, although the six sampling stations within each site were not selected randomly, the adopted stratified selection approach maximised within-site variation in prescribed environmental factors and so minimised any spurious between-site variation due to bias in selection of within-site sampling stations. Of more concern is the selection of whole sites. In the floodplain, small sites which dried out quickly in the summer were undoubtedly under-represented in the data set. In fact the smaller sites which were visited in 1991 were found to be unsuitable for sampling after June using the adopted methods. However, the larger sampling sites represented a high proportion all the available sites in the study area. Ungraded stretches of the main-channel riverbank were found to be largely vertical, eroded structures, interspersed with occasional shallower slopes. The vertical banks were impossible to sample, both because of lack of area to sample and because of difficulty of access. This left a limited number of discrete sites for sampling which consisted of exposed sedimentary deposits and banks which had collapsed due to the trampling of cattle. Logistic considerations led to a bias in favour of easily accessible sites. This bias would have important consequences for any analysis, if it led to an environmental gradient being poorly represented in the sites used to collect the sample set, because such a gradient would not be expressed in any identifiable axis of variation in species composition. Consequently, the conclusions of this investigation assume that all important environmental gradients are covered in the range of sites which were sampled.

Despite the observed variation in seasonal and annual fluctuations in the abundances of individual species, the DCA ordinations described in section 4.2 were found to yield consistent ordinations of sites between April and July and from year to year. The only exception was for main-channel sites between years and this may reflect genuine annual fluctuations in species composition due to the dynamic nature of the main-channel environment. The robustness of these ordinations suggests that methods based on weighted averages can provide a powerful, cost-effective tool for classifying sites as a preliminary stage in site evaluation as recommended by Margules (1986). Classification and quality scoring of sites at this scale has some application in the detailed design of river management schemes, where individual sites have to be prioritised for protection or enhancement. It is also be useful for designating floodplain sites for protection under local planning processes. However, individual sites are subject to modification by natural or human-induced fluvial processes and so the validity of an individual site classification and quality assessment has a limited lifespan. For most purposes, rivers are normally classified and evaluated for conservation priority at a larger scale because of the ecological integrity of the whole system (Boon 1992).

7.1.2 Species diversity indices

The evenness, E, for unpooled samples collected in the spring by hand, ranged from 2.50 to 13.77. Although the value of E would not be expected to vary with sampling effort, it was found that the value of E increased in the pooled samples used in section 5.2 to a range of 3.39 to 17.88. In fact, this increase may be unconnected with sampling effort. The pooled samples were collected in different months and so species with peaks of abundance at different seasons were all included in the same samples. This could have led to lower proportional species abundances in the aggregated species lists and, consequently, higher values of E. Therefore, the apparent sensitivity of E to sampling effort, may, in fact, be caused by pooling samples from different times of the season. By the same argument, E may be sensitive to the length of trapping period in pitfall trap studies.

The species richness, S, ranged from 7 to 39 for unpooled, hand-collected samples. The dependence of S on sampling effort is well known (Southwood 1978) and the similar arguments to those used for E can be applied to S with regard to repeat visits. Therefore, it is no surprise that values of S increased to between 14 and 45 for the pooled samples used in section 5.2.

E and S performed in a very similar fashion in nearly all investigations. Figure 7.1 shows the graph of the square root of evenness (E) plotted against species richness (S) for the sample set used in the investigation described in section 5.2. These two quantities are clearly related and can be expected to give similar responses to environmental variables. The observed close relationship is probably connected with the sampling method employed. At densely populated sites, most of the sampling time is taken up by collecting rather than searching. Approximately equal numbers of specimens were collected at each of these sites, because an equal amount of time was spent at all sites.

In section 3.2.1, E was related to the slope of the graph of log species abundance plotted against species rank abundance using the equation:

$$E = -1 / r \qquad (3.1)$$

where r is the regression coefficient. If all samples contain equal numbers of individuals, then the area under the graph becomes a constant and E becomes proportional to S^2 for a linear plot.

Deviations from this relationship will occur

1) where there is a non-linear relationship between log species abundance and rank abundance,

2) in samples from sparsely populated sites where the number of recorded specimens is relatively small.

3) in samples containing species which are easier or more difficult to catch.

If sampling had been conducted by unit area rather than unit time, it is likely that this relationship would not have been observed. At sites with low population densities and high evenness, far fewer specimens would have been collected and the measured value of S would have been lower, although E would have remained relatively unaffected.

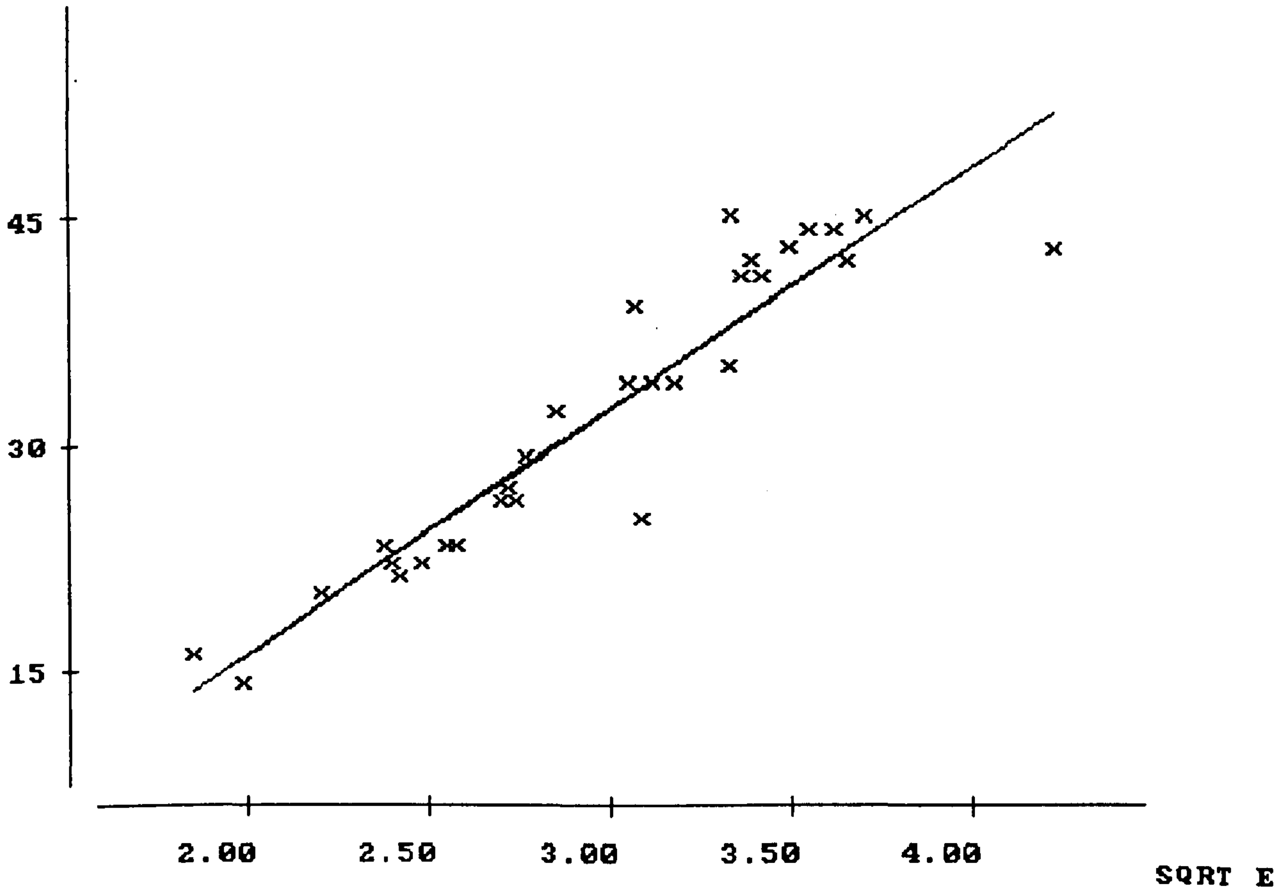

Figure 7.1: Plot showing relationship between Species Richness, S and the square root of Evenness, E for pooled samples from April and May 1991.

Both E and S failed to provide consistent ranking of sites between different months and years (see tables 4.18 and 4.19). The only exception was for ranking of sites between years which was unexpected, because the equivalent lack of robustness of DCA axis scores and the large annual variations in values of S for main-channel sites both suggest a large annual turnover of species. In any case, the large annual fluctuations make impossible the comparison of main-channel sites sampled in different years. The lack of robustness of these indices disqualifies their use for evaluating sites. Consequently, the general recommendation by Usher (1986) for using species richness as a conservation criterion, cannot be applied to beetle assemblages on semi-aquatic habitat structures in the Soar valley. However, species diversity indices may be more useful for conservation evaluation at a larger scale.

One reason for the poor performance of species diversity indices at the site scale may be connected with the vagrant species identified in the previous section. These form Shmida and Wilson's (1985) *mass effects* component of species diversity, but for the purposes of site evaluation or functional analysis, they lead to noisy data (Gauch 1982) by stochastically inflating values. Beetle assemblages may be more unsuitable for deriving species diversity indices than some other groups, because of the dispersive capabilities of many species. This is particularly the case for rove beetles. Bauer (1989b) estimated that 59% of rove beetle species recorded in a study of moorland were vagrants from other biotopes. In the present study, 54% of all recorded rove beetle species were represented by 10 or fewer specimens compared with 38% of ground beetle species (see table 7.1), although not all of these species were vagrants.

7.1.3 Rarity

Of the 281 target species recorded, 34 are currently designated as of national significance on grounds of rarity (Hyman 1992, 1994). They are listed in table 7.3. They tended to be less frequently recorded than other species with 62% of them being ranked below the median rank of total abundance.

The use of national rarity scores has several inherent theoretical advantages over the use of local rarity scores. Firstly, on a national scale, individual species rarities are derived from a wider information base and, therefore, less likely to suffer from any bias in the base line data used to calculate individual species rarities. Secondly, locally rare species are, by definition, unlikely to be regularly recorded and useful for comparing a large number of sites. By

Family	Species	Total Abundance	Rank Abundance	Conservation Status
Carabidae	*Bembidion clarki*	671	7	n
Carabidae	*Bembidion gilvipes*	339	19	n
Carabidae	*Agonum livens*	208	29	n
Staphylinidae	*Gnypeta ripicola*	97	49	n
Staphylinidae	*Atheta hygrobia*	49	69.5	n
Staphylinidae	*Gabrius bishopi*	30	94	n
Staphylinidae	*Carpelimus similis*	25	101	n
Staphylinidae	*Dochmonota clancula*	23	105.5	n
Staphylinidae	*Gnypeta velata*	22	108.5	n
Carabidae	*Trechus discus*	16	119	n
Staphylinidae	*Oxypoda exoleta*	16	119	n
Staphylinidae	*Brachyusa concolor*	14	129.5	n
Staphylinidae	*Calodera uliginosa*	11	139.5	r
Staphylinidae	*Myllaena elongata*	9	148	n
Staphylinidae	*Platystethus nodifrons*	8	151.5	n
Carabidae	*Pterostichus gracilis*	6	161	n
Carabidae	*Chlaenius nigricornis*	5	169	n
Staphylinidae	*Anotylus insecatus*	4	182.5	n
Staphylinidae	*Oxytelus fulvipes*	4	182.5	n
Staphylinidae	*Tachyusa coarctata*	4	182.5	n
Carabidae	*Acupalpus consputus*	3	200.5	n
Carabidae	*Pterostichus anthracinus*	3	200.5	n
Staphylinidae	*Stenus argus*	3	200.5	n
Carabidae	*Bembidion fumigatum*	2	221.5	n
Carabidae	*Bembidion obliquum*	2	221.5	n
Carabidae	*Tachys parvulus*	2	221.5	n
Staphylinidae	*Carpelimus obesus*	2	221.5	n
Staphylinidae	*Carpelimus subtilis*	2	221.5	n
Staphylinidae	*Lathrobium pallidum*	2	221.5	r
Elateridae	*Selatosomus nigricornis*	1	258	r
Staphylinidae	*Aloconota planifrons*	1	258	r
Staphylinidae	*Calodera riparia*	1	258	n
Staphylinidae	*Deleaster dichrous*	1	258	n
Staphylinidae	*Ilyobates propinquus*	1	258	n

Table 7.3: Species of national conservation significance in samples collected during the investigation. Conservation status taken from Hyman (1992, 1994) where n = notable and r = provisional red data book status.

contrast, nationally scarce species which are locally widespread and easily sampled would make very good quality indicators. It was, therefore, unfortunate that rarity indices based on national rarity did not give enough separation of samples to be useful over the whole range of sites. This was because there were insufficient classes of national rarity. All except the richest sites supported insufficient numbers of nationally rare species. In order to solve this problem, national rarity criteria could be extended to cover a wider range of sites by adding more rarity classes, as done by Archer (1996) who introduced classes of nationally *restricted* species, nationally *widespread* species and nationally *universal* species for aculeate bees and wasps. Alternatively, regional rarity scores could be appended below the national scores to give a hybrid system as proposed by Falk (1996).

Local rarity indices achieved good separation of samples because of the fine classification which separated relatively widespread species. Moreover, they produced consistent rankings of floodplain sites against seasonal and annual fluctuations which were generally small over the whole range of sites. Where they could be calculated, national rarity indices also proved to be robust for floodplain sites. Significantly consistent rankings of main-channel sites were not achieved using rarity indices. However, there was much more concordance in the ranking of sites than in the ranking of either months or years and further experimentation with different methods of calculation or sampling protocols might achieve better results.

Because of their robustness, rarity indices have much more potential for conservation evaluation in the study sites than species diversity. They are possibly less affected by stochastic movements, because many vagrant species score low for rarity and have less influence on index values than resident rare species due to the geometric scoring system.

7.1.4 Land use indices

Apart from odd cases, the land use indices investigated did not produce significantly consistent rankings of sites. They were primarily designed to investigate sampling bias and environmental gradients within the context of this study, but they could have some theoretical potential for conservation evaluation as a measure of typicalness, if the land use categories were converted to a finer classification based on habitat structures. Essentially, they would be a weighted average of the fidelities of each recorded species to a particular habitat structure with stenotopic species contributing high scores and eurytopic species contributing low scores.

Unfortunately the fidelity of a species to a habitat structure varies regionally and measures of fidelity are likely to be skewed by the baseline data used in their calculation (see section 1.3.4). Nevertheless, such an index may prove useful in predicting the effects of habitat structure management, if the index is based on data of local relevance.

7.2 How are these descriptors affected by natural fluvial and successional processes?

7.2.1 Species composition

Species composition, as interpreted by multivariate analysis of weighted averages of species abundances, proved to be far more responsive to a wider range of environmental gradients than any other species assemblage parameter investigated. The observed importance of substrate particle size and percentage vegetation cover is in agreement with the results of previous work carried out on the microhabitat preferences of riparian ground beetles (e.g. Palmen & Platanoff 1943, Andersen 1969, 1983, Reid & Eyre 1985, Plachter 1986, Gerken *et al.* 1991). These preferences can be linked to the morphological adaptations of some riparian, adult ground beetles for a cursorial lifestyle (Evans 1990) or for hiding under coarse particles (Andersen 1985a, Desender 1989). The importance of litter and shade has been less often mentioned and their observed importance in this study may be due to the inclusion of rove beetles in the analysis, the inclusion of floodplain sites in the study area, the sluggish, lowland nature of the River Soar, or a combination of these factors. However, in this study, the whole range of physical features at a site was found to be as important and possibly more important for species abundance than the features present at the microsite sampled (see section 5.1), even though previous studies have tended to concentrate on microhabitat preferences.

All these physical features can be related to more fundamental environmental variables which can be related to the dynamics of natural fluvial processes. CCA was used to relate species composition directly to linear combinations of these environmental variables. Several important environmental factors were detected despite the coarse, ordinal values assigned to these variables at each site. A general disturbance factor related to both frequency and severity of flooding was found to operate across the whole range of sites and its effects could be detected in all the three sample sets analysed. These results agree with those of Sustek (1994) and Zulka (1994), who cited frequency of flooding as an important factor influencing ground beetle species composition in floodplain sites in two areas of central Europe. Sustek interpreted differences between sites flooded by fast-flowing water and sites flooded by stagnant water as a response to a productivity gradient between oligotrophic and eutrophic poles, but functionally this gradient would appear to be related to severity of flooding. In studies on main-channel sites, many authors have described the habitats of individual ground beetle species (Lindroth 1945, Andersen 1969, 1983, Reid & Eyre 1985, Plachter 1986, Desender 1989, Gerken *et al.* 1991) or assemblages (Desender *et al.* 1994) in terms of substrate particle size and vegetation cover, but these parameters are both functions of the underlying disturbance factor connected with flows during floods.

A hydrological factor related to water level stability was found to be the most important factor in the floodplain sample set. There are very few published studies of beetle assemblages which attempt to identify important environmental variables away from main-channel sites. No influence of water level fluctuations on floodplain ground beetle assemblages was identified by Sustek (1994), although it is possible that the major axis of variation which he associated with frequency of flooding was more related to hydroperiod than disturbance by flooding. Away from river systems, studies of peatland ground beetle assemblages have shown the degree of saturation in the substrate to be an important influence (Butterfield & Coulson 1983, Holmes *et al.* 1993), while Landry (1994) characterised the habitats of marshland *Agonum* species by vegetation characters and these could be related to hydrological factors. Essentially, however, the conclusions in these works relate to a static hydrological model. In summary, the degree of instability in water levels has not previously been identified as important for semi-aquatic beetle assemblages, although permanence or temporary nature of open water can be an important factor for aquatic beetles assemblages (Eyre *et al.* 1992) and in a literature review, Jeffries (1991) cited 12 references which found that variations in physical stability (by which he meant drying out and flooding) had a significant effect on aquatic plants and animals in temperate ponds. The detection of its influence in the Soar valley may be a consequence of including rove beetles in the analysis. Ground beetles alone might exhibit a poor response to this variable because of their lower species diversity in floodplain habitat structures.

Both the general disturbance factor and the degree of water level stability can be related to the equilibrium model wherein habitat structures are produced by the opposing forces of vegetational succession and disturbance by flooding. Figure 5.8 shows that the degree of water level stability has a non-linear relationship with the position of this equilibrium. Kangas (1990) regarded fluctuations in water level as a type of disturbance which regulated succession. However, its effects on species composition are unrelated to those of the general disturbance factor.

As well as the detection of influential combinations of environmental factors, CCA axis scores were also used to represent values of these factors and often achieved more significant results in the investigation of responses of other species assemblage parameters, than using raw environmental measurements. This may be because the CCA axis scores have the practical benefit of being based on gradients which maximise variation in species composition. A possible further reason lies in the coarse and ordinal measures used for raw environmental data.

7.2.2 Species diversity

Despite the lack of robustness of species diversity indices, they were found to be responsive to environmental gradients. However, they were very selective, in that they were almost exclusively sensitive to gradients connected with the general disturbance factor even when the gradient was associated with less important axes of variation in species composition. Their response to the general disturbance factor appeared to fit predictions made from the intermediate disturbance theory (Huston 1979) (see section 6.1).

7.2.3 Rarity

Despite the robustness of rarity indices, they were found to be much less responsive to environmental gradients than diversity indices. Undisturbed floodplain sites with fluctuating water levels were found to produce relatively high rarity scores, but, because they occupied intermediate positions along the main axis of ordination of floodplain samples, they did not exhibit a linear relationship with the associated environmental gradient (see section 6.2).

7.2.4 Land use indices

As with species diversity indices, land use indices generally lacked robustness, but were responsive to some environmental variables. However, in direct contrast to species diversity indices, land use indices were affected by stability of the water level in the floodplain and not by the general disturbance factor. Of course, this may be a function of the particular categories used to derive the indices used in this study.

7.3 Are these descriptors sensitive to management operations along the river and on adjacent land?

All of the assemblage parameters exhibited sensitivity to at least one management factor, although, in the case of rarity, it proved difficult to detect. Regular access of cattle and bank regrading were both found to strongly affect the species composition of semi-aquatic beetle assemblages at a site, while species diversity indices varied with grazing pressure. The effects of impoundment were less marked, but still detectable. As with other environmental factors, land use indices exhibited a response to management operations which had a significant effect on species composition. The responses of species composition and species diversity to grazing were found to be very similar to their responses to the general disturbance factor, while the effects of impoundment on species composition were correlated with those of the general disturbance factor.

7.4 Can we predict the impact of management operations from the response patterns of assemblages to natural processes?

The observed responses of species assemblage parameters to management factors within the Soar valley suggest that, within the conceptual model of how fluvial and successional processes affect habitat structures, management operations influence beetle assemblages in three different ways:

1) they directly affect fluvial and successional processes and so modify habitat structures;

2) they mimic fluvial and successional processes in the way that they affect habitat structures;

3) they affect beetle assemblages in ways that are not predicted in the model.

7.4.1 Management which affects fluvial and successional processes

In section 5.5, the observed influence of impoundment for navigation was explained in terms of reduction of severity of disturbance and consequent modification of habitat structures, particularly through the deposition of fine sediment and the creation of conditions suitable for dense vegetation cover.

Similarly, the altered disturbance regime and consequent modifications of geomorphic structures produced by rechannelling works (Brooker 1985, Brookes 1985, 1988, Bravard *et al.* 1986) and changes in catchment land use (Walling & Gregory 1970, Park 1977) can be expected to produce predictable changes in beetle assemblages. Floodplain assemblages may be particularly sensitive to changes in the equilibrium between flooding disturbances and successional processes which influence water level stability (Bravard *et al.* 1986). In the Soar valley, the flood alleviation scheme will probably affect beetle assemblages outside the embankment through an acceleration of vegetational succession leading to terrestrialisation of carr and destabilisation of water levels in fen. Unfortunately, this prediction could not be tested within the timescale of this study.

A reliable model of how fluvial processes modify habitat structures has considerable application in planning the restoration of engineered rivers. Engineered rivers whose maintenance is subsequently neglected only have limited powers of natural recovery in the short term, depending on their stream-power (Brookes 1992). Consequently, active intervention may be necessary to restore river channels and floodplains to a natural state which can support a full range of biodiversity. Many river management techniques have been developed for creating habitat structures as part of normal maintenance work (RSPB *et al.* 1994). Although these techniques are rarely designed for terrestrial invertebrates, the creation of meanders may result in the formation of point bars suitable for occupation by riparian beetles, the creation of floodplain pools may result in sites suitable for occupation by floodplain species and the creation of buffer strips to intercept agricultural run-off may provide suitable hibernation sites. Driver (1997) describes several schemes which have restored sections of English rivers and their floodplain. However, Brookes (1992) stressed the importance of assessing long term channel stability in the planning of such works.

7.4.2 Management which mimics the effects of fluvial and successional processes

Section 5.2.4 gives possible explanations for why regular access of cattle to a site affects species composition and species diversity along the Soar in a similar fashion to the general disturbance factor. Favoured wetland management practices not infrequently include at least low intensity grazing (e.g. Kirby 1992, Fojt 1994, Chatters 1995, Drake 1995). Grazing by wild animals would have been a natural phenomenon before the advent of agriculture. However, for the conservation of riparian and floodplain beetles, it is doubtful that grazing can be successfully used to replace natural disturbance by flooding, because some species appear to be differentially sensitive to grazing pressure, at least within the Soar valley.

The long term effects of regrading can be seen as the result of artificially setting the steepness of the bank profile. Along the Soar, grassland species have replaced more specialist riparian species on older regraded banks which have subsequently been unaffected by natural fluvial processes (see section 5.5). Better design of bank profiles might encourage a more appropriate riparian fauna. An even better approach would be the imaginative use of natural fluvial processes to produce replacement natural structures which did not interfere with the drainage function of the watercourse.

The presence of riparian beetles at recently excavated gravel pits (Koch 1977, Plachter 1986) suggests that gravel extraction can also mimic fluvial processes by reproducing riparian habitat structures in the floodplain. However, Plachter's claim that pits can serve as refuges for endangered species associated with plant-free habitat structures takes no account of the long term vegetational succession that floodplain biotopes undergo. Gravel pits probably have more conservation value as artificial analogues of floodplain wetlands.

7.4.3 Management whose effects are not predicted by the present model

The failure of the current model to predict the short term responses of beetle assemblages to bank regrading (see sections 5.5 and 6.3) can be attributed to the false equation of regrading disturbance to the general disturbance factor. Regrading disturbance differs from flooding and grazing disturbance in three of Sousa's (1984) descriptors of disturbance.

1) It is more severe, because it results in greater modification of the habitat.

2) It occurs at a much lower frequency.

3) It is much less predictable.

It is now necessary to examine how these differences might find expression in the species traits of assemblages affected by each type of disturbance.

Southwood (1977) viewed disturbance as the disruption of favourableness of the environment in time and space. He characterised environments according to the length of time between periods suitable for breeding in comparison with the time required to complete a life cycle. He also characterised environments according to the predictability of the disturbance. According to habitat templet theory, frequency and predictability of flooding are therefore critical in selecting species traits in the riparian and floodplain environment. Table 7.4 shows how the temporal scale of flooding may result in the selection of different species traits.

On an annual timescale, flooding in the Soar valley occurs according to a predictable seasonal pattern which includes a high frequency of flooding during the winter. Superimposed on the seasonal pattern is a much more unpredictable high frequency pattern of flooding, often termed spates. Because spates happen on a much shorter timescale than the riparian beetle life cycle, a strategy based on investment in reproduction would be unsuccessful. Of course such a strategy would be possible if the life cycle was shortened, but known riparian beetle life cycles appear to be almost exclusively univoltine perhaps because of phylogenetic constraints. Instead there is evidence that riparian species are selected for a variety of morphological and behavioural traits which are used to escape the deleterious effects of spates. These traits include swimming ability (Joy 1910, Jenkins 1959, Andersen 1968, Zulka 1994), running or flying away from rising water (Andersen 1968) and survival of inundation (Joy 1910, Palmen 1945, 1949, Andersen 1968). The various hibernation strategies adopted by riparian beetles (Palmen 1945, 1949, Krogerus 1948, Andersen 1968) can be seen as a behavioural trait of advantage in surviving predictable annual disturbances. In life history terms these strategies represent an investment in survivorship, termed A-strategy (Greenslade 1983), appropriate for adversity and environmental stress which varies along the second templet axis of Southwood (1988) rather than the r-strategy considered to be the usual selection for disturbed habitats. Riparian beetles view subannual (=subgenerational) flooding as an environmental stress rather than a disturbance. Similar conclusions were reached by Richoux (1994) for floodplain water beetles which he considered to be closer to K-strategists than r-strategists.

If there is any r-selection of life-history traits within the natural riparian environment, we can expect it to operate through unpredictable disturbances that occur on average at frequencies greater than or equal to one year. Consequently we might expect to find r-strategists along active rivers where new habitat structures are created or severely modified by floods which

Type of flooding	**spates**	**seasonal pattern**	**channel-forming floods**
Frequency	daily / weekly	annual	usually superannual
Predictability	unpredictable	predictable	unpredictable
Timescale compared with life cycle	subgenerational	equigenerational	supergenerational
Severity	low to moderate	low to moderate	high
Species traits favoured	allocation of resources to survivorship through morphological and behavioural traits (A-selection)	allocation of resources to survivorship during winter flooding by hibernation (A-selection)	allocation of resources to dispersal and reproductive effort (r-selection) ?

Table 7.4. Predicted selection of species traits by flooding in riparian and floodplain environments

occur at superannual (= supergenerational) frequencies. Suitable structures for r-strategists should occur on rivers with high stream power or on sandy substrates and within river systems on unstable medial bars rather than more stable point bars. These conditions are not found along the River Soar, but were present in the past and may still be locally present on the nearby Trent (Petts *et al.* 1992, Salisbury 1995).

A lack of knowledge about lifespans and fecundity makes it difficult to identify r-strategists among riparian beetles, although r-strategists would be expected to be good dispersers and colonisers. Very few brachypterous species were recorded along the Soar and this made it difficult to differentiate between dispersive abilities as responses to disturbance factors. Holeski (1984) characterised the beetle fauna on the banks of channelised rivers in Ohio as r-strategists, but gave no data on either the reproductive strategies or the dispersal abilities of the beetles as evidence for his assertions. Furthermore he claimed that all shore beetles are r-strategists, because they are frequently required to recolonise their sites after flooding. This assertion does not necessarily stand scrutiny from a comparison of the timescale of riparian disturbances with that of the beetles' generation time as recommended by Southwood (1977). Similarly, the discussions of Lehmann (1965) and Rehfeldt (1984) are based on assumptions which may have placed too much emphasis on recolonisation by flight as opposed to survival of floods *in situ*.

The severity of grazing disturbance is of a similar order of magnitude to the subgenerational flooding disturbances that predominate along the Soar. Grazing disturbance occurs at higher frequencies than flooding disturbances, but its subgenerational periodicity may be the factor that produces similar species assemblage responses and favours A-strategists. On the other hand, bank regrading is an unpredictable, supergenerational and relatively severe disturbance. Habitat templet theory predicts that it should favour r-strategists. Support for this prediction comes from the higher values of the post-industrial land use index at regraded sites along the Soar. This index is based on the proportion in the assemblage of species which colonise highly disturbed demolition sites.

Disturbance from bank regrading does not appear to have a natural analogue along the Soar in the same way that grazing disturbance mimics subgenerational flooding disturbance. However, a natural analogue may be present on more powerful rivers than the Soar. Indeed, the Trent may have been an immigration source of some of the r-strategist colonisers of regraded banks on the Soar. More likely sources, however, can be found in artificial biotopes such as arable land.

The characterisation of subgenerational flooding and grazing disturbances as environmental stresses throws an interesting slant on the intermediate disturbance hypothesis. The responses of species diversity indices observed in section 6.1 must now be interpreted as responses to environmental stress. By contrast their lack of response to regrading disturbance, which is much closer to Huston's (1979) concept of disturbance, must be interpreted as a contradiction of the intermediate disturbance hypothesis.

In addition to the problem of regrading, it must be acknowledged that the present model does not predict assemblage responses to several potentially important factors involving nutrient enrichment. While the model deals with the transport of Coarse Particulate Organic Matter to and from floodplain wetlands, Dissolved Organic Matter remains uncovered. However, there are indications (Hammond 1971, Green 1983, Holmes *et al.* 1993) that agricultural run-off and sewage discharge are all likely to have important effects on beetle assemblages.

7.5 Practical applications

7.5.1 Evaluation and management of fine exposed riverine sediments in the main channel

This investigation has established the conservation value associated with fine sediments along the River Soar. This interest is probably repeated in other lowland river systems and the maintenance of these structures should be considered when drawing up catchment management plans. Proposed developments which cause changes in channel morphology and sediment load, need to be assessed for their impact on these sediments. The reduction of interest associated with intensive grazing suggests that influence over adjacent land use is a necessary supplement to positive river management.

7.5.2 Design of rechannelling works

The investigation also detected a long-term loss of characteristic riparian species from regraded banks, but there are indications that this can be redressed by creating more natural profiles and allowing sediments to build up naturally within the river channel.

7.5.3 Evaluation and protection of floodplain wetlands

The high level of interest associated with undisturbed floodplain wetlands suggests either that Environment Agency river habitat surveys need to be extended into the floodplain, or that a parallel habitat survey is required for the floodplain. The evaluation of such features in the Soar floodplain has been combined with that of other features of existing or potential conservation interest in a new rapid assessment system for the Soar valley which uses just four main criteria: stages of vegetational succession represented, size of feature, estimated age of feature and recent management history. Sites of potential interest for beetles are identified as those which meet the following criteria:

a) carr, transitional fen or grassland,

b) any size,

c) over fifty years old,

d) not subject to intensive grazing.

It is likely that this system could be adapted to cover a wide range of lowland rivers.

Identification of these sites for protection is a priority in lowland river systems, because they are often small-scale features which are vulnerable to changes in land use. The equilibrium model developed in this investigation demonstrates that they are also sensitive to hydrological changes caused by drainage and flood alleviation schemes.

7.5.4 Gravel pit restoration

Disused gravel pits are often managed for amenity purposes or as bird reserves. This management often involves the maintenance of open water bodies. In the absence of frequent flooding, the coarse sediments on the banks of these water bodies would quickly become clogged up with silt and overgrown with vegetation making them unsuitable for main channel beetles without regular mechanical disturbance. This would be costly and difficult to sustain. However, there is potential in reserving small pools for a minimum-intervention style of management which would lead to the establishment of fen or carr.

7.5.5 River restoration

The variation in species composition associated with different types of disturbance has implications for river restoration design. Habitat diversity, and therefore species diversity, can be maximised by building in a variety of flow regimes both in the main channel and in associated floodplain wetlands.

8 Summary

(1) A conceptual model for river floodplains was developed to postulate how fluvial and successional processes produce a variety of geomorphic and vegetational structures which serve as semi-aquatic habitats for terrestrial beetle assemblages exhibiting appropriate species traits. Disturbance by flooding was regarded as an important process which interacts with vegetational succession to produce a dynamic equilibrium. It was argued that this model could be used to predict the effects of land use changes and river management operations.

(2) 281 species from five target ground-living families were recorded from 69 sites in the floodplain of the lower Soar, a lowland river in an agricultural landscape in Leicestershire. 33 species were of national conservation significance, indicating that terrestrial beetles with semi-aquatic habitats form a major component of biodiversity within the riverine ecosystem.

(3) Two methods of sampling ground-living beetles in semi-aquatic habitat structures were evaluated using multivariate analysis and non-parametric paired comparisons. Differences in species composition between timed hand-collected samples and pitfall trap samples were smaller than those produced by environmental and seasonal factors. Ground beetles were more abundant and rove beetles less abundant in pitfall trap samples. Smaller species were less likely to be captured by pitfall traps, but no significant differences in sampling efficiency were found for nocturnal, fossorial and cursorial species. Pitfall traps were found to be vulnerable to flooding during spates and interference by humans and grazing stock and failed to collect a representative sample from a floating mat of *Glyceria maxima* or from any site during September. Timed hand collected samples were used for all investigations of variations in species assemblage parameters.

(4) DCA was found to give significantly consistent rankings of sites between April and June in each of two years, despite heavy flooding of sites in June of one of those years. Significantly consistent ranking of sites between years was only achieved for floodplain sites away from the main channel.

(5) DCA was used to examine within-site variations in species composition at the microhabitat scale. Correlation of DCA scores with the two most important environmental

variables was found to be slightly better at the *ecohabitat* scale (c 50m long sampling sites) than at the microhabitat scale as might be expected from a consideration of an organism's requirement for several microhabitats during its whole life cycle.

(6) Correlation of DCA ordination scores with environmental variables from 30 sites showed the important influence on species composition of several physical resources which could be related to the more fundamental fluvial process of disturbance by flooding. The severity of disturbance was represented by an index derived from substrate particle size. The frequency of disturbance was represented by an index derived from hydrological continuity with the main channel. An additional index of grazing pressure was also calculated and all three indices were shown to have similar effects on species composition using CCA. Brachypterous species were found to be rare at all study sites. Wing-dimorphic species were found to favour less disturbed sites away from the main channel, but no comprehensive relationship could be derived between disturbance and dispersive ability.

(7) Frequency of flooding and grazing pressure also influenced species composition according to a CCA ordination of samples from 27 floodplain sites, but were found to be less important than an index related to water level stability which varied in a non-linear fashion with vegetational succession.

(8) In a sample set of 30 main channel sites which included engineered sites, CCA found that bank regrading had a major effect on species composition which lasted for less than five years. The long term effects of bank regrading were less important and were possibly connected with the steeper profile of artificial banks. Impoundment for navigation also had a less important effect which could be explained by its influence on the disturbance regime.

(9) In order to evaluate the suitability of various species assemblage parameters for comparing sites, their robustness against seasonal and yearly factors was tested using Kendall's coefficient of concordance. Seasonal variations in site rankings of species diversity indices indicated a lack of robustness. Significant rankings of sites between years was achieved for species richness, but consistent variations of each yearly set indicated potential problems for comparison of sites sampled in different years. Rank correlation of CCA axis scores and species assemblage parameters was found to be an effective method of detecting relationships. Species diversity indices proved to be exclusively sensitive to disturbance by flooding and

grazing among the environmental variables investigated. These results could not be fitted to predictions of the intermediate disturbance hypothesis, because the frequency of these disturbances does not match the concept of disturbance used in the hypothesis. The recorded species richness and evenness of sites were found to be closely related, probably as a result of using timed hand collecting as the sampling method.

(10) A rarity index based on local species rarity was found to be robust for floodplain sites away from the main channel and insensitive to most environmental variables. It, therefore, has potential in conservation for evaluating site quality. Undisturbed floodplain wetlands with fluctuating water levels were frequently found to have high rarity indices, despite their lack of recognition for conservation interest in other taxonomic groups.

(11) For each sample, land use indices were calculated from the average of the proportion of local records of each species which were associated with wetlands, grasslands and highly disturbed post-industrial sites. They were not robust against seasonal and yearly factors, but were sensitive to a number of environmental variables. They were used to interpret variations in rarity indices and species composition, but they could be adapted as a measure of typicalness for conservation purposes.

(12) The effects of impoundment could be explained by the conceptual model in terms of modification of the severity of flooding disturbance. The effects of grazing pressure could be explained in terms of a disturbance which mimics disturbance by flooding. The short term effects of bank regrading could not be explained by the model without distinguishing between two types of disturbance based on differences in severity, predictability and frequency compared to the generational timespan of beetles. Further work on a larger river than the Soar is required to study a natural analogue of this type of disturbance.

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Species	Site numbers																	
	1992			1994														
				April			May			June			July			September		
	4	5c	8w	4	13	18	4	13	18	4	13	18	4	13	18	4	13	18
Carabidae																		
Agonum albipes	46		8	44	33	5	27	14	9	6	25	13	12		2			
A. assimile						12			8			5			3			
A. dorsale								1		2			1					
A. fuliginosum		2	12			1			1		4	2		5	6			
A. livens			171															
A. micans	3		15	2	2	1	1	15	5		10	51		2	18			
A. moestum	1	1									1	1			2			
A. muelleri								1										
A. obscurum								1						1	1			
A. thoreyi		10										1						
Amara communis	1																	
A. familiaris		3	5															
A. similata												1						
Asaphidion stierlieni				1					1									
Badister bipustulatus	2																	
Bembidion aeneum	1				1								1					
B. articulatum	11																	
B. biguttatum	2		90		2			1			8	4		4	13			
B. clarki			187															
B. dentellum	15		4		3	1	4	3	1		8	15	6	3	13	1	2	
B. genei	2																	
B. gilvipes	4		15		1	2	3	5	1		1	3	3	8	5			
B. guttula	3		3	2			3			2		1	10	7	15			
B. lunulatum					2			1					2					
B. obtusum			28	7			18			1								

Appendix 1 - Abundances of species recorded in pitfall trap samples

Species	Site numbers																	
	1992			1994														
				April			May			June			July			September		
	4	5c	8w	4	13	18	4	13	18	4	13	18	4	13	18	4	13	18
B. properans	1																	
B. quadrimaculatum								1										
B. tetracolum	16		3	18	9		6	9			5	3	1		1			
Carabus granulatus					15	11		2	1		2	7		1				
Chlaenius nigricornis						2			1			1						
Clivina collaris					1			2				1	1	1	1			
C. fossor			1		1	1			2			1						
Elaphrus cupreus		1	2	1			1		3		1	3	1		4			
E. riparius	13				3		4	4		2	2	1	15		1			
Harpalus latus				1														
H. rufipes												1						
Loricera pilicornis	1	2	12	2	6	5	1	8	7	1	6	11	41	4	76			
Nebria brevicollis	4		2					1										
Notiophilus biguttatus	1		4															
Patrobus atrorufus				1									2			2	7	
Pterostichus cupreus	1					1												
P. macer			1															
P. melanarius					1								2					
P. minor	1		14						1			1			4			
P. nigrita	11	6	160	1	2	3	1	1	3			7	1		10			
P. strenuus			11		2			3	2		1	2	1					
P. vernalis	1				3	2		5	5		3	8		3	1			
P. versicolor	2																	
Stenolophus mixtus	9																	
Stomis pumicatus	1		2															
Trechus discus													1	2		1		

Appendix 1 - Abundances of species recorded in pitfall trap samples

Species	Site numbers																	
	1992			1994														
				April			May			June			July			September		
	4	5c	8w	4	13	18	4	13	18	4	13	18	4	13	18	4	13	18
T. obtusus			1															
Staphylinidae																		
Aleochara bipustulata			1															
Aloconota gregaria	1		4		1				1			2			1			
Amischa analis	1	1				1												
A. cavifrons				1			1			6			7					
A. decipiens			1															
Anotylus insecatus	2			1														
A. rugosus	1		3	3	5			3	5	2		2	37	31	27			
A. sculpturatus	1	2	23	1									2					
A. tetracarinatus			5															
Atheta crassicornis														1	1			
A. elongatula	2				2			2		1	2		34	43	39		1	
A. fungi agg.	2	1	6			1					1	7		9	57	2		2
A. graminicola		7	26		3	7			2		6	4	1	11	53	2	15	4
A. hygrotopora					1													
A. laticollis											4		2	16	29			1
A. luteipes	3		1										2		1			
A. malleus	2																	
A. obfuscata								1										
A. vilis			1															
Callicerus obscurus	2		7															
C. rigidicornis	3		58	1														
Calodera aethiops			3															
C. riparia			1															
Carpelimus bilineatus											1							

Appendix 1 - Abundances of species recorded in pitfall trap samples

Species	Site numbers																	
	1992			1994														
				April			May			June			July			September		
	4	5c	8w	4	13	18	4	13	18	4	13	18	4	13	18	4	13	18
C. elongatulus			1															
C. gracilis	1			1							1							
C. impressus			1												4			
C. rivularis	3		1				1			3			11	1	24			
C. subtilicornis	3			2	32	1	3	20	2	7	5	6	53	21	22		2	
C. subtilis				1	1													
Chiloporata longitarsis	8		1			1	12	1				1		1				
Deleaster dichrous												1						
Deubelia picina		6																
Dinaraea angustula	2		4				2			2			1					
Gabrius pennatus	3				1													
Geostiba circellaris	2		3		1		4			124		1	36	1				
Gnypeta carbonaria	1																	
Gyrophaena angustata												2						
Hygronoma dimidiata		3										1						
Ilyobates propinquus			1															
Lathrobium brunnipes			6				1	3										
L. fulvipenne	10		1	7			3			4			4	1				
L. geminum	1				2		2				2		1					
L. pallidum													1					
L. quadratum															1			
Lesteva longoelytrata	1		2				1		1									
L. pubescens			2															
Liogluta nitidula			128															
Micropeplus porcatus															1			
Myllaena dubia		2																

Appendix 1 - Abundances of species recorded in pitfall trap samples

Species	Site numbers																	
	1992			1994														
				April			May			June			July			September		
	4	5c	8w	4	13	18	4	13	18	4	13	18	4	13	18	4	13	18
Neobisnius villosulus	1				1								1					
Omalium caesum			21															
Othius punctulatus			1															
Oxypoda brachyptera	1										1			1	2			
O. elongatula					1													
O. exoleta															1			
O. lentula			2															
O. opaca			1															
O. rivulare		2	10															
O. umbrata			3												1			
Pachnida nigella		1																
Philonthus cognatus		1	1															
P. laminatus	1		7						1			1			2			
P. quisquiliarius												2						
P. sordidus			1															
P. varians											1							
P. varius			1												1			
Platystethus cornutus	6																	
Proteinus macropterus													17	19	5	3		1
P. ovalis			1															
Quedius curtipennis			3					1										
Q. maurorufus		1																
Q. scintillans			2															
Sepedophilus marshami	1																	
Staphylinus melanarius			2															
Stenus bimaculatus		1	4						1						2			

Appendix 1 - Abundances of species recorded in pitfall trap samples

Species	Site numbers																	
	1992			1994														
				April			May			June			July			September		
	4	5c	8w	4	13	18	4	13	18	4	13	18	4	13	18	4	13	18
S. boops	8		1	2	1		3	2	2		6	7	9	3	16			
S. formicetorum												2						
S. juno	1	4	5			2		1	3	1		1	1	1	1			
S. olens			4															
S. pusillus													1					
S. tarsalis					1	5					1							
Tachinus corticinus			4															
T. signatus	1	3	81						2	1	1	2	63	10	32			
Tachyporus dispar	1																	
T. laticollis			1															
T. hypnorum	4		6				1											
T. nitidulus			2															
T. obtusus	3							1			1			9	4			
T. pallidus	4	1	2															
Tachyusa atra	1														2			
Xantholinus linearis	5		8	1			1											
X. longiventris	6		23	1			3			1	1							
Pselaphidae																		
Rybaxis longicornis											1							
Tychus niger					1													
Heteroceridae																		
Heterocerus fenestratus	4																	
H. marginatus	2																	
Elateridae																		
Adrastus pallens													1					
Hypnoides riparius				8									1					
Selatosomus incanus															1			

Appendix 1 - Abundances of species recorded in pitfall trap samples

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Carabidae																														
Agonum albipes	2	3	3	2				1	1	5		4	11	13	1		6	6	3	4	1	3	4	7	5	5	10	5	1	
A. assimile																			2											
A. dorsale		1												1																
A. fuliginosum		2			4		1	1					1	2	1	1		1	1	2	1				1		1			
A. marginatum						1																	1				2		1	1
A. micans				3	1							2	13	2		3	4		1	8	6				3	4	5			
A. moestum					1																				1					
A. obscurum																											2			
A. thoreyi	2				25																									
A. viduum		6										1																		
Amara aenea					1																									
A. familiaris													1		1	1														
A. plebeja														1																
A. similata				1									1																	
Asaphidion curtum												1					1											2		
A. stierlieni																					1									
Bembidion aeneum	6		16			40	17		7	5	38	8	2	1	18	10	1	21	2		1	4	15	5	5	10	9		23	11
B. biguttatum	2	1		4			13	12	2		1	12	14	8	18	19	39	6	13	26	19	7	5	3	19	11	5	2	11	4
B. bruxellense																								1						
B. clarki							9	56																	1					
B. dentellum			1	3				2	1			8	3	1	1		1		3	3	2		1	2		4	1		1	
B. gilvipes	1			1		1	12	1	1			4	5	6	1	6	1	6	16	5	2	4	2		3		2	1	3	1
B. guttula	1		3	1			7	2	5	3		2	1	4	5	8	4	4	10	1	7	1	1	3	1		2	4	4	
B. harpaloides																2				4				1						
B. lampros				1											1															
B. lunulatum	1		3			7	2	1	7	3	18	5		1			1	1	1				10	4		1			5	2
B. obtusum				2			2	1							2															

Appendix 2A - Abundances of species recorded in samples collected in March and April, 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
B. properans	1	1										1		3		1									1		4			
B. punctulatum											5																			
B. quadrimaculatum				1				4						1						1										
B. tetracolum		1	15	1		1			6	15		9	10	6	10		1	2			1			7		2	4	13		
Clivina collaris									1		2		3															2		
C. fossor						2		1																	1					
Demetrias atricapillus																6		1									1			
Dromius linearis								2																						
Elaphrus cupreus		1											2												3					
E. riparius																			1				1							
Loricera pilicornis				1								1	1				1				1					1				
Nebria brevicollis		1																												
Notiophilus biguttatus																					3					1		1		
Patrobus atrorufus														1																
Pterostichus cupreus																				1							3	1		
P. melanarius																											1			
P. minor							1	5																						
P. nigrita	1						1	2	1			1								1			1		1			1		
P. strenuus		1			4	3	8	2	1			1	2	1	3	8	2	9	1	10	1						9	2		2
P. vernalis												1	2	3		2		2	1	1	3				2	1	2			
P. versicolor						1																								
Trechus quadristriatus							1					1																		
Staphylinidae																														
Aloconota gregaria	1		1		1		1		1		7	4										1	2	1	1					1
Amischa analis		4			1									1		1		3	1	1										2
A. decipiens					1																									
A. forcipata																									1					
Anotylus rugosus				1	2		1				1	1	1					3	2	4	1	1								

Appendix 2A - Abundances of species recorded in samples collected in March and April, 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
A. tetracarinatus																			1											
Atheta celata																						1								
A. elongatula											2	5			1					1		2			1					1
A. fungi					4		4				1	1																		
A. graminicola	11	1		1	9	2		1	3			2	10	2	1			4	2	4	4	1			15	1	2	2	1	7
A. hygrobia								1																						
A. luteipes		1																												
A. malleus	1		1								1	4	1						3				1							
A. volans		2										3																		
Brachyusa concolor			1																											1
Calodera uliginosa							6																							
Carpelimus bilineatus												2	2				1										3	8		
C. corticinus		1			1													1												
C. elongatulus																1			1		2									
C. impressus	2															2			9		1									
C. obesus													1																	
C. rivularis	10		2	1							1	37	1		1			2	1		1						5			3
C. subtilicornis												20	6	2									4				6	19		
Deinopsis erosa					1												3													
Deubelia picina					14																									
Gabrius bishopi																			1											
Geostiba circellaris							1																							
Gnypeta carbonaria			1								1	1	1									1	5							2
G. rubrior																							1							
Hygronoma dimidiata																		2												
Lathrobium brunnipes								3					1	1					4		1									
L. elongatum																1														
L. fulvipenne				2		2	8		1			5		1											2					

Appendix 2A - Abundances of species recorded in samples collected in March and April, 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
L. longulum																		1												
Lesteva heeri		1													1	3						2								
L. longoelytrata														1									1					1	4	2
Myllaena dubia					2																									
M. elongata					1																									
Neobisnius villosulus													2																	
Oxypoda brachyptera										1																				
O. elongatula		1			2															1										
O. exoleta	1										8																			
O. lentula							2	1																						
Pachnida nigella					3																									
Philonthus micantoides						1							1																	
P. quisquiliarius						1																								
P. varius												1																		
Platystethus cornutus	1										3	1																		
Proteinus ovalis				1	1																									
Quedius maurorufus		1			3																									
Rugilus orbiculatus				1																										
R. rufipes																											1			
Stenus bimaculatus														1						1										
S. boops		2		1	1				1			6	7						2	1		3	1		1			2	1	
S. cicindeloides		1																												
S. juno	4			3	6	2						2	1	1				3	1	1		2			2		1			
S. nitidiusculus		2																												
S. pubescens														1																
S. pusillus																				1							1			
S. solutus					1																									
S. tarsalis														7								2								

Appendix 2A - Abundances of species recorded in samples collected in March and April, 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Tachinus signatus								1																			1			
Tachyporus dispar		2							1	1		1		2											1					1
T. hypnorum						1		1		1	3			2											3	1	3	2		
T. nitidulus		2																							1				1	
T. obtusus																	1										1			
T. pallidus					2																						1			
T. pusillus																3			1		1			1						
Tachyusa atra				1		2							1																	1
Xantholinus longiventris		2			2	1	1				1										1						2			

Appendix 2A - Abundances of species recorded in samples collected in March and April, 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Carabidae																														
Acupalpus consputus																												1		
Agonum albipes	1	2	1	3				2	3	10		4	10	13	2	4	6	2	6	1	9		1	12	2	3	4	4	12	1
A. assimile																					2									
A. dorsale																											1			
A. fuliginosum					21			3					1	1	2	11	1	1	1		3						4		1	
A. livens								2												1										
A. marginatum	1								1						1		1	1					3				1			
A. micans				1	9			5	4	1		8	13	4	5	16	4	10	3	2	14					3	3			
A. moestum																									2					
A. obscurum														1				1			1						4	1		
A. thoreyi					18																									
A. viduum		2															1			1										
Amara aenea																							1							
A. communis																		2												
A. familiaris							2								2	10														
A. plebeja					1													1										2		
A. similata					3		2																							
Asaphidion curtum																		1			1									
Badister bipustulatus					1																									
Bembidion aeneum	1	1	22	1		10	2		10	3	36	8	2		10		1	18					28	6	3	2	4		22	14
B. articulatum	1									1																				
B. biguttatum	1		1		3		11	16	2	3	2	10	8	7	15	27	11	10	4	8	15	8	7	3	15	7	15	9	3	1
B. clarki							5	41								1					1								1	
B. dentellum			1	3				4				11	5	1	8	4	13	15	9	10	13		1	1	1	2	6	3		1
B. genei																											1			
B. gilvipes			1	4			4	1	3			3		6	15	22	2	9	1	1	1	4		2	6		5	2	1	
B. guttula		1		10			1		6	1	1	2	2	2	5	1					1		3	1	1		7	6	1	1

Appendix 2B - Abundances of species recorded in samples collected in May 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
B. harpaloides														1		2														
B. lampros			1													6											1			
B. lunulatum		1	5	2		8			10	9	7	5			1			2					17	4		3			9	5
B. obtusum			1	3			1	1				1									1									
B. properans	1									1																	3			
B. punctulatum											5																			
B. quadrimaculatum	1				1										1															
B. tetracolum			2	3					4	21		4	3	2	8			2			1			2		4	2	14		
Carabus granulatus												1	1																	
Clivina collaris				1					3		1				1		2			1								1		
C. fossor						1	11		1	1		2				3						4	1							
Demetrias atricapillus					1											1											1			
Dromius linearis					1											1												1		
D. melanocephalus		1										1		1				1												
Dyschirius aeneus		1																												
D. luedersi				1																			1							
Elaphrus cupreus		7						2						1			1				2					1				
E. riparius			1	4								1						1					2							
Harpalus rufipes										1								2												
Loricera pilicornis				1									1																	
Microlestes maurus			1																											
Nebria brevicollis	15																													
Pterostichus cupreus														3		1										1				
P. minor								15						1		2			2											
P. nigrita		1				1	4	3				1	1	1	3	3	7		1		1		1			2		1		
P. strenuus		1			3	1	1	1	2			1	1		11	6	1	4		1		3			1	2	8	1		
P. vernalis					1									1	5		3	6			2		2		2		3			
P. versicolor																9														

Appendix 2B - Abundances of species recorded in samples collected in May 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Stenolophus mixtus																		1												
Stomis pumicatus				1												2					2									
Trechus quadristriatus	1									1																1	1			
Trichocellus placidus																3														
Staphylinidae																														
Aleochara lanuginosa																1														
Aloconota gregaria	2	1						2			4	2				1					1									
Aloconota insecta											1																			
Amischa analis		1			1	1	5								1	5				2		2			3					
A. cavifrons				1			1																							
A. decipiens		1																												
A. forcipata		2																												
A. soror		4																												
Anotylus rugosus			1		1						1					2		2								1		1		
A. tetracarinatus																				1										
Atheta elongatula				1				1		1	1			3				2				2			1					
A. fungi	1	2			3	1		1				2	2	3				1				2			1					
A. graminicola	27	1		2	11		2	1	4	4		4	1	6	1	2	1	7	1	7	5	1			10	1	1	1	4	11
A. hygrobia								1																						
A. luridipennis													1																	
A. malleus	1			3				1		2				1			1				1				1					
A. obfuscata				1																										
A. volans											1		1												1					
Brachyusa concolor																								1						
Callicerus rigidicornis				1																										
Calodera aethiops								3																						
C. uliginosa							3	2																						
Carpelimus bilineatus												2	1				4		1		4		1							

Appendix 2B - Abundances of species recorded in samples collected in May 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
C. corticinus		2			6			2					1				1	3												
C. impressus								19				6				3	2		18	37	41									
C. obesus				1																										
C. rivularis	6	4		33				6					1	3	3		4	7	7	2	5					1	3	1		4
C. similis					2												1				1							9		
C. subtilicornis				13					2	1		20	8		2			6	2	3	3		1			8	3	19		
Deinopsis erosa																	1											1		
Deubelia picina					10																									
Dochmonota clancula								1																						
Gabrius bishopi									1							1	1	2												
G. pennatus													1								2				2					
G. trossulus								1																						
Geostiba circellaris																						1								
Gnypeta carbonaria												1																		
G. ripicola													1	3					2											
G. rubrior			2	11								1																		5
G. velata												1																		
Hygronoma dimidiata		1			1										1		1													
Lathrobium brunnipes							1	4				1	1		1		2		1	5	1									
L. fulvipenne				1		6	16	3		1		6				2				2										
L. geminum												1					2													
L. impressum																1														
L. longulum		1																												
Lesteva heeri																	8													
L. longoelytrata	9	1	3	6				1	2	5	3	8	12	8			2	4	2	2	2		4	2	1			6	8	7
Myllaena dubia					7																									
Neobisnius villosulus													2				1													
Omalium rivulare													1		1	1														

Appendix 2B - Abundances of species recorded in samples collected in May 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Oxypoda brachyptera									1																					
O. elongatula		1			3	1																								
O. exoleta											1																			
O. lentula							7	35														1								
O. umbrata																					1									
Pachnida nigella					16																									
Philonthus cognatus																			1											
P. laminatus																		1								1				
P. micantoides						1																								
P. varius						1																								
Platystethus cornutus	1	1		4									1												1					
P. nitens	1			1																										
P. nodifrons								1									2													
Quedius maurorufus		1			1																									
Rugilus orbiculatus						1																								
Sepedophilus marshami					1					1																		1		
Stenus bimaculatus				1	1			1								1	1		1											
S. boops		7	1	3					2			3	6		3		2	11	3	1	2		1		2					
S. clavicornis																				1										
S. juno	5			5	6		1	3					5	4	1	2	4	1		3	3	2			1		2		1	
S. melanopus	2																													1
S. nitidiusculus		1																												
S. pallitarsis																						1								
S. pusillus		1																												
S. solutus					2																									
S. tarsalis									1								2	1		2							1			
Tachinus signatus								1													1	1								
Tachyporus chrysomelinus																									1					

Appendix 2B - Abundances of species recorded in samples collected in May 1991

Species	Site numbers																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
T. dispar							1							2		2	1								2					
T. hypnorum		2														3					1						2			
T. nitidulus		2																3			1		1							
T. obtusus				1	1									1																
T. pallidus				1	1					1				3	1	4	1	1							2		4			
T. pusillus															1	1														
T. solutus		2											1	5		1														
Tachyusa atra													1	1																
Xantholinus linearis								3																						1
X. longiventris				2			3		1													1				1	1		1	
Heteroceridae																														
Heterocerus fenestratus				1														1												
H. marginatus				1					1																					
Elateridae																														
Agriotes linearis						1																								
A. obscurus																						1								

Appendix 2B - Abundances of species recorded in samples collected in May 1991

Species	Site numbers																											
	1	2	3	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Carabidae																												
Agonum albipes	4	1	5				1	2		1	3	26		8	3	2	1	3	7		3	7	2	6	3	8	4	1
A. assimile												1				1			1					1				
A. dorsale			1					1																1	1	7		
A. fuliginosum				1		1						2	3	2			2										1	
A. livens							1																					
A. marginatum	1															1					2						1	3
A. micans				1			4			1	7	1	2	5		8	3	2	9				6	4				
A. obscurum												3							1							4		
A. thoreyi				4																								
A. viduum		1																										
Amara aenea																										2		
A. familiaris				1																								
A. plebeja					1	1																						
A. similata						1			1																			
Asaphidion curtum												1				1												
A. stierlieni					1																							
Bembidion aeneum			2		13				3	2		2									8	1	1				5	10
B. articulatum	2								1																			
B. biguttatum	1					2	8		1	1	6	3	1	26	1	1	1	2	5	1	1	1	24	3	3	1	4	2
B. clarki						4	20																					
B. dentellum			1				4				4	1	3	4	2	3	2	6	15		3		3					
B. fumigatum													1															
B. gilvipes						3						1	1		1					1		1	1					
B. guttula						2		1				1	1	1						1			1			1		
B. lampros			1								2	2																
B. lunulatum	1				3								1								8						2	8
B. obtusum						5	1	1																				

Appendix 2C - Abundances of species recorded in samples collected in June, 1991

Species	Site numbers																											
	1	2	3	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
B. properans												1																
B. punctulatum									5																			
B. tetracolum								3			7	3										2		1		7		
Carabus granulatus											1						1											
Chlaenius nigricornis																					1							
C. fossor					1	8																1		1				
Demetrias atricapillus				2																								
Dromius linearis						1																						
D. luedersi											1																	
Elaphrus cupreus		1												1		2			1				1					
E. riparius	3		1							1	3					1												1
Nebria brevicollis	3													1														
Notiophilus biguttatus								1		2	2																	
Patrobus atrorufus	1																		4			7		3				
Pterostichus cupreus																										1		
P. melanarius																	1											
P. minor							10																					
P. nigrita		2				2					1	2	2		1			2	2				1	2				1
P. strenuus				1		3		1				5	2						1	1		1			3	1		2
P. vernalis				1	1							3		1		1										3		
P. versicolor																						2		8				
Trechus quadristriatus																					1	6						
T. secalis				1																3						1		
Trichocellus placidus						1																						
Staphylinidae																												
Aloconota gregaria	1		1																			2						
Amischa analis						1								1														
A. decipiens						1																						

Appendix 2C - Abundances of species recorded in samples collected in June, 1991

Species	Site numbers																											
	1	2	3	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Anotylus rugosus											1																	
A. sculpturatus		1					2																					
Atheta elongatula								2		1			1			1								1				
A. fungi				1		2	1			1		2		3														
A. graminicola				6	1		2				4	13	5	8	2	4		1	2	1			13					
A. hygrobia																	1											
A. luteipes		2																										
A. malleus								2								2												
A. nigra																									1			
A. volans											1		1			1												
Carpelimus bilineatus										1	2								1									
C. corticinus		1		1																								
C. impressus							72							28					9									
C. rivularis	4	3	1				1			2	15					4					1		8				1	
C. similis									1																			
C. subtilicornis											6					1			1									
Chiloporata longitarsis			1				5					5		8								3	2					
Deinopsis erosa													1		3													
Deubelia picina				6																								
Dochmonota clancula							1																					
G. pennatus														1		1												
Gnypeta carbonaria											1										1	2						
G. ripicola										2							3											
G. rubrior																					6						1	
Hygronoma dimidiata				1									2															
Lathrobium brunnipes				5			6							2				1	3				1					
L. elongatum							1																					
L. fulvipenne			1			1				1														1				

Appendix 2C - Abundances of species recorded in samples collected in June, 1991

Species	Site numbers																												
	1	2	3	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
L. geminum																						1						
L. quadratum																2												
Lesteva heeri				4							1			1						1			1					
L. longoelytrata							1				1			2			1						1					
Myllaena dubia				2																								
M. intermedia													1															
Omalium oxyacanthae							1																					
Oxypoda brachyptera						1																						
O. lentula						3	14																					
Pachnida nigella				19																								
Philonthus fimetarius																			1									
P. laminatus									1																			
P. marginatus																								1				
P. quisquiliarius	1						1															1						1
Platystethus cornutus			2								6					2					5							1
P. nitens																			1									
P. nodifrons														1														
Quedius maurorufus		1		1																				1				
Q. molochinus				1																1								
Q. schatzmayri		1																										
Rugilus orbiculatus											1																	
Staphylinus mealanarius														1														
Stenus argus																			1	1								
S. bimaculatus				1										1														
S. boops								3		1	1		2			3			8								1	
S. cicindeloides																									1			
S. fulvicornis				1																								
S. juno	1	1		5			1				3	1			1			1	1									

Appendix 2C - Abundances of species recorded in samples collected in June, 1991

Species	Site numbers																											
	1	2	3	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
S. melanopus	5																1											
S. nanus											1																	
S. nitidiusculus		2																										
S. picipes		1																										
S. pusillus		1		1																								
S. solutus				1																								
S. tarsalis											4	1												1				
Tachinus signatus							1																					
Tachyporus chrysomelinus					1	1				1												1		1			1	
T. dispar		1				2	6	4				1		1														
T. hypnorum			1		1	1	1	5						1	1							1				5		
T. nitidulus							1							1														
T. obtusus	1						4				1	2			1		1		1			1			1			1
T. pallidus							2					1	1	3						2								
T. solutus											2	5										1						
Tachyusa atra															1													
T. coarctatus																					1							
Xantholinus linearis		1					5																					
X. longiventris					1		1					2			1					1				1				
Heteroceridae																												
Heterocerus fenestratus	3															1												
H. marginatus															1													
Elateridae																												
Agriotes obscurus																						1						
Selatosomus nigricornis						1																						

Appendix 2C - Abundances of species recorded in samples collected in June, 1991

Species	Site numbers																												
	1	2	3	4	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Carabidae																													
Agonum albipes	6	3	4	5				1	5		3	4	10	6		2		1	1	1		1	3	1	5	3	5	5	
A. assimile																											1		
A. dorsale																										1			
A. fuliginosum					3						1		2		3	1										2			
A. marginatum	3									1																			1
A. micans									3		4			6	1	4	7	2	1	1				2	1	2			
A. moestum																								1					
A. obscurum																												3	
A. thoreyi					1																								
A. viduum		1																											
Amara plebeja						1	1																						
Asaphidion curtum																											1		
Bembidion aeneum			10			16				3			1									10	4					4	3
B. articulatum											1																		
B. biguttatum				6		1					3		4	1	1	1	4	4		3	1	4	1	8	1	6	2	4	1
B. clarki								6																					
B. dentellum			2	1		2					5		1	3	2		4	4	5	7		1		4					1
B. gilvipes								1													2					1			
B. guttula					7	1			2							2						1		1		2	1		5
B. lampros			2																										
B. lunulatum			4	1	2	1				1	1	1						1				16	4					8	11
B. obliquum				1																									
B. properans						1																							
B. punctulatum										14																			
B. quadrimaculatum		1																											
B. tetracolum	2		1					1	1	1	1											1					3		
Clivina fossor						1	1														1								

Appendix 2D - Abundances of species recorded in samples collected in July 1991

Species	Site numbers																												
	1	2	3	4	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Elaphrus cupreus		1						1											1	1									1
E. riparius	3		3																			2							
Loricera pilicornis				1							1					1	1		1						1				
Notiophilus biguttatus						1																							
Pterostichus minor								2																					
P. nigrita				1	1									1		2	1			1									
P. strenuus		1				1							1	1					1		2		1			2	1		
P. vernalis							1										1										1		
Stenolophus mixtus																2	1												
Trechus micros				1																									
T. quadristriatus																								1					
T. secalis																					5								
Trichocellus placidus							1																						
Staphylinidae																													
Aloconota gregaria								1																	1				
A. sulcifrons																		1											
Amischa analis		1													1						1								
A. decipiens							1																						
Anotylus rugosus				1	4						1			2															
Atheta elongatula	2	6		14	10			9	22	4	10	10	1	10	7	3	12	7	9	9		1		3	3	3			
A. fungi				3	2	1	1	1	6		11	4		2	3	6	5	2	2	4	11	2			5	2	3	5	4
A. graminicola	4			1	5	1	2	4	5		11	7	2	4	2	3	3	1	4	1				5	6	2		2	2
A. gyllenhali																								1					
A. hygrobia																		1		1									
A. hygrotopora			1								1																		
A. indubia																									1				
A. luridipennis																		1											
A. luteipes																				2									

Appendix 2D - Abundances of species recorded in samples collected in July 1991

Species	Site numbers																												
	1	2	3	4	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
A. malleus				1		1					4				1	1		4	2	3				1					1
A. melanocera																	1												
A. volans			1	1					1		1						1												
Brachyusa concolor																							2						
Carpelimus bilineatus																			2										
C. corticinus								1									1												
C. impressus								6							19	1		1	8	10				3	3				
C. rivularis	3	6		11							7	2			3		3	8	4	6		6			2				1
C. subtilicornis									1		1	8						2	3			1			3	1	32		
Chiloporata longitarsis		1		2						1	2	2												1					
Deinopsis erosa																1													
Deubelia picina					9																								
Dochmonota clancula								1																					
Gnypeta carbonaria	1		4																				3						1
G. ripicola											1				7		3	25	2	1			2						
G. rubrior			1															1					9						4
G. velata											1																		
Lathrobium brunnipes							1	5							2	1			2	3									
L. elongatum																		2											
L. fulvipenne				2		2		1																					
L. quadratum									1	1																			
L. terminatum																	1												
Lesteva heeri																					1								
Myllaena dubia					22																								
M. elongata																											1		
Neobisnius villosulus				1							1																		
Oxypoda elongatula					2																								
O. exoleta												1																	

Appendix 2D - Abundances of species recorded in samples collected in July 1991

Species	Site numbers																												
	1	2	3	4	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
O. lentula							1	3																					
Pachnida nigella					4																								
Philonthus laminatus						1																							
P. quisquiliarius	1		1														2												
P. umbratilis																	1												
P. varius						1																							
Platystethus cornutus			1	1																									1
P. nodifrons															1														
Quedius maurorufus					2																								
Q. tristis			1																										
Rugilus orbiculatus						1																							
Sepedophilus marshami																											1		
Stenus bifoveolatus					4																								
S. bimaculatus				1									1			4	2	2			1				1				
S. boops	2	6		2					1	1		2	5	3		1	1		1	2			2						
S. canaliculatus	2																												
S. cicindeloides		1								1																			
S. juno	3			1	10			1	1		1		2	3	4	2	4		4	6	3					1			1
S. melanopus	4																												2
S. nitidiusculus		4																											
S. solutus														1															
S. tarsalis									1			2				1	2												
Tachinus signatus				1					1							1	2								1				
Tachyporus atriceps		1																											
T. chrysomelinus						1					1																	1	
T. dispar							1																						
T. hypnorum				1		2				1												2				1		2	
T. nitidulus																									1				

Appendix 2D - Abundances of species recorded in samples collected in July 1991

Species	Site numbers																												
	1	2	3	4	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
T. obtusus				5					10		1	3	1			2	1					1				3	7	1	
T. pallidus				3				1				1		2	2	1	1	1		1	1					6	3		
T. solutus									1			2	1									1					5		
Tachyusa atra											1			2	1		1					3	4	1					
Xantholinus longiventris	1																		1										
Heteroceridae																													
Heterocerus fenestratus										1	2																		
H. marginatus	2																												

Appendix 2D - Abundances of species recorded in samples collected in July 1991

Species	Site numbers																										
	1	2	3	4	5	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Carabidae																											
Agonum albipes		1	1	9		2		1		5	3	2	1	5	9						3	2	15	2		1	4
A. assimile											1				1												
A. fuliginosum					1	1											1		1								
A. livens						4											4	1									
A. micans	2						1	1	1			8		1	7								1				
A. obscurum																		1									
A. thoreyi	1				2																						
A. viduum		1																									
Asaphidion curtum																		1									
A. stierlieni					1																						
Bembidion aeneum			3	2				4		3		1															1
B. articulatum	1													1											1		
B. biguttatum			2			12	2	1	3	1	1	4	8		2	1	3	7	1				8	3	2		2
B. clarki						4																					
B. dentellum				1		4			2	1		1	4		3		5	9		1		3	1				1
B. gilvipes													1			1	1		1						1		
B. guttula	7	3	1	10	11		5	1	3	15	2	14	2	9	4	2	1			2		4	1	1	4		3
B. harpaloides																										1	
B. lunulatum		3	7	5		2	2	4	1	3		1	1	2	1							1	4	1		1	3
B. obtusum										1																	
B. punctulatum								1																			
B. tetracolum				1		1	2			3													3		3		
B. varium								1																			
Demetrias atricapillus	3																					2					
Dromius linearis									1																		
Elaphrus cupreus		3			3	3				2				1	1												1
E. riparius																				1							

Appendix 2E - Abundances of species recorded in samples collected between August and October, 1991

Species	Site numbers																										
	1	2	3	4	5	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Loricera pilicornis	1	1		1				1	4			1		4									1				
Nebria brevicollis																				1						1	1
Patrobus atrorufus													1	1													
Pterostichus nigrita		1	1			1		1				1		1													
P. strenuus			1	1						2		1							2								
P. vernalis										1						1			2								
Trechus discus								1																	1		
T. quadristriatus		1							1																		1
Staphylinidae																											
Amischa analis					1														1								
A. decipiens									1																		
Anotylus rugosus		1			5		1			1	1	1	1	1				3									
A. sculpturatus																		1	1								
Atheta elongatula		1	3	4			5	1	4		1			6				1				3	5	2			
A. fungi	5				2	1	4	1	7			3	15			1	1		1			1	2	2			
A. graminicola	9			24	17	1	39	2	11	19	13	10	2	5	11	2		1				10	18	18	9		9
A. gyllenhali						1																					
A. hygrobia																1											
A. hygrotopora			1					2			4										8	2					
A. laticollis	1			10	2									1	4							2		4	3		
A. malleus	1		2	1		1			1		1				1	1	1				1	3		1	2		1
A. melanocera						1																					
A. nigra													1											1			
A. parvulus																				1							
A. volans							2				1					1											
Brachyusa concolor																					3						
Carpelimus bilineatus	1												3	3	3												1
C. corticinus					1																						

Appendix 2E - Abundances of species recorded in samples collected between August and October, 1991

Species	Site numbers																										
	1	2	3	4	5	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
C. impressus						1							35			1						2					
C. rivularis	4		2	5		4	3		6		2	1	3	1	3	1					2	1	2		5		2
C. subtilicornis									1	1	1	1			1								5		9		
Chiloporata longitarsis																										1	
Deinopsis erosa														3													
Deubelia picina					7																						
Gabrius bishopi										2		6		2	2							1			1		1
G. pennatus															1			2									
G. trossulus						1																					
Gnypeta carbonaria	3													1							4						
G. ripicola	3		1			2					13	1	1			7					4						
G. rubrior	12		1												1						8						2
G. velata	9														1						1						
Hygronoma dimidiata					1							2		3													1
Lathrobium brunnipes						1							4	2		1	1										
L. geminum																1											
Lesteva heeri						1										7		1	1								
Megarthrus sinuaticollis					1																						
Mycetoporus						1																					
Myllaena dubia					21																						
Neobisnius villosulus													1														
Omalium caesum																			1	1							
O. excavatum													1														
Oxypoda elongatula		1			4																	1					
O. lentula						1																					
O. umbrata					1																	1					
Oxytelus laqueatus						1																					
Pachnida nigella					3																						

Appendix 2E - Abundances of species recorded in samples collected between August and October, 1991

Species	Site numbers																										
	1	2	3	4	5	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Philonthus fimetarius	2								1			2			1							3		1			
P. laminatus								1																			
P. marginatus																								1			
P. quisquiliarius	3				2		2								2												
P. umbratilis					2																			2			
Platystethus cornutus	1		1	1	1																						
P. nitens												1															
P. nodifrons												1															2
Quedius fuliginosus																			1								
Q. maurorufus					4																						
Q. nitipennis													1														
Sepedophilus marshami													1														
Stenus argus																			1								
S. bimaculatus						1			3				6														
S. boops		13	2		3	1	5	1	1	2		2	1	2	3	1		1				1		1	1		1
S. cicindeloides		1																									
S. juno	8			2	12	3	1	1	2		1	5	3	2	9	1			2			15		2			
S. melanopus	1																										
S. nitidiusculus		1																									
S. pubescens	11																										
S. solutus	1											1															
S. tarsalis							1		1		1			1	1		5		9			1	1	1			
Tachinus laticollis													1														
T. signatus				1	2		1			1										1							
Tachyporus chrysomelinus						1																					
T. dispar																			3						3	1	1
T. hypnorum					2			1								1		1	8					2	2		
T. nitidulus		1					1													1							

Appendix 2E - Abundances of species recorded in samples collected between August and October, 1991

Species	Site numbers																										
	1	2	3	4	5	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
T. obtusus	2			4	2	1	14	6	6	1	1	2	1	1		1						1	7	3	3		
T. pallidus					1			1	3		1	3	1					1	3				1	4	3		
T. pusillus					1																						
T. solutus														1											3		
Tachyusa atra			1								3	1										1			2		
Xantholinus longiventris													1									1	1			1	
Pselaphidae																											
Rybaxis longicornis					2																						
Heteroceridae																											
Heterocerus fenestratus	7																										
H. marginatus		1																			1						

Appendix 2E - Abundances of species recorded in samples collected between August and October, 1991

Species	Site numbers																													
	4	9	11	13	17	18	23	30	31	32	33	35	36	38	39	42	44	46	48	49	50	51	52	53	54	55	58	60	62	63
Carabidae																														
Acupalpus consputus																					1									
A. meridianus												1												1						
Agonum albipes	3	8	1	2		2	2	2	8		1	5	2	10	2	2	2	3	8	6	11	4		3	21	9	11	5	6	16
A. fuliginosum															2															
A. marginatum	1						2	1	1																3		1	1		
A. micans		1		9	1	5	2	2	1						7															
A. muelleri									1																					
A. obscurum								1																						
Amara similata							1																				2			
Badister bipustulatus															1															
Bembidion aeneum		1				1	3	2		3		2							3	1		2	14	4	1	1			5	1
B. articulatum		1				3				3			3					1					2	16		4	4	1		
B. assimile					1																	2								
B. biguttatum	4	3		9	4	9	3	1		1	1		1		12	1		1	3	2	1				2					
B. clarki						1																								
B. dentellum	13	5		2	7	5		3	11		2		1		10	1	1	8	1	2	3				3		1	2		
B. femoratum												1											1			1				
B. genei			8						1	5														3		1				
B. gilvipes		1		2	2	7					1		1	1	7									1	1			1	3	
B. guttula	2	2		1	1	3	1	2	1				3			3	1		3	1			3		1	1			4	
B. harpaloides																				1										
B. lampros												1			1	1			1		1							1		
B. lunulatum	1		1		1	2	1	13		1		2		1		7	1					1		3		1	9	1		2
B. obliquum						1																								
B. obtusum	2														1	4			3		1									
B. properans	1					1				6								1				1						2	2	
B. punctulatum			10									1		7														8		

Appendix 2F - Abundances of species recorded in samples collected in main-channel sites in 1992

Species	Site numbers																													
	4	9	11	13	17	18	23	30	31	32	33	35	36	38	39	42	44	46	48	49	50	51	52	53	54	55	58	60	62	63
B. quadrimaculatum																						1								
B. tetracolum	3	8		2			1		1	1	5	11	2	10		3	1		5		3	1	4	2	1	3	2	11	7	1
Clivina collaris	1			1	1					1				1	1															
C. fossor										1					1															
Demetrias atricapillus															1									1						
Dromius linearis															2				1	1										
Dyschirius aeneus						2			1	10							1					1					1			
D. luedersi						4				2							1										1			
Elaphrus cupreus							1				1				1										1					
E. riparius	1		8			1	1	1	2	8	1	4		3				1						1	2	4	4	12	5	3
Loricera pilicornis								1																						
Nebria brevicollis								2										3			1	5					2			
N. salina																							1							
Notiophilus biguttatus																							1				5			
Pterostichus cupreus																			1											
P. gracilis															1															
P. minor					1																									
P. nigrita					4	1			3	1	1		1		2			3	2	2	1				1					
P. strenuus		2				1	1	1						1	2						1									
P. vernalis				1	1	2									1	1		2												
Stenolophus mixtus					9					1					1		1			1							1			
Trechus quadristriatus																			1			2								
Staphylinidae																														
Aloconota gregaria			1	2														1					1			1				
A. planifrons																								1						
A. sulcifrons	1																													
Amischa cavifrons										1																				
Anotylus insecatus	1																													

Appendix 2F - Abundances of species recorded in samples collected in main-channel sites in 1992

Species	Site numbers																													
	4	9	11	13	17	18	23	30	31	32	33	35	36	38	39	42	44	46	48	49	50	51	52	53	54	55	58	60	62	63
A. rugosus	1	1				2				2			1											3					1	
A. sculpturatus					1																			1						
Atheta debilis																	1													
A. elongatula				2	2				1					1															1	
A. fungi agg.		1				2												1												
A. graminicola		12		1			2									2		5			1				1					
A. hygrotopora				1																										
A. luteipes					3	2			2	1			4																	
A. malleus	16	5		14		1	8	1	4	1			2		3			5			2				3		3			
A. volans								1										1		1					1					
Bledius gallicus						2																								
Carpelimus bilineatus	1			4		2	2		1	2	1		5		3			1	2	1	1								1	
C. corticinus					1	3																								
C. impressus					1																									
Ç. rivularis	15		6	32	1	21	6	5	6	19	2	1	12			1		5		2				3	2	1	4	6		
C. similis									3	4				1									1	2						
C. subtilicornis				40	1	3			1	2			3		1									4		1	2	4		
Chiloporata longitarsis			10		24	39		49		2	7	9	1			14					1	45	18				40			
Deinopsis erosa	1			1	7	1				1					3					2	2									
Dochmonota clancula				1																										
Drusilla canaliculata																1														
Gabrius bishopi						5																								
G. pennatus					2	6											1													
Geostiba circellaris																					1									
Gnypeta carbonaria	21	2		1			1	1		1				1		1		3							8		1			
G. ripicola				2																										
G. velata								1		3								2												
Hygronoma dimidiata					2										1															

Appendix 2F - Abundances of species recorded in samples collected in main-channel sites in 1992

Species	Site numbers																													
	4	9	11	13	17	18	23	30	31	32	33	35	36	38	39	42	44	46	48	49	50	51	52	53	54	55	58	60	62	63
Lathrobium brunnipes					8													1		3	1									
L. fulvipenne	4				1	1			5	9		2	1					1	1		2	4		1					1	
L. geminum				1	1										2															
L. pallidum			1																											
L. terminatum					1																									
Lesteva heeri		1			2										2					4	1									
L. longoelytrata	5	2	2	6			2		1	1		1		2			1	5		3		1	1	6	3				1	4
Myllaena elongata													2							2				3						
M. intermedia					2		2	1																						
Neobisnius villosulus	2			1										3											1					
Oxypoda brachyptera																			1											
O. exoleta										1																			1	
O. longipes																					1									
Oxytelus laqueatus								1																						
Philonthus quisquiliarius				2	7		1	1		4			8			1											2	3		
P. umbratilis					1																				1					
P. varians								1																						
Platystethus cornutus					3		3	2	1	3				11	1										1		9	2		
Rugilus rufipes													1			1														
Stenus bimaculatus					3	1														3										
S. boops	1	6		2	1	7			4	2				5	1	2		9		5				2	12	6	3		1	1
S. canaliculatus										2																				
S. cicindeloides								1																						
S. comma										2												2	1	1		4		1		
S. juno	1					5		7	1	2	1				4			1		5	2			1	6					
S. melanopus								5																						
S. pubescens				1																										
S. pusillus						1														1						1				

Appendix 2F - Abundances of species recorded in samples collected in main-channel sites in 1992

Species	4	9	11	13	17	18	23	30	31	32	33	35	36	38	39	42	44	46	48	49	50	51	52	53	54	55	58	60	62	63
S. tarsalis				1		2																			2					
Tachinus signatus					2				1											1					1					
Tachyporus chrysomelinus																								1						
T. dispar														1																
T. hypnorum							1					1						1	1				2	1		3	8	1		5
T. nitidulus												1																		
T. obtusus											1													1			5			
T. pallidus	1				1	1							1		1	1			1	4	2									
T. solutus												1																		
Tachyusa atra				1			10											2		1										
Thinodromus arcuatus																				2										
Xantholinus linearis	1											1	1							1										
X. longiventris	1			2		1					1	13	3		1	2		2	4	2	2	2	1			1				
Hetroceridae																														
Heterocerus fenestratus	4		1	2			1	4	1	3														1	1					
H. marginatus	1																							5		4	1			
Elateridae																														
Hypnoidus riparius													3		3															

Appendix 2F - Abundances of species recorded in samples collected in main-channel sites in 1992

Species	Site numbers															
	1c	1e	1w	5c	5w	8e	8w	40	43	45	47	57	66	67	95	96
Carabidae																
Agonum albipes		1	9		1	2		1	6	3	17		3			
A. fuliginosum			2		7	1		3	7						18	3
A. livens						2	2									
A. marginatum											3					4
A. micans			5				2	1	1		15	1		1	2	
A. obscurum													2			
A. thoreyi	1		2	7	16			5	2			2			5	1
Amara communis																1
Bembidion aeneum			1					1		1				9		3
B. articulatum		5														2
B. assimile								3	5						1	1
B. biguttatum			5	3	1	44	38	6	12		9			10		1
B. clarki						70	78						1		2	
B. dentellum	1		1			1	2		4		17		4			4
B. fumigatum													1			
B. gilvipes			1			4	2				1			4		
B. guttula			1			1					1			12		
B. lunulatum		3												1		4
B. obtusum						1	5				1					
B. tetracolum			1						1							
Clivina fossor														4		
Demetrias atricapillus		1						1								
Elaphrus cupreus		1	3			1			1	4		1				1
Elaphrus riparius		14									3					2
Loricera pilicornis										1						
Nebria brevicollis													1			
Notiophilus biguttatus					1		4									

Appendix 2G - Abundances of species recorded in samples collected in floodplain sites in 1992

Species	Site numbers															
	1c	1e	1w	5c	5w	8e	8w	40	43	45	47	57	66	67	95	96
Patrobus atrorufus									1							
P. gracilis								3	1						1	
P. minor						8	1		1			1	2	2		
P. nigrita			1			2	1	2		2	5					1
P. strenuus					1	2	1	4				9		4		
P. vernalis											1			2		1
Stenolophus mixtus										4						
Trichocellus placidus								7								
Staphylinidae																
Aleochara lanuginosa				1												
Aloconota gregaria							1									
Amischa analis				3	1											
A. decipiens					1											
Anotylus rugosus				2	3			2				2	1		2	1
A. sculpturatus													2			1
A. tetracarinatus					1											
Anthobium atrocephalum						2										
Atheta elongatula										1			1			
A. fungi agg.				4	2	2	2	3		1		1	1	1	1	
A. graminicola	18		2	13	21				1		1	20	5	1	10	3
A. gyllenhali			1													
A. hygrobia						9	5									
A. hygrotopora																1
A. laticollis					1											
A. luteipes									1						1	
A. malleus	1		6				2	1	2	3	1	1	5		4	
A. volans			1	1						1						
Carpelimus bilineatus					1			1		3		2				

Appendix 2G - Abundances of species recorded in samples collected in floodplain sites in 1992

Species	Site numbers															
	1c	1e	1w	5c	5w	8e	8w	40	43	45	47	57	66	67	95	96
C. corticinus				1	2			6				1				
C. elongatulus						2		5								
C. impressus			1			4	2		2				13	1	2	
C. rivularis	4		1			1		1	3	3		2	3		3	1
Chiloporata longitarsis													6			1
Deinopsis erosa									3							
Deubelia picina				4	9											
Dinaraea angustula														1		
Dochmonota clancula													4			
Gabrius pennatus									5	2		2	4		3	1
Geostiba circellaris						4		2								
Gnypeta carbonaria		1	1								5					
G. ripicola											1		1			
G. rubrior			1													
G. velata											1					
Habrocerus capillaricornis						1										
Hygronoma dimidiata	1		1	1				1	2			2			1	1
Lathrobium brunnipes						11	7	9	12				3		8	
L. fulvipenne		1	1						1				1			
L. geminum						1							3		1	
L. longulum						1					1					
L. quadratum											1					
L. terminatum															2	
Lesteva heeri								1	2			4				
L. longoelytrata	10		12							2	6					1
Liogluta nitidula			8													
Mycetoporus splendidus																1
Myllaena dubia				24	5											

Appendix 2G - Abundances of species recorded in samples collected in floodplain sites in 1992

Species	Site numbers															
	1c	1e	1w	5c	5w	8e	8w	40	43	45	47	57	66	67	95	96
M. infuscata				1	1											
M. intermedia								1								
Omalium rivulare			1		1											
Oxypoda elongatula				9	5		1									
O. exoleta						1										
O. lentula						6	13				1					
O. umbrata					4											
Oxytelus fulvipes						2										
Pachnida nigella				7	2											
Philonthus micans												1				
P. quisquiliarius										3						1
P. umbratilis									1	1						
Platystethus cornutus								4				1				
P. nitens								1								
Proteinus ovalis					1											
Quedius curtipennis								1								
Q. maurorufus				2	1											
Q. molochinus																1
Q. nitipennis														1		
Stenus bifoveolatus					5											
S. bimaculatus				1	2			1	4			2				1
S. boops	9	8	8					1	1	15	1		2		10	1
S. canaliculatus										1						
S. cicindeloides		1							1							
S. formicetorum		1														
S. juno	35	5	9	13	9	4	5	2	4	4	4	24	3	1	10	1
S. pallitarsis															1	1
S. pubescens									1							

Appendix 2G - Abundances of species recorded in samples collected in floodplain sites in 1992

Species	Site numbers															
	1c	1e	1w	5c	5w	8e	8w	40	43	45	47	57	66	67	95	96
S. pusillus										2						
S. solutus				1	3							1				
Tachinus signatus									2							
Tachyporus chrysomelinus					1	1										
T. dispar						3	1									
T. hypnorum							1									
T. nitidulus					1											
T. obtusus				1												
T. pallidus								1	2			1			6	
Xantholinus linearis							2									
X. longiventris										2	2					1
Pselaphidae																
Bryaxis bulbifer				1												
Rybaxis longicornis													1			
Heteroceridae																
Heterocerus fenestratus			1						1							
Elateridae																
Agriotes obscurus							1									

Appendix 2G - Abundances of species recorded in samples collected in floodplain sites in 1992

Species	Site numbers																																
	1993																			April 1994													
	1c	1e	1w	4	5c	5e	5w	8e	8w	9	11	13	16	17	18	23	30	72	73	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30
Carabidae																																	
Acupalpus consputus			1																														
A. meridianus										1																							
Agonum albipes		2	4	7						10	1	2	7	5	3	1	1	5	6		1	1	8				1	2	6	5	3	19	2
A. assimile															3				2												3		
A. dorsale					1					1																					1		
A. fuliginosum					3	5	1	1	1				2					4	1					2	4						1		
A. livens								2										2								5	2						
A. marginatum																2														1		3	1
A. micans	2		3			1	1	2		1	1	1	1		4			2		2		4						1	2	1	8		
A. moestum			1											1																			
A. obscurum													1																				
A. thoreyi	9	1	1		18	4	12						1							12		4		14	17								
Bembidion aeneum		4																			1								1			1	3
B. articulatum										1																							
B. assimile			3																														
B. biguttatum		3	7	4		1	1	9	13				14	1		1		11	12		2	5	1		1	6	17	1	4	11	5	6	
B. clarki			2					60	46									2			1	3				9	16						
B. dentellum		1	1			1			1	4				3	2			2			2	3	1				1	1	1	1	1	1	
B. gilvipes	1	1	2					1				1	2					1	3	1	3	3	3					2		2	5	2	3
B. guttula		1										1									2		5								2	1	
B. harpaloides					1								1													1							
B. lampros						1										1					1												
B. lunulatum		4															3				1											2	4
B. obtusum				4					2												1		15				1						1
B. properans		1																											1				
B. punctulatum											5																						

Appendix 2H - Abundances of species recorded in samples collected in 1993 and April 1994

Species	Site numbers																																
	1993																			April 1994													
	1c	1e	1w	4	5c	5e	5w	8e	8w	9	11	13	16	17	18	23	30	72	73	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30
B. quadrimaculatum																1			1														
B. tetracolum			1													5		1	1				10					3	2		1	3	
Clivina collaris				2																												1	
C. fossor																		1	8									1					
Demetrias atricapillus							2																										
Dromius linearis									1																								
D. melanocephalus				1																													
Dyschirius luedersi		2																			2												
Elaphrus cupreus			2		1	4	1	2												1	2				1	1							
E. riparius		3		2						1						1					2	1							1				
Loricera pilicornis			1														1							1				1			1		
Notiophilus biguttatus		2																										1					
N. substriatus																							1										
Patrobus atrorufus			1																														
Pterostichus													1																				
P. minor						1		3										5	3														
P. nigrita		1	1		1	1														1										2			
P. strenuus							1											3	5	2											1		1
P. vernalis			1										1						2												4		
Stenolophus mixtus		3	1																														
Staphylinidae																																	
Aloconota gregaria																						1	1			2		1		3			6
Amischa analis								1																2									
Anotylus rugosus																		1		1					3					2	2	1	
Atheta elongatula		1	4	4		1				3		6			1		1		1									1				1	
A. fungi agg.			1	2	2			3		1					6			3		1		2		1	1	1	1						
A. graminicola	7				3	9	12	1					6					5	3	12		4		11	10	9	5	2		3	6		1

Appendix 2H - Abundances of species recorded in samples collected in 1993 and April 1994

Species	Site numbers																																
	1993																			April 1994													
	1c	1e	1w	4	5c	5e	5w	8e	8w	9	11	13	16	17	18	23	30	72	73	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30
A. gyllenhali			1																														
A. hygrobia									2																		1						
A. hygrotopora			1									12										1											
A. indubia												1																					
A. laticollis										1		1																					
A. luteipes	1																																
A. malleus	1		6	2	1	1						1									2	22	1								1	1	1
A. vilis								14	25																	2							
A. volans			1			1															1	1							1				
Carpelimus bilineatus	1													2	1							8								1		1	
C. corticinus							1															1		1									
C. elongatulus					1																												
C. impressus			11					27	8				4					4	5			13				1	1						
C. rivularis		5	2	3				1	1			3			7						14	48										1	1
C. subtilicornis																							8						3		1	1	
Chiloporata			1							1			2						3							1							
Deinopsis erosa						2			1				1																				
Deubelia picina					9		16																	8	9								
Dinaraea angustula																												1					
Dochmonota clancula			1				1	3	4																								
Gabrius pennatus									1													4											
Gnypeta carbonaria		3	1																		32	26										1	1
G. ripicola				2																		4											
G. rubrior										1																							
G. velata																													1				
Gyrohypnus fracticornis																								1									
Hygronoma dimidiata	5												2																				

Appendix 2H - Abundances of species recorded in samples collected in 1993 and April 1994

Species	Site numbers																																
	1993																			April 1994													
	1c	1e	1w	4	5c	5e	5w	8e	8w	9	11	13	16	17	18	23	30	72	73	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30
Lathrobium brunnipes						1	1	1	2									3											1				
L. elongatum																		2															
L. fulvipenne			2	3					1					1																			
L. geminum																							3						1				
Lesteva heeri	1				3	1	6	1					10						3											2			
L. longoelytrata						3	4	2	12				2					4	3													1	2
Liogluta nitidula								1	3																								
Mycetoporus																	1																
Myllaena dubia					14	12	4	1	1															8	9								
M. infuscata					1		1																										
Neobisnius villosulus				1																													
Omalium caesum									1																								
Othius laeviusculus	1																																
Oxypoda elongatula					11																	1		5	2								
O. exoleta								1																									
O. lentula								1	2																								
Oxytelus laqueatus																											1						
Pachnida nigella					5		9																	3	2								
Philonthus	1	6															1					1											
P. umbratilis	2																																
Platystethus cornutus			3														2	1															
P. nitens					1																												
Quedius maurorufus					1															1					2								
Q. nemoralis																		1															
Stenus bifoveolatus					1		3																		11								
S. bimaculatus							2						1	1					1			3											
S. boops	13	8	12	2		3			3					1	1	1		1		11	12	35	5	1	1			1	2	3	2		

Appendix 2H - Abundances of species recorded in samples collected in 1993 and April 1994

Species	Site numbers																																
	1993																			April 1994													
	1c	1e	1w	4	5c	5e	5w	8e	8w	9	11	13	16	17	18	23	30	72	73	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30
S. canaliculatus		1																															
S. cicindeloides	2		1															1		3		1			3								
S. formicetorum																		1		7													
S. fulvicornis							1																										
S. juno	3	1	5		8	7	7	1	2				2	2	1			3	2	8	2	3		12	9	2	1	1		3	6		
S. melanopus			3																	1	2	1											
S. pubescens																				18		8											
S. solutus	2				2		2								1					6					3								
S. tarsalis																												1			1		
Tachinus signatus																								2									
Tachyporus hypnorum													1										1					1					1
T. obtusus										2			2		1																		
T. pallidus				1									1					2															
Tachyusa atra	1		1																		1												
T. coarctata				1																													
T. leucopus						1																											
Thinodromus arcuatus													2																	1			
Xantholinus longiventris		1					2																					1					
Heteroceridae																																	
Heterocerus fenestratus		1																															
H. marginatus																					1												
Elateridae																																	
Agriotes obscurus																			1														

Appendix 2H - Abundances of species recorded in samples collected in 1993 and April 1994

Species	Site numbers																																
	May															June															July		
	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30	91	1c	1e	1w	4	5c	5w	8e	8w	9	11	13	17	18	23	30	4	13	18
Carabidae																																	
Acupalpus meridianus																													1				
Agonum albipes			1	4		2	2	1	28	19	14	22	11		20			2	2				1	4	4	20	7	8	16	2	3	3	1
A. assimile												8															1						
A. dorsale						1																							1				
A. fuliginosum	1		5		8	1	4	1				4			1					3	1	2						3					
A. livens							2	3														2	2										
A. marginatum														1															1	3			
A. micans	2		4	2					9	5	10	26			6			1	1							5	2	2				1	
A. moestum															1																		
A. obscurum															1																		
A. thoreyi	16		1		21	17									1	1		1		1	6						1	1					
A. viduum			1																														
Asaphidion stierlieni											2																						
Bembidion aeneum		1											1	2			4								2				4	2	2		
B. articulatum																			1														
B. assimile																		1															
B. biguttatum		4	3				7	7	3	4	14	4	3	2	14		2	1				5	14	2		8	5	7	3	1		3	
B. clarki							10	14														8	12										
B. dentellum		2	1	2			3	2	4	7	14	4			1		2		4				4			5	5			3		2	1
B. genei																								1									
B. gilvipes									3	2		2	1		6									2									
B. guttula				2								4	1			1	2		1					1	1						19	1	14
B. lampros		1																															
B. lunulatum													1	4		1	10				1				2				5	8	12	2	21
B. obtusum				13				1											4														
B. properans	1													1																			

Appendix 2I - Abundances of species recorded in samples collected from May to July 1994

Species	Site numbers																																
	May															June															July		
	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30	91	1c	1e	1w	4	5c	5w	8e	8w	9	11	13	17	18	23	30	4	13	18
B. punctulatum																									3								
B. quadrimaculatum																									1								
B. tetracolum				2					3	2		2							2				1	5	1	2			2				1
Chlaenius vestitus										1																							
Clivina collaris										2		2							1														
Elaphrus cupreus		1	1		1		2										2																
E. riparius		5								3		2	3	1					1										2	3	3		
Harpalus rufibarbis									1																								
Loricera pilicornis												2			1				1						1	1					1		
Nebria brevicollis														2												2				1			
Notiophilus biguttatus																									1						1		
Patrobus atrorufus																											3						
Pterostichus anthracinus															1												1						
P. minor							16	1														2	3										
P. nigrita	1										2							1											2				
P. strenuus											2			1		1		1															
P. vernalis										1		4			1											1		1					
Stenolophus mixtus													2																				
Tachys parvulus											2																						
Staphylinidae																																	
Alianta incana					1	3														1													
Aloconota gregaria										3				2	1																		
Amischa cavifrons				2																													
Anotylus rugosus							1	1				2			1	4				2	3	1									11	5	15
A. sculpturatus																			1				1										
A. tetracarinatus							2	2															1										
Atheta elongatula							2									8	9	19	2	17	35	74	74		3			1			38	188	36

Appendix 2I - Abundances of species recorded in samples collected from May to July 1994

Species	Site numbers																																
	May															June															July		
	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30	91	1c	1e	1w	4	5c	5w	8e	8w	9	11	13	17	18	23	30	4	13	18
A. fungi agg.	2	1	1	1	6		1									4					4	1		1			2	4	1		3	1	7
A. graminicola	19		1		20	6	1		1	7	6	12			21	7		2		11	14	11	1	2		9	4	25	12			9	6
A. hygrobia																						12	14										
A. hygrotopora			2				1																2			1							
A. indubia																						4											
A. luteipes							1																										
A. laticollis												4																1					
A. malleus			1				1			2		2			3			2	1			5	7							1		1	2
A. vilis							20	1														4	1										
A. volans																																	1
Brachyusa concolor																	6																
Carpelimus bilineatus					1					1	2				1			1								1							5
C. corticinus																							1										1
C. elongatula							1																						1				
C. gracilis																														1			
C. impressus	1		7				20	2							13			4				7	3				1	1					4
C. rivularis		21	16	5						14		18			1		5	2	23						2			3		1	8		55
C. subtilicornis			1	44						30	4	6	1						6					1	1	1				2	24	5	2
Chiloporata longitarsis		3	6	34					3	1					1	1			5		2			1	3	2		7	1			1	1
Deinopsis erosa			1								2																						
Deubelia picina					9	8														4	8												
Dinaraea angustula																			1														
Dochmonota clancula							3	2															1										
Gabrius bishopi										1							1						1										1
Geostiba circellaris				1															2														
Gnypeta carbonaria		9	1	4						1							35						1	1									
G. ripicola										2								1															

Appendix 2I - Abundances of species recorded in samples collected from May to July 1994

Species	Site numbers																															
	May															June															July		
	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30	91	1c	1e	1w	4	5c	5w	8e	8w	9	11	13	17	18	23	30	4	13	18
G. rubrior																	12					1											
G. velata																			1														
Lathrobium brunnipes					2		5				4											1										1	
L. fulvipenne																																1	
L. geminum				4							2											1					3						
L. quadratum										1																							
Lesteva heeri					4	7					16				9												1						
L. longoelytrata	8		5		1	2	5	13	1	6	24	6		4		1						1											
Myllaena dubia	1				9	1														7													
Nehemitropia sordida					1																												
Neobisnius villosulus				1																													
Omalium caesum	1																																
O. rivulare								1																									
Oxypoda elongatula					2	3										1																	
O. lentula								1																									
O. opaca																							2										
O. umbrata							1															8	5										
Oxytelus fulvipes							2																										
Pachnida nigella					5	8														4	3												
Philonthus cognatus																												1					
P. quisquiliarius		1								1		2					3													1			
P. umbratilis												2					1																
P. varians																	1																
P. varius																														1			
Platystethus cornutus																	8		1														
Quedius maurorufus					2	2														2	1							1					
Q. schatzmayri																5					4												

Appendix 2I - Abundances of species recorded in samples collected from May to July 1994

Species	Site numbers																																
	May															June															July		
	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30	91	1c	1e	1w	4	5c	5w	8e	8w	9	11	13	17	18	23	30	4	13	18
Stenus bifoveolatus					5	4														4	5											1	
S. bimaculatus			1		1	1	1								2								1										
S. boops	1	18	12	2			2	2		3	6	28	1		2	2	10	10	2							3	5	2		1	4	3	12
S. cicindeloides	2				2	2										1												1		1	1		
S. formicetorum	5															7																	
S. juno	11				16	12	5	1		1	2	8			12	4				2	12					3	2	2	4	1	1	1	1
S. melanopus	1	1																															
S. picipennis																1																	
S. pubescens	2															12		1															
S. solutus	9				1	2															1												
S. tarsalis									1																								1
Sunius propinquus																			1														
Tachinus signatus	1						1		1																					1	4	2	
Tachyporus dispar							1																										
T. hypnorum					1				1																								
T. nitidulus			1																														
T. obtusus	1				1										1										1	6					2	1	
T. pallidus	1						1									1										2	1						
Tachyusa atra													1		1			1				1											
T. coarctata				1																											1		
T. leucopus				1																													
Xantholinus longiventris				1					1														1										
Pselaphidae																																	
Rybaxis longicornis					1															1													
Heteroceridae																																	
Heterocerus fenestratus				1																													
H. marginatus			1																														

Appendix 2I - Abundances of species recorded in samples collected from May to July 1994

Species	Site numbers																																
	May															June															July		
	1c	1e	1w	4	5c	5w	8e	8w	9	13	17	18	23	30	91	1c	1e	1w	4	5c	5w	8e	8w	9	11	13	17	18	23	30	4	13	18
Elateridae																																	
Adrastus pallens																															1		

Appendix 2I - Abundances of species recorded in samples collected from May to July 1994

Species	Site			Species	Site			Species	Site		
	4	13	18		4	13	18		4	13	18
Carabidae				*P. strenuus*			1	*Chiloporata longitarsis*	1		
Agonum albipes	2	6	7	*P. vernalis*			1	*Gabrius bishopi*			2
A. fuliginosum			1	*Staphylinidae*				*Geostiba circellaris*	1		
A. micans		1	11	*Alianta incana*		1		*Philonthus cognatus*			1
Bembidion biguttatum	1	3	2	*Anotylus rugosus*			2	*Stenus boops*	1	1	4
B. dentellum	9	7	15	*Atheta fungi agg.*	2		2	*S. juno*			1
B. gilvipes		1	1	*A. graminicola*	19	9	18	*S. pubescens*	1		
B. guttula			2	*A. laticollis*	5			*S. solutus*			1
B. lunulatum	3	3		*A. malleus*			2	*Sunius propinquus*	1		
B. obtusum	1			*A. volans*			1	*Tachinus signatus*			1
B. tetracolum	4	2		*Carpelimus bilineatus*			2	*Tachyporus obtusus*	3	4	1
Carabus granulatus			1	*C. corticinus*			2	*T. pallidus*	1		
Loricera pilicornis			1	*C. rivularis*	1		1	*T. solutus*		1	
Pterostichus nigrita			3	*C. subtilicornis*	1			*Tachyusa atra*	1		1

Appendix 2J - Abundances of species recorded in samples collected in September 1994

Values of environmental measurements at sampling stations in May 1991

Sampling Station	Substrate composition			Surface moisture	Bare ground		Surface litter	
	silt	sand	litter		sub-sample	whole site	sub-sample	whole site
S1A	1	0	9	3	0	2.7	2	0.8
S1B	6	0	4	1	1	2.7	0	0.8
S1C	6	0	4	1	6	2.7	1	0.8
S1D	10	0	0	1	0	2.7	0	0.8
S1E	10	0	0	1	9	2.7	0	0.8
S1F	0	0	10	3	0	2.7	2	0.8
S2A	0	10	0	1	3	3.8	0	0.2
S2B	4	4	2	2	8	3.8	0	0.2
S2C	0	8	2	1	5	3.8	1	0.2
S2D	2	2	6	2	1	3.8	0	0.2
S2E	6	2	2	1	3	3.8	0	0.2
S2F	6	0	4	2	3	3.8	0	0.2
S3A	0	4	0	0	7	6.3	0	0
S3B	8	2	0	0	10	6.3	0	0
S3C	10	0	0	0	5	6.3	0	0
S3D	8	0	2	0	6	6.3	0	0
S3E	8	0	2	0	5	6.3	0	0
S3F	8	0	2	1	5	6.3	0	0
S4A	4	2	4	1	8	7	1	0.8
S4B	4	2	4	2	9	7	1	0.8
S4C	2	6	2	1	6	7	1	0.8
S4D	4	2	4	1	9	7	1	0.8
S4E	2	4	4	1	5	7	1	0.8
S4F	2	6	2	1	5	7	0	0.8
S5A	0	0	10	2	0	0	3	2.7
S5B	0	0	10	1	0	0	3	2.7
S5C	0	0	10	2	0	0	3	2.7
S5D	0	0	10	2	0	0	3	2.7
S5E	2	0	2	1	0	0	2	2.7
S5F	2	0	4	1	0	0	2	2.7
S6A	8	0	2	0	0	0.5	1	0.5
S6B	4	0	6	1	1	0.5	0	0.5
S6C	6	0	4	1	0	0.5	0	0.5
S6D	8	0	2	2	2	0.5	0	0.5

S6E	8	0	2	0	0	0.5	1	0.5
S6F	6	0	4	1	0	0.5	1	0.5
S7A	1	0	9	0	0	0.2	2	1.5
S7B	0	0	10	1	0	0.2	2	1.5
S7C	2	0	8	1	0	0.2	2	1.5
S7D	4	0	6	0	1	0.2	1	1.5
S7E	4	0	6	0	0	0.2	1	1.5
S7F	4	0	6	0	0	0.2	1	1.5
S8A	2	0	8	1	0	0.8	2	1.2
S8B	2	0	8	1	2	0.8	1	1.2
S8C	6	0	4	1	2	0.8	1	1.2
S8D	6	0	4	1	3	0.8	1	1.2
S8E	6	0	4	1	0	0.8	0	1.2
S8F	6	0	4	1	0	0.8	2	1.2
S9A	8	2	0	1	6	3.2	0	0.3
S9B	4	6	0	1	6	3.2	0	0.3
S9C	2	8	0	1	6	3.2	0	0.3
S9D	8	0	2	1	7	3.2	1	0.3
S9E	2	8	0	0	2	3.2	1	0.3
S9F	4	6	0	1	2	3.2	0	0.3
S10A	8	0	2	1	10	5.7	0	0.5
S10B	0	10	0	1	9	5.7	1	0.5
S10C	0	10	0	1	3	5.7	1	0.5
S10D	0	10	0	0	0	5.7	0	0.5
S10E	0	10	0	1	2	5.7	1	0.5
S10F	10	0	0	1	10	5.7	0	0.5
S11A	2	4	0	1	8	6.5	0	0
S11B	8	0	2	1	3	6.5	0	0
S11C	8	0	2	1	7	6.5	0	0
S11D	8	0	2	1	2	6.5	0	0
S11E	0	0	0	1	10	6.5	0	0
S11F	2	2	0	1	9	6.5	0	0
S12A	8	0	2	1	9	5.7	0	0.8
S12B	4	0	6	2	6	5.7	1	0.8
S12C	4	0	6	1	8	5.7	2	0.8
S12D	6	0	4	2	0	5.7	2	0.8
S12E	6	0	4	1	4	5.7	0	0.8

S12F	8	0	2	1	7	5.7	2	0.8
S13A	6	0	4	2	7	4.5	1	1.1
S13B	4	0	6	1	1	4.5	2	1.1
S13C	4	0	6	1	7	4.5	1	1.1
S13D	2	6	2	1	3	4.5	1	1.1
S13E	2	6	2	1	1	4.5	1	1.1
S13F	8	0	2	2	8	4.5	1	1.1
S14A	2	2	0	1	9	5	0	0.3
S14B	2	2	2	2	6	5	1	0.3
S14C	2	4	0	1	9	5	0	0.3
S14D	2	6	0	1	1	5	0	0.3
S14E	4	2	0	1	2	5	1	0.3
S14F	0	10	0	1	3	5	0	0.3
S15A	4	0	6	1	0	3.2	2	1.7
S15B	4	0	6	2	0	3.2	3	1.7
S15C	6	0	4	1	1	3.2	2	1.7
S15D	6	0	4	1	4	3.2	1	1.7
S15E	6	0	4	1	7	3.2	1	1.7
S15F	6	0	4	1	7	3.2	1	1.7
S16A	4	0	6	1	0	0.8	1	1.2
S16B	2	0	8	1	0	0.8	1	1.2
S16C	2	0	8	2	1	0.8	1	1.2
S16D	2	0	8	1	1	0.8	1	1.2
S16E	2	0	8	1	3	0.8	1	1.2
S16F	2	0	8	1	0	0.8	2	1.2
S17A	6	0	4	1	7	2.3	1	1.2
S17B	6	0	4	1	2	2.3	2	1.2
S17C	6	0	4	1	0	2.3	0	1.2
S17D	6	0	4	1	1	2.3	1	1.2
S17E	8	0	2	1	3	2.3	1	1.2
S17F	8	0	2	1	1	2.3	2	1.2
S18A	4	0	6	1	0	4	3	1.2
S18B	8	0	2	1	7	4	0	1.2
S18C	0	0	10	2	0	4	3	1.2
S18D	8	2	0	2	7	4	0	1.2
S18E	4	6	0	1	6	4	0	1.2
S18F	2	8	0	1	4	4	1	1.2

S19A	4	0	6	2	8	3.8	1	1
S19B	8	0	2	1	0	3.8	1	1
S19C	2	0	8	2	4	3.8	1	1
S19D	6	0	4	1	2	3.8	1	1
S19E	8	0	6	2	0	3.8	2	1
S19F	2	8	0	1	9	3.8	0	1
S20A	6	0	4	1	5	2	1	1.8
S20B	6	0	4	1	0	2	2	1.8
S20C	4	0	6	2	4	2	2	1.8
S20D	4	0	6	1	3	2	2	1.8
S20E	4	0	6	1	0	2	2	1.8
S20F	4	0	6	1	0	2	2	1.8
S21A	8	0	2	2	4	2.3	1	1.3
S21B	8	0	2	1	2	2.3	0	1.3
S21C	6	0	4	2	0	2.3	3	1.3
S21D	2	0	8	2	3	2.3	2	1.3
S21E	6	0	4	1	0	2.3	1	1.3
S21F	2	0	8	2	5	2.3	1	1.3
S22A	8	0	2	1	0	0	2	1.3
S22B	10	0	0	0	0	0	0	1.3
S22C	8	0	2	0	0	0	2	1.3
S22D	8	0	2	1	0	0	2	1.3
S22E	8	0	2	1	0	0	1	1.3
S22F	8	0	2	0	0	0	1	1.3
S23A	8	0	2	2	7	3.7	1	0.8
S23B	8	0	2	1	3	3.7	1	0.8
S23C	8	0	2	2	8	3.7	0	0.8
S23D	8	0	2	1	8	3.7	1	0.8
S23E	8	0	2	2	9	3.7	1	0.8
S23F	8	0	2	2	5	3.7	1	0.8
S24A	10	0	0	2	9	7.3	0	0
S24B	8	0	2	1	7	7.3	0	0
S24C	10	0	0	1	8	7.3	0	0
S24D	10	0	0	1	8	7.3	0	0
S24E	10	0	0	1	9	7.3	0	0
S24F	10	0	0	0	3	7.3	0	0
S25A	8	0	2	1	7	1.8	0	1

S25B	4	0	6	2	0	1.8	2	1
S25C	4	0	6	2	0	1.8	1	1
S25D	8	0	2	2	1	1.8	0	1
S25E	8	0	2	2	3	1.8	0	1
S25F	2	0	8	1	0	1.8	3	1
S26A	8	0	2	1	6	4.8	2	0
S26B	8	0	2	1	3	4.8	1	0
S26C	10	0	0	1	6	4.8	0	0
S26D	8	0	2	1	4	4.8	1	0
S26E	8	0	2	1	3	4.8	0	0
S26F	8	0	2	1	5	4.8	1	0
S27A	2	2	6	1	0	3.3	3	0.8
S27B	2	6	2	0	6	3.3	0	0.8
S27C	4	4	2	0	4	3.3	0	0.8
S27D	8	0	2	0	2	3.3	2	0.8
S27E	8	0	2	0	6	3.3	0	0.8
S27F	8	0	2	0	2	3.3	0	0.8
S28A	0	6	4	2	4	6.3	1	1
S28B	0	4	6	1	8	6.3	1	1
S28C	1	7	2	1	8	6.3	0	1
S28D	2	2	6	1	9	6.3	1	1
S28E	8	0	2	1	8	6.3	1	1
S28F	2	6	2	0	0	6.3	2	1
S29A	6	2	2	2	1	3	0	0.7
S29B	10	0	0	1	1	3	1	0.7
S29C	8	0	2	1	1	3	1	0.7
S29D	6	2	2	1	3	3	1	0.7
S29E	10	0	0	1	7	3	0	0.7
S29F	10	0	0	1	5	3	1	0.7
S30A	8	2	0	1	6	4.5	0	0.5
S30B	8	2	0	2	9	4.5	0	0.5
S30C	2	0	8	2	0	4.5	2	0.5
S30D	6	0	4	1	2	4.5	0	0.5
S30E	6	0	4	1	5	4.5	0	0.5
S30F	6	0	4	2	7	4.5	1	0.5

Environmental and management scores for sites sampled in April and May 1991

Site no.	Grid ref.	Dates visited	Values for environmental and managemement factors													
			SHINGLE	SAND	SILT	CPOM	LITTER	SHADE	BAREGRD	HIBSITES	DWATER	CONNECT	NATDIST	GRAZING	RECR	IMPOUND
S1	525219	11/4 7/5	0	0.5	5	4.5	1.1	2	3.2	1	1	2	0.8	1	0	1
S2	534221	25/4 10/5	0	4.5	3	2.5	0.2	3	4.1	1	1	1	1.3	2	0	0
S3	535220	22/4 10/5	1	6.3	1.4	1	0.1	3	6	1	2	4	1.4	2	0	0
S4	539220	22/4 13/5	0	3.2	3.3	3.5	0.9	0	6.4	1	2	4	1.3	0	1	0
S5	541220	3/4 8/5	0	0	1.1	7.6	2.7	4	0	1	1	1	0.2	0	0	0
S6	537217	22/4 13/5	0	0	6.8	3.2	0.3	0	0.3	0	4	1	0.9	2	0	0
S7	539215	3/4 8/5	0	0	2	8	1.6	0	0.1	1	4	1	0	0	0	0
S8	541216	3/4 8/5	0	0	4.7	5.3	1.4	9	0.9	1	3	1	0.7	0	0	0
S9	543216	11/4 9/5	0	4.2	5.5	0.3	0.3	0	4.8	0	2	3	1.4	2	0	0
S10	544215	9/4 9/5	0	5.8	3.7	0.5	0.5	0	5.8	0	2	4	1.6	2	0	0
S11	553206	12/4 10/5	3.3	1.8	4.2	0.7	0	0	6.8	0	2	4	2	0	0	0
S12	553203	12/4 10/5	0	0	6	4	0.8	6	5.8	1	2	2	0.8	1	0	0
S13	565183	26/4 15/5	0	2	4.8	3.2	1.2	0	4.3	1	2	4	1.2	0	1	0
S14	565182	26/4 14/5	2.3	4.1	3.3	0.3	0.6	2	5	1	2	3	1.8	0	0	0
S15	566179	28/3 9/5	0	0	5.8	4.2	1.3	0	3.2	1	1	4	0.7	0	1	1
S16	567178	29/3 8/5	0	0	2.5	7.5	0.9	9	0.5	1	3	1	0	0	0	1
S17	568177	29/3 9/5	0	0	6.7	3.3	1.5	1	1.8	1	1	4	1	0	1	1
S18	571174	28/3 9/5	0	2.5	3.8	3.7	1.3	2	3.3	1	1	4	1	0	1	1
S19	568170	10/4 19/5	0	1.3	3.8	4.8	1.1	9	3.3	1	2	2	0.5	0	0	0
S20	568169	10/4 19/5	0	0	4.2	5.8	1.9	7	1.6	1	3	1	0.2	0	0	0
S21	567168	10/4 19/5	0	0	5	5	1.3	9	4.1	1	3	1	0.6	0	0	0

S22	566165	10/4 19/5	0	0	8.3	1.7	1.5	3	0.2	1	4	1	1	2	0	0
S23	575163	28/4 19/5	0	0	8	2	0.6	0	7	0	2	4	1	2	1	0
S24	577165	15/4 13/5	0	0	9.8	0.2	0	3	7.4	0	2	4	1	2	0	0
S25	578166	28/4 18/5	0	0	6	4	0.8	7	1.4	1	3	1	0.6	1	0	0
S26	576167	20/4 12/5	0	0	8.2	1.8	0.3	3	4.3	1	2	3	1	0	0	0
S27	577167	14/4 13/5	0	2	5.3	2.7	1.1	0	2.8	1	2	3	1.1	0	0	0
S28	578167	26/4 13/5	0	4.4	2.8	2.8	0.8	5	6.1	1	2	4	1.7	0	0	0
S29	578167	27/4 15/5	0	0.7	8.2	1.2	0.4	1	3.3	0	2	4	1.3	2	0	0
S30	582168	27/4 19/5	0	1	6.7	2.3	0.6	0	4.6	0	1	4	0.9	2	0	1

Environmental and management scores for floodplain sites

Site no.	Grid ref.	Date visited	Values for environmental and managemement factors			
			SHADE	GRAZING	IMPOUND	DWATER
S1c	525219	30/05/94	1	1	0	1
S1e	525219	30/05/94	0	2	0	2
S1w	525219	31/05/94	6	2	0	2
S5c	541220	8/5/93	4	0	0	1
S5e	541219	8/5/93	2	0	0	2
S5w	540220	8/5/93	5	0	0	1
S6	537217	13/5/91	0	2	0	4
S7	539215	8/5/91	0	0	0	4
S8e	542216	4/5/93	8	0	0	3
S8w	541216	4/5/93	9	0	0	3
S16	567178	19/5/93	9	0	1	3
S20	568169	19/5/91	7	0	0	3
S21	567168	19/5/91	9	0	0	3
S22	566165	19/5/91	3	2	0	4
S25	578166	18/5/91	7	1	0	3
S40	492281	11/5/92	3	0	1	2
S43	492278	23/5/92	1	0	1	2
S45	491261	14/5/92	0	0	1	2
S47	498249	13/5/92	8	1	1	4
S57	534217	22/4/92	0	0	0	2
S66	586153	7/6/92	9	1	1	3
S67	588153	10/4/92	2	2	1	4
S72	570175	19/5/93	9	0	1	3
S73	569176	19/5/93	8	0	1	4
S91	569175	10/5/94	8	0	1	3
S95	488298	19/5/92	0	0	1	2
S96	483294	11/6/91	0	2	1	2

Appendix 3D

Environmental and management scores for main channel sites sampled in 1992

Site no.	Grid ref.	Date visited	Values for managemement factors				
			REGRAD0	REGRAD1	REGRAD5	GRAZING	IMPOUND
4	539220	22/4	1	0	0	0	0
9	543216	23/4	1	0	0	1	0
11	553206	20/5	1	0	0	0	0
13	565183	7/5	1	0	0	0	0
17	568177	26/5	1	0	0	0	1
18	571174	26/5	1	0	0	0	1
23	575163	7/5	1	0	0	1	0
30	582168	26/5	1	0	0	1	1
31	491306	19/5	0	0	1	1	1
32	491305	19/5	0	0	1	1	1
33	491302	19/5	0	0	1	0	1
35	488294	19/5	0	0	1	1	1
36	495293	23/5	0	0	1	0	0
38	494290	14/5	1	0	0	0	0
39	491285	14/5	0	0	1	0	1
42	491279	23/5	0	0	1	1	1
44	491262	14/5	0	0	1	0	1
46	496250	13/5	0	0	1	0	1
48	497244	13/5	0	0	1	1	1
49	497241	13/5	1	0	0	0	1
50	498241	13/5	0	0	1	1	1
51	510233	26/5	0	1	0	1	1
52	519221	17/5	0	1	0	0	1
53	523219	3/5	0	1	0	0	1
54	524218	3/5	1	0	0	1	0
55	526219	3/5	0	1	0	1	0
58	544215	26/5	0	1	0	1	0
60	550208	20/5	1	0	0	0	0
62	550208	4/5	0	1	0	0	0
63	553207	4/5	0	1	0	1	0