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An Assessment of the Conservation Potential of Forest Fire Ponds

by

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of the requirements for the degree of
Master of Science in Ecology**

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ABSTRACT

1. Fourteen forest fire ponds were sampled at Hamsterley Forest (NZ 0030) to determine the composition of their aquatic Coleoptera, Hemiptera-Heteroptera and plant macrophyte assemblages. Two moorland pools were included for comparative purposes. Environmental variables including the physical attributes and water chemistry of the ponds were measured.

2. The ponds were classified on the basis of their invertebrate assemblages and also on the basis of their flora using two-Way indicator species analysis (TWINSPAN). Ponds were ordinated on the basis of their invertebrate assemblages using detrended correspondence analysis (DECORANA). Community composition was related to environmental variables by means of canonical correspondence analysis (CANOCO).

3. TWINSPAN and DECORANA indicated major divisions between the communities of small heavily shaded peat-based forest fire reservoirs, larger exposed forest ponds and moorland pools.

4. CANOCO revealed that the major environmental determinants of invertebrate community composition were shade, area, age, pH and conductivity.

5. The ponds were found to support mostly common species assemblages, but nevertheless exhibited important differences which have implications for the construction and subsequent management of forest fire ponds for conservation. The ponds

undoubtedly contribute to the diversity and conservation value of the forest habitat as a whole.

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INTRODUCTION

Throughout history the drainage and reclamation of wetlands has been second only to forest clearance among the major human impacts on the environment. The need for well drained fertile farmland has been a major factor in the loss of natural wetlands, particularly in lowland Britain. The drainage of fertile, but wet lowland ecosystems provides the conditions necessary for the cultivation of a range of cereal crops. In Britain control of the snails that are an intermediary host of the liver fluke is also an important factor in the drainage of some farmland.

Not all wetland drainage has been for agriculture. The drainage of lowland and upland peat bog ecosystems has long been a consequence of their exploitation for fuel and horticultural use. But recently, with the expansion of British forestry, the drainage of these ecosystems has been widespread. At the time of the establishment of the Forestry Commission in 1919 less than five per cent of Britain's land was wooded. The total area of forest in Britain is now over two million hectares or approximately 10 per cent of the total land area. The two million hectares is divided approximately into two-thirds conifer and one-third broadleaved species. Approximately 80 per cent of the conifer area is under 35 years old (Forestry Commission, 1988a). The total area of blanket bog in Caithness and Sutherland is estimated to have covered 401,375 hectares before afforestation. Since then, at least 79,350 hectares have been planted or are programmed for planting (Nature Conservancy Council, 1987). Successful afforestation requires deep ploughing and draining which disrupts water-tables and surface flow patterns and leads to longer-term erosion, shrinkage, deep cracking and oxidation of peat. As the trees become established, higher evapo-transpiration rates lower the water-table and further change soil structure. The more hydrophilous plant species are lost, though the drier facies of bog communities may persist. Flush bog, flush and spring communities usually depend on the maintenance of a concentrated water flow at or near the ground surface and are particularly vulnerable to hydrological disturbance.

Wetland drainage has led to the decline or loss of many wetland animals in Britain. Earlier drainage following the Saxon colonisation and opening up of the valleys was probably mainly responsible for the loss of the beaver (*Castor fiber*). Otter (*Lutra lutra*) populations are now declining throughout the lowlands, due mainly to the canalisation and pollution of waterways, and to wetland drainage (Nature Conservancy Council, 1977). The bittern (*Botaurus stellaris*), a species largely confined in Britain to a few extensive East Anglian reedbeds, has declined in recent years. In 1976 a national census estimated 45 to 47 pairs (Day & Wilson, 1978). Many smaller animals and plants have survived drainage better because they do not need the same extensive and continuous tracts as do the larger species. In many old wetland areas, the dykes and ponds harbour the remnants of plant and animal communities typical of the once vast wetland ecosystems. Foster *et al* (1989) found that a rich water beetle fauna has survived in drainage systems in arable fen around the Wash despite intensification of water management.

Reservoirs, gravel pits and other man-made wetlands have to some extent compensated for the loss of natural wetlands. They have, for example, led to the increase and spread of populations of many species of wildfowl including the great crested grebe (*Podiceps cristatus*), tufted duck (*Aythya fuligula*), pochard (*A.ferina*) and smew (*Mergus albellus*) (Green, 1985). However, loss and degradation of these habitats is also taking place. Surveys in several counties of lowland England indicate that in mixed farming and arable areas at least half the farm ponds have disappeared in the last fifty years (Nature Conservancy Council, 1986). With increasing areas being ploughed and the advent of piped water supplies for stock, ponds have lost their usefulness and many have been filled in, used as refuse tips, or through neglect have reverted to dry ground.

On land where the water table has been artificially lowered, ponds and shallow ditches may dry out permanently and a network of shallow ditches can become reduced to a few deep water courses. Even the deeper ditches may have unnaturally fluctuating water levels. Lack of water in ditches in spring is particularly disastrous for breeding amphibians.

Driscoll (1985) emphasised the differences between the dykes of grazing fen and those of arable fen. Arable land dykes are used solely for drainage and levels need only be high when water is being supplied for irrigation. These dykes can be replaced by piping and much of the loss of habitat quality in arable fens has been due to their removal. In grazing fen the dykes must be maintained to provide water for stock. Consequently the bank slopes are low and grazed short and water levels are kept high. In arable fens dykes can be steep-sided and grazing is replaced by cutting, burning or herbicide treatment. Inevitably there is a loss of plant diversity which could result in a loss of invertebrate diversity.

Degradation of existing ponds and ditches may also occur through contamination with refuse, pesticides, fertilisers and agricultural or domestic effluent. Silage liquor can be a serious pollutant. Domestic water birds or visiting cattle can also cause fouling of the water. Nutrient enrichment from both organic and inorganic sources can lead to algal blooms which may inhibit the growth of higher plants and cause the death of fish and other animals through deoxygenation. Aquatic herbicides may produce similar effects.

The decline of the common frog (*Rana temporia*) in the past thirty years is almost certainly attributable to land drainage and loss of suitable wetland habitat. In 20 Km^2 around Kimbolton in Huntingdonshire 35 per cent of ponds were lost between 1950 and 1969 (Relton, 1972). The density of frogs in the Huntingdon area is now only about one adult per 40 hectares, which represents a loss since the 1930's of over 99 per cent (Nature Conservancy Council, 1986). The frog is one of the chief items in the diet of many larger birds and mammals. It's decline may have implications for other species.

The sensitive management of existing ponds and the construction of new ponds both make a significant contribution to the conservation of freshwater communities. This is particularly relevant in forestry plantations as the Wildlife and Countryside (Amendment) Act 1985 amended the Forestry Act 1967 to place a duty on the Forestry Commission to endeavour to achieve a reasonable balance between the interests of forestry and those of the environment. Pond construction primarily for conservation purposes has lately been encouraged by the Forestry Commission (Forestry Commission, 1985) and an increased awareness of forestry practices designed to protect freshwaters now exists (Forestry Commission, 1988b).

At Hamsterly Forest (NZ 0030) the Forestry Commission have constructed approximately twenty ponds and water holes in the past fifty years. Of these, about half have been established since 1983 (B.Walker pers comm). Earlier ponds were constructed solely as fire reservoirs and tend to be small, steep-sided, heavily shaded and polluted by large quantities of coniferous litter. At least two were lined with concrete. Recently ponds have been constructed with greater emphasis on conservation. Later ponds are larger, less steep sided and located in open situations, avoiding heavy shading and large inputs of coniferous litter.

In the present study I have investigated the diversity and composition of assemblages of aquatic Coleoptera and Hemiptera-Heteroptera in ponds at Hamsterley Forest. The ponds considered varied in terms of their age, area and physico-chemical and biotic characteristics. The influence of such factors on the nature of Coleoptera and Hemiptera-Heteroptera assemblages was assessed, using multivariate analysis, with a view to identifying factors of importance in designing, constructing and managing fire reservoirs of high conservation potential.

SITE DESCRIPTION

Study area

The study was carried out in Hamsterly Forest in Weardale (NZ 0030), approximately 32 Km south-west of Durham City. The forest covers an area of 2000 ha and extends approximately from 150 to 400m in altitude.

The land was purchased by the Forestry Commission in 1927 and the initial planting of the forest took place between 1927 and 1951. Harvesting of the initial crop has been taking place for some years and as this proceeds the forest is being restructured to incorporate new ideas and practices for forestry, and landscape and wildlife conservation. These include the development of a varied forest structure and the establishment of additional conservation areas and ponds. The figures below show the proportional landuse of the forest at the present time:

Coniferous woodland	82.5%
Broadleaved woodland	8.0%
Pastures and meadows	4.5%
Conservation areas	2.0%
Recreational grassland	1.0%
Forest rides and roads	2.0%

The underlying geology of the area is sand and mudstone of millstone grit age with the small volcanic Hett Dyke running north-east to south-west through the eastern section of the forest. The soils are mostly peaty gleys.

Description of ponds studied

The approximate locations of the sixteen ponds studied are shown in Fig. 1. The exact locations and year of construction of the ponds are given in Table 1.

Fire Reservoirs 1, 2, 3 & 4

Fire Reservoirs 1, 2, 3 & 4 are situated in the south-west region of Hamsterly Forest (Fig. 1, Table 1). These ponds were constructed in 1948 when the present crop was planted. Reservoirs 1, 2 & 3 are situated in peat and Reservoir 4 in a peaty gley. The four ponds are relatively small ($<26m^2$), steep-sided and do not exceed 1.2m in depth. Reservoirs 1, 2 & 4 are heavily shaded by sitka spruce (*Picea sitchensis*) and are devoid of vegetation, with the exception of Reservoir 4, which supports a little *Juncus effusus*. Fire Reservoir 3 receives less direct shading from the surrounding crop and supports an abundance of submerged *Sphagnum* moss. The ponds receive a large input of coniferous litter and drainage from the nearby forest roads, which are surfaced with pulverised brick, probably influences their water chemistry.

Fire Reservoirs 5 & 6

Fire Reservoirs 5 & 6 are situated towards the north-west corner of the forest (Fig. 1, Table 1). The ponds were constructed in 1951 at the time of the establishment of the present crop. They are of similar size to those ponds discussed above and have a depth of approximately 1.5m.

Fire Reservoir 5 is sited in a peaty gley. The pond receives no direct shading and consequently supports an abundance of

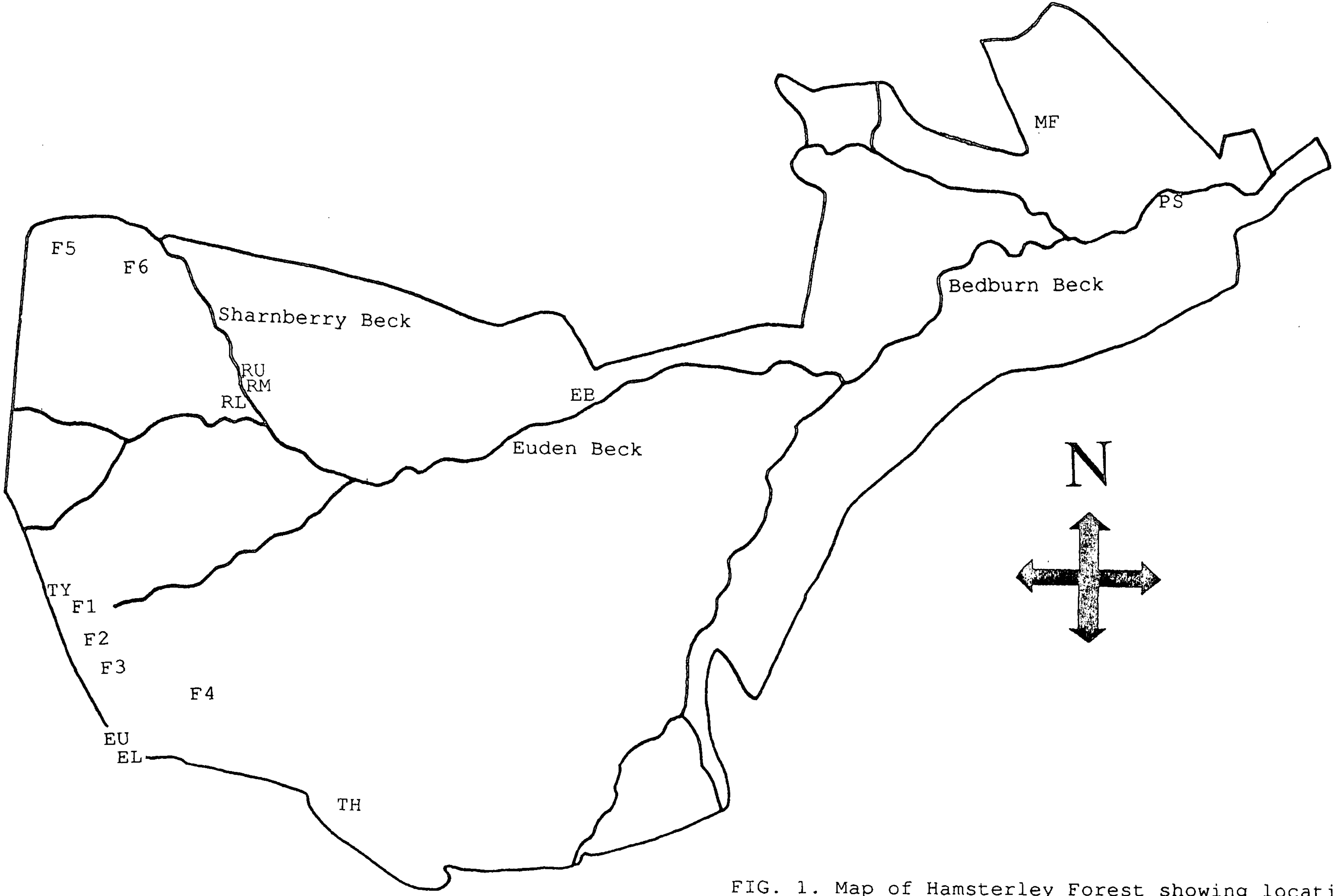


FIG. 1. Map of Hamsterley Forest showing locations of the ponds studied.

TABLE 1. Locations and year of construction of ponds studied.

Nº	GRID REF	NAME	YEAR
01	NZ 018 282	F1 Fire Reservoir 1	1948
02	NZ 019 281	F2 Fire Reservoir 2	1948
03	NZ 019 280	F3 Fire Reservoir 3	1948
04	NZ 027 279	F4 Fire Reservoir 4	1948
05	NZ 018 307	F5 Fire Reservoir 5	1951
06	NZ 024 305	F6 Fire Reservoir 6	1951
07	NZ 029 298	RL Redgate Shield (lower)	1983-87
08	NZ 029 299	RM Redgate Shield (middle)	pre 1927
09	NZ 029 299	RU Redgate Shield (upper)	pre 1927
10	NZ 088 311	PS Pooh Stick Pond	1985
11	NZ 050 298	EB Euden Beck Pond	1985-86
12	NZ 079 317	MF Millfield Pond	1987
13	NZ 021 276	EU Everpool (upper)	pre 1851
14	NZ 021 276	EL Everpool (lower)	pre 1851
15	NZ 016 286	TY Tulleys Pond	1985-86
16	NZ 036 272	TH Tinker Hills Pond	1986-87

aquatic macrophytes. The pond surface is covered almost entirely by *Potamogeton natans* and its margin fringed, in part, by *Juncus effusus*. The sediment is comprised largely of small organic debris (<5mm) and contains little decomposing coniferous litter.

Fire Reservoir 6 is sited over podzolic gley, but is lined throughout with concrete and is devoid of vegetation with the exception of one small stand of *Juncus effusus*. The pond receives little direct shading from nearby trees. There is a thin layer of small organic debris (<5mm) over the bottom of the pond, but few decomposing needles.

Redgate Shield Ponds

These ponds are situated in the bottom of the Sharnberry Beck valley in close proximity to the stream (Fig. 1, Table 1). The underlying geology at the site comprises river-bed gravels overlain by an alluvial brown earth. The area is open in character and the ponds receive little shading from the surrounding trees which are mostly confined to the valley slopes. The lower pond was constructed from 1983 to 87 by the Forestry Commission. It is a relatively large pond with a surface area of approximately 500m^2. Its depth does not exceed 1.0m. The pond receives water at a high rate directly from the beck via a small channel and is drained at its lower end by a second channel, also linked to the beck. Being of recent origin, the margins of the pond are sparsely vegetated in parts. However, there is an abundance of emergents such as *Juncus bulbosus* and *Glyceria fluitans* in shallow areas and submerged *Callitriche stagnalis* in deeper areas. The sediment comprises mostly fine organic and inorganic debris (<1mm) and little larger organic debris or litter. Larger stones (>10cm) are strewn over the sediment surface. The pond is inhabited by trout which may have implications for invertebrate populations.

The upper ponds were in existence when the Forestry Commission purchased the area in 1927 and probably owe their origin to some early small-scale industry, such as iron smelting. These ponds receive water indirectly from the Beck, probably by seepage. The middle pond has a surface area of approximately 350m^2 and is shallow throughout (<0.5m). The surface of the pond is covered almost entirely by emergent and floating-leaved macrophytes, particularly *Equisetum fluviatile* and *Potamogeton natans*. The pond is surrounded by wet meadow, which supports a diverse flora. The sediment is composed mainly of organic debris derived mainly from decomposing aquatic macrophytes. There is little coniferous litter present.

The upper pond is both small (approx.18m^2) and shallow (<0.3m). It supports a few aquatic macrophytes including *Juncus bulbosus* and *Potamogeton natans*. The sediment is comprised mostly of gravel (<5mm), as well as finer organic and inorganic debris (<1mm) and small stones (<3cm). A thin layer of coniferous litter covers the sediment surface.

Pooh Stick Pond

Pooh Stick Pond is situated close to Bedburn Beck, towards the eastern edge of the forest (Fig. 1, Table 1). The pond was constructed by the Forestry Commission in 1985. It has a surface area of approximately 100m^2 and does not exceed 0.6m in depth. The pond is sited in an alluvial brown earth and being shallow does not penetrate the gravels below. Overhanging trees on one side cause partial shading of the pond. The aquatic flora is somewhat sparse, although the pond's margin is fringed, in part, by *Juncus effusus*. The sediment comprises mainly organic debris (<5mm) as well as decomposing leaves and needles. The surrounding area is heavily used by the public for recreational purposes resulting in considerable disturbance of the pond.

Euden Beck Pond

Euden Beck pond is situated in the Euden Beck valley (Fig. 1, Table 1). The pond was constructed by the Forestry Commission from 1985 to 86. It has a surface area of approximately $400m^2$ and exceeds little more than 1m in depth. The substratum comprises river bed gravels overlain by alluvial brown earth. The site is open in character and the pond receives little shading. Emergent macrophytes occupy approximately 50 per cent of the pond's surface area. Species present include *Juncus effusus*, *Glyceria fluitans* and *Holcus mollis*. The sediment comprises mostly organic debris (<5mm) together with a fine inorganic fraction and a small amount of decomposing coniferous litter.

Millfield Pond

Millfield Pond is situated in the north-east region of the forest (Fig. 1, Table 1). The pond which is spring-fed, was constructed by the Forestry Commission in 1987 and occupies an area of approximately $300m^2$. The underlying rock is gritstone overlain by a surface water gley. The pond is relatively deep in parts (>2m), but also comprises an extensive shallow area (<0.5m) dominated by *Juncus bulbosus*. Common emergent grasses include *Deschampsia cespitosa* and *Holcus mollis*. The sediment is mostly a fine ooze, but also includes larger organic debris (<5mm). There is little decaying litter. The pond supports a large quantity of photosynthetic algae indicating high nutrient levels, probably associated with disturbance of the soil when the pond was constructed.

Everpools

The Everpools are situated to the south-west of Hamsterley Forest, just outside the Forestry Commission boundary on adjacent moorland (Fig. 1, Table 1). The pools are at least 140 years of age, being present on the 1851 O.S. map. The upper pool has a surface area of approximately $500m^2$ and a depth of up to 2m. The lower pool has an area of approximately $60m^2$ and a depth of up to 0.8m. The pools are sited in peat and support an impoverished flora dominated by *Sphagnum* and *Juncus effusus*. The sediment in the pools comprises mostly organic debris (<5mm).

Tulleys Pond

Tulleys Pond is situated on the western edge of the forest (Fig. 1, Table 1), in a shallow peaty gley soil. The pond was constructed from 1985 to 86 and has a surface area of approximately $480m^2$ and depth not exceeding 1m. The pond is in an open situation and supports emergent and floating-leaved macrophytes which occupy approximately 30 per cent of the total area and include species such as *Juncus effusus, Agrostis stolonifera, Glyceria fluitans* and *Potamogeton natans*. The sediment comprises mostly small organic and inorganic debris (<1mm), but also grit (1-5mm) and decomposing litter.

Tinker Hills Pond

Tinker Hills Pond is located on the south-west side of the forest (Fig. 1, Table 1). The pond lies at the junction of three soil types: typical podsol, peaty gley and brown clay, and has a rocky base in parts. The pond was constructed by the Forestry Commission from 1986 to 87 and occupies an area of approximately 160m . It's depth does not exceed 1m. Much of the margin of the pond is fringed with *Juncus effusus* but the flora is otherwise impoverished. The sediment comprises mainly organic debris (<5mm), together with large quantities of grit (1-5mm) and some decomposing needles.

Feed, comprising decomposing vegetable matter, is deposited into the pond to encourage wildfowl for sporting purposes.

METHODS

Sampling

Invertebrates

Ponds were sampled for aquatic Coleoptera and Hemiptera-Heteroptera from May to July inclusive. Sampling was carried out using a long-handled pond net of 1mm mesh size.

Method 1: One sample comprised two figure of eight sweeps made just above the sediment surface. All sweeps were approximately equal in length. Samples were taken in all major micro-habitats such as stands of rushes (*Juncus* spp.), marginal grasses and open water. Successive samples were taken in each pond until few, or no, new species were found. Eight successive samples were taken on the same day from the most species-rich pond (Middle Redgate Shield Pond) to determine the sampling efficiency.

At least five samples were taken from each of the sixteen ponds and a total of 126 samples were collected by this method. More samples were taken in larger ponds and also in ponds of greater species-richness.

Method 2: A second sampling technique, that of the National Pond Survey (Pond Action, 1989), was also employed. This technique involved taking one sample of three minutes duration per pond. This sampling time was divided equally amongst the different micro-habitats present. For comparative purposes this technique was employed in eight of the larger ponds. The six fire water-holes, Pooh Stick Pond and Upper Redgate Shield pond were excluded as they were considered too small for the technique to be appropriate.

All samples were sorted and all adult Coleoptera and Hemiptera-Heteroptera were removed and identified to species level. The mean number of individuals of each species per sample was determined for each pond.

Difficulties arose in distinguishing between *Helophorus grandis* and *H. aequalis* and consequently the species were grouped under their previous name *H. aquaticus* agg., which was used prior to the separation of the two species. A single female of the genus *Oulimnius* could not be identified to species level and also a single female of the genus *Haliplus* could only be identified, with certainty, as far as the *ruficollis* group. In both cases certain identification to species level could have only been achieved through examination of male genitalia.

For the purposes of the analysis the data from the two sampling methods was combined by equating one Method 2 three-minute sampling period to nine Method 1 samples (one Method 1 sample was found to have a mean duration of 20 seconds). A paired t-test indicated no significant difference between the numbers of species found in the Method 2 timed samples and in the first nine Method 1 samples (Table 2).

In addition to the sampling techniques discussed above, whirligig beetles (*Gyrinus* spp.) and pond skaters (Gerridae and Velidae) were collected and identified. The populations of species in these groups were estimated for each pond. The following abundance classes were used:

(1) 1 to 10 individuals.

(2) 11 to 100 individuals.

(3) 100+ individuals.

TABLE 2. Numbers of species found by Method 1 (9 samples) and Method 2 (three minute sample) sampling techniques.

Pond	Method 1 (9 Samples)	Method 2 (3 Minutes)
Redgate Shield (middle)	18	12
Redgate Shield (lower)	9	8
Euden Beck Pond	10	12
Millfield Pond	7	6
Everpool (upper)	4	5
Everpool (lower)	2	2
Tulleys Pond	5	4
Tinker Hills Pond	10	10

($t=0.93$, $df=7$, $p > 0.1$)

Vegetation

The proportion of the total area of each pond covered by emergent, floating-leaved and submerged aquatic plants was estimated in the following percentage cover classes (Pond Action, 1989):

(0) no cover
(1) 1 to 20%
(2) 21 to 40%
(3) 41 to 60%
(4) 61 to 80%
(5) 81 to 100%

All species of aquatic macrophyte were identified and ascribed one of the following abundance classes:

(1) Rare
(2) Occasional
(3) Frequent
(4) Abundant
(5) Dominant

Pond characteristics

The surface area of the ponds was estimated from measurements of their length and width. For the purposes of the calculation the ponds were assumed to be elliptical in shape (excepting the Fire Reservoirs which were rectangular). The depth of each pond was measured at its deepest point.

The proportion of each pond surface overhung directly by surrounding trees was estimated as follows (Pond Action, 1989):

(0) no overhang
(1) 1 to 20%
(2) 21 to 40%
(3) 41 to 60%
(4) 61 to 80%
(5) 81 to 100%

Each pond was ascribed a score from one to five based on the size of its sediments (only the component contributing most to sediment bulk was considered here).

The contribution of coniferous litter to total sediment bulk was scored on a scale of zero (no litter) to three (largest component of sediment).

Water quality

Turbidity could not be measured by secci disk in particularly clear or shallow ponds and was therefore assessed by taking Water samples in transparent bottles that were placed against a white background and ranked in order of increasing turbidity from 1 to 16.

Dissolved oxygen (% saturation) was measured in the field using a portable probe.

Water samples of 1.0 litre were taken from each pond and analysed for the following qualities:

pH.

Conductivity.

Biological Oxygen Demand.

Ammoniacal Nitrogen.

Nitrate.

Nitrite.

Solids (particulate).

Data analysis

The aquatic Coleoptera and Hemiptera-Heteroptera data were analysed using the multivariate techniques of classification and ordination using two-way indicator species analysis (TWINSPAN, Hill, 1979a) and detrended correspondence analysis (DECORANA, Hill, 1979b). Canonical correspondence analysis (Ter Braak 1986) was employed in order to relate species composition to environmental parameters. Vegetation data were also analysed using two-way indicator species analysis.

These particular analytical techniques were selected for their robustness and their capacity for rapid analysis of multidimensional data sets.

Classification

The ponds were classified on the basis of their Coleoptera and Hemiptera-Heteroptera assemblages and also on their vegetation by means of two-way indicator species analysis using the TWINSPAN computer programme (Hill, 1979a). TWINSPAN first classifies the samples and then uses this classification to obtain the classification of the species according to their ecological preferences.

This technique not only produces a hierarchical classification of the sites, grouping those with similar composition, but also constructs an ordered two-way table in which the correlation between the sites and the species is maximised (Hill, 1979a).

TWINSPAN makes its dichotomies by dividing ordinations in half. There are three ordinations involved (Hill, 1979a):

1.- The primary ordination (reciprocal averaging), which is divided to obtain an initial dichotomy.

2.- The refined ordination, which is derived from the primary ordination through the identification of differential species.

3.- The indicator ordination, which is based on a few of the most highly preferential species. These "indicator-species" differentiate the groups of sites produced at each dichotomy in the classification.

Input of TWINSPAN is composed of the data matrix itself and parameters determining details of the analysis and the output. In order that similarities between the level of abundance of each species are taken into account pseudospecies are created to indicate high levels of abundance. The cut levels were chosen to reflect typical levels of abundance (Hill, 1979a) and were set at 0, 1, 6 and 36. Thus the first pseudospecies was added to indicate the capture of more than five individuals and the second to indicate the capture of more than 35 individuals.

TWINSPAN is attractive as a method of analysing lists of aquatic insects because it provides an objective method of subdividing community types without regard to preconceived ideas about habitats based on their appearance and vegetation (Foster, 1987).

Ordination

Ordination of the invertebrate data by detrended correspondence analysis was carried out using the DECORANA computer programme (Hill, 1979b). This programme provides a species ordination as well as a site ordination, grouping the sites with similar species composition.

Detrended correspondence analysis is derived from a simpler method of ordination known as reciprocal averaging (Hill, 1973) or correspondence analysis (Hill, 1974), but differs from this in two respects: a) the scaling of the axes; and b) the way in which the second and higher axes are calculated. It avoids the "arch effect" (Gauch *et al*, 1977) which is the tendency in reciprocal averaging for the second axis (and sometimes higher axes) to be strongly related to the first axis. It also permits a better scaling of the samples and the equivalent ecological distances between them, which are not preserved in reciprocal averaging (Hill & Gauch, 1980).

DECORANA has several advantages over other ordination programmes: a) its performance is the best of the ordination techniques tested; b) both species and samples ordinations are produced simultaneously; c) the axes are rescaled in standard deviation units with a definitive meaning, and d) large amounts of data can be analysed without difficulty (Hill & Gauch, 1980).

A piecewise linear transformation (reflecting the TWINSPAN pseudospecies cut levels) was applied to the invertebrate data as follows:

0.0	0.0
1.0	1.0
6.0	2.0
36.0	3.0

Canonical correspondence analysis

The relationships between the composition of aquatic Coleoptera and Hemiptera-Heteroptera assemblages and the environmental variables were investigated by means of canonical correspondence analysis (Ter Braak, 1986) using the CANOCO computer programme (Ter Braak, 1987). Canonical correspondence analysis is an extension of correspondence analysis (reciprocal averaging) and is a multivariate direct gradient analysis technique whereby a set of species is related directly to a set of environmental variables. The technique identifies an environmental basis for community ordination by detecting patterns of variation in community composition that can be explained best by the environmental variables.

In the resulting ordination diagram, species and sites are represented by points and environmental variables are represented by arrows. Such a diagram shows the main pattern of variation in community composition as accounted for by the environmental variables, and also shows, in an approximate way, the distributions of the species along each environmental variable. The technique thus combines aspects of regular ordination with aspects of direct gradient analysis.

Canonical correspondence analysis allows a quick appraisal of how community composition varies with the environment.

Input of CANOCO comprises both species and environmental data matrices. The piecewise linear transformation described above was again applied to the invertebrate data.

When environmental variables are strongly inter-correlated, the effects of different variables cannot be separated out and consequently the canonical coefficients are unstable. This is known as the multicolinearity problem (Ter Braak, 1986).

The initial data set in the present study comprised 15 environmental variables which included pond age (Table 1), total vegetative cover (Appendix 3), physical characteristics (Appendix 4) and water quality variables (Appendix 5). These variables were found to show a considerable degree of inter-correlation. Five strongly correlated environmental variables were therefore removed from the data set, leaving at least one variable per set of strongly correlated variables. The five least important variables were then removed from the remaining data set on the basis of the significance of their regression coefficients. The final input of CANOCO comprised five variables with a low degree of inter-correlation.

The significance of the first axis eigen-value was tested using the Monte Carlo permutation test.

RESULTS

Species recorded

Sampling revealed 41 species: 28 species of Coleoptera and 13 species of Hemiptera-Heteroptera.

Sampling efficiency

The eight successive samples taken on the same day from Middle Redgate Shield Pond to test the efficiency of sampling revealed 16 species. Of these, 15 (94%) were obtained in the first five samples and 16 (100%) in the first seven samples (Fig. 2). No new species were found in the eighth sample. Four additional species were found at other times of which two species had been obtained in earlier sampling and two species were obtained in a later timed (Method 2) sample. The eight successive samples therefore contained 80% of the total species found at the site. Thus eight Method 1 samples should adequately reflect species composition at any one time provided that sampling is representative of all micro-habitats. Fewer samples are adequate in smaller, low diversity ponds.

Multivariate analysis

Ponds were classified into five groups on the basis of their Coleoptera and Hemiptera-Heteroptera assemblages and into three groups on the basis of their aquatic vegetation using the TWINSPAN computer program (Hill, 1979a). These classifications

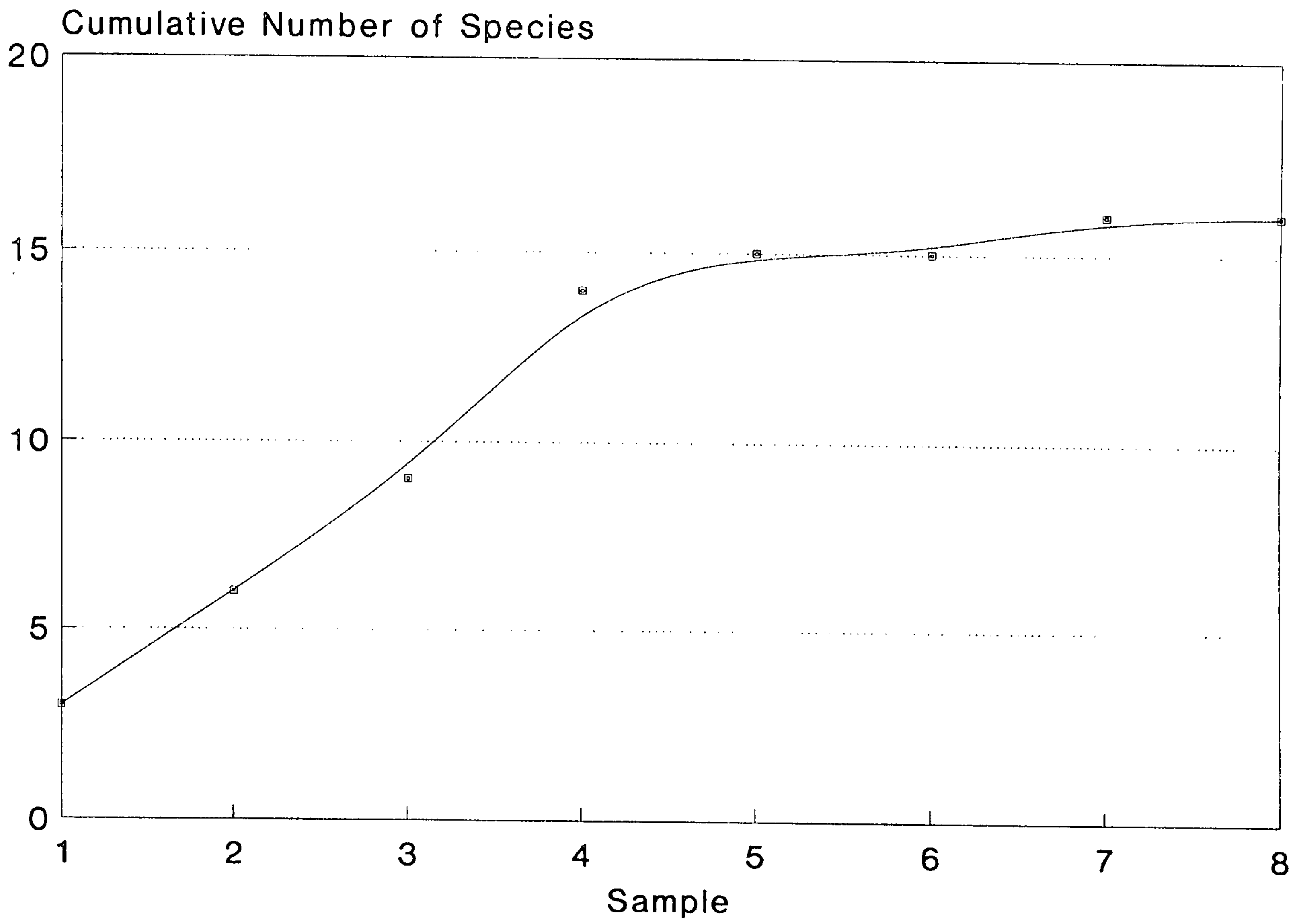


FIG. 2. Cumulative number of species found in eight successive samples taken on the same day from Middle Redgate Shield Pond.

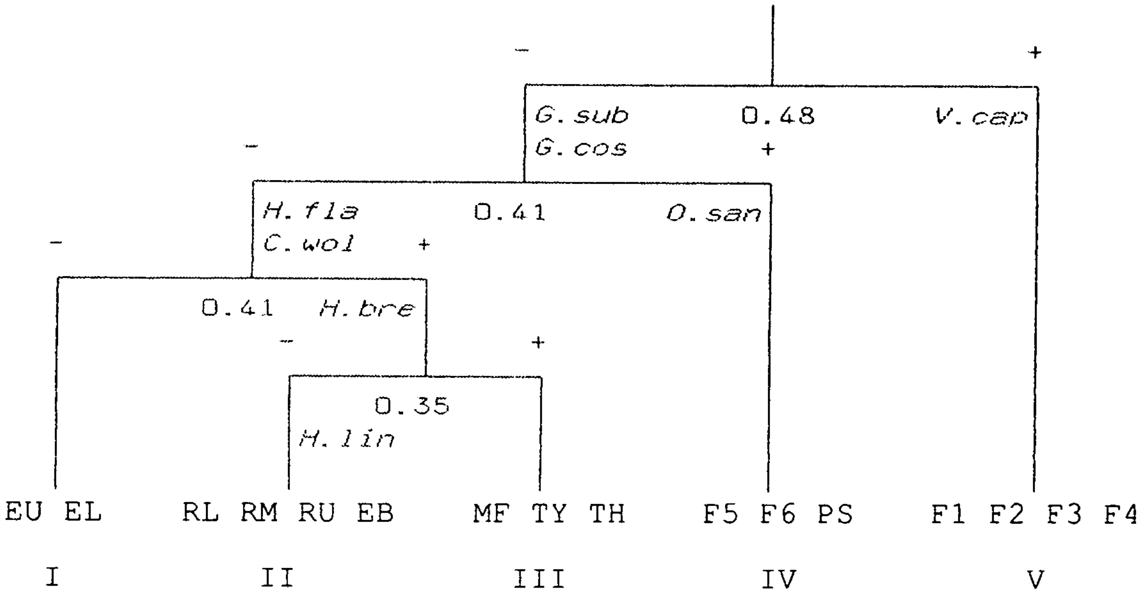
are illustrated by means of dendrograms and species frequency tables. DECORANA (Hill, 1979b) was used to identify the major community gradients from the invertebrate data and these are represented in an Axis 1 by Axis 2 ordination plot. Five important environmental variables were identified and these were related to species composition using the CANOCO computer program (Ter Braak, 1987), the results of which are represented in a canonical correspondence analysis ordination diagram.

Classification of ponds based on their invertebrate assemblages

The dendrogram (Fig. 3) shows the hierarchy and relationships between the sixteen ponds based on their aquatic Coleoptera and Hemiptera-Heteroptera assemblages, as indicted by TWINSPAN (Hill, 1979a). The indicator species at each TWINSPAN division are also shown. Five end-groups were identified from the classification, the species assemblages of which are summarised in the frequency table (Table 3). The sequence of the species in Table 3 is that produced by TWINSPAN in the final tabulation.

Agabus bipustulatus was the only species to appear in all end-groups reflecting the catholic nature of its habitat requirements. Species more selective in their habitat requirements featured among the commoner species in some end-groups, particularly Groups I and II. For example, the upland sphagnophiles *Hydroporus tristis* and *H. obscurus* occurred in the upper moorland pool in Group I. *Strictotarsus duodecimpustulatus*, a species associated with fast flowing water, was found in Lower Redgate Shield Pond in Group II. Group V (Fire Reservoirs 1, 2, 3 and 4) contained only common species and none that were not found in other groups (Table 3).

FIG. 3. Dendrogram of TWINSPAN classification of ponds based on their aquatic Coleoptera and Hemiptera-Heteroptera assemblages. Eigen-values and indicator species are shown at each division.



G.sub = *Gyrinus substriatus*. *G.cos* = *Gerris costai*.
V.cap = *Velia caprai*. *H.lin* = *Haliplus lineatocollis*.
C.wol = *Callicorixa wollastoni*. *O.san* = *Oreodytes sanmarki*.
H.bre = *Helophorus brevipalpis*. *H.fla* = *Helophorus flavipes*.

TABLE 3. Percentage occurrence of invertebrate species in ponds in the TWINSPAN end-groups.

Species	I	II	III	IV	V
Oreodytes sanmarkii				67	
Potamonectes depressus		25		67	
Strictonectes lepidus				33	
Oulimnius sp				33	
Micronecta poweri			33	33	
Gerris gibifer				33	
Arctocorisa germari			67	33	
Gerris lacustris		25	67	67	
Gyrinus substriatus	50	50	100	67	
Sigara nigrolineata			100	33	
Gerris costai	100	100	100	67	
Callicorixa wollastoni	100	25	100		
Hydroporus obscurus	50				
H. tristis	50				
Glaenocorisa propinqua	100				
Hesperocorixa castanea	50				
Hydroporus erythrocephalus	50	25			
Helophorus aquaticus agg.	50	100	67	33	
H. brevipalpis		100	100	33	
Agabus sturmii		75	33		
Hydroporus nigrita		25			
Ilybius subaeneus		50	33		
Strictotarsus duodecimpustulatus		25			
Haliplus lineatocollis		100			
Haliplus ruficollis agg.		25			
Limnebius truncatellus		50			
Anacaena lutescens		50			
Helophorus flavipes		100	67		
Hydrobius fuscipes		75	67		
Hesperocorixa sahlbergi	50	75	33		
Agabus nebulosus			33		
Laccobius atratus			33		
Corixa punctata		25	67		
Sigara distincta		25	33		
Hydroporus incognitus		100	33		50
H. pubescens		75	100	33	25
Anacaena globulus		75	67		25
Agabus bipustulatus	50	100	100	67	100
Hydroporus gyllenhalii		25	33		50
H. palustris		25		33	50
Velia caprai				33	75
No. of ponds in end-groups	2	4	3	3	4

Group 1: This group comprises the two moorland pools of which the lower pool is species poor, only four species being found here. However, the group does contain four typically acid water species, *Hydroporus obscurus, H. tristis, Glaenocorisa propinqua* and *Hesperocorixa castanea* which were not found in the forest ponds. The Corixid, *Glaenocorisa propinqua,* occurs typically in moorland or bog pools where the sides are sheer and the depth uniform and 1-2m (Macan 1965). *Hesperocorixa castanea* was found in one sample in the upper moorland pool. This species is generally associated with thick *Carex* and *Sphagnum* beds in very base-defficient water (Macan, 1965). *Callicorixa wollastoni,* although found also in forest ponds in Groups II and III, was particularly abundant in the lower moorland pool. The species has a restricted range, occurring in the North and West in peat pools (Macan 1965). The indicator species for the division of the moorland pools from the ponds in Groups II and III was *Helophorus brevipalpis,* an abundant and wide-ranging lowland species (Eyre *et al,* 1985). It's absence from the moorland pools could be due to a range of factors, but it appeared to be most abundant in shallow ponds with emergent vegetation such as Middle and Upper Redgate Shield Ponds. The moorland pools lack such micro-habitat.

Group II: This group comprises the Redgate Shield and Euden Beck Ponds which are located either close or adjacent to streams on river-bed gravels. Six species were restricted to Group II (Table 3). Of these *Strictotarsus duodecimpustulatus, Limnebius truncatellus* and the negative indicator species *Haliplus lineatocollis* are associated with running water (Friday, 1988). The presence of these species reflects the close proximity and probable influence of the streams, particularly at Redgate

Shield. Also of interest is the high abundance of *Helophorus* beetles at these sites, particularly *H. brevipalpis* and the *H. aquaticus* group, the latter of which is associated with grassy pools and ditches (Friday, 1988).

Group III: This group comprises Millfield, Tulleys and Tinker Hills Ponds. One obvious feature of the Group is the recent origin of it's constituent ponds, all of which were constructed during the past five years. Two species were restricted to this group: *Agabus nebulosus* and *Laccobius atratus.* The former occurred only in Millfield Pond, the most recent pond studied, and is thought to be associated particularly with new ponds (Friday, 1988). Eyre *et al* (1985) found the species to be associated with lowland temporary water, especially subsidence ponds, which again reflects its preference for recent or unstable habitats. Millfield and Tulleys Ponds were very similar in terms of their species composition and 10 of the 12 species found at Tulleys Pond also occurred at Millfield Pond. Tinker Hills Pond was found to be the most favourable pond for corixids, supporting six of the nine species found in the survey. *Sigara nigrolineata* was particularly abundant here, although it's habitat is not easily defined, being found across a range of conditions (Macan, 1954).

Group IV: This group comprises the two exposed Fire Reservoirs (5 and 6) and Pooh Stick Pond. Four species occurred here which were restricted to this group. The positive indicator species, *Oreodytes sanmarkii*, is associated with flowing water (Eyre *et al*, 1985; Friday, 1988), particularly small gravelly burns in the North (Balfour-Brown, 1940). *Strictonectes lepidus* occurs also in streams, as well as dam pools and quarry and sand pit pools (Eyre *et al*, 1985; Friday, 1988). Pooh Stick Pond also supports a large population of *Potamonectes depressus*, which is also characteristic of fast flowing streams and rivers (Eyre *et al*, 1985). The close proximity of Bedburn Beck to Pooh Stick Pond may account for the presence of these species here, since they would be capable of flying from the stream to the pond. Fire Reservoir 6 and Pooh Stick Pond are characterised by particularly high pH and it may be that this factor is responsible for the absence of *Helophorus flavipes* and *Callicorixa wollastoni*, the negative indicator species for the division. The former is characteristic of upland acid water (Eyre *et al*, 1985) and the latter of peat pools (Macan, 1965).

Group V: This is a distinctive group comprising the Fire Reservoirs 1, 2, 3 and 4. These ponds are of the same age and share a number of common features, being heavily shaded, steep-sided and set in peat. They support a limited invertebrate fauna and the group contained no species which were not found in other groups. The majority of the species found here occur in at least two other groups. Fire Reservoirs 1, 3 and 4 supported a large number of *Velia caprai*, the positive indicator species for the division. Brinkhurst (1959) states that the species is predominantly a stream inhabitant. However *Velia caprai* is carnivorous and feeds on insects disabled or killed by falling into the water rather than on living prey captured by itself (Butler, 1923) and the trees which overhang these ponds would of course provide an abundance of such prey. The requirement of the first negative indicator species *Gyrinus substriatus* for open habitat (Balfour-Brown, 1950) may be an important factor in its exclusion from these ponds. The second negative indicator *Gerris* *costai* may be precluded for similar reasons.

Ordination of ponds based on their invertebrate assemblages

Fig. 4. shows Axis 1 by Axis 2 ordination plots of the sixteen ponds based on detrended correspondence analysis (Hill, 1979b). The TWINSPAN end-groups, discussed above, have been superimposed onto the plot. The primary and secondary axes of ordination, which together explained 81 per cent of the variance in the data set, were respectively 3.8 and 2.7 standard deviations in length reflecting the relative lengths of the community gradients represented by the two axes (Gauch, 1982) (Table 4). The remaining axes (3 and 4) explained only 19 per cent of the variance.

Axis 1 represents a strong gradient (Fig. 4). The moorland pools lie at the left, the exposed forest ponds at the centre and the heavily shaded fire reservoirs (1, 2, 3 and 4) at the right of the axis. Generally speaking larger ponds lie on the left of the axis and smaller ponds on the right. The axis thus appears to represent both a shade and an area gradient. The lower moorland pool and Fire Reservoir 3 lie at opposite ends of Axis 1 and are therefore least similar in terms of their species composition, having no common species. The previously identified TWINSPAN end-groups are clearly separated along this axis.

Axis 2 reflects a community gradient which is less clearly related to environmental factors, although there is a tendency for the more acid ponds to lie along the lower half of the axis. The lower moorland pool and Fire Reservoir 5, which mark the ends of the axis, are least similar in terms of their species composition, possessing no common species. There is little

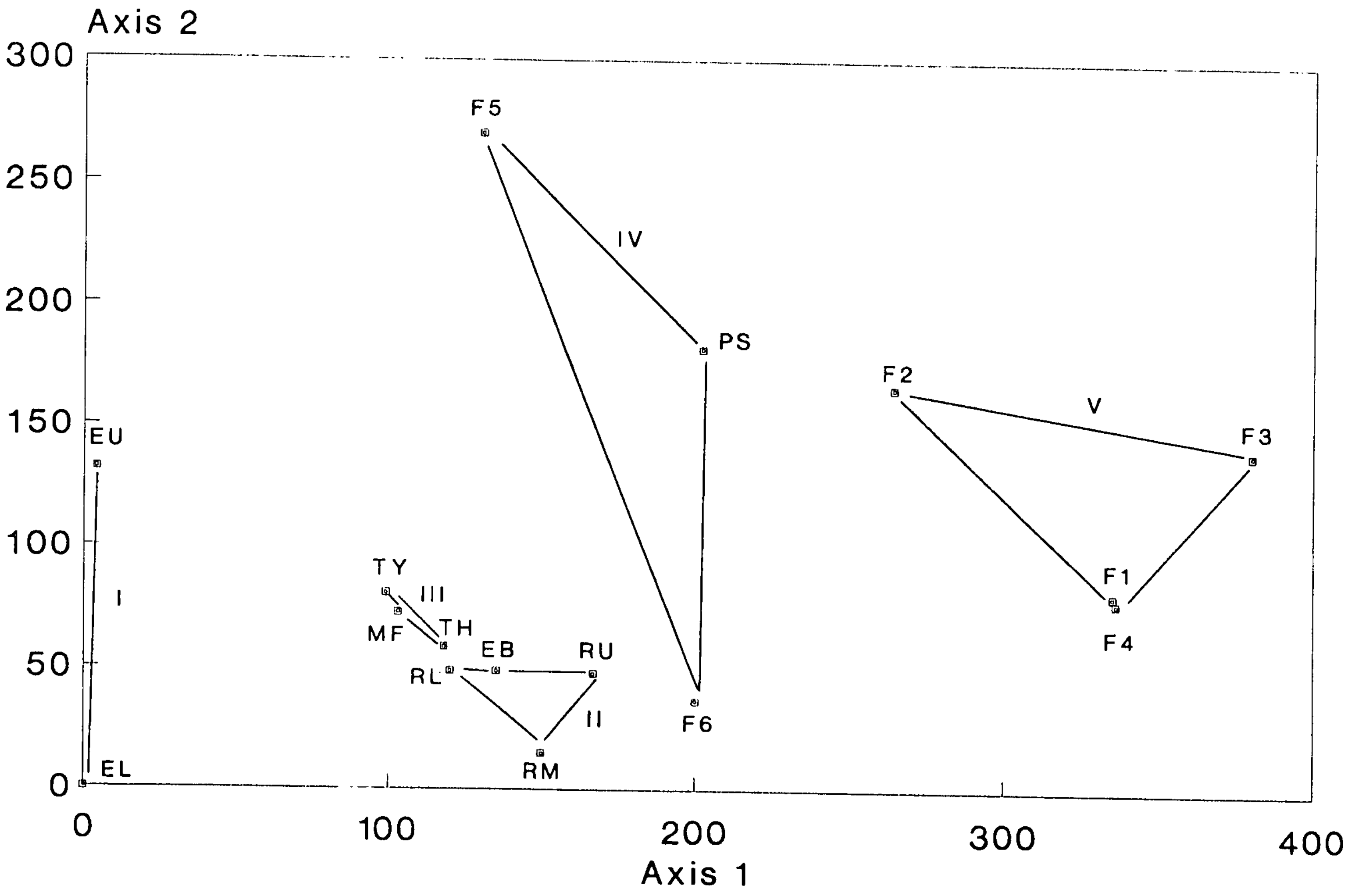


FIG. 4. DECORANA ordination plot (Axis 1 x Axis 2) of the ponds based on their Coleoptera and Hemiptera-Heteroptera assemblages. The TWINSPAN end-groups are also shown.

TABLE 4. Eigen-values, cumulative percentage variance explained and lengths (standard-deviations) of each DECORANA axis.

Axis	Eigen-value	Cumulative (%) Variance Explained.	Length (SD)
1	0.507	50.8	3.80
2	0.304	81.3	2.70
3	0.138	95.1	1.83
4	0.049	100.0	2.78

separation of the TWINSPAN end-groups along this Axis.

Classification of ponds based on their vegetation

The dendrogram (Fig. 5) shows the results of the classification of the ponds based on their vegetation, as indicated by TWINSPAN (Hill, 1979a). Three end-groups were identified from the classification, the species assemblages of which are summarised in the frequency table (Table 5).

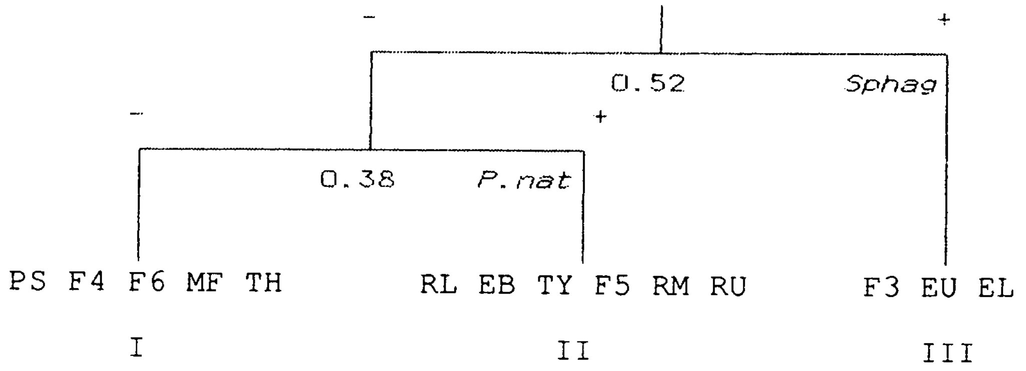
Fire Reservoirs 1 and 2, which were devoid of aquatic macrophytes and bryophytes, do not appear in the dendrogram, although they may be considered a separate group in their own right. *Juncus effusus* is the only species to occur in all three groups and is the most general in terms of its habitat requirements. The species is very abundant and locally dominant in bogs, wet pastures and damp woods, especially on acid soils, throughout the British Isles (Clapham *et al*, 1987).

The moorland pools are separated at the first division together with Fire Reservoir 3 (Group III). *Sphagnum,* the positive indicator at this division, is abundant in these three ponds. The moorland pools also support an abundance of *Juncus effusus*, but are otherwise devoid of aquatic macrophytes.

The division of Groups I and II is based on the presence of *Potamogeton natans* (the positive indicator species) in all ponds in Group II. The species is absent from all other ponds (Table 4). *Potamogeton natans* occurs in lakes, ponds, rivers and ditches, especially on a highly organic substratum and usually in water less than 1.0 metre deep. The species is common throughout the British Isles (Clapham *et al*, 1987).

Group II comprises the Redgate Shield and Euden Beck Ponds,

FIG. 5. Dendrogram of TWINSPAN classification of ponds based on their vegetation, together with eigen-values and indicator species at each division.



Sphag = *Sphagnum* *P.nat* = *Potamogeton natans*

TABLE 5. Percentage occurrence of plant species in ponds in TWINSPAN end-groups.

Species	I	II	III
Glyceria fluitans		50	
Ranunculus omiophyllus		50	
Sparganium emersum		17	
Equisetum fluviatile		17	
E. palustris		67	
Potamogeton natans		100	
Juncus bulbosus	60	83	
Ranunculus flammula	20	33	
Agrostis stolonifera	20	17	
Carex demissa	20		
Calitriche hamulata agg.	20	17	
Deschampsia cespitosa	40		
Callitriche stagnalis agg.	20	17	
Juncus effusus	100	100	67
Sphagnum		33	100
No. of ponds in end-groups	5	6	3

which together constitute end-group II of the pond-invertebrate classification (Fig. 3)

Group I however, includes components from Groups III, IV and V of the pond-invertebrate classification.

The number of invertebrate species found at each site was found to be significantly correlated with both plant cover ($r=0.601$, $df=14$, $p<0.05$) and number of aquatic plant species ($r=0.714$, $df=14$, $p<0.05$). Generally, ponds such as Middle Redgate Shield Pond, which supported extensive emergent and floating-leaved macrophytes also supported the richest aquatic Coleoptera and Hemiptera-Heteroptera assemblages. Fire Reservoirs 1, 2, 3 and 4 failed to support rich invertebrate and plant communities. However, this does not necessarily imply a causal relationship, since the composition of the pond's faunal and floral assemblages may be ultimately dependent on the same environmental factors, such as shading, which would account for the correlation. Nevertheless, aquatic macrophytes and bryophytes undoubtedly provide important micro-habitats for many of the invertebrate species considered here.

Canonical correspondence analysis

A preliminary analysis was carried out using the environmental variables listed in Appendices 4 and 5, together with pond age (Table 1) and total vegetative cover (Appendix 3). In the final analysis five environmental variables were identified as important on the basis of the t-values of their regression coefficients: pH, shade, pond age, area and conductivity. The t-values are relative rather than absolute values, but allow the importance of each variable to be assessed

(Table 6).

The variance accounted for by each canonical correspondence ordination axis was 33%, 26%, 18% and 16% for Axes 1, 2, 3 and 4 respectively. In total these axes accounted for 93.4 per cent of the variance in the data. The first axis, which alone accounted for 33 per cent of the variance, had an associated eigen-value of 0.422, p=0.03 (Monte Carlo permutation test) (Table 7).

Axis 1 was correlated most strongly with the degree of overhang or shading by neighbouring trees (Table 8). Pond surface area was of secondary importance. Small, heavily-shaded ponds, notably Fire Reservoirs 1, 2, 3 and 4 are situated towards one end of the gradient and larger exposed ponds such as Tulleys Pond and the upper moorland pool lie towards the other (Fig. 6). Shade is the longest and thus the most important environmental gradient, along which species composition changes most. The least species-rich ponds generally lie at the upper end of the shade gradient.

The second CCA ordination axis was found to be most strongly correlated with pH and secondly with age (Table 8). The acid moorland pools lie at one end of the gradient and those ponds characterised by high pH lie at the other.

Axes 1 and 2 were not strongly correlated with conductivity, although this variable was found to be the strongest correlate of Axis 3 (Table 8).

The pond and site points in Fig. 6. jointly represent the dominant patterns in community composition insofar as they can be explained by the environmental variables: shade, area, age and pH. The species points and arrows of the environmental variables jointly reflect the species distribution along each of

TABLE 6. t-values of regression coefficients of environmental variables with the CCA ordination axes (x1000).

Variable	Axis 1	Axis 2	Axis 3	Axis 4
pH	-121	-260	102	605
Conductivity	146	-2	218	-610
Shade	302	240	108	468
Age	-361	264	132	487
Area	-348	-22	68	451

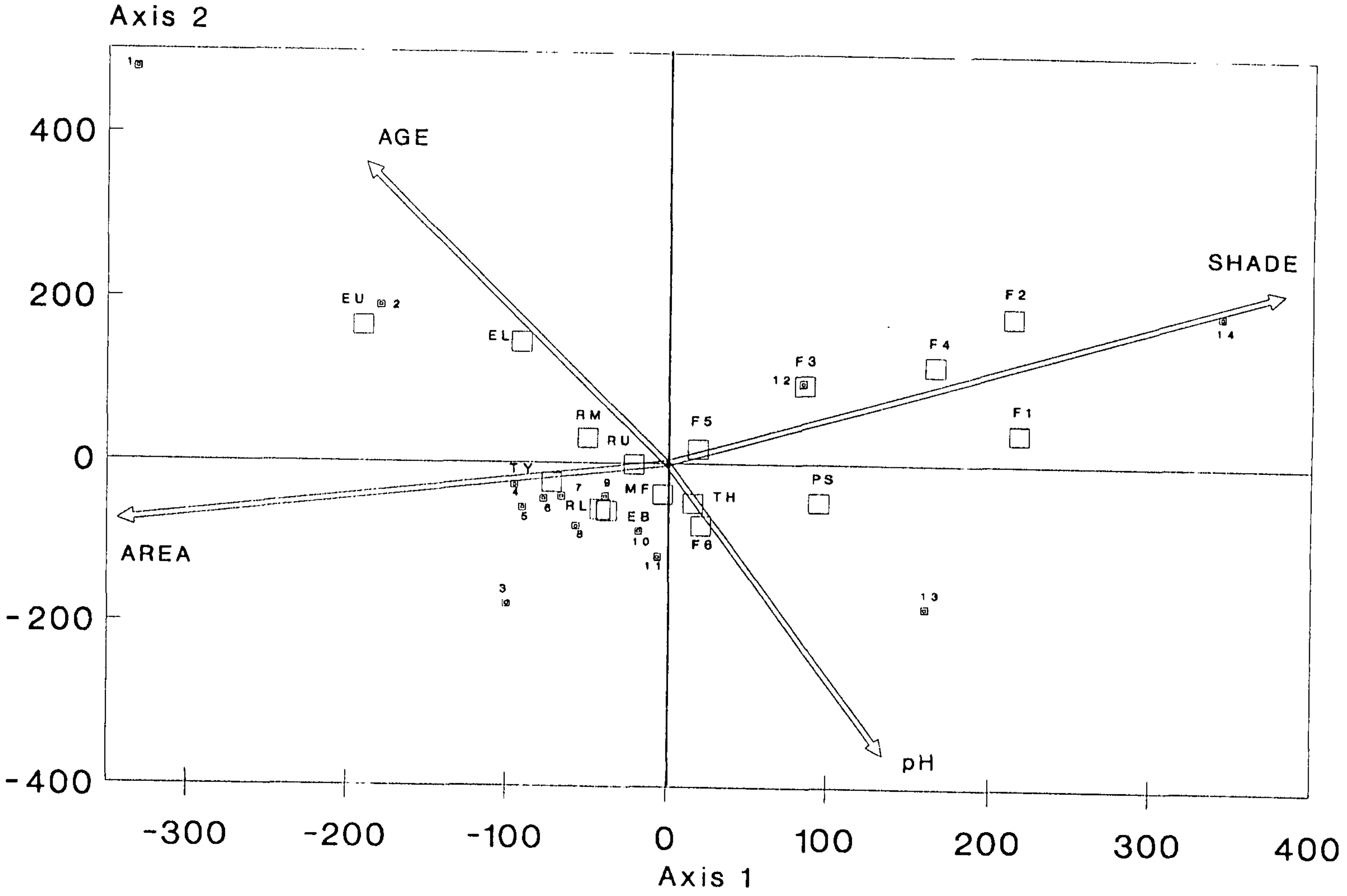
TABLE 7. Eigen-values and cumulative percentage variance explained by CCA ordination axes.

Axis	Eigen-value	Cumulative (%) Variance Explained
1	0.422	33.3
2	0.329	59.3
3	0.234	77.7
4	0.198	93.4
Trace	1.267	

TABLE 8. Inter-set correlations of environmental variables with the CCA ordination axes (x1000).

Variable	Axis 1	Axis 2	Axis 3	Axis 4
pH	228	-712	428	223
Conductivity	-14	-116	851	-203
Shade	716	417	262	243
Age	-361	687	325	65
Area	-649	-139	119	-77

FIG. 6. Canonical correspondence analysis (CCA) ordination diagram (Axis 1 x Axis 2) showing positions of ponds (□) and species (▣) in relation to environmental variables (arrows).



KEY

1. *Glaenocorisa propinqua*
2. *Callicorixa wollastoni*
3. *Strictotarsus duodecimpustulatus*
4. *Haliplus lineatocollis*
5. *Helophorus flavipes*
6. *Gyrinus substriatus*
7. *Helophorus aquaticus*
8. *H. brevipalpis*
9. *Gerris costai*
10. *Sigara nigrolineata*
11. *Agabus bipustulatus*
12. *A. nebulosus*
13. *Oreodytes sanmarki*
14. *Velia caprai*

the environmental variables. As each pond lies at the centroid of the species points that occur at that site (Ter Braak, 1986), it is possible to infer which species are likely to be present at a particular site. *Callicorixa wollastoni* (2) occurs in the two moorland pools, but is unlikely to appear in the Fire Reservoirs. The species points are approximately the optima, therefore the abundance or probability of occurrence of a species decreases with distance from its location in the diagram. The arrows determine a direction or axis in the diagram and projecting species points onto the axis or environmental variable indicates the relative position of the centre of the species distribution along the axis. The centre of distribution of *Velia caprai* (14) is towards the upper end of the shade axis suggesting that the species is tolerant of heavy shading. *Oreodytes sanmarkii* (13) has a centre of distribution at the upper end of the pH axis reflecting the requirement of the species for a relatively high pH environment. *Glaenocorisa propinqua* (1), which is a species of acid habitats has its centre of distribution towards the end of the pH axis, while the ubiquitous Agabus bipustulatus (11) is represented towards the centre of the diagram. The majority of the species shown lie to the left of the origin reflecting their preference for unshaded ponds. Generally shade and pH increase along the first axis or major community gradient, whilst age and area decrease.

DISCUSSION

During the survey of fire ponds at Hamsterley Forest two sampling methods were compared. The method of successive sampling until few or no new species are revealed was found to be an effective sampling technique, provided that all micro-habitats are represented. The technique was found to reveal as many species as the timed sampling technique (Method 2) recommended for the National Pond Survey (Pond Action, 1989) when the two methods were equated in terms of the total sampling time. The latter method is less flexible in that it offers no less than a three minute period of sampling, which may be inappropriate for smaller ponds such as Upper Redgate Shield Pond and the Fire Reservoirs. In ponds of this size such a lengthy sample may well prove destructive, both in terms of the number of individual organisms removed in relation to the total population and the physical damage inflicted, particularly to aquatic vegetation. Equally a three minute sample may be inappropriate for large ponds. At present the National Pond Survey sampling technique is not recommended for use in ponds larger than 0.25 hectares.

In the National Pond Survey Method, equal sampling time is allocated to different micro-habitats, with the possibility that micro-habitats, such as open water, which are impoverished in terms of the numbers of species and of individuals that they contain are over-represented. In addition, the National Pond Survey technique recommends sampling on two occasions: once in the summer (June-August) and again in the autumn (September-November) (Pond Action, 1989), but smaller sampling units spaced at regular intervals throughout the period would provide a more continuous representation of the species present. This is particularly relevant when sampling groups which do not have aquatic adults and thus appear only temporarily.

The aquatic Coleoptera are a particularly useful group in the assessment of the conservation status of wetlands (Foster, 1987). Their value as indicator species is related to a number of characteristics: they are not subject to extreme seasonality and adults are found throughout the year, they occupy all types of wetland habitat, the majority are either predators or scavengers and there are no host-specific phytophages, they contain both pollution sensitive and resilient species and, finally, while some species are usually among the first to colonise a new water body, there are many species incapable of dispersal from isolated relict habitats.

The classification of ponds at Hamsterley Forest identified five groups of sites based on their invertebrate assemblages. These can be loosely defined as follows: moorland pools, stream-influenced ponds on river-bed gravels, very recent ponds, small exposed fire reservoirs and small heavily-shaded peat-based fire reservoirs. The groupings reflect genuine physico-chemical and biological differences between the ponds. The small number of plant species in some ponds made the classification of the ponds on the basis of their vegetation less precise, although the dissimilarity of the moorland and forest ponds was again emphasised.

In the present study five factors were identified by canonical correspondence analysis as important determinants of the major community gradients and the composition of invertebrate assemblages. These were shade, area, age, pH and conductivity, with shade being the longest and most important gradient.

In a classification of the habitats of aquatic Coleoptera in North-east England Eyre (1986) found that the major environmental influences on the formation of assemblages of aquatic Coleoptera were firstly pH and secondly the amount of oxygen in the water. The study which was based on 384 sites encompassed a wide range of aquatic habitats including rivers, large permanent lakes, transition mires, lowland marshes and saltmarshes. River sites contained little vegetation with beetles living either in the gravel e.g. *Oreodytes* spp., or in moss on boulders, e.g. *Hydraena gracilis*. Large permanent lakes or ponds contained some weed but were generally bare. *Haliplus lineolatus* and *Potamonectes assimilis* were characteristic. Transition mires contained a mixture of *Sphagnum* spp., *Glyceria* spp., *Carex* spp. and *Juncus* spp. The prevalent species were not only those favouring grassy conditions, mud and temporary water, e.g. *Hydroporus palustris* and *Hydrobius fuscipes*, but also acid water-species such as *Hydroporus gyllenhali* (Balfour-Brown, 1940). Lowland marshes contained *Glyceria* spp., *Carex* spp., *Juncus* spp. and *Typha* spp. but rarely Sphagnum spp. The Coleoptera present were those favouring neutral-basic conditions (Balfour-Brown, 1940), e.g. *Hydroporus planus*. The present study has been of a relatively restricted habitat range and it is therefore not surprising that the determinants of the major community gradients should be different.

In a study of forest ponds in Scotland, Jeffries (1990) demonstrated that the major division from the classification and ordination of ponds, based on macrophytes was due to acidification. The dominant patterns in the non-acid division were linked to pond establishment, with new or disturbed ponds separating out, or to drying out regime. The study included natural and artificial ponds in clear felled, replanted and closed canopy areas on a range of sediment types (e.g. peat, clay, sand, gravel, pebble, cobble, boulder and bed-rock). In this greater range of habitats two of the major environmental gradients, pH and age, proved to be the same as in the present study, indicating their wider importance.

The presence of a dense crop of conifers around the boundary of a pond plays an important role both directly and indirectly in shaping the biota of the pond. The intensity and quality of light reaching a pond surface will directly determine the level of primary productivity of that pond. Moss (1979) has shown that light availability is a very significant factor in determining the distribution of submerged aquatic plants. The level of shading will also influence the pond's temperature regime, damping the oscillations. The surrounding trees will serve to shelter the pond thus preventing disturbance of the water surface by the wind which would result in increased levels of dissolved oxygen. In addition to this the trees provide a large input of coniferous litter which accumulates at the bottom of the ponds resulting in anoxic sediments and an increased biological oxygen demand of the water. The heavily shaded fire reservoirs consequently support an impoverished macrophyte community consisting of no more than the occasional stand of *Juncus effusus*. The macro-invertebrate assemblages of these ponds are also restricted consisting of a few species of Coleoptera, but no species of Corixidae.

The possible effects of pond area on community composition have both biogeographic and biotic elements. As area increases so the number of different micro-habitats and their associated species are likely to increase. Population sizes should also increase with area thus reducing the extinction rate of resident species (MacArthur & Wilson, 1967); and large target areas may simply receive a larger number of colonizing propagules and therefore have more chance of receiving a greater variety of species than smaller ponds. Area, as an expression of the size of a water body is also related to its persistence. Small ponds, such as Upper Redgate Shield Pond, tend to be less persistent than larger ones. The water level in this pond fluctuated considerably during the course of the study and by the end of the summer the pond had almost dried up. Smaller ponds may therefore exhibit greater fluctuations in physical and chemical conditions and so present a changing habitat. Habitat stability has been shown to influence the identity and possibly the diversity of corixid species in a water body (Macan, 1954, 1962). Corixids were absent from Upper Redgate Shield Pond, the least stable of the ponds studied, and also Fire Reservoirs (1, 2, 3, and 4) and were mostly confined to the larger ponds. However both *Agabus bipustulatus* and *Helophorus brevipalpis* were particularly abundant in Upper Redgate Shield Pond, these active flying species are characteristic of temporary or unstable ponds (Eyre, 1986).

In the present study, pond age was an important determinant of species composition, but is not necessarily correlated directly with species diversity. For instance, the moorland pools, constructed in the earlier half of the last century, were no more diverse in terms of their species composition than some of the larger ponds constructed in the past ten years. In the moorland pools species may have been precluded by the acidity and oligotrophic status of the water.

During the initial colonisation of newly created ponds there is a general increase in the numbers of species of invertebrates and macrophytes (Gates, 1927; Street & Titmus, 1979; Barnes, 1983). Where dispersal distances are short the rate of acquisition of new species is likely to decline within a few years (Barnes, 1983), suggesting an approach to an equilibrium number of species as predicted by the theory of Island Biogeography (MacArthur & Wilson, 1967). However, the numbers of less vagile species may continue to rise over many decades (Godwin, 1923). As a pond ages the habitat it presents to colonists changes, partly due to the extent and diversity of aquatic vegetation and partly due to the production of autochthonous detritus. Such changes are accompanied by changes in the identity of the invertebrate taxa (Street & Titmus, 1979; Barnes, 1983). Invasion by an individual species depends on the availability of suitable source propagules in source habitats, the species dispersal mechanisms and the dispersal distances, but is also subject to stochastic factors (Talling, 1951). Within Hamsterly Forest dispersal distances are short, ponds tend to be in close proximity to one another and to the becks which run through the forest and at least three of the ponds studied are fed directly by these streams. These factors may partly explain the relative diversity of the recent ponds.

The aquatic Coleoptera and Hemiptera-Heteroptera are relatively vagile by comparison with other insect groups with non-aquatic adults and have been shown to be the earliest colonists of water bodies (Barnes, 1983). In both orders adults are present throughout the year and fly whenever temperature and weather conditions are suitable (Popham, 1964). Species of both orders can migrate over quite large distances. In a study of the colonisation of ball-clay ponds Barnes (1983) found that the number of species immigrating from beyond the immediate source area was greater for the Coleoptera and Hemiptera-Heteroptera than for any other order. Within the Hemiptera, the Corixidae in particular are highly vagile and colonise very quickly. Fast immigration rates are not however universal within the Corixidae. The earliest colonists *Sigara nigrolineata* and *Corixa punctata* are typical species of temporary water bodies, which must be recolonised seasonally and flightless morphs are rare (Young, 1965). Both species occurred in Millfield Pond, the most recent and isolated pond in the present study and in at least two other recent ponds. In contrast *Sigara distincta* is a late colonist and is characteristic of permanent waters (Macan, 1954), the species is markedly polymorphic in flight musculature. Although in the present study this species occurred in two comparatively recent ponds, Euden Beck Pond and Tinker Hills Pond, it is possible that it arrived via the adjacent streams rather than by flight. The sequence of colonisation of Corixids is closely related to their relative rates of migration.

Correlations between biotic diversity and water chemistry have been demonstrated by many workers (e.g. Aho, 1987; Green, 1986; Okland, 1980). In the present study pH was found to be the aspect of water chemistry most strongly related to community composition and to be inversely correlated with species diversity. An increase in the number of taxa in a pond with increasing pH was demonstrated by Friday (1983). Individual taxa generally exhibit one of a number of distributional patterns in response to pH: (a) Many taxa are not present below a pH of 5.5. (b) Few taxa occur only in acid ponds. (c) Some species occurring across a range of pH show changes in their abundance with pH. Extreme acidity is likely to exclude all but the most tolerant species for physiological reasons (Sutcliffe & Carrick, 1973), but indirect effects on habitat also influence invertebrate colonisation. For example, the macrophyte vegetation in acid and neutral ponds differs in the dominant species. *Potamogeton natans* is replaced by *Juncus bulbosus* in acid ponds. *Juncus bulbosus* creates a more complex structure of submerged surfaces, but does not die-back annually to produce large amounts of litter unlike *Potamogeton natans* (Hendrey et al, 1976). Thus the detritus food chain, which is an essential component of maturing ecosystems is virtually absent from new acid ponds. The acid water fauna in such ponds tends to be dominated by a few algivorous or carnivorous species which tolerate the impoverished conditions and may flourish in the absence of competitors. However in the present study the moorland pools were not devoid of organic debris, and the lower pool in particular contained a considerable amount of litter derived from the *Juncus effusus* and *Sphagnum* mosses which line the pool. Upland mire sites in the region which are dominated by *Carex* and *Sphagnum* have been found to contain considerable amounts of litter (Eyre, 1986). Nevertheless the moorland pools appear to be retarded in a relatively immature state by the effects of low pH.

In the ponds at Hamsterley Forest electrical conductivity was found to be of some importance in the shaping of invertebrate communities. Conductivity is likely to correlate with ionic composition of the water both quantitatively and qualitatively and succession in corixids has been shown to occur in relation to conductivity and the accumulation of organic matter (Savage, 1989). The majority of corixids found in the present study are characteristic of oligotrophic waters (40-110 uS/cm) e.g. *Micronecta poweri*, *Sigara distincta* and *Hesperocorixa castanea* (Savage, 1989). None of the ponds studied could be described as being of more than mesotrophic status (100-300 uS/cm). *Hesperocorixa sahlbergi* was the only species of corixid normally associated with eutrophic waters (Savage, 1989) to be found in the study. This species occurred in five ponds, but was most numerous in Middle Redgate Shield Pond which was found to have a relatively high conductivity.

Both the extent of vegetative cover and diversity of plant species present were found to correlate with invertebrate diversity, although these factors also appear to correlate with the environmental variables discussed above. Middle Redgate Shield Pond, in particular, supported a high diversity of both macrophytes and invertebrates. The heavily shaded fire reservoirs were least diverse in terms of both macrophytes and invertebrates. Palmer (1981) demonstrated a close relationship between macrophyte species diversity and the number of species of Coleoptera and Hemiptera-Heteroptera in base-rich ponds in Norfolk. Structural factors such as bank topography and changes in substratum associated with irregularities in shoreline are of particular importance for pond macrophytes.

There is some evidence that biotic interactions such as competition and predation might be an important influence from the earliest stages of pond colonisation. In new ponds extensive pure stands of emergent or floating-leaved macrophytes may establish within a few years (Barnes, 1983) and preclude other species by competition for light and space. They may constitute very distinctive habitats for invertebrates and if by chance different aggressive species colonise neighbouring ponds then quite different invertebrate communities may result.

Balfour-Brown (1940) distinguished between silt ponds and detritus ponds in a broad classification of aquatic Coleoptera habitats based on obvious physical and vegetative characteristics. The silt pond is one sited in gravel, marl or sand, free from or with very little vegetation, and it is frequented by more species of aquatic Coleoptera than any other type of habitat, although few of these beetles are characteristic of silt ponds as such. As vegetation increases, the subsequent senescence of plants leads to an accumulation of organic matter and the sediment is transformed from silt to mud. The recently constructed ponds at Hamsterley Forest probably fall into the first category, but are still undergoing colonisation and have not yet reached a state of maximum diversity. Middle Redgate Shield Pond may be considered to lie further along this gradient, and has probably reached a state of maximum diversity. The accumulation of organic matter will bring about the eventual infilling of the pond and subsequent loss of aquatic invertebrates. The pond will eventually succeed in its entirety to wet meadow, such as that which currently surrounds it. The heavily-shaded Fire Reservoirs may be considered as extreme examples of detritus ponds supporting impoverished Coleoptera assemblages, but have not followed the usual course of succession. These ponds closely resemble their original form, having never supported any significant macrophyte assemblage, the source of detritus being the surrounding trees.

The Coleoptera assemblages of ponds at Hamsterley Forest comprised mostly common species. Two "local" species, *Hydroporus obscurus* and *Strictotarsus duodecimpustulatus* and three "notable" species *Laccobius atratus*, *Ilybius subaeneus* and *Strictonectes lepidus* (Ball, 1987) were found. Although the ponds contained no rare species they nevertheless exhibit important differences in terms of their species compositions which reflect their physico-chemical and biotic characteristics. The identification of the five most important determinants of community composition has important implications for the future construction and management of forest ponds. It is important that trees are planted sufficiently far from pond margins so as to avoid direct shading of the ponds and pollution arising from large inputs of litter. Larger ponds are preferable to smaller ones both in terms of their stability and the potentially greater number of distinct micro-habitats they contain. Water quality characteristics such as pH and conductivity are less amenable to direct manipulation, although the nature of the water source and type of underlying substrate are probably important determinants of water quality. Stream fed ponds sited on silt or river-bed gravels are likely to provide better habitat for both macrophytes and macroinvertebrates than peat pools fed by ground or drainage water. The avoidance of direct drainage from road surfaces would undoubtedly prove beneficial. Although age is an important determinant of species composition it does not necessarily correlate directly with species diversity. The colonisation of recent ponds at Hamsterley Forest is likely to occur at different rates for a number of reasons, including the degree of isolation of the ponds and range of available microhabitats, but most ponds will eventually reach a state of maximum species diversity beyond which subsequent infilling and succession will result in loss of diversity. At this point some form of management such as deepening and the removal of invasive scrub may be required in order to limit succession and prevent a subsequent transition to semi-aquatic and terrestrial habitat.

The fire ponds at Hamsterley Forest undoubtedly make a very important contribution to the diversity and wildlife interest of the forest habitat and the future construction of additional ponds can only add to the conservation potential of the area as a whole.

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APPENDICES

APPENDIX 1.

Total numbers of individuals of species in samples.

	Pond							
Species	F1	F2	F3	F4	F5	F6	RL	RM
Dytiscidae								
Agabus bipustulatus	1	3	4	20	4	5	2	18
A. nebulosus								
A. sturmii							3	10
Hydroporus erythrocephalus								3
H. gyllenhalii			3	4				1
H. incognitus	7			3			4	25
H. nigrita								1
H. obscurus								
H. palustris	2			4		11		2
H. pubescens				1		4	4	4
H. tristis								
Ilybius subaeneus							2	1
Oreodytes sanmarkii						1		
Potamonectes depressus					1			
Strictonectes lepidus								
Strictotarsus duodecimpustulatus							1	
Elmidae								
Oulimnius sp					1			
Gyrinidae								
Gyrinus substriatus					(2)	(2)	(1)	
Haliplidae								
Haliplus lineatocollis							2	29
H. ruficollis agg.								1
Hydraenidae								
Limnebius truncatellus							1	1
Hydrophilidae								
Anacaena globulus	1							14
A. lutescens								3
Helophorus aquaticus agg.							14	143
H. brevipalpis							52	83
H. flavipes							2	12
Hydrobius fuscipes								10
Laccobius atratus								
Corixidae								
Arctocorisa germari						3		
Callicorixa wollastoni								1
Corixa punctata								
Glaenocorisa propinqua								
Hesperocorixa castanea								
H. sahlbergi							2	4
Micronecta poweri								
Sigara distincta								
S. nigrolineata					1			
Gerridae								
Gerris costai						(2)	(2)	(2)
G. gibifer					(1)			
G. lacustris					(2)		(3)	
Veliidae								
Velia caprai	(3)		(3)	(3)				

	Pond							
Species	RU	PS	EB	MF	EU	EL	TY	TH
Dytiscidae								
Agabus bipustulatus	13		12	1	3		2	4
A. nebulosus				2				
A. sturmii			18					3
Hydroporus erythrocephalus					1			
H. gyllenhalii								1
H. incognitus	3		22					3
H. nigrita								
H. obscurus					2			
H. palustris								
H. pubescens			2	1			2	4
H. tristis					1			
Ilybius subaeneus								4
Oreodytes sanmarkii		8						
Potamonectes depressus		24	5					
Strictonectes lepidus		1						
Strictotarsus duodecimpustulatus								
Elmidae								
Oulimnius sp								
Gyrinidae								
Gyrinus substriatus			(2)	(2)	(2)		(2)	(3)
Haliplidae								
Haliplus lineatocollis	1		1					
H. ruficollis agg.								
Hydraenidae								
Limnebius truncatellus								
Hydrophilidae								
Anacaena globulus	15		1	1				1
A. lutescens	1							
Helophorus aquaticus agg.	43	3	57	7	1			3
H. brevipalpis	26	1	35	19			3	4
H. flavipes	2		6	2			1	
Hydrobius fuscipes	1		1				6	2
Laccobius atratus							1	
Corixidae								
Arctocorisa germari				1			1	
Callicorixa wollastoni				2	5	22	1	2
Corixa punctata			1	1				4
Glaenocorisa propinqua					2	2		
Hesperocorixa castanea					1			
H. sahlbergi			6			1		5
Micronecta poweri		15						1
Sigara distincta			2					5
S. nigrolineata				2			5	26
Gerridae								
Gerris costai	(1)	(3)	(2)	(3)	(1)	(2)	(1)	(3)
G. gibifer								
G. lacustris		(2)		(2)			(1)	
Veliidae								
Velia caprai		(2)						

APPENDIX 2.

Numbers of samples taken in ponds at Hamsterley Forest.

Pond	F1	F2	F3	F4	F5	F6	RL	RM
Method 1	5	5	5	5	6	5	10	12
Method 2							*	*

Pond	RU	PS	EB	MF	EU	EL	TY	TH
Method 1	5	10	10	10	10	8	10	10
Method 2			*	*	*	*	*	*

APPENDIX 3.

Plant species in ponds at Hamsterley Forest, together with their cover values.

	Pond							
Species	F1	F2	F3	F4	F5	F6	RL	RM
Agrostis stolonifera								
Carex demissa								
Callitriche hamulata								
C. stagnalis							4	
Deschampsia cespitosa								
Equisetum fluviatile								3
E. palustre							3	4
Glyceria fluitans							4	
Juncus bulbosus					3		4	3
J. effusus				2	3	1	4	3
Potamogeton natans					5		3	5
Ranunculus flammula							1	2
R. omiophyllus							1	
Sparganium emersum								
Sphagnum sp			4		2			3
Total Cover	0	0	1	1	5	1	3	5

	Pond							
Species	RU	PS	EB	MF	EU	EL	TY	TH
Agrostis stolonifera							2	2
Carex demissa		1						
Callitriche hamulata		3					1	
C. stagnalis		3						
Deschampsia cespitosa		1		3				
Equisetum fluviatile								
E. palustre	3		2					
Glyceria fluitans			3				3	
Juncus bulbosus	4	3		4			2	3
J. effusus	3	3	4	4	4	5	4	4
Potamogeton natans	3		3				2	
Ranunculus flammula				1				
R. omiophyllus			3				1	
Sparganium emersum							1	
Sphagnum sp					5	5		
Total Cover	2	1	3	3	1	1	2	1

APPENDIX 4.

Pond Characteristics

Pond	Area (m^2)	Depth max(m)	Over -hang	Sed Size	Litter
F1 Fire Reservoir 1	16	0.7	4	3	2
F2 Fire Reservoir 2	10	1.0	5	5	3
F3 Fire Reservoir 3	12	1.1	1	4	3
F4 Fire Reservoir 4	26	1.1	4	5	3
F1 Fire Reservoir 5	24	1.4	0	3	1
F6 Fire Reservoir 6	27	1.5	1	3	1
RL Redgate Shield (lower)	492	1.0	0	2	0
RM Redgate Shield (mid)	353	0.4	1	3	1
RU Redgate Shield (upper)	18	0.3	0	3	2
PS Pooh Stick Pond	97	0.6	1	3	1
EB Euden Beck Pond	428	1.0	0	4	1
Millfield Pond	292	2.5	0	1	1
EU Everpool (upper)	517	1.8	0	3	0
EL Everpool (lower)	59	0.8	0	3	0
TY Tulleys Pond	478	0.9	0	2	1
TH Tinker Hills Pond	164	0.8	0	3	1

APPENDIX 5.

Results of water quality analysis.

	Pond							
Variable	F1	F2	F3	F4	F5	F6	RL	RM
Oxygen (%)	22	9	42	26	26	97	97	65
pH	7.29	4.49	4.30	5.35	5.57	8.38	6.61	6.60
Conductivity (uS/cm)	275	50	59	72	53	125	185	225
BOD 5 Total (mg/l)	14.0	9.0	3.0	5.0	1.1	1.8	3.0	1.4
Amm. nitrogen (mg/l)	0.52	1.36	0.50	2.26	0.72	0.64	0.57	0.59
Nitrate (mg/l)	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Nitrite (mg/l)	0.09	0.08	0.04	0.10	0.06	0.07	0.07	0.07
Solids (mg/l)	41	21	3	21	4	5	6	4
Turbidity (rank)	14	13	12	16	10	7	1	4

	Pond							
Variable	RU	PS	EB	MF	EU	EL	TY	TH
Oxygen (%)	96	85	63	100	90	43	92	82
pH	6.95	7.02	6.55	6.16	3.86	4.50	5.80	6.50
Conductivity (uS/cm)	166	170	150	110	125	79	65	89
BOD 5 Total (mg/l)	1.4	1.6	1.8	1.4	1.0	5.0	1.6	2.0
Amm. nitrogen (mg/l)	0.70	0.63	0.70	0.69	0.91	0.92	0.86	0.75
Nitrate (mg/l)	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Nitrite (mg/l)	0.05	0.08	0.08	0.07	0.04	0.04	0.07	0.08
Solids (mg/l)	4	3	4	2	5	15	2	5
Turbidity (rank)	3	5	6	2	11	15	8	9