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ECOLOGY OF EUROPEAN PONDS

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

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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

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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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