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ECOLOGY OF EUROPEAN PONDS

How can we make new ponds biodiverse? A case study monitored over 7 years

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Abstract A new pond complex, designed to enhance aquatic biodiversity, was monitored over a 7-year period. The Pinkhill Meadow site, located in grassland adjacent to the R. Thames, proved unusually rich in terms of its macrophyte, aquatic macroinvertebrate and wetland bird assemblages. In total, the 3.2 ha mosaic of ca. 40 permanent, semi-permanent and seasonal ponds and pools was colonized by approximately 20% of all UK wetland plant and macroinvertebrate species over the 7-year survey period. This included eight invertebrate species that are Nationally Scarce in the UK. The site supported three breeding species of wading bird and was used by an additional 54 species of waders, waterfowl and other wetland birds. The results from four monitoring ponds investigated in more detail showed that these ponds significantly supported more plant and macroinvertebrate species than both minimally impaired UK reference ponds, and other new ponds for which compatible data were available. Comparisons of the physico-chemical, hydrological and land-use characteristics of the Pinkhill pools with those of other new ponds showed that the site was unusual in having a high proportion of wetlands in the near surrounds. It also had significantly lower water conductivity than other ponds and a higher proportion of (non-woodland) semi-natural land in its surroundings. Given that ponds are known to contribute significantly to UK biodiversity at a landscape level, and that several thousand new ponds are created each year in the UK alone, the findings suggest that well designed and located pond complexes could be used to significantly enhance freshwater biodiversity within catchments.

Keywords Constructed ponds · Compensatory wetlands · Pond age · Colonisation · Hydroperiod

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Introduction

Ponds are an important freshwater habitat in Britain. They are species-rich, supporting populations of at least two-thirds of Britain's freshwater plant and animal species (Williams et al., 1999) and, in terms of both species richness and rarity, the biodiversity of ponds appears to compare well with that of other freshwater ecosystems, such as lakes, rivers, streams and ditches (Godreau et al., 1999; Williams et al., 2004; Davies, 2005). A considerable number of new ponds are created in Britain each year, with around 2000 excavated annually in the lowlands alone (Williams et al., 1998). Yet, despite the popularity of pond creation, a little is known of the ecological value or characteristics of new pond sites. Across Europe as a whole in the last decade, a mere handful of papers describe the value of new ponds for amphibian and macrophyte assemblages (e.g., Gee et al., 1997; Stumpel & van der Voet, 1998; Baker & Halliday, 1999; Fleury & Strehler Perrin, 2004; Hansson et al., 2005), and fewer still the biodiversity value of new ponds for other groups, such as macroinvertebrates, or wetland birds (Gee et al., 1997; Fairchild et al., 2000; Hansson et al., 2005).

Perhaps most significantly, there has been exceptionally little research into the factors that drive new pond quality. In particular we know little of the key locational and physico-chemical characteristics likely to promote development of high biodiversity in new ponds. This is an important omission. If ponds both support a large proportion of freshwater biodiversity in catchments and, are continually being created in large numbers, then, through the application of good design principles, there is considerable potential to use the creation of highly biodiverse pond sites as a tool for enhancing catchment biodiversity.

This article describes the biodiversity value of a new pond complex, created in the early 1990s in southern England and subsequently monitored over a 7-year period. The richness of the wetland plant, aquatic macroinvertebrate and wetland bird assemblages is compared with other available datasets, and the factors likely to promote the development of biodiverse new ponds are evaluated.

Methods

Site description

Pinkhill Meadow in Oxfordshire, England (UK national grid coordinates: SP 439 067), lies in an area of floodplain grassland surrounded on two sides by a meander of the upper River Thames and on the third side by Farmoor Reservoir, which is the largest area of standing open water in the county. Pinkhill Meadow as a whole is small (approximately 4.5 ha), and relatively disturbed by the public using perimeter footpaths that surround the site.

Soil cores through the meadow substrata show that the site is underlain by clayey alluvium (0.8 to >4 m thick). This, in turn, overlies Quaternary gravels that support a shallow confined aquifer. Excavations into the gravel are filled rapidly by groundwater that fluctuates by approximately 0.4 m during the year. Excavations into the alluvial layer alone fill with surfacewater that fluctuates by ca. 1 m during the year. The area is subject to inundation from 1 in 15 year floods from the River Thames. During the monitoring period described here, the new pond complex was flooded twice: in the winters of 1991/2 and 1992/3.

Construction of the pond complex

The Pinkhill Wetland Enhancement Project was conceived in 1990 as a joint initiative by Thames Water Utilities Ltd (TWUL) and the Environment Agency (Thames Region). Pond Conservation provided ecological guidance for the design of the site and on-site supervision during construction work. A principle objective of the Pinkhill scheme was to provide complementary breeding and feeding habitats for wetland birds that would extend the existing feeding and roosting areas provided by the concrete-rimmed reservoir. Associated objectives were to provide habitats for a diverse range of wetland plant and aquatic macroinvertebrate species.

The final design of the wetland comprised a complex of approximately 40 permanent, semi-permanent and seasonal pools, sited within a low wetland area ca. 3.2 ha in total. The ponds ranged in area from the largest waterbody (the Main Pond) which is about 0.75 ha and has a number of mud and gravel small islands, to many tiny permanent and seasonal pools ca. 1–2 m^2 in area. Most ponds were dug into groundwater, but some were surfacewater fed. Winter pond depths ranged from a few centimetres to 2.5 m. Part of the site perimeter, adjacent to footpaths, was planted-up with a narrow reed bed and willow hedge to act as a screen.

Excavation of the new wetland occurred in two stages. Phase 1 excavation was undertaken in June and July 1990 and involved the creation of the four waterbodies (the Main Pond, Scrape, Groundwater Pond and Surfacewater Pond), which were subsequently the main focus of site monitoring. Phase 2, undertaken in winter 1991/92, extended the areas of shallow water, wet meadow, mudflats and temporary pool habitats.

The ponds were allowed to colonise naturally, so that, with the exception of *Phragmites australis* (Cav.) Trin. ex Steud which was planted around the edge of the site as a screen, no plants were deliberately introduced to the site.

Survey methods

Water chemistry samples were collected to provide background data describing the site's water quality. Water sampling focused on the four waterbodies created during Phase 1 of the project (above). For these ponds, replicate samples were taken monthly from April 1991 to March 1992 and then bimonthly from July 1992 to July 1993 except during the bird-breeding season. Water samples and meter readings were taken from the centre of each pond at mid column depth. Samples were analysed at an accredited laboratory for the following determinands: pH, conductivity, total oxidised nitrogen, ionised ammoniacal nitrogen ($NH_4^+ \cdot N$), unionised ammoniacal nitrogen (NH_3N), soluble reactive phosphorus (SRP) and biochemical oxygen demand (BOD). Water temperature was recorded on site on each sampling occasion.

Physico-chemical data were collected from each of the four main monitoring ponds. Details of the methods used to collect data are given in Pond Action (1998). However, in summary: pond area was measured from a 1:500 scale map of the site levelled after construction. Land-use cover was estimated in the field within the 100 m zone supplemented by map evidence where necessary. Water and sediment depth measurements were an average from 5 measurements taken along two perpendicular transects. Organic matter and sediment particle size categories were estimated in the field. Inflow velocity was estimated as the number of seconds for a floating object to travel 1 m downstream × average water width × average water depth.

Wetland macrophyte species were recorded in August 1991–1996. On each occasion, plant species lists were compiled for the site as a whole and individually for each of the four monitoring ponds. Plants were surveyed while walking and wading the margin and shallow water areas of the waterbodies. In the deep Main Pond, submerged macrophytes were surveyed using a grapnel thrown from the bank or islands. 'Wetland macrophytes' were defined as plants listed in the National Pond Survey methods guide (Pond Action, 1998), which comprises a standard list of the ca. 400 submerged, floating-leaved and marginal wetland plants recorded in the UK.

Aquatic macroinvertebrate species lists were compiled annually for the four monitoring ponds between 1990 and 1997. These surveys were undertaken in July, except in 1991 (May) and 1995 (August). Water areas were sampled using a standard 1 mm mesh hand-net, frame-size 0.26 × 0.30 m. The sampling method followed the National Pond Survey protocol (Pond Action, 1998), with each site sampled for 3 min and the sampling time divided equally between major mesohabitats identified at the pond. In addition, for the years 1994–1997, the samples from the available mesohabitats (either 2, 4 or 8, depending on the pond in that year) were sub-divided, as appropriate, to give a total of 16 sub-samples from each pond. In the current article, these data were used to provide a means of comparing Pinkhill results with other survey data collected using shorter sampling durations (see below), but for the majority of the analyses the data were collated to give a single 3-min sample for each pond. The samples collected 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. In 4 years (1992–1994 and 1997) a more comprehensive survey of the site as a whole was carried out in autumn. This used a field sorting approach and covered all parts of the site. In order to standardise this field survey, the site was divided into 14 specified water areas of similar size or potential. Each of these areas was searched for macroinvertebrate species (using a pond-net and large white sorting tray), for 1 h per water area on each occasion. Most species were identified on site. Taxa requiring microscopic identification were preserved in 70% ethanol for return to the laboratory. In order to reduce the possibility of recorder bias, the same two surveyors carried out the survey on each occasion. 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.

Data describing wader and waterfowl use of the site as a whole (but not of the individual waterbodies) were derived from records entered in the log-books located in the hide overlooking Pinkhill and from the adjacent Farmoor Reservoir. In 1991, during the Phase I monitoring programme, J. Biggs evaluated the accuracy of the log-book data compared to a complete survey (i.e., full-day observations) of Pinkhill (Pond Action, 1992). The results indicated that for recording breeding species, birdwatchers visited the site sufficiently regularly to provide accurate and near daily summaries of the progress of breeding species. Records of the daily peak count of individuals were also sufficiently reliable for waders and scarce species (e.g., Shoveler *Anas clypeata* L., Redshank *Tringa totanus* (L.). and Water Rail *Rallus aquaticus* L.). Peak numbers of common waterfowl (e.g., Tufted Duck *Aythya fuligula*, (L.) and Mallard *Anas platyrhynchos* L.) were more likely to be underestimated, since many observers ignored these birds. However, the observations still provided an indication of the relative abundance of the common species across the site as a whole.

Analysis of biodiversity

Macrophyte and macroinvertebrate data were analysed to assess the biodiversity value of the different waterbody types in terms of: (i) species richness and (ii) species rarity. Richness was measured as the number of species, or distinctive taxa, recorded. Wetland plant richness was further subdivided into aquatic species (i.e., the total number of submerged and floating-leaved taxa) and marginal emergents. Measures of plant richness excluded *Phragmites australis*, which was deliberately introduced using plants purchased from commercial suppliers, for use as a screening reed bed around the periphery of the site. Two other common ornamental species that appeared in this reed bed the year after planting (*Mimulus guttatus* DC and *Bolboschoenus maritimus* (L.) Palla), were also excluded because of the likelihood that they were introduced with the *Phragmites* plants. For both plant and macroinvertebrate assemblages, comparisons of species rarity were made within the following two categories: (a) “Local”, defined for invertebrates as species either confined to certain limited geographical areas, where populations may be common, or of widespread distribution but with few populations, and for plants as those species recorded from fewer than 25% of the 10×10 km grid squares ($n = 2823$) in Britain (Preston et al., 2002) and (b) “Nationally Scarce” (both invertebrates and plants), species recorded from 15 to 100 10×10 km grid squares in Britain.

Comparison with other data

The Pinkhill plant and macroinvertebrate data were compared with results from a range of national pond surveys, and surveys of new ponds. The national surveys were (i) the National Pond Survey (NPS): a survey of high quality reference sites located in areas of semi-natural land use across the UK (Biggs et al., 2005) (ii) the Impacted Ponds Database (IPD): a stratified random survey of ponds in England and Wales excluding ponds in semi-natural landscapes (Biggs et al., 2005), and (iii) Lowland Pond Survey (LPS96): a plant only survey of ponds representative of lowland countryside areas of the UK (Williams et al., 1998). Both the IPD and LPS96 datasets were, predominantly composed of ponds exposed to a wide range of anthropogenic stresses including urban and road runoff, agricultural runoff, organic pollution, hydrological stresses and overstocking with fish and waterfowl. Sub-sets of data specifically describing new ponds were extracted from these three datasets. For the NPS and IPD datasets this included ponds $<$10-years-old. LPS ponds were all less than 12 years old. In addition, the Pinkhill data were compared with results from the Welsh Farm Pond Survey (Gee et al., 1994, Gee & Smith, 1995), a study of new and renovated ponds located in mid and west Wales. For the current assessment, a subset of the Welsh data was used which included ponds 3–10 years in age (mean 5.2 years) and which excluded renovated sites.

For plants, the field methods used for data collection were, in all cases, directly comparable with those used at Pinkhill (see above). Macroinvertebrate data were collected using directly compatible 3-min survey data for (i) the NPS (summer season data) and (ii) the IPD survey. Gee et al.'s survey of farm ponds in Wales provides useful invertebrate data from new ponds, but was based on surveys using only a 1-min sample. In order to enable a direct comparison with the Pinkhill ponds, sub-sample data from Pinkhill were analysed (see above). In order to provide these data five of the 16 sub-samples (each 11 s duration) were selected at random for each survey pond and the data collated to give a 55 s sample from each pond. The Pinkhill dataset spans a 7-year period. In order to provide the fairest comparison with the other new pond datasets (for which the average or median pond age was 5 years), the 1995 Pinkhill data was used, when the four monitoring ponds were also 5-years-old. Physico-chemical data compatible with the Pinkhill survey results were available from all three national pond surveys (NPS, IPD, LPS96), although LPS96 lacked a full suite of chemical determinands (limited to pH, calcium, conductivity).

Statistical analysis

Differences between (i) the four Pinkhill monitoring ponds and (ii) the monitoring ponds and other new ponds, were analysed in terms of species richness and physico-chemical characteristics. These data differed in the extent to which they approached normality and were, therefore, compared using non-parametric methods. The significance of differences was tested using two-tailed Mann–Whitney U, Kruskal–Wallis or Friedman tests.

Results

Physico-chemical data

The four Pinkhill monitoring ponds were un-shaded permanent pools between 0.75 ha and 0.02 ha in area, with a mean water depth of 0.2–1.5 m. In general, their water chemistry profiles were typical of calcium-rich ponds in lowland Oxfordshire with a mean pH of 7.9. Conductivity was low with a mean of 208 μS. Total oxidised nitrogen (TON), Soluble reactive phosphorus (SRP) and ammoniacal nitrogen ($NH_4^+ \cdot N$ and $NH_3 \cdot N$) levels were also low: falling below the analysis detection limits on most occasions (<0.2, <0.06 and <0.05 mg/l respectively). The exception was winter TON levels where there was a maximum of 0.3–6.05 mg/l: almost certainly the result of inputs of groundwater from the adjacent River Thames.

Plant species

The Pinkhill site was colonised rapidly by both marginal and aquatic plants. Within 6 months of the site's creation the new pool complex as a whole had been colonised by 34 species of wetland plant, and richness in the four main monitoring ponds ranged from 9 to 19 species (Fig. 1a). By 1997 the complex as a whole supported at least 67 plant species (Appendix 1). Four early colonist plant species had been lost by this time, but overall the site was still accumulating taxa (Fig. 1b). Plant richness in the four main monitoring ponds after 7 years varied from 27 to 50 species (mean 36 species).

During its first 7 years the Pinkhill site supported between three and nine locally uncommon plant species. Two early colonising local aquatics (*Potamogeton obtusifolius* Mert. & W.D.J. Koch and *Potamogeton perfoliatus* L.) disappeared co-incidentally with the invasion of two non-native taxa: *Elodea nuttallii* (Planch.) H. St. John and *Lagarosiphon major* (Ridl.) Moss.

Macroinvertebrate species

The four monitoring ponds were relatively slowly colonised by macroinvertebrate species. Four to eight species (mainly Coleoptera and Hemiptera) were recorded from the waterbodies in summer 1990, a few months after they were dug. However, in the 3 years after this, species richness increased rapidly so that in 1993, invertebrate richness in the four ponds averaged 52 species (range 46–57). After 3 years, average invertebrate richness plateauxed (Fig. 1c), although there were considerable differences between individual ponds in different years. In the 4 years when the Pinkhill site as a whole was surveyed, the field survey recorded between 87

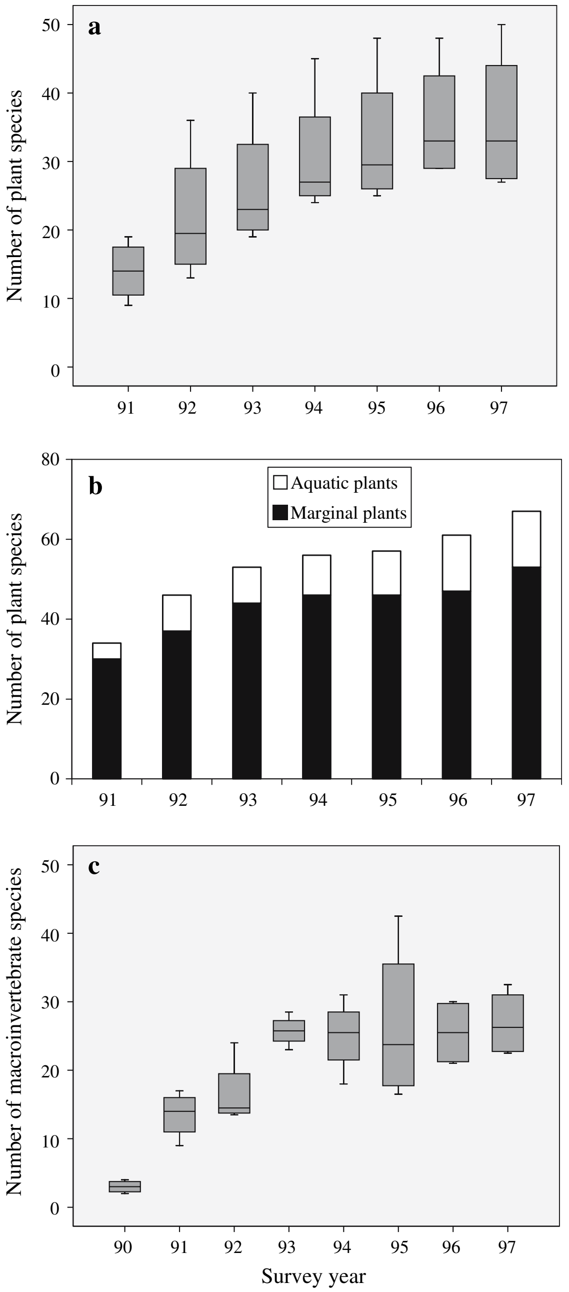

Fig. 1 Species richness from the Pinkhill Site (**a**) Plant richness from the four monitoring ponds (**b**) Plant richness from the whole site (**c**) Macroinvertebrate richness in the four monitoring ponds. Plots show median, inter-quartile and extreme values

(1992) and 110 (1997) macroinvertebrate species, and in total 165 macroinvertebrate species were recorded from all surveys over the 7 year period (Appendix 2).

Out of this total, eight species (all Coleoptera) are listed as Nationally Scarce in the UK. A further 13 could be considered locally uncommon. Most of these were Hemiptera, but local species in the orders Hirudinea, Coleoptera, Tricoptera and Hiudinea were also recorded.

Wetland birds

Between May 1990 and December 1997, 57 species of non-passerine wetland birds were recorded on the Pinkhill Meadow wetlands (excluding feral or escaped species). These included 24 species of wader and 33 other wetland species (Table 1). Most waterfowl showed marked seasonal patterns in their use of the site, the majority being present only in spring and summer.

Of the wading birds, the most commonly recorded species at Pinkhill Meadow were Lapwing *Vanellus vanellus* (L.), Snipe *Gallinago gallinago* (L.), Little Ringed Plover *Charadrius dubius* Redshank and Common Sandpiper *Actitis hypoleucos* (L.). All other waders were recorded much less frequently (Appendix 3). Three wading species (Lapwing, Little Ringed Plover, Redshank) and up to six species of waterfowl all bred on Pinkhill in one or more years (Table 1).

Comparison with other survey data

Wetland plants

Species-richness comparisons with ponds from other datasets suggest that the Pinkhill ponds supported unusually species-rich plant assemblages (Table 1). Compared to ponds in national UK datasets (which include ponds of all ages) the Pinkhill ponds supported, on average, two to three times more wetland plant species than the impaired countryside ponds of the IPD and LPS96 surveys (significance $P < 0.001$). Pinkhill typically supported ca. 30% more species than the high-quality reference sites of the National Pond Survey (NPS), although this difference was only marginally significant ($P = 0.03$, one-tailed test). The plant richness of the Main Pond also exceeded the maximum number of plants recorded in any pond survey.

Table 1 Comparison of the plant species richness of the four Pinkhill monitoring ponds with other survey data

	Number of plant species recorded: average (range)		
	Marginal species	Aquatic species	All wetland plant species
Pinkhill			
Pinkhill monitoring ponds (All 5 years old, $n = 4$)	28 (21–38)	5 (2–10)	33 (25–48)
National surveys			
National pond survey ($n = 102$)	18 (1–42)	5 (0–14)	23 (1–46)
Impacted pond database ($n = 148$)	11 (1–32)	3 (0–11)	14 (1–38)
LPS96 DETR ($n = 377$)[a]	8 (0–30)	2 (0–10)	10 (0–35)
New ponds only			
National Pond survey (<10 years old $n = 8$)	14 (3–28)	3 (1–5)	16 (4–30)
Impacted pond database (<10 years old $n = 12$)	13 (7–23)	3 (1–5)	16 (9–26)
LPS96 DETR ponds (<12 years old, $n = 26$)[a]	10 (0–24)	2 (0–4)	12 (0–27)
South Wales farm ponds (3–10 years old $n = 26$)[b]	7 (2–13)	3 (0–5)	10 (2–17)

[a] LPS96 = Lowland Pond Survey 1996, DETR = Department of the Environment, Transport and the Regions

[b] Modified from Gee et al. (1994)

Comparisons with the smaller datasets of new ponds (Table 1) shows that the Pinkhill ponds, again, supported at least two to three times more plant species than other new sites. This relationship was significant in all cases (all $P < 0.01$, except NPS where the relationship was week: $P = 0.046$, one-tailed test). The richness of new ponds in semi-natural areas (NPS survey) was lower than older ponds in these landscapes. For ponds in other countryside areas (IPD, LPS96), average plant richness was marginally greater in the new ponds.

Macroinvertebrates

The richness of Pinkhill's macroinvertebrate assemblages mirrored the richness of its plants (Table 2). Compared to national survey data, Pinkhill samples supported around double the number of invertebrate species typical of impaired wider countryside ponds ($P < 0.01$) and, on average, around a third more species than the high quality sites of the NPS (a marginally significant difference at $P = 0.046$, one-tailed test). The Pinkhill ponds also supported significantly more species ($P < 0.05$) than the subset of new ponds in these datasets. Comparison between the 1-min invertebrate sample of new Welsh farm ponds and the 1-min microhabitat samples from Pinkhill (see methods), showed a highly significant difference ($P < 0.001$). In high quality landscapes (NPS) new ponds typically supported fewer macroinvertebrate species than older ponds. In the more impaired ponds of the wider countryside (LPS96, IPD) new ponds were marginally richer in macroinvertebrates than older ponds.

Table 2 Comparison of the macroinvertebrate richness of the four Pinkhill monitoring ponds with other survey data

	No. invert. spp: average (range)
Pinkhill standard survey (3 min)	
Pinkhill ponds (5 years old, $n = 4$)	53 (33–85)
National surveys	
National pond survey ($n = 149$)	35 (6–78)
Impacted pond database ($n = 161$)	25 (2–64)
New ponds only	
National pond survey (<10 years old $n = 8$)	29 (17–39)
Impacted pond database (<10 years old, $n = 12$)	29 (15–52)
Pinkhill ponds, 1 min sample (5 years old, $n = 4$)	39 (23–62)
South Wales farm ponds 1 min. sample (3–10 years old, $n = 26$)[a]	14 (1–26)

[a] Modified from Gee & Smith (1995)

Wetland birds

Bird data from pond complexes comparable to Pinkhill are rarely published, with most studies of wetland birds being concerned with much larger sites. However, in terms of regional comparisons, the wading bird records represent just over half of the total number of wader species that had been seen in Oxfordshire since records were first kept. At its peak, the number of pairs of Little Ringed Plover and Redshank breeding at Pinkhill probably represented about 10% of the Oxfordshire's breeding population for these species. Overall wader densities were high for such a small area. For example, peak Redshank densities in Britain are around 100 pairs/km^2 (= 1 pair/hectare) in optimum habitat (Gibbons et al., 1993), and densities at Pinkhill were similar to this.

Environmental data comparisons

Compatible environmental data from new ponds in the three national datasets (NPS, IPD and LPS96) were combined and compared with data from the Pinkhill monitoring ponds. The results show that there were a few significant differences in terms of most environmental parameters including their area, water source and sediment characteristics. A major exception was a significant relationship with easting ($P < 0.001$), linked to Pinkhill's location in the southern lowlands. There were, however, no difference in pH or calcium concentrations suggesting that, the species-richness differences were unlikely to be related to the major SE (alkaline) to NW (acid) trends that broadly shape the UK's major bio-geographic zones. In terms of surrounding land use, the Pinkhill ponds were also relatively unusual within the dataset in being unshaded ($P < 0.05$) and located in an open (i.e., un-wooded) semi-natural landscape ($P < 0.01$). They had a significantly higher proportion of wetlands in their near vicinity than other ponds in the data-sets ($P = 0.01$). Unfortunately, one of the national datasets (LPS96) had only field meter water chemistry data (see methods), giving limited potential to compare water quality at the sites. However, conductivity data showed that Pinkhill ponds had significantly lower conductivity than other ponds in the datasets ($P < 0.01$). Other relationships between species richness and the physico-chemical variables were not significant.

Discussion

Pond colonisation

Data from the current survey show that new ponds can colonise quickly. Not only did plant and macroinvertebrate species accumulation in the Pinkhill monitoring ponds typically plateaux after only 3–4 years for macroinvertebrates and after 6 years for macrophytes, but new ponds in the Impacted Pond Database and Lowland Pond Survey 1996 were as species-rich as much older ponds in less than 10 and 12 years, respectively. Indeed, further analysis of LPS96 ponds (Williams et al., 1998) showed that 6–12-year-old ponds were significantly more species rich ($P < 0.01$) and supported more uncommon species ($P < 0.05$) than older ponds in this dataset.

The propensity for new ponds to colonise rapidly has long been recognised, in many cases colonisation may come from an existing seed, egg or spore bank in the soil or near surrounds, but authors from Darwin onwards have also noted the inherent mobility of freshwater taxa, which confers on individuals of many aquatic animal and plant species a strong potential for dispersal and colonisation (Darwin, 1859; Talling, 1951; Bilton et al., 2001).

Given that ponds are a natural habitat type, and that pond creation is likely to have been a common process through evolutionary history (Gray, 1988; Biggs et al., 1994), the rapid colonisation of new ponds may also be, in part, attributable to species adaptations to new pond conditions. In terms of their physico-chemical environment, new ponds are clearly different to older ponds: they are typically dominated by inorganic substrates, have a little vegetation cover, and may, at least in their early years, lack predation from higher predators, such as fish. A range of taxa appear to specifically thrive in such conditions. In the United Kingdom, new ball-clay pits, turf ponds and gravel pits have, for example, all been shown to support aquatic invertebrates or plants not found at later stages of succession. This includes uncommon plants, such as Lesser Water-plantain, *Baldellia ranunculoides*, damselflies, such as the Scarce Blue-tailed Damselfly, *Ischnura pumilio*, and rare water beetles such as *Helophorus longitarsus* (Barnes, 1983; Kennison, 1986; Foster, 1991; Fox & Cham, 1994). Other authors have found similar results in seasonal ponds: Fleury & Perrin (2004), for example, showed that pioneer plant assemblages of high conservation interest showed a rapid population increase in the first 2–3 years after ponds were created, followed by a progressive decline.

A third reason for the relative rapidity with which new ponds are colonised may be related to their nutrient status. Previous analysis of ponds in the LPS96 dataset (Williams et al., 1998), showed, for example, that new ponds had significantly lower Trophic Ranking Scores (*sensu* Palmer, 1992) than older ponds, suggesting that they were less enriched than more mature sites. It is possible that new ponds may lack the nutrient burden that accumulates in the sediments and water of many older countryside ponds and that the cleaner new ponds have, as a result, greater potential to support diverse plant and invertebrate assemblages. Such a suggestion is given some credence by the current analysis, which shows that new ponds supported similar numbers of plant and invertebrate species regardless of whether they were located in semi-natural or anthropogenically impaired landscapes. This contrasts with older ponds, where waterbodies located in semi-natural surrounds supported significantly more species than those in the wider lowland landscape (Williams et al., 1998).

Pond richness

It is clear from the current study that Pinkhill was unusually species rich, both at an individual pond scale and across the larger pond complex. In such new ponds where, it may be assumed, biological interactions are little developed, it seems likely that the particular richness of individual ponds should be explicable either in terms of (i) bottom-up effects produced by the physico-chemical environment created during or after pond construction, or (ii) stochastic processes influencing propagule arrival. Comparison of the Pinkhill ponds with other new ponds suggested that, in terms of their physical characteristics, the unusual richness of the Pinkhill ponds could not be explained in terms of difference in size, depth, substrate type or water source. However, differences in shading, land use and conductivity between the Pinkhill ponds and other new ponds indicated that some of the former's richness might be attributable to their open unshaded aspect, their semi-natural grassland surrounds and/or their low chemical conductivity. Of these, shade, is known to be associated with lower species richness, particularly for macrophyte assemblages (Gee et al., 1997; Craine & Orians, 2004; Biggs et al., 2005). Semi-natural grassland land use and conductivity (assuming the latter to be a surrogate for nutrient pollution) are also clearly plausible influences promoting the richness in the Pinkhill ponds. Both minimally impaired land use and water quality have been strongly positively correlated with species richness in ponds (Biggs et al., 2005; Menetrey et al., 2005; Williams et al., 1998).

Clearly, for the Pinkhill site to colonise so rapidly and richly, a wide range of plant and animal propagules must have been available to reach the site from other wetland areas. Comparisons with other new ponds in the current study showed that individual Pinkhill ponds were indeed unusual in having a significantly higher proportion of wetland in their surroundings than was typical of other new ponds. Thus in their near surrounds, the Pinkhill ponds were closely adjacent to (i) other ponds created in the new complex, (ii) the River Thames and its backwaters, and (iii) the large, but barren concrete-sided, Farmoor Reservoir. Further afield, Pinkhill may also have received plant and animal propagules from more distant ditches, streams, ponds and gravel pits which are widespread along the Thames Valley. Other studies, too, have emphasised the importance of propagule availability in ponds. In LPS96, ponds were shown to be significantly richer and to support more rare species when located on, or immediately adjacent to, floodplains and other traditionally wetland areas (Williams et al., 1998). The floristic assemblages of newly created turf ponds and species-richness of more mature ponds has also been shown to be positively related to the proximity of other ponds and wetlands in the neighbourhood (Moller & Rordam, 1985; Beltman et al., 1996; Linton & Goulder, 2000, 2003).

Site richness

In the 7 years following its creation the Pinkhill Meadow site as a whole supported at least 71 plant and 167 macroinvertebrate species: approximately 20% of all the UK's freshwater plants and macroinvertebrates in the groups assessed. The site was also valuable for birds; used both by a wide range of waders and waterfowl, and significant as a breeding area for species such as Redshank, Lapwing and Little Ringed Plover which have either declined markedly or are rare in the UK. For birds, the value of the site is likely to have been strongly influenced by its location. The Thames valley is a well-known flyway for migratory species, and the adjacent Farmoor Reservoir is one of the best areas for recording wetland birds in the county of Oxfordshire (Brucker et al., 1991). The value of Pinkhill as a whole for plants, macroinvertebrates and birds may, in addition, have been influenced by the new site's physical heterogenity and complexity (e.g., Froneman et al., 2001). The waterbody mosaic includes ponds that differ in size, substrate and water source but, more particularly, hydrological regime: it includes pools that are highly seasonal, semi-permanent ponds that dry up in drought years, as well as six large permanent ponds. Seasonality gradient has been clearly shown to drive community type in pond (as well as other freshwaters), in a number of studies at a range of landscape scales (Collinson et al., 1994; Schneider & Frost, 1996; Wellborn et al., 1996) and it seems probable that its range of waterbody hydroperiods contributed to the richness of the Pinkhill site.

Implications

We have argued elsewhere (Williams et al., 1997) that pond creation is a natural and ecologically valid method for maintaining pond biodiversity in the landscape. Man's creation of new ponds mimics age-old processes of natural pond formation, creating new sites that are of value in their own right and that eventually pass through a range of successional stages, each exploited by freshwater taxa.

The value of the current case study is that it suggests that it may be possible to use well-designed and targeted pond creation schemes to some considerable effect in the landscape. Wetland bird observations at Pinkhill suggest that through the development of a number of small-scale habitat-creation schemes it may be possible to significantly influence national breeding populations of wading birds such as Little Ringed Plover (national population ca. 1000 pairs), and perhaps, regional populations of Redshank (Oxfordshire's population ca. 30 pairs in 1997). However, for birds, habitat-creation work of this type seems most likely to succeed in areas where some wetland habitat already exists: for example, alongside rivers, in existing areas of damp grassland, or beside reservoirs and gravel-pits. In these areas, some feeding habitat may already be available, even when habitats are unsuitable for breeding. This appears to be the case at Pinkhill, at least for Little Ringed Plover and Redshank, which spend a certain amount of time feeding on the reservoir margin during the breeding season, and probably also visit sites further afield.

For wetland plant and aquatic macroinvertebrate species the Pinkhill data suggest that, by creating small pond complexes with semi-natural surrounds, good water quality and strong colonisation potential, it may be possible to create exceptionally biodiverse aquatic sites in very short periods of time. Ponds have recently been shown to be surprisingly significant as freshwater habitats, supporting a relatively high proportion of the total freshwater biodiversity present in a range of landscape types (Godreau et al., 1999; Williams et al., 2004). One implication from this finding is that pond creation might have the potential to be a more powerful ecological enhancement tool than is commonly credited. Ponds are relatively simple and cost effective habitats to create. The techniques for creating them are well developed and commonplace, and there are many areas of the landscape where the creation of high quality pond complexes is feasible. Thus, it may prove possible to use well-designed and located pond creation schemes not only to protect pond habitats, but also to enhance freshwater biodiversity across wider catchment areas.

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References

Baker, J. M. R. & T. R. Halliday, 1999. Amphibian colonization of new ponds in an agricultural landscape. Herpetological Journal 9: 55–63.

Barnes, L. E., 1983. The colonisation of ball-clay ponds by macroinvertebrates and macrophytes. Freshwater Biology 13: 561–578.

Beltman B., T. van den Broek, K. van Maanen & K. Vaneveld, 1996. Measures to develop a rich-fen wetland landscape with a full range of successional stages. Ecological Engineering 7: 299–313.

Biggs, J., A. Corfield, D. Walker, M. Whitfield & P. Williams, 1994. New approaches to the management of ponds. British Wildlife 5: 273–287.

Biggs, J., P. Williams, M. Whitfield, P. Nicolet & A. Weatherby, 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 15: 693–714.

Bilton D. T., J. R. Freeland & B. Okamura, 2001. Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics 32: 159–181.

Brucker J. W., A. G. Gosler & A. R. Heryet (eds) 1991. The Birds of Oxfordshire. Pisces Publications, Oxford.

Collinson, N. F., J. Biggs, A. Corfield, M. J. Hodson, D. Walker, M. Whitfield & P. J. Williams, 1994. Temporary and permanent ponds: an assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. Biological Conservation 74: 125–133.

Craine, S. I. & C. M. Orians, 2004. Pitch pine (*Pinus rigida* Mill.) invasion of Cape Cod pond shores alters abiotic environment and inhibits indigenous herbaceous species. Biological Conservation 116: 181–189.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life, 6th edn. John Murray, London.

Davies, B. R., 2005. Developing a strategic approach to the protection of aquatic biodiversity. PhD thesis. Oxford Brookes University.

Fairchild, G. W., A. M. Faulds & J. F. Matta, 2000. Beetle assemblages in ponds: effects of habitat and site age. Freshwater Biology 44: 523–534.

Fleury, Z. & C. Strehler Perrin, 2004. Vegetation colonisation of temporary ponds newly dug in the marshes of the Grande Caricaie (lake of Neuchatel, Switzerland). Archives des Sciences 57: 105–112.

Foster, G. N., 1991. Conserving insects of aquatic and wetland habitats, with special reference to beetles. In Collins, N. M. & J. A. Thomas (eds), The Conservation of Insects and Their Habitats. Academic Press, London: 237–262.

Fox, A. D. & S. A. Cham, 1994. Status habitat use and conservation of the Scarce Blue-tailed damselfly *Ischnura pumilio* (Charpentier) (Odonata: Coenagrionidae) in Britain and Ireland. Biological Conservation 68: 115–122.

Froneman, A., M. J. Mangnall, R. M. Little & T. M. Crowe, 2001. Waterbird assemblages and associated habitat characteristics of farm ponds in the Western Cape, South Africa. Biodiversity and Conservation 10: 251–270.

Gee, J. H. R. & B. D. Smith, 1995. The conservation value of farm ponds: macroinvertebrates. Report to the Countryside Council for Wales.

Gee, J. H. R., K. M. Lee & S. Wyn Griffiths, 1994. The conservation and amenity value of farm ponds. Report to the Countryside Council for Wales.

Gee, J. H. R., B. D. Smith, K. M. Lee & S. Wyn Griffiths, 1997. The ecological basis of freshwater. Pond management for biodiversity. Aquatic conservation: Marine and Freshwater Ecosystems 7: 91–104.

Gibbons, D. W., J. Reid & R. A. Chapman, 1993. The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991. T. & A. D. Poyser Ltd, London.

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

Gray, J., 1988. Evolution of the freshwater ecosystem: the fossil record. Palaeogeography, Palaeoclimatology, Palaeoecology 62: 1–214.

Hansson, L. A., C. Bronmark, P. A. Nilsson & K. Abjornsson, 2005. Conflicting demands on wetland ecosystem services: nutrient retention, biodiversity or both? Freshwater Biology 50: 705–714.

Kennison G. C. B., 1986. Preliminary observations on the plant colonisation of experimental turf ponds in a Broadland fen. Transactions of the Norfolk Naturalists Society 27: 193–198.

Linton, S. & R. Goulder, 2000. Botanical conservation value related to origin and management of ponds. Aquatic Conservation: Marine and Freshwater Ecosystems 10: 77–91.

Linton, S. & R. Goulder, 2003. Species richness of aquatic macrophytes in ponds related to number of species in neighbouring water bodies. Archiv für Hydrobiologie 157: 555–565.

Menetrey, N., L. Sager, B. Oertli & J. B. Lachavanne, 2005. Looking for metrics to assess the trophic state of ponds. Macroinvertebrates and amphibians. Aquatic Conservation: Marine And Freshwater Ecosystems 15: 653–664.

Moller, T. R. & C. P. Rordam, 1985. Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark. Oikos 45: 8–16.

Palmer, M., 1992. A Botanical Classification of Standing Waters in Great Britain and a Method for the Use of Macrophyte Flora in Assessing Changes in Water Quality. Joint Nature Conservation Committee, Peterborough, UK.

Pond Action, 1992. Experimental management of wetland habitats at Pinkhill Meadow. NRA National R&D project F01(91) 2 383.

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

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

Schneider, D. W. & T. M. Frost, 1996. Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society 15: 64–86.

Stumpel, A. H. P. & H. van der Voet, 1998. Characterizing the suitability of new ponds for amphibians. Amphibia-Reptilia 19: 125–142.

Talling, J. F., 1951. The element of chance in pond. Populations. The Naturalist 839: 157–170.

Wellborn G. A., D. K. Skelly & E. E. Werner, 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337–363.

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

Williams, P., J. Biggs, C. J. Barr, C. P. Cummins, M. K. Gillespie, T. C. G. Rich, A. Baker, J. Baker, J. Beesley, A. Corfield, D. Dobson, A. S. Culling, G. Fox, D. C. Howard, K. Luursema, M. Rich, D. Samson, W. A. Scott, R. White & M. Whitfield, 1998. Lowland Pond Survey 1996. Department of the Environment, Transport and the Regions, London.

Williams, P., J. Biggs, M. Whitfield, A. Thorne, S. Bryant, G. Fox & P. Nicolet, 1999. The Pond Book: A Guide to the Management and Creation of Ponds. Ponds Conservation Trust, Oxford.

Williams P., M. Whitfield & J. Biggs, 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biological Conservation 115: 329–341.