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FRESHWATER ECOLOGY

Pond ecology and conservation: research priorities and knowledge gaps

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Abstract. Ponds are among the most biodiverse and ecologically important freshwater habitats globally and may provide a significant opportunity to mitigate anthropogenic pressures and reverse the decline of aquatic biodiversity. Ponds also provide important contributions to society through the provision of ecosystem services. Despite the ecological and societal importance of ponds, freshwater research, policy, and conservation have historically focused on larger water bodies, with significant gaps remaining in our understanding and conservation of pond ecosystems. In May 2019, pond researchers and practitioners participated in a workshop to tackle several pond ecology, conservation, and management issues. Nine research themes and 30 research questions were identified during and following the workshop to address knowledge gaps around: (1) pond habitat definition; (2) global and long-term data availability; (3) anthropogenic stressors; (4) aquatic–terrestrial interactions; (5) succession and disturbance; (6) freshwater connectivity; (7) pond monitoring and technological advances; (8) socio-economic factors; and (9) conservation, management, and policy. Key areas for the future inclusion of ponds in environmental and conservation policy were also discussed. Addressing gaps in our fundamental understanding of pond ecosystems will facilitate more effective research-led conservation and management of pondscapes, their inclusion in environmental policy, support the sustainability of ecosystem services, and help address many of the global threats driving the decline in freshwater biodiversity.

Key words: aquatic–terrestrial linkages; biodiversity; connectivity; ecosystem services; management; policy; small lentic water bodies.

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Introduction

Biodiversity is declining worldwide with significant reductions particularly in freshwater fauna and flora (Grooten and Almond 2018). With anthropogenic pressures such as agricultural intensification, urbanization, hydrological alterations, habitat fragmentation, climate change, and pollution likely to continue and intensify, biodiversity loss and species extinctions within freshwater environments are expected to increase in the future (Jantz et al. 2015). Ponds, defined here as lentic water bodies between 1 m^2 and <2 ha in area (Williams et al. 2010*b*), and pondscapes (a network of ponds and their surrounding terrestrial matrix) are a significant freshwater resource in the landscape. There are an estimated 547 million–3.19 billion ponds globally, although significant uncertainty surrounds pond numbers at national and international scales in many regions (Holgerson and Raymond 2016). As such, the management and conservation of ponds offer considerable opportunities to mitigate some threats faced by freshwater habitats and reverse the decline of freshwater biodiversity globally.

Cumulatively, ponds often support a greater biodiversity than other freshwater habitats (e.g., lakes and rivers), sustain many rare and endangered aquatic taxa, and act as important "refuges" in heavily modified landscapes (Davies et al. 2008). Alongside aquatic species, many terrestrial species, including insect pollinators, birds, bats, and other mammals rely on ponds for water, food, and habitat (Nummi et al. 2011, Lewis-Phillips et al. 2020). Ponds also play a significant role in the provision of ecosystem services to society including water purification, flood alleviation, irrigation, watering livestock, fish production, support for pollinators, and climate change mitigation (Lundy and Wade 2011; Coutts et al. 2012; Stewart et al. 2017; Pereira Souza et al. 2019; Vico et al. 2020). Ponds also have significant amenity and educational value (Bastien et al. 2012) and can be used to raise awareness of biodiversity and nature conservation as well as providing a space for physical activity and relaxation (Higgins et al. 2019). Despite their biodiversity and societal value, ponds have historically been dismissed as unimportant and have been drained and removed as a result of changes in agricultural practices and urban development (Wood et al. 2003), or because they are seen as breeding grounds for disease vectors (e.g., mosquitos; Dos Reis et al. 2015).

In recent decades, there has been a growing interest among scientific and non-scientific communities in pond biodiversity, their conservation and contribution to ecosystem services (Biggs et al. 2017), reflected in the rapid rise of publications between 2000 and 2019 (Fig. 1). Despite this growing recognition of the ecological and societal importance of ponds, freshwater scientific research, policy, and conservation remains disproportionately focused on rivers and larger lakes (Fig. 1), leaving significant gaps in our understanding of these valuable ecosystems. In addition, ponds are threatened by anthropogenic activities but remain a low priority of national and international conservation and environmental legislation in most countries (Hill et al. 2018). International collaboration and commitment is urgently needed to increase fundamental understanding of pond ecology, develop more effective practical conservation and management strategies, and for the implementation of detailed national and international conservation policies (Hill et al. 2018).

In May 2019, leading pond researchers, regulators, and practitioners across the United Kingdom (including Natural England, the Environment Agency and the Freshwater Habitats Trust) came together at a workshop (*Pond Ecology and Conservation in the Anthropocene*), to discuss the current status and future directions of key pond ecology, conservation, and management issues. The workshop objectives were to (1) identify critical knowledge gaps where research is

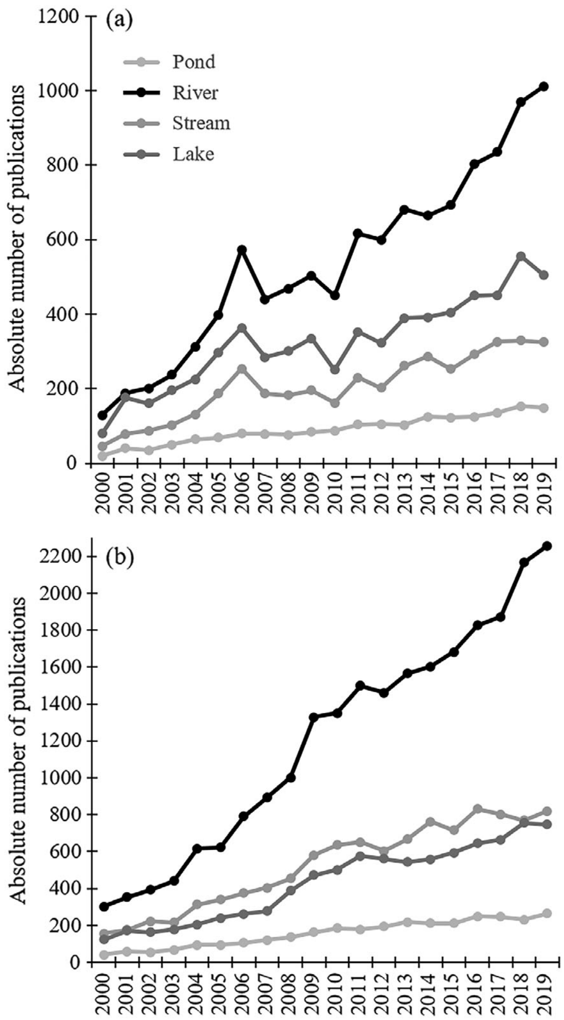

Fig. 1. Total number of peer-reviewed publications based on the search topic (a) "biodiversity" or (b) "conservation," with "pond," "stream," "lake," or "river" between 2000 and 2019, using the Scopus database.

required to advance understanding of pond ecosystems; (2) develop and/or facilitate more effective conservation and management strategies; and (3) establish the required evidence base to support the future inclusion of pond ecosystems in wider environmental and conservation policy initiatives. Initially, attendees individually and independently listed the "key challenges" and "research priorities" for pond ecosystems, based on theoretical (e.g., fundamental understanding) and applied (e.g., management, conservation, and wider societal functions) topics. Detailed group discussions followed, which reduced individual lists (over >30 research priorities in total) to nine research themes: (1) definition of pond habitats; (2) global and long-term data; (3) anthropogenic stressors; (4); aquatic-terrestrial interactions; (5) succession and disturbance; (6) freshwater connectivity; (7) pond monitoring and technological advances (8) socio-economic factors; and (9) conservation, management and policy (Fig. 2; Table 1). Subsequently, workshop organizers collated research questions from attendees, based on the research themes, and refined them into 30 questions for future pond research, building upon previous studies by Calhoun et al. (2017) and Biggs et al. (2017). The research themes and questions are outlined below by theme and are not ordered by importance or relevance.

Research Priorities

Definition of pond habitats

Since the 19th century there have been numerous attempts to define ponds (see Appendix 1 in Biggs et al. 2005). The distinction between smaller lakes and ponds has proved particularly difficult, as well as between ponds and virtually all other small standing freshwaters into which they merge (Biggs and Williams 2021), although several factors can be used to distinguish larger lakes from smaller lakes and ponds (e.g., littoral zone size, catchment size, wind protection, and environmental heterogeneity; Søndergaard et al. 2005). Despite this, distinguishing between small lakes and large ponds can still be problematic as they share many characteristics (Biggs et al. 2017). This discrepancy in definition is likely to have implications for our understanding of ecological processes in small water bodies and the development of pond management and conservation strategies.

In operational terms, ponds have been defined based on their size as water bodies between 1 m^2 and 2 ha in the UK (Williams et al. 2010*a*, *b*), although the upper size limit used to define a pond varies considerably among countries. Values between 1 ha and 6 ha are often employed (Ilg and Oertli 2017), and the Ramsar Convention on Wetlands proposed an area of 8 ha to distinguish between ponds and lakes (Ramsar Convention Secretariat 2013). To

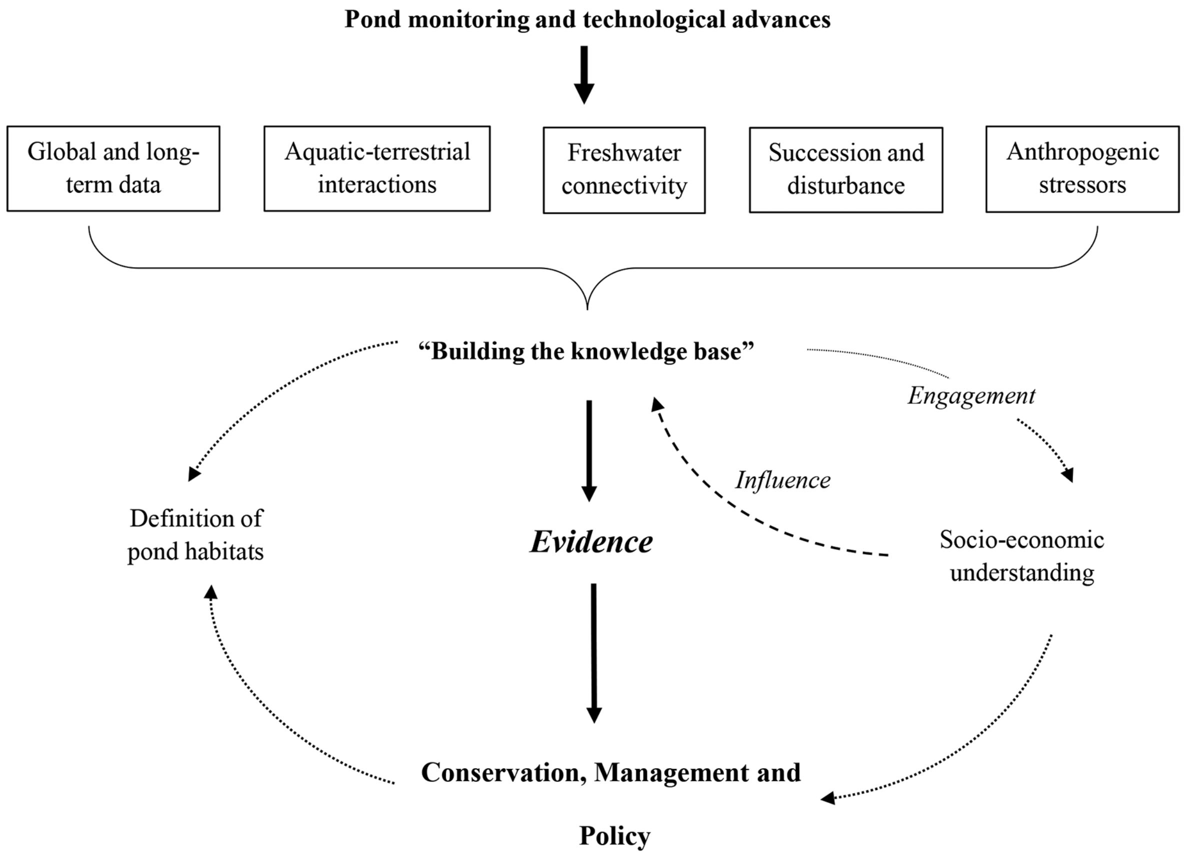

Fig. 2. The nine priority research themes and their contribution to the conservation and management of pond ecosystems.

provide a consistent, scientifically derived definition, research is required to examine the significance of depth, wind action, nutrient transport, and light penetration across a range of water body sizes, as these factors may have a large influence on biological communities. Recent research has found that small water bodies may experience strong diurnal stratification and mixing (due to convection), and seasonal stratification (Sayer et al. 2013), a process which can influence pond environmental conditions, patterns in freshwater biodiversity, and the performance of organisms, particularly sessile taxa (Andersen et al. 2017, Martinsen et al. 2019). A threshold in water body size where there is a change in mixing processes may provide a suitable characteristic to distinguish between ponds and lakes, although this currently remains inadequately quantified. The wide range of pond definitions partly reflects the wide range of perennial and temporary pond types that exist internationally, all of which demonstrate significant variability in environmental conditions and origin (Biggs et al. 2017). Given the complexity of this task, simple size-based definitions will probably continue to play an important role in practical identification and management of small standing waters. But clearly an overarching, process-based definition of a pond is required to allow researchers to undertake more targeted and comparable research and for practitioners to develop effective conservation and management strategies and policies.

Key research question.—

1. Are there critical thresholds in physical, biological, and chemical processes, and ecosystem function, which reflect changing lentic water body size?

Table 1. Key research themes, research questions, and future research identified in this paper to advance understanding of pond ecology and increase opportunities for pond conservation.

Key research theme	Context	Future research	Key research question(s)
Definition of pond habitats	A long-standing lack of congruency of how pond habitats are identified and defined	Development of an overarching, process-based global definition of a pond	1. Are there critical thresholds in physical, biological, and chemical processes, and ecosystem function, which reflect changing water body size?
Global and long-term data	Minimal research examining global- and international-scale patterns in pond numbers, diversity, and functioning. Pond studies dominated by single-season or single-year data collection	Systematic consolidation of existing datasets and international collaborative studies to examine global-scale biodiversity patterns Collection of long-term data to examine temporal trends in response to global environmental change	1. What are the abiotic and biotic drivers of pond environmental and biological patterns at different spatial and temporal scales? 2. How do biological communities within ponds respond to global environmental change along spatial and temporal gradients?
Anthropogenic stressors	Little research examining the effect of the interaction/ additive effect of multiple stressors (pollution, invasive species, and climate change) on pond habitats	Increased understanding of water chemistry standards for ponds Examine the effects of neonicotinoid and microplastics pollution, invasive species colonization, and changes in pondscape connectivity on pond biodiversity Examine the interaction between short- and long-term climate effects in ponds Greater research focus on the value of small water bodies as a scalable solution to carbon sequestration	1. What are the interactive effects of multiple stressors on pond ecosystem resilience? 2. How do pollutants impact pond ecological functioning and resilience? 3. How widely are ponds affected by non-native species and what are the dynamics of their spread? 4. How do non-native species introductions affect trophic interactions in pond ecosystems? 5. What are the potential ecological implications for pond communities associated with different climate change scenarios? 6. How will climate change affect the interactions between aquatic and terrestrial food webs?
Aquatic-terrestrial interactions	A lack of understanding on the role that pond communities play in metaecosystem dynamics, trophic, and food web structure of terrestrial communities and the role of predation for aquatic–terrestrial communities	Examine the interaction between freshwater ecological health and terrestrial ecological health Identify the role of aquatic biota in structuring terrestrial communities and food webs	1. Does the nutritional value of aquatic macroinvertebrates for terrestrial predators reflect pond water quality? 2. How important are terrestrial vertebrates for the dispersal of pond biota and for maintaining local environmental heterogeneity and does this vary systematically with pond setting? 3. How do aquatic–terrestrial interactions in predation influence pond community structure and vice versa?
Succession and disturbance	The effect of disturbance on pond communities (at local and landscape scales) is poorly understood, in part due to the lack of long-term data and anthropogenic location of many ponds	Increase fundamental understanding of how disturbance structures pond communities spatially and temporally across different land-use types Examine the life-history strategies and mechanisms that species and communities employ to survive disturbance events	1. What role do natural disturbances play in structuring aquatic and terrestrial biodiversity in pond habitats across landscapes minimally impacted by human influences? 2. What are the best management strategies to reduce detrimental disturbances and increase positive disturbance in anthropogenically dominated landscapes? 3. What are the principal trajectories, timescales, and outcomes of pond succession across different pond types?
Freshwater connectivity	Research is focused on lotic habitats and typically examines freshwater habitats in isolation. The lack of high-resolution pond mapping is inhibiting research understanding the role of connectivity in the large-scale patterns of pond communities	Examine how spatial processes influence the patterns of actively and passively dispersing pond taxa across landscape types Examine spatial processes operating across the watery landscape by incorporating multiple freshwater habitats Characterize where connectivity is an advantage and where it represents a risk to pond biodiversity	1. How does connectivity between pond habitats influence trophic interactions that bridge aquatic–terrestrial divides? 2. How do species move between ponds and other freshwaters and what are the dominant mechanisms? 3. How are pond networks (pondscapes) best designed or managed to ensure that rarer and less mobile species benefit? 4. What is the role of spatial processes in assemblage structure and does pond context or landscape create regional differences?

Table 1. Continued.

Key research theme	Context	Future research	Key research question(s)
Pond monitoring and technological advances	eDNA, remotely sensed and drone-based data have been poorly applied to pond monitoring and multi-taxon assessments. Advances in biostatistics may increase effectiveness of pond conservation	The use of remote sensing and drone technologies to identify the distribution and physicochemical properties of pond environments Using multiple technologies (eDNA, UAV) effectively to answer fundamental, multitrophic ecological questions	1. Can molecular tools be used to assess the distribution of conservation priority and invasive species as well as community diversity at the pondscape scale? 2. Are molecular tools and remote sensing able to identify the effects of anthropogenic stressors and climate change on ponds and improve management strategies to mitigate stressors? 3. Can UAV-based data collection record physico-chemical and spatial characteristics of ponds and pondscapes more accurately than conventional data collection? 4. How can the development of new statistical analyses in biodiversity assessment contribute to more effective pond conservation planning?
Socio-economic factors	Limited understanding of the personal, social, and educational contributions made by ponds, and governance conflicts that exist between users of ponds. There remain gaps in our knowledge of the contribution of ponds to human health and wellbeing	Studies of the human dimensions of stakeholder engagement in pond creation and management are needed Explore the relationships between ponds, well-being, access, and habitat quality Assess the complexities of engagement, the educational value of ponds, and the use of ponds in fostering an environmental conscience	1. How do ponds contribute to human physical and mental health and wellbeing within urban and rural populations? 2. What are the barriers (including social, cultural, institutional, emotional, communicative, and governance) in stakeholder–pond conservation interactions, and how might these be addressed? 3. What are the short- and long-term effects of environmental education for pond conservation?
Conservation, management, and policy	There is a need to increase fundamental understanding of pond ecosystems to inform practical pond conservation and management. Ponds are largely excluded from environmental policy and legislation	Examine the mechanisms that affect pond creation and restoration success A need for studies to assess medium to long-term pond conservation and management measures Identify opportunities for the inclusion of ponds in environmental and conservation policy Quantify the distribution of rare species in ponds and high-quality pond sites for conservation	1. Where are the most ecologically important ponds at national and international scales? 2. How does pond creation and management affect biotic communities at local and landscape scales in different environmental settings? 3. How can we best conserve pondscapes in anthropogenically dominated landscapes? 4. What are the mechanisms required to better incorporate ponds into national and international environmental policy and legislation?

Global and long-term data

While global-scale research has been undertaken for lotic (Tiegs et al. 2019) and lake ecosystems (Alahuhta et al. 2017), there has been no equivalent research examining global- and international-scale patterns in pond diversity and functioning, despite the threats facing freshwater habitats worldwide (but see Downing et al. 2008). Some studies have examined pond communities at a national-scale (Hill et al. 2017), but it is not clear whether similar ecological patterns and processes occur at continental or global scales. To enable more effective international management and conservation of the biodiversity and associated ecosystem services of ponds, there is a need for the systematic consolidation of existing datasets to examine global-scale biodiversity patterns and the community assembly processes at multiple spatial scales. Key to these studies will be placing ponds in the context of other freshwater habitats (e.g., lakes, rivers) across the aquatic landscape (Sayer 2014). The development of an open-access, global pond database of biotic and environmental data will facilitate significant global-scale research and increase our understanding of these important water bodies; although this database does not currently exist. New large-scale collaborative studies will be critical to understand how global pressures (e.g., land-use change and pollution) are affecting pond diversity (e.g., total biodiversity and rare species distributions) and ecosystem service provision (e.g., stormwater collection, water purification, and human well-being).

A further scaling issue that inhibits conservation efforts and the development of effective policy for ponds is the lack of long-term datasets. With a few exceptions (see Jeffries 2011, Williams et al. 2020), most pond research has been dominated by studies covering a single season or year (Hill et al. 2016), with studies covering timescales longer than 10 yr largely missing. Consequently, there are significant knowledge gaps regarding the long-term dynamics and patterns in pond environments, biological diversity, and functioning. As for larger lentic water bodies, paleoecological approaches could provide critical information for inferring long-term (c.100s–1000s years) changes in pond ecology in response to environmental change and, in turn, inform restoration strategies (Walton et al. 2021). This is of particular importance for demonstrating the scope for returning communities to those recorded prior to major human impacts. As well as encouraging long-term data collection, the comparison of contemporary samples with older records (Hassall et al. 2012) and mesocosm experimentation may elucidate long-term processes (Yvon-Durocher et al. 2017).

Key research questions.—

1. What are the abiotic and biotic drivers of pond environmental and biological patterns at different spatial and temporal scales?
2. How do biological communities within ponds respond to global environmental change along spatial and temporal gradients?

Anthropogenic stressors

Ponds are increasingly being subjected to multiple anthropogenic stressors which can affect the diversity and resilience of their communities (Ryan et al. 2014). The cocktail of anthropogenic stressors may include chemical (e.g., pollution), biological (e.g., invasive species), and physical (e.g., infilling, management, and climatic warming) pressures. In addition, stressors may originate from anthropocentric perceptions of ponds, such as the high values placed upon neatness, carefully managed plant communities (removal of "weedy" and aesthetically unpleasing species), and large areas of open water, perceptions which often do not reflect the natural functioning of ponds (Nassauer 2004). Many stressors remain poorly understood, and in this section, we focus on the impacts of pollution, non-native species, and climate change on pond communities, and identify knowledge gaps and key areas for future research.

*Pollution.—*One of the most pervasive threats to pond communities is pollution. Nutrient enrichment, which is known to decrease species diversity at a landscape-scale (Rosset et al. 2014), is one of the better understood threats to pond communities in agricultural and heavily populated landscapes. In urban landscapes, runoff from impermeable surfaces can result in an increase in heavy metals, nutrients, road salts, and chloride in ponds (Moss 2017). However, many natural and anthropogenic ponds in urban landscapes are designed and managed to hold stormwater runoff and are thus intended to be polluted as a means to protect water quality in the catchment downstream (Gold et al. 2017). As such, there is a paradox in urban landscapes, where ponds have high biodiversity value but are being designed to hold pollutants to improve downstream water quality of more highly valued (but not actually more biodiversity rich) freshwater habitats, such as larger lakes and rivers. Given urban areas are predicted to increase in size across the globe (Seto et al. 2012), more ponds are likely to experience pollution, but the impacts on urban pond biodiversity are not fully understood (Hintz and Relyea 2019). Higher numbers of polluted ponds also pose potential risks from increasing the number of water bodies which are producing large quantities of climate heating gases (Peacock et al. 2019, Rosentreter et al. 2021).

The process of suburbanization also poses a major threat to freshwater biodiversity (Van Acker et al. 2019). Pond habitats frequently survive the conversion from natural to suburban land cover, but they are often subject to wastewater runoff (chemical loading), physical changes (e.g., decreased canopy cover and increased temperature), and isolation which can have large effects on food web dynamics, species health, and taxa richness (Homan et al. 2004, Holgerson et al. 2018, Van Acker et al. 2019). Pesticide pollution in freshwaters also represents a long-term persistent issue (Ito et al. 2020), yet quantifying concentrations remains challenging due to high spatiotemporal variability, limitations of instrument availability, and difficultly in identifying new/emerging chemicals (Lorenz et al. 2017). In particular, neonicotinoid pesticides (Raby et al. 2018) are contaminants of freshwaters which have been given little attention in pond environments thus far. Moreover, despite a large body of literature in lotic systems (Calabrese et al. 2020), there has been little research examining interactive effects of multiple stressors on pond communities, which could be additive, subtractive, antagonistic, or synergistic (Hassall 2014).

Non-native species.—Non-native species are one of the greatest threats to many freshwater systems, but are probably less common in ponds than other highly connected freshwater environments associated with their hydrological isolation (Williams et al. 2010*a*, *b*), although ponds in urban areas are highly vulnerable to intentional introductions (Patoka et al. 2017).

Where non-native species become highly invasive after successfully colonizing and establishing in ponds, impacts are invariably detrimental. For example, the effects of New Zealand Pigmywort (*Crassula helmsii)* on pond communities in Europe are widely acknowledged (e.g., loss of plant biomass and abundance, plant germination suppression; Langdon et al. 2004; Smith and Buckley 2020), and the introduction of the Topmouth Gudgeon (*Pseudorasbora parva)* into European pond habitats has been shown to shift the trophic position of fishes (Britton et al. 2010). However, there are a wide range of non-native invasive species that are expanding their habitat range and of which we know little about their impacts for pond ecosystem functioning and biodiversity (e.g., *Dikerogammarus villosus* and *Pacifastacus leniusculus*).

While it is clear that the establishment of non-native invasive species can be detrimental to native communities, not all introductions of non-native taxa are negative. For example, in Oregon, USA, the non-native Reed Canary grass (*Phalaris arundinacea*) has been beneficial to breeding amphibians in many ponds, providing suitable sites for oviposition, increasing tadpole survival, and the abundance of adult amphibians (Holzer and Lawler 2015) and in Washington State, USA, Holgerson et al. (2019) found that non-native bullfrogs (*Lithobates catesbeianus*) did not impact pond amphibian occupancy (but non-native fish did). Should ponds be less widely affected than other freshwaters they may represent refugia for some taxa otherwise threatened by non-native invasive species in shallow lakes and rivers (Sayer et al. 2011). Historically, the effects of non-native species on trophic interactions within ponds have been poorly studied compared to their lotic counterparts, and as such, further consideration is required to identify the implications of predator–prey interactions between non-native and native species, as well as how non-native species may be driving shifts in pond ecosystem functioning. Research is clearly required to examine the full range of ecological effects (negative, positive, and negligible) that non-native taxa may have on native pond communities, and how they can be managed to facilitate conservation of native species.

Climate change.—As small but abundant habitats, ponds are sensitive to the effects of environmental change and are therefore essential to consider within climate feedbacks. Agricultural impoundment ponds are among the most significant habitats for carbon sequestration due to their high nutrient loads and associated high primary productivity (Downing et al. 2008). Even accounting for their relatively small size, research has demonstrated that carbon burial rates in small ponds are at least equivalent to woodland or grassland habitats (Taylor et al. 2019). However, other studies have suggested that small water bodies can switch between carbon sources and sinks, while boreal ponds and small agricultural reservoirs may even act as significant sources of greenhouse gas emissions (Holgerson and Raymond 2016; Webb et al. 2019). Given recent drives toward afforestation for climate mitigation (Brown 2020), determining the net value of ponds within the carbon cycle may reveal their potential, helping diversify climate mitigation beyond forestry alone.

Understanding the different dimensions of climate change—gradual warming, heat waves, droughts, and floods—and how they interact and affect pond communities is vital to the future conservation of pond environments. Extreme climatic events may result in homogenized pond communities, reducing the biodiversity value of pondscapes (Bertoncin, et al. 2019). Drought is likely to increase the proportion of ponds that experience hydrological intermittency resulting in changing community structures of existing temporary ponds, extirpation of species unable to adapt to increasing ephemerality (Ryan et al. 2014, Abney et al. 2019), and potentially influence greenhouse gas emissions from ponds (Holgerson and Raymond 2016). These climate shifts typically favor freshwater communities from warmer regions that can take advantage of higher temperatures to circumvent the increasingly ephemeral nature of the ponds. However, a better understanding of the interaction between short- and long-term climate effects on ponds to predict future effects is required.

Climate change has been shown to interact with other stressors, for example by exacerbating the effects of pesticides (Janssens and Stoks 2013) and sedimentation (Piggott et al. 2012) due to climatic changes to rainfall and runoff regimes altering the delivery of fine sediment and its associated contaminants. In contrast, some studies suggest that climate change may be antagonistic to biological invasions, where non-native species increase their functional capacity to the same level as native species under warming (Kenna et al. 2017), but climate change has also been found to intensify the effects of non-native introductions (Bellard et al. 2012). While some progress has been made in understanding how co-occurring stressors interact (if at all), a synthetic approach to gathering evidence across spatial and temporal scales could yield further insights across ponds and the wider freshwater network and inform new research.

Climate change also potentially mediates interactions among species through driving spatio-temporal patterns of occurrence. While phenological change has been described for some freshwater taxa (Hassall 2015), the ecological and fitness implications of phenological changes in pond communities have received little attention. The existing focus has largely been on birds (Radchuk et al. 2019), and changes in synchrony of interacting taxa have mostly been studied in larger water bodies (Winder and Schindler 2004). Given the importance of links between aquatic and terrestrial food webs (Stenroth et al. 2015), more research examining the effect of climate change on aquatic–terrestrial networks and the flow of nutrients and services between these habitats is required (Soininen et al. 2015).

Key research questions.—

1. What are the interactive effects of multiple stressors on pond ecosystem resilience?
2. How do pollutants impact pond ecological functioning and resilience?
3. How widely are ponds affected by non-native species and what are the dynamics of their spread?
4. How do non-native species introductions affect trophic interactions in pond ecosystems?
5. What are the potential ecological implications for pond communities associated with different climate change scenarios?
6. How will climate change affect the interactions between aquatic and terrestrial food webs?

Aquatic–terrestrial interactions

The importance of freshwater habitats is not limited to the water body itself. Interactions between aquatic and terrestrial ecosystems can be significant, demonstrated by the importance of terrestrial vegetation shading in structuring freshwater invertebrate assemblages (Suh and Samways 2005), the negative effects of land-use change on terrestrial insectivores reliant on aquatic insects, and the effect of predation (e.g., dragonflies preying on bees) on aquatic–terrestrial interactions (Knight et al. 2005, Stenroth et al. 2015). There is a growing recognition of the importance of interactions between ponds and terrestrial species, especially farmland birds (Lewis-Phillips et al. 2020) and insect pollinators (Stewart et al. 2017). The reliance of terrestrial organisms on ponds may be largely due to trophic interactions that bridge the aquatic–terrestrial divide. Farmland ponds managed by scrub and sediment removal (to re-establish macrophyte dominance) have been shown to increase avian diversity and abundance due to enhanced emerging of invertebrate food sources (Lewis-Phillips et al. 2020) and support distinct diurnal pollinator communities (Walton et al. 2020). An increased abundance of local pollinators enhances pollination services in neighboring crop fields (Stewart et al. 2017), while increased numbers of spiders and beetles adjacent to some ponds have been linked to emerging insect prey from ponds (McCaffery and Eby 2016) and might promote natural pest control over wider scales.

Of particular note, ponds can act as important components of the food web and energy flow between aquatic and terrestrial organisms. For example, birds feeding on aquatic invertebrates have crucial access to higher levels of unsaturated omega-3 fatty acids needed for improved physical and cognitive development than birds relying primarily on terrestrial invertebrates (Twining et al. 2016). However, it is unclear how pollution and other anthropogenic stressors in ponds may influence the nutritional value of aquatic macroinvertebrates and therefore their value to terrestrial predators. Conversely, nutrients that have moved from aquatic to terrestrial systems can eventually be transported back when semi-terrestrial organisms such as amphibians return to ponds to lay eggs (Regester et al. 2006, Capps et al. 2015). Amphibian larvae often also form part of pond fish diets which can act as a limiting factor on amphibian richness and abundance within ponds (Hecnar and M'Closkey 1997; Hartel et al. 2007). Furthermore, terrestrial leaf litter and other detritus that falls into ponds provide nutrients (Fey et al. 2015) as well as food for invertebrate communities (Holgerson et al. 2016). These examples highlight the significance of ponds as food and energy links between the aquatic and terrestrial realms.

Despite this emerging knowledge, there is still a lack of understanding regarding the role that ponds play in aquatic–terrestrial interactions. For example, bats and other small mammals may benefit from pond resources including emerging aquatic insects and the provision of drinking water (Nummi et al. 2011), while vertebrate herbivores, including waterfowl, beaver, elk, and moose are attracted by shallow water and extensive palatable vegetation (Law et al. 2014). Furthermore, terrestrial vertebrate visitors to ponds may provide important ecosystem processes, including trampling, grazing, and poaching which could arrest successional processes, stimulate seed bank emergence, disperse propagules (Cieminski and Flake 1997), and enhance fine-scale spatial heterogeneity (Willby et al. 2019). Such dynamics are considered critical in maintaining populations of many endangered plant species. More research on pond aquatic–terrestrial interactions and food web structures that transcends traditional aquatic–terrestrial boundaries is clearly needed.

Key research questions.—

1. Does the nutritional value of aquatic macroinvertebrates for terrestrial predators reflect pond water quality?
2. How important are terrestrial vertebrates for the dispersal of pond biota and for maintaining local environmental heterogeneity and does this vary systematically with pond setting?
3. How do aquatic–terrestrial interactions in predation influence pond community structure and vice versa?

Succession and disturbance

Due to their small size and shallow depth, hydroseral succession may operate faster in ponds compared to larger water bodies. However, little is known regarding the timescales or pathways of succession across ponds, particularly in relation to their origin, climatic, and geological settings (Biggs and Williams 2021). Disturbance, both natural and anthropogenically driven, is an important influence on succession, but remains poorly studied among pond habitats. Natural disturbances, including beaver damning, natural tree fall, wetting and drying cycles, floods (resulting in meander cutoff and channel avulsion), and the activities of large herbivores (both domestic and wild), may act to create ponds, or delay and reset succession trajectories. Equally, human-induced disturbances can create new ponds, for example, wartime bomb craters supporting high-diversity pondscapes in Central Europe (Vad et al. 2017). In pondscapes where natural disturbances occur, it is generally accepted that ponds will be at different stages of succession, which may enhance both beta and gamma diversity (Hill et al. 2017). In contrast, in landscapes where natural disturbances have been reduced, uninterrupted succession can result in areas entirely dominated by late-succession ponds, thus reducing biodiversity (Sayer et al. 2012). The influence of succession and disturbance regimes (natural and anthropogenic) on landscape-scale species distribution and diversity patterns remains poorly understood, in part due to a lack of long-term monitoring, but could provide critical information for the development of landscape-scale conservation and management strategies.

Many pond species possess life cycles and adaptive strategies enabling them to persist across the landscape in the face of disturbance, such as dormant and resistant propagules of aquatic invertebrates and plants (Alderton et al. 2017; Williams et al. 1997), and relatively long lifespans for amphibians and some invertebrates. Efficient dispersal mechanisms by many invertebrates allow rapid recolonization when favorable conditions return including endozoochary (Kleyheeg and van Leeuwen 2015), aerial dispersal (Bilton et al. 2001), and "hitch-hiking" (Okamura et al. 2019). Research focused on the life-history strategies that enable species and communities to persist after a disturbance will be especially valuable to conservation managers as manipulating and facilitating disturbance via active management or passively by rewilding may be key to the survival and protection of many pond species.

Key research questions.—

1. What role do natural disturbances play in structuring aquatic and terrestrial biodiversity in pond habitats across landscapes minimally impacted by human influences?
2. What are the best management strategies to reduce detrimental disturbances and increase positive disturbance in anthropogenically dominated landscapes?
3. What are the principal trajectories, timescales, and outcomes of pond succession across different pond types?

Freshwater connectivity

Connectivity is important because it facilitates the movement of energy, materials, organisms, and genetic resources within and between habitats in a landscape or more widely. Published studies examining connectivity have accelerated greatly during the 21st century alongside the growing debate on the relative roles of dispersal limitation and local species sorting across all ecosystem types (Heino et al. 2017). A growing number of studies have reported the importance of spatial factors (Juračka et al. 2019), or biological traits linked to dispersal ability (De Bie et al. 2012) in determining assemblage structure, indicating that dispersal limitation is likely to be an important influence on pond communities. Contrasting active and passive dispersers, both within and across taxon groups, has confirmed expectations that dispersal limitation among ponds is stronger among less mobile taxa (De Bie et al. 2012; Hill et al. 2017*a*). The transferability of these patterns across a range of landscape types and pond characteristics now needs to be determined as most studies on connectivity in freshwater systems focus on longitudinal connectivity in rivers and tend to examine freshwater habitats in isolation. In the case of ponds, two-way connectivity both across the aquatic–terrestrial interface and with other freshwater habitats in the wider landscape are likely to be especially important.

Connectivity is complex to quantify and is typically estimated using simple indicators, including Euclidean distances to similar habitats (Juračka et al. 2019), hydrological pathway lengths or percentage of surrounding freshwater with a buffer zone (Law et al. 2019), waterbird migration flyways (Viana, et al. 2016), and human population densities or proximity to recreational facilities (Chapman et al. 2020). Measures of geneflow or similarity in assemblage composition are often used to infer realized connectivity (Bilton et al. 2001). Metrics based on the structural properties of spatial networks (e.g., centrality and percolation thresholds) or species-specific dispersal distances and costs to crossing different habitats have also been suggested as possible solutions (Thornhill et al. 2018; Hunter-Ayad and Hassall 2020). Rapid increases in the quality and availability of national biological recording datasets are improving understanding of the role of connectivity on the large-scale distribution of freshwater taxa. However, among ponds, the lack of high-resolution mapping may confound such attempts. It is also important to acknowledge that connectivity is not a static property and varies temporally, for example, with hydroperiod or hydrological events, or seasonality linked to water bird migration, and can be fundamentally altered by anthropogenic activities or ecosystem engineers (Bilton et al. 2001). Moreover, rare or long-distance colonization events may be important for connectivity (Jordano 2017), but accurately modeling or predicting these events will be complex when related to local physicochemical variables. Freshwater habitats are not discrete entities but often exist in networks (e.g., an interconnected system of ponds, rivers, streams, and lakes; Sayer 2014), and ubiquitous species are recorded across these freshwater habitats (Davies et al. 2008). As such, it will be misleading to study ponds in isolation, and more holistic research is required to understand the ecological processes operating across a range of connected freshwater habitats (the "waterscape"), which will likely provide more accurate information for future landscape-scale conservation initiatives (Heino et al. 2021).

Management strategies to increase habitat patch connectedness is a common response to fragmentation; however, the relative isolation of some ponds may be an asset in insulating them from common stressors such as diffuse nutrient loading, pathogens or invasive species that are easily transmitted between more connected water body types. Understanding the aspects of connectivity that confer an advantage in terms of enhanced resilience, and those where it represents a risk in terms of accelerated transfer of stressors, is therefore critical in terms of future restoration or the design of pondscapes and wider waterscape.

Key research questions.—

1. How does connectivity between pond habitats influence trophic interactions that bridge aquatic–terrestrial divides?
2. How do species move between ponds and other freshwaters and what are the dominant mechanisms?
3. How are pond networks (pondscapes) best designed or managed to ensure that rarer and less mobile species benefit?
4. What is the role of spatial processes in assemblage structure and does pond context or landscape create regional differences?

Pond monitoring and technological advances

Recent developments in pond monitoring techniques and biostatistics can advance our understanding of the ecology and conservation of pondscapes. There are several challenges facing pond monitoring including (1) often being located difficult to access and remote landscape settings, (2) identifying representative sites due to their high abundance, (3) their high environmental heterogeneity, resulting in multiple ponds needing to be monitored to capture abiotic and biotic diversity, and (4) the availability of taxonomic specialists to identify the highly diverse floral and faunal taxa recorded within ponds. However, the utilization of new technologies may help to overcome some of these challenges. In this section, we first outline the contribution that molecular tools have made to pond monitoring (Biggs et al. 2015; Deiner et al. 2017) and then discuss the opportunities that recent technological advances in remote sensing, unmanned aerial vehicles, and biostatistics have provided for pond ecology and conservation.

*Pond monitoring using molecular tools.—*The emergence of environmental DNA (eDNA) analysis has the potential to transform freshwater biodiversity assessment. eDNA is genetic material released by organisms into their environment, which can be sampled and analyzed to target specific species or passively screen entire communities (Harper et al. 2019*a*). Targeted eDNA analysis can be used to assess the distribution and range of threatened, rare, or non-native pond species (Biggs et al. 2015; Mauvisseau et al. 2018), and estimate relative abundance or biomass, and detection probability (Buxton, et al. 2017). Similarly, eDNA metabarcoding could be employed to assess multi-species distribution, reveal species interactions (Harper et al. 2019*b*), and characterize genetic diversity (Parsons et al. 2018), all of which are only beginning to be considered for pond ecosystems. Community DNA is distinct from eDNA samples, being sourced from biological material such as invertebrate blood meals (invertebrate-derived DNA: iDNA), feces, and collected specimens (Deiner et al. 2017). iDNA analysis uses DNA that was ingested by invertebrates, such as leeches, to detect biodiversity within freshwater habitats (Abrams et al. 2019). iDNA metabarcoding could identify vertebrate biodiversity and enable multi-species occupancy modeling (Abrams et al. 2019), while fecal metabarcoding could be used to assess diets of threatened or invasive species and construct pond food webs (Kaunisto et al. 2017). Although bulk tissue DNA and eDNA metabarcoding have been used for macroinvertebrate assessment in other freshwater ecosystems (Elbrecht et al. 2017), these techniques have rarely been applied to ponds. Using bulk tissue DNA and eDNA metabarcoding in pond research may provide more holistic estimates of alpha and beta-diversity (Harper et al. 2020). Similarly, stable isotope analysis can complement metabarcoding to determine trophic relationships among pond taxa (Compson et al. 2019). These tools could more accurately quantify target species distribution and ranges and determine the interactive effects of anthropogenic stressors, such as invasive species on communities and food webs.

Technological advances in remote sensing, unmanned aerial vehicles, and biostatistics.—Conventional data collection methods for some environmental variables within ponds (e.g., visual estimation of macrophyte coverage) are typically subjective or at best semi-quantitative and/or lack sufficient detail of wider environmental conditions. Remote sensing has been widely used in water quality assessment and resource management within lakes and rivers (Gholizadeh et al. 2016). Remote sensing can accurately measure certain catchment characteristics (e.g., land cover, productivity), physical properties (e.g., surface area, turbidity), and biological properties (e.g., aquatic macrophyte coverage) of freshwater environments across large spatiotemporal scales in a cost-effective and standardized manner (Giardino et al. 2010). Remote sensing could provide an efficient means to collect large-scale environmental and spatial metadata (e.g., pond numbers, connectivity, pond spatial structure, and physical barriers) for pond research and assistance in the development of effective monitoring strategies, particularly for remote ponds and pond networks (Rose et al. 2015). Recent research, using remote sensing, was able to determine the number (>1000 ponds) and distribution of ponds across the Greater Kuala Lumpur region (~2950 km^2) in Malaysia and quantify particular environmental conditions of each pond including the surface area, shape, connectivity, and surrounding land use (Teo et al. 2021). Despite this, it remains a largely unused tool in pond research. However, given the spatial resolution of remotely sensed data, it is unclear how remote sensing could be used to record small (<10 m^2) or intermittent ponds (during the dry phase), and those located under forest canopy (Gallant 2015, Kissel et al. 2020).

In lotic settings, the recent use of small unmanned aerial vehicles (UAV) and structure-from motion (SfM) photogrammetric processing has provided a significant improvement in the objectivity, accuracy, and efficiency of physical habitat data collection (Woodget et al. 2015). The parallels between streams and ponds suggest that similar advancements could be made for surveying surface area (particularly of small ponds), substrate composition, aquatic and riparian vegetation structure, habitat complexity, pollution events, and the spatial structure of ponds and pondscapes. UAVs can generate fine spatial resolutions (<10 cm/pixel; Lucieer et al. 2014) and, as such, have the potential to significantly increase the accuracy and consistency of pondscape data, elucidating the processes impacting their ecology and providing detailed site information to underpin effective monitoring strategies. However, no empirical studies have thus far examined the use of UAVs to characterize pondscapes.

Recent developments in biostatistics may also provide considerable advances to our understanding of pond ecology and their conservation. Research on the drivers of species richness and community composition among lentic systems has focused almost exclusively on local environmental and spatial factors and has largely ignored the potential influence of biotic interactions (Heino et al. 2015). Recently, new statistical analysis has enabled the influence of biotic interactions, environmental conditions, and spatial factors to be considered together providing a more realistic understanding of the factors that govern the spatial and temporal patterns in pond biodiversity (García-Girón et al.

2020). Similarly, Local Contributions to Beta Diversity (LCBD; Legendre 2014) analyses goes beyond traditional measures of beta-diversity (a single measure of dissimilarly across the landscape) and calculates the contribution to overall beta-diversity by individual sites (provides a measure of ecological uniqueness for individual sites; Heino and Grönroos 2017). LCBD may contribute to pond conservation by identifying ponds with high numbers of unique species (that may be missed by traditional conservation practices that focus on taxonomic richness), whose protection can increase the number of species that are conserved at a landscape-scale. Recent research by Hill et al. (2021) found 70–97% of the regional species pool was protected when ecologically unique (sites with high LCBD values) and high taxonomic diversity sites (sites with >50 taxa) were considered together compared to 54%–94% when only sites with high taxonomic diversity were considered. Applying these new statistical techniques to different ecological and geographical settings will facilitate a greater understanding of pond ecology and more effective and targeted conservation strategies.

Key research questions.—

1. Can molecular tools be used to assess the distribution of conservation priority and invasive species as well as community diversity at the pondscape scale?
2. Are molecular tools and remote sensing able to identify the effects of anthropogenic stressors and climate change on ponds and improve management strategies to mitigate stressors?
3. Can UAV-based data collection record physicochemical and spatial characteristics of ponds and pondscapes more accurately than conventional data collection?
4. How can the development of new statistical analyses in biodiversity assessment contribute to more effective pond conservation planning?

Socio-economic factors

Ponds form an intrinsic component of urban and rural landscapes and many were historically created for a range of purposes, including industrial processes such as mineral extraction, provision of food and water, irrigation, watering livestock, and as ornamental features (Gledhill and James 2012). In much of the world, many of the historical purposes of ponds are now redundant and today ponds are often managed as amenity features (e.g., angling) or have been abandoned. Angling ponds have been demonstrated to support limited faunal diversity (Wood et al. 2001), but there remains a paucity of research considering social elements associated with angling ponds. Research is needed to assess the personal, social, and educational contributions made by angling ponds and to better understand the practical and emotional governance conflicts that exist between anglers and other users of ponds to increase opportunities for sustainable management (Arlinghaus 2005). Given that the origin of many ponds is a by-product from industrial processes, their presence in rural areas is unwanted by some landowners (Wood et al. 2003). As a result, there are still numerous barriers to the creation of new ponds and the management of existing ponds, despite recent evidence of biodiversity gains (Williams et al. 2020). Studies of the human dimensions (including social, cultural, institutional, emotional, communicative, governance, and lifestyle tolerance factors) of stakeholder engagement with pond creation and management are currently largely absent but are required to ensure the success of any local or landscape-scale pond initiatives.

There is emerging evidence of the importance of blue space for the health and well-being of individuals by promoting psychological restoration and providing spaces for physical activity, recreation, and social interaction (Gascon et al. 2017; Foley and Kistemann 2015). Blue space regeneration could also help foster a sense of civic pride and ownership (Higgins et al. 2019). However, existing research has primarily focused on coastal areas or lotic ecosystems, and there remain considerable gaps in our knowledge of the contribution of ponds to human health and well-being (Foley and Kistemann 2015). The immersive benefits of ponds in terms of their contribution to physical health, imaginative, emotional, and therapeutic aspects, and the range of meanings for individuals and groups of pond ecosystems all require a greater understanding. In addition, research is needed to explore the relationships between ponds, well-being, access, and habitat quality, particularly in urban landscapes (Higgins et al. 2019).

With increased urban living, the incorporation of ponds as blue spaces into the aesthetic design of urban areas represents an opportunity to engage the public with freshwater ecosystems (de Bell et al. 2017). Online packs of pond dipping materials and citizen science pond initiatives can reconnect individuals with nature, while engaging non-professionals in scientific research and practical freshwater conservation (Dickinson et al. 2012). Ponds also provide opportunities for education as the presence of ponds within schools may provide an important resource for educational study and can encourage an initial interaction and familiarization with ponds and wildlife from an early age (Braund 1997). Research that considers the complexities of engagement, the educational value of ponds, barriers to environmental education, and the use of pond ecosystems for the development of an environmental conscience in individuals and society will be particularly beneficial in addressing freshwater environmental and ecological degradation and increase opportunities for pond conservation.

Key research questions.—

1. How do ponds contribute to human physical and mental health and well-being within urban and rural populations?
2. What are the barriers (including social, cultural, institutional, emotional, communicative, and governance) in stakeholder–pond conservation interactions, and how might these be addressed?
3. What are the short- and long-term effects of environmental education for pond conservation?

Pond conservation, management, and policy

While lake and riverine habitats have overwhelmingly dominated historic freshwater policy, conservation, and management research, more recently there has been a growing focus on ponds. Research on strategies for pond creation, pond and pondscape design, and where best to locate new ponds to maximize aquatic conservation benefits has developed significantly (Thiere et al. 2009). In addition, there is a growing body of research and expertise centered on the successful restoration and management of ponds in a variety of landscape settings, in particular European farmland and semi-natural habitats (Sayer et al. 2012; Sayer and Greaves 2020), Mediterranean coastal plains (Sebastián-González and Green 2014), and the prairies of Canada and the United States (Bortolotti et al. 2016). Pond creation and restoration studies are typically short-term in duration, and studies assessing the medium to long-term success of measures alongside natural dynamics are needed (Seabloom and van der Valk 2003). These studies will ultimately determine the need (or not) for subsequent policy and management activities to maintain conservation benefits (Sayer et al. 2012). Further, research is also required on the mechanisms that affect pond creation and restoration success, covering key issues such as water quality, grazing regimes, hydrology, connectivity, and invasive species. In this respect, studies that compare and combine pond restoration with creation at the landscape-scale will be important to inform pond conservation planning and prioritization.

Policy on the conservation and management of ponds has generally suffered from the assumption that small water bodies were not important due to their size (Biggs and Williams 2021). This long-standing assumption, noted since the 1950s, has generally led to the absence of small water bodies from environmental and conservation policy globally (Hill et al. 2018). For example, the European Union's Water Framework Directive, although intended to protect "all" water bodies specifically excludes those <50 ha from monitoring schemes, thereby excluding millions of ponds (although some are specially selected for nature conservation under the EU Habitats Directive). Similarly, in North America and Asia, ponds are generally not directly considered in environmental policy or legislation despite the establishment of the Clean Water Rule clarifying freshwater protection under the Clean Water Act in the United States (Department of Army, Corps of Engineers and US Environmental Protection Agency 2015*)* and various national-scale environmental legislation across Asia (e.g., Environment Protection Act 1986 and the Wildlife Protection Act 1972 in India). However, the policy failure relating to small water bodies is slowly being reversed as awareness of the importance of these water bodies appears to be increasing. For example, the Intergovernmental Science Policy Platform on Biodiversity and Ecosystem Services (IPBES) included temporary and perennial ponds in its classification of freshwater habitats in 2018 (IPBES 2018).

The future inclusion of ponds in environmental and conservation policy should focus on four areas: (1) stopping further deterioration, especially of the most vulnerable high-quality sites. Although evidence is scarce, the quality of the most protected ponds continues to decline (Williams 2019); (2) protecting species and communities that are a special feature of ponds. Increasing knowledge of pond communities and the distribution of freshwater species will refine our understanding of the role of ponds play in protecting endangered freshwater species and inform policy; (3) encouraging the creation of new clean water ponds (clean water ponds reflect pond water chemistry and biology that is typical for a given area in the absence of human activity; (Williams et al. 2010*a*, *b*)) and ensuring the effective restoration and management of existing ponds to maximize opportunities for maintaining and increasing species diversity at the landscape-scale; and (4) creating/restoring ponds for ecosystem service measures for land and water management. Emerging evidence suggests that this could be one of the most effective means of enhancing landscape-scale freshwater biodiversity, but to maintain their long-term contribution, management interventions may be required (Williams et al. 2020). However, it is important to recognize that ponds for ecosystem service purposes such as sediment retention or to attenuate flood flows may not always provide suitable conditions for biodiversity provision (Williams et al. 2020).

Key research questions.—

1. Where are the most ecologically important ponds at national and international scales?
2. How does pond creation and management affect biotic communities at local and landscape scales in different environmental settings?
3. How can we best conserve pondscapes in anthropogenically dominated landscapes?
4. What are the mechanisms required to better incorporate ponds into national and international environmental policy and legislation?

Conclusion

Large knowledge gaps remain in our understanding of pond ecosystems. Yet, it is clear that ponds can benefit society and wildlife by providing habitats that support significant freshwater and terrestrial biodiversity across a range of landscapes, while also providing ecosystem services required by society. Although ponds have received less research attention than other freshwater habitats to date, there is an increasing community of researchers and practitioners interested in pond ecology and conservation and a rapidly increasing awareness of the importance of ponds by society. This paper has highlighted some of the major themes and provides key questions for future pond research, which aim to address existing knowledge gaps and increase fundamental and practical understanding of pond ecology. However, to continue to progress interest, knowledge and awareness of pond ecosystems, international collaboration, and commitment among researchers and end-users is required. A better understanding of pond ecosystems will benefit society and wildlife by enabling more effective research-led conservation and management of pondscapes, facilitating their inclusion in environmental policy more clearly while simultaneously addressing many of the threats driving the decline in global freshwater biodiversity.

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