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Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England

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Abstract

Information about the relative biodiversity value of different waterbody types is a vital pre-requisite for many strategic conservation goals. In practice, however, exceptionally few inter-waterbody comparisons have been made. The current study compared river, stream, ditch and pond biodiversity within an 80 km^2 area of lowland British countryside. The results showed that although all waterbody types contributed to the diversity of macrophytes and macroinvertebrates in the region, they differed in relative value. Individual river sites were rich but relatively uniform in their species composition. Individual ponds varied considerably in species richness, with the richest sites supporting similar numbers of taxa to the best river sections, but the poorest sites amongst the most impoverished for all waterbody types. At a regional level, however, ponds contributed most to biodiversity, supporting considerably more species, more unique species and more scarce species than other waterbody types. Streams typically supported fewer species and fewer unique species at local and regional level than either ponds or rivers. Ditches (most of which were seasonal) were the least species-rich habitat, but supported uncommon species, including temporary water invertebrates not recorded in other waterbody types. Multivariate analysis indicated that permanence, depth, flow and altitude were the main environmental variables explaining invertebrate and plant assemblage composition. The findings, as a whole, suggest that ponds and other small waterbodies can contribute significantly to regional biodiversity. This contrasts markedly with their relative status in national monitoring and protection strategies, where small waterbodies are largely ignored.

Keywords: Wetland; Community; Similarity; Macroinvertebrate; Macrophyte

1. Introduction

Over the last 10 years, the concept of integrated catchment management has begun to gain wide acceptance amongst water managers (Gardiner, 1994; Everard, 1999; Verdonschot, 2000). Its central premise, that land and water need to be managed together at a catchment level to ensure long-term ecological and socio-economic sustainability, has also been increasingly emphasised in legislation and policy. Most recently, the new EC Water Framework Directive (2000/60/EC) has placed catchment management at the centre of European water protection policy by requiring Member States to maintain the ecological quality of all fresh waters in a catchment context.

Achieving sustainable catchment management requires, inter alia, knowledge of the biodiversity characteristics and importance of different waterbody types within catchments (Schneiders and Verheyen, 1998). This includes information about the relative richness of different waterbody types, their variability across the landscape, and net contribution to catchment biodiversity. In practice, however, such data are exceptionally scarce. This is, in part, because traditional freshwater research has generally been waterbody-specific with very few comparisons made between different waterbody types. In addition, most research on specific waterbody types has focused on rivers, streams and lakes with little data describing other smaller natural or man-made habitats such as ditches, ponds, headwater

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streams, springs and flushes. In the few cases where wider catchment studies have been undertaken, their relevance and applicability has usually been restricted, because they either cover a limited range of taxa (Gontcharov, 1996; Sanoamuang, 1998), focus on restricted or atypical habitat types (Abernethy and Willby, 1999; Godreau et al., 1999; Pollock et al., 1998; Vincent and James, 1996; Ward et al., 1999) or use methodologies which differ between the waterbody types, making direct comparison difficult (Doledec and Statzner, 1994; Verdonschot, 1990). There remains, therefore, a paucity of information describing freshwater biodiversity across wider catchment areas, either semi-natural or managed. The need for such data is particularly urgent because it has immediate relevance for many areas of catchment management including the strategic location of agri-environment schemes, water resource management, pesticide strategic risk assessment and catchment restoration.

The aim of this paper is to present some of the first data to compare the biodiversity of different freshwater ecosystems in a lowland agricultural landscape. The survey area, on the Oxfordshire/Wiltshire border of southern England, includes a representative range of waterbody types, both permanent and seasonal, including streams, ponds, ditches, rivers and lakes. The comparative biodiversity of these waterbodies was assessed in terms of their wetland macrophytes and aquatic macroinvertebrates, with comparisons made of assemblage type, the occurrence of rare species and the alpha, beta and gamma diversity of each waterbody type.

2. Study area

The study area comprised an 80 km^2 square (ca 9×9 km), centred on the River Cole at Coleshill, Oxfordshire (national grid reference SU234935) (Fig. 1). Land use in

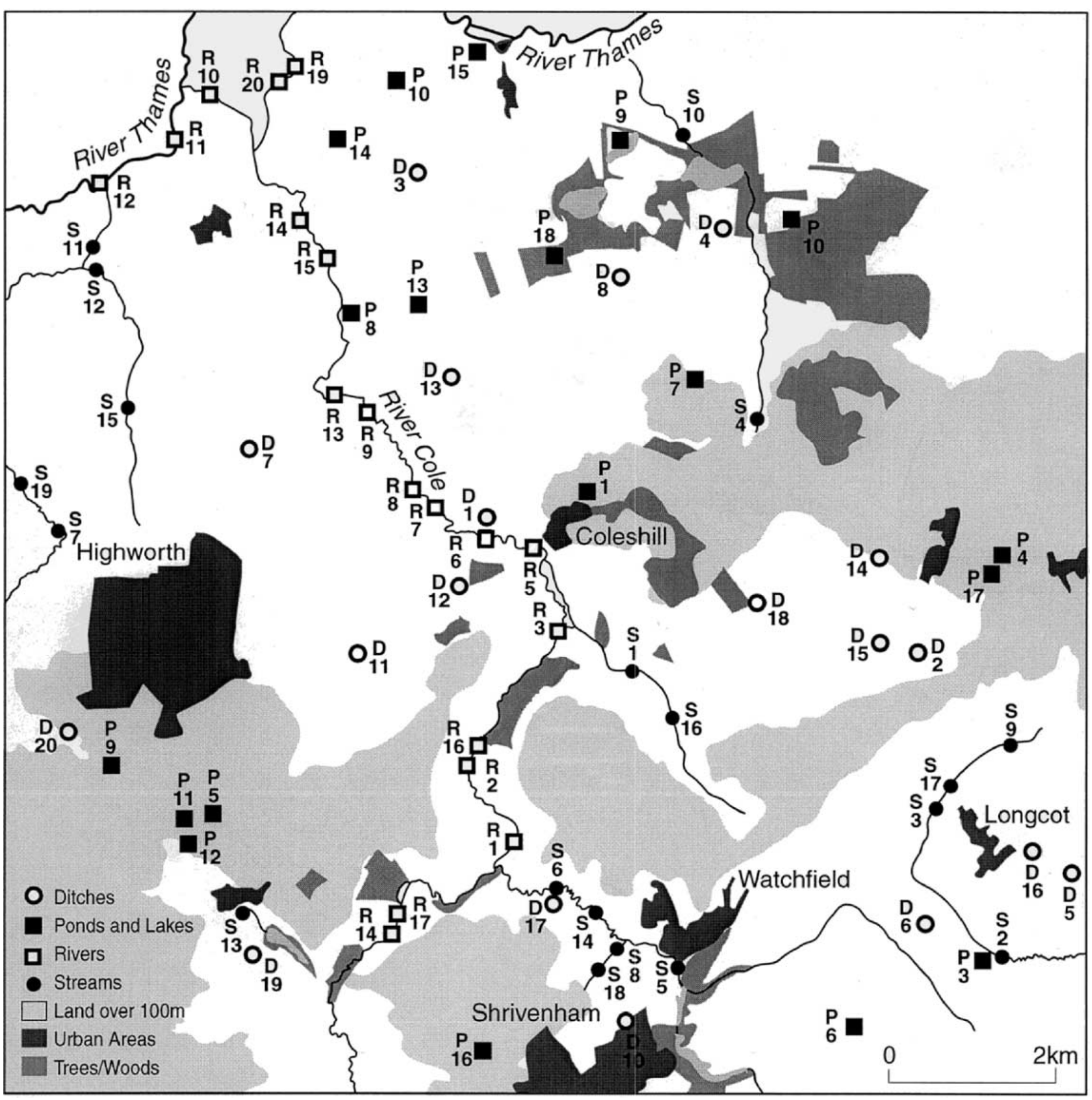

Fig. 1. The study area showing location of river, pond, stream and ditch sampling sites.

Table 1
Summary of definitions of aquatic habitats used in the survey

Waterbody type	Definition
Lakes	A body of water >2 ha in area (Moss et al., 1996). Includes reservoirs and gravel pits.
Ponds	Waterbodies between 25 m^2 and 2 ha in area which may be permanent or seasonal (Collinson et al., 1995). Includes both man-made and natural waterbodies.
Ditches	Man-made channels created primarily for agricultural purposes, and which usually: (i) have a linear planform, (ii) follow linear field boundaries, often turning at right angles, and (iii) show little relationship with natural landscape contours.
Streams	Small lotic waterbodies created mainly by natural processes. Marked as a single blue line on 1:25,000 Ordnance Survey (OS) maps and defined by the OS as being <8.25 m in width. Stream differ from ditches by (1) usually having a sinuous planform, (2) not following field boundaries, or if they do, pre-dating boundary creation, and (3) showing a relationship with natural landscape contours e.g. running down valleys.
Rivers	Larger lotic waterbodies, created mainly by natural processes. Marked as a double blue line on 1:25,000 OS maps and defined by the OS as >8.25 m in width.

the region was mainly mixed grassland and arable agriculture with ca 9% of the area woodland and 8% urban. The geology is largely Oxford Clay to the south and mixed strata of limestone, sands and clays of Corallian age to the north. Topographically, the region is dominated by low rolling hills with ca 10% of the area lying within the floodplains of the Rivers Thames and Cole. Altitude varies between 72 and 158 m above sea level.

Within the survey area five main waterbody types were distinguished using the map criteria described in Table 1. Using these definitions the region was found to have four lakes, 65 ponds, seven streams, an extensive network of ditches, and two rivers: a small portion of the River Thames and the River Cole, a 3rd order tributary of the Thames (Table 2).

3. Methods

3.1. Sampling strategy

In total, 80 sites were sampled within the survey area. Of these, half were surveyed in spring 2000 (April and May) and the remainder in autumn 2000 (October and November). Sample sites were stratified by waterbody type with 20 sites surveyed in each of the following categories: (i) ditches, (ii) streams, (iii) rivers, and (iv) ponds and lakes. In each season, equal numbers of each waterbody type were surveyed (i.e. 10 in spring, 10 in autumn). Within this stratification, sites were selected randomly from all potential sites shown on the Ordnance Survey 1:25,000 scale maps of the area. Within the combined pond and lake category the random selection identified 19 ponds and one lake. This category is referred to as 'ponds' in later sections.

Table 2
Length of lotic waterbodies and number of lentic waterbodies in the survey area

Rivers	Streams	Ditches	Ponds	Lakes
17.25 km	28.75 km	70.00 km	65 sites	4 sites

Data derived from analysis of 1:25,000 scale Ordnance Survey maps.

To ensure that ecological data gathered from different waterbody types could be directly compared, the sampling was area-limited with data from each site collected from a 75 m^2 area of the waterbody. Thus for a 1 m wide ditch a 75 m length of ditch was surveyed. For discrete waterbodies, like ponds and lakes, the 75 m^2 area was approximately triangular with the apex at the middle of the waterbody and the base following the waterbody margin. Although this area-based survey method enabled waterbodies with widely differing dimensions and characteristics to be compared, it had the disadvantage that small waterbodies less than 75 m^2 could not be included in the survey. In practice three ponds were excluded for this reason.

3.2. Field data collection

All wetland macrophytes present within the 75 m^2 sample area were recorded. Plants were surveyed while walking and wading the margin and shallow water areas of the waterbody. In deeper water (two sites) submerged macrophytes were surveyed using a grapnel thrown from the bank. 'Wetland macrophytes' were defined as those plants listed as wetland plants in the National Pond Survey methods guide (Pond Action, 1998) which comprises a standard list of ca 300 submerged, floating-leaved, emergent and marginal wetland plants.

Aquatic macroinvertebrates were collected using a standard 1 mm mesh hand-net, frame-size 0.26×0.30 m. Each site was sampled for a total of 3 min with the total sampling time divided equally between major mesohabitats identified in the 75 m^2 area. Samples from deeper water were collected using a long-handled pond net. Samples were exhaustively live-sorted in the laboratory to remove all individual macroinvertebrates, with the exception of very abundant taxa (>100 individuals) which were sub-sampled. Macroinvertebrate taxa were identified to species level in the groups for which reliable UK distribution data and Red Data Book information is available. These were Tricladida (flatworms), Hirudinea (leeches), Mollusca (snails and bivalves, but excluding *Pisidium* species), Malacostraca (shrimps and slaters), Ephemeroptera (mayflies), Odonata (dragonflies and damselflies), Plecoptera (stoneflies), Heteroptera (bugs), Coleoptera (water beetles), Neuroptera (alderflies and spongeflies) and Trichoptera (caddis flies). Other taxa (mainly Diptera larvae and Oligochaeta) were noted at family or genus level, but were not included in the analysis of species richness.

From each site physico-chemical data were collected describing water body area (or channel width), water and sediment depths, permanence, rate of flow, shade, substrate type, bank height and angle, surrounding land use, grazing intensity (Table 3). Details of the methods used to collect data are given in Pond Action (1998). Conductivity and pH were measured in the field to broadly characterise the waterbodies chemically. Analysis of other determinands could not be undertaken contemporaneously. To provide these data a chemical survey was undertaken in February 2002. This included field analysis of pH, conductivity and dissolved oxygen and collection of samples for laboratory analysis of total phosphorus, nitrate-nitrogen and suspended solids.

In total the full survey took ca 220 person days to design, organise and complete.

Table 3
Physico-chemical parameters measured

1. Northing
2. Easting
3. Altitude
4. Permanence (ranked 1 = permanent to 4 = dries annually)
5. Flow volume ($cm^3 s^{-1}$)
6. Area of waterbody shaded (%)
7. Margin of waterbody shaded (%)
8. Wood and scrub in 0–100 m zone (%)
9. Semi-natural grassland in 0–100 m zone (%)
10. Total grassland in 0–100 m zone (%)
11. Wetlands in 0–100 m zone (%)
12. Total semi-natural land use in 0–100 m zone (%)
13. Total intensive agriculture in 0–100 m zone (%)
14. Water depth (mean)
15. Sediment depth (mean)
16. Organic matter in sediment (%)
17. Sediment size (phi)
18. Bank angle (mean)
19. Bank height (mean)
20. Waterbody margin grazed (%)
21. Grazing intensity (ranked 0–5)
22. Turbidity (ranked 1 = clear, 4 = turbid)
23. pH (mean)
24. Conductivity (mean)
25. Dissolved oxygen
26. Nitrate–nitrogen
27. Total phosphorus
28. Suspended solids

3.3. Analytical methods

The data were analysed to assess the biodiversity value and characteristics of the different waterbody types in terms of three main biotic attributes: (i) species richness, (ii) species rarity, and (iii) assemblage type.

Richness was measured as the number of species, or distinctive taxa, recorded. Alpha diversity was measured as the richness of individual samples. Beta diversity was described using Jaccard's coefficient (Southwood, 1984) and multivariate assessment techniques (see later). Gamma (regional) diversity was calculated as the total number of species recorded in each waterbody type within the survey area. Species richness data differed in the extent to which they approached normality. Differences in alpha, beta and gamma diversity were, therefore, tested using non-parametric methods (e.g. Mann–Whitney U test). An estimate of true regional gamma diversity was made using the abundance-based coverage estimator (ACE) (Colwell and Coddington, 1994). ACE is based on the concept of 'sample coverage' developed by Chao and Lee (1992). Using this technique, species richness is estimated by considering the probabilities of encountering species ('coverage'), taking into account the species present but not observed. Species accumulation curves for each waterbody type were calculated from the species lists using a run of 500 sample randomisations in the computer programme EstimateS (Colwell, 1997).

Comparisons of species rarity were made using a species rarity index (SRI). This index is conceptually based on the Species Quality Score developed by Foster and colleagues in the 1980s (Foster et al., 1990) and was derived in the following manner: (I) all species present were given a numerical value depending on rarity/threat (see later), (ii) the score of all species in each sample were summed to give a Species Rarity Score, (iii) the Species Rarity Score was divided by the number of species recorded in the sample to give the SRI.

Six rarity categories were recognised and given the following conservation scores:

- Common species (score 1).
- Local (2): Invertebrates: either confined to certain limited geographical areas, where populations may be common or of widespread distribution, but with few populations. Plants:

recorded from fewer than 25% ($n \leqslant 705$) of 10×10 km grid squares in Britain (Preston et al., 2002).
- Nationally Scarce (4) recorded from 15 to 100 10×10 km grid squares in Britain.
- Red Data Book—conservation dependent or near threatened (8).
- Red Data Book—endangered or vulnerable (16).
- Red Data Book—critically endangered (32).

Plant and invertebrate assemblage types were described, and related to major environmental gradients, using canonical correspondence analysis (CCA), implemented in the computer programme CANOCO 4.0 (ter Braak and Smilauer, 1998). Species data were converted to presence/absence values and CCA was undertaken without downweighting of rare species. Environmental variables were chosen by forward selection in CANOCO with only those significant at $P < 0.05$ included in the model. Table 3 lists the environmental variables for which data were collected.

4. Results

4.1. Chemical data

Data summarising the chemical characteristics of the four main waterbody types are given in Table 4. As a whole, the waterbodies were circum-neutral to slightly alkaline with similar mean and range pH values. Mean conductivity and dissolved oxygen levels were also similar across the waterbody types. Ponds had the lowest mean values for nitrate-nitrogen and suspended solids but also by far the widest range values for these parameters. The mean total phosphorus concentrations for streams was unusually high. This was due to highly elevated total phosphorus levels at three closely grouped sites, probably caused by recent agrochemical applications to adjacent fields. Compared with other waterbodies, rivers showed a more limited range of conductivity, dissolved oxygen and nitrate-nitrogen values.

4.2. Richness (alpha diversity) and rarity values for individual samples

The number of plant and macroinvertebrate species recorded from individual samples in each waterbody type showed a consistent pattern, with mean alpha diversity for both groups showing the following trend: rivers > ponds > streams > ditches (Table 5). Ponds were generally more variable in their richness than other habitat types, particularly in terms of their invertebrate communities (Fig. 2). Thus the richest pond site (67 species) had a similar invertebrate species richness to the richest river site (66 species) but the poorest pond was amongst the most impoverished of all sites with only five invertebrate species recorded (Table 5). Assessment of the number of uncommon species in the waterbody types showed that, at site level, ponds had the highest mean invertebrate SRI. Ponds also had the highest mean plant SRI although, in practice, the mean plant rarity values for all waterbodies were similar (Table 6).

4.3. Sample similarity (beta diversity)

Jaccard's coefficients of similarity (C_j) calculated for each pair of the 20 sites within each waterbody type (Table 7) showed that, for macroinvertebrate species, river sites had significantly higher C_j values (i.e. samples were more uniform) than other waterbody types ($P < 0.001$). Comparisons of wetland plant assemblages showed that pond sites had significantly fewer species in

Table 4
Mean and range values for water chemistry determinands in waterbodies in the River Cole catchment

	Ponds	Rivers	Streams	Ditches
pH	8.1 (7.5–8.9)	8.3 (7.7–8.6)	8.0 (7.1–8.4)	8.0 (7.3–9.2)
Conductivity (μS cm^{-1})	654 (322–1265)	688 (593–785)	767 (571–1244)	791 (564–1402)
Dissolved oxygen (% saturation)	136 (63–255)	139 (104–158)	105 (43–140)	117 (55–222)
Nitrate nitrogen (mg l^{-1})	3.7 (0.1–38.3)	5.8 (3.2–9.7)	8.1 (2.3–19.8)	5.6 (0.4–17.7)
Total phosphorus (mg l^{-1})	0.27 (0.002–2.490)	0.24 (0.060–1.300)	0.74 (0.005–5.730)	0.14 (0.002–0.880)
Suspended solids (mg l^{-1})	73 (1–794)	24 (7–101)	20 (1–86)	35 (1–150)

Table 5
Mean number of species recorded in individual samples, with range in parentheses

	Rivers	Ponds	Streams	Ditches
Invertebrates	45.3 (18–66)	32.6 (5–67)	18.7 (3–50)	12.9 (2–35)
Wetland plants	10.7 (6–19)	10.1 (2–17)	7.3 (1–17)	6.1 (1–14)

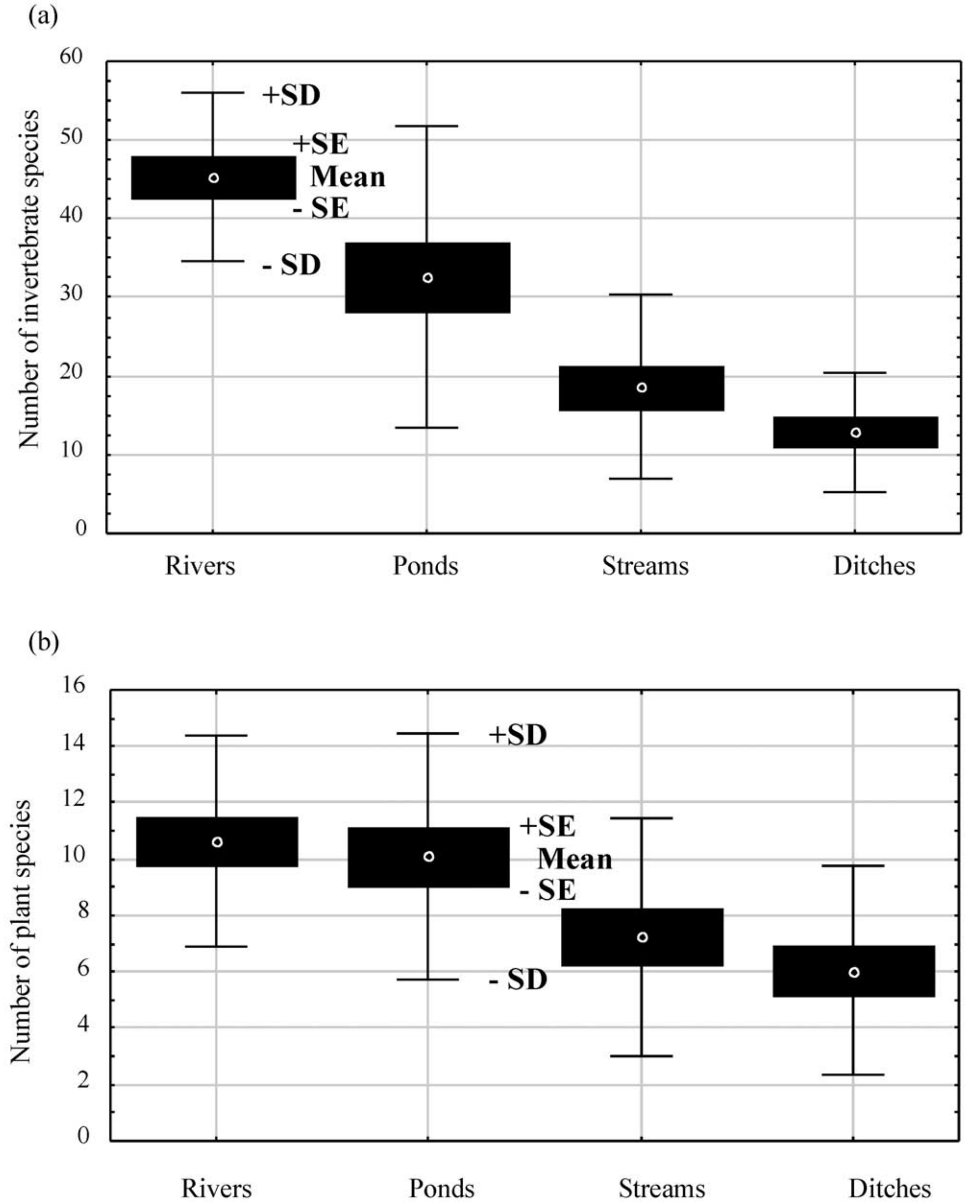

Fig. 2. Species richness in each waterbody type: (a) aquatic macroinvertebrates (b) wetland macrophytes (SE = standard error, SD = standard deviation).

Table 6
Mean species rarity in rivers, ponds, streams and ditches in the River Cole catchment, with range in parentheses

	Rivers	Ponds	Streams	Ditches
Species rarity index (SRI)				
Per site				
Invertebrates	1.10 (1.02–1.28)	1.19 (1.00–1.60)	1.09 (1.00–1.36)	1.14 (1.00–1.44)
Wetland plants	1.03 (1.00–1.09)	1.04 (1.00–1.22)	1.01 (1.00–1.08)	1.00 (1.00–1.00)
Number of species				
Region (i.e. total number of species)				
Nationally scarce invertebrate species	3	14	3	7
Local invertebrate species	14	15	11	6
Nationally scarce plant species	0	0	0	0
Local plant species	3	7	1	0

Table 7
Mean Jaccard's coefficient (C_j) values for each of the waterbody types

	Rivers	Ponds	Streams	Ditches
Invertebrate C_j	0.36	0.18	0.14	0.15
Wetland plant C_j	0.20	0.14	0.24	0.24

common (i.e. they were more variable) than other habitat types ($P < 0.005$). Differences in Jaccard's coefficients between other waterbody types were not significant.

4.4. Regional species richness (gamma diversity) and rarity

Ponds supported the greatest number of plant and invertebrate species across the survey region as a whole, followed by rivers, streams and ditches respectively (Table 8). The high observed gamma diversity for ponds reflected the large number of unique species recorded in this habitat, which was about twice that recorded in rivers, and six to eight times the number of unique species found in streams and ditches (Table 8). Out of the total 337 species of plants and invertebrates recorded in the survey, ponds supported 71%, rivers 60%, streams 48% and ditches 35%. This general pattern was consistent for both wetland plants and aquatic macroinvertebrates (Table 8). Sequentially combining waterbody data to achieve maximum biodiversity with the smallest number of waterbody types indicated that 71% of the area's species were supported by ponds alone. Addition of river habitats increased the total to 91%. Ditches added 6%, and streams a final 3% to total species richness.

Accumulation curves were calculated from the species lists for each waterbody type, based on 500 sample randomisations. The results show that plant and invertebrate species were still accumulating in all waterbody types with no consistent indication of the asymptotes (Fig. 3). To indicate true gamma diversity (i.e. the total rather than observed number of species present in the study area) Colwell's ACE was applied. Overall, the predicted values showed a similar pattern of waterbody richness to the observed data, with ponds contributing most species to the area (279 species predicted) followed by rivers (235), streams (220) and ditches (147).

At regional level, all the waterbody types supported nationally uncommon species but, overall, ponds consistently supported more uncommon species than other types of waterbody. Thus, of the 18 Nationally Scarce species recorded in the survey, the majority (14 species) were found in ponds. Ditches, despite being a generally species poor habitat, supported seven Nationally Scarce species, higher than both streams and rivers, which supported, respectively, four and three Scarce species (Table 6).

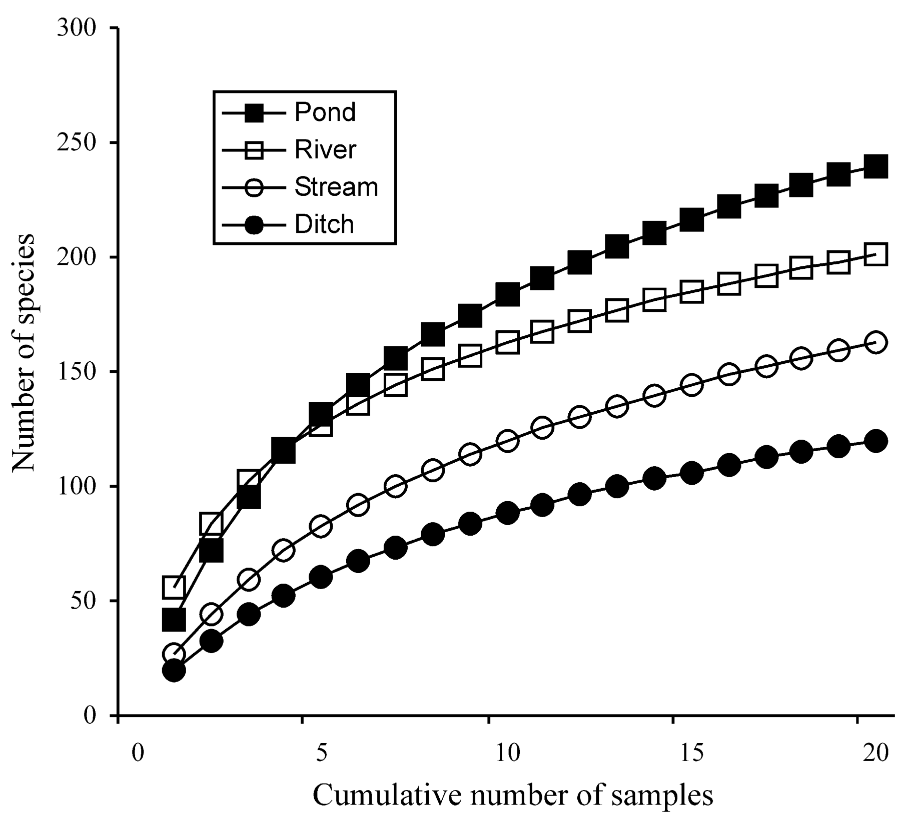

Fig. 3. Accumulation curves for plant and invertebrate species from the four waterbody types.

Table 8
Total number of species (gamma diversity) recorded across the survey region

	Rivers	Ponds	Streams	Ditches	All habitats
Invertebrate species					
Total number of species	152	173	124	90	249
Percentage of total species richness	61	70	50	36	100
Number of species unique to the waterbody type	26	50	6	8	–
Wetland plant species					
Total number of species	49	67	39	30	88
Percentage of total species richness	56	76	44	34	100
Number of species unique to the waterbody type	9	24	3	3	–
Invertebrates and wetland plants combined					
Total number of species	201	240	163	120	337
Percentage of total species richness	60	71	48	35	100
Number of species unique to the waterbody type	35	74	9	11	–
Total number of species in all habitats					337

4.5. Invertebrate and plant assemblages

CCA ordination of the invertebrate assemblage data (Fig. 4, Table 9) showed a broad continuum between the assemblages of rivers, streams and ditches along a water depth and seasonality gradient. Pond invertebrate assemblages were relatively distinct, but seasonal ponds showed some overlap with ditches (most of which were seasonal). The close grouping of river sites evident in the CCA indicate that river invertebrate assemblages were relatively similar across the catchment. Invertebrate assemblages from the ponds and ditches showed, in contrast, a relatively high degree of dispersion suggesting a more varied assemblage composition. Across the data set as a whole, altitude was the major correlate with Axis 1 of the CCA, largely separating rivers and streams, most of which were associated with valley landscapes, from ponds and ditches which were more widely spread across the survey region.

CCA ordination of wetland plant assemblage data (Fig. 5, Table 9) showed a strong overlap between the assemblages of the four waterbody types with only two

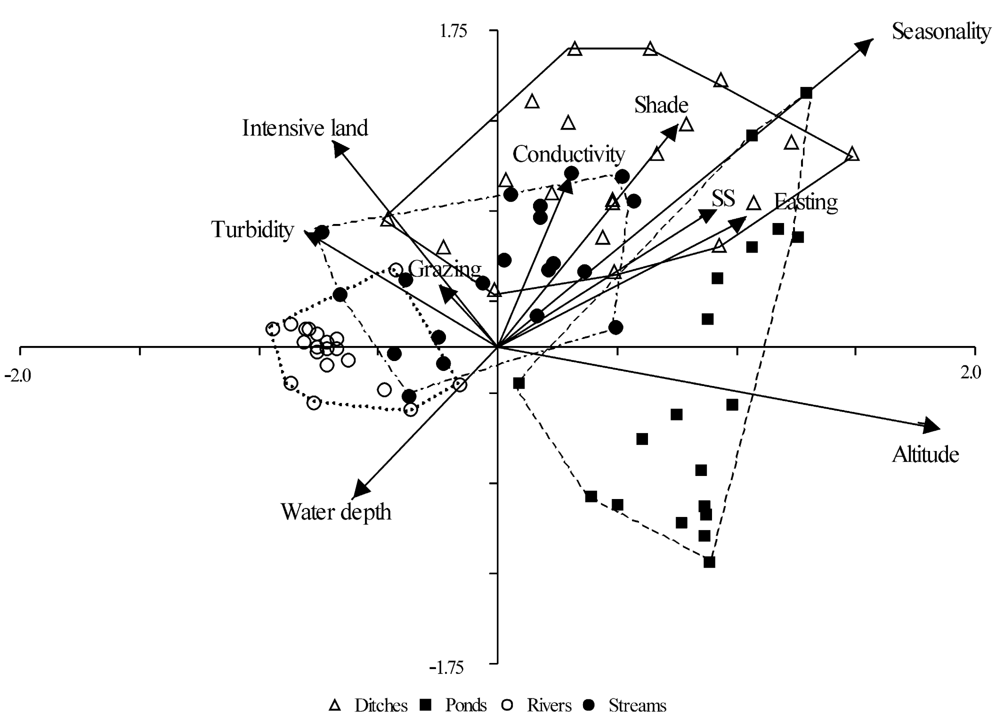

Fig. 4. Invertebrate canonical correspondence analysis. Polygons enclose each waterbody type. Arrows represent the correlation of physico-chemical variables with canonical axes.

Table 9
Summary statistics for canonical correspondence analyses of waterbody assemblage data and environmental variables

	Invertebrates		Wetland plants	
	Axis 1	Axis 2	Axis 1	Axis 2
CANOCO summary statistics				
Eigenvalue	0.434	0.263	0.429	0.360
Species-environment correlations	0.921	0.889	0.912	0.878
Cumulative percentage variation				
Explained by species only	5.6	9.0	4.1	7.6
Explained by species + environmental variables	26.4	42.4	19.9	36.7
Interset correlations with axes				
Northing	–	–	−0.285	0.397
Easting	0.297	0.214	0.433	0.197
Altitude	0.597	−0.220	0.748	−0.407
Permanence	0.434	0.674	–	–
Flow volume	−0.761	−0.036	−0.277	0.194
Area of waterbody shaded	0.179	0.446	–	–
Margin of waterbody shaded	–	–	−0.010	−0.545
Wood and scrub in 0–100 m zone	0.296	−0.296	–	–
Water depth	−0.211	0.192	–	–
Organic matter in sediment	−0.176	−0.598	–	–
Bank height	−0.191	0.067	–	–
Waterbody margin grazed	−0.155	−0.028	–	–
Grazing intensity	–	–	−0.202	0.423
Turbidity	−0.352	0.032	−0.189	0.367
Conductivity	−0.185	0.304	–	–

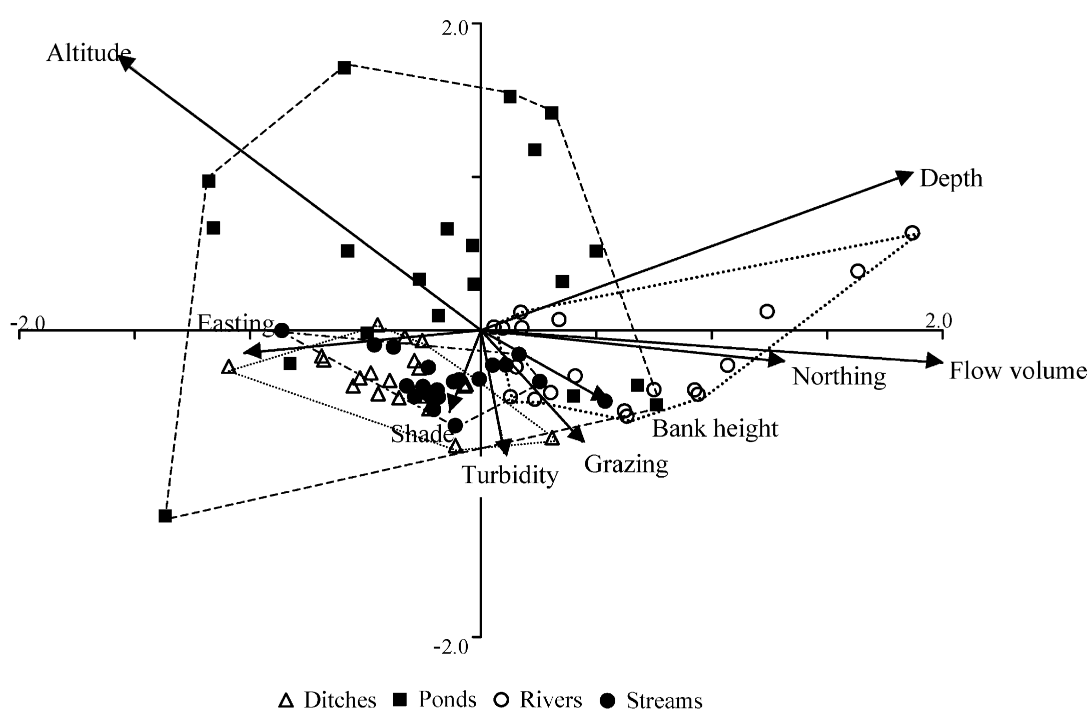

Fig. 5. Wetland plant canonical correspondence analysis. Polygons enclose each waterbody type. Arrows represent the correlation of physico--chemical variables with canonical axes.

outlying groups suggesting plant assemblages that were different to the majority of sites. These were (i) a relatively small group ($n=6$) of larger and faster flowing rivers, and (ii) a large, well dispersed group of ponds ($n=15$). As in the invertebrate CCA there was a continuum between the assemblages of rivers, streams and ditches along a gradient linked to water depth and flow. This was, however, less marked, with more assemblage overlap than in the invertebrate plot. Across the data set as a whole, altitude was, again, a strong environmental gradient on Axis 1, particularly differentiating low altitude floodplain waterbodies from ponds located on the surrounding hillsides.

5. Discussion

5.1. Patterns in catchment aquatic biodiversity

The limited availability of multi-waterbody biodiversity data makes it difficult to identify how typical the current findings are of other regions and landscape types. A preliminary evaluation can, however, be undertaken using data from studies that have made pair-wise comparisons between waterbody types.

5.1.1. Stream and river comparisons

Species-richness comparisons between streams and rivers are moderately common in the published literature, partly because there has been interest in testing the validity of the river continuum concept (RCC) which predicts that lotic biodiversity will be greatest at intermediate stream orders (Vannote et al., 1980). Within the range of stream orders encompassed by the current study, most published studies (including the RCC) have concurred with Cole catchment data in finding greater alpha and/or gamma diversity in rivers than in streams (e.g. Furse et al., 1993; Gehrke and Harris, 2000; Malmqvist and Hoffsten, 2000; Wiberg et al., 2000; Riis et al., 2001). This pattern is generally attributed to the greater physical habitat complexity present in larger watercourses (Vinson and Hawkins, 1998), with factors such as variation in substrate size, disturbance regime and annual temperature range contributing to the relationship (Stanford and Ward, 1983; Hawkins, 1984; Minshall et al., 1985; Death and Winterbourn, 1995).

5.1.2. Comparison of ponds with other waterbody types

Studies comparing the alpha diversity of ponds with other waterbody types have been rather few, with the notable exception of research on the Upper Rhône in France. Aquatic macrophyte data from the latter showed similar trends to the current study with the river richer in plant species than adjacent ponds. Invertebrate richness, however, differed from the Cole findings, with invertebrate assemblages in the River Rhône generally poorer than in floodplain ponds (Richoux, 1994; Bornette et al., 1998; Ward et al., 1999). The explanation for the Rhône patterns has been variously related to factors associated with connectivity, disturbance and/or productivity, but Bornette et al. (1998) suggest that, in practice, the interplay between these factors is complex, so that richness is often difficult to predict at any location. In the current study of an impacted landscape, field observations suggested that factors such as pollution and seasonality reduced the richness of some ponds (bringing down the mean) relative to the consistently species-rich river sites.

In contrast to site diversity, regional pond diversity in the current study was unusually high relative to other waterbody types. This pattern is consistent with the few other surveys that have gathered similar data. Thus, in Britain, comparison of national pond and river data sets showed that pond macroinvertebrate assemblages were richer, and supported more rare species than rivers and streams (Biggs et al., 2000). At a smaller scale, similar trends were found by Verdonschot (1990) in OverIjssel province in the Netherlands and in the Upper Rhône by Usseglio-Polatera (1994). The consistency of these results suggests that there may be factors operating at landscape level to create and maintain ponds as a regionally important biodiversity resource. This seems an important finding, and the reasons that such a pattern could arise are worth briefly considering. Theoretically, both landscape heterogeneity and connectivity processes can be invoked to explain high regional pond biodiversity. It is likely, for example, that ponds are physically heterogeneous habitats. These waterbodies often have small catchment areas and can, as a result, have highly individual physico-chemical characteristics that vary considerably between ponds depending on local geology and land use (e.g. entirely wooded, heavily grazed, draining acid- or base-rich strata). Rivers and large streams, in contrast, usually have extensive catchments and this, combined with the homogenising action of flowing water, will usually ensure that they are characterised by less variable physico-chemical conditions than small lentic waters (see, for example, chemical data from the current study in Table 4). It is possible, therefore, that such heterogeneity in water chemistry and habitat has a bottom-up effect on biodiversity, maintaining ponds as regionally rich habitats.

Differential connectivity processes could, however, also explain trends towards high pond gamma diversity. Rivers and streams are highly connected waterbodies, linked both morphologically and by flow. Dispersion of species, facilitated by high connectivity, may lead to more uniform vegetation and fauna in lotic waters (Bornette et al., 1998; Ward et al., 1999). Many ponds, in contrast, are relatively isolated and may, therefore, show greater community heterogeneity as a result of stochastic effects acting on the colonisation process (Jeffries, 1988). Variability in pond isolation has the potential to further enhance gamma diversity, because ponds directly connected to streams or located on floodplains are likely to be colonised by species with relatively low aerial dispersal ability whereas isolated sites are likely to be dominated by good dispersers.

5.1.3. Comparison of ditches with other waterbody types

The alpha and gamma diversity patterns shown by ditches in this study are particularly difficult to evaluate because there have been surprisingly few comparisons between ditches and other waterbody types. The main exception is Verdonschot's study in OverIjssel province which showed that ditches supported similar species numbers to streams and rivers, despite the smaller number of sites sampled (Verdonschot, 1990). These findings contrast with the current study where ditches had lower alpha and gamma diversity than other waterbody types. The likely explanation for this difference is study location. The OverIjssel ditches were located in low-lying areas and were largely permanent. Most ditches in the River Cole catchment were small, highly seasonal and located away from floodplain areas. The seasonality of these waterbodies is, in particular, likely to explain their comparatively low species richness (Collinson et al., 1995). It is worth noting, however, that although ditches were the most species-poor of the waterbody types surveyed, they were still a valuable habitat. In particular, the Cole ditches supported specialist temporary water invertebrates including the common caddis fly *Limnephilus sparsus* and the Nationally Scarce water-scavenger beetle *Helophorus nanus* (Wallace, 1991; Foster, 2000) that were not recorded elsewhere in the survey. It is possible that these 'unique' species might eventually be found in other waterbodies than ditches if a more exhaustive search of the survey area was undertaken. However, they would be expected from few other habitats, except perhaps temporary ponds (a relatively uncommon waterbody type in the region), and it seems more probable that the estimated 50–60 km of temporary ditches in the survey area are a significant habitat for these and other temporary water species.

5.1.4. Assemblage composition

Only a few studies have compared plant or invertebrate assemblage composition across several waterbody types, including the work of Verdonschot (1990), Bornette et al. (1994), Usseglio-Polatera (1994), and Godreau et al. (1999). For macroinvertebrates, at least, these authors showed somewhat similar trends to those found here. Thus Verdonschot, the only author to have published regional comparisons, found that ponds supported very different invertebrate assemblages to those of streams, rivers and ditches. At a smaller scale Usseglio-Polatera (1994), working on the Upper River Rhône, found differences in invertebrate assemblages in the main river channel, side channels and isolated floodplain ponds. Similar results were obtained from the floodplain of the River Saône in France (Godreau et al., 1999). In the current study, seasonality and flow/depth were the main environmental factors linked to the gradual change in assemblage type between rivers, streams and ditches and these factors also partially explained the broad spread of pond assemblages. For ponds at least, the results concur with other pond-only data sets from the UK in showing permanence and depth to be major factors differentiating pond invertebrate assemblages at both regional and national levels (Collinson et al., 1995; Nicolet, 2003). The most striking feature of the macrophyte CCA from the Cole area is the marked overlap between the plant assemblages of different waterbody types. The relative uniformity of macrophyte composition in different aquatic habitats can probably be explained by the generalist habitat requirements of many wetland plants. Marginal species, in particular, often show relatively few habitat preferences amongst different waterbody types, being found at the edge of rivers, ponds, streams and ditches (Grime et al., 1988).

5.2. Implications of the study

On the basis of the current project findings, a number of preliminary observations can be made on the wider implications of the data.

First, it is worth emphasising that all waterbody types contributed to the biodiversity of the survey region, each supporting species or assemblage types not found in other habitats. Such findings reinforce the importance of maintaining a diversity of waterbody types in any landscape including, our data suggest, waterbodies with different flow and permanence regimes.

The results of this and other studies suggest that ponds may be particularly important for maintaining regional freshwater biodiversity. This finding has significant practical implications for waterbody monitoring and protection in catchments. Most European countries now have river, stream and sometimes lake monitoring programmes. However, none undertake routine pond or ditch surveillance. Even the recently adopted EC Water Framework Directive (2000/60/EC), which emphasises a catchment management approach, does not specifically included the terms 'pond' and 'ditch', making it unlikely that their surveillance will be widely undertaken. Rivers, streams and large lakes clearly support an important component of biodiversity, but monitoring that focuses on these exclusively risks missing potentially significant degradation trends in smaller waterbodies. To ensure that biodiversity loss can be avoided within catchments requires a more representative monitoring approach that both encompasses small and seasonal sites, and is stratified to recognise the differing scale and intensity of factors that can impact on small waterbodies.

More positively, the high biodiversity value of small waterbodies shown by the current study suggests that there may be a range of easy-win opportunities for enhancing biodiversity at landscape level. Rivers and lakes drain relatively large catchment areas and are, as a result, both expensive and technically challenging to manage successfully. Ponds, with their small catchments are, in contrast, a highly viable option for protection and enhancement. Putting a field with a pond into an agri-environment scheme can often, for example, buffer its entire surface water catchment. Similarly, the creation of new ponds in areas where it is easy to keep them relatively unpolluted, has the potential to be a cost-effective method for enhancing freshwater biodiversity in impacted landscapes (Williams et al., 1997).

A significant wider benefit of gathering landscape scale biodiversity data is that it can help to push the boundaries of what is possible in sustainable catchment management. There is increasing interest, both amongst regulators and the agrochemical industry, in probabilistic risk assessment methods (Maund et al., 1997; Hendley et al., 2001). Indeed data from the work presented here are already being used by UK regulators for this purpose. It is anticipated that, in the long term, regional scale biodiversity data will provide the essential foundation for more sophisticated agrochemical application strategies that can minimise levels of damage by predicting those waterbodies likely to be particularly vulnerable to degradation.

Finally, it is important to recognise that the current work has inherent limitations; it is a study of a single survey area, that area was anthropogenically impacted, not semi-natural, and the information collected relates only to macrophytes and macroinvertebrates. To protect the freshwater environment requires more data and greater understanding. Investigations of freshwater biodiversity in semi-natural areas are especially necessary because only this can give information about the natural distribution of aquatic biodiversity and the processes that drive it in the (near) absence of anthropogenic impacts. Such areas, typically support a range of small-scale features such as flushes, temporary pools and runnels, that are often completely eliminated from intensively managed and drained agricultural catchments such as the Cole. The role that these often abundant features play in supporting the diversity and integrity of the freshwater environment has yet to be adequately assessed in any European landscape type.

Investigation of other countryside areas and other taxonomic groups are likewise required. With increasing legislative and policy emphasis on monitoring, maintaining and restoring wider countryside areas, an understanding of the distribution of the freshwater biota across managed landscapes becomes a key requirement to ensure appropriate allocation of funds and adequate protection of the freshwater resource across the landscape as a whole.

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References

Abernethy, V.J., Willby, N.J., 1999. Changes along a disturbance gradient in the density and composition of propagule banks in floodplain aquatic habitats. Plant Ecology 140, 177–190.

Biggs, J., Whitfield, M., Williams, P., Fox, G., Nicolet, P., 2000. Factors affecting the nature conservation value of ponds: results of the National Pond Survey. In: Proceedings of the Ponds Conference 1998. Pond Action, Oxford.

Bornette, G., Henry, C., Barrat, M.H., Amoros, C., 1994. Theoretical habitat templets, species traits, and species richness: macrophytes in the Upper Rhône River and its floodplain. Freshwater Biology 31, 487–505.

Bornette, G., Amoros, C., Lamouroux, N., 1998. Aquatic plant diversity in riverine wetlands: the role of connectivity. Freshwater Biology 39, 267–283.

Chao, A., Lee, S.M., 1992. Estimating the number of classes via sample coverage. Journal of the American Statistical Association 87, 210–217.

Collinson, N.H., Biggs, J., Corfield, A., Hodson, M.J., Walker, D., Whitfield, M., Williams, P.J., 1995. Temporary and permanent ponds: an assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. Biological Conservation 74, 125–134.

Colwell, R.K., 1997. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 5. User's Guide and Application available from <http://viceroy.eeb.uconn.edu/estimates>.

Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society B 345, 101–118.

Death, R.G., Winterbourn, M.J., 1995. Diversity patterns in stream benthic invertebrate communities—the influence of habitat stability. Ecology 76, 1446–1460.

Doledec, S., Statzner, B., 1994. Theoretical habitat templets, species traits, and species richness—548 plant and animal species in the upper Rhône river and its floodplain. Freshwater Biology 31, 523–538.

Everard, M., 1999. Towards sustainable development of still water resources. Hydrobiologia 396, 29–38.

Foster, G.N., 2000. A Review of the Scarce and Threatened Coleoptera of Great Britain. Part 3 Aquatic Coleoptera. JNCC, Peterborough.

Foster, G.N., Foster, A.P., Eyre, M.D., Bilton, D.T., 1990. Classification of water beetle assemblages in arable fenland and ranking of sites in relation to conservation value. Freshwater Biology 22, 343–354.

Furse, M.T., Winder, J.M., Symes, K.L., Clarke, R.T., Gunn, R.J.M., Blackburn, J.M., Fuller, R.M., 1993. The Faunal Richness of Headwater Streams: Stage 2—Catchment Studies. R & D Note 221. National Rivers Authority, Bristol.

Gardiner, J.L., 1994. Sustainable development for river catchments. Journal of the Institution of Water and Environmental Management 8, 308–319.

Gehrke, P.C., Harris, J.H., 2000. Large-scale patterns in species richness and composition of temperate riverine fish communities, southeastern Australia. Marine and Freshwater Research 51, 165–182.

Godreau, V., Bornette, G., Frochot, B., Amoros, C., Castella, E., Oertli, B., Chambaud, F., Oberti, D., Craney, E., 1999. Biodiversity in the floodplain of Saône: a global approach. Biodiversity and Conservation 8, 839–864.

Gontcharov, A.A., 1996. The algal flora of the Primorsky region, Russian Far East. Hydrobiologia 336, 93–97.

Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative Plant Ecology: A Functional Approach to Common British Species. Unwin Hyman, London.

Hawkins, C.P., 1984. Substrate associations and longitudinal distributions in species of Ephemerellidae (Ephemeroptera: Insecta) from western Oregon. Freshwater Invertebrate Biology 3, 181–188.

Hendley, P., Holmes, C., Kay, S., Maund, S.J., Travis, K.Z., Zhang, M.H., 2001. Probabilistic risk assessment of cotton pyrethroids: III. A spatial analysis of the Mississippi, USA, cotton landscape. Environmental Toxicology and Chemistry 20, 669–678.

Jeffries, M., 1988. Measuring Talling's element of chance in pond populations. Freshwater Biology 20, 383–393.

Malmqvist, B., Hoffsten, P.O., 2000. Macroinvertebrate taxonomic richness, community structure and nestedness in Swedish streams. Archiv für Hydrobiologie 150, 29–54.

Maund, S.J., Sherratt, T.N., Stickland, T., Biggs, J., Williams, P., Shillabeer, N., Jepson, P.C., 1997. Ecological considerations in pesticide risk assessment for aquatic ecosystems. Pesticide Science 49, 185–190.

Minshall, G.W., Petersen, R.C., Nimz, C.F., 1985. Species richness in streams of different size from the same drainage basin. American Naturalist 125, 16–38.

Moss, B., Johnes, P., Phillips, G., 1996. The monitoring of ecological quality and the classification of standing waters in temperate regions: a review and proposal based on a worked scheme for British waters. Biological Reviews of the Cambridge Philosophical Society 71, 301–339.

Nicolet, P., 2003. The classification and conservation value of wetland plant and macroinvertebrate assemblages in temporary ponds in England and Wales. Unpublished PhD Thesis, Oxford Brookes University.

Pollock, M.M., Naiman, R.J., Hanley, T.A., 1998. Plant richness in riparian wetlands—a test of biodiversity theory. Ecology 79, 94–105.

Pond Action, 1998. A Guide to the Methods of the National Pond Survey. Pond Action, Oxford.

Preston, C.D., Pearman, D.A., Dines, T.D., 2002. New Atlas of the British and Irish Flora. Oxford University Press, Oxford.

Richoux, P., 1994. Theoretical habitat templets, species traits, and species richness—aquatic Coleoptera in the Upper Rhone River and its floodplain. Freshwater Biology 31, 377–395.

Riis, T., Sand-Jensen, K., Larsen, S.E., 2001. Plant distribution and abundance in relation to physical conditions and location within Danish stream systems. Hydrobiologia 448, 217–228.

Sanoamuang, L.O., 1998. Rotifera of some freshwater habitats in the floodplain of the River Nan, Northern Thailand. Hydrobiologia 387, 27–333.

Schneiders, A., Verheyen, R., 1998. A concept of integrated water management illustrated for Flanders (Belgium). Ecosystem Health 4, 256–263.

Southwood, T.R.E., 1984. Ecological Methods. Chapman and Hall, London.

Standford, J.A., Ward, J.V., 1983. Insect species diversity as a function of environmental variability and disturbance in stream systems. In: Barnes, J.R., Minshall, G.W. (Eds.), Stream Ecology: Application and Testing of General Ecological Theory. Plenum, New York.

ter Braak, C.J.F., Smilauer, P., 1998. CANOCO Reference Manual and User's Guide to CANOCO for Windows. Centre for Biometry, Wageningen.

Usseglio-Polatera, P., 1994. Theoretical habitat templets, species traits, and species richness: aquatic insects in the Upper Rhône River and its floodplain. Freshwater Biology 31, 417–437.

Vannote, R.L., Minshall, G.W., Cummings, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37, 120–137.

Verdonschot, P.F.M., 1990. Ecological Characterisation of Surface Waters in the Province of OverIjssel (The Netherlands). Unpublished PhD Thesis, University of Wageningen.

Verdonschot, P.F.M., 2000. Integrated ecological assessment methods as a basis for sustainable catchment management. Hydrobiologia 422, 389–412.

Vincent, W.F., James, M.R., 1996. Biodiversity in extreme aquatic environments: lakes, ponds and streams of the Ross Sea Sector, Antarctica. Biodiversity and Conservation 5, 1451–1471.

Vinson, M.R., Hawkins, C.P., 1998. Biodiversity of stream insects: variation at local, basin, and regional scales. Annual Review of Entomology 43, 271–293.

Wallace, I.D., 1991. A Review of the Trichoptera of Great Britain. Research and Survey in Nature Conservation, 32. Nature Conservancy Council, Peterborough.

Ward, J.V., Tockner, K., Schiemer, F., 1999. Biodiversity and river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management 15, 125–139.

Wiberg-Larsen, P., Brodersen, K.P., Birkholm, S., Gron, P.N., Skriver, J., 2000. Species richness and assemblage structure of Trichoptera in Danish streams. Freshwater Biology 43, 633–647.

Williams, P., Biggs, J., Corfield, A., Fox, G., Walker, D., Whitfield, M., 1997. Designing new ponds for wildlife. British Wildlife 8, 137–150.