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SMALL WATER BODIES

Review Paper

The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers

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Abstract Small waterbodies, including ponds and small lakes, low-order streams, ditches and springs, are the most numerous freshwater environments globally, are critical for freshwater biodiversity and are increasingly recognised for their role in ecosystem service delivery. Small waters often represent the best remaining examples of intact freshwater habitats and are the most likely to remain unpolluted, often being a refuge for species which have disappeared from larger, more damaged, waterbodies. Practically all water-related ecosystem services are initially mediated by small waters and some, such as carbon cycling, may be dominated by them. Small waters are exposed to all the threats affecting larger waters, and some experienced only by small waters. Despite this, small waters remain the least investigated part of the water environment and are largely excluded from water management planning. We identify the priorities for research to underpin better protection of small waters and recommend policy actions needed to better integrate small waters into the management of catchments and landscapes. The primary requirements are to identify reliable monitoring programmes for small waters, develop effective measures to protect the biodiversity and ecosystem services they provide and ensure that regulators take full account of this critical part of the water environment.

Keywords Ponds · Small lakes · Headwaters · Springs · Biodiversity · Ecosystem services

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Introduction

There is growing awareness of the importance of small waterbodies in terms of their abundance, importance for freshwater biodiversity, role in contributing to ecosystem services and their sensitivity and vulnerability to anthropogenic disturbances (Williams et al., 2004; Downing et al., 2006; Verdonschot et al., 2011; Bartout et al., 2015; US EPA, 2015). At the same time, there is a recognised lack of knowledge on the functioning of small waters to effectively inform policy and practice measures to protect them (Cereghino et al., 2008; Kelly-Quinn & Baars, 2014). This has led to a range of recent initiatives aiming to highlight the importance of small waters and encourage interactions between scientists, policy makers, practitioners and others with interests in their protection and management (e.g. Meyer et al., 2007a; Anon 2012; Biggs et al., 2014a; Kelly-Quinn & Baars, 2014). Better understanding, and more effective management, of small waters has considerable potential to help address some of the many threats to freshwater ecosystems, and the services they provide, summarised by Dudgeon et al. (2006) and Vörösmarty et al. (2010). This paper seeks to refocus attention on small waters by drawing together the key literature on what constitutes small waters, their extent, importance, vulnerability and threats they face, and to evaluate the main fundamental and practical knowledge gaps. Reflecting the concerns of Strayer and Dudgeon (2010), we aim to stimulate practical action by encouraging rational planning of responses to climate change and other threats to freshwater ecosystems, to stimulate freshwater conservationists to act now to prevent further losses of species and habitats, particularly by working with small waters, and to bridge the gap between freshwater ecology and conservation biology. We particularly encourage researchers who have substantially increased our fundamental understanding of freshwaters through the use of small waters as model systems (e.g. De Meester et al., 2005; Hildrew, 2009) to continue emphasising to policy makers and practitioners the importance of the waterbodies themselves, not simply as surrogates for something bigger and, by implication, more important.

Previous reviews of small waters have typically focussed on single waterbody types, considering either running or standing waters (e.g. Clarke et al., 2008; Oertli et al., 2009; Downing 2010; Larned et al., 2010; Dollinger et al., 2015). Here we consider all types of small waters, both running and still, to highlight the commonalities of structure and function, and the concepts of relevance to policy makers which apply to all kinds of small waterbodies. As far as possible, we have attempted to evaluate all relevant recent information but this inevitably leads to some imbalances in coverage. Although small waters have been neglected generally, more information is available about ponds, small lakes and headwater streams than for springs and, especially, ditches, which have only begun to attract detailed attention quite recently. Acknowledging the gaps in available data, recommendations are made for policy makers and legislators to increase the effectiveness of management of these habitats, with particular reference to the European Water Framework Directive and Habitats Directive as examples (European Commission, 2000, 2002).

Definitions

'Small waterbodies' is an ambiguous term with, as yet, no universally accepted or legal definition. In this paper, we use the term to refer to ponds and small lakes, small streams including headwaters, ditches and springs. In the following section, the approaches which have been taken to derive these definitions are described.

Ponds and small lakes

Ponds are small standing waters varying in size from 1 m^2 to about 2-5 ha in area and may be permanent or seasonal, man-made or naturally created (Pond Conservation Group, 1993; Collinson et al., 1995; Biggs et al., 2007; E.P.C.N., 2007; Cereghino et al., 2008). Although there is a long history, dating back to the nineteenth century, of attempts to define the difference between a pond and a lake (Biggs et al., 2005), large ponds and small lakes share many characteristics in terms of structure and function, and the transition zone between the two types of habitat is very gradual (Søndergaard et al., 2005; De Meester et al., 2005). Indeed, ponds merge imperceptibly into virtually all other freshwater habitat types (Biggs et al., 1997). However, for practical purposes, such as estimating waterbody numbers or comparing waterbody types, most authors have adopted a size-based classification with a size boundary somewhere between 1 and 5 ha, which can be fairly easily measured in the field (e.g. Williams et al., 2004; Kalettka & Rudat, 2006; Davies et al., 2008a, b; De Bie et al., 2008; Williams et al., 2010a). Occasionally, 'pond' studies are restricted to waters of no more than 0.5 ha (e.g. Lafitte et al., 2009) or extended to include those up to 8 m in depth or 10 ha in area (e.g. Oertli et al., 2000, 2005). The Ramsar Convention adopted a cut-off between ponds and lakes of 8 ha, although in practice this has not been widely applied by workers investigating these habitats (Ramsar Convention Secretariat, 2013). Other approaches to distinguishing ponds from lakes based on depth, wind action and light penetration are impractical to measure and now rarely used in Europe, although all are factors which can influence waterbody ecology. In North America, many waterbodies which European freshwater biologists would call ponds are termed wetlands (see, for example, US EPA, 2015) or, increasingly, *Geographically Isolated Wetlands* (Lane & D'Amico, 2016). Ponds include a wide variety of temporary waterbodies such as dune slack pools, vernal pools, rock pools, smaller pingos, playas and other temporary small standing waters which range from, at one extreme, tiny puddles that might only hold water for a few days after rain, to more permanent waterbodies that may only dry up for a few weeks in most years and in some years remain permanently wet (Holmes et al., 1968; Nicolet et al. 2004; Smith, 2006; Ruiz 2008; Walmsley, 2008; Huggins et al., 2011; Faccio et al., 2015; Brendonck et al., 2016).

Small lakes can be defined as standing waters of greater than 1–5 ha up to around 50–100 ha. There is no strict definition of what constitute small or large lakes, although in Europe the size of lake considered significant in the Water Framework Directive, 50 ha, provides a *de facto* cut-off point for small lakes. Both small lakes and ponds include brackish waters. Small lakes may also be temporary: for example, in Ireland many turloughs fall into this category, as do the UK's 'aquifer-fed fluctuating waterbodies' and Breckland meres and Mediterranean lagoons in the south of France (Sheehy-Skeffington et al., 2006; Maddock 2008; Muller et al., 2008; Cohez et al., 2011). In Australia, billabongs (which are floodplain ponds and lakes) may be permanent or seasonal (Hillman, 1986).

Small streams

The term small stream is perhaps the most ambiguous of all and is often used interchangeably with the term headwater, with no clear consensus on a definition of either. Furthermore, as noted by Moore & Richardson (2003) not all small streams are headwaters. Despite this, most small streams probably lie within headwater reaches. Headwater streams have been defined by Furse et al. (1993) as the length of stream within 2.5 km from the source, most often encompassing zero-, first- or second-order watercourses (e.g. Meyer et al., 2007a; Callanan et al., 2008a; Clarke et al., 2008; Barmuta et al., 2009; Finn et al., 2011), although some European headwater studies have extended to third-order streams (Dunbar et al., 2010) and may be located in lowland or upland areas. Some small coastal streams are first- and at most second-order channels for their entire length which often extends to just a few kilometres (Whelan, 2014).

So is there an all-encompassing definition of small streams? In a workshop held in Carlingford, Northern Ireland, in 2010, steam order, width and flow were considered as potentially defining small streams, and although no definition was derived, it was generally agreed that width was the most easily measured and, when combined with stream order, widths would vary from <3 to 6 m (Anon, 2012). The same workshop proposed that priority be given to streams with widths <1.5 m because of their vulnerability to anthropogenic impact. Barmuta et al. (2009) presented similar discussion on what constituted headwater streams and adopted a working definition which included zero- and first-order, and where necessary, second-order stream segments but within a maximum catchment area of about two square kilometres. As noted by Richardson & Danehy (2007), the best accepted definition of a headwater at a meeting convened by the Oregon Headwater Research Cooperative was based on widths (<3 m) and mean annual discharge (<57 l/s), although the latter was recognised as problematic. The term headwater system was used by Gomi et al. (2002) which they described as containing four topographic units (hillslopes, zero-order basins, temporary or transitional channels and first- and second-order streams), each differing in biological and hydrological processes. They proposed that the largest catchment of headwater systems is likely to be 1 km^2, but these systems are probably better defined by hydrologic, geomorphic and biological processes rather than simply catchment area. The latter definition might capture short coastal streams whose total stream length may be less than 3 km. These are often extremely numerous in coastal areas with fringing uplands, e.g. Ireland. In the Water Framework Directive, small linear headwaters are those with catchments less than 10 km^2. Overall, the term headwater is probably the most useful and most widely used to capture the location of the smallest stream elements, including intermittent streams. However, the precise definition and spatial extent of headwater will be regionally variable. Furthermore, it will depend on the scale of mapping data and where one selects the start of the stream, which can vary seasonally and with land use (e.g. Montgomery & Dietrich, 1989; Hanson, 2001; MacDonald & Coe, 2007). The term headwater is generally used in the studies cited throughout this paper.

Ditches

In the United Kingdom and other parts of Europe, studies by Williams and colleagues (Williams et al., 2004; Biggs et al., 2007; Davies et al., 2008a, b; Biggs et al., 2014b) and others (Shaw et al., 2015; Hill et al., 2016) comparing ditches to other freshwater habitats have used a definition of the habitat first proposed in Williams et al. (2004): '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) showing little relationship with natural landscape contours'. In the UK landscape, the majority of ditches are 1–3 m wide, with only a small proportion narrower or wider than this (Brown et al., 2006). A survey of the ditch network by Shore et al. (2015) in two agricultural catchments in the southeast of Ireland recorded an average width of 2.3 m and depth of 1.1 m, and cross-sections that were generally U-shaped or trapezoidal.

Although ditches occur in all kinds of human-modified environments where land drainage is needed, they have only been the subject of limited investigation as freshwater habitats (e.g. Scheffer et al., 1984; Higler & Verdonschot, 1989; Painter, 1999; Williams et al., 2004; Verdonschot et al., 2011). Despite this, ditches in some areas are of exceptional importance for freshwater biodiversity, normally because they retain patches of clean water in otherwise drained long-established wetland environments. In England, for example, there are currently 74 Sites of Special Scientific Interest (SSSIs), areas designated by the government as being of high importance for nature conservation, with lowland ditches identified as one of the reasons that the site has legal protection (Clarke, 2015). Most of these are found within the approximately 31,000 ha of coastal and floodplain grazing marsh habitat protected within SSSIs, but as ditches can occur in other land uses there is not complete overlap. Typically, these high-value systems occur in Land Classes 1 and 2 identified by Brown et al. (2006). Here they may be important biodiversity refuges especially where more 'natural' waterbodies are exposed to near-universal water pollution. Consequently, they have been valued by nature conservation organisations since the late 1970s (Drake et al., 2010; Clarke, 2015) when their value was first initially appreciated.

Springs

Hydrologically, springs are defined as strictly delimited places where the groundwater emerges at the surface (Cantonati et al., 2006). They can also be seen as points of natural, concentrated discharge of groundwater, at a rate high enough to maintain flow on the surface (van Everdingen, 1991). The German Institute for Norms (DIN) precisely defines a spring as a "spatially restricted groundwater emergence, which at least temporally leads to a superficial discharge" (DIN, 1994). This definition also includes anthropogenically modified springs such as wells. Geohydrological spring types, such as overflow springs or artesian springs, are distinguished depending on the geology and the characteristics of the aquifer (Martin et al., 2015). In general, the aquifer is the storage body of water gained by precipitation and lost by spring flow after a certain time lag (Glazier, 2014). Depending on the geology, storage times in the aquifer differ considerably from a few hours to over 10,000 years (Glazier, 2014).

From an ecological perspective, springs are ecotones at the interface between surface water and groundwater (Webb et al., 1998; Cantonati et al., 2006). Since the start of spring research at the beginning of the twentieth century, it has almost been a paradigm that springs are stable habitats providing the biota, such as macroinvertebrates, with relatively constant abiotic conditions (e.g. Thienemann, 1926; Nielsen, 1950). Thermal stability in particular was identified as a key factor characterising springs fed by deep groundwater (e.g. Illies, 1952; Minshall, 1968; van der Kamp, 1995). More recent spring research has revealed doubts about this apparent stability (Fischer et al., 1998; Gräsle & Beierkuhnlein, 1999). However, at least for lowland springs and springs in low mountain ranges, low temperature variability indeed seems to be an indicator for separating the springhead, the actual spring, from the adjacent springbrook (Erman & Erman, 1995; Von Fumetti et al., 2007).

Extent and abundance of small waterbodies

Ponds and small lakes

Ponds and small lakes are globally abundant habitats (Downing et al., 2006; Downing, 2010). However, there is currently considerable controversy about their numbers, mainly owing to difficulties in estimating the numbers of small ponds (Bartout et al., 2015). As the significance of small standing waterbodies has become increasingly clear, the ability to estimate their abundance reliably has become more important. However, current suggestions for global abundance of standing waters vary by more than an order of magnitude with low estimates ranging from 64 and 100 million (respectively, McDonald et al., 2012; Bartout et al., 2015) to c.300 million (Downing et al., 2006), c.500 million (Holgerson & Raymond, 2016) and about 3 billion (Oertli & Frossard, 2013). Bartout et al. (2015) suggest that the higher estimates are unlikely. However, they consider waterbodies only down to 100 m^2 and in some regions (e.g. the United Kingdom, southeast Great Plains in the United States) half to two-thirds of all waterbodies are in the 25–400 m^2 category, suggesting that omitting these from global counts could substantially underestimate total numbers (Williams et al., 2010a; Chumchal et al., 2016). Ponds and small lakes outnumber large lakes roughly 100:1 (Downing et al., 2006; Cereghino et al., 2008). In Europe as a whole, it is likely that there are between 5 and 10 million small lakes and ponds and in the United States about 17 million ponds up to 1 ha in area (McDonald et al., 2012) although the latter total excludes waters less than 1000 m^2 so underestimate the true number.

Probably, the most reliable estimates of pond numbers currently come from field surveys, such as those carried out in the United Kingdom Countryside Survey, which has evaluated a stratified random national sample of 1 × 1 km squares on several occasions since the 1980s with surveyors walking the land to map ponds (Barr et al., 1994; Williams et al., 1998b, 2010a). Field observations of smaller waters are generally necessary because of the difficulty of remotely sensing (a) waters beneath trees (although it may be possible to solve this problem (Wu et al., 2014), (b) temporary waters, which will often be dry when surveys are undertaken and undetectable by satellites looking for water, but are often readily identifiable on the ground by analysing vegetation patterns, and (c) in wetland environments, where an element of biological knowledge is needed to separate ponds and small lakes from other wetland types (e.g. mires, fens).

Downing et al. (2006) originally suggested that the area of lakes and ponds up to 10 ha was about 30% of the global total standing water area. Although more conservative estimates are probably appropriate (e.g. Holgerson & Raymond, 2016), it is clear that small standing waters make an important contribution to the global total freshwater area.

Extent of small streams in river networks

About 80% of the global river network is estimated to be represented by headwater streams (0–2nd order) (EEA, 2012; Downing et al., 2012). A similar figure was estimated for Europe by Kristensen & Globevnik (2014). The latter authors compiled available figures for some European countries which included a figure of 70% for England (Natural England, 2008), and noted that 75% of the channel length in Denmark had a stream width less than 2.5 m and in Slovenia 80% of the total river network has widths less than 5 m. In Ireland, 77% of the river network is first (52.2%)- and second (24.5%)-order streams (McGarrigle, 2014). Despite their extensive channel length, small streams represent a small percentage (11.4%) of the total global lotic habitat area. Overall, there has been no comprehensive mapping of small streams in most countries, a fact highlighted by Meyer et al. (2007a) and Roy et al. (2009) for the United States. As noted by Wilding & Parkyn (2005), the first step in understanding the importance of small waterbodies is to determine their extent and nature.

Ditches

Ditches are man-made waterbodies although, particularly in flood plain and coastal grazing areas, their attributes (still or slow-flowing interconnected channels) are an analogue of the multi-thread and anatomising channels of the floodplains and coastal alluvial plains they often drain. This drainage is essential for maintaining productive agricultural areas around the globe: the International Commission on Irrigation and Drainage has estimated that, globally, 190 million ha of agricultural lands are drained artificially, with most of that land in the Americas (65 Mha), Asia (58 Mha) and Europe (47 Mha), about 12% of the estimated 1,500 Mha of arable land and permanent crops (Ausubel et al., 2012; Leslie et al., 2012).

The length of ditch networks has not been assessed globally or regionally, although they are extensive in agriculturally intensive countries. In the heavily drained Netherlands, the total length of ditches is around 300,000 km and ditch densities are 400–1000 m ditch per hectare (Verdonschot, 2012). In the United Kingdom, where ditch densities have been calculated for both lowland and upland landscapes, using data presented by Brown et al. (2006), it can be estimated that there are around 600,000 km of ditches, including small ditches which only flow intermittently. This is three to four times greater than the 165,000 km length of the river and stream network (Maltby et al., 2011).

Springs

Emergence of groundwater occurs globally, making springs and seeps commonplace in all but the most arid or cold regions, although even the latter have their own characteristic upwellings e.g. those found in the Chihuahuan Desert in Texas (Wallace et al., 2005) and on Axel Heiberg Island in the High Arctic (Lay et al., 2013). Glazier (2014) gave a comprehensive review of the number of springs all over the world. As an approximate estimate, there are thought to be over 43,000,000 springs worldwide. Certain geographical "hotspots" for springs can be distinguished. In alpine regions such as the Alps, but also the South Island of New Zealand, spring density is high. In Berchtesgaden National Park in the Alps, 330 springs are documented in an area of 208 km^2 (Gerecke & Franz, 2006). For the Kalkalpen National Park, 3808 springs per 1000 km^2 were extrapolated (Cantonati et al., 2012). Recently, over 1300 mostly alpine springs have been mapped in the Canton of Berne in Switzerland (Felder & Bruppbacher, 2016). In New Zealand, 1400 springs were recorded in an area of 42,200 km^2 (Barquin & Scarsbrook, 2008). Lowland areas still strongly influenced by the last glacial period are also rich in springs: for northeastern Germany, the presence of more than 10,000 springs has been estimated in an area of 29,000 km^2 (Krüger, 1996). For central Finland, the presence of 1300–1500 springs per 1000 km^2 was extrapolated (Särkkä et al., 1998). In arid regions, the density of springs is naturally low. In the Great Artesian Basin in Australia, only 1.2 springs per 1000 km^2 were found (Ponder, 2004), and for Nebraska and Texas in the USA estimated densities were only 0.1 and 1.1 springs per 1000 km^2, respectively (Stevens & Meretsky, 2008). Owing to anthropogenic influences such as drinking water supply and land-use changes, the density of springs has declined considerably all over the world (e.g. Ponder, 2004; Zollhöfer, 1997). In central Europe, natural springs are now mostly restricted to forested areas, where they are not in conflict with agriculture (Hotzy, 1996; Zollhöfer, 1997).

Conclusion

Overall, it is clear that small waterbodies are exceptionally abundant globally and that their numbers and distribution are strongly affected by human activity. Large numbers of ponds and small lakes, and all ditches, have been created by people and perhaps similar, or greater, numbers of natural small waters destroyed. Small streams and springs, on the other hand, are rarely created by human activity, but have often been eliminated, or reduced in extent, by the modification of physical structure or water supply.

Types of small waterbodies

Types of pond and small lake

There has been no systematic global analysis of types of ponds, but several regional descriptions have been made, mainly, but not exclusively, in Europe (e.g. Biggs et al., 2000a; Oertli et al., 2000; Declerck et al., 2006; Kalettka & Rudat, 2006; Ruiz, 2008; Pinto-Cruz et al., 2011). This is despite the fact that many areas are known globally for their abundance of small waters, including the Arctic tundra and northern peat-forming landscapes, the vernal pool systems of North America (e.g. in California and the Pacific north west), kettle holes of the Central European Plain, the prairie pothole regions of North America, Mediterranean temporary ponds of southern Europe and North Africa, mountain and upland pools in all major mountain regions (e.g. Alps, Himalayas, Rockies, Andes) and the ponds and pools of arid and desert regions, such as South Africa and Australia (Hobbie, 1980; Shiel 1994; Dahl 2014; Boix et al., 2016; Wissinger et al., 2016).

In the United Kingdom, Biggs et al. (2000a) used macroinvertebrate data to group ponds into 16 categories in which permanence, pH and hydrology were the dominant driving environmental variables (Fig. 1). In Switzerland, Oertli et al. (2000) identified between 4 and 7 pond types, depending on the biotic groups (amphibians, macrophytes, dragonflies, molluscs, water beetles) used to characterise types. Martens et al. (2008), working in Belgium, showed that pond assemblage composition was driven mainly by the presence of fish and macrophytes, with water turbidity and sediment quality also being important influences. Water quality in turn was influenced by the presence of trampling cattle, and probably broader land-use factors. However, the classification of ponds is complicated by their acknowledged heterogeneity, which is greater than that seen in the running water network. Although this heterogeneity is most apparent in studies comparing different waterbody types (e.g. Williams et al., 2004; Biggs et al., 2014b; De Bie et al., 2008), it may also explain the conclusion of Batzer (2013) working on North American wetlands that little consensus has so far emerged about how environmental factors influence invertebrate communities.

Although it has traditionally been assumed that ponds are 'isolated islands in a sea of dry land', they clearly form networks linked by physical and biological processes, not just with other ponds but with all other kinds of freshwater habitat. This is reflected in the fact that, at least in north temperate environments, a large proportion of the freshwater species in any landscape is found in a range of waterbody types, including both still and flowing waters. For example, in the landscape of southern England (Williams et al., 2004) (Fig. 2, unpublished data) found that in a stratified random sample of ponds, rivers, streams and ditches, of 230 aquatic macroinvertebrate taxa recorded, 33% were found only in ponds, 32% only in rivers and 45% in both ponds and rivers. This points to the existence of 'freshwater landscapes' in which plants and animals move around a network of habitats, small and large, all of which contribute to the protection of freshwater biodiversity (Sayer, 2014). It seems quite likely that this trend is fairly general, at least in the temperate zone, although there are currently few data available to test the idea.

Standard lake typologies commonly incorporate small lakes, such as those developed by the OECD based on lake trophic status (OECD, 1982), the United Kingdom national lake typology developed by Duigan et al. (2007) or the lake assessment methods developed in Denmark for the Water Framework Directive (Søndergaard et al., 2010). In some instances, these typologies specifically identify 'small' lake types (e.g. Duigan et al. 2007), whereas others treat small lakes as part of a continuum. Wellborn et al. (1996) suggested some years ago that studies of standing waters on size gradients from small to large would be of general value, but until quite recently most work was still concentrated on relatively large waterbodies, with few studies specifically concerned with whether or not there are significant differences between small and large lakes. For example, Søndergaard et al. (2005), specifically evaluating whether ponds and lakes differed, found structural and functional differences above and below

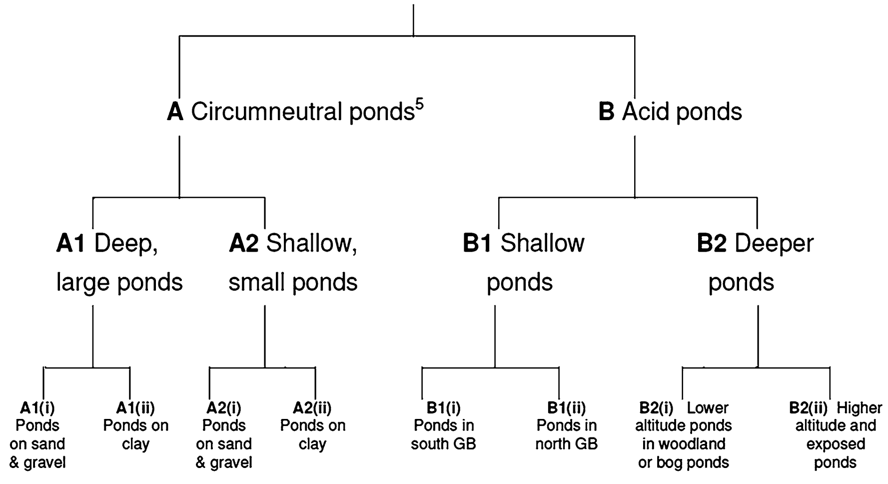

Fig. 1 TWINSPAN classification of ponds in Great Britain based on macroinvertebrate species assemblage data. Reproduced from Biggs et al. (2000a) with permission

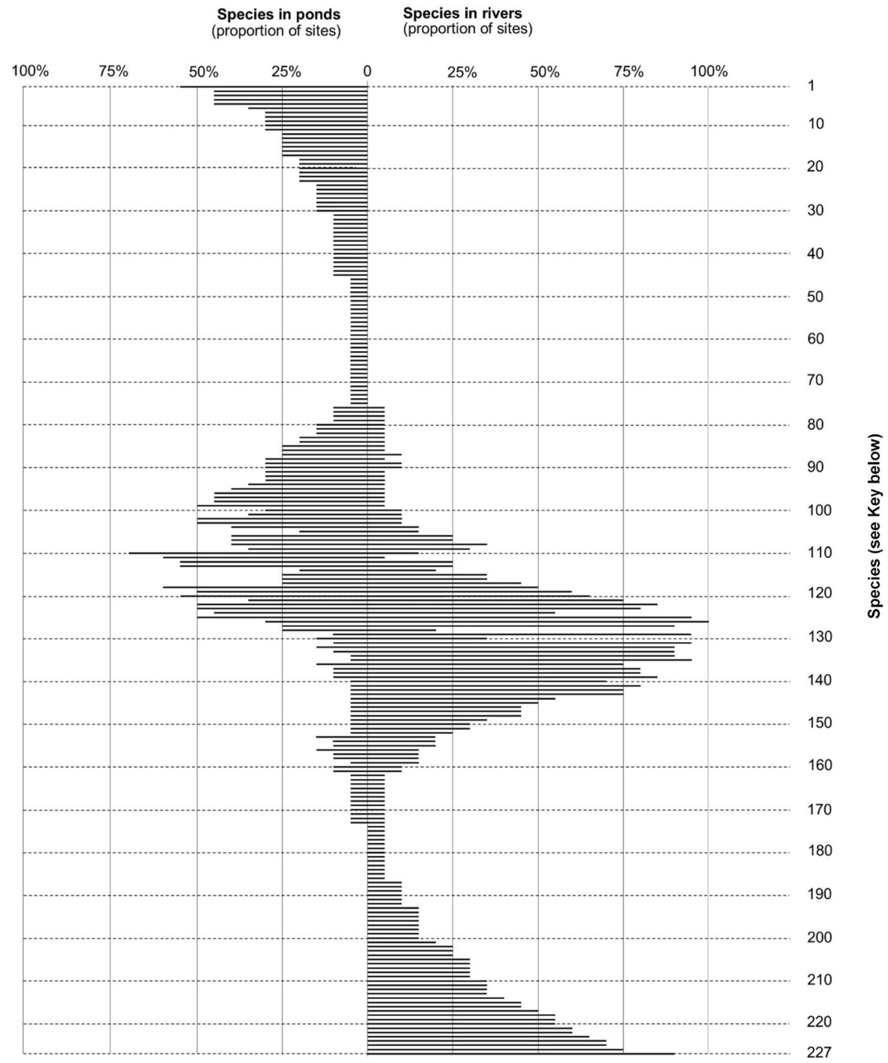

Fig. 2 Proportion of species found in ponds only (*left* of the *central line*), rivers only (*right* of the *central line*) and both ponds and rivers (both sides of the *central line*) in a stratified random sample of waterbodies in southern England. The *X*-axis scale indicates the proportion of sites in which the species occurred. Data derived from Williams et al. (2004). Species identities, from 1 to 227, are shown in Online Resource Table 1

1 ha, but no obvious transitions in the lakes above this size. However, apart from macrophyte assemblages, relatively few other relationships between biota and lakes size have been explored. Thus, Borics et al. (2016) noted that, for algae, some prefer what these authors called 'small habitats', some 'middle-sized' and some 'large habitats'. At present, there remains little information with which to assess whether small lakes really are different, or to explore more complex ideas of relevance to practitioners such as: Are small lakes easier to protect from damaging impacts than larger lakes? To what extent do interactions between lakes and other waterbodies affect their ecology? Which processes differ in small and large lakes, and which are similar?

Types of small streams

Within the small stream or headwater network, channel types or features are likely to be highly variable due to differences in geomorphic, hydrological, precipitation and ecological conditions (Gomi et al., 2002), thus leading to the heterogeneity that is typical of small stream networks. There have been some attempts to classify small streams on the basis of some or all of these conditions. They have been classified in terms of flow duration into perennial, intermittent and ephemeral, with the latter two often collectively being called temporary streams. Intermittent streams do not flow for certain parts of a year, whereas ephemeral streams typically only flow during storm events (Hanson, 2001; Meyer et al., 2007a, b). Datry et al. (2014) included ephemeral streams in their definition of intermittent streams. However, as noted by Hanson, flow duration is often difficult to determine and therefore he proposed a number of other type indicators such as channel definition, bed water level, movement of benthic materials and level of scouring as well as the presence of aquatic insects. McDonagh et al. (2011) synthesised available information on temporary streams, describing them as the most abundant, widely distributed and dynamic freshwater ecosystem on Earth. They presented reported estimates of their global representation ranging from 60% to >70% of river networks. According to Datry et al. (2014), most Arctic, Alpine and Antarctic streams are intermittent. In a study by Hanson (2001), the Chattooga stream network was estimated to have 28% perennial, 17% intermittent and 55% ephemeral streams. Sánchez-Montoya et al. (2007) made further divisions of intermittent and ephemeral streams based on the number of seasons that flow ceased (viz. intermittent streams) or dried up (viz. ephemeral streams). Scoring systems to distinguish intermittent, ephemeral and perennial streams, incorporating a range of geomorphic and biological indicators, have been employed in some areas (e.g. NCDWQ, 2010). Regardless of how they are classified, intermittent streams, as outlined by Larned et al. (2010), are characterised by hydrological discontinuities with advancing and retreating wetted fronts which have consequences for aquatic communities and biogeochemical processes. These vary both spatially and temporally and are determined by local climatic and topographical factors.

Headwater streams also differ in their sources: most studied appear to be seepage-fed (e.g. Furse, 2000; Heino et al., 2003a; Meyer et al., 2007a; Callanan et al., 2008b), but others arise from groundwater and glacier feeds (Friberg et al., 2001; Hieber et al., 2002) and lake outlets (Friberg et al., 2001). Typological classification within the context of the European Water Framework Directive has generally excluded headwater streams because their catchment size falls below 10 km^2. Consequently, within Europe there have been few attempts to define types of headwaters apart from the work of Furse (2000) in the UK, Heino et al. (2003a) in Finland, Triest (2006) in Belgium and Callanan et al. (2012) in Ireland. With the exception of Triest (2006) working on macrophytes, the classifications were based on macroinvertebrates. The site groupings based on macroinvertebrates were largely due to differences in site elevation, stream geology and its effect on pH, and to a lesser extent substrate type. However, in some areas there were high degrees of overlap among assemblage types (Heino et al., 2003a). Furthermore, Paavola et al. (2003) noted in their work in Finland that community classifications in headwater streams are not concordant across taxonomic groups and care should be taken when the results based on one taxonomic group are extrapolated to other groups to create typologies.

Types of ditches

Studies of ditch types are best developed in the Netherlands and the United Kingdom with relatively few other studies worldwide. Biggs et al. (2007) compared the richness and conservation value of ditch macrophyte and macroinvertebrate assemblages throughout Great Britain, showing that those associated with old fen landscapes (Defra Landscape Class 2) were, in α diversity terms, of similar richness and greater conservation value (in terms of occurrence of species of conservation concern) than rivers. Drake et al. (2010) focussing specifically on the ditch systems of drained fen landscapes near the English and Welsh coast (Fig. 3) identified seven main botanical assemblages with a clear distinction between vegetation dominated by floating duckweed species and the more species-rich vegetation typified by the presence of Frogbit (*Hydrocharis morsus-ranae* L.) and Ivy-leaved duckweed (*Lemna trisulca* L.). The principle environmental variables influencing ditch vegetation types were salinity, water depth, substrate and hydroseral stage. Invertebrate classifications were influenced by the pronounced east–west preference of some species in their national distribution but it was not possible to derive a classification that was robust for the entire spectrum of ditch types at a national scale, perhaps reflecting a greater heterogeneity in invertebrate assemblages. Water conductivity and pH, ditch dimensions, water depth, vegetation structure, the presence/absence of algae and grazing were the most important environmental factors influencing invertebrate assemblages. However, the study did not include laboratory analysis of water chemistry so it

Fig. 3 Location of old fenland ditch networks described by Drake et al. (2010) in England. Note that ditches occur throughout the UK landscape but the old fen areas (Landscape Class 2, Brown et al., 2006) are of exceptional biological richness

may have underestimated the role of pollution caused by excess nutrients, sediments or biocides in shaping assemblages. In the Netherlands, Verdonschot (1990) found eleven ditch assemblage types in the Overijjsel Province based on aquatic macroinvertebrates. Assemblage composition was shaped mainly by ditch dimensions, duration of drought, acidity and flow but also reflected successional stage and time since previous management, effectively existing along a spatio-temporal continuum.

Types of springs

At the beginning of the twentieth century, three principal eco-morphological spring types were differentiated by Steinmann (1915) and Thienemann (1922). The so-called *rheocrenes* are characterised by a single point of outflow where the outflow stream is formed immediately and is dominated by coarse inorganic substrates (Hahn, 2000). *Helocrenes* are swampy springs, where the water seeps out of the ground at several points. Such lentic springs are dominated by fine organic and inorganic substrates (Von Fumetti & Nagel, 2011). *Limnocrenes* occur when the groundwater emerges in a natural basin. The basin is first filled with spring water before the water runs off. Helocrenes and limnocrenes mainly occur in the North European Lowlands. Here, they can reach large spatial extents and a high density (Lindegaard et al., 1998; Ilmonen & Paasivirta, 2005; Martin & Brunke, 2012). In low mountain ranges such as the Palatine forest in Central Europe and the Swiss Jura Mountains, rheocrenes and rheohelocrenes dominate (Hahn, 2000; Küry, 2013). In high alpine areas, large spring bogs, but also many, partly steep, rheocrenes typically occur. Combined rheocrenes and helocrenes are known as *rheohelocrene* (Schwoerbel, 1959). In natural alluvial river floodplains, alluvial springs are common. They occur where alluvial groundwater is upwelling owing to geologic constraints (Zollhöfer et al., 2000). They usually exhibit low discharge variability and are characterised by extremely clear water, promoting the growth of submerged macrophytes. In springs with pronounced karst characteristics, discharge strongly depends on precipitation in the catchment area. Such karstic rheocrenes tend to dry out in summer and can then be described as intermittent. In limestone-dominated regions, so-called "limestone-precipitating springs" (LPS, Cantonati et al., 2016) are quite often found. They can be eco-morphologically impressive with large calcite terraces, but are faunistically poor. The differentiation of spring types in the field is, however, critical and intermediate types or transitions from one type to the other are often much more frequent (Von Fumetti et al., 2006; Cantonati et al., 2006; Martin & Brunke, 2012).The eco-morphological appearance of springs strongly depends on the slope and the underlying geology. The differentiation of cold water and hot water springs is hydrologically and ecologically relevant. The latter occur in high frequency, e.g., in New Zealand (Tillyard, 1920), but also in North America (Meffe & Marsh, 1983; Hayford & Hermann, 1998), India (Jana, 1973) and China (Keshi, 1980). In desert regions, such as the Sonoran Desert or the Great Basin, the existence of cold water springs is especially remarkable (Myers & Resh, 2002).

Naturally, the ecology of thermal springs differs clearly from that of cooler, non-thermal springs (Glazier, 2014). Water chemistry is another feature for classifying springs. For example, the extent of salinity is an important characteristic of a spring (Williams & Williams, 1996; Hahn, 2000). Owing to high salinity and high water temperatures, some springs are used for the health benefits they provide. The various approaches to classifying springs are reviewed by Glazier (2014).

Small waterbodies: biodiversity

Why are small waterbodies so important for biodiversity?

A wide range of studies have now confirmed that, particularly for macrophytes, aquatic micro- and macroinvertebrates and amphibians, small waterbodies are areas of high biodiversity. Thus, although individual small waters have lower average α diversity than larger waters, at regional level small waters, especially ponds and small lakes, typically have high γ diversity (Williams et al., 2004; Clarke et al., 2008). The possible explanations of this high inherent richness are as follows: (i) the history and temporal abundance of small waters; in most landscapes and over long geological periods, it seems likely that small waterbodies have been the numerically dominant freshwater habitat type, commonly available to freshwater organisms able to move between temporally dynamic habitat patches, (ii) the physico-chemical heterogeneity of small waters, which is typically greater than that for larger waterbodies (Williams et al., 2004; Demars & Edwards, 2007; Gooderham et al., 2007; Lischeid & Kalettka, 2012) and (iii) in the contemporary environment, the more frequent occurrence of near-natural conditions, especially freedom from pollution, in small waters (Freshwater Habitats Trust, unpublished data).

It has been suggested that the patchy and comparatively isolated nature of freshwater habitats, particularly compared to the sea, should promote greater speciation rates than open oceans. Support for this idea comes from recent studies which have highlighted the surprisingly high species richness of freshwater habitats, which are nearly equal to marine environments despite their much smaller area (~2% of Earth's surface vs. 70% for marine habitats) (Wiens, 2015). If isolation is an important driver of species richness in freshwaters, the very large proportion of small waters that comprise freshwater ecosystems may make an important contribution to this pattern.

The heterogeneity of small waters is well documented and in part this reflects their small catchments: small waterbodies are strongly affected by local conditions (e.g. wooded or open surrounds, heavily or lightly grazed grassland, acid or neutral chemistry), which leads to considerable variation between waterbodies in physical and chemical characteristics, compared with larger waterbodies (e.g. Williams et al., 2004; Demars & Edwards, 2007).

Small waterbodies, both still and flowing, are also now an important 'refuge' for clean water ecosystems in many landscapes, especially in those areas where agriculture and urbanisation represent a substantial portion of land use. As a consequence of their small catchments, where small waters occur in pockets of semi-natural habitat, they can remain near-pristine (e.g. Feeley & Kelly-Quinn, 2012). In contrast, larger waterbodies, with their extensive catchments, are almost inevitably subject to pollution and other impacts except in the most pristine landscapes. As a result, small waters are often amongst the least damaged freshwaters in the areas where they have been investigated.

The protection of small waterbodies and the biodiversity they support is a concern. For example, in the EU, the Water Framework Directive in theory is intended to protect all waters. However, in the delineation and selection of waterbodies, many Member States have used size thresholds that exclude small waterbodies without necessarily taking into account their importance in the basin (EC, 2012). Some Member States have explicitly included smaller waterbodies if they are protected under other legislation or if they are ecologically important in the basin. In Europe, several priority habitat types recognised in the Habitats Directive occur extensively in ponds (Keeble et al., 2009) but, in practice and with the exception of Mediterranean temporary ponds, most EU states only protect or monitor large examples of these priority habitats, i.e. lakes (EEA, 2012; EC, 2012, pp. 72–73). Also in Europe, although ponds are recognised as 'stepping stone' habitats in the Habitats Directives, most states have made limited efforts to maintain the extent or quality of these stepping stones. In North America, recent attempts have also been made to bring small waters more into the regulatory system, although as yet it is too early to judge success (US EPA, 2015).

Table 1 summarises comparisons of biodiversity discussed in this section, focusing on studies which have compared two or more waterbody types (e.g. ponds vs rivers vs ditches; headwater streams vs mid-order streams), principally in terms of alpha, beta or gamma diversity.

Pond and small lake biodiversity

A wide body of international evidence now shows that ponds are exceptionally important waterbodies for biodiversity at catchment and landscape levels. They have consistently been shown to support more freshwater species than rivers or lakes at landscape scale (Williams et al., 2004; Karaus et al., 2005; Davies et al., 2008a, b; Martinez-Sanz et al., 2012), a pattern repeated at national level (Biggs et al., 2005). 'Single Large Or Several Small' analyses (SLOSS) have also shown that ponds support more species and a higher conservation value than lakes of the same total area (Oertli et al., 2002; Martinez-Sanz et al., 2012). A number of studies show that ponds are particularly important for endangered species, supporting a similar or higher portion of endangered species than rivers or lakes. In many landscapes, these endangered species are now restricted to a very few ponds making these taxa exceptionally vulnerable to extinction (e.g. U.S. Fish and Wildlife Service, 2005; Feber et al., 2011; Rhazi et al., 2012; Lukács et al., 2013).

The contribution to regional freshwater biodiversity made specifically by small lakes has not been evaluated in the same way as for ponds, but it is clear that many also make an important contribution. For example, in Denmark, Søndergaard et al. (2005) in a study of ca.800 lakes, of which roughly half were in the size range 1–10 ha, found a low impact of lake size on the species richness of several taxonomic groups. These findings implied that small lakes made an important contribution to freshwater biodiversity in the landscapes studied and are probably typical of small lakes generally (e.g. Scheffer et al., 2006; Mosscrop et al., 2015).

Small stream biodiversity

Meyer et al. (2007b) presented an overview of the importance of headwater streams for biodiversity and placed the aquatic biota in four categories which included species that are unique to this part of the river network, species that occur there but also in larger rivers, species that move into headwaters seasonally and those that migrate there to complete particular life history stages (e.g. salmonids for spawning). Interestingly, recruitment from the aforementioned small coastal streams may be important for the maintenance of sea trout fisheries in neighbouring coastal areas (Whelan, 2014). A fifth grouping proposed by Meyer et al. (2007b) included species that live near these streams in semi-aquatic or riparian habitats.

Headwaters may be particularly important in terms of habitat for rare and threatened species, a contribution also noted by Furse (2000) and Heino (2005). Thus, as noted by several studies, headwaters may be fundamental to the ecological integrity of the entire river network (Gomi et al., 2002; Heino, 2005; Freeman et al., 2007; Meyer et al., 2007a, b; Clarke et al., 2008). The significant contribution of headwaters to regional biodiversity was highlighted in the global-scale study of Finn et al. (2011) and they emphasised the need to consider the contribution of headwaters to whole-stream biodiversity and the pressing need to conserve each headwater branch to prevent the loss of unique biota. They suggested that effective conservation of headwaters would protect biodiversity at the catchment scale. Small streams may individually support naturally low (<20) taxon richness but collectively the network of small streams can make a large contribution to regional biodiversity. This is supported by the findings of some studies which showed that approachng one third (29%) of a catchment's macroinvertebrate biodiversity can be unique to headwaters (Feeley & Kelly-Quinn, 2012; Callanan et al., 2014). Indeed, Heino et al. (2003b) drew attention to the role of regional factors in structuring headwater communities, which in part is attributed to their highly heterogeneous environments (Furse, 2000; Heino et al., 2003a; Lowe and Likens 2005; Clarke et al., 2008; Callanan et al., 2014). Such habitat heterogeneity can give rise to heterogeneous aquatic plant communities as reported by Weekes et al. (2014). Callanan et al. (2014) also reported that many headwater macroinvertebrate species (c.38% in their study)

Table 1 Biodiversity of small and larger waterbodies: a summary of comparative studies

Study	Type of comparison, including taxon units compared	Diversity measure	Ponds	Small lakes (up to 50 ha)	Streams	Rivers	Ditches
Williams et al. (2004)	Landscape level comparison of wetland plant and aquatic macroinvertebrate mean alpha and gamma species richness in four waterbody types in the United Kingdom	Invertebrate α	32.6	33.1	18.7	45.3	12.9
		Invertebrate γ	173	140	124	152	90
		Plants α	10.1	6.7	7.3	10.7	6.1
		Plants γ	67	46	39	49	30
Davies et al. (2008a, b)	Landscape level comparison of wetland plant and aquatic macroinvertebrate mean alpha and gamma species richness in four waterbody types in Whitchurch, United Kingdom; Funen, Denmark; Avignon, France and Braunschweig, Germany	UK					
		Invert. α	29.7		18.5	np	17.3
		Invert. γ	118		74	np	91
		Plants α	15.3		7.3	np	6.1
		Plants γ	67		35	np	44
		DK					
		Invert. α	–		–	–	–
		Invert. γ	–		–	–	–
		Plants α	9.4		8.9	12.0	6.5
		Plants γ	83			50	42
		F					
		Invert. α	–		–	–	–
		Invert. γ	–			–	–
		Plants α	7.9		7.3	9.8	6.2
		Plants γ	75		–	67	58
		D					
		Invert. α	–		–	–	–
		Invert. γ	–			–	–
		Plants α	7.73		6.31	6.25	5.87
		Plants γ	96			44	47
Biggs et al. (2014a, b)	Landscape level comparison of wetland plant mean alpha and gamma diversity in all waterbodies in an English Midlands farmed landscape. There were no lakes or rivers in the study area	Plants α	8.5	np	5.6	np	4.3
		Plants γ	57.3	np	33.0	np	25.7
Karaus et al. (2005)	Analysis of 1 km^2 section of natural Alpine river system comparing Jackknife estimated gamma species diversity in main river channel and parafluvial floodplain ponds	Invertebrates γ	57	np	np	32	np
Biggs et al. (2005)	Comparison of macroinvertebrate species gamma diversity at national level in ponds and rivers in the United Kingdom	Invertebrates γ	431	np	np	377	np
		Plants γ					
Hamerlík et al. (2014)	Comparison of macroinvertebrate alpha and gamma taxa diversity in ponds and lakes in Tatra Mountains, Slovakia and Poland	Invertebrates α	6.6	8.9	–	–	–
		Invertebrates γ	44	48			

Table 1 continued

Study	Type of comparison, including taxon units compared	Diversity measure	Ponds	Small lakes (up to 50 ha)	Streams	Rivers	Ditches
Finn et al. (2011)	Global comparison of headwaters (order 1-2) and mid-order (order 3-5) streams and rivers using Sørensen's dissimilarity index to assess beta diversity	Invertebrates β	–	–	0.50	0.40	–
Furse (2000)	National (Great Britain) invertebrate alpha species diversity in headwaters (up to 2.5 km from source) and higher order streams and rivers (more than 2.5 km from source)	Invertebrates: unique species	–	–	16.6	20.4	–
Feeley & Kelly-Quinn (2012)	Proportion of unique invertebrate species in headwaters (0, 2 km) and higher order rivers (5 and 10 km) in two regions (Killarney, Slieve Bloom Mountains), Republic of Ireland	Invertebrates: unique species	–	–	0, 2 km: 29%; 12%	5, 10 km: 16%; 12%	–
Callanan et al. (2014)	Proportion of unique invertebrate species in headwaters (0, 2 km) and higher order rivers (4, 7 and 10 km) in Republic of Ireland	Invertebrates: unique species	–	–	0 km: 29% 2 km: 2%	4 km: 2% 7 km: 2% 10 km: 6%	–
Biggs et al. (2007)	National level assessment of species invertebrate and wetland plant alpha and gamma diversity in Great Britain in 13 landscape classes (summary data only shown for invertebrates; landscape range shown for plants). Includes lakes > 50 ha	Invertebrate α	25.1	–	15.0	28.2	18.5
		Invertebrate γ	–	–	–	–	–
		Plants α	9.2–17.2	24.5–40.0	18.5–29.5	22.0–37.0	7.0–18.5
		Plants γ	–	–		–	–
Webb et al. (2010)	Comparison of national gamma diversity of priority freshwater species for conservation in coastal grazing marsh ditches, ponds, lakes (includes waters > 50 ha) and streams/rivers	Plant and animal γ	77	40			47
Verdonschot et al. (2011)	Comparison of macroinvertebrate alpha and gamma diversity in drainage ditches and small lakes in the Netherlands	Invertebrates α	–	81	–	–	75
		Invertebrates γ	–	201	–	–	226
Kavanagh & Harrison (2014)	Comparison of invertebrate alpha and gamma diversity of ditches (average of four types) with streams in a southern Ireland landscape.	Invertebrate α	–	–	30.8	–	26.0
		Invertebrate γ	–	–	96	–	120

Data are from studies in which a major objective was to compare two or more small and larger waterbody types in terms of alpha, beta or gamma diversity. *np* not present: waterbody types which did not occur in the study area. – waterbody types for which comparable data were not collected. Note that in Davies et al. (2008a, b), for gamma diversity assessment, streams and rivers were combined to create equal sample sizes are common to reaches further downstream, highlighting their potential to act as sources to downstream sites if natural or anthropocentric pressures cause local extinctions. Thus, headwaters species pools will be critical for the restoration of downstream sites to good status as required, for example, by the EU Water Framework Directive. According to Meyer et al. (2007a), headwater diversity is underestimated and therefore the importance of headwaters could be considerably higher that currently documented.

Ditch biodiversity

A growing number of studies show the value of drainage ditches for freshwater biodiversity, although the ditches themselves have also extensively damaged, or eliminated, wetland habitats (Armitage et al., 2003; Herzon & Helenius, 2008). Despite this, ditch networks, especially in coastal areas and on river floodplains, may be of exceptionally high biodiversity value. In the UK, Biggs et al. (2007) in a study characterising wetland plant and macroinvertebrate biodiversity in all widespread freshwater habitat types (ponds, lakes, rivers, streams and ditches) found that ditches in floodplain and coastal environments supported the most species-rich plant and animal assemblages. Webb et al. (2010) in a literature review of aquatic species habitat requirements in England showed that there were 47 UK Biodiversity Action Plan species associated with ditches in coastal and floodplain grazing marshes compared with 77 species for ponds, 40 for lakes and 76 for rivers. Away from flat, low-lying, coastal and floodplain landscapes, in ‘ordinary’ farmed environments, ditch systems resemble other parts of the headwater network and are often subject to significant pollution (e.g. Biggs et al., 2014b). Even here, however, there is some evidence that they can provide a useful biodiversity resource (Williams et al., 2004). Although it has long been known that ditches can be critical freshwater habitats in areas with low-intensity grassland agriculture, it is also increasingly clear that, even in intensively cultivated drained wetlands, they can support a range of species of conservation concern in areas that might superficially be regarded as ‘arable deserts’ (Graham & Hammond, 2015). They may also be dispersal corridors for water plants otherwise restricted to nature reserves (Favre-Bac et al., 2016).

Elsewhere in Europe (Ireland, Denmark, Germany, France), ditch systems have been found to be similar to (Davies et al., 2008a, b; Verdonschot et al., 2011) or exceed (Kavanagh & Harrison, 2014) streams, in α or γ diversity, and to support similar numbers of endangered species to semi-natural small lakes (Verdonschot et al., 2011). In North America, studies of ditches are still at an early stage but work in Florida (Simon & Travis, 2011) confirms that they can make a similar contribution to regional freshwater biodiversity to that seen in Europe. Away from floodplains, where many ditches are seasonal, they are often more impoverished, but even these seasonal ditches may support uncommon species not recorded in other waterbody types at regional level (Williams et al., 2004). There is recent evidence that ditch networks can also sustain functional connectivity and influence patterns of gene flow in intensively agricultural landscapes (Favre-Bac et al., 2016).

Spring biodiversity

Due to their ecotonal character, springs are inhabited by species of different ecotonal areas: spring specialists restricted to springheads, the so-called crenobionts, co-exist with species also occurring in springbrooks (i.e. crenophiles). Groundwater-associated stygobiont species, species occurring in adjacent streams (i.e. rhithrobionts) and species adapted to the transition zone between land and water, also occur. Water temperature has traditionally been identified as the key factor determining the close relationship between crenobionts and springs (e.g. Erman & Erman, 1995) with characteristic species amongst the water mites, certain dipteran families and mosses (Cantonati et al., 2006). Recently, evidence has been found for other environmental factors of equal importance to thermal stability for crenobiosis, with substrate diversity and spatial heterogeneity seeming to especially enhance spring biodiversity (Bonettini & Cantonati, 1996; Hahn, 2000; Von Fumetti et al., 2006; Cantonati et al., 2012).

Despite usually low alpha diversity in springs, beta diversity is high due to heterogeneous faunistic assemblages. Their contribution to regional biodiversity must not be underestimated (Gerecke et al., 2011; Wigger et al., 2015). Regionally, springs can collectively be seen as hotspots of biodiversity (Cantonati et al., 2012). For example, more than 500

Table 2 Names and description of main ecosystem services categories, with examples focused on freshwater ecosystems

Final services	
Provisioning services	The material or energy outputs from ecosystems such as water for domestic and non-domestic use, fish, fibre or other renewable materials
Regulating and maintenance services	The various ways in which living organisms can mediate or moderate the ambient environment. For example, they provide for water quality by removing excess nutrients and degrading waste and toxic substances through biological processes
Cultural services	The non-material benefits people obtain from contact with ecosystems such as recreation, sense of place, spiritual and educational value
Intermediate services	
Supporting processes[a]	These underpin almost all other services. In fresh waters they relate to all levels of aquatic biodiversity from genetics to community diversity, primary production and other ecosystem processes and functions which occur in well-functioning ecosystems and support their resilience to internal and external pressures

[a] Also known as *supporting services* and *habitat services*

macroinvertebrate taxa were found in 792 springs in Kalkalpen National Park (121, 1998). In the 1970s, 1500 aquatic animal species associated with springs were described for Europe, a third of them being crenobionts or crenophiles (Zollhöfer, 1997). Spring biodiversity is strongly influenced by geology and altitude. Hard-water springs are dominated by non-insect taxa such as amphipods and snails, whereas in soft-water springs insect taxa dominate (Glazier, 1991). Along an altitudinal gradient, springs below the treeline are dominated by shredders and collectors and springs above the treeline are dominated by scrapers (Wigger et al., 2015). Species richness seems to decrease with altitude (Wigger et al., 2015). Overall, springs are excellent experimental outdoor laboratories as they are of small spatial extent, hydrologically stable and ecologically simple. This was realised by Odum (1957), who conducted the first holistic study of an aquatic ecosystem in Silver Springs, Florida.

Small waterbodies for terrestrial species

As well as providing habitats for aquatic organisms, small waterbodies are often an important part of the matrix of habitats used by terrestrial organisms. For example, farmland birds and pollinating insects may make use of ponds in agricultural environments (Davies et al., 2016; Stewart et al., 2016), and bats make use of ponds, small lakes in a wide variety of environments and intermittent streams (Freshwater Habitats Trust, 2012; Seidman & Zabel, 2001). A range of non-aquatic plants and animals depend upon (technically, are obligate users of) the riparian zones of small forest headwater streams (Richardson et al., 2005). As these small patches of habitat often seem less significant than large habitat patches, reflecting the normal alpha diversity/gamma diversity contrast of large and small habitats, the role of smaller waterbodies for terrestrial species generally has received less attention than for larger waters.

Small waterbodies and ecosystem services

Ecosystem services are most commonly defined as ‘the benefits people obtain from ecosystems’ or ‘the contributions that ecosystems make to human well-being’, based on the MEA (2005) report or the Common International Classification of Ecosystem Services report (Haines-Young & Potschin, 2013), respectively. Four main categories of ecosystem services have been recognised: (1) provisioning, (2) regulating and maintenance, (3) cultural and (4) a range of supporting processes (also referred to as supporting or intermediate services), which underpin the services of the first three categories (Table 2). To avoid double counting, the latter is not considered in the valuation of ecosystem services. Apart from providing water to sustain life on earth, freshwater habitats provide a wide range of other benefits to human well-being. The contribution of small waterbodies is likely to be particularly high but poorly quantified. Here, we highlight the key provisioning, regulating and maintenance, and cultural ecosystem services that have been highlighted within the literature and refer to others that are likely to be important but have not been considered.

Ponds and small lakes

As fundamental ecological understanding of ponds and small lakes has grown, awareness of their role in providing ecosystem services has also developed. Three areas are of particular importance: pollution control, carbon cycling and small-scale water supply. There is an extensive worldwide literature on the role of natural and constructed small standing waters in pollution control, which have been extensively investigated (e.g. Braskerud, 2002; Vymazal, 2011; Tournebize et al., 2016). These studies show that pond systems are able to retain nutrients, although with substantial variations in efficiency depending on geology, soils, topography, hydrology, season and climate. At present, it is unclear to what extent such systems reduce pollutant loads generally, although evidence suggests that the gains at catchment and landscape scale are so far modest (e.g. Ockenden et al., 2012; Díaz et al., 2012; Arheimer & Pers, 2016). In terms of carbon cycling, understanding of the role of ponds and small lakes is growing rapidly at present, reflecting the awareness of the intensity of geochemical process in small waters and their abundance which appears to give them a role disproportionate to their physical extent. Thus, Downing et al. (2008) proposed that, globally, ponds trapped as much carbon as the ocean, a striking suggestion which has prompted substantial interest in the role of small waters in the carbon cycle. However, there is increasing evidence that certain conditions in small standing waters can lead to elevated methane emissions and the need to develop greater understanding of this disadvantage of small waters in regulating carbon should be noted. For example, ponds in the Arctic permafrost can contribute three quarters of landscape-level carbon dioxide emissions (Abnizova et al., 2012). Similarly, Holgerson & Raymond (2016) report substantial emissions of methane from very small ponds, which are also the most abundant type of waterbody. As yet, it remains unclear whether burial of carbon first highlighted by Downing et al. (2008) compensates for the high rates of the production of CO_2 and other greenhouse gases from ponds. Additionally, despite their apparent isolation from other surface waters, it is also becoming evident that ponds and other small wetlands, including those which do not have direct surface connections with adjacent waterbodies, still influence downstream waters (US EPA, 2015; Cohen et al., 2016). Wetlands and open waters away from floodplains provide numerous functions that benefit downstream waterbody integrity, including storage of floodwater; recharge of groundwater, retention and transformation of nutrients, metals and pesticides and export of organisms or reproductive propagules to adjacent waters. They can be connected to downstream waters through surface water, shallow subsurface water and groundwater flows and through biological and chemical connections. Although there is ample evidence of hydrologic, chemical and biological links between these ‘upstream’ and ‘downstream’ waterbodies, few studies specifically address the magnitude of these fluxes. Some effects of ponds and wetlands on downstream waters are due to their isolation, rather than their connectivity, particularly because of the wetland’s ability to isolate material fluxes (US EPA, 2015).

Finally, small-scale water supply is provided by ponds throughout the world but has attracted little scientific attention. In Eurasia, small-scale water storage using ponds has occurred for centuries and many ponds in Europe have been created for water supply reasons. In the Americas, as agricultural intensification continues, a large number of agricultural ponds have been created, probably having a substantial, but little investigated, impact on hydrology. For example, small farm ponds are now the dominant lentic ecosystem in the Great Plains of the United States (Huggins et al., 2011) and are common in parts of Brazil (Bichsel et al. 2016).

Importance and ecosystem services of small streams

A considerable number of papers have documented the importance of small streams and headwaters but few have done so from the perspective of ecosystem services. The ecosystem services, or direct and indirect benefits, humans derive from headwaters include water provision, recharge of ground waters, flood control, trapping of sediment and pollutants, nutrients recycling, maintenance of biological diversity and support of downstream water quality and productivity (Meyer & Wallace, 2001; Meyer et al., 2007a).

In terms of water provision, it is intuitively obvious that small streams collect and deliver a considerable volume of the water to higher order streams and rivers, lakes and reservoirs but there are few calculations of that contribution. According to Saunders et al. (2009), some 90% of a river’s flow is derived from headwater streams. Alexander et al. (2007), in a study in the north-eastern United States, concluded that first-order headwaters contribute approximately 70% of the water volume and 65% of the nitrogen flux in second-order streams and that their contributions to mean water volume and nitrogen flux decline only marginally to about 55 and 40% in fourth-order and higher order rivers that include navigable waters and their tributaries. Other studies also attribute a high proportion of surface water, nutrient and organic matter retention to headwater capture (Meyer & Wallace, 2001; MacDonald & Coe, 2007; Hill et al., 2014). However, the contribution depends on whether the outflow from headwaters is synchronised or desynchronised (Gomi et al., 2002).

The regulating and maintenance services and supporting processes are more poorly documented. Small streams, for example, have been popularly characterised as the 'capillaries' of the water system and are critically important for flow regulation both through water storage/groundwater recharge and through flood amelioration. As our climate changes in coming decades, the buffering function of the small water system will increase through a need for water conservation, and to ameliorate exceptional and damaging flood events. Small waters play a critical role in the transfer of nutrients and carbon to downstream reaches (Dodds & Oakes, 2008) and are increasingly seen as playing a role in urban and rural water pollutant interception (e.g. Kadlec 2012, Merilla & Tonjes, 2014). They also show greater response to precipitation events than larger systems, which shapes instream habitats and influences the supply of sediment from hillslopes and subsequent delivery to downstream reaches (Gomi et al., 2002). Fine sediment is a vital element in freshwater systems and important to nutrient cycling, substrate composition and heterogeneity, all of which influence instream habitats and thus aquatic community composition (Rabeni & Minshall, 1977; Wood & Armitage, 1997). Headwater streams provide both storage conditions for sediment, especially where there are debris dams, as well as influencing its distribution downstream (Gomi et al., 2002). Thus, small streams have a strong influence on downstream water quality. The central role of small streams in the maintenance of catchment biodiversity, both in terms of unique species and contribution to downstream communities, has already been highlighted in this paper. The maintenance of fish population by the spawning and nursery habitat in small streams is well documented in contrast to many of the other services in this category.

With respect to cultural services, small streams have an aesthetic value and contribute to a sense of place. They are likely to contribute to recreation where they are part of walking routes and can be enjoyed for the aquatic and riparian wildlife they support.

Ecosystem services provided by ditches and springs

Comparatively little information is available concerning the contribution of ditches and spring to ecosystem services other than their specific drainage function. Clearly, it is axiomatic that ditches provide a very substantial land drainage and flood control function (Smedema et al., 2004), as well as contributing similar ecosystem services to those known for natural and constructed ponds and wetlands (see review by Dollinger et al., 2015). As in other small waters, the potential for ditches to provide ecosystem services varies substantially. For example, Dollinger et al. (2015) conclude that the reduction in nutrient loads along a ditch reach varies from 3 to 92% depending on the nutrient considered and the characteristics of ditches. They note that total nitrogen and phosphorus are preferentially reduced along ditches with regard to nitrates and ammonium. Similarly, reductions in pesticides vary widely from 5 to 95%.

Since ancient times, the most obvious ecosystem service provided by springs is drinking water supply. Other services include hot water either for heating purposes such as in Iceland or for bathing. This is then often coupled with high mineral content and is proposed to have therapeutic values. Already in Roman times, hot spring water was used for leisure activities and also Japanese macaques are famous for taking hot baths in spring water. Spring water is also irreplaceable for brewing and it is still important for livestock watering and crop irrigation (Glazier, 2014).

Impacts on small waterbodies

Ponds and small lakes

The extent of our knowledge of environmental of impacts on ponds and small lakes is markedly contrasting. For ponds, we understand the general extent of impacts, and some broad patterns, such as the significance of land-use intensification for water quality and biota (Declerck et al., 2006; Williams et al., 2010a; Novikmec et al., 2016; Bichsel et al., 2016). However, we lack detailed understanding of the relative importance of specific stressors and the mechanisms through which they operate in ponds. For small lakes, in contrast, including those in the 5–10 ha size range (Sayer et al., 2010), there are a wide range of studies investigating the importance of a range of stressors, and many detailed studies of the processes which those stressors influence. These have led to well-developed conceptual models of the effects of stressors on lakes (see Fig. 4).

Ponds are threatened by many human activities such as development and intensive agriculture, and by climate change. Several studies indicate that, at a landscape level, ponds can experience both more impacts and fewer impacts than nearby larger waters. For example, because ponds have small volumes, there may be less potential for dilution of pollutants. Conversely, because ponds have small catchments, their catchments are much more likely to fall entirely within areas of natural forest, heathland or unfertilised grassland which produce unpolluted water, and to be less exposed to point source pollutions (sewage effluent, road runoff). In contrast, larger waterbodies with larger catchments are more likely to be exposed to such pollutants. For example, Williams et al. (2004) showed that in a stratified random sample of freshwater habitats typical of UK lowland farmed landscape, ponds had phosphate concentrations that ranged from 2 to 2490 μg/l^{-1} (mean 270 μg/l^{-1}), whereas larger rivers in the same landscape showed a range from only 60 to 1300 μg/l^{-1} (mean 240 μg/l^{-1}). Shade can also play an important role in influencing pond biodiversity, especially where once open, grazed landscapes have been converted to arable land or lost their grazing for some other reason. At least in the UK landscape, this local influence is clearly more important for small waters than larger lakes, although there are no comparative studies with which to evaluate the generality of this apparently ubiquitous pattern. However, although the extent of impacts on ponds in some regions is now reasonably well understood, impacts which have been extensively investigated in larger waters, such as the role of multiple stressors (Sayer et al., 2006; Phillips et al., 2016), the comparative importance of climate, nutrients, depth and waterbody size (Scheffer & van Nes, 2007) and the relative importance of biotic and physico-chemical stressors (e.g. fish, nutrients, grazers) (Gorman et al., 2014)

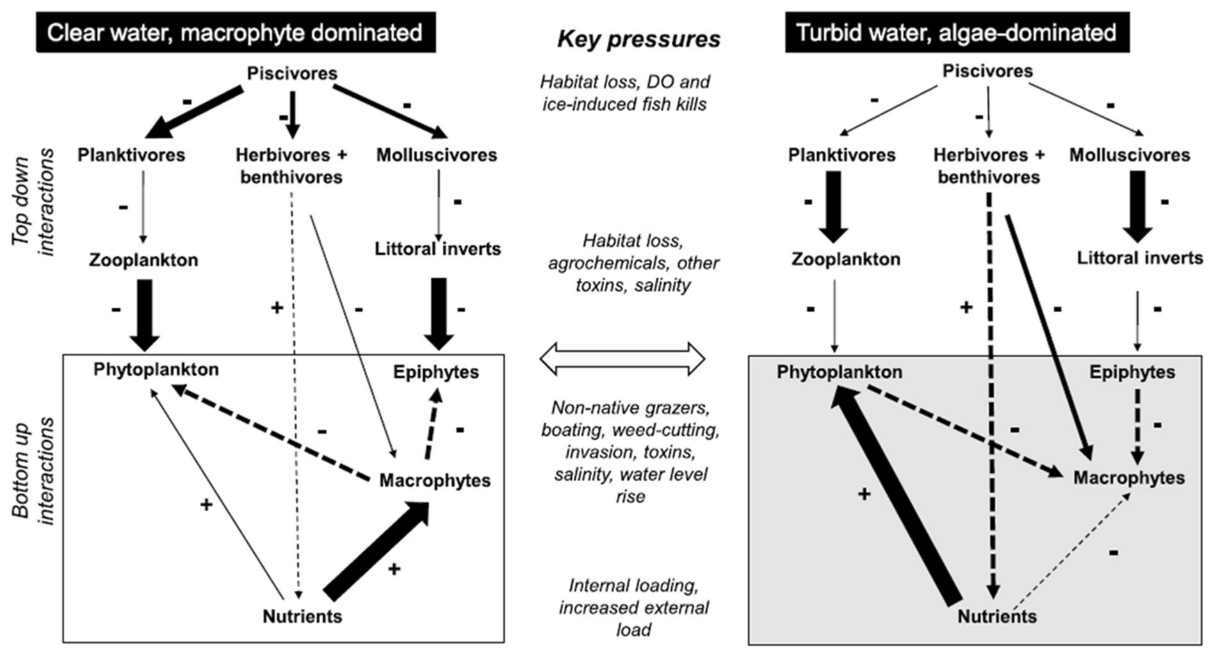

Fig. 4 Process and pressures in the two alternative stable states seen in shallow lakes. Reproduced with permission from Phillips et al., (2016)

have barely been examined in ponds. Consequently, it is not yet clear to what extent models for larger standing waters, such as the alternative stable states hypothesis and the concept of tipping points, apply to ponds (Scheffer et al., 1993).

In contrast, there is a very extensive literature on the effect of anthropogenic impacts on small lakes, particularly those resulting from the suite of processes leading to the phenomenon labelled 'eutrophication' (Phillips et al., 2016). In small lakes, a large body of theory and observation can give the impression that we clearly understand the main mechanisms and, in particular, the corrective steps needed to rehabilitate systems. However, as Phillips et al. (2016) have recently argued, despite 40 years of work, it is still uncertain what causes one of the major impacts seen on small and shallow lakes, the loss of macrophytes associated with eutrophication, and, critically, how to reverse that problem.

Small and large lakes have experienced substantial impacts as a result of atmospheric deposition with the clearest impact resulting from increased acidity on poorly buffered geologies (Battarbee et al., 2014). The effects on ponds have been little studied and may be different to those seen in both small and larger lakes (Campbell et al., 2004). Atmospheric deposition on base-rich soils probably affects small waterbodies mainly by adding to the nitrogen load but detecting these effects has been difficult given that much higher loads are commonly supplied from surface water sources.

Impacts on small streams

The high land contact and relatively low water volume of small streams make them particularly vulnerable to degradation from land-use and other anthropogenic activities (McGarrigle, 2014). Meyer & Wallace (2001) and later Meyer et al. (2007a) summarised the wide range of anthropogenic activities that impact small streams including drainage, deforestation, piping and culverting and discharges of a range of pollutants. Small streams flowing through urban area are at risk from the greatest range of pollutants and habitat alteration (e.g. Nelson et al., 2009). Nutrient enrichment is probably the most pervasive of impacts affecting hydrochemical conditions, organic matter processing and export, trophic responses and structure of aquatic communities (Benstead et al., 2009; Davies et al., 2009). Nutrient impacts may be due to both nitrogen and phosphorus (Dodds & Smith, 2016), although measures to reduce nitrogen pollution in streams have lagged behind efforts to control phosphorus. For example, Rosemond et al. (2015) have shown that both nitrogen and phosphorus added to streams accelerate carbon (leaf litter, woody debris) breakdown with potentially substantial and very wide ranging impacts on ecosystem structure and function. Both removal of natural forests (Meyer & Wallace, 2001) and planting of non-native commercial conifers in headwater catchments have resulted in a range of impacts. Commercial forest operations have the potential to cause impacts right through the forest cycle, from planting to felling (Kelly-Quinn et al., 2016). Diffuse nutrient and sediment pollution has been associated with preparation for both planting and felling (e.g. Cummins & Farrell, 2003; Reynolds et al., 1995; Stone & Wallace, 1998, Nieminen, 2003; Clarke et al., 2015). In acid-sensitive catchments, conifer forests have been associated with increased surface water acidification and impacts on aquatic biota (e.g. Harriman & Morrison, 1982; Ormerod et al., 1989; Ormerod & Jenkins, 1994; Kelly-Quinn et al., 1996; Dangles & Guérold, 2000; Kowalik & Ormerod, 2006; Tixier et al., 2009; Feeley et al., 2013; Feeley & Kelly-Quinn, 2014). Acidification has been driven largely by the interception of atmospheric sulphate and nitrate and the release of organic acidity from peaty soils, the former reducing in its severity in recent years due to reductions in emissions (e.g. Feeley et al., 2013).

Dodds & Oakes (2008) and Lassaletta et al. (2010) emphasised the linkages between headwater and downstream chemistry and that land-use impacts in headwaters as described also have significant effects on downstream conditions. It is also increasingly clear that, for streams, the preservation of regional biodiversity requires both freedom from stressors (e.g. water pollution, intensive land use) and proximity to other high-quality streams to facilitate dispersal of sensitive taxa and suppress the proliferation of tolerant groups (Merriam & Petty, 2016).

Impacts on springs

The density of natural springs decreased rapidly, and to a remarkable extent, in the twentieth century in Europe (Zollhöfer, 1997; Barquin & Scarsbrook, 2008). Less is known of impacts outside of Europe, but is presumably substantial in all cultivated and drained landscapes. Now, in Switzerland for example, natural springs in the Jura Mountains are found almost exclusively in forested areas (Zollhöfer, 1997). The main reasons for the loss of springs are water abstraction for drinking water supply, construction of wells for cattle or drainage of farmland. Anthropogenic degradation of springs also happens via acidification or heavy metal pollution and mechanical stress such as cattle trampling. Like all other small waterbodies, in Europe springs are not included in the EU Water Framework Directive (WFD) although in some countries there is protection under national laws. For example, in Germany springs are covered by the Federal Nature Conservation Act (2009) and in Finland, at least potentially, by the Finnish Forest and Water Acts (Ilmonen et al., 2009). In Switzerland, protection is still lacking, but progress is expected by the Federal Office for the Environment (Lubini et al., 2014). Management plans and efforts to systematically catalog the conservation status of springs have been made all over the world (e.g., Lischewski, 1999; Fatchen, 2000; Sada et al., 2001; Hotzy & Römheld, 2008; Barquin & Scarsbrook, 2008). Although springs are outside the WFD, limestone-precipitating springs are protected under the provisions of the Habitats Directive due to the presence of mosses of the genus *Palustriella* and aesthetic aspects created by sinter deposits. Despite existing regional conservation and restoration strategies, the exclusion of springs from, e.g., the WFD makes protection difficult, and owing to globally ongoing climatic changes, the utilisation pressure will increase in the future.

Impacts on ditches

The available evidence indicates that ditches experience the same spatial extent of water pollution as is seen in the rest of the water environment, with in excess of 90% of ditches having nutrient levels associated with biological impairment of communities (Williams et al., 2004; Biggs et al., 2014b). However, because ditches often have quite small catchments, they also offer greater opportunities for protection from water pollution than larger waterbodies. This can be seen in the heterogeneity of water quality when compared to other freshwater habitats. For example, Biggs et al. (2014b) in a stratified random sample of waterbodies in the lowland English farmed landscape found that ditches surveyed in late winter/early spring generally had the greatest range of values in most of the common water quality determinants including nutrients, heavy metals and organic pollutants. As a result of this, networks of ditches in areas draining land which is not farmed intensively, especially in old wetlands, can be reservoirs of water with near-natural nutrient, and other potential pollutant, levels. This is one of the main factors explaining the exceptional biodiversity of such sites.

Research needs

Introduction

Despite the growth of interest in, and understanding of, small waters, much ‘basic’ science remains to be done. Gaps in our understanding include quite fundamental aspects of function and structure: for example, the hydrology, geochemical processes, assemblages of organisms and the population ecology of the species that make up those assemblages all remain poorly studied. Other than for the large and obvious macroinvertebrates, macrophytes and amphibians, even basic inventories are lacking for algae and other micro-organisms, microcrustaceans, non-vascular plants, Diptera (which make up about half of all larger invertebrates in small waterbodies) and the semi-terrestrial invertebrate fauna in small waterbodies. The role of small waters as refuges for freshwater biodiversity and techniques for protecting that biodiversity all remain relatively under-researched even though these waterbodies are some of the most tractable when it comes to tackling the main impacts of human activity on freshwaters. Perhaps, the most important need is for more studies comparing different types of waterbody, large and small. This approach has proved fruitful for understanding freshwater biodiversity in ponds, but has been adopted to a very limited extent in virtually all other studies of the structure and function of freshwaters (for a recent exception, see Schriever & Lytle, 2016). However, we anticipate that for many aspects of practical freshwater biodiversity conservation, and the understanding of ecosystem services, such comparative studies will be vital.

Ponds and small lakes

Despite the work of pioneers of freshwater ecology, like Charles Elton, who produced the first categorisation of freshwater habitats (for Elton, ponds were waterbodies less than 1 acre (Elton & Miller, 1954)), TT 'Kit' Macan (Macan, 1973) and Jack Talling (Talling, 1951), the study of ponds became a backwater in the second half of the twentieth century, really only gaining momentum in the twentyfirst century, in Europe particularly as a result of the work of the European Pond Conservation Network (Oertli et al., 2009) and in North America by ecologists interested in wetlands (e.g. Batzer et al., 1999; Batzer & Boix, 2016).

Although it is well understood that ponds, at least in the temperate zone, are more heterogeneous than larger waters, both in terms of their physico-chemistry and biota (De Meester et al., 2005; Jeffries, 2008), there are very few long-term studies of ponds enabling us to evaluate the extent to which assemblages change over time in response to deterministic factors, compared to the role of stochastic processes. We are aware of only one long-term repeat survey of a group of ponds (Nicolet, 2000). Additionally, important knowledge often remains largely anecdotal: for example, one pond first surveyed in the 1970s (Palmer, 1973), and subsequently revisited over more than 40 years, provides the only currently available evidence of the potential for pond plant communities to remain exceptionally rich, and retain specific endangered species, over reasonable lengths of time (Palmer, 2010).

Just as we lack knowledge of the biota and function of individual waterbodies, we know comparatively little about the ways in which ponds interact both with each other and other freshwaters. A major area of uncertainty remains the role of connectivity between different types of waterbodies, and the probably critical role of ponds as refuges in landscapes which are increasingly hostile to freshwater biodiversity. Understanding of the extent to which ponds function as networks, how they interact with other freshwaters, the frequency of movement between sites and factors controlling how species move between sites are poorly understood and restricted to a few better-studied groups, particularly amphibians and dragonflies (e.g. Pittman et al., 2014; Hassall & Thompson, 2012) and to specific river floodplain scenarios (Karaus et al. 2005, 2013). There are two sides to this question: organisms must be able to move between suitable habitat patches if their population are to persist. But equally, for many freshwater organisms, isolation between habitats is also important. Increasingly in human-modified landscapes, isolation is essential for the maintenance of populations through keeping waterbodies isolated from pollutant sources, maintaining barriers to non-native species, and providing "water-friendly" management regimes, especially those involving low-intensity grazing on high-nature-value farmland, which appear to simulate aeons-old natural disturbance regimes. Recent observations of ponds in England (Williams, unpublished data) indicates that losses of sensitive biota from high-quality, relatively unimpaired, ponds first surveyed in the late 1980s and early 1990s have continued. We do not know whether this is due to an extinction debt (Kuussaari et al., 2009) or simply reflects short-term changes in habitat quality which could be ameliorated.

Practically, there is a need to characterise further pond and small lake (especially lakes less than 5–10 ha) assemblages and further refine assessment methodologies, particularly looking for rapid techniques which can be applied at low cost. Monitoring tools such as those developed by Williams et al. (1996, 1998a), Biggs et al. (2000b), Boix et al. (2005) and Oertli et al. (2005) have provided a first-generation of assessment tools but further developments of these methods are needed. It seems possible that the potential offered by environmental DNA, which has already started to revolutionise protected species monitoring (Biggs et al., 2015), will have a role to play here.

There remain many questions of importance for protecting pond ecosystems and their biota that have not been answered. How quickly do ponds change? Is change accelerated by anthropogenic impacts? What are the biota of the main successional stages of ponds? One of the most important practical conservation issues to assess is the balance between protecting, and increasing the number of, currently high-quality ponds (Williams et al., 1997) versus the management of degraded or fish impacted sites (Lemmens et al., 2015), particularly those exposed to agricultural pollution. Should we dredge ponds or remove fish to benefit biodiversity (removing pollutants, reducing physical disturbance and resetting the successional stage) or focus first on the protection of water quality followed by the maintenance of low-intensity physical interventions, such as achieved by low-density grazing, to maintain a range of successional states? Given the well-demonstrated risks of damaging pond assemblages by invasive physical management first highlighted by Biggs et al. (1994), a risk which is still apparent (Biggs, personal observations), this remains an important issue.

In addition to managing ponds, can we use ponds to re-build freshwater biodiversity across landscapes in which near-universal water pollution has made larger waterbodies (such as lakes or rivers) inhospitable to many species? The first evidence that ponds can protect landscape-scale biodiversity has been obtained in the UK Water Friendly Farming project (Biggs et al., 2014b) in which pond creation was shown to have stopped a landscape-wide decline in the diversity of aquatic plants. This approach could play a major role in protecting freshwater biodiversity given the inherent richness of ponds, their disproportionate numbers of endangered species and the evidence of success from practical programmes. It has been exploited practically in the UK's Million Ponds Project, detailed evaluations of which are just beginning but which show promising colonisation of new, high-quality clean water ponds by species of conservation concern. As pond creation projects are not automatically successful, it is clear that further evaluation of their potential is needed (Calhoun et al., 2014).

Streams

As noted by Alexander et al. (2007), the recent U.S. Supreme Court rulings, related to Clean Water Act decisions by agencies such as the U.S. Army Corps of Engineers and U.S. Environmental Protection Agency, highlight the need to improve scientific understanding of the contribution of headwaters to the physical, chemical and biological integrity of downstream waters. Research needs and priorities have also been highlighted by researchers such as Heino et al. (2003b), Lowe & Likens (2005) and Meyer et al. (2007a, b) and Barmuta et al. (2009).

The primary need is to further document the biological diversity of headwaters and the spatial population dynamics of species within stream networks, including the relative importance of environmental factors and links to other aquatic and terrestrial habitats. The diversity of some groups such as the Diptera is poorly described and is likely to further elevate the biodiversity importance of small streams. The aquatic communities of short coastal streams are also largely unknown; in western Europe, their contribution to migratory fish production (sea trout) and coastal fisheries is important, and similar patterns probably occur elsewhere. Given the heterogeneity of small stream habitats, studies will have to be extensive in their site coverage.

Given the threats to freshwater biodiversity generally, there is a need to better understand the environmental conditions which support the high regional biodiversity of some biological groups—e.g. macroinvertebrates. Studies have typically developed through an upstream/downstream paradigm, but interactions across landscapes may be as important.

All running waters originate in their headwaters so there is a need to quantify how cumulative inputs to and impacts on headwaters affect downstream resources. In particular, there is a need to further quantify the effects of nutrient processing (autotrophic and heterotrophic uptake,), cycling and export of nutrients in headwaters on nutrient status further downstream. Equally, we need to establish how hydrological and habitat alteration of headwaters affects ecological processes in the larger catchment.

Given the importance of small streams and at the same time their high vulnerability to land use and other inputs, there is a need for research on both the resistance and the resilience of small stream processes to anthropogenic disturbance.

The aforementioned investigations need to incorporate and model the impact of climate on hydrological and physico-chemical conditions and ecological processes in small streams. As noted for ponds, long-term studies are needed to characterise natural temporal changes in physico-chemical and ecological conditions, and responses to management. If these knowledge gaps are addressed, it will provide a better understanding of the ecosystem services derived from small streams and what is required to maintain services supply. Therefore, in addition to fundamental research on ecosystems structure and function, there is a need for operationally focussed investigations including the development of specific guidance on management and restoration of small streams. This may be particularly critical for temporary streams. For example, Larned et al. (2010) called for conservation and management options that address their unique properties. They noted that effective management requires 'preservation or restoration of aquatic-terrestrial habitat mosaics, preservation or restoration of natural flow intermittence, and identification of flow requirements for highly valued species and processes'.

Finally, monitoring of water quality in the very extensive small stream network will remain a challenge for regulatory authorities. Thus, there is an opportunity to engage citizen science but this will require selection of determinants and development of kits or tools, both physico-chemical and ecological, that would generate useful and reliable data. Some initiatives are already in place, for example the Angler's Riverfly Monitoring Initiative run by the UK Riverfly Partnership (http://www.riverflies.org/rp-riverfly-monitoring-initiative).

Springs

Until recently, it was commonly thought that crenobiont species are primarily adapted to constant environmental conditions. Now, we know that especially water temperature is often much less constant than assumed. Why then are crenobiont species bound to springs? Approximating the answer will help understand, e.g., how sensitive crenobiont species really are towards climatic changes. In this context, autecological studies are needed including, e.g., experimental approaches on how crenobiont species react to changes in their environment but also broader approaches at higher levels of organisation such as food web analysis (see e.g. Robinson et al., 2008; Woodward et al., 2010). Concepts for long-term monitoring of springs in different biogeographical regions are also needed to understand future developments of species diversity and ecosystem functioning in springs.

The most striking question, which will also provide important information for conservation strategies, is how isolated populations of species exclusively inhabiting springs really are. Isolation would make conservation of each spring in a certain region necessary, while connected populations, i.e. metapopulations, may justify the further use of some springs, e.g. for drinking water supply or the abandonment of some natural springs in a region with a similar or even identical genetic pool. This indicates that research should focus on genetic analyses at population and species level and on metapopulation modelling (see Von Fumetti and Blattner, 2016).

Knowing the degree of genetic exchange and population connectivity is an important step for the conservation of springs to be brought in line with the sustainable use of spring water, which is an urgent future challenge. For spring conservation and restoration, an international concept is needed in concordance with the river types of the WFD. Such a concept should define international standards and, on a regional scale, regional spring types, their eco-morphological features and species assemblages (see e.g. Zollhöfer et al., 2000; Von Fumetti & Nagel, 2011; Martin & Brunke, 2012). This is crucial for assessing the ecological status of springs in relation to a reference status and to evaluate their restoration potential. In this regard, it will also be desirable to develop consistent evaluation sheets, which also consider regional aspects as they are implemented in the WFD. Moreover, a further raising of awareness of policy makers, NGOs and the general public including farmers and land owners is necessary to demonstrate the need for better legislation.

Ditches

As the least investigated part of the freshwater environment, ditches have remained largely outside the realm of traditional freshwater ecology. Despite this, ditches have been of considerable practical significance in two areas: pesticide risk assessment where they have become a model system (e.g. Renaud & Brown, 2008; Renaud et al., 2008) and, in some countries, where they have been the focus of a very large body of practical conservation activity and survey work (see Drake et al., 2010 for an example from the United Kingdom). These projects are mostly in places where ditches represent the remaining vestiges of freshwater habitats in otherwise drained wetlands.

Little is known about the ecology of ditches. Most studies have been carried out on the classic permanently wet ditches typical of drained wetlands. However, most ditches are found outside this landscape type (Brown et al., 2006) and it is clear that ditches can be broadly divided into stream-like and standing water-like habitats. In one southern England landscape, stream-like 'upland' ditches showed greater heterogeneity than rivers or streams themselves (Fig. 5).

Key research areas for ditch systems are, therefore, as follows:

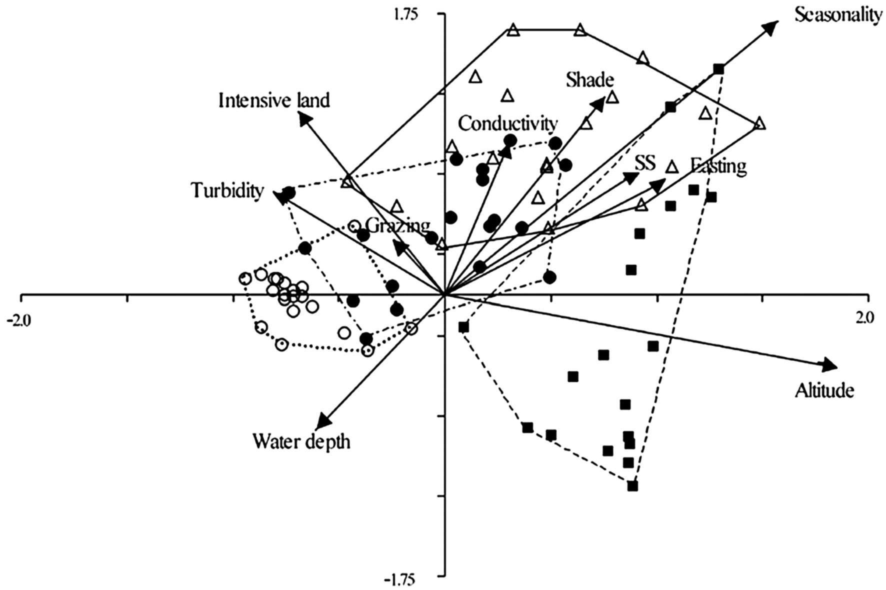

Fig. 5 Heterogeneity of aquatic macroinvertebrate assemblages in four waterbody types in a southern England agricultural landscape. The figure shows a CANOCO analysis of macroinvertebrate species data collected from four waterbody types in a typical southern England lowland landscape. Polygon size provides a measure of macroinvertebrate assemblage heterogeneity showing that rivers have the least, and ponds and ditches the most, heterogeneous assemblages. *Triangle* = ditches, *filled square* = ponds, *filled circle* = streams, *circle* = rivers. From Williams et al. (2004)

- Understanding similarities to, and differences from, other freshwater habitats.
- Understanding the extent to which they provide refuges for endangered species.
- In some locations, the threat faced from sea-level change. At least in Europe, ditch networks are both important freshwater biodiversity reserves and, in coastal regions where many occur, vulnerable to the complete elimination of this special freshwater biota by saline water intrusion.
- A critical practical question for ditch networks is the extent to which they can be linked to inland habitats and their rich and vulnerable biota successfully 'moved inland' to avoid coastal squeeze (Clarke, 2015). This is likely to prove a very challenging problem as little is known about the interaction between ditch connectivity, hydrology, water quality, metapopulation dynamics and the achievement of successful conservation outcomes in ditch networks.

Recommendations for policy makers and legislators

Small waters, still and flowing, are an intrinsic and highly significant component of the freshwater environment, of equal importance to the larger waters that are the focus of most current legislation and practical action. There needs to be better integration of international, national and regional networks and organisations to ensure that current and new policies, legislation and funding opportunities support the conservation and effective management of small waters (Biggs et al., 2014a).

The primary recommendation for policy makers and legislators is to recognise the importance of small waterbodies for freshwater biodiversity and ecosystem function as well as the maintenance of ecosystem services. It is clear that in all landscapes, a starting point in the management of the water environment should include an evaluation of the role of both small and large waters, including those which are man-made.

Because of their size, small waterbodies are easier to protect than larger waters and there is evidence that it may be easier to maintain them in a near-natural condition (in the terminology of the WFD, at 'High' status). There is also good evidence that ponds and small lakes can be created in a way which mimics natural processes and can be used to help restore freshwater biodiversity at landscape level, increasing connectivity, resilience and biodiversity. In terms of restoration of existing freshwaters, current evidence indicates that the vast majority of stream restoration projects rarely demonstrate a biodiversity recovery post-hydrogeomorphic adjustment (Palmer et al., 2014; Law et al., 2016), and increasingly emphasise the critical need to improve water quality (e.g. Turunen et al., 2016), which may be more achievable in small rather than larger waters. This is in part because small waters are more likely to have catchments dominated by predominantly 'water-friendly' land uses which are less likely to act as pollutant sources, such as natural forest, extensive grasslands, high-nature-value farmland or other natural or semi-natural vegetation types. However, restoration of water quality in small streams in high-intensity agricultural catchments is more challenging. Finally, because small waterbodies are also both common and 'people friendly', they are ideal habitats with which to engage individual citizens in water policy decision making and practical action.

Overall, policy makers and legislators need to develop clear processes for assessing the status of smaller waters and ensuring their effective management in catchment plans. Small waterbodies are abundant, and many are badly degraded, so it is necessary to identify important sites based on high biodiversity, high water quality or other valuable attributes. These should be identified in catchment plans and measures implemented for their protection.

Because small waterbodies are abundant, it is reasonable to identify groups or networks of important sites as management units, an approach recommended in the WFD (EC, 2003), to stratify sites for monitoring purposes and identify generic objectives/measures for each waterbody group. There are a number of options for grouping small waterbodies including the adoption of the Important Freshwater Areas approach being adopted in the UK (Nicolet & Biggs, 2015) or the Key Biodiversity Approach adopted by IUCN (Langhammer et al., 2007), as well as identifying areas that are important for specific groups, such as Important Stonewort Areas developed by the UK NGO Plantlife (Stewart, 2004).

Specifically, policy makers and legislators should ensure the following:

- Small waters are formally included in relevant sections of international and national nature conservation and water management legislation (for example, in Europe, the WFD).
- Small waters are adequately represented in statutory networks of protected sites (e.g. Ramsar, Natura 2000, national designations).
- Monitoring networks are established to better represent small waters. At present, few countries/regions regularly monitor small waters so there are likely to be opportunities to share experiences to design efficient monitoring networks. It is likely that novel applications of citizen science will be valuable here; for example, in the UK 'WaterNet' provides a model for a citizen-based monitoring network (http://freshwaterhabitats.org.uk/projects/waternet/). However, equally it is clear that given the critical role of small waters in protecting freshwater biodiversity and ecosystem function, professional programmes must incorporate small waters as needed. New eDNA technologies for monitoring freshwater ecosystems may play a particularly important role in this respect. For example, in the UK, the world's first national monitoring programme for a protected species, the Great Crested Newt (*Triturus cristatus* (Laurenti, 1768)) (Biggs et al., 2015) has been applied to a national network of ponds and it is clear that other species and species groups in small waters could be monitored using eDNA approaches. Lawson Handley (2015) described the potential for eDNA work, and Turak et al. (2016) note the value of eDNA for developing Essential Biodiversity Variables for measuring change in global freshwater biodiversity.
- Species protection and management measures in small waters are adequately enforced (e.g. by ensuring that endangered freshwater species receive sufficient legal protection in national legislation and through tighter restrictions on the sale of invasive non-native species).
- National development and planning policies should adequately safeguard small waters through their recognition in water management and nature conservation legislation.
- Relevant international, supra-national and national funding bodies should ensure that protection of small waterbody biodiversity is given equal attention to that of larger waters.
- Opportunities for climate change mitigation policies which benefit the protection of small waterbodies are adopted.

- Unpolluted waters, defined here as those with water quality at near-natural or reference condition, (i.e. equivalent to WFD 'High' status) should be specially protected.

Given the critical losses occurring worldwide to freshwater biodiversity, and the clear role that small waters can play in protecting freshwater biota, a central goal of small water management should be to make the most of their potential to protect freshwater biodiversity.

Conclusions

Small waterbodies include natural, artificial and heavily modified waterbodies. They are important in their own right, and also important for their influence on larger waters. They are the commonplace freshwater habitats in virtually all landscapes but have been overlooked by freshwater science until recently. They are often both the most and least degraded remaining examples of freshwater habitats because their small catchments make them both more vulnerable to stresses, and more likely to escape those stresses. Despite this, they still largely lie outside the mainstream of freshwater science and policy making although practitioners, landowners and ordinary people are as likely to interact with them as a great lake or large river.

The protection and management of small waterbodies presents a substantial, and achievable, opportunity to protect an important component of the freshwater environment. We encourage policy makers and legislators to help facilitate this goal.

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