# Pond Conservation in Europe

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# Pond Conservation in Europe

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# The ecology of European ponds: defining the characteristics of a neglected freshwater habitat

R. Céréghino · J. Biggs · B. Oertli · S. Declerck



**Abstract** There is growing awareness in Europe of the importance of ponds, and increasing understanding of the contribution they make to aquatic biodiversity and catchment functions. Collectively, they support considerably more species, and specifically more scarce species, than other freshwater waterbody types. Ponds create links (or stepping stones) between existing aquatic habitats, but also provide ecosystem services such as nutrient interception, hydrological regulation, etc. In addition, ponds are powerful model systems for studies in ecology, evolutionary biology and conservation biology, and can be used as sentinel systems in the monitoring of global change. Ponds have begun to receive greater protection, particularly in the Mediterranean regions of Europe, as a result of the identification of Mediterranean temporary ponds as a priority in the EU Habitats Directive. Despite this, they remain excluded from the provisions of the Water Framework Directive, even though this is intended to ensure the good status of *all* waters. There is now a need to strengthen, develop and coordinate existing initiatives, and to build a common framework in order to establish a sound scientific and practical basis for pond conservation in Europe. The articles presented in this issue are intended to explore scientific problems to be solved in order to increase the understanding and the protection of ponds, to highlight those aspects of pond ecology that are relevant to freshwater science, and to bring out research areas which are likely to prove fruitful for further investigation.

**Keywords** Biodiversity · Conservation · Ecosystem services · European Pond Conservation Network · Small water bodies · Temporary pools · Water policy · Wetlands

Guest editors: R. Céréghino, J. Biggs, B. Oertli and S. Declerck
The ecology of European ponds: defining the characteristics of a neglected freshwater habitat

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## Introduction

Ponds are small (1 $m^2$ to about 5 ha), man-made or natural shallow waterbodies which permanently or temporarily hold water (De Meester et al., 2005). They are numerous, typically outnumbering larger lakes by a ratio of about 100 to 1 (Oertli et al., 2005), and occur in virtually all terrestrial environments, from polar deserts to tropical rainforests. Despite this they have, until recently, been mostly ignored by freshwater biologists or regarded simply as smaller versions of larger lakes. In contrast, practitioners spend considerable amount of effort on the management and creation of ponds, largely without a rigorous scientific framework for their actions (Williams et al., 1999; Pyke, 2005). However, recent research, driven both by the need to improve pond conservation strategies and by increasing interest in fundamental aspects of pond ecology (Biggs et al., 2005; McAbendroth et al., 2005), has started to shed interesting new light on pond ecosystem structure and function. As a result, there is growing evidence that ponds are functionally different from larger lakes (Oertli et al., 2002; Sondergaard et al., 2005) and that, despite their small size, they are collectively exceptionally rich in biodiversity terms (Williams et al., 2004). Thus, ponds often constitute biodiversity "hot spots" within a region or a landscape, challenging conventional applications of species-area models ('big is best') in practical nature conservation (see also Scheffer et al., 2006). Ponds also show greater biotic and environmental amplitudes than rivers and lakes (Davies, 2005). Thus they pose interesting questions about the relationships between waterbody size, the heterogeneity of catchments, the role of small water bodies as refugia, and the existence of networks of aquatic. Ponds also provide an ideal model for investigating metapopulation and metacommunity processes in aquatic systems and the importance of between-waterbody movements, compared to better known within-waterbody movements (Jeffries, 2005). They fit nicely into the basic scheme of metapopulation and metacommunity theory: for obligatory aquatic organisms, ponds are suitable patches in an unsuitable habitat matrix. This in turn plays a significant role in understanding population persistence and recovery from disturbance. Finally, in addition to their inherent biological importance, the small size of ponds and the ease with which they may be manipulated experimentally, makes them ideal models for controlled studies of many basic ecosystem processes (Blaustein & Schwartz, 2001; De Meester et al., 2005), from community assembly rules (Warren & Spencer, 1996) to diversity–productivity relationships (Chase & Ryberg, 2004). In this special issue, therefore, we aim to bring together a set of articles which provide an overview of the developing science describing the ecology of ponds with the objective of (i) exploring the major scientific problems which will need to be solved in order to increase understanding and protection of these vulnerable and neglected habitats, (ii) exploring those aspects of pond ecology that are of relevance to freshwater science generally and (iii) highlighting research areas which are likely to prove fruitful for further investigation.

## The second European Pond Workshop

In October 2004, the first European Pond Workshop devoted to the "Conservation and Monitoring of Pond Biodiversity" (Geneva, Switzerland) launched a European network of people and institutions involved in fundamental scientific issues and practical applications needed to protect ponds, the European Pond Conservation Network (EPCN, http://campus.hesge.ch/epcn/, see also Oertli et al., 2005). The second EPCN Workshop was held in Toulouse (France, 23–25 February 2006), under the topic "Conservation of Pond Biodiversity in a Changing European Landscape". The aim of this second workshop was to yield a multi-disciplinary framework on how to maintain ponds and the biodiversity they host, in a landscape subjected to a wide array of potential stressors such as intensification or abandonment of agriculture, socio-economical pressures, climate change. The workshop was divided into plenary sessions and working group meetings. The 55 communications (oral and poster) were related to three sub-topics: (i) Understanding pond ecology (biodiversity, spatial and temporal patterns and ponds as research tools for hypothesis testing), (ii) Added value of ponds (biological indicators, ecosystem services) and (iii) Management of ponds (practical tools for management and monitoring, pond conservation). Three working group meetings were devoted to "The Pond Manifesto" (a publication aiming at presenting the background and the motivations for the EPCN), EPCN management and activities, and joint research programs. The meeting brought together 60 participants from Austria, Belgium, Denmark, France, Germany, Hungary, Ireland, Italy, Poland, Spain, Switzerland and the UK. This special issue presents a selection of 12 contributions.

## Special issue content

Recent studies, mainly in Europe (Williams et al., 2004; Angélibert et al., 2007), have indicated that ponds harbour a significant portion of aquatic biodiversity at the landscape scale. Several contributions in this issue have confirmed and reinforced this idea. For instance, in their comparative study on zooplankton diversity in different freshwater water body types (lakes, rivers, ditches, ponds and wheel tracks), De Bie et al. (2007) found that ponds may disproportionately contribute to total zooplankton species richness at the landscape scale. Ponds also often contain rare, endemic and/or Red Data List species (Oertli et al., 2007) and may as such form an irreplaceable type of habitat for a variety of freshwater biota (Céréghino et al., 2007; Williams et al., 2007).

Owing to their important contribution to aquatic biodiversity, ponds should be considered as an important target system in strategic plans that aim at conserving or developing aquatic biodiversity at the landscape scale. Such plans can only be effective if based on a solid knowledge of the factors that affect pond community structure and diversity. In this issue, several studies document clear associations between the communities of organism groups (macrophytes, zooplankton, macroinvertebrates and waterbirds) and a variety of ecologically relevant gradients, such as hydroperiod (Boix et al., 2007; Della Bella et al., 2007), surface area (Céréghino et al., 2007), salinity (Boix et al., 2007) and among-pond connectivity (Boix et al., 2007; Gascón et al., 2007; Oertli et al., 2007). If these associations are causal, it is clear that the conservation of such environmental gradients at the landscape scale is essential for the conservation of among-pond variability (beta diversity) and total landscape biodiversity (gamma diversity). There is a clear differentiation among communities of macroinvertebrates (and to a lesser extent of macrophytes) between temporary and permanent ponds. Although temporary ponds tend to have lower species richness than permanent ponds, temporary ponds are at least as important as a habitat for uncommon and rare species. In Mediterranean regions, temporary wet habitats are important for conservation. Nevertheless, both temporary and permanent ponds are important for the conservation of regional biodiversity: in Central Italy, both type of ponds present high dissimilarity in the taxonomic composition of aquatic plants (Della Bella et al., 2007), the former containing more annual fast-growing species while in the latter, species with long life-cycles are abundant. Some aquatic species are exclusively found in each pond type.

Essential for the conservation of pond biodiversity is a good knowledge of its threats. Land use practices in the surroundings of ponds may, to an important extent, affect pond characteristics through a diversity of processes that play at the scale of the pond catchment (e.g. nutrient loading, increased erosion, pesticide contamination; Declerck et al., (2006)). Davies et al. (2007) contrasted catchment characteristics among different water body types within a landscape and noted that the small scale of pond catchments combined with their relatively high contribution to landscape scale biodiversity offers a lot of opportunities for cost-efficient conservation strategies. An important reason for this is that deintensification of agriculture at the scale of pond catchments is far more feasible and effective than it is on the catchment scale of larger aquatic systems, such as rivers or lakes. It means that efforts on the pond scale can be, relatively, easily implemented and have the potentiality to yield visible biodiversity benefits on a relatively short term, even in areas where large scale deintensification is not an option.

Due to their small scale, ponds can also be easily created. Pond creation has a lot of potential for nature development plans: new ponds are rapidly colonised by a variety of organisms and well designed and located, pond complexes could be used to significantly enhance freshwater biodiversity within catchments (Williams et al., 2007). Furthermore, pond density in the landscape can be an important factor determining the persistence of metapopulations of rare species. In such development plans, one may also take advantage of the opportunities offered by ponds that are not necessarily created as a part of nature conservation programmes such as ponds that aim at supporting agricultural activities (Céréghino et al., 2007; Williams et al., 2007).

Owing to their small sizes and simple community structure, small aquatic ecosystems may also function as early warning systems for long-term effects on larger aquatic systems. For instance, global warming may lead to higher local and regional richness in high altitude ponds through an increase in the number of colonisation events resulting from the upward shift of geographical ranges of species, while cold stenothermal species may be subject to extinction (Oertli et al., 2007). On the other hand, a survey on crucian carp body condition in ornamental ponds in the UK revealed no correlation with climatic variables (Copp et al., 2007). More direct threats to ponds include habitat destruction (in-filling ponds; deepening of ephemeral pools so that they become permanent) or other forms of strong human impact (e.g. urban runoff, acidification, diffuse agricultural pollution, introduction of exotic species, excessive trampling by livestock). Efficient bioindication metrics based on macroinvertebrate taxa richness and functional feeding groups as well as pollution tolerance are sensitive to nutrient enrichment (Solimini et al., 2007). The species richness of insect and crustacean taxa also respond well to eutrophication (Menetrey et al., 2007, Solimini et al., 2007) or salinity (Boix et al., 2007), while the presence of some indicator species can be associated to the trophic state of the ponds in a given area (Menetrey et al., 2007). However, sampling biodiversity in ponds is still a critical issue, because ponds are rich in microhabitats, often structured by macrophytes. Therefore, standardised methods are required. Becerra et al. (2007) present an effective sampling regime to maximise total taxon richness while minimising sampling effort.

## Perspectives

To understand how the biological diversity sustained by ponds is maintained and how ponds function, future research should involve complementary approaches, and focus on the relevant ranges of temporal and spatial scales. Several directions can be identified for relevant research on ponds, ranging from the fields of biological monitoring to evolutionary ecology (reviewed in De Meester et al., 2005). Here, we specifically emphasise those perspectives which call for intense collaborative research at a European level.

Whereas much research has been undertaken at the EU level towards developing robust methodologies and tools for the implementation of the Water Framework Directive (examples include the STAR, AQEM and ECOFRAME projects), small water bodies such as shallow lakes and ponds have not been well represented, despite their ecological role at the landscape—regional scales. Active research into the ecology and conservation of ponds is being undertaken in many European states, addressing different areas of relevance. One of the chief problems is the lack of integration between these research areas, and a general poor level of understanding of patterns of variation in habitats and biota across Europe. Some national environment agencies from countries such as France, the United Kingdom and Switzerland, have recently developed elements of a national strategy for pond conservation, but such efforts remain in the minority across the rest of Europe. Obtaining a typology of small water bodies at a European scale, should be a first step towards optimising the design of new surveys and standardising sampling schemes and monitoring applications. Exploration of fundamental ecological patterns and definition of a typology of European small waterbodies should cover the range of habitats found along broad geographical (North-South, East-West), altitudinal and environmental gradients. The analyses should try to involve the full range of taxonomic groups (i.e. different trophic levels, keystone taxa, umbrella and flagship species). These analyses, in addition to giving a vital understanding of large-scale patterns, are also expected to reveal gaps in existing knowledge. An important issue is the capacity for ponds and pond communities to respond to disturbance and to global change (early-warning systems). This implies that near-pristine systems should be identified as references in the investigated areas, and that long-term monitoring is necessary to assess temporal responses of ponds to local practices and/or global changes. Assessments of responses to various types and/or intensity and frequency of disturbance should preferably be hypothesis-based, in order to reduce (and thus better target) the number of variables that will be assessed. Experimental work should include the main driving forces of community dynamics in ponds, and should thus include both regional (dispersal, external forcing) and local factors (abiotic conditions, biotic interactions). Suggested practical applications should not only be based on the patterns derived from fundamental research, they must be tested and evaluated in the field.

Although there are clear gaps still to fill in our knowledge on pond ecology, this special issue of Hydrobiologia demonstrates that notable improvements have been made these last ten years. For effective conservation of pond biodiversity, this knowledge has now to be communicated to managers, in order to be put into practice. This will be one of the priority tasks for the European Pond Conservation Network, with an important stepping stone at the third European Ponds Workshop, to be held in Valencia (Spain) in May 2008.

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ECOLOGY OF EUROPEAN PONDS

# A comparison of the catchment sizes of rivers, streams, ponds, ditches and lakes: implications for protecting aquatic biodiversity in an agricultural landscape

**B. R. Davies · J. Biggs · P. J. Williams · J. T. Lee · S. Thompson**



**Abstract** In this study we compared the biodiversity of five waterbody types (ditches, lakes, ponds, rivers and streams) within an agricultural study area in lowland England to assess their relative contribution to the plant and macroinvertebrate species richness and rarity of the region. We used a Geographical Information System (GIS) to compare the catchment areas and landuse composition for each of these waterbody types to assess the feasibility of deintensifying land to levels identified in the literature as acceptable for aquatic biota. Ponds supported the highest number of species and had the highest index of species rarity across the study area. Catchment areas associated with the different waterbody types differed significantly, with rivers having the largest average catchment sizes and ponds the smallest. The important contribution made to regional aquatic biodiversity by small waterbodies and in particular ponds, combined with their characteristically small catchment areas, means that they are amongst the most valuable, and potentially amongst the easiest, of waterbody types to protect. Given the limited area of land that may be available for the protection of aquatic biodiversity in agricultural landscapes, the deintensification of such small catchments (which can be termed microcatchments) could be an important addition to the measures used to protect aquatic biodiversity, enabling 'pockets' of high aquatic biodiversity to occur within working agricultural landscapes.

**Keywords** Watershed · Microcatchment · Aquatic biodiversity · Agri-environment schemes · Diffuse pollution

Guest editors: R. Céréghino, J. Biggs, B. Oertli & S. Declerck
The ecology of European ponds: defining the characteristics of a neglected freshwater habitat

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## Introduction

Pollution from agriculture is recognised as having a significant negative impact on water quality and aquatic biota (Allan, 2004; Foley et al., 2005; Declerck et al., 2006; Donald & Evans, 2006). These pollutants include nutrients and other chemicals used to maximise production on arable land; animal waste and animal health biproducts, e.g. antibiotics and sheep dip, from pastoral land; as well as sediment resulting from eroded soils. They affect aquatic ecosystems both by altering the physicochemical characteristics and quality of a waterbody (e.g. eutrophication, changes to sediment composition) and by direct toxicity impacts on the organisms within it. Many of these pollutants are diffuse in nature, and the broad areas from which they emanate and multiplicity of pathways by which they reach waterbodies, make such pollutants difficult to control and mitigate.

The quantity and concentration of diffuse pollutants reaching waterbodies can potentially be reduced by two mechanisms: (i) source control through reduction in chemical loads, better targeting in the timing of chemical applications and the use of appropriate farming techniques to reduce runoff, e.g. minimum tillage; and (ii) measures to prevent pollutants from reaching waterbodies through deintensifying areas of land, e.g. buffer zones. Although the source control mechanisms go someway towards reducing pollution (e.g. Yates et al., 2006) diffuse pollutants will not be completely eliminated by such means. Thus, methods of land management and pollutant interception are likely to remain important in the effective long-term protection of aquatic biota under current agricultural systems. Typically such methods involve leaving areas adjacent to waterbodies out of agricultural production, through whole field conversion or more commonly, the creation of buffer strips. Although widely used and much tested, this approach has shown mixed results in terms of pollution reduction, e.g. Schmitt et al. (1999), Dosskey (2002), Borin et al. (2004, 2005), and recent evidence (e.g. Wang et al., 1997; Quinn, 2000; Fitzpatrick et al., 2001; Donohue et al., 2006) implies that where such methods have proved relatively ineffective, this has often been because the deintensified area has not included a sufficient proportion of the catchment area of a waterbody.

The catchment of a waterbody is the area over which water, and hence diffuse pollutants, will travel (both by overland and subsurface movement) to enter the waterbody. Catchments have long been recognised as the key to understanding the ecology of freshwaters (Hynes, 1975; Allan et al., 1997; Allan, 2004) and although underlying geology and morphology are the fundamental determinants of water characteristics (Host et al., 1997; Johnson et al., 2004; Wiley et al., 1997; McRae et al., 2004), in areas where landcover is heavily modified, the landuse composition of the catchment will dominate (Hynes, 1975; Lund & Reynolds, 1982; Moss et al., 1996; Allan et al., 1997; Muir, 1999; Cresser et al., 2000; Johnson & Goedkoop, 2002; Tong & Chen, 2002). Thus, the proportion of intensive landuse in a catchment as well as the catchment's size will influence the cost and potential success of a waterbody's protection from diffuse pollution.

Catchment areas are generally perceived as large and are usually described only in the context of rivers or large lakes. For example, in the UK, small river and stream catchments are generally termed 'sub-catchments'. However, in reality all waterbodies, large or small, have a catchment area. The association of catchment areas with larger rivers and lakes is likely to have resulted from the historic use of these waterbodies for navigation, drainage, food supply, water supply, recreation and removal of wastes. This considerable socio-economic value has resulted in a vested interest in the protection of these waterbodies and consequently, both scientific research and environmental protection has tended to be focused at larger waterbodies. The more limited economic value of small waterbodies has meant that until recently, their biodiversity potential has tended to be overlooked with a general presumption that they are inferior versions of their larger equivalents. However, recent evidence has shown that small waterbodies may in fact make a disproportionately large contribution to aquatic biodiversity across landscapes in terms of both their species richness and their species rarity (Biggs et al., 2003, 2007; Williams et al., 2004; De Bie et al., 2008; Davies et al., in press), implying that they are likely to warrant a higher priority in terms of conservation concern. The ease and success of their protection from diffuse agricultural pollution will depend to some extent, as for larger waterbodies, on the proportion of their catchment areas that can be incorporated into protection strategies.

This study investigates the aquatic biodiversity (species richness and rarity) of a suite of waterbody types across an area of UK lowland agricultural landscape in the context of their catchment sizes. The results are used to explore the potential ease and success of the protection of different waterbody types from diffuse agricultural pollution.

## Material and methods

### The study area and its aquatic biodiversity

A 13 × 11 km study area of lowland agricultural landscape in Britain on the borders of Oxfordshire, Wiltshire and Gloucestershire was selected. The study area contained three Department for Environment, Food and Rural Affairs (Defra) agricultural landscape classes (Table 1) (Biggs et al., 2003) and was considered typical of lowland agricultural landscapes (Brown et al., 2006). Arable cultivation dominated the landcover (75%), with 9% under woodland, 7% improved grassland, 2% urban and the remaining 7% made up of water, semi-natural grassland and bare rock (Fig. 1). Agricultural land was predominantly arable, comprised mainly of cereals, permanent grass, oil-seed rape, potatoes peas and sugarbeet. There were 205 ha of surface water in the study area comprising 3 rivers, 97 streams, 236 ponds, 8 lakes and 340 ditches. The rivers included lengths of the Thames (c. 16.7 km), Cole (c. 16.8 km) and Coln (c. 4.3 km).

Data on the macrophyte and macroinvertebrate species present in the five dominant waterbody types in the study area (ditches, lakes, ponds, rivers and streams) were collected in two phases. In 2000, a stratified random sample of 20 sites was surveyed for each of four waterbody types (ditches, ponds, rivers and streams), i.e. 80 sites in total (reported in Williams et al., 2004). During 2002–2003, comparable data were collected from a further 20 sites in a fifth waterbody type, lakes. Due to the size division between a lake and a pond (Table 2; Biggs et al., 2003; Williams et al., 2004), data were also collected for a pond to replace one from the existing dataset which would have been categorised as a small lake under Table 2.

Within each waterbody, the sample area and survey methods followed those used by Williams et al. (2004). Each sample area was 75 $m^2$ to enable direct comparison of data from different waterbody types with inherently different sizes. For linear waterbodies, this area comprised a rectangular section of the waterbody, while for circular waterbodies, the area comprised a triangular wedge with the base following the margin and the apex at the centre of the waterbody. At each site, all wetland macrophytes (marginal, emergent, submerged and floating-leaved plants) were recorded by walking and wading the margin, using a grapnel thrown from the bank and sampling from a boat in the deeper lake sites. A three-minute hand net sample was taken for macroinvertebrates using a standard 1 mm mesh net, with the three minute sample time being divided equally between the mesohabitats in the 75 $m^2$ area. Macroinvertebrate samples were exhaustively live-sorted in the lab and all individuals (except Diptera larvae and Oligochaeta which were omitted from the analysis) were identified to species level, except very abundant taxa (>100 individuals) which were sub-sampled.

The macrophyte and macroinvertebrate data provided information on aquatic species richness and rarity for each survey site in the ditches, lakes, ponds, rivers and streams (100 sites in total). The species richness of a site was the total number of species found at that site, whilst species rarity was calculated using the Species Rarity Index (SRI). This rarity index follows a process developed by Foster et al. (1990) whereby each species is given a numerical value according to its rarity or threat within Britain, the total for each site is then summed and finally divided by the number of species found at the site, resulting in an index which is not biased towards

**Table 1** Defra agricultural landscape classes occurring within the study area

| Landscape | Area-km$^2$ (% of area) | Description | Associated agriculture |
|---|---|---|---|
| LC1—River floodplains and low terraces | 16.27 (11.5) | Level to very gently sloping river floodplains and low terraces | Permanent grass, some cereals and oil-seed rape, probably more intensive on terraces |
| LC6—Pre-quaternary clay landscapes | 95.46 (67.1) | Level to gently sloping vales. Slowly permeable, clays (often calcareous) and heavy loams. High base status (Eutrophic) | Permanent grass, cereals (>10–15%), leys, oil-seed rape maize and beans |
| LC7—Chalk and limestone plateaux and coombe valleys | 30.44 (21.4) | Rolling 'Wolds' and plateaux with 'dry' valleys; shallow to moderately deep loams over chalk and limestone | Cereals (and oil-seed rape, beans), sugar beet, potatoes, peas |

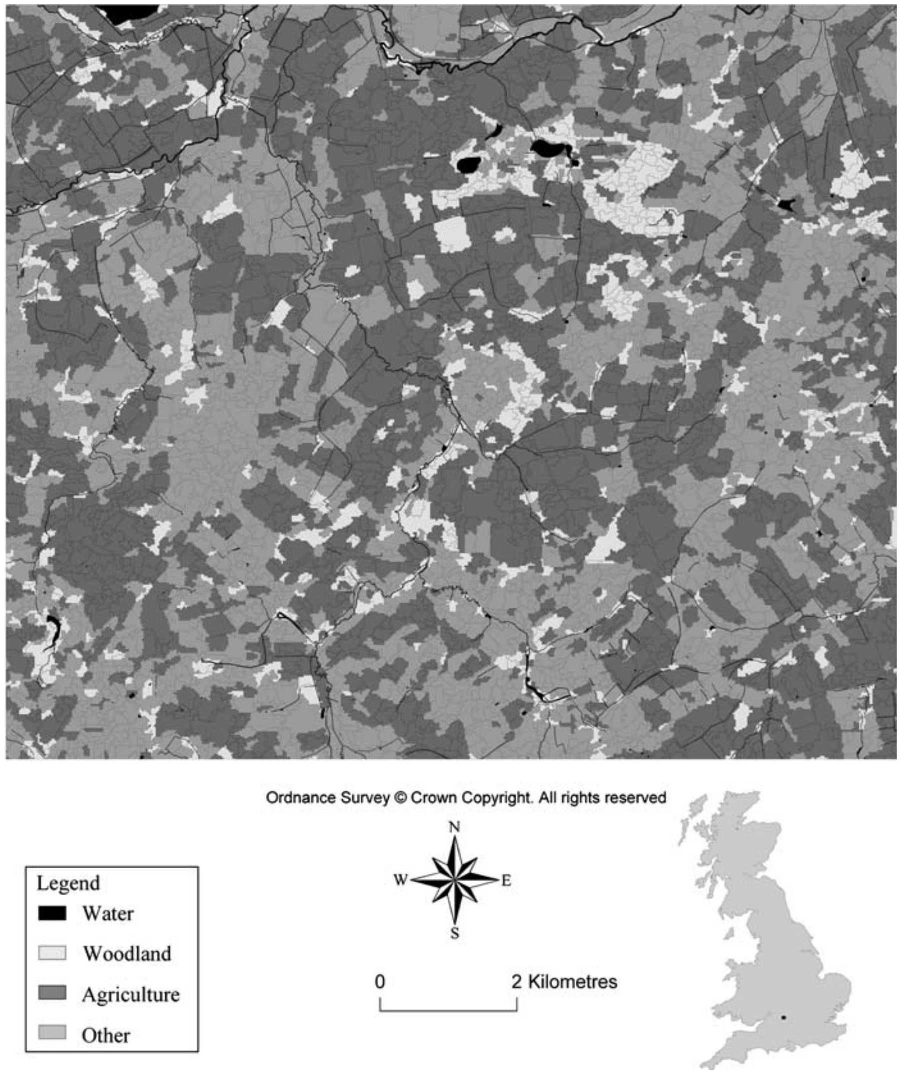


**Fig. 1** The study area and its landuse composition

**Table 2** Definitions of waterbodies used in this study

| Waterbody type | Definition |
|---|---|
| Lakes | Bodies of water, both natural and man-made, greater than 2 ha in area (Johnes et al., 1994). Includes reservoirs, gravel pits, meres and broads. |
| Ponds | A body of water, both natural and man-made, between 25 $m^2$ and 2 ha in area, which may be permanent or seasonal (Collinson et al., 1995). |
| Rivers | Relatively large lotic waterbodies, created by natural processes. Marked as a double blue line on 1:25,000 OS maps and defined by the OS as greater than 8.25 m in width. |
| Streams | Relatively small lotic waterbodies, created by natural processes. Marked as a single blue line on 1:25,000 OS maps and defined by the OS as being less than 8.25 m in width. Streams differ from ditches by usually: (i) having a sinuous planform; (ii) not following field boundaries; and (iii) showing a relationship with natural landscape contours, usually by running down valleys. |
| 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. |

species-rich sites (see Williams et al., 2004 for further details).

Catchment delineation and landcover

Ordnance Survey (OS) Landform Profile and MasterMap data were used to create the underlying Digital Elevation Model (DEM) upon which catchment delineation was based, for an area extending 8 km outside the study area, using the Geographical Information System (GIS) software, ArcGIS 8.2. MasterMap data include topographic information on every landscape feature, each with its own unique identifying code. Landform Profile data comprise height data at 10 m intervals in *x* and *y* and recorded to the nearest 0.1 m in *z*, with a planimetric accuracy of ±1 m and a vertical accuracy of ±1.8 m.

All waterbody polygons were extracted from the MasterMap data. Misclassified features were removed and polygons split by overlying features, such as bridges, were joined. Separate data layers were created for ditches, lakes, ponds, rivers and streams according to the definitions in Table 2. A new river or stream was defined at confluence sites and a new ditch was defined at both confluence sites and where it turned by approximately 90°. Results were visually compared with 1:25,000 OS maps, aerial photographs and site visits to ensure that the network of catchments and waterbodies generated from digital data were consistent with the real landscape.

Each waterbody polygon was assigned a constant minimum height value from the OS Landform Profile data and the waterbodies layer converted to a 5 m grid. The 10 m Landform Profile raster data were also converted to a 5 m grid using bilinear resampling, so that it could be combined with the waterbodies whilst retaining their continuity. The waterbodies were 'burnt' into the DEM at their height value minus 10 m to ensure that modelled runoff would flow into the waterbodies and that they would be retained during the catchment delineation process.

The catchments of each waterbody type were delineated separately using the DEM with the depressed waterbodies and the ArcGIS extension ArcHydro Tools (Version 1.1 Beta 2; ESRI, 2001). ArcHydro Tools only modelled surface water flow. Although the study area was predominantly underlain by impermeable clay and so overland flow would have been a dominant process, some throughflow and transport via field drains would have occurred but this was not modelled and is a limitation of the method. ArcHydro Tools also had the underlying assumption that all water will flow to the edge of the DEM. This ignores standing waterbodies which provide natural sinks that retain water within a landscape and so all ponds and lakes were 'seeded' with 'no-data' points at their deepest locations or centre point, to ensure that water flowed towards these points.

River catchments that extended beyond the limit of the data held were estimated using published statistics on catchment size from gauging stations present in the study area (Environment Agency, 2006). Additional manipulation of one river catchment boundary was required by hand due to the very flat nature of the northwest corner of the study area, which meant that ArcHydro Tools was not able to accurately define the catchment boundary in this instance. The landuse composition of the catchments was ascertained by intersecting each catchment with Land Cover Map 2000 data (remotely sensed landuse data in 25 $m^2$ cells; copyright NERC). For the river catchments that extended beyond the limit of data available, the proportions of different landuse types were taken as those modelled in the GIS for the area over which data was held.

## Results

Of the total area of water (205 ha) within the study area (13 × 11 km), lakes comprised the greatest proportion of the water area (38%), followed by rivers (24%), ditches (20%), streams (14%) and ponds (4%) (Fig. 2). There was a broadly inverse relationship between surface water area and number of waterbodies, with rivers and lakes being fewest in number but covering the largest surface area and ponds being one of the most numerous waterbody types but having the smallest total surface area.

Across the study area, the pond sites supported the greatest number of both macrophyte and macroinvertebrate species, followed by rivers, lakes, streams and lastly ditches, which contained no aquatic (submerged or floating) plants (Fig. 3a). Overall, the pond sites supported 238 species, river sites

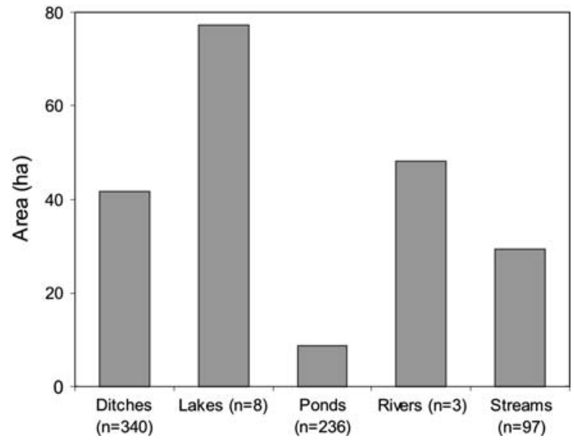


**Fig. 2** Surface water area of the different waterbody types within the study area

supported 201 species, lakes 186 species, streams 163 species and finally, ditch sites supported 120 species.

The pond sites had the highest SRI for macrophytes, followed by lakes, rivers, streams and lastly ditches which supported no rare plant species (Fig. 3 b). The ponds also had the highest macroinvertebrate SRI, followed by ditches, lakes, streams and lastly rivers (Fig. 3b).

Catchment sizes were significantly different between waterbody types (Kruskall–Wallis, $P < 0.001$). Rivers had the greatest average catchment areas (43,850 ha), followed by lakes (141 ha), streams (86 ha), ditches (29 ha) and lastly, ponds (18 ha) (Fig. 4). The total catchment areas followed a different pattern: overall, rivers had the greatest total catchment area (131,550 ha), followed by ditches (9,904 ha), streams (8,354 ha), ponds (4,237 ha) and lastly, lakes (1,124 ha) (Fig. 4). This difference arose because ditches had catchments that were small in size but numerous giving a large total catchment area, whilst lakes had large catchments but were few in number. Although river catchments were clearly the largest, there were too few in the sample for this to be confirmed with post hoc Mann–Whitney $U$ tests. However, significant differences ($P < 0.001$) in catchment size were seen between ponds and streams, ponds and lakes, ditches and streams and ditches and lakes, whilst no significant difference was observed between the size of pond and ditch catchments and between stream and lake catchments. This showed that ponds and ditches had similarly small catchments, whilst streams and lakes had similarly larger catchments and rivers had the greatest catchment sizes.

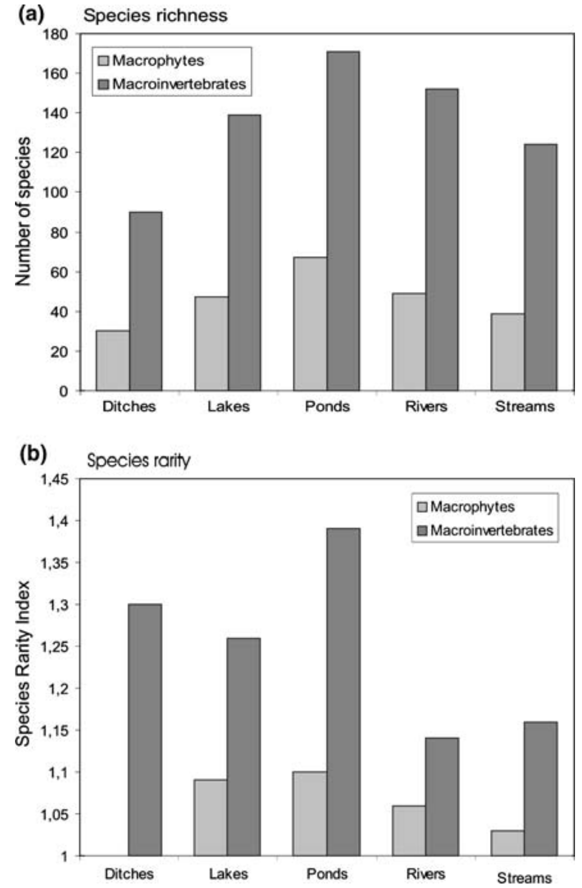


**Fig. 3** Macrophyte and macroinvertebrate (**a**) species richness and (**b**) species rarity across the study area

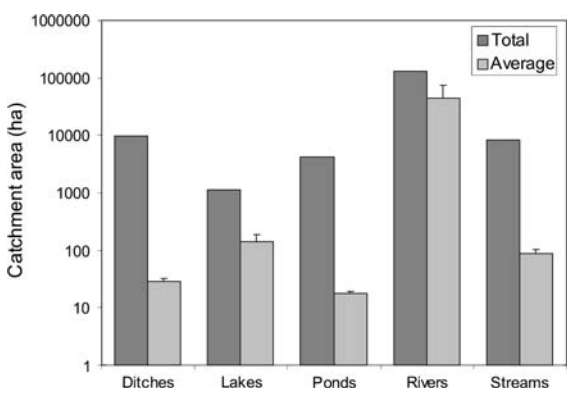


**Fig. 4** Average and total catchment areas of the different waterbody types within the study area

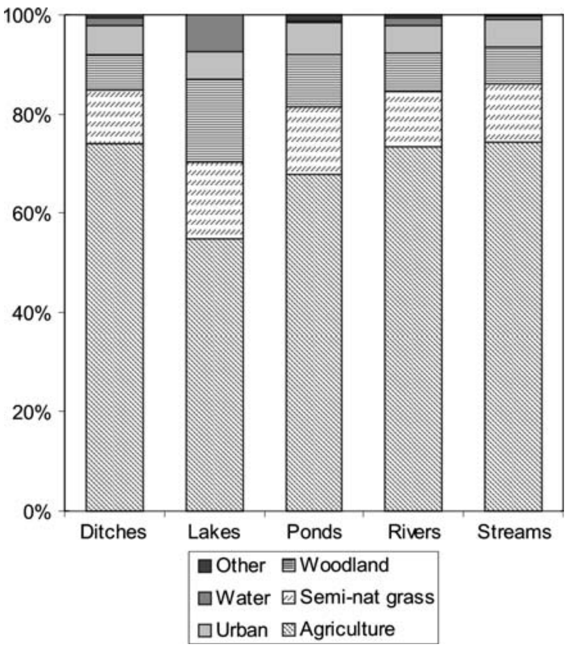


**Fig. 5** Proportion of landuses within the total catchment area of each waterbody type

The catchments of all waterbody types were dominated by agricultural landuse, with river, stream, pond and ditch catchments all containing similar proportions of agricultural land (69–74%) together with similar proportions of woodland (7–10%), semi-natural grassland (10–13%) and water (1–2%) (Fig. 5). Lake catchments differed, typically containing less agricultural land (55%) and larger proportions of semi-natural grassland (c. 4% more), woodland (c. 9% more) and water (c. 6% more) than those of the other waterbody types. The proportion of urban land within catchments was similar for all waterbody types (c. 5%).

## Discussion

### Catchment sizes and the area needed for protection of aquatic biota

Hynes (1975), in his classic work on the ecology of running waters, described rivers as, "*a manifestation of the landscapes that they drain*". Since this pioneering work, many studies have sought to characterise river, stream and sometimes lake catchments, analysing relationships between factors such as catchment area, landuse composition and waterbody ecology. Practically all of these studies have reinforced Hynes' original comments. The extent of agriculture in the developed world is such that it is a dominant component of many waterbodies' catchment areas, with its associated diffuse pollutants having well accepted and largely detrimental impacts on aquatic biodiversity.

Recent research has investigated the importance of such widespread agriculture within catchments, typically finding streams to remain in good condition until agriculture exceeds 30–50% of the catchment (Allan, 2004). For example, working in the US, Wang et al. (1997) found that habitat quality and scores of biotic integrity declined when agricultural landuse exceeded 50% of the catchment. Fitzpatrick et al. (2001) working in the same region, found declines in fish biotic indices above 30% agricultural land, whilst Quinn (2000), working in New Zealand, found 30% agricultural land to be a critical value for macroinvertebrates. More stringent levels were identified by Donohue et al. (2006) who investigated the relationship between the ecological quality of aquatic networks and landcover, identifying thresholds at which 'good' ecological status could be attained in Ireland. They predicted that with more than 1.3% arable land in a catchment or 37.7% pastoral land, ecological status would fall below 'good' levels. Within the current study area, the average landuse composition of the catchments of all the waterbody types exceeded these thresholds. The waterbody type with the least intensive catchment landuse composition was lakes, which were, on average, associated with 55% agricultural land. This implied that within the study area, lakes were already fairly well buffered, largely due to their frequent location on large private estates. This may not, of course, be the situation in other areas.

Agriculture currently covers approximately half of the earth's habitable surface (Clay, 2004) and in many countries covers more than 70% of the land surface. This implies that vast areas would need to be deintensified to reach the maximum thresholds of 30–50% identified as important in the literature. Given the anticipated doubling of food demand forecast for the next 50 years (Donald & Evans, 2006), this may be very difficult to achieve and impractical in landscapes where agricultural production is needed. However, not all waterbodies have large catchment areas and it may be possible to deintensify those with 'microcatchments' to reach the critical thresholds of 30–50%, or even to completely deintensify them. The present study found that, as might be expected, larger waterbodies, (i.e. rivers and lakes), had larger catchments than smaller ponds, streams and ditches. Using the study area as an example, rivers would require a comparatively large amount of land to be deintensified to reach the thresholds of 30 and 50%, compared with the smallest waterbody type, ponds (Table 3). To attain levels of no more than 50% agricultural land in an average catchment, rivers would require 10,086 ha to be deintensified, compared with just 4 ha for ponds. To reach 30% agricultural land, rivers would require 18,856 ha to be deintensified, compared with just 7 ha for ponds.

Therefore, if ponds and other waterbodies with small catchments can be demonstrated to support high levels of biodiversity they may play an important part in a strategy for the protection of aquatic biodiversity because they could be afforded very high levels of protection, e.g. complete deintensification, for a comparatively low land area.

## Macrophyte and macroinvertebrate species richness and rarity across the study area

Ponds made a high contribution to both the aquatic macrophyte and macroinvertebrate biodiversity of the study area in terms of both species richness and species rarity. Results for the other waterbody types were more mixed, with rivers supporting a relatively large number of species but low species rarity, whilst ditches supported few species but had a high macroinvertebrate SRI. Studies comparing the aquatic biodiversity of different types of waterbody are few and, as far as the authors are aware, none have compared the range of waterbody types undertaken for this study. However, those studies that have compared aquatic biodiversity for a more limited range of habitats have often found smaller waterbodies, particularly ponds and ditches, to make an important contribution (e.g. Painter, 1999; Armitage et al., 2003; Biggs et al., 2007; Davies et al., in press). These small waterbody types have often been overlooked in biodiversity protection and rarely enjoy the statutory protection afforded to larger waterbodies. The results of this study, supported by other work on comparative biodiversity including smaller waterbody types (Davies, unpublished data; Davies et al., in press), suggest that this may be both a considerable oversight and a missed opportunity. In particular, the valuable contribution of smaller waterbodies to regional aquatic biodiversity means that they could have an important role in the strategic protection of aquatic biota.

**Table 3** Areas requiring deintensifying within the study area to reach identified thresholds of 50% and 30% agricultural land

| Waterbody type | Average area (ha) requiring deintensification to reach: | |
|---|---|---|
| | 50% Agricultural land | 30% Agricultural land |
| Rivers | 10085.5 | 18855.5 |
| Streams | 20.6 | 37.8 |
| Lakes | 7.1 | 35.3 |
| Ditches | 6.7 | 12.8 |
| Ponds | 3.6 | 7.2 |

## The potential role for small waterbodies in protection strategies

As identified above, waterbodies with larger catchments require a much greater area to be deintensified to reach the levels that are suggested as needed for the sufficient protection of aquatic biota. In the study area, the largest catchments (associated with rivers) were on average 300 times larger than those of lakes (which had the second largest catchments) and almost 2,500 times larger than those of ponds, which had the smallest mean catchment sizes. Equally, in the area required to deintensify a single average-sized river catchment to 50% agricultural landuse, it would be possible to fully deintensify more than 560 average-sized pond catchments. Thus, the relatively small catchment sizes of smaller waterbodies, and in particular ponds, combined with their important contribution to aquatic biodiversity, means that their inclusion amongst the measures used for biodiversity protection from diffuse agricultural pollution is likely to enhance the effectiveness and economic efficiency of protection across whole landscapes.

The common perception, mentioned above, that catchment areas are associated with larger waterbodies and in particular rivers (and hence cover large areas), may be one of the reasons that whole catchment or large-scale deintensification are not generally proposed as protection measures. Instead, buffer strips (involving much smaller areas) are often employed. The disadvantage of such methods for larger waterbodies is that, depending on the proportion of the catchment that they occupy, they are unlikely to provide sufficient protection for the aquatic biota of the waterbody. For example, under the English Agri-Environment Scheme, Environmental Stewardship, the maximum buffer width offered at the edge of a field to protect a river is six metres. Published data on the effectiveness of buffer zones at varying widths suggest that a six metre buffer is highly unlikely to result in reduced nutrient pollution loads to rivers. Due to the large edge length of a river, the agricultural land-take that would be involved in even a limited buffer area would be considerable, implying that large areas of agricultural land are likely to be taken out of production to protect a river, with very little chemical or ecological gain.

The mechanisms most likely to be used to protect aquatic biodiversity in agricultural landscapes in the UK, are agri-environment schemes (AESs) whose structure would facilitate small catchment deintensification. These schemes remunerate farmers for environmentally sensitive farming, including reducing chemical and nutrient inputs as well as land management to reduce the impacts of diffuse pollution. The scheme is voluntary and is applied to by individual farmers and consequently, the measures offered are at a farm-scale. Such a scale and the potentially ad hoc uptake would favour microcatchment deintensification over that of larger catchments which would require the efforts of many farmers to be coordinated, increasing administrative costs and the complexity of operation, as well as increasing the chances of failure because the lack of cooperation of even a single landowner could jeopardise the success of a waterbody's protection. In contrast, the microcatchment of a smaller waterbody may be wholly encompassed by one land manager. Additionally, microcatchment deintensification has the potential to provide farmers with locally visible, biodiversity benefits. Such local returns are very important for improving satisfaction and a sense of ownership of the AES measures, as opposed to employing measures for broader scale improvements where results are harder to observe at a site level.

Supplementary to the deintensification of small catchments is the possibility of creating small waterbodies. Ponds and ditches are relatively easy to create and can be located so as to have small, completely unintensive catchments with good water quality, providing the best possible chance of supporting high levels of aquatic biodiversity, whilst involving minimum amounts of land (Williams et al., 2008). This is particularly important given evidence of the time lag between landuse change and improved ecological quality (Harding et al., 1998).

Protection of the aquatic biodiversity of smaller waterbodies through catchment deintensification and the creation of small waterbodies can be undertaken relatively quickly. This means that such initiatives could be employed immediately, providing benefits for aquatic biodiversity across a region much more quickly than could be achieved for larger waterbodies through catchment deintensification, whose complex implementation would take some time to execute.

Clearly, the protection of small waterbodies through catchment deintensification and the creation of ponds cannot deliver the complete protection of aquatic biota within agricultural landscapes (Davies, unpublished data). However, their inclusion amongst measures for aquatic biodiversity protection should provide 'pockets' of high biodiversity in working agricultural landscapes, making aquatic biodiversity protection more effective and more economically efficient.

## Conclusion

This study appears the first in the literature to compare both the biodiversity and catchment size of such a range of waterbody types. Small waterbodies, and in particular ponds, were found to support a relatively high proportion of the aquatic biodiversity in the study location, which confirmed the results of the few other studies that have made biodiversity comparisons between a more limited range of waterbody types. Smaller waterbodies were also found to have smaller catchment areas than larger waterbodies, which was not a surprising result, but the implications that arise from it are important.

Calculation of the areas of agricultural land within the catchments of the different waterbody types that would need to be deintensified to provide adequate protection, indicated that, for larger waterbodies, such a method of deintensification would be inappropriate and uneconomic due to the scales that are likely to be involved. In contrast, complete catchment protection would be quite feasible for smaller waterbodies. Given that the smaller waterbodies supported higher levels of aquatic biodiversity, deintensification of their relatively small catchments should afford effective protection from many pollutants, enabling pockets of high biodiversity to exist in a working agricultural landscape. Combined with alternative methods to protect waterbodies with larger catchments, and the creation of strategically located new ponds a landscape matrix should result which incorporates minimally impacted aquatic habitats whilst still being economically and socially productive.

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ECOLOGY OF EUROPEAN PONDS

# A comparative analysis of cladoceran communities from different water body types: patterns in community composition and diversity

**Tom De Bie · Steven Declerck · Koen Martens · Luc De Meester · Luc Brendonck**



**Abstract** To develop strategies for the management and protection of aquatic biodiversity in water bodies at the landscape scale, there is a need for information on the spatial organization of diversity in different types of aquatic habitats. In this study, we compared the cladoceran composition and diversity between wheel tracks, pools, ponds, lakes, ditches, and streams, in 18 different areas of Flanders (Belgium). Multivariate analysis revealed significant differences in the composition of cladoceran communities among the different water body types. Average local and total diversity tended to be highest for lakes and lowest for streams. Despite the relatively high number of species supported by lakes, small water bodies seem to contribute considerably more to the total cladoceran richness of an average landscape in Flanders than lakes, because of their high abundance. With respect to biodiversity conservation at the landscape scale, our results point to the importance of maintaining a diversity of water body types of different size, permanence and flow regimes.

**Keywords** Zooplankton · Cladoceran · Ditch · Pool · Pond · Lake · Wheel track · Stream · Species richness · Biodiversity

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The ecology of European ponds: defining the characteristics of a neglected freshwater habitat

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## Introduction

So far, most studies on biodiversity in aquatic habitats have focused on rivers, streams and lakes, and little research has been done on smaller aquatic systems. Small water bodies, such as ponds, pools, ditches, and wheel tracks are, nevertheless, ubiquitous features of the landscape and form no doubt the most common type of freshwater habitat in many areas of Europe. Despite their high abundance and the fact that they can support unique floral and faunal elements, these small ecosystems have only recently been recognized as important habitats for the maintenance of biodiversity (Armitage et al., 2003; Nicolet et al., 2004; Biggs et al., 2005; Oertli et al., 2005). In many regions these small and hence vulnerable types of water bodies are highly threatened due to eutrophication, pollution or physical destruction (Boothby, 2003). Pools, ponds, and ditches differ from lakes and rivers in many aspects (Oertli et al., 2002; Søndergaard et al., 2005) and can therefore be expected to be affected by anthropogenic stress in different ways and at different spatial scales (Allan et al., 2004; Declerck et al., 2006).

A good knowledge of patterns of species diversity within and among different types of aquatic habitat is necessary to direct strategies for the management and protection of aquatic biodiversity at the landscape scale. However, there are only few studies that have investigated aquatic biodiversity on a large catchment scale (Stendera & Johnson, 2005) or on a diverse set of water body types (Williams et al., 2004). Williams et al. (2004) compared the diversity of macroinvertebrates and macrophytes between different water body types within an entire part of a river catchment. They found that small water bodies contributed substantially to the regional biodiversity. This was to a large extent due to the high beta diversity of these systems, especially of ponds. The aim of this article is to compare the community composition and species diversity of cladocerans of different water body types and to assess the contribution of each of these water body types to average landscape cladoceran diversity.

## Methods

### Study area

We studied zooplankton communities in aquatic habitats from 18 different regions distributed over the major part of Flanders (Belgium) (Fig. 1). In each of the regions, we defined a circular area of 28 $km^2$. Within each of the areas, we sampled the zooplankton of on average 14 (range 10–21) water bodies belonging to six different water body types (see Table 1 for the definitions of water body types used in this study). In each area, the water bodies were chosen upon haphazard encounter in the field while walking in the surroundings of ponds and lakes. The number of sampled water bodies in each of the areas is presented in Table 2. Not all water body types were equally represented in each of the sampled areas. In total, we sampled ten wheel tracks, 38 pools, 151 ponds, 13 lakes, 26 ditches, and nine streams. The water bodies had no surface connections with other water bodies.

Land use in Flanders is dominated by intensive crop culture and pasture. Forest patches are scarce, fragmented, and small. The 18 areas were part of a larger survey that was carried out in the framework of the pond project MANSCAPE (Declerck et al., 2006) and each area represented a wide range in land use intensity.

### Sample collection

We sampled the zooplankton of the water bodies once during the period June–August 2003. Cladoceran zooplankton samples were obtained with a conical plankton net (mesh size: 64 μm, diameter: 26 cm). Each water body was sampled for a total of 2 min with the total sampling time equally divided between the shore and the central zone of the water body. At both shore and central zone we sampled at four different spots equally distributed over the entire surface area (wheel tracks, pools, ponds, and lakes), or along a stretch of at least 10 m (ditches and streams). In very shallow habitats, water was collected with a beaker (5 l) and filtered through the

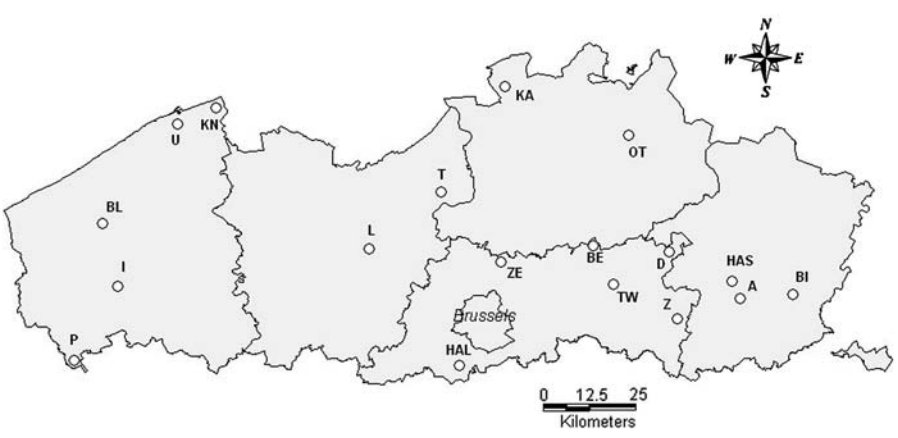


**Fig. 1** Geographic location of the 18 study areas on the map of Flanders (Belgium). KN, Knokke; U, Uitkerke; BL, Diksmuide; I, Ieper; P, Ploegsteert; L, Lede; T, Temse; Ka, Kalmthout; OT, Oud Turnhout; ZE, Zemst; BE, Begijnendijk; D, Diest; HAL, Halle; TW, Tielt-Winge; Z, Zoutleeuw; HAS, Hasselt; A, Alken; BI, Bilzen

**Table 1** Summary of definitions of aquatic habitats used in the survey (adapted from Williams et al., 2004)

| Water body type | Definition |
|---|---|
| Wheel track (W) | Small shallow and elongated water bodies situated on sandy roads or tracks created by transport of vehicles. These aquatic habitats are temporarily and can vary strongly over time. |
| Pool (PL) | Temporary water bodies smaller than 25 $m^2$. Includes both man-made and natural water bodies. |
| Pond (PN) | Water bodies 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 water bodies. |
| Lake (L) | Permanent water bodies larger than 2 ha in area. Includes reservoirs and gravel pits. |
| Ditch (D) | Man-made channels created primarily for agricultural purposes, and which usually: (i) have a linear plan form, (ii) follow linear boundaries, often turning at right angles, and (iii) show little relationship with natural landscape contours. |
| Stream (S) | Small lotic water bodies created mainly by natural processes. Streams differ from ditches in (i) usually having a sinuous plan form, (ii) not following field boundaries, or if they do, pre-dating boundary creation, and (iii) showing a relationship with natural landscape contours e.g., running down valleys. All selected streams were less deep than 1 m and less width than 5 m. |

**Table 2** Number of water body types sampled in each of the 18 studied areas in Flanders

| Area | Date | Water body type | | | | | |
|---|---|---|---|---|---|---|---|
| | | W | PL | PN | L | D | S |
| Alken (A) | 1/7/03 | 0 | 4 | 7 | 0 | 1 | 2 |
| Begijnendijk (BE) | 12/7/03 | 1 | 6 | 7 | 0 | 1 | 1 |
| Bilzen (BI) | 12/6/03 | 1 | 1 | 7 | 1 | 1 | 1 |
| Diest (D) | 20/6/03 | 0 | 1 | 7 | 0 | 2 | 0 |
| Diksmuide (BL) | 2/7/03 | 1 | 1 | 10 | 2 | 3 | 0 |
| Halle (HAL) | 4/7/03 | 1 | 3 | 8 | 1 | 1 | 1 |
| Hasselt (HAS) | 12/6/03 | 1 | 1 | 17 | 1 | 3 | 0 |
| Ieper (I) | 23/6/03 | 0 | 1 | 9 | 1 | 1 | 0 |
| Kalmthout (KA) | 15/7/03 | 2 | 1 | 7 | 2 | 1 | 0 |
| Knokke (KN) | 19/7/03 | 0 | 1 | 8 | 0 | 0 | 1 |
| Lede (L) | 14/7/03 | 0 | 2 | 9 | 0 | 1 | 0 |
| Oud-Turnhout (OT) | 6/8/03 | 1 | 3 | 5 | 2 | 2 | 1 |
| Ploegsteert (P) | 19/7/03 | 0 | 1 | 12 | 0 | 2 | 1 |
| Temse (T) | 13/7/03 | 0 | 4 | 7 | 1 | 1 | 1 |
| Tielt-Winge (TW) | 12/7/03 | 0 | 4 | 9 | 0 | 1 | 0 |
| Uitkerke (U) | 24/6/03 | 0 | 1 | 7 | 0 | 2 | 0 |
| Zemst (ZE) | 13/7/03 | 1 | 1 | 8 | 2 | 0 | 0 |
| Zoutleeuw (Z) | 27/6/03 | 1 | 2 | 7 | 0 | 3 | 0 |

Area, location of sampled area; date, time of sampling; W, wheel tracks; PL, pools; PN, ponds; L, lakes; D, ditches; S, streams

plankton net. Samples from deeper water were collected with a long-handled plankton net (64 µm, diameter: 26 cm). The zooplankton samples were preserved in formaldehyde (4%) saturated with sucrose. Cladocerans in the samples were analyzed up to species level following Flössner (2000). For each water body a subsample of at least 100 cladocerans was identified. Water bodies of which samples contained less than 70 cladoceran specimens in total were excluded from further data analysis (four wheel tracks, one pool, two ditches, and two streams).

## Data analysis

### *Community composition*

We formally tested for differences among the zooplankton communities of the different water body types by applying redundancy analysis (RDA) on percentage abundance data (arcsine-transformed) and canonical correspondence analysis (CCA) on species lists (presence/absence data) using the software CANOCO v5 (Lepš and Šmilauer, 2003). In these analyses, the different water body types were specified using dummy variables. We also specified the 18 studied areas as co-variables to avoid biases introduced by geographic patterns. We assessed the statistical significance of differences among water body types with random Monte Carlo permutations ($n = 999$). These permutations were restricted to areas (areas specified as 'blocks'; see Lepš and Šmilauer, 2003).

### Species richness

Species richness of a water body (local species richness) was estimated as the total number of species recorded in its sample upon rarefaction to a standard number of 100 individuals with the statistical program PRIMER-5 (Clarke & Gorley, 2001). For each of the studied regions, we calculated the average local species richness for each type of water body.

We created species accumulation curves for each type of water body with the likelihood-based method developed by Mao et al. (2005). This method allowed an estimate to be made of the rate at which new species accumulate with an increasing number of samples. Through extrapolation of the available data the procedure also allowed, for each water body type, for a graphical evaluation to be made of whether the species accumulation curve approximates its asymptote and for an estimate to be made of total expected species richness with associated bootstrap confidence intervals. It should, however, be noted that extrapolations should be restricted to triple the number of samples available (Colwell et al., 2004).

Since, low sample numbers prevented us from making reliable estimates of total expected species richness for each water body type with extrapolation methods, we compared total richness among water body types with standard estimates of total richness based on a fixed number of six water bodies. We chose the number of six because this is equal to the total number of systems of the least represented water body type (wheel tracks). This procedure had the additional advantage of obtaining independent replicate estimates of total diversity for most of the water body types (except wheel tracks and streams). Replicate sets of six systems were randomly chosen within each of the water body categories without replacement.

We tested for differences in diversity among water body types with ANOVA and Tukey's post-hoc testing. All variables were log-transformed prior to analysis. ANOVA-analyses were performed with the software package STATISTICA v6. The species accumulation curves were computed with the programme R (version 2.4.0.) and algorithms were provided by C. X. Mao.

## Results

### Community composition

CCA and RDA revealed significant differences in both species lists ($F = 1.78$; $p < 0.01$) and proportional species composition ($F = 1.75$; $p < 0.01$) among the different water body types (Fig. 2). Pairwise post-hoc RDA tests indicated significant compositional differences between all possible pairs of water body types, except for the combinations of wheel tracks with pools and ditches with streams. The

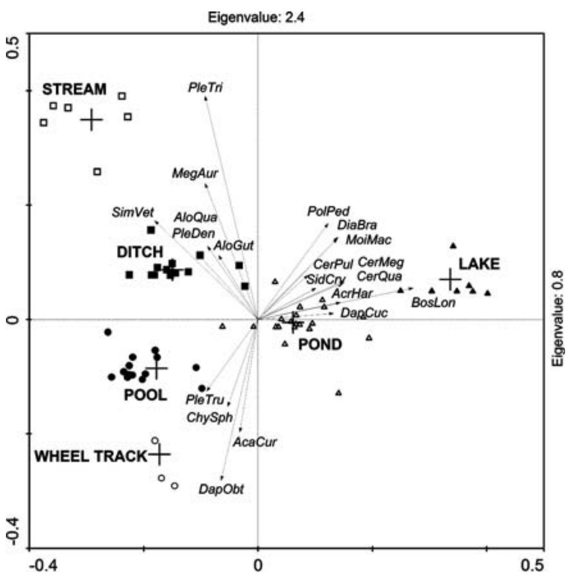


**Fig. 2** Results of a redundancy analysis (RDA) showing patterns of association between species and water body type. Regional differences were partialled out by defining the 18 studied areas as co-variables. The water body types were specified as nominal variables and are represented by centroids. The samples are represented by symbols indicating the water body type: ■ = ditches, □ = streams, ▲ = lakes, △ = ponds, ● = pools and ○ = wheel tracks. AloQua, *Alona quadrangularis*; BosLon, *Bosmina longirostris*; ChySph, *Chydorus sphaericus*; DapObt, *Daphnia obtusa*; DiaBra, *Diaphanosoma brachyurum*; MegAur, *Megafenestra aurita*; MoiMac, *Moina macrocopa*; PleTri, *Pleuroxus trigonellus*; PolPed, *Polyphemus pediculus*; SimVet, *Simocephalus vetulus*; PleTru, *Pleuroxus truncatus*; AcaCur, *Acantheloberis curvirostris*; PleDen, *Pleuroxus denticulatus*; AloGut, *Alona guttata*; DapCul, *Daphnia cucullata*; CerMeg, *Ceriodaphnia megops*; Cer pul, *Ceriodaphnia puclhella*; CerQua, *Ceriodaphnia quadrangula*; SidCry, *Sida crystallina*; AcrHar, *Acroperus harpae*

most important axis of variation in the RDA analysis (Eigen value = 2.4) mainly represented the difference between lakes and other water body types, with ponds taking an intermediate position. The second axis (Eigen values = 0.8) mainly appeared to differentiate between small temporary lentic water bodies (wheel tracks and pools) and the larger systems (in terms of total surface area: lakes, ditches, and streams). The relative abundance of *Bosmina longirostris*, *Polyphemus pediculus*, *Moina macrocopa*, and *Diaphanosoma brachyurum* was higher in lakes than in the other water body types, while *Daphnia obtusa* was best represented in wheel tracks and pools (Table 3). The relative share of *Simocephalus vetulus* of total clacoderan density was highest in streams and ditches. *Pleuroxus trigonella* and *Alona quadrangularis* had their highest relative abundances in streams and ditches, respectively, whereas *Chydorus sphaericus* was most abundant in wheel tracks.

## Species richness

We detected a total of 53 cladoceran species in the entire set of samples. Overall, local species richness differed significantly between water body types ($F(5) = 2.34$; $p = 0.04$). Average local species richness was highest for lakes (5.7; range: 3–11.1) (Fig. 3a). Average richness in ditches (4.1; range: 1–10.8 species) and ponds (4.2; range: 1–12.4 species) was similar and tended to be slightly higher than in pools; the difference was however not significant.

Results of the species accumulation curves (Fig. 4) show a rapid increase in total species number with an increasing number of lakes compared to pools, whereas ponds and ditches take an intermediate position. According to the curves, a total count of 20 species appears to correspond approximately with a total of six lakes, nine ditches, 11 ponds, or 18 pools. The curves also show that lakes and, to a smaller extent pools, do not approximate their asymptote within the range of samples. In contrast, the curves for ponds and ditches tend to approximate much better their asymptote. According to the likelihood-based extrapolation, total richness equals 49 species in pools (95% confidence interval: 46–51) and 40 species in ditches (95% confidence interval: 34–55). The accumulation curves of wheel tracks and streams could not be reliably characterized due to low number of available samples.

Our standardized measure of total richness showed a similar pattern as local species richness (Fig. 3b).

**Table 3** Summary of all significant differences (Tukey post-hoc tests) between the studied water body types for the relative abundances of the ten most dominant species

| Species | | Tukey post-hoc tests | | | | | |
|---|---|---|---|---|---|---|---|
| | | W | PL | PN | L | D | S |
| *Alona quadrangularis* (O.F. Müller, 1776) | D | | > | > | > | | |
| *Bosmina longirostris* (O.F. Müller, 1785) | L | > | > | > | | > | > |
| | PN | | > | | | > | |
| *Chydorus sphaericus* (O.F. Müller, 1785) | W | | | > | > | | |
| *Daphnia obtusa* (Kurz, 1874) | W | | | | > | | |
| | PL | | | > | > | > | |
| *Diaphanosoma brachyurum* (Liévin, 1848) | L | > | > | > | | > | > |
| *Megafenestra aurita* (S. Fischer, 1849) | S | > | > | > | > | > | |
| *Moina macrocopa* (Straus, 1820) | L | > | > | > | | > | > |
| *Pleuroxus trigonellus* (O.F. Müller, 1776) | S | > | > | > | > | > | |
| *Polyphemus pediculus* (Linnaeus, 1761) | L | > | > | > | | > | > |
| *Simocephalus vetulus* (O.F. Müller, 1776) | PL | | | | > | | |
| | D | | | > | > | | |
| | S | > | | > | > | | |

The symbol '>' indicates that the relative abundance of a species is significantly higher in the water body type of the first column than in the corresponding water body type of the first row (see Table 1 for the abbreviations of the water body types)

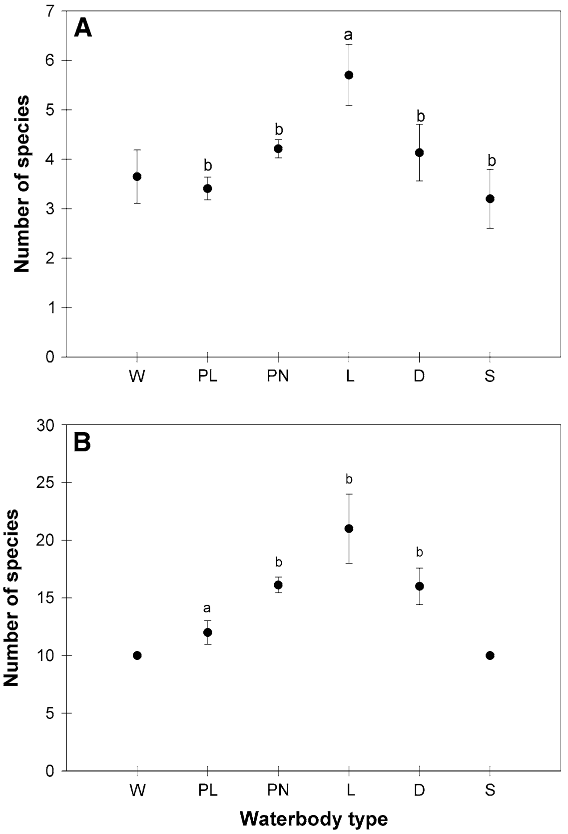


**Fig. 3** Differences between water body types with respect to: (**a**) average of the mean local zooplankton diversity observed in each of the selected regions. Error bars denote SE; (**b**) average total diversity expressed as the total species richness observed in sets of six randomly selected systems. Error bars denote SE and reflect the variation among randomly chosen sets of six systems within each water body category. Significant differences between water body types according to Tukey post-hoc tests are indicated by different characters. Abbreviations of the water body types are explained in Table 1

Lakes tended to have the highest total richness, but the difference was not significant with ponds and ditches. Pools had significantly lower total richness than ponds, lakes, and ditches (Tukey post-hoc: $p < 0.05$). Due to lack of replicate values, wheel tracks and streams could not be incorporated in this analysis.

## Discussion

### Community composition

Our survey revealed a high variation in cladoceran community composition among different water body

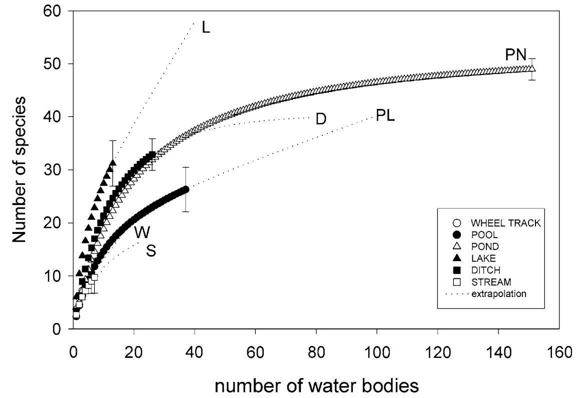


**Fig. 4** Species accumulation curves for the six water body types. Expected species richness values (dotted line) were computed using the likelihood-based estimator. Extrapolations for each water body type are limited to three times the number of available samples. For reasons of clarity, 95% bootstrap confidence intervals are only presented for the total number of samples available

types (wheel tracks, pools, ponds, lakes, ditches, and streams) in Flanders. Species composition differed considerably among the different types of systems and many species showed pronounced affinities with one or a few specific water body types. Pelagic zooplankton species, like *B. longirostris*, *D. brachyura*, *P. pediculus*, and *M. macrocopa* were clearly more associated with lakes than with other water bodies. In contrast *D. obtusa* was mainly found in small temporary systems, such as pools and wheel tracks. This species and *C. sphaericus* have been shown to be very rapid colonizers of newly created habitats (Louette & De Meester, 2005) and have often been reported for temporary waters during spring (Forró et al., 2003). Ditches and streams were quite similar in community composition and were dominated by species like *A. quadrangularis*, *P. trigonelus*, *M. aurita*, and *S. vetulus*. An important reason for the difference between the ditches and streams and the other water body types is probably that they are lotic systems. Water flow in lotic systems may act as an important source of disturbance for zooplankton communities. Cladoceran zooplankton tends to be underrepresented in flowing zones of lotic systems (Dole-Olivier et al., 2000) as complete washout of their populations can occur at water velocities higher than 3.2 cm $s^{-1}$ (Richardson, 1992). Persistence of a zooplankton population in a lotic system is also strongly determined by the availability of flow