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The ecological role of permanent ponds in Europe: a review of dietary linkages to terrestrial ecosystems via emerging insects

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Abstract :

Permanent ponds are valuable freshwater systems and biodiversity hotspots. They provide diverse ecosystem services (ESs), including water quality improvement and supply, food provisioning, and biodiversity support, despite significant pressure from multiple anthropogenic stressors and the impacts of ongoing global change. However, ponds are largely overlooked in management plans and legislation, and ecological research has focused on large freshwater ecosystems, such as rivers or lakes. Protection of ponds is often insufficient or indirectly provided via associated habitats such as wetlands. This situation is likely exacerbated by the lack of a full-scale understanding of the importance of ponds. In this review, we provide a detailed overview of permanent ponds across Europe, including their usages and the biodiversity they support. By discussing the concepts of pondscape and metacommunity theory, we highlight the importance of connectivity among and between ponds and identified fluxes of emerging insects as another ES of ponds. Those insects are rich in essential nutrients such as polyunsaturated fatty acids (PUFAs), delivered through them to the terrestrial environment; however, the extent and impact of this ES remains largely unexplored. Several potential stressors, especially related to ongoing global change, that influence pond diversity and integrity are discussed. We provide our insights on future pond management. Adaptive measures, taking into account the pond system per se within the pondscape, are the most promising to mitigate the loss of natural ponds and restore and conserve natural small waterbodies as refuges and diversity hotspots in increasingly urbanized landscapes.

Keywords : aquatic insects, biodiversity, dietary subsidies, emergence of insects, pondscape, small waterbodies

1. Introduction

Ponds are found across multiple landscape types, often occurring in high numbers which surpass those of lakes or rivers. Despite this, they have been historically overlooked by research focusing on larger aquatic ecosystems. Since ponds share many characteristics with shallow lakes, wetlands, or more region-specific ecosystems (e.g., vernal pools, billabongs), their structural distinction is often unclear. However, certain features can help to distinguish ponds from other standing water bodies (Søndergaard et al. 2005; Richardson et al. 2022). There is a long history of debate around the definition of ponds which continues to the present (Richardson et al. 2022). Ponds were frequently defined as small and shallow, natural or artificial standing water bodies, which can contain water permanently or fall dry occasionally (Biggs et al. 2005; De Meester et al. 2005). Some much larger water bodies were also sometimes considered as ponds, for instance, many man-made and shallow fish ponds in some European countries (e.g., Austria or the Czech Republic) cover many hectares (Lhotský 2010). These should, according to a recent publication, not be referred to as ponds but as shallow lakes (Richardson et al. 2022). A maximum depth of 5 meters and a surface area of no more than 5 hectares were proposed to classify a pond. Characteristics that were also included within this study are the aphotic zone, which is typically absent in ponds unless they are very turbid, and macrophytes, which can grow throughout the entire water column (Biggs et al. 2005) should cover no more than 30% of the water body (Richardson et al. 2022).

Ponds are not isolated systems. They are strongly linked to other aquatic systems and their surrounding terrestrial environment. One of the most important linkages between ponds and their terrestrial surroundings is the export of dietary energy from ponds to the associated terrestrial environment via emerging insects. Within this review, we incorporate both the historical background of ponds in the landscape and novel insights on their contributions to export of energy and essential biomolecules, investigating: the publication bias despite the abundance and ecological importance of ponds (Section 2); the importance of pond biodiversity in relation to pond connectivity within the pondscape (Section 3); the influence of stressors on the local and regional scale of ponds in the pondscape (Section 4); the effect of emerging insects on the terrestrial environment and the role of this ES (Section 5); and perspectives and future challenges especially regarding ongoing global change (Section 6).

2. Ponds - ubiquitous but often overlooked systems

Present in all biogeographical regions, ponds are heterogeneously distributed in the landscape, with densities that decrease from arctic and boreal regions towards the tropics (Verpoorter et al. 2014). A global assessment suggested that the number of natural ponds with a surface area of 0.1-1 ha exceeds 277 million and a total area of 692,600 km^2 is covered, representing 91% of standing freshwater bodies worldwide and 16% of their surface area (Downing et al. 2006). In Europe, estimates are lacking for most countries. However, there are some data for ponds between 0.01 ha and 5 ha in size in Switzerland (32,000 ponds; Oertli et al. 2005), Denmark (120,000 ponds; Søndergaard et al. 2005) and Great Britain (size: 0.0025 ha - 5 ha; 400,000 ponds; Biggs et al. 2005). For Austria (>25,000 standing waters larger than 0.025 ha; BMLRT 2021) and Ireland (12,206 freshwater lakes, mostly smaller than 1 ha; Kristensen and Globevnik 2014), studies on small water body abundances have not exclusively focused on ponds. The reliability of these high estimates has been questioned (Biggs et al. 2017), considering changes in the number of small water bodies over time (Pekel et al.

2016).

Despite their wide distribution, high abundance, and distinctiveness, smaller-scale ecosystems, such as ponds, brooks or springs are underrepresented in the scientific literature (Oertli et al. 2002; De Meester et al. 2005; Cantonati et al. 2021) and excluded from management plans (Biggs et al. 2017). A literature search for “ponds” returns three times fewer results than “lakes” and six times fewer results than “rivers/streams” (Figure 1). A potential confounding factor might be the inclusion of “ponds” in other classifications, due to the aforementioned overlaps in definitions, thus leading to insufficient clarity regarding the contents of the research. This is problematic since research on ponds is hindered if varying definitions complicate literature searches for previous studies. A straightforward approach during the development of protection policies would certainly also benefit from a common definition, which very recently has been proposed in the aforementioned Richardson et al. (2022) publication.

Lacking a full-scale understanding of the ecological value of ponds might be one of the reasons for the continuous degradation and decline of ponds in anthropogenic landscapes (Oertli 2018). Recent studies on pond management and protection have improved their conservation status in some European countries (Oertli et al. 2005; Boix et al. 2012; Labat et al. 2022). Awareness of the ecological value of ponds has greatly increased in recent years (Oertli et al. 2009; Oertli and Parris 2019), as pointed out by many studies on different pond types, such as urban ponds (Hassall 2014; Hill et al. 2017), farm ponds (Lewis-Phillips et al. 2020) or even garden ponds (Hill et al. 2015). However, ponds remain excluded from key freshwater management strategies, both at national and continental levels. For example, the European Water Framework Directive (WFD; Council of the European Communities 2000) only considers standing water bodies larger than 50 ha, whereas the European Habitats Directive (Council of the

European Communities 1992) only defines two types of ponds that should be protected, namely “Mediterranean temporary ponds” and Irish “Turloughs” (Hill et al. 2018; Oertli 2018). In some cases, ponds are indirectly protected by being included in association with wetlands under the Ramsar convention (Kingsford et al. 2021), which leads to enhanced protection despite not being properly named in conservation plans. We argue that the WFD and Habitats Directive should be adapted to include all permanent and temporary ponds rather than relying on indirect protection from associated habitats. Thus, their ecological importance in the rapidly changing landscapes of Europe would be better acknowledged, and monitoring of their status in response to ongoing global change improved.

3. Intrinsic biodiversity of ponds and "the pondscape"

Despite their small size in comparison to other water bodies, ponds constitute biodiversity hotspots, both in terms of community composition and functional traits, and are vital for a wide range of rare and protected species (e.g. Oertli et al. 2002; Williams et al. 2004; EPCN 2008; Céréghino et al. 2014). These small but valuable ecosystems host many critically endangered taxa, including emblematic "flagship groups" of wetland biodiversity, such as amphibians, dragonflies and aquatic plants (Sahlén et al. 2004; Semlitsch et al. 2015; Law et al. 2019). The high biodiversity generally associated with ponds is related to their particular structural and biotic features, such as rich ecotone zones and complex interactions with the surrounding terrestrial environments (Céréghino et al. 2014; Bolpagni et al. 2019). A large part of these cross-ecosystem interactions can be attributed to species which require both environments to complete their life-cycle, such as emerging aquatic insects (Schriever et al. 2014; see Section 4). These act as a vector for dietary energy (as measured in lipids), exporting essential molecules from the aquatic into the terrestrial environment (see Mathieu-Resuge et al. 2021).

3.1 Characterization of "the pondscape" and its implications for biodiversity

Pond size is often highlighted as one of the main determinants of pond species diversity (Oertli et al. 2002; Kadoya et al. 2004; Hill et al. 2015). Like other aquatic habitats, ponds might also be subject to the species-area effect in this regard (Dodson et al. 2000). Likewise, pondscapes are mainly characterized by the size and density of ponds, along with surrounding land use and pond connectivity (Boothby 1997; Fang 2011; Jooste et al. 2020). However, the role of pond size in shaping biodiversity can be difficult to assess as several other environmental (e.g., depth, hydroperiod, and connectivity; Carchini et al. 2007; Hamer et al. 2012; Tornero et al. 2016) and biotic factors (e.g., fish presence and predation, presence of macrophytes; Pearman 1995; Semlitsch et al. 2015; Kolar and Boukal 2020) may also influence species richness and the community composition of ponds within the pondscape. The biodiversity within pondscapes increases with the diversity of environmental factors and landscape heterogeneity by enhancing the number of ecological niches available to species and metapopulations (Williams et al. 2004; Boix et al. 2012; Oertli and Parris 2019). A diverse mosaic of ponds provides a good variety of characteristics at the landscape scale, and is crucial to promote and maintain biodiversity at the regional level (Oertli et al. 2002; Goertzen and Suhling 2013; Oertli and Parris 2019). In urban environments, species richness is mainly affected by artificial barriers (e.g., roads, buildings), especially in densely populated areas, and by the reduction of, and connection to, natural areas (Oertli and Parris 2019).

Since metacommunities largely depend on the potential to move between interconnected aquatic habitat patches, enhancing connectivity within the pondscape will promote species dispersal and ultimately may increase its biodiversity (Oertli and Parris 2019). The idea of pondscapes comes hand in hand with the metacommunity concept. Metacommunity refers to a set of local communities connected through spatial dispersal. The metacommunity concept incorporates the importance of local processes and regional dispersal effects into four main mechanisms that act alone or in interaction within a habitat: species sorting, mass effects, patch dynamics, and neutral processes (Leibold et al. 2004). The need for pond connectivity poses unique management challenges at the landscape scale: the aim should be an integration of small water bodies into densely human-populated landscapes.

3.2 Dispersal abilities and life-histories: how life in the pond interconnects with the pondscape

Ponds are inhabited and used by a large set of organisms with widely different life histories and dispersal abilities that define their interactions with the pondscape (Rundle et al. 2002; Massol et al. 2017; Sarremejane et al. 2020). The ability of organisms to disperse is crucial for finding new refuges or more suitable conditions within the pondscape when facing challenges that threaten their individual fitness (e.g., heightened predation pressure, habitat instability, or harsh competition; Baguette et al. 2013). Dispersal can be passive (i.e., the organism relies on a vector to disperse) or active (i.e., the organism can move and disperse by itself) (Bilton et al. 2001; De Bie et al. 2012). Dispersal strategies can change dramatically within the life cycle. Emerging insects are actively dispersing organisms in their adult stage (Bilton et al. 2001). How frequently and how far organisms move within the pondscape depends mainly on individual (physiological) needs, their sensory organs and environmental conditions. Certain dragonfly individuals (Odonata) have been found to cover large distances from their natal ponds (Conrad et al. 1999), with dragonflies generally being known as rather strong flyers. For instance, as an exceptional case, the globe skimmer (Pantala flavescens) takes advantage of the wind to cross the Indian Ocean (Hobson et al. 2012; Bomphrey et al. 2016). Around 2 km dispersal distances have been recorded for some caddisfly (Trichoptera) species, depending on body size, with larger species dispersing further (Kovats et al. 1996). Particularly for rare species with low dispersal abilities such as certain freshwater beetles (Iversen et al. 2017), connectivity is a major driver ensuring the functioning of the pondscape at metacommunity level (Chase et al. 2020).

3.3 Local and regional diversity

With high variability in their physicochemical characteristics and an intrinsically changing spatiotemporal distribution within the terrestrial landscape, ponds are good examples of systems hosting metacommunities which are connected, in part, via food webs (Wilbur 1997; De Meester et al. 2005). Spread across a wide range of geographic and environmental gradients with generally small catchment areas, ponds typically reflect local variation in geology, hydrology, climate and vegetation and can harbor a proportionally higher species richness than larger catchments of lakes and rivers, where environmental conditions are more uniform (Biggs et al. 2005; Davies et al. 2008). Previous studies from Great Britain indicated that when comparing the biodiversity of water bodies within an area of 80 km^2, ponds contributed the most to biodiversity at the regional level, supporting considerably more species, including more unique and rare species, than other aquatic systems (Williams et al. 2004; see also Anton-Pardo et al. 2019). Individually, ponds may contain relatively few species (α-diversity) in comparison to larger freshwater ecosystems. However, at the regional level, variations in the environmental characteristics among ponds create heterogeneity that result in differentiation between local communities (β-diversity), allowing the coexistence of a greater number of species at the regional level (γ-diversity) (Akasaka and Takamura

2012; Horváth et al. 2019).

Ponds also play an essential role in supporting biodiversity in environments considered less favorable for most taxa, such as urban, fragmented and intensively cultivated areas (Hassall 2014; Hill et al. 2017). For instance, urban ponds host diverse communities of aquatic macroinvertebrates (Hill et al. 2015), including dragonflies and damselflies of conservation concern (Goertzen and Suhling 2015) as well as other threatened taxa (Oertli and Parris 2019). Despite their small size and artificial construction, ponds in urban areas (e.g., garden ponds) or post-industrial sites (e.g., gravel pit ponds) can significantly contribute to regional biodiversity (Williams et al. 2004; Davies et al. 2008; Oertli and Parris 2019; Kolar et al. 2021).

4. Ecosystem services of ponds and the influence of stressors

For centuries ponds have been created, modified or managed to provide a variety of valuable ES to humans, for example, being used as a source of drinking water and food (e.g. fish production; Fu et al. 2018) or as a tool for flood control (Pokorný and Hauser 2002; Oertli and Parris 2019). Besides this, they provide ES covering social, environmental, and economic aspects related to climatic regulation, biodiversity support, as well as cultural and recreational activities (Céréghino et al. 2008; Moore and Hunt 2012; Céréghino et al. 2014; Hassall 2014; Figure 2). Even small ponds that were created exclusively to serve human populations play an important role in the ecosystem well beyond that of the individual waterbody (Le Viol et al. 2009) and have vital functions for the human population.

4.1 Land use changes and stressors - influences and consequences

Land-use changes can be highly detrimental to ponds, particularly in landscapes which are heavily impacted by human activities (Declerck et al. 2006; Dudgeon 2010; Wezel, Chazoule, et al. 2013). For instance, biodiversity in farm ponds is especially threatened by the increased demand for land consolidation and changes in pond management over time, including macrophyte removal or the introduction of fish which can lead to increased bioturbation or top-down effects via predation on zooplankton with corresponding increases in phytoplankton biomass (Usio et al. 2017). Land-use change in catchment areas and management activities, such as agricultural drains and dams, may have strong impacts on pond ecosystems, constituting serious threats to their preservation (Wood et al. 2003; M.E.A 2005; Haidary et al. 2013). Changes in land use during the last few centuries resulted in the loss of a proportion of natural ponds as high as 90% in some developed European countries (Oertli 2018), where many ponds have been in-filled and disappeared (Boothby and Hull 1997; Wood et al. 2003). Pond degradation and loss have also been associated with a decrease in grasslands, an increase in agricultural areas (Curado et al. 2011) and, more recently, with urbanization (Hassall 2014). However, the creation of artificial ponds, typically used for livestock water storage, agriculture irrigation, fire protection, erosion control and various industrial processes (Oertli 2018), has partially mitigated the effects of the loss of natural ponds (Williams et al. 1997; Zamora-Marín et al. 2021). Many human-made and, to a lesser extent, natural ponds are now part of the urban landscape and contribute to human well-being. Even though species richness of some taxa, including certain zooplankton and macroinvertebrate groups, may be higher in human-made than in natural ponds, and urban species pools may include some threatened species of conservation interest, the impact of urbanization and improper management practices on pond species diversity is often negative at the local scale (Oertli and Parris 2019).

Eutrophication, sediment disturbance, water scarcity and chemical stressors, such as pesticides, also pose a significant threat to ponds and inland waters in general (M.E.A 2005; Benslimane et al. 2019; Ito et al. 2020). Fish ponds in particular often display high eutrophic levels following the addition of manure and other fertilizers. Nutrient inputs can occur via water-inflow or directly from the surrounding terrestrial ecosystems (Declerck et al. 2006; Wezel, Arthaud, et al. 2013; Wezel, Chazoule, et al. 2013; Francová et al. 2019). According to Rosset et al. (2014), eutrophic or even hypertrophic ponds can host high biodiversity, as many communities are adapted to high nutrient levels, but climate warming shifts naturally eutrophic ponds towards hypertrophic, which further leads to homogenization of pond networks that are dominated by hypertrophic ponds.

Another emergent challenge concerns the changes in the natural hydrological regimes of inland water bodies, as a result of climate change. Ponds are generally small, and many rely primarily on rainfall for their water supply, which makes them highly vulnerable to climate change (Winter 2000; Woodward et al. 2010; Davis et al. 2013). The hydrological state of ponds is directly influenced by climate, with a high sensitivity to precipitation, evaporation and snowmelt, especially but not exclusively in mountainous environments (Lee et al. 2015). Climate change projections estimate an overall reduction in pond water levels, shorter hydroperiods and transitions from permanent to intermittent ponds during the 21st century (Lee et al. 2015). At its most intense degree, hydrological stress can cause the disappearance of ponds, particularly at high elevations and in arid regions (Davis et al. 2013). Additionally, decreasing precipitation and increasing evaporation following global change are expected to increase salinization in lakes in some regions (Jeppesen et al. 2020), which certainly also holds true for other freshwater systems such as ponds (Cunillera-Montcusí et al. 2022).

Stressors may not only cause species losses but can also change the functional roles of key persisting taxa, such as macroinvertebrates. Thus, it is reasonable to assume that the effects of multiple interacting stressors on the diversity and structure of communities may strongly affect critical ecosystem functions and pond ES, as already observed in streams (Burdon et al. 2020).

4.2 Stressors on the local and regional scale

How stressors influence ponds in the pondscape largely depends on their mode of action and the extent of their impact (Figure 3). While some of them are local (e.g., land consolidation and urbanization), others extend over large spatial scales (e.g., climate change associated stressors), influencing multiple ponds and interfering with the flux of aquatic and semi-aquatic organisms (Hanashiro et al. 2019; Chase et al. 2020; Voelker and Swan 2021). Recent advancements in metacommunity theory provided answers to some of the interplays between local and global stressors influencing ecosystem patches such as ponds, linking abiotic filtering on communities with dispersal capabilities and limitations (Hanashiro et al. 2019; Chase et al. 2020; Voelker and Swan 2021). In summary, the effects of stressors across the pondscape depend on the ability of organisms to either tolerate (abiotic filtering) or evade stressors (dispersal processes). Therefore, stressors expanding past the tolerance and dispersal range of an organism are likely to induce severe effects and may even lead to local extinctions and drastic diversity reductions (Relyea 2005; Beketov et al. 2013). This is particularly problematic as once key taxa have been removed from the regional species pool following filtering, the local and regional recovery of the biodiversity, even after stressor mitigation, may not be possible due to the absence of key dispersers (Voelker and Swan 2021). As aforementioned, connectivity between ponds is a critical determinant of biodiversity in ponds. Provided that connectivity is maintained, multiple local stressors resulting from anthropogenic activity and landscape management practices may even increase β-diversity to some extent by creating a gradient of environmental conditions that promote the coexistence of different taxa (De Meester et al. 2005; Chase et al. 2020). This phenomenon has been coined "biotic differentiation" (Chase et al. 2020). By contrast, wide-ranging stressors, such as spread out local management practices or climate-related stressors, or stressors benefiting tolerant and generalist species over specialists, may lead to biotic homogenization and a decrease in β-diversity (Socolar et al. 2016; Chase et al. 2020; Voelker and Swan 2021).

4.3 Management approaches

Effective management can play a key role in reducing the effects of stressors and in improving the overall ecological status of ponds (Figure 3). Restoration strategies to recover natural pond structure and functioning can range from the more intensive, such as dredging to remove sediments (Sychra and Adámek 2011; Jurczak et al. 2018), to simpler actions, such as riparian vegetation removal, to increase light availability and decrease excessive leaf litter input (Janssen et al. 2018). The removal of fish (e.g. benthivorous carp) that increase bioturbation can allow sediment to settle and improve macrophyte growth (Roberts et al. 1995; Matsuzaki et al. 2007). Additionally, measures taken to decrease the trophic status of ponds can increase microhabitat heterogeneity and enhance macrophyte-richness (Sayer et al. 2012). Post-dredging, measures should be taken for longer term water quality improvement (Pokorný and Hauser 2002), such as the inoculation of ponds with pioneer green algae (e.g. Characeae) which has demonstrable benefits for water quality by regulating turbidity and phytoplankton growth (Crawford 1979). Regular high-resolution monitoring is indispensable for appropriate management policies, and can be more easily achieved with the support of modern technologies, improving accuracy and efficiency. The use of satellite imaging (Clark et al. 2017) or environmental DNA (Harper et al. 2019) can help monitor the spread of invasive species and facilitate environmental impact assessment, such as ecological responses to eutrophication. Policy-based solutions that consider pondscapes as management units and seek their implementation as sustainable drainage systems in urban planning (Charlesworth 2010) and natural flood plains (Collentine and Futter 2018) are likely to positively impact ponds. Finally, these pond management solutions may be improved from a societal standpoint, for example, focussing on measures which compensate farmers for maintaining biodiverse farmland ponds. The creation of public engagement programs to reach a broader public audience can increase awareness of the value of ponds, particularly of the ecosystem services they provide, and improve pond stewardship.

5. Effects of emerging insects on terrestrial environments - an understudied ecosystem service of ponds

The small size of ponds results in high perimeter-to-area ratios that enhance the relative importance of cross-boundary processes between ponds and their surrounding terrestrial environment. Boundaries between ponds and their environment are critical sites for the exchange of organisms, energy, and nutrients, which establish important linkages between aquatic and terrestrial ecosystems (Polis et al. 1997; Bartels et al. 2012; Schindler and Smits 2017). With both aquatic and terrestrial life stages, semi-aquatic organisms can be vectors of energy and nutrients and can contribute to the functioning of the terrestrial ecosystem.

The linkage of the aquatic system with the surrounding terrestrial environment via emerging insects constitutes an important flux of dietary energy and nutrients for recipient terrestrial food webs. The emergence of aquatic insects is one of the most important and extensively studied fluxes from aquatic to terrestrial food webs (see

Schindler and Smits 2017), however, those studies focus on larger water bodies and in-depth research for ponds is lacking.

Furthermore, emergent insects can affect ecosystem functioning and wider ecosystem services (e.g., pollination, soil fertilization, or pest control) in adjacent terrestrial environments. For example, the high emergence of predatory dragonflies can lead to reduction of terrestrial pollinators (Knight et al. 2005), but also of pests (Sathe and Shinde 2008). By feeding on pollen and nectar, adult Diptera within the dipteran families Stratiomyidae and Syrphidae contribute to plant pollination in adjacent terrestrial ecosystems (Courtney and Merritt 2009; Walton et al. 2021).

The interplay between trait diversity in emerging insects and the associated ecological processes is often complex. However, ultimately, its understanding will provide new insights into the functional roles of these organisms and help pond management and provisioning of pond ecosystem services beyond aquatic boundaries.

5.1 Export of insects from ponds to terrestrial systems

The annual export of insect biomass from ponds to the surrounding terrestrial environments is rarely quantified. Reported values suggest high variability in insect emergence across ponds, which can range from 0.04 to 3.32 g C m^{-2} yr^{-1} (Leeper and Taylor 1998; Stagliano et al. 1998; Schriever et al. 2014), comparable to those reported in lakes (0.07–1.23 g C m^{-2} yr^{-1}) and river ecosystems (0.42–3.12 g C m^{-2} yr^{-1}) (Gratton and Vander Zanden 2009). The large range in insect biomass exports from ponds is not surprising, given that the intrinsic features of ponds, such as pond size and depth, microhabitat availability or physicochemical parameters, are highly variable (Bennion and Smith 2000), influencing the community composition and abundances of taxa in the ponds. The often higher productivity (Bennion 1994) and the lack of predatory fish in many ponds (Dorn 2008) could explain the higher proportional exports of aquatic insects in comparison to individual lakes and rivers.

Insect phenology controls the time of emergence and leads to spatiotemporal fluctuations that tend to have pronounced seasonal patterns, often differing from the dynamics of terrestrial insects (Nakano and Murakami 2001). The number and timing of emergence peaks are determined mainly by temperature, light and food availability (Ivković et al. 2013; Raitif et al. 2018). Both interannual weather variation and environmental heterogeneity affect the distribution of emergence throughout the year (Anderson et al. 2019). Pond size is also expected to be a strong determinant of overall insect emergence, where a tenfold increase in pond radius may cause a tenfold increase in the fluxes of insects to land (Gratton and Vander Zanden 2009; Schriever et al. 2014). In addition to pond size, pond productivity is another likely key factor driving insect emergence, with almost twice as many emerging in hypereutrophic compared to mesotrophic conditions in a mesocosm experiment (Scharnweber et al. 2020). The high irradiance associated with shallow depths promotes the development of submerged aquatic vegetation that may provide food sources and refuge for macroinvertebrates, thus increasing insect emergence compared to macrophyte-free zones in open water (Stagliano et al. 1998; Lewis-Phillips et al. 2020). Biotic interactions within ponds can also affect insect emergence fluxes. For example, the presence of invertivorous fish has been reported to cause a 39% decline in insect emergence (Wesner 2016).

The colonization distance of actively dispersing insects is limited to their dispersal traits (see Section 3.2) and environmental characteristics of the recipient terrestrial ecosystem. Overall, the majority of insect biomass deposition is expected within the first 100 meters from the shoreline (Gratton and Vander Zanden 2009; Martin-Creuzburg et al. 2017). Steep topography or more open habitats around the pond can constitute a strongly limiting factor for Diptera dispersal (Carlson et al. 2016).

Conversely, riparian forests that provide shade and protection from the wind have been linked to higher dispersal distances in semi-aquatic insects, compared to more open agricultural landscapes (Carlson et al. 2016).

The magnitude of the effects of semi-aquatic insect fluxes on adjacent terrestrial systems is noticeable at small spatial scales and on a high fraction of the terrestrial surface at the landscape level (Bartrons et al. 2013). Therefore, studies focused on the variability of insect emergence and their spatiotemporal dispersal into the adjacent environments are key to understanding the processes whereby ponds and other small water bodies affect terrestrial ecosystems.

5.2 Impact of aquatic insect subsidies on terrestrial consumers and food webs

Similarly to observations in lakes and streams (Gratton et al. 2008; Sullivan and Manning 2019), terrestrial and pond nutrient cycles are expected to be linked. On land, energetic inputs of emerging insects from aquatic ecosystems can surpass local secondary production in low to moderately productive terrestrial ecosystems, as shown for streams and lakes (Bunn et al. 2006; Gratton and Vander Zanden 2009). Either as prey or detritus, aquatic insects constitute an important resource for a wide variety of terrestrial consumers in riparian zones, for example comprising up to 80% of beetle diets (Paetzold et al. 2005), 77% of spider diets (Gergs et al. 2014) and 40% of bird diets (McCarty and Winkler 1999), along streams. Emerging semi-aquatic insects can provide a key additional food resource for terrestrial consumers during winter, when terrestrial productivity is generally low (Nakano and Murakami 2001; Wesner 2010). Further evidence of the importance of these energy subsidies can be found in terrestrial predator populations feeding on aquatic insects, which are often higher in abundance and biomass than those consuming terrestrial prey alone (rivers: Henschel et al. 2001;

streams: Iwata et al. 2003; Marczak and Richardson 2007). There is a lack of knowledge on the contribution of pond-derived resources for terrestrial predator diets, with most of the aforementioned studies focused on larger aquatic ecosystems. However, as similar aquatic insect taxa emerge from ponds as from other water bodies it can be assumed that aquatic insects are integrated into terrestrial food webs surrounding ponds. Also, similar recipient consumer communities (e.g. spiders, lizards, birds, bats) may be present in the riparian zone of lakes, rivers and ponds.

Semi-aquatic insects are sources of essential nutrients, such as polyunsaturated fatty acids (PUFA), including highly unsaturated fatty acids (HUFA) (Gladyshev et al. 2009), which are scarce at the base of terrestrial food webs (Hixson et al. 2015; Ruess and Müller-Navarra 2019). Feeding on aquatic insects, which are richer in omega-3 PUFAs than strictly terrestrial insects, can improve the fitness of riparian consumers and help them meet nutritional demands (Twining et al. 2016; Fritz et al. 2017; Twining et al. 2018). Migrating songbirds use aquatic insects to refuel during migration (MacDade et al. 2011). Currently, many species of aerial insectivores, which rely on the consumption of emerging aquatic insects along their life cycle, are experiencing unprecedented declines in some continents, in part due to decreased prey abundance (Spiller and Dettmers 2019). Additionally, insects are a key food source for several bird species which are not generally insectivorous during the breeding season or to enrich their diet (Yanega and Rubega 2004; Twining et al. 2021).

Semi-aquatic insects may differ significantly in fatty acid content, partly due to taxonomic differences (Lau et al. 2012; Martin-Creuzburg et al. 2017) and differences in their feeding strategies during the larval phase (Guo et al. 2018; Kühmayer et al. 2020). Although the factors driving the variability of PUFA exports to terrestrial systems by emerging insects have been studied in lakes (Borisova et al. 2016; Martin-

Creuzburg et al. 2017), rivers (Chari et al. 2020) and mesocosms (Scharnweber et al. 2020), little is known about the driving factors in ponds. Thus, studying PUFA fluxes and dietary exports from ponds is pivotal for an integrative assessment of their role as providers of high-quality nutrients to terrestrial food webs.

Habitat heterogeneity within and among ponds may also affect pond dietary exports, as it promotes asynchronies in the timing of the emergence pulses of semi-aquatic insects by modulating the life history of their larvae (Schriever et al. 2014). This potentially benefits mobile terrestrial consumers (i.e., bats or birds), which can follow resources in the landscape, whereas less mobile consumers, such as ants or spiders, may benefit more from local time-prolonged emergence (Anderson et al. 2019). On the other hand, habitat homogenization may promote more synchronous pulses of insect emergence, shortening the provision of aquatic subsidies to mobile terrestrial consumers (Schindler and Smits 2017).

Through their effects on predator populations, pond subsidies can indirectly affect the broader terrestrial ecosystem (Leroux and Loreau 2008). If predators switch from terrestrial to aquatic prey, local terrestrial prey may increase in abundance following the relief in predatory pressure (Sabo and Power 2002; Baxter et al. 2005). Alternatively, if aquatic prey provides a complementary diet source alongside terrestrial prey, bolstered predator populations may exert a more significant top-down pressure on local prey. Aquatic-subsidized spiders have been shown to suppress terrestrial herbivores in temperate rivers (Henschel et al. 2001), tropical streams (Recalde et al. 2016), and rice paddies (Radermacher et al. 2020), but evidence from ponds is still lacking. The indirect interactions arising from shared predation across pond-terrestrial boundaries can substantially affect the dynamics and stability of recipient terrestrial communities. For example, asynchronies in the availability of resources used by generalist predators are expected to promote community stability. Maintaining the asynchronies between terrestrial production and aquatic fluxes and between the pulses of peaks of the emergence of semi-aquatic insects across the landscape might be critical to increase community stability and reduce local extinctions (McCann and Rooney 2009).

6. Perspectives and future challenges

Considering the importance of ponds as biodiversity hotspots, the ecosystem services they deliver and their vulnerability to global change, it is critical to protect ponds more efficiently and preserve their ecological integrity at both regional and global scales. Small permanent water bodies are exposed to various external stressors that not only impoverish pond biodiversity and reduce their ecological status but also impact crucial ecological contributions of ponds to the adjacent terrestrial ecosystems. This can also affect the provision of high-quality nutrients through the emergence of aquatic insects. However, this influence remains poorly studied, and further collaborative research efforts should focus on different aspects:

1. Climate change and human population growth will increase impacts on freshwater quality and availability (e.g., the need for drinking water). Until now, research efforts have mainly focused on the ecological services provided by ponds at local and regional scales (Oertli and Parris 2019), but have largely ignored continental scales (but see Davies et al. 2008; Epele et al. 2022). Research covering broader temporal and spatial scales (i.e., ecoregions and even continents) and a higher diversity of pond types would allow the identification and clearer definition of different pond types. Specific and common features could be discovered that may inform conservation and management efforts to

preserve the ecological status of these ponds and the valuable ecosystem services they deliver. Collaborative projects on pond research should also consider pondscape heterogeneity as an important factor at a regional scale, promoting the coexistence of different pond types within the landscape and contributing to the conservation of biodiversity (Oertli 2018; Zamora-Marín et al. 2021).

2. Future research (field studies, mesocosm experiments and modeling) should always consider the ponds as a singular system within a bigger context, integrating them throughout the management process in landscape scale approaches. In a multi-faceted approach, knowledge of the entire pondscape should be generated. Ponds are still insufficiently protected and are usually not included in water monitoring programmes, unlike other surface freshwater habitats. Pond attributes are strongly correlated to the landscape features where they occur and subject to the effects of land use in their surroundings (Declerck et al. 2006). Their effective conservation requires robust knowledge of the exact ecological contributions of these small freshwater habitats. Including the pond types present within the landscape, differing in their structural features (e.g., farm ponds, small reservoirs, stormwater ponds, gravel pit ponds and fish ponds) and their origin and substrate (near-natural vs artificial ponds) would ensure an adequate representation of the taxa inhabiting ponds. Finally, large-scale research would allow to cover a representative sample of permanent ponds occurring along broad geographical, altitudinal and environmental gradients (e.g., alpine vs lowland systems, forest vs steppe systems, continental vs coastal regions, wet vs arid zones), ensuring a better understanding of patterns in pond ecosystems and biota across continents (Céréghino et al. 2008). Surroundings of

ponds should also be included in conservation and management strategies by preserving green spaces and limiting the construction of artificial structures that pose obstacles to species dispersal among sites (Oertli and Parris 2019) and would thus inhibit potential positive effects of pondscape management. Furthermore, appropriate land management would also be key to preserve the pond ecological state since pond attributes are strongly correlated to the landscape features where they occur and are subject to the effects of land use in their surroundings (Declerck et al. 2006).

3. To achieve these goals, we propose to develop specific recommendations and interventions for different ponds based on their type (e.g., permanent or temporary), successional stages and their connectivity to other aquatic ecosystems in order to incorporate pond and landscape variability in pond conservation. This pondscape-based approach, which preserves heterogeneity among pond types and stages of succession, would enhance the overall ecological value and increase species richness at the regional scale (Sayer et al. 2012; Hassall et al. 2016; Hill et al. 2018; Oertli and Parris 2019).

Artificial, near-natural ponds are sometimes suggested as a complementary solution to mitigate biodiversity declines and compensate for declining natural ponds (Deacon et al. 2018). However, this approach should be assessed carefully from a functional and multi-taxa point of view, maintaining desired biodiversity enhancing functional targets whilst creating it. For instance, some intensively managed artificial fish ponds have been reported to act as ecological traps for various taxa, such as dragonflies (Šigutová et al. 2015). Nevertheless, artificial systems can play an important role in protecting rare and endangered freshwater species, for example, in areas with no natural water reservoirs (Sousa et al. 2021).

We also suggest further collaborative international initiatives targeting ponds that include a variety of stakeholders from science, management, policy, and the general public, working together towards a holistic, sustainable base for the conservation and management of ponds. International collaborative research projects are key to assessing the contributions of permanent ponds to biodiversity and ecosystem functioning at larger scales. Within the EUROPONDS project, we aim to contribute to the knowledge about permanent ponds at European scale, especially concerning the dietary energy transfers and export of biomass via emerging insects from small water bodies to their adjacent terrestrial environments, enabling an argumentation for the protection of ponds as valuable sources of essential nutrients of high importance for terrestrial consumers.

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Figure 1: Number of recorded publications per year mentioning the terms "*pond*", "*lake*" and ("*river*" or "*stream*") in the Web of Science database. All publications within the field of Ecology from 1970 to 2021 were included (date of search query: 17.01.2022).

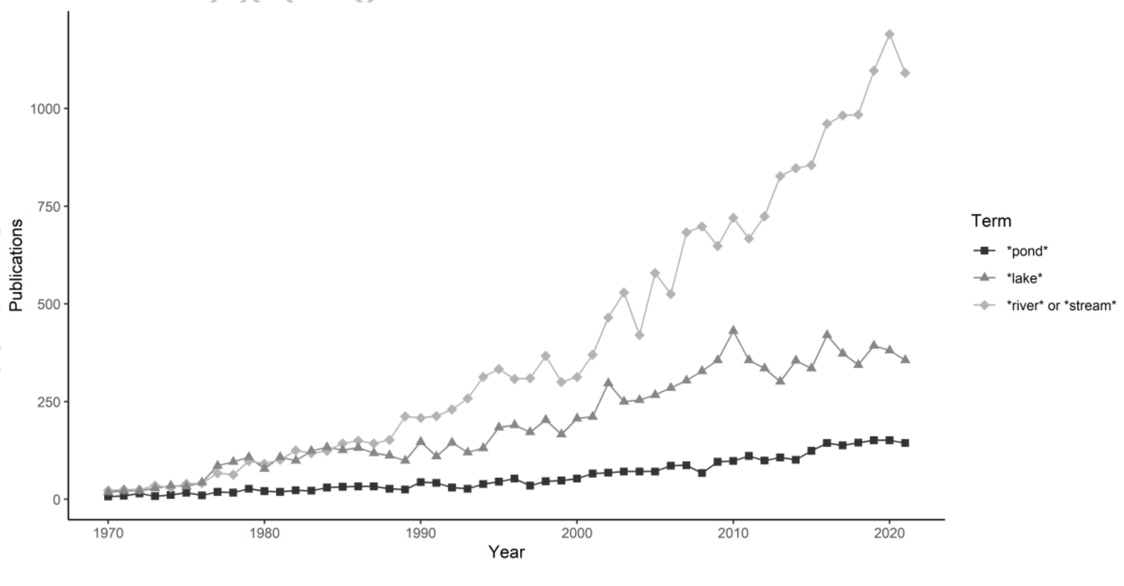


Figure 2: **Schematic overview of pond ecosystem services**. 1. Culture and recreation: recreational activities (see e.g., EPCN 2008; Ghermandi and Fichtman 2015), educational programmes (Ghermandi and Fichtman 2015), wildlife viewing and bird watching (Sebastián-González and Green 2014), enabling of research projects e.g., for schools (Ghermandi and Fichtman 2015); 2. Hydrology: increase groundwater discharge (Cheng et al. 2021), reduce peak runoff rates (Fiener et al. 2005; Krivtsov et al. 2022), control stormwater flow (Moore and Hunt 2012), act as water reservoirs (Fu et al. 2018), erosion control (Fiener et al. 2005); 3. Air quality: filtration and absorption of particulates by vegetation and substrates (Xu et al. 2016; Krivtsov et al. 2022); 4. Gas balance: gas storage through vegetation, burial and sediment accretion (Gilbert et al. 2021), CO2 release: microbial and benthos respiration, production of methane and other greenhouse gasses (GHG) (Malyan et al. 2022); 5. Climate: regulation of microclimate through shading and evapotranspiration, influence on humidity and heat exchange, mitigation of urban heat islands (Steeneveld et al. 2014; Ampatzidis and Kershaw 2020); 6. Food and energy: provision of energy to (terrestrial) consumers via e.g., emerging insects (Schriever et al. 2014), globally used for food production (fish) (Boyd and Tucker 1998); 7. Water quality and supply: improvement of runoff quality (Krivtsov et al. 2022), removal of sediments and heavy metals via sediments and macrophytes (Fiener et al. 2005), carbon sequestration in sediments and plants (Moore and Hunt 2012), water reserves for livestock, irrigation and fire protection (Oertli 2018); 8. Biodiversity: enhance landscape biodiversity (γ-diversity), essential for migration, dispersal and genetic exchange among wild species (Oertli and Parris 2019), biodiversity hotspot especially in anthropogenic areas (Hill et al. 2017), refuges for rare and endemic species, support of semi-aquatic and terrestrial flora and fauna (Usio et al. 2017); 9. Aesthetics: pleasant environments that provide soothing benefits, promote health and well-being (Rey-Valette et al. 2022).

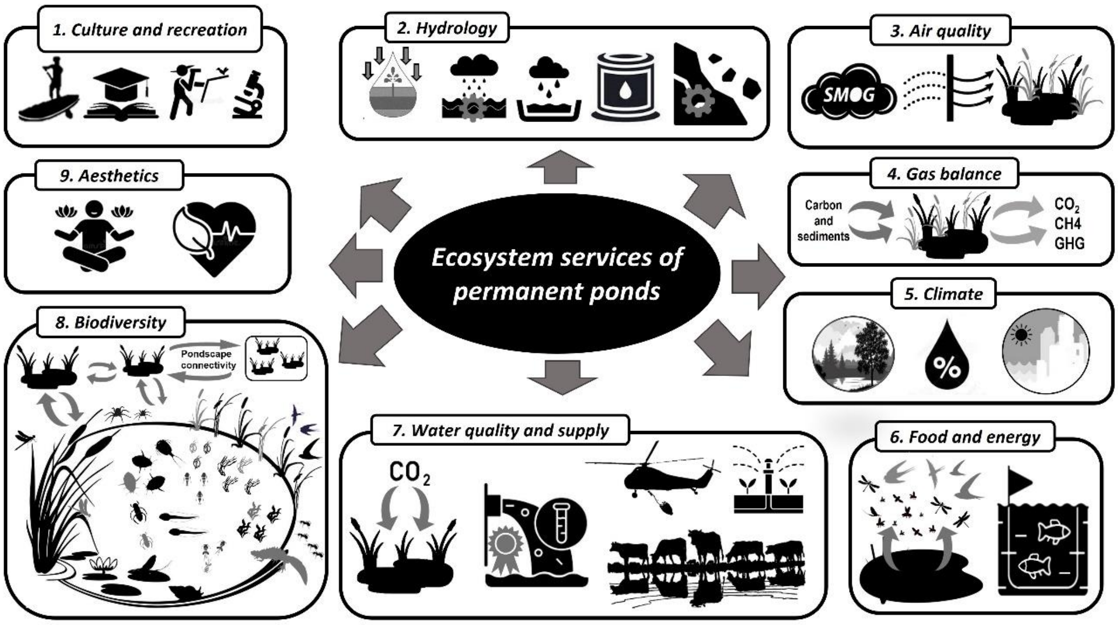
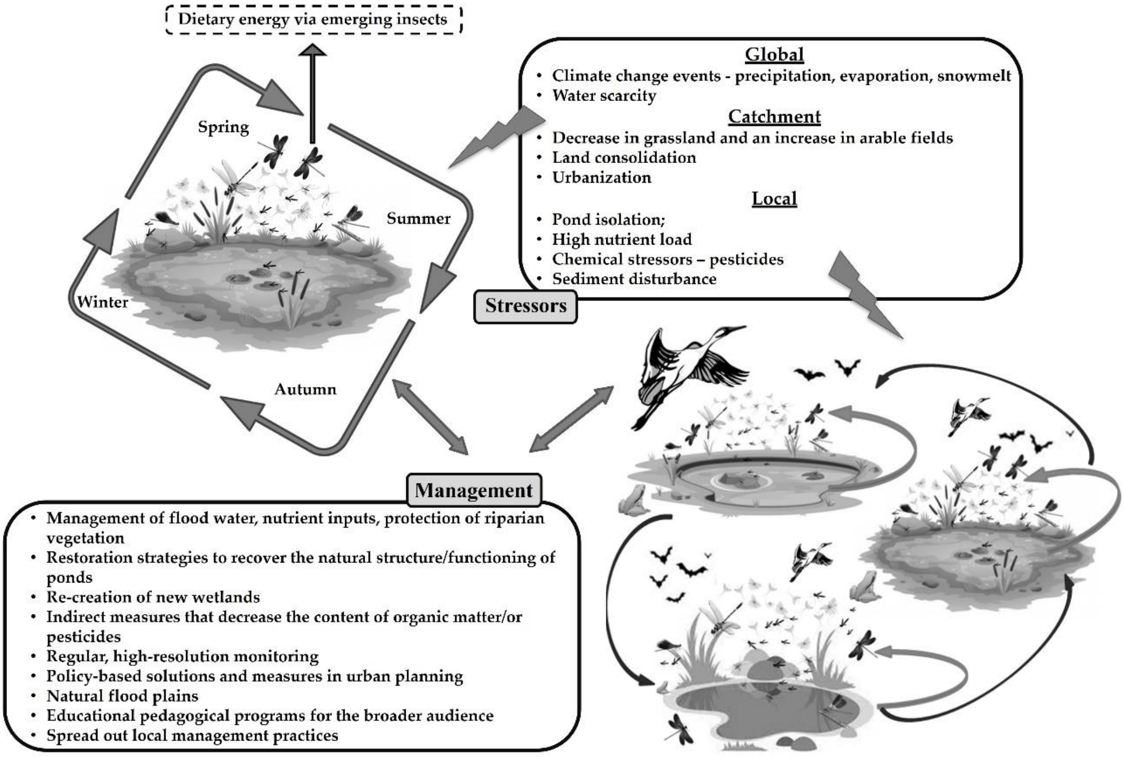


Figure 3: Schematic representation of seasonal dietary energy flow via emerging insects, the stressors influencing the individual pond ecosystems and the pondscape and the management approaches for biodiversity conservation and pond restoration. **Stressors** associated with a) Climate Change: precipitation regime, evaporation and snowmelt changes, water scarcity (Brönmark and Hansson 2002); b) Catchment Area: decrease in grassland and increase in arable fields (Liu et al. 2005), land consolidation (e.g., Yu et al. 2010), urbanization (Holgerson et al. 2018); c) Local processes: pond isolation (Marsh et al. 1999), high nutrient load (Rosset et al. 2014), chemical stressors (e.g., pesticides; Brönmark and Hansson 2002), sediment disturbance (Eggleton and Thomas 2004); **Management approaches**: Management of flood water (Tang et al. 2020), nutrient inputs (Pouil et al. 2019), protection of riparian vegetation (Blinn and Kilgore 2001), restoration strategies to recover the natural structure and functioning of ponds (Davies et al. 2016; Lewis-Phillips et al. 2019), recreation of new wetlands (Moore and Hunt 2012), indirect measures to decrease organic matter and or pesticide content (Peretyatko et al. 2010), regular high-resolution monitoring (Biggs et al. 2005), policy-based solutions and measures in urban planning (Hassall 2014), natural flood plains (Sayer 2014), educational pedagogical programs for the broader audience (Sousa et al. 2016), dispersed local management practices (Hill et al. 2018).


Dietary energy via emerging insects
Spring
Summer
Autumn
Winter
Global
• Climate change events - precipitation, evaporation, snowmelt
• Water scarcity
Catchment
• Decrease in grassland and an increase in arable fields
• Land consolidation
• Urbanization
Local
• Pond isolation;
• High nutrient load
• Chemical stressors – pesticides
• Sediment disturbance
Stressors
Management
• Management of flood water, nutrient inputs, protection of riparian vegetation
• Restoration strategies to recover the natural structure/functioning of ponds
• Re-creation of new wetlands
• Indirect measures that decrease the content of organic matter/or pesticides
• Regular, high-resolution monitoring
• Policy-based solutions and measures in urban planning
• Natural flood plains
• Educational pedagogical programs for the broader audience
• Spread out local management practices