REPORT HYDROLOGY No. 22, 2022

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A literature study and development of hydrological indicators

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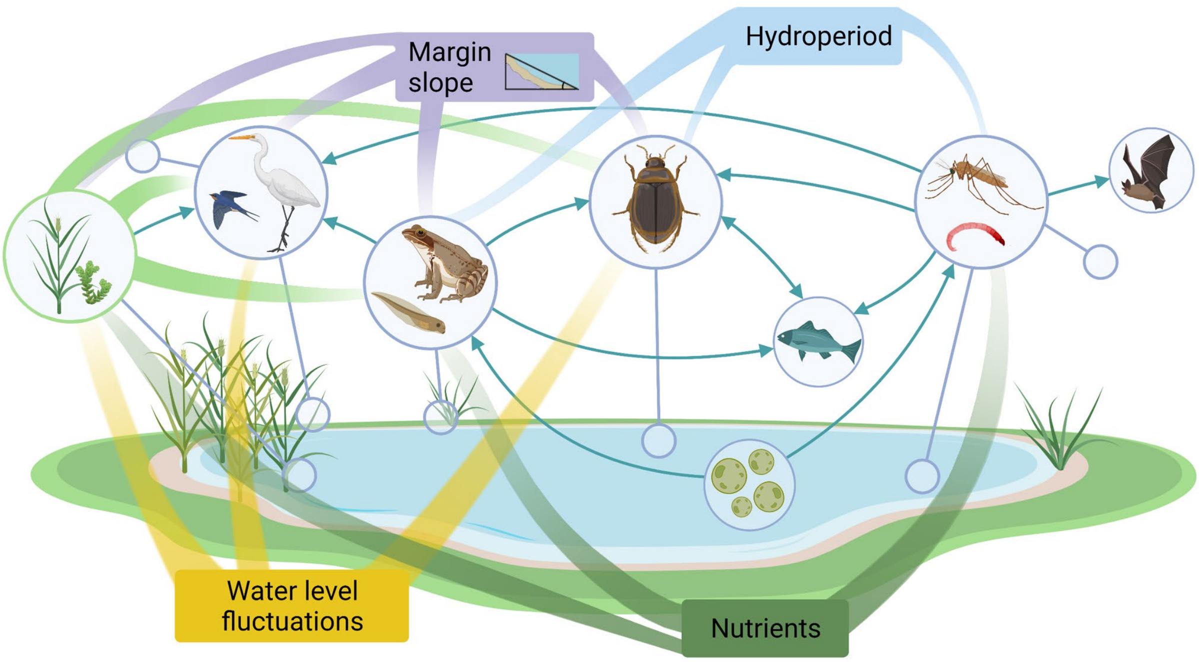

Front:
Figure showing an overview of the effects of hydrological variables on a selection of wetland organisms, as well as interactions between organisms. Figure created with BioRender.com.

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Summary

Wetlands are one of the most species rich environments in Sweden and provide habitat to for example plants, insects, amphibians, and birds. Since the 19th century, expansion and intensification of agriculture and forestry have been associated with extensive drainage of wetlands, resulting in population declines of many wetland-dependent species, and habitat construction and restoration are now important measures for conservation of wetland biodiversity. Hydrology shapes the physiochemical properties of wetlands and is the main driver of wetland community assemblage and species richness. An improved understanding of the effects of hydrology on wetland organisms can thus potentially facilitate optimization of wetland design and management for increased biodiversity. Here, we synthesize current evidence of relationships between hydrology and local scale (i.e. within wetlands) species richness of five groups of wetland organisms: vegetation, chironomids (non-biting midges), dytiscids (diving beetles), amphibians, and birds.

Vegetation plays a key role in wetland ecosystems by providing food and habitat to numerous other organisms, and a complex and diverse vegetation community can provide a fundament for further biodiversity. Due to differences in water level tolerances among plant species, the spatial and temporal variation of wetland vegetation communities is primarily determined by the water regime, and a high species richness can be attained by creating various water depths over small distances, for example by microtopographic variation. Water levels exceeding the tolerance ranges of plant species cause an ecological disturbance and, in accordance with the Intermediate Disturbance Hypothesis, low-amplitude water level fluctuations can thus facilitate species coexistence and promote a high biodiversity. Chironomids, dytiscids, and amphibians have aquatic larval development and are sensitive to desiccation before they transition into adult stages. Their use of wetland habitats is therefore largely determined by wetland hydroperiod (the length of time there is standing water in the wetland), with highest species richness typically in wetlands with long hydroperiods, as they can be utilized also by species with long development times. Most amphibians, however, are very sensitive to predation by fish, and amphibian species richness is therefore generally highest in wetlands with intermediate hydroperiods, where risk of fish presence is lower than in permanent wetlands. For wetland birds, water depth is a key parameter determining accessibility to foraging habitats, and water level fluctuations and topographic variation promote species richness by creating a high spatial and temporal variability of water depths. Further, flooding increases foraging efficiency by increasing soil penetrability and keeping vegetation short, and shallow, temporarily flooded areas are thus especially important foraging habitats for wetland birds.

Though some relationships between hydrology and species richness are similar between organism groups, there is a large variation between species that makes it difficult to predict the effects of hydrology on wetland biodiversity. Further, the effects may vary depending on species interactions, which, in turn, are often affected by hydrology. To facilitate the application of hydrology-biodiversity relationships to conservation work, we suggest using biologically relevant hydrological indicators to quantify aspects of the hydrological regime relevant to biodiversity. The indicators can be used to optimize biodiversity when creating and restoring wetlands, assess anthropogenic impacts, predict effects of climate change, and as tools for further research. In this report, we develop suggestions of indicators based on known relationships between hydrology and biodiversity, including for example indicators related to wetland hydroperiod, amplitude of seasonal water level fluctuations, and slope of wetland margins. In future research, the suggested indicators should be tested against data on species richness in wetlands.

Sammanfattning

Våtmarker är en av de artrikaste miljöerna i Sverige, och de utgör habitat för till exempel växter, insekter, groddjur och fåglar. Sedan 1800-talet har expandering och intensifiering av skogs- och jordbruket lett till omfattande dräneringar av våtmarker, vilket har resulterat i att populationerna av många våtmarksbundna arter har minskat, och anläggning och restaurering av våtmarker är därför viktiga åtgärder för bevarandet av våtmarkers biologiska mångfald. Hydrologi formar våtmarkers fysikaliska och kemiska egenskaper och är den huvudsakliga faktorn som påverkar våtmarkers artsammansättning och artrikedom. En ökad förståelse för hydrologins effekt på organismer i våtmarker har därför potential att bidra till optimering av våtmarkers utformning och skötsel med avseende på biologisk mångfald. I den här rapporten sammanställer vi befintlig kunskap om sambanden mellan hydrologi och lokal (inom våtmarker) artrikedom av fem organismgrupper i våtmarker: vegetation, fjädermyggor, dykarbaggar, groddjur och fåglar.

Vegetation spelar en nyckelroll i våtmarkers ekosystem genom att bilda habitat och utgöra en födoresurs för ett flertal andra organismer, och ett komplext och artrikt vegetationssamhälle kan utgöra en grund för vidare biologisk mångfald. Eftersom växtarter kan tolerera olika vattennivåer uppstår variationer i våtmarkers vegetationssamhällen framför allt på grund av skillnader i vattenregim, och en hög mångfald kan uppnås genom att skapa en variation av vattennivåer på liten skala, till exempel genom mikrotopografisk variation. Vattennivåer utanför det spann som växter tolererar orsakar en ekologisk störning och vattenfluktuationer med låg amplitud kan därför, i enlighet med 'the Intermediate Disturbance Hypothesis', gynna samexistens av arter och därmed en hög biologisk mångfald. Fjädermyggor, dykarbaggar och groddjur har alla akvatisk larvutveckling och är känsliga för uttorkning innan de når adult form. Deras användning av våtmarker som habitat styrs därför i stor utsträckning av hydroperioden (hur länge det finns vatten i våtmarken), och högst artrikedom finns generellt i våtmarker med lång hydroperiod, eftersom de kan nyttjas även av arter med lång utvecklingstid. Många groddjur är däremot väldigt känsliga för predation av fisk, och högst artrikedom av groddjur återfinns därför ofta i våtmarker med medellång hydroperiod, där risken för fisk är lägre än i permanenta våtmarker. För våtmarksfåglar är vattendjup en viktig parameter som avgör åtkomsten till födosöksmiljöer, och vattennivåfluktuationer och topografisk variation gynnar artrikedom genom att skapa en hög rumslig och temporal variation i vattendjup. Översvämningar kan dessutom öka födosökseffektiviteten genom att göra marken lättare att tränga igenom samt genom att hålla vegetationen låg, och grunda, översvämmade områden är därför extra viktiga födosöksmiljöer för våtmarksfåglar.

Även om vissa samband mellan hydrologi och artrikedom återkommer för flera organismgrupper finns det en stor variation mellan arter som gör det svårt att förutse effekten av hydrologi på biologisk mångfald. Dessutom kan effekten variera beroende på interaktioner mellan arter, som i sin tur också kan påverkas av hydrologi. För att underlätta användningen av sambanden mellan hydrologi och biologisk mångfald i bevarandearbete föreslår vi användandet av biologiskt relevanta hydrologiska indikatorer för att kvantifiera aspekter av den hydrologiska regimen relevanta för biologisk mångfald. Indikatorerna kan användas för att optimera biologisk mångfald vid våtmarksanläggning eller -restaurering, för att bedöma effekten av mänsklig påverkan, förutsäga effekten av klimatförändringar, och som verktyg för vidare forskning. I den här rapporten utvecklar vi förslag på hydrologiska indikatorer baserat på kända samband mellan hydrologi och biologisk mångfald, till exempel indikatorer relaterade till hydroperiod, amplituden av säsongsvariationer i vattenstånd, och strandkantens lutning. Vidare forskning bör testa indikatorerna mot data över biologisk mångfald i våtmarker.

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Glossary

Aerenchyma	Airy plant tissue that allows for gas transportation to and from plant roots
Amphibians	Sv. groddjur, taxonomic group including for example frogs, toads, and newts
Chironomidae	Sv. fjädermyggor, non-biting midges
Coenocline	A sequence of communities along an environmental gradient
Community	A group of species in a common location
Competitive exclusion	Exclusion of a species due to competition
Dabbling bird	Birds that forage either on the water surface, or by tipping forward (but not diving) to forage under water
Disturbance	An event or force causing a perturbation in an ecological system, e.g. a mechanism which removes biomass
Dytiscidae	Sv. dykarbaggar, diving beetles
Exploitative competition	Indirect competition between species utilizing a common resource
Guild	A group of organisms that exploit the same resources, or exploit different resources in a similar way
Habitat connectivity	The degree to how and to which degree different habitat patches are connected, i.e. how easily different organisms can move between patches
Herbivore	An animal consuming plants
Heterophylly	Presence of leaves with different morphology in response to different environmental conditions
Hydroperiod	Number of days there is standing water in a location
(Macro-)invertebrates	Animals that lack a vertebral column (i.e. backbone), for example insects or spiders. Macroinvertebrates refer to invertebrates large enough to see without the aid of a microscope
Macrophytes	Plants that grow in or near water, can be emergent, submerged, or floating. Does not include for example unicellular algae, i.e. microphytes.
Mesic	(As an environment trait) containing moderate moisture
Mesocosm	Outdoor experimental system with controlled conditions
Minerotrophic	(As an environment trait) receives water that has been in contact with mineral soil, e.g. groundwater or stream water
Niche	The role of a species in an ecosystem: both the environmental conditions it requires and its interactions with other species and the abiotic environment
Ombrotrophic	(As an environment trait) receives water only from precipitation
Periphyton	Algae and other microbes growing on submerged surfaces

Productivity	Rate of increase of biomass
Refuge	An area or habitat in which an organism obtain protection from predation
Rhizosphere	Part of soil or substrate directly influenced by root secretions or root-associated microbes
Stomata	Sing. stoma, pores in plant tissues used to control gas exchange
Succession	Directional change in community structure over time
Tadpole	Amphibian larva
Taxa	Sing. taxon, taxonomic units, commonly species or genus
Trophic cascade	Indirect interactions between organisms in a food chain resulting from a change on a trophic level, such as increased abundance of a predator
Trophic interaction	An interaction where one organism feeds on another

1 Background and aim

Wetlands are one of the most species rich environments in Sweden and provide habitats to a wide variety of plants and animals, including for example mosses, invertebrates, amphibians, and birds. Due to expansion and intensification of agriculture and forestry, many wetlands in Sweden were drained mainly during the 19th and 20th centuries, leading to a loss of approximately 25 % of the original wetland area. Wetland losses were greatest in southern Sweden, where 90 % of wetlands were destroyed (Naturvårdsverket, 2019). Due to the extensive habitat loss and degradation, abundance of many wetland species has declined, and almost 16 % of species for which wetlands are important habitats have been registered on the Swedish red list (a regionalized version of the International Union for Conservation of Nature Red List of Threatened Species; https://www.iucnredlist.org/) (Naturvårdsverket, 2021a). Ditching and vegetation overgrowth have the largest effect on wetland species (Naturvårdsverket, 2019), but other factors, such as increased temperature and evaporation, nitrogen deposition, and anthropogenic acidification, are also important (Gunnarsson & Löfroth, 2009). Some wetland types, including rich fens and shoreline wetlands, are more affected by habitat degradation than others (Naturvårdsverket, 2019).

Since the late 20th century, wetland losses have diminished, and great efforts have been made to construct and restore wetlands to improve nature values and ecosystem services. Wetlands are constructed or restored with a range of different aims, including for example improved nutrient or water retention, flow regulation, carbon sequestration, or biodiversity, and habitat multifunctionality has become the aspiration of many wetland projects. Habitat construction and restoration is an important tool in nature conservation, and the recent increase in wetland area has already improved the population trends of some wetland organisms, such as amphibians (Naturvårdsverket, 2021a). However, we need to improve our understanding of what factors are important for biodiversity in wetlands to be able to (i) assess effects of anthropogenic impacts, (ii) predict effects of climate change, and (iii) optimize wetland construction and management for increased biodiversity.

Hydrology is widely recognized as one of the most important factors shaping wetland communities, and the importance of variation in flow regimes and water levels, as well as abundance of different wetland types and successional stages in the landscape, have previously been highlighted (Naturvårdsverket, 2017). Further, Rolls et al. (2018) synthesized information on the effects of hydrology on biodiversity across different spatial scales, aiming to draw general conclusions about freshwater habitats. They highlighted three different mechanisms by which hydrology affects biodiversity: (i) as a vector of connectivity and transportation of material and organisms, (ii) as a disturbance, and (iii) as habitat and resource for organisms. However, to our knowledge, no previous work has synthesized existing literature of the relationships between hydrology and biodiversity in wetlands specifically, which we aim to do in this report. As this aim encompasses an extensive set of scientific literature, we focus on local scale biodiversity (i.e., within wetlands) of a selected group of wetland organisms, to enable a more detailed review of important mechanisms and how they differ between organism groups. We further aim to provide a basis for future development of hydrological indicators (i.e., quantitative measures of hydrological regime characteristics) relevant for wetland biodiversity, as tools for habitat optimization in construction and restoration projects, as well as for future research. Richter et al. (1996) proposed a similar use of biologically relevant measures to assess the degree of hydrological alteration caused by anthropogenic impacts: the Indicators of Hydrological Alteration (IHA). IHA is a collection of 32 indicators measuring five components (magnitude, duration, frequency, timing, and rate of change) of the hydrological flow regime, and they have for example been used to assess impacts of flow alterations in rivers and lakes in Europe (EU, 2015). These indicators have, however, not been developed to assess site-specific potential for wetland biodiversity, and though the flow regime likely has a large impact on wetlands connected to streams and rivers, the IHA may not be optimal as tools for planning wetland construction and management. Here, we instead suggest a smaller suite of hydrological indicators based on known direct impacts of hydrology on wetland biodiversity. Finally, we aim to highlight implications of identified relationships between the hydrological regime and biodiversity for wetland construction and management, as well as identify needs for future research.

The great diversity of wetland ecosystems makes them suitable habitats for many kinds of organisms. *Top left*: semiaquatic spiders can use the surface tension to move across water when they hunt. *Top right*: The grass snake (*Natrix natrix*, Sw. snok) is often found near water. *Bottom left*: Flowers in wetlands can be an important food source for pollinators. Here, the painted lady butterfly (*Cynthia cardui*, Sw. tistelfjäril). *Bottom right*: wetlands are often rich in prey for small mammals. Photos by Maria Nilsson.

2 Definitions and delimitations

2.1 Wetland definition and classification

Wetlands are habitats strongly characterized by the presence of water at or near the ground surface. In this report, the wetland definition from the Swedish Wetland Survey (Våtmarksinventeringen, VMI) is used, as it is broadly accepted in Swedish environmental protection and nature conservation. In VMI, wetlands are defined as: “areas where the water table during the main part of the year is close below, at or above the ground level, including vegetation covered water surface. An area is called a wetland when at least 50 % of its vegetation is hydrophilic, i.e., water loving. Exceptions are temporarily exposed lake-, sea-, and riverbeds; they are classified as wetlands despite a lack of vegetation” (Gunnarsson & Löfroth, 2009).

The wetland definition encompasses a wide variety of habitats, including for example the shallow, vegetated areas of ponds and lakes, and wetlands are often further divided into classes based on their characteristics. In VMI, wetlands were divided into three main classes: mires, containing peat-accumulating wetlands, shore wetlands, containing wetlands on the shores of lakes and rivers or along the coast, and other wetlands. Brief descriptions of the wetland types are given below.

It is not always obvious if a habitat is a wetland or not. For example, parts of many lakes (shallow areas, shorelines, low islands, etc.) are, by definition, wetlands. Photo by Maria Nilsson.

2.1.1 Mires

Due to a high water table causing anoxic conditions, mires are characterized by partially decomposed organic material accumulating in the form of peat. Mires are the most common wetland type in Sweden (Gunnarsson & Löfroth, 2009), and can be further divided into bogs and fens. Bogs are ombrotrophic, which means that they receive water and nutrients solely from precipitation. Such wetlands are naturally nutrient-poor and acidic, with a pH typically below four. Bogs are often characterized by Sphagnum mats but, due to the harsh conditions, overall species diversity is generally low. By contrast, fens receive minerogenic water (i.e., water that has been in contact with mineral soil, such as water from streams or groundwater) and are generally more productive and diverse than bogs. Some mires have features of both bogs and fens and are thus classified as mixed mires within the VMI methodology.

2.1.2 Shore wetlands

Situated along the shores of rivers and lakes, or along the coast, shore wetlands are strongly affected by or dependent on these water bodies. Wetlands affected by limnic waters are classified as limnic wetlands, while wetlands affected by salt or brackish water are classified as marine wetlands.

2.1.3 Other wetlands

Other wetlands include all wetlands that are not peat-accumulating nor strongly affected by marine water or water from lakes and rivers. They are further divided into open wetlands, such as wet meadows, and wet forests, such as swamp forests.

2.2 Biodiversity definition and delimitation

In the Convention on Biological Diversity (1992), biodiversity is defined as the variability of living organisms and environments, including diversity within species, between species, and among ecosystems. As such, biodiversity is a multifaceted concept that encompasses taxonomic, functional, and evolutionary variation. Here, we focus on species diversity (a type of taxonomic diversity) on a community level. Further, we differentiate between species richness, which is the number of species, and species diversity, which is high if both species richness and species evenness (similarity of the number of individuals of each species) is high.

In this report, we focus on the relationship between hydrology and species richness within wetlands, to facilitate optimization of biodiversity on a local scale. However, species have such various habitat requirements that it is impossible to accommodate all species within a single wetland. For example, the species composition of vegetation communities in bogs is distinctly different from that in fens, and both habitat types are thus necessary to support a full range of wetland species. Therefore, to attain an extensive and sustainable conservation of species and biodiversity, it is necessary to promote habitat variability and other conditions essential for biodiversity (e.g., connectivity) on a larger scale, i.e., within landscapes or regions. In general, some species or organism groups are more common than others on a regional level, and they are thus rarely focal species of conservation projects. For example, lack of both management and natural mechanisms for habitat rejuvenation are causing many wetlands to overgrow, and late-succession vegetation such as reeds or shrubs are common elements in wetlands. Though such vegetation are important habitats to for example birds, it is therefore rarely necessary to explicitly promote late-succession species within wetland habitats. Accordingly, which species should be promoted in a wetland construction or restoration project needs to be decided in the context of regional biodiversity. Thereupon, individual wetlands can be optimized to support high abundances of focal species, or a high species richness of focal organism groups.

2.3 Organism groups in this study

As previously mentioned, in this study, we focus on some selected organism groups for which wetlands are an important habitat. Two criteria were used when selecting organism groups: (i) they should represent different niches or roles in the ecosystem, and (ii) they should be easily identifiable either as a taxonomic group or as an ecological guild relevant for ecosystem functioning, to promote future use as indicator or focal species. Focal organism groups are:

- vegetation, which provides a foundation for further biodiversity by providing habitat and food,
- Chironomidae (non-biting midges), a ubiquitous invertebrate group and important food item in both terrestrial and aquatic food chains,
- Dytiscidae (diving beetles), one of the primary aquatic invertebrate predators in wetlands,
- amphibians, which are sensitive to both aquatic and terrestrial habitat quality, and are focal species of many wetland projects, and
- birds, which occupy many different niches, are easily recognizable, and are focal species of many wetland projects.

3 Overview of non-hydrological factors affecting wetland biodiversity

Hydrology shapes the physiochemical properties of wetlands and is widely recognized as the main driver of wetland community assemblage and biodiversity. Nevertheless, several other factors also affect species richness in wetlands, such as wetland area, age, and management, as well as characteristics of the surrounding landscape. These factors are briefly described here, to provide context to our main focus on the effects of hydrology, which is described in section 4.

Species-area relationships, describing the increase of species richness with increasing habitat area, are one of the most documented patterns of biodiversity across ecosystems and regions. The relationship has been found for various organism groups in wetlands, for example plants (Møller & Rørdam, 1985), snails (Brönmark, 1985), birds (Kačergytė, Arlt, et al., 2021), mammals, reptiles, and amphibians (Findlay & Houlahan, 1997). Several hypotheses have been suggested to explain the species-area relationship. One hypothesis states that larger areas are inherently more likely to contain more habitat heterogeneity and thus more niches to support different species (Williams, 1943), while another suggests that organisms of a species are randomly distributed spatially within their suitable habitat, and each site can thus be seen as a random sample of such a distribution (Arrhenius, 1921). Larger areas would then contain a larger sample of organisms, and likely a higher species richness. It is possible that more than one mechanism causes the increase of species richness with habitat area, and that the relative importance of different mechanisms varies between sites. Further, for wetlands, area generally correlates with both water depth and hydroperiod, and habitat area can thus be a surrogate measure of hydrological factors important for species richness, as was likely the case for amphibians (Semlitsch et al., 2015) and birds (Ma et al., 2010).

The relationship between species richness and productivity (the rate of increase of biomass) has been widely studied in plant communities. A classic hypothesis suggests a unimodal relationship ("hump-backed" or bell-shaped curve; Figure 1), where species richness is highest at intermediate productivity (Connell, 1978; Grime, 1973). At low productivity levels, abiotic stresses such as nutrient limitation inhibit establishment of many species, and at high productivity levels competitive exclusion of all except a few highly competitive species cause low species richness. In wetlands, multiple studies have found a unimodal relationship between productivity and plant species richness (Keddy & Fraser, 2000; Olde Venterink et al., 2003; Vermeer & Berendse, 1983), and threatened species have been found to be particularly sensitive to high productivity levels (Olde Venterink et al., 2003). However, the diversity-productivity relationship is debated among ecologists, and though some studies have found global evidence for a unimodal relationship (Fraser et al., 2015), others have not (Gillman & Wright, 2006). Further, the underlying mechanisms of this relationship are still poorly understood.

Studies of species richness in wetlands of different ages have shown varying results. Møller & Rørdam (1985) found that newly created or restored ponds had a higher macrophyte richness than natural ponds of corresponding sizes, while others have found an increased species richness with wetland age of macrophytes (Galatowitsch & van der Valk, 1996; Hansson et al., 2005) and invertebrates (Hansson et al., 2005). Møller & Rørdam (1985) hypothesized that the high diversity in young wetlands is the result of rapid colonization of wetland species, but that competition dynamics become more important as wetland ages. Thus, vegetation communities in young wetlands, not yet substantially affected by competition and subsequent exclusion of non-competitive species, can be very high. If so, the positive relationship between species richness and wetland age observed by Galatowitsch & van der Valk (1996) and Hansson et al. (2005) could be explained by the relatively young age (≤ 8 years) of studied wetlands, and that they had not yet reached a stage governed by competition dynamics. Wetland age can also affect species composition, as different types of species benefit from different successional stages. For example, species richness of birds utilizing open wetland habitats decreased with wetland age, while species richness of reed-dependent birds increased with age, likely as a result of the changing vegetation communities (Strand & Weisner, 2013).

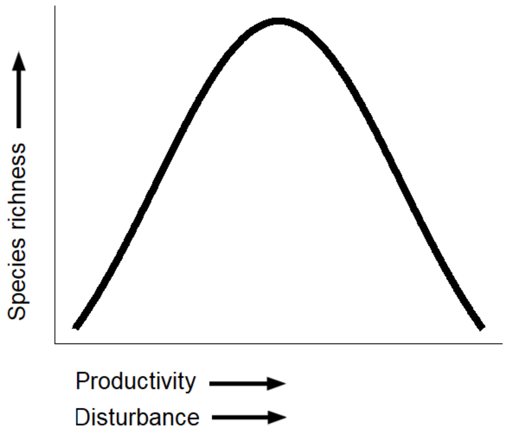


Figure 1. Ecological theories suggest that both productivity and disturbance have a unimodal relationship with species richness, i.e., species richness peaks at intermediate productivity or disturbance.

To prevent a reduced species richness from competitive exclusion in vegetation communities, management such as grazing or mowing can be used to facilitate coexistence of species. According to the intermediate disturbance hypothesis, species richness is maximized by disturbances (i.e., biomass removal) of intermediate strength (Figure 1), as they are strong enough to stop highly competitive species from dominating communities, but not strong enough to render the environment uninhabitable (Connell, 1978; Grime, 1973). Grazing and mowing can slow or reverse succession, such as wetland overgrowth, and especially low-intensity grazing can further increase species richness by generating habitat heterogeneity. This heterogeneity consists of, for example, vegetation of different heights, and patches of exposed soil from trampling, which can facilitate seed germination. Long-term grazing of herbivorous birds can have an effect on vegetation nutrient use and growth pattern (van den Wyngaert et al., 2003), however, bird density must be very high to have an effect on vegetation communities (Marklund et al., 2002), and grazing of for example cattle or sheep is thus preferred for wetland management.

The surrounding landscape of a wetland may also influence biodiversity, but the effect likely varies between organism groups. For example, forests surrounding wetlands has been associated with a low species richness of birds (Kačergytė, Arlt, et al., 2021; Wilson et al., 2014; Żmihorski et al., 2016), while it increases diversity of amphibians (Brown et al., 2012) and mammals (Findlay & Houlahan, 1997). Other landscape factors that likely are important include proximity to other wetlands and habitat connectivity, as they affect the dispersal possibilities of wetland species. For example, macrophyte richness was higher in an area where wetlands were closely spaced than in an area with large distances between wetlands (Møller & Rørdam, 1985), and amphibian use of wetlands was negatively affected by intersecting roads between wetlands and overwintering habitats (Nyström & Stenberg, 2009; Stenberg & Nyström, 2008).

Grazing keeps wetlands open and increases habitat heterogeneity. Photo by John Strand.

4 Effects of hydrology on the studied organism groups

4.1 Overview and hydrological indicators

As described by Rolls et al. (2018), hydrology affects biodiversity in freshwater habitats by three main mechanisms: as a vector of transportation of organisms and materials, as a disturbance, and by providing habitat and resources for organisms. Chemicals transported with water, mainly minerals, have a large effect on wetland characteristics and are an important factor for wetland classification. For example, mires are divided into bogs and fens based on where they receive water from, which in turn largely determines concentrations of substances in the water. Fens are minerotrophic and generally less acidic and more nutrient rich than ombrotrophic bogs (see section 2.1), but even within the fen class there is a nutrient and pH gradient. Rich fens, distinguished by a high pH and high concentrations of minerals, particularly calcium, are among the most threatened wetland types in Sweden. Due to their unique characteristics, they provide habitat for a set of specialized wetland species, many of them red listed. Differences in wetland chemistry is not unique to mires; all wetlands exist on a gradient between nutrient rich and nutrient poor, and wetlands of a certain type generally have pH values within a restricted range, though these ranges can overlap between types (Sjörs, 1950). Wetland chemistry is fundamental in determining which species can inhabit a wetland, and different wetland types often have different species assemblages.

Water depth is a fundamental characteristic of wetlands, and it largely affects the set of species able to inhabit the environment. Some species, such as fish and most aquatic invertebrates, are dependent on standing water and cannot inhabit wetlands where the water level is below the ground surface. The hydroperiod, i.e., the amount of time the water level is above the ground surface, is also an important determinant of wetland diversity and, in general, permanent waters can inhabit more species. However, shorter hydroperiods can benefit species sensitive to predation, such as many amphibians, as it reduces risks of for example fish presence. In such cases, the length of the hydroperiod becomes a trade-off between reducing predation risks and still being able to complete aquatic larval development.

Rich fens have a unique flora, including many orchids. Here, the fly orchid (*Ophrys insectifera,* Sw. flugblomster), whose flowers mimic a fly to attract pollinators. It also releases a scent that mimic sexual pheromones of female flies. Photo by Johanna Orsholm.

Water depth is also the main factor affecting vegetation distribution in wetlands, as most plants can tolerate only a range of water levels. In the extremes, some submerged species do not tolerate exposure, and some terrestrial species do not tolerate waterlogging. Accordingly, water level fluctuations act as an ecological disturbance, increasing the abiotic stress species experience by for example exceeding their preferred water level range. Provided that the water level fluctuations are relatively moderate, this disturbance increases vegetation diversity and complexity, which in turn affects numerous other wetland species using vegetation for habitat, food, and shelter. Most shrubs are very sensitive to high water levels, and water level fluctuations can reduce the distribution of fast-growing woody species, thus preventing wetlands from becoming overgrown. When shrubs are prevented from invading the wetland, it increases the area of species-rich wet meadow vegetation, and generally overall wetland diversity. Water level fluctuations can also affect wetland biodiversity by for example causing a nutrient flush or enabling germination of many plant species. However, the effects of water level fluctuations can be complex and difficult to predict, as they depend on fluctuation duration, frequency, amplitude, and timing.

Wetland morphology plays an important role in determining biodiversity and species assemblage. Many species, including amphibians, dytiscids, and birds, use the shallow areas of a wetland for foraging or shelter, and thus prefer wetlands with gently sloping margins. Similarly, wetland elements such as islands, or temporary pools separated from the main water body, increase habitat heterogeneity and promote wetland diversity. Finally, the effects of hydrological factors on wetland species vary depending on individual species characteristics, and what promotes diversity of one organism group, or increases abundance of a certain species, might be detrimental for another. Therefore, diversity of wetland habitats within the landscape is crucial for maintaining a high regional diversity.

Inventories of biodiversity or species richness are typically time-consuming and may require expert knowledge of species identification, and biodiversity surveys are thus often limited by lack of resources. If we can identify and quantify the main hydrological factors affecting species richness and abundances in wetlands, those variables can potentially be used as proxy measures of biodiversity, creating opportunities for more resource-efficient biodiversity estimations. The hydrological variables can be used to optimize wetland construction and restoration for biodiversity, estimate potential for species richness, and model the effects of anthropogenic impacts or environmental change, such as climate change, on biodiversity via their impact on hydrology. Therefore, we suggest a suite of hydrological indicators of factors that likely affect species richness in wetlands. These indicators are based on the evidence of relationships between species richness and hydrology found in literature, but they have not yet been tested for this purpose. It is possible that some indicators are not suitable for measuring the hydrological aspect relevant to species richness, or that some other indicator would better measure the relationship. However, these indicators are likely a good starting point for further research and development. Because the effects of hydrology on species richness are complex and vary with multiple characteristics of the hydrological regime, we further suggest some supplementary indicators, for example to measure the timing of high and low water levels. The hydrological indicators are defined in table 1, and a summary of their expected effect on each focal organism group is presented in table 2. Some measures relevant to wetland species, such as water level and pH, are not included as indicators, because they don't have a directional relationship with species richness within individual wetlands. However, on a landscape scale, variation of these characteristics between wetlands is crucial for supporting a high regional diversity. Detailed information on the relationship between hydrology and species richness for each organism group is given in their respective subsection.

Table 1. Definitions of indicators suggested for quantifying hydrological aspects relevant to wetland biodiversity. Depending on the aim, statistical measures can be based on single or multiple years. Water levels should be measured in the deepest part of the wetland.

Indicator	**Definition**
MHW - MLW	Yearly mean difference between highest and lowest water levels.
MW - MLW	Yearly mean difference between mean and lowest water levels.
MHLW_day	Yearly mean difference between daily high and low water levels. Retrieved from for example Fourier analysis of high-frequency time series, or from seiche calculations.
DD_wet_5	Number of consecutive days with water level more than 5 cm. If there are multiple periods within a year meeting this criterion, use the longest period.
DD_wet_MLW_50	Number of consecutive days with water levels more than 50 cm over the yearly mean low water level. If there are multiple periods within a year meeting this criterion, use the longest period.
Julian date of W < 5	Julian date of the first day of a period where water levels are less than 5 cm. If there are multiple periods within a year meeting this criterion, use the longest period.
Julian date of HW/LW	Julian date of yearly highest/lowest water levels.
Area MW - Area MLW	Difference between water-covered area during yearly mean water level and water-covered area during yearly mean low water levels.
Area_W_10_50	Yearly mean area where water level is between 10 and 50 cm.
HW_5years_1day	High water level with return period of five years and duration of one day.
Mean slope	Mean slope of wetland margin.
Conductivity	Water conductivity.

Table 2. Effects of hydrological factors on the abundance and species richness of organism groups in this report. For each factor, we suggest a main hydrological indicator, as well as additional indicators suitable for quantifying different aspects of the hydrological regime, such as seasonality. Positive relationships between the main indicator and abundance/species richness are denoted '+', negative relationships '-', and neutral 'No effect'. Unimodal relationships or relationships changing between seasons are denoted '+/-' and unknown relationships '?'.

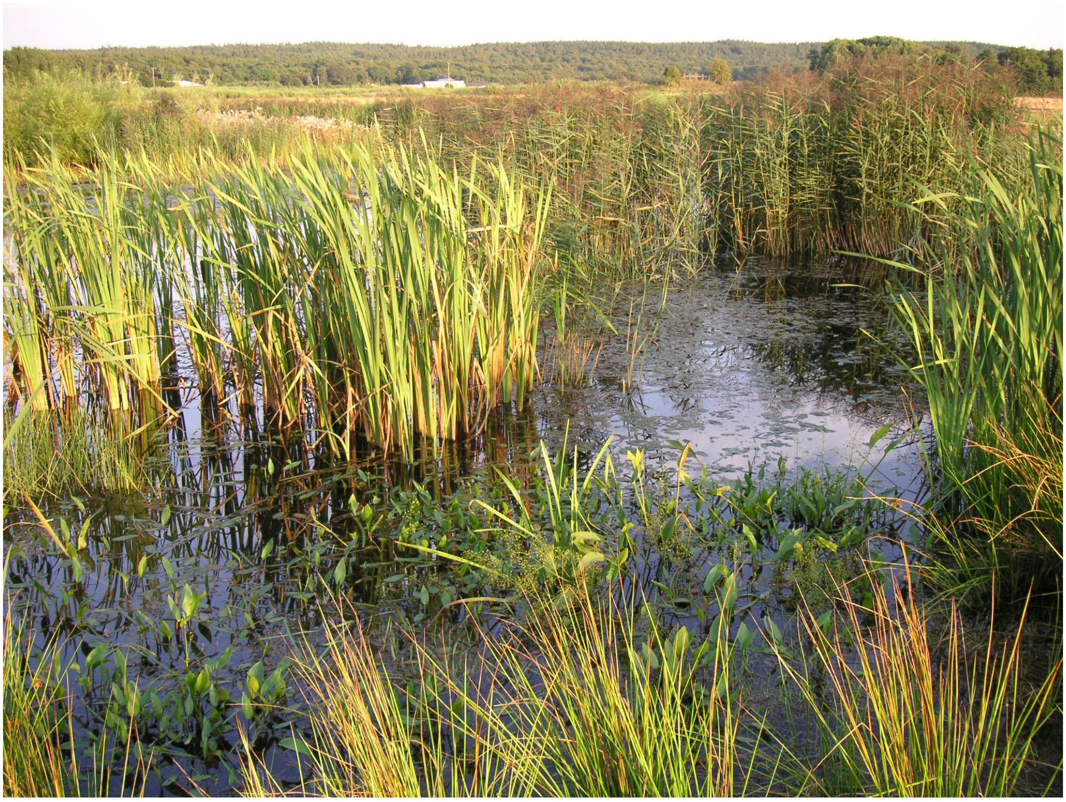
	Hydrologic factor	**Hydroperiod**	**Yearly water fluctuations**	**Daily water fluctuations**	**Drawdown**	**Extreme flood events**	**Shoreline slope**	**Nutrient content**
	Suggested indicator	*DD_wet_5*	*MHW - MLW*	*MHLW_day*	*MW - MLW*	*HW_5years_1day*	*Mean slope*	*Conductivity*
	Additional indicators	*Julian date of W < 5*	*Julian date of HW/LW, DD_wet_MLW_50, Area MW – Area MLW*				*Area_W_10_50*	
Abundance	Emergent vegetation	?	?	?	?	-	-	+
	Submerged vegetation	?	+/-	?	?	+	?	?
	Terrestrial vegetation	?	+	?	?	-	?	?
	Shrubs	?	-	?	?	-	?	?
	Chironomids	+	?	?	?	?	?	+
	Dytiscids	?	?	?	?	?	-	?
	Amphibians	?	?	?	?	?	-	+/-
	Diving birds	+	?	?	+/-	?	?	?
	Dabbling/wading birds	?	+/-	?	+/-	?	-	?
Species richness	Emergent vegetation	?	+/-	+	+	?	?	+/-
	Submerged vegetation	?	+/-	*No effect*	+	?	?	+/-
	Terrestrial vegetation	?	+/-	+	+	?	?	+/-
	Shrubs	?	?	-	?	?	?	+/-
	Chironomids	?	?	?	?	?	?	?
	Dytiscids	+	+	?	?	?	-	?
	Amphibians	+/-	?	?	?	?	-	?
	Diving birds	?	?	?	?	?	?	?
	Dabbling/wading birds	?	+/-	?	?	?	-	?

4.2 Vegetation

4.2.1 Background

Vegetation is the major primary producer of wetland ecosystems, and especially macrophytes play an important role in shaping their biological, physical, and chemical characteristics. Macrophytes provide crucial habitat and food for numerous other organisms, as well as shape the abiotic properties of wetlands by, for example, nutrient uptake and soil stabilization. Here, we will focus on the interactions between macrophytes and hydrology.

Wetland macrophytes can be classified based on where in relation to the water level they (predominantly) grow – submerged, floating, emergent, or terrestrial plants. Submerged species grow entirely under water and often lack certain characteristics found in terrestrial plants, such as stomata – leaf structures which are used to control gas exchange. An example of submerged species found in Swedish wetlands is the perfoliate pondweed (*Potamogeton perfoliatus*, Sw. ålnate). Floating vegetation can either be rooted in soil, such as water lilies, or free-floating, such as duckweeds (*Lemna spp*.). Emergent vegetation is rooted under water but grows with the main part of the stem and leaves above the surface. Fluctuating water levels can reduce or increase the proportion of a plant emerging from the water, and emergent species can even be found growing in completely exposed areas. Common emergent species in Swedish wetlands include the common reed (*Phragmites australis*, Sw. bladvass) and cattails (*Typha spp*., Sw. kaveldun). Finally, rarely flooded parts of wetlands can support terrestrial plants that thrive in mesic conditions.



Wetland vegetation can be very structurally diverse. Here, we see a mix of emergent and floating species of macrophytes, including cattails and reeds in the background, and broad-leaved pondweed (*Potamogeton natans*, Sw. gäddnate) in the open water. Photo by John Strand.

Water saturated soils rapidly become anaerobic, as microbial oxygen consumption exceeds the diffusion rate of oxygen into the soil. Most plants growing in wetlands need to tolerate some degree of flooding or waterlogging, as well as the anaerobic conditions associated with soil saturation. The lack of oxygen is the main stress affecting vegetation growing in wet conditions, and it can affect survival, growth rate, and propagation. Anaerobic soils can further lead to accumulation of substances to toxic concentrations, such as reduced metals ($Mn2+$, $Fe2+$) or intracellular ethanol from anaerobic metabolic pathways (Colmer & Voesenek, 2009). Many wetland plants have evolved adaptations to tolerate these conditions, such as a porous tissue, known as aerenchyma, that can transport gasses to and from plant roots. Oxygen transportation to the roots enables aerobic metabolism in anaerobic conditions and, through a process known as radial oxygen loss, where excess oxygen diffuses to the rhizosphere, reduces toxicity of the soil by oxidizing the aforementioned metal ions. Other adaptations to flooded conditions include rapid stem elongation in response to increasing water levels, or heterophylly, where plants evolve different types of leaves above and below the water surface.

4.2.2 Distribution and species richness - effects of water level fluctuations

Spatial and temporal variation in wetland vegetation is primarily determined by the water regime. One of the most conspicuous patterns of vegetation distribution in wetlands is the zonation of communities along the wet-dry gradient. This is also known as a coenocline – a sequence of communities along an environmental gradient (Figure 2) – and its establishment and maintenance are mainly driven by differences in flood tolerance among plant species. Survival of adult plants is the main factor controlling vegetation distribution (Seabloom et al., 2001), but plant characteristics such as seed dispersal, germination patterns, and seedling mortality are also important drivers (van der Valk & Welling, 1988). Water depth and duration of flooding are likely the most important properties of the water regime in shaping vegetation patterns (Casanova & Brock, 2000; Todd et al., 2010; van der Valk, 2005). Though coenocline establishment is driven by complex mechanisms, there are some general limitations observed for common wetland plants: cattails are restricted to depths less than 70 cm, and reeds are restricted to depths less than two meters (Feuerbach, 2014).

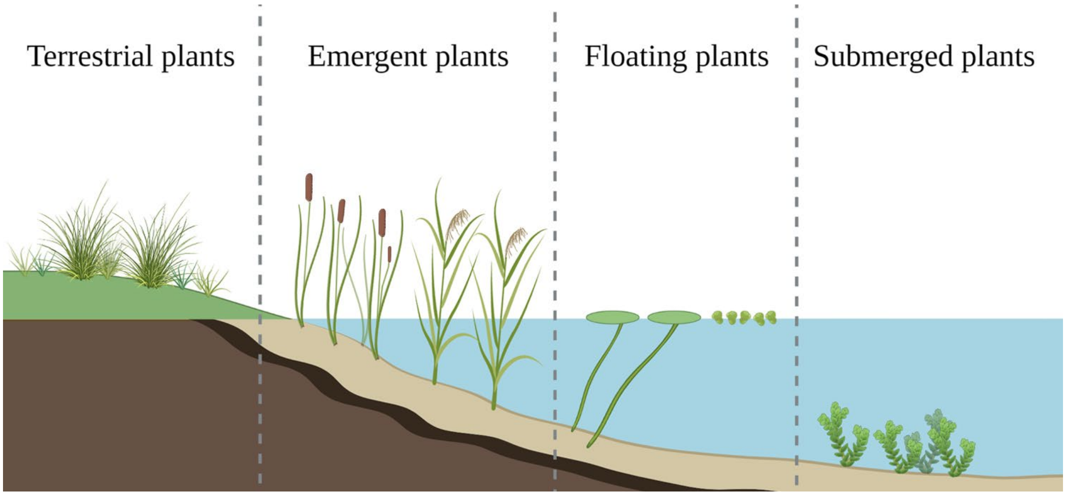


Figure 2. An example of a coenocline along a dry-wet gradient in a wetland, spanning from terrestrial plants to fully submerged aquatic plants. [Created with BioRender.com]

Knowledge of which mechanisms are important for shaping coenoclines is primarily derived from studies in wetlands with large interannual variations of water levels. In many of these studies, wetlands are surveyed during a period with high water levels, maintained for at least one year, followed by one or more years with low water levels. Duration of high and low water levels, as well as the number of fluctuation cycles, vary between studies. Results show that different mechanisms are important during high and low water levels. When water levels are high, flooding and anaerobic soil conditions eliminate many species, and the main driver of vegetation distribution is flooding toleration of adult plants (Keddy & Reznicek, 1986; Seabloom et al., 2001; van der Valk, 2005). When water levels are low, propagation abilities become of increased importance, as many species can colonize and grow in mesic conditions (Seabloom et al., 2001). Plants can propagate either vegetatively or via seeds, and it is possible that soil seed bank contents are of greater importance for vegetation distribution patterns during dry periods (Keddy & Reznicek, 1986; Seabloom et al., 2001). When ground is exposed, it is also likely that many annual species germinate, which could increase species richness (Keddy & Reznicek, 1986).

The effects of water level fluctuations on wetland vegetation depend on what conditions plants are adapted to. For example, shrubs are very sensitive to high water levels, and both long-term and short-term water level fluctuations have been shown to decrease shrub abundance (Grabas et al., 2019; Keddy & Reznicek, 1986; Raulings et al., 2010; Smith et al., 2021). Occasional increases in water levels can thus prevent wetlands from being overgrown by woody species, increase the area of terrestrial (wet meadow) vegetation (Keddy & Reznicek, 1986; Smith et al., 2021), and promote a high species richness in vegetation communities. Very high water levels have also been shown to decrease the abundance of terrestrial and emergent vegetation, while the abundance of submerged vegetation either remained unchanged or increased (Smith et al., 2021). Most emergent species are unable to germinate in flooded conditions, and decreased propagation rates could contribute to the extensive elimination of vegetation observed after a long period of high water levels (van der Valk, 2005). Similarly, germination of some submerged plant species is also facilitated by exposed soil, and, accordingly, occurrence of low water levels has been associated with high species richness of terrestrial and emergent vegetation (Raulings et al., 2010), and high species richness and abundance of submerged vegetation (Van Geest et al., 2005).

After a period of flooding had eliminated communities of emergent vegetation in a wetland, van der Valk & Welling (1988) studied the development of new coenoclines. When comparing newly established coenoclines to vegetation patterns that prevailed before the flooding, they found that the distribution of species was very similar. However, most species did not form monodominant stands, as they had in previous coenoclines. The authors hypothesized that, over time, exploitative competition becomes more significant and may lead to local exclusion of less competitive species.

So far, the described mechanisms causing vegetation distribution patterns in wetlands have largely been the result of interannual water level fluctuations. Short-term variations of water levels, such as seasonal fluctuations caused by precipitation patterns and snowmelt, or daily variations caused by waves or winds, likely have different effects on vegetation (Keddy & Reznicek, 1986). For example, many perennial macrophytes, especially emergent species, can tolerate short periods of sub-optimal water levels by temporarily shifting to anaerobic metabolic pathways. Furthermore, annual species often respond rapidly to environmental conditions and can likely germinate and exploit favourable sites even when water levels vary. Short-term fluctuations, provided that the amplitude is not too large, thus primarily act as a natural disturbance of vegetation communities, increasing vegetation diversity and possibly the annual component of the community (Keddy & Reznicek, 1986).

The intermediate disturbance hypothesis suggests that peak species richness is found in areas exposed to ecological disturbances, such as water level fluctuations, of intermediate strength or frequency, as such disturbances can facilitate coexistence of species and thus increase diversity. Due to their long duration and often high amplitude, interannual fluctuations generally constitute a strong disturbance and are associated with community shifts rather than increased diversity (van der Valk, 2005). Natural short-term fluctuations typically have a lower amplitude, associated with changing relative abundance of species rather than community composition, and are likely more important in enhancing species richness through disturbance. This was the case in three lakes with water fluctuations of different amplitudes, where the lake with intermediate fluctuations supported the most species rich vegetation communities (Wilcox & Meeker, 1991).

Daily fluctuations of water levels, primarily caused by seiches, have been associated with high species richness of both emergent and terrestrial vegetation in wetlands (Grabas et al., 2019). Fluctuations decreased shrub species richness near the shoreline, while submerged vegetation remained unaffected, likely because, provided that the plants are not completely exposed, fluctuations do not substantially change the sub-aquatic environmental conditions. In addition to serving as a disturbance of vegetation communities, fluctuations likely fostered establishment of flood tolerant species in frequently inundated areas, as well as created a broad range of hydrological niches, thus supporting species with a range of different water tolerances. For example, water level fluctuations were associated with high richness of species existing at elevations more than one meter above the mean water level, possibly because high water levels during spring flood facilitated germination of certain species. A similar relationship between water fluctuations and species richness was found in New Zealand, where Riis & Hawes (2002) compared diversity of low-growing vegetation communities found along the shores of two lakes. Water levels in the two lakes fluctuated between or within years, respectively. Species richness was higher in the lake with short-term water fluctuations, and peak diversity was found in areas with intermediate water level ranges.

4.2.3 Importance of topographic variation on a small spatial scale

It is well established that vegetation has various water regime requirements and that these differences influence vegetation distribution in wetlands. Accordingly, an important variable for supporting high macrophyte richness and abundance in wetlands is topographic variation, as it can create a range of various water depths. For example, gently sloping wetland margins create large areas of relatively shallow water, and such wetlands should thus support higher abundances of emergent macrophytes than wetlands with steep sides. Further, microtopographic variation can create a range of water regimes on a small spatial scale, and thus promote a complex macrophyte distribution pattern (van der Valk, 2012). Raulings et al. (2010) found that microtopographic variation promoted coexistence of plant species with different water regime requirements over small distances, and Hansson et al. (2005) found that a complex shoreline, which could be associated with large microtopographic variation, increased macrophyte diversity. Further, when tillage was used to increase the microtopographic variation in constructed wetlands, species richness increased compared to created wetlands that were not tilled (Moser et al., 2007).

4.2.4 Effects of water chemistry

Water chemistry in wetlands is often described with regard to pH, base richness (calcium and magnesium), and nutrients, as these components have considerable effects on vegetation communities (van der Valk, 2012). The primary factor influencing these environmental gradients in wetlands is the main water source (e.g., whether the wetland is minerotrophic or ombrotrophic), but other factors such as vegetation composition and soil type can also have an effect. For example, nutrient cations are often adsorbed in peat soils, resulting in low plant availability (Rydin et al., 2013). An example demonstrating the importance of water source in shaping wetland properties is the differentiation between ombrotrophic and minerotrophic mires – bogs and fens, as described in section 2.1.

Wetland pH has been found to strongly correlate with distribution of plant species (Sjörs, 1948). Typically, wetlands of a certain type have pH-values within a specific range, thus potentially supporting a distinct assemblage of plant species. However, pH-ranges largely overlap between wetland types (Sjörs, 1950), resulting in large similarities of vegetation communities between related wetland classes. Patterns of conductivity, which is often used as a proxy measure of dissolved substances important for vegetation, such as nutrients, are less consistent within wetland types. Sjörs (1950) found that rich fens had a higher conductivity than poor fens, as expected, but intermediate fens could have either a high or a low conductivity. Further, the correlation between plant distribution and conductivity appeared less distinct than the correlation with pH, and species typical of intermediate fens often occurred in areas with conductivity values that corresponded to poor fens.

Groundwater generally has a high concentration of dissolved substances, and inflowing groundwater can be an important source of nutrients in wetlands (van der Valk, 2012). Groundwater inflow rate and concentrations of dissolved substances can vary both spatially and temporally (Schot & Pieber, 2012), thus resulting in heterogeneity of water chemistry within a wetland, and this variation is likely to affect vegetation distribution. For example, Wassen et al. (1988) studied water chemistry and macrophyte richness in a wetland where only part of the area received calcium-rich groundwater. They found that the concentration of calcium was strongly influenced by the hydrological gradient, and that rare species occurred only in areas with high calcium concentrations. Simkin et al. (2013) found that variation in concentrations of groundwater-derived phytotoxic sulphide could explain observed local decreases in plant species richness. Finally, nutrient levels affect abundance and distribution of plant species, and there is evidence of a unimodal relationship between species richness and conductivity, with highest richness at intermediate conductivity (Johnson & Leopold, 1994; Keddy & Fraser, 2000; Olde Venterink et al., 2003; Vermeer & Berendse, 1983). Though conductivity is not a direct measure of nutrient availability, this could be in accordance with the richness-productivity relationship described in section 3. High nutrient levels generally promote competitive emergent species, such as reeds and cattails, and abundance of emergent vegetation can be high in wetlands receiving nutrient-rich water (Feuerbach, 2014).

4.3 Chironomidae

Chironomids (Diptera: Chironomidae), or non-biting midges, can be found in virtually all aquatic habitats, and they are an important component of both aquatic and terrestrial food chains in wetlands. The aquatic larvae are preyed upon by for example diving beetles, newts, and fish, while the flying adult stages are important food items for birds and bats. The larvae often live in burrows in bottom soils where they feed on small particles in the water, such as algae and disintegrated plant detritus (van der Valk, 2012). Chironomid larvae are well-adapted to low oxygen levels, and many species contain hemoglobin to increase oxygen uptake and storage. Larvae also use an undulating movement to cause water flow through their burrows and thus facilitate oxygen uptake from the water (van der Valk, 2012).

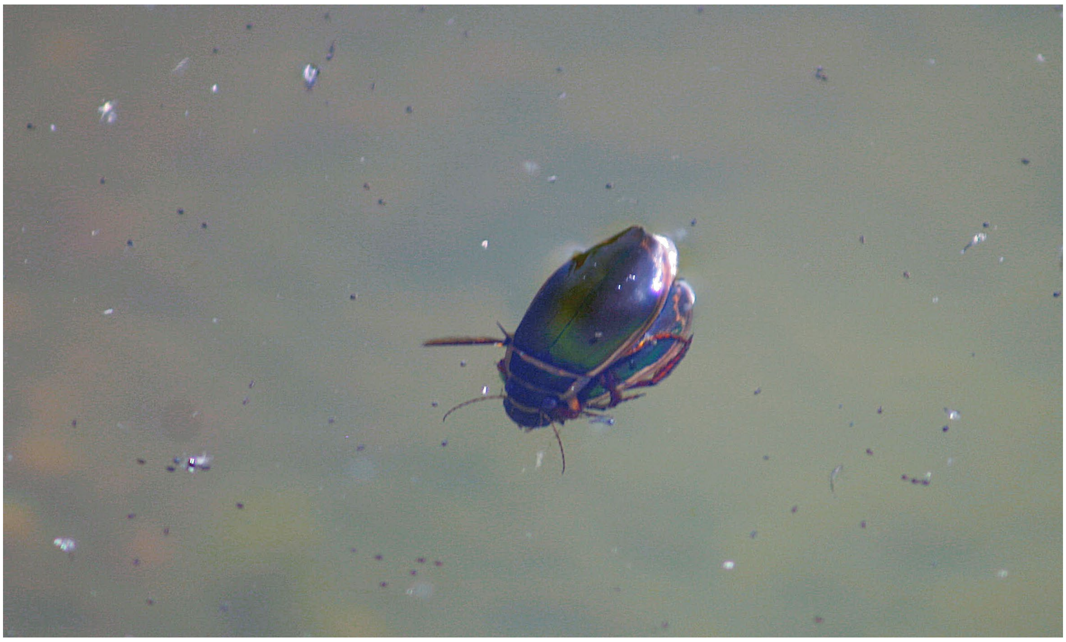
In a review of the invertebrate fauna in 447 wetlands, chironomids were present at 97.3 % of the sites (Batzer & Ruhí, 2013). However, chironomid abundance varies both temporally and between different wetlands. In the Delta Marsh in Canada, more than 10 000 larvae per m2 have been recorded (van der Valk, 2012), while the average abundance in temporary wetlands along River Dalälven in Sweden was about 2 000 larvae per m2, which was similar to the production in terrestrial habitats (Lundström et al., 2010). Chironomid abundances has been found to be higher in permanent than in temporary wetlands (Lundström et al., 2010; Whiles & Goldowitz, 2001), and species richness has been found to be higher in lakes than in peatlands (Rosenberg et al., 1988), which could suggest that water permanence is an important factor for chironomid production and diversity. However, in another study, there was no relationship between hydroperiod and species richness, but wetlands with different wet phase duration had different species assemblages (Bazzanti et al., 1997). The authors suggested that smaller species might develop faster, thus enabling them to utilize wetlands with a shorter hydroperiod. Further, it is possible that some species have eggs or larvae that can tolerate periods of drought, allowing them to inhabit temporary wetlands.

Organic matter content, oxygen levels, and nutrient levels have been shown to affect chironomid species assemblage (Bazzanti et al., 1997; Blumenshine et al., 1997). Further, in a mesocosm experiment, nutrient enrichment increased the proportion of chironomids, possibly because an increased abundance of phytoplankton decreased food limitations (Blumenshine et al., 1997).

4.4 Dytiscidae

Dytiscids (Coleoptera: Dytiscidae), also known as diving beetles, are one of the most ubiquitous macroinvertebrate taxa in wetlands. In a review of the invertebrate fauna in 447 wetlands, dytiscids were present at 87.5 % of the sites (Batzer & Ruhí, 2013), and they were the dominating predatory insect taxa in wetlands along River Dalälven in Sweden (Persson Vinnersten et al., 2009). Dytiscids are generalist predators in both larval and adult stages, and they feed on insects, small crustaceans, tadpoles, and juvenile fish. They can have a large impact on other wetland organisms, and in a mesocosm experiment they affected abundances of species throughout a food chain in what is known as a trophic cascade (indirect interactions between organisms in a food chain resulting from a change on a trophic level) (Cobbaert et al., 2010). In the experiment, dytiscid predation led to a decreased abundance of grazing macroinvertebrates, such as gastropods (snails and slugs), which in turn led to a decrease in grazing pressure and a subsequent increase in periphyton abundance. Dytiscids also predate on mosquito larvae (Diptera: Culicidae) and could possibly decrease mosquito production in wetlands. However, the effect of dytiscid predation on abundances of adult mosquitoes is still unclear (Persson Vinnersten et al., 2009), though some evidence suggests that high abundances of large dytiscid species can decrease abundances of mosquito larvae (Lundkvist et al., 2003). The effect could also depend on species assemblage, as some dytiscid species have been shown to prefer mosquitoes over other prey (Culler & Lamp, 2009), while others do not (Lundkvist et al., 2003). Chironomids (Diptera: Chironomidae) are another important prey item of dytiscids, and in Swedish lakes, dytiscid abundance and species richness was positively associated with abundance of chironomid and mosquito larvae, suggesting that prey abundance can affect dytiscid diversity (Nilsson et al., 1994).

Adult dytiscids are generally good fliers and can disperse over distances of several kilometres (Bilton, 1994 in Lundkvist et al., 2003). Therefore, their species assemblage and richness in wetlands are likely the result of both individual wetland characteristics and the distribution of wetlands within the landscape. Dytiscids are dependent on aquatic habitat both as larvae and as adults and are thus sensitive to wetland hydroperiod and flooding regimes. However, larval dytiscids are more sensitive to desiccation than adults, as they are unable to migrate between wetlands. In Swedish wetlands, dytiscid species richness increased with hydroperiod, as more species were able to utilize wetlands with longer hydroperiods (Nilsson & Svensson, 1994; Schäfer et al., 2006). Flooding regime has been identified as an important factor in shaping dytiscid communities (Persson Vinnersten et al., 2009) and, in lakes, seasonal flooding has been related to high species richness, possibly due to associated nutrient pulses (Nilsson et al., 1994). Species-area relationships were weak in a study of dytiscid species richness in Swedish wetlands (Lundkvist et al., 2001). However, vegetation cover and complexity has been related to high species richness and abundance (Liao et al., in press; Nilsson et al., 1994), and it is possible that vegetated area is a better predictor of dytiscid diversity than total wetland area, as has been found for other invertebrates (Gee et al., 1997). Liao et al. (2020) found that dytiscid abundance and species richness were lower in wetlands with presence of fish and in wetlands with steeply sloping margins, suggesting that predation could be an important factor affecting wetland dytiscids, and that shallow, vegetated areas could be important refuges from predators such as fish and dragonfly larvae.



Mating dytiscids at the water surface. Dytiscids trap air in a bubble below their elytra (the hardened front-wings that cover most of their body, including the membranous wings used in flight) to breathe when under water. Photo by John Strand.

Dispersal is likely one of the main drivers of dytiscid community assemblage in wetlands, and multiple studies have found that abundance and species richness are associated with surrounding open landscapes (Lundkvist et al., 2001; Schäfer et al., 2006), likely because such wetlands are easier to locate from the air and thus have higher immigration rates than wetlands surrounded by forests (Nilsson & Svensson, 1995). Studies have also found that dytiscid species richness is very similar between different types of wetlands, but that species assemblage varies with environmental characteristics (Lundkvist et al., 2001; Persson Vinnersten et al., 2009). Therefore, a landscape perspective might be necessary when considering dytiscid diversity, and it has been suggested that high regional species richness is better achieved with multiple small wetlands of varying characteristics than a single large wetland of corresponding area (Gee et al., 1997; Lundkvist et al., 2001).

4.5 Amphibians

Amphibians inhabit both terrestrial and aquatic habitats during their life cycle; mating and development of eggs and tadpoles occur in water, while adults predominantly inhabit terrestrial environments. Since the late 20th century, scientists have reported wide-spread amphibian population declines, and amphibians are now more threatened than for example birds and mammals (IUCN, n.d.). The declines are probably caused by various mechanisms, both known and unknown, but loss of suitable habitats is considered one of the main drivers in Europe (Stuart et al., 2004). In Sweden, there are thirteen species of amphibians: eight frogs, three toads, and two newts. Five of these species are listed as threatened on the national red list, and eleven are included in the EU Habitats Directive (92/43/EEC), which means that the species and their habitats should be protected or restored to ensure a favorable conservation status throughout their natural range within the EU. Many amphibian species in Sweden only occur within restricted geographical ranges in the far south, and they have been especially affected by the considerable wetland losses in the area. Extensive conservation measures during the last decades have however resulted in stabilized or improved population trends for most amphibian species in Sweden (Naturvårdsverket, 2019, 2021a; Strand & Weisner, 2013). Nonetheless, compared to before the start of large-scale wetland degradation, populations are still very small, and further measures are likely necessary to ensure long-term viable populations.

Table 3. Amphibian species occurring in Sweden, their status on the national red list and their inclusion in the EU Habitats Directive. Two red list categories occur: Least Concern (LC), meaning that the species is not considered threatened nor included on the red list, and Vulnerable (VU), which means that the species is red listed and considered threatened. Annex 2 of the EU Habitats Directive include species for which their habitat should be protected, annex 4 species that require strict protection regimes, and annex 5 species for which the exploitation need regulation.

Species	**Swedish name**	**Scientific name**	**National red list status (2020)**	**EU Habitats Directive**
Great crested newt	Större vattensalamander	*Triturus cristatus*	LC	Annex 2 and 4
Smooth newt	Mindre vattensalamander	*Lissotriton vulgaris*	LC	-
European fire-bellied toad	Klockgroda	*Bombina bombina*	LC	Annex 2 and 4
Common spadefoot toad	Lökgroda	*Pelobates fuscus*	VU	Annex 4
Common toad	Vanlig padda	*Bufo bufo*	LC	-
Natterjack toad	Strandpadda	*Epidalea calamita*	VU	Annex 4
European green toad	Grönfläckig padda	*Bufotes viridis*	VU	Annex 4
European tree frog	Lövgroda	*Hyla arborea*	LC	Annex 4
Common frog	Vanlig groda	*Rana temporaria*	LC	Annex 5
Moor frog	Åkergroda	*Rana arvalis*	LC	Annex 4
Agile frog	Långbensgroda	*Rana dalmatina*	VU	Annex 4
Edible frog	Ätlig groda	*Pelophylax kl. esculentus*	LC	Annex 5
Pool frog	Gölgroda	*Pelophylax lessonae*	VU	Annex 4

One of the main determinants of amphibians' colonization and use of wetlands as breeding habitats is presence of fish (Brown et al., 2012; Nyström & Stenberg, 2009; Semlitsch et al., 2015). Fish are important predators on tadpoles, and wetlands containing fish have been associated with lower amphibian production (number of metamorphosing juveniles) and species richness than wetlands without fish (Shulse et al., 2012). Further, when fish were extirpated from wetlands due to drought, amphibian species richness increased (Werner et al., 2007). Though most amphibians benefit from fish absence, sensitivity to predation varies between species. For example, the common toad (*Bufo bufo*, Sw. vanlig padda) is generally not preyed upon by fish due to its toxicity, and it can even prefer wetlands with fish (Beebee, 1979), possibly because it reduces competition from other amphibians. Coexistence of amphibians and fish could also be facilitated by habitat heterogeneity, specifically from varying wetland vegetation, shape, and structure, as it creates refuges from predation, but further studies are needed to confirm such mechanisms (Kačergytė, Petersson, et al., 2021). Predatory macroinvertebrates, such as dytiscids or dragonfly larvae, potentially have similar effects on amphibians as fish, and during a conservation project in Australia, amphibians were more abundant in ponds without dytiscids (Valdez, 2019). However, it is uncertain how common such effects of invertebrate predation are, as other studies on the effects of macroinvertebrate abundance on amphibians are inconclusive (Semlitsch et al., 2015; Werner et al., 2007).

Tadpoles in a shallow littoral zone. Tadpoles are predated on by many different organisms, including birds, dytiscids, and dragonfly larvae, and they can use the shallow, vegetated areas of wetlands as a refuge. Photo by John Strand..

Wetland hydroperiod is a key driver of amphibian community assemblage (Babbitt et al., 2003; Drayer & Richter, 2016), and it affects species richness by two main mechanisms: risk of desiccation and probability of fish presence (Brown et al., 2012). If a breeding site dries before tadpoles reach the critical body size for metamorphosis to the terrestrial stage, the tadpoles will either desiccate or concentrate in small water bodies, becoming easy prey to for example birds. Long hydroperiods can thus promote species richness by providing habitat even for slow-developing amphibians, and some studies have found a positive relationship between hydroperiod and species richness (Pechmann et al., 1989; Werner et al., 2007). However, because long hydroperiods are associated with increased risk of fish presence, amphibian species richness is generally highest in wetlands with intermediate hydroperiods, provided that the wetland does not dry out during the breeding season (Brown et al., 2012). Wetland size often correlates with hydroperiod and, accordingly, amphibian diversity and larval density peak in wetlands of intermediate size (Semlitsch et al., 2015). Because species assemblage varies between wetlands with different hydroperiods, a range of hydroperiods within the same landscape is likely optimal for amphibian conservation (Brown et al., 2012).

The moor frog (*Rana arvalis*, Sw. åkergroda), one of the most common frogs in Sweden. Photo by Gabriella Rinaldo.

Habitat connectivity is crucial for allowing amphibians to find suitable overwintering habitats, and to enable dispersal between breeding sites. Amphibian populations experience large natural fluctuations, and to maintain viable populations, colonization from nearby wetlands may be necessary (Brown et al., 2012). However, connectivity by waterways, such as streams and ditches, increases probability of fish colonization and, accordingly, amphibians were less common in interconnected than in isolated wetlands, in a study performed in south-central Sweden (Kačergytė, Petersson, et al., 2021). Similarly, the great crested newt (*Triturus cristatus*, Sw. större vattensalamander) has been negatively associated with wetland inflow, which could be related either to increased probability of fish presence or changed water quality (Harper et al., 2020).

Emergent and submerged vegetation increase habitat heterogeneity and create important habitats and predation refuges for amphibians (Brown et al., 2012). Established wetland vegetation is important for amphibian colonization (Brown et al., 2012; Nyström & Stenberg, 2009; Stenberg & Nyström, 2008), and high vegetation cover has been associated with high amphibian species richness and production (Shulse et al., 2012). Hydrological regimes promoting diverse and structurally complex vegetation communities, such as inter-annual water level fluctuations, thus likely promote amphibian diversity, provided that other wetland characteristics (e.g., hydroperiod) are suitable for amphibian use. Flooding could potentially also benefit amphibians by providing a nutrient flush, thus promoting growth of algae, the main food source for many amphibian larvae (Pechmann et al., 1989). However, there is currently not enough evidence to conclude such effects from wetland flooding.

The shallow littoral zone is an important element to amphibian habitats and refuges, and Shulse et al. (2012) found that amphibian production was highest in wetlands with gently sloping margins. Other studies on the effects of margin slopes on amphibians have shown mixed results, possibly because the effect varies between species. However, it is likely that gently sloping wetland margins generally promote amphibian abundance and species richness (Brown et al., 2012). Sun-exposed shallow waters may be especially important, as the sunlight increases temperatures and enhances primary productivity, thus facilitating amphibian metabolism and increasing availability of algae (Shulse et al., 2012). Wetland canopy cover affects amphibian community assemblage (Drayer & Richter, 2016) and has been negatively associated with species richness (Nyström & Stenberg, 2009; Werner et al., 2007). A hypothesized mechanism is that canopy cover affects resource quality and quantity by altering wetland nutrient contents and abiotic conditions, such as temperature and sun exposure. Accordingly, newts, which primarily feed on invertebrates and thus depend on a detritus-based food chain, was found to be unaffected by canopy cover (Werner et al., 2007).

Areas of intensive agriculture surrounding wetlands have been found to negatively affect amphibians, likely because they do not provide suitable habitats for adults, and because water runoff contains high concentrations of nutrients and agricultural chemicals, such as pesticides, negatively affecting water quality (Nyström & Stenberg, 2008). Generally, amphibians benefit from intermediate water nutrient levels, as it increases resource availability by promoting algal growth without creating eutrophic conditions (Brown et al., 2012). However, sensitivity to high concentrations of nutrients and other chemicals likely varies between species. For example, the great crested newt was found to prefer ponds located on golf courses, which are often heavily exposed to pesticides and fertilizers, over ponds located in parklands and reserves, while no such preference was found for other amphibian species (Colding et al., 2009). Similarly, though many amphibians colonized wetlands in Sweden irrespective of whether they were created to promote biodiversity or nutrient retention, the natterjack toad (*Epidalea calamita*, Sw. strandpadda) and the agile frog (*Rana dalmatina*, Sw. långbensgroda) were only found in wetlands aimed at increasing biodiversity (Strand & Weisner, 2013), which could suggest a greater sensitivity to heavy nutrient loads.

4.6 Birds

Wetlands are highly important habitats for birds, and various bird species utilize wetlands for foraging, breeding, resting during spring and fall migration, and over-wintering. Globally, about 55 % of the waterbird species are declining (BirdLife International, 2017), and wetland protection, restoration, and construction are important conservation measures aimed at mitigating the negative population trends. Habitat construction and restoration have positively impacted Swedish populations of wetland birds, especially rare species and species that have experienced substantial population declines during the last decades (Pärt, 2020; Strand & Weisner, 2013). Wetland construction can even positively impact bird species that are not water-dependent, such as swifts or swallows, likely by increasing the abundance of flying insect prey, such as chironomids (Strand & Weisner, 2013). Some evidence, however, suggests that natural wetlands might be more suitable as breeding habitats for waterbirds than constructed wetlands. For example, Sebastian-Gonzales and Green (2016) found that the diversity of breeding birds was higher in natural or restored wetlands than in constructed wetlands, and therefore urged for caution when interpreting studies emphasizing the importance of constructed habitats for wetland birds. Nevertheless, both wetland construction and restoration have a positive impact on many threatened or declining species and are valuable measures for bird conservation (Kačergytė, Arlt, et al., 2021; Pärt, 2020).

Depending on species characteristics, such as foraging strategy and nesting site preferences, birds have various habitat requirements and therefore utilize different parts of wetlands. Diving birds, for example, need deep water to forage, while dabbling and wading birds mainly reside in shallow water and along wetland edges. Nesting sites include, for example, the ground along wetland shores, among wet meadow vegetation, on floating vegetation or islands, in reeds or shrubs, or in nearby trees. In addition to the large variation between species, habitat requirements may vary between seasons, as birds have different needs for breeding, migration, and over-wintering (Ma et al., 2010). Though the diverse, and sometimes conflicting, habitat requirements of wetland birds are unlikely to be accommodated within a single wetland, habitat heterogeneity can generally promote a high species richness and abundance of birds (Ma et al., 2010; Verhulst et al., 2011). Here, we highlight three important aspects for providing suitable habitats to a diversity of wetland birds: topographic variation, water level fluctuations, and vegetation diversity.

Water depth is a key parameter determining accessibility to foraging habitats, largely because of morphological constraints, such as neck or leg length, which can restrict birds from foraging in deep water (Ma et al., 2010). Conversely, diving birds can be restricted by water too shallow to forage in, and the optimal water depth to promote a high abundance and species richness of wetland birds thus largely depends on which group dominates the regional bird fauna. In most regions, wading and dabbling birds are the dominant waterbird groups, and peak density thus generally occurs at water depths of 10-20 cm (Taft et al., 2002). However, a range of water depths is likely preferred to support a high species richness, and topographic variation is thus an important factor for promoting a diverse bird fauna (Ma et al., 2010; Taft et al., 2002). Other important topographic elements include gently sloping wetland margins, which create large, variable areas with shallow water, thus attracting species with diverse water depth requirements and promoting high abundance of wading and dabbling birds (Ma et al., 2010), and islands, which constitute nesting habitats sheltered from some mammal predators (Feuerbach, 2014; Ma et al., 2010; but see Kačergytė et al., 2021).

Predators such as foxes and minks prey on birds, especially eggs and chicks. Islands can create nesting habitats sheltered from fox predation, but not from the semiaquatic minks. Photo by Maria Nilsson.

Wading birds use the shallow areas of wetlands to forage, primarily for invertebrates. Here, two ruffs (*Calidris pugnax*, Sw. brushane). Photo by Maria Nilsson

In addition to topographic variation, heterogeneity of water depths can be created by fluctuating water levels, which provides diverse foraging opportunities and thus support a high species richness and abundance of birds (Ma et al., 2010; Murkin et al., 1997). Flooded areas are important foraging habitats for wading and dabbling birds (Eglington et al., 2007), and local species richness and abundance of breeding birds have been positively associated with the area of spring-flooded grassland and soil wetness (Kačergytė, Arlt, et al., 2021; Żmihorski et al., 2016). The biomass of soil macroinvertebrates, an important food source for wetland birds, have been found to be lower in flooded than in unflooded grasslands (Ausden et al., 2001). However, flooding likely enhances forage efficiency by increasing soil penetrability and keeping vegetation short, thus creating a net positive effect on resource availability (Ausden et al., 2001; Green et al., 1990; Żmihorski et al., 2016). Accordingly, wading birds have been found to prefer breeding sites close to wet features, likely due to the enhanced foraging conditions (Eglington et al., 2007). However, the effect of flooding varies between seasons, and high water levels during the breeding season may be detrimental for ground-nesting birds, as flooding of nests can increase the mortality of eggs and chicks, or cause birds to abandon the breeding attempt (Żmihorski et al., 2016). Accordingly, stable water levels provided the best habitat for summer-breeding wetland birds (Farley et al., 2021), and brood densities were higher in wetlands with stable water levels than in seasonally flooded wetlands (Ma et al., 2010). Water level fluctuations can further affect availability of aquatic prey, including dytiscids (Culler et al., 2014), amphibian larvae (Toledo et al., 2007), and fish (Ma et al., 2010), by mechanisms caused by both flooding and drawdown. Flooding can create small pools of water, constituting an additional and easily accessible source of aquatic prey (Ausden et al., 2001), and low water levels can enhance foraging efficiency by concentrating prey in smaller water bodies, increasing visibility, and hinder prey from escaping vertically (Ma et al., 2010). Low water levels during early autumn have been shown to increase resource abundance and quality of both vegetation and macroinvertebrates (Farley, 2020; Farley et al., 2021), which is especially important during bird migration. Some studies have found that bird abundance is positively associated with abundance of prey, such as amphibians (Kloskowski et al.,

2010) and fish (Baschuk et al., 2012; Gawlik, 2002). The effect of fish abundance, however, likely varies between bird species, as fish is known to compete with birds for macroinvertebrate prey (Eriksson, 1979). Further, fish presence has been negatively associated with duck breeding success, likely due to either competition or predation on chicks (Dessborn et al., 2011; Väänänen et al., 2012). Due to the various effects of water level fluctuations on resource availability and bird habitat use, optimal conditions for supporting a high diversity of birds are likely provided by creating a mosaic of unflooded and flooded conditions, with partial drawdowns as a possible compromise in small wetlands (Ausden et al., 2001; Farley et al., 2021).

Water level fluctuations are further important for maintaining a complex and diverse wetland vegetation, which in turn is associated with high species richness and abundance of birds (Ma et al., 2010; Żmihorski et al., 2016). Wetland vegetation provides habitat and increases food availability, both as a direct food source for herbivorous birds and indirectly, by providing habitat for and increasing abundance of invertebrate prey. The relationship between bird species richness and vegetation is however complex, and Kačergytė et al. (2021) found a negative relationship between emergent vegetation and abundance of breeding birds. The negative relationship could be a result of limited visibility, decreasing the detection probability during bird censuses, but it could also be a result of tall and dense vegetation limiting accessibility to foraging habitats. Accordingly, many bird species prefer sparsely vegetated or unvegetated areas for foraging, and therefore benefit from fluctuating water levels (Ma et al., 2010).

Vegetation heterogeneity has been associated with a high species richness and abundance of birds. Here, a family of Whooper swans (*Cygnus cygnus*, Sv. sångsvan) among the tall macrophyte vegetation. Photo by Maria Nilsson.

5 Discussion

Wetland physiochemical properties, community assemblage, and biodiversity are strongly governed by the hydrological regime, and understanding these relationships is of immense importance for conservation of wetland biodiversity. Though some relationships between habitat characteristics and species richness recur for multiple organism groups, the large variation of species-specific responses to hydrological variables makes it difficult to predict the effects of hydrology on wetland species richness. Here, we have suggested the use of indicators to quantify the hydrological aspects relevant to biodiversity, with the aim to optimize wetland design and management for high species richness, and as a tool for further research on the relationship between hydrology and biodiversity. The indicators may facilitate discerning the effect of hydrology from other variables affecting biodiversity, such as landscape characteristics, management, and species interactions.

Species interactions can have a substantial impact on wetland biodiversity, and many interactions are affected by hydrology. For example, vegetation plays a key role in wetland ecosystems by affecting environment conditions and providing food and habitat to an array of different organisms, and vegetation complexity has been associated with species richness of for example dytiscids (Liao et al., 2021; Nilsson et al., 1994), amphibians (Shulse et al., 2012), and birds (Ma et al., 2010; Żmihorski et al., 2016). Consequently, hydrological regimes that promote vegetation species richness and complexity, such as fluctuating water levels, by extension also affect species that utilize and depend on the vegetation community. Trophic interactions, where one species feed on another, are fundamental in structuring biotic communities and can have a large effect on species richness and abundance. For example, mild disturbances caused by grazing increase species richness of vegetation communities, and moderate nutrient enrichment can increase chironomid abundance (Blumenshine et al., 1997) and amphibian species richness (Brown et al., 2012; Werner et al., 2007). Many birds use wetlands as resting habitats before or during migration, and resource abundance, availability, and spatial distribution largely determines their use of foraging habitats (Ma et al., 2010). As indicated by the effects of fish presence on dytiscids (Liao et al., 2020), amphibians (e.g., Brown et al., 2012), and birds (Eriksson, 1979), trophic interactions can also negatively affect organisms, and excluding predators such as fish can increase wetland biodiversity. However, wetlands are important breeding habitats for fish, and populations of wetland-dependent species, such as the Northern pike (*Esox lucius*, Sw. gädda), have decreased due to habitat loss and degradation (Hansen et al., 2020). Allowing fish in wetlands is therefore crucial to achieve and maintain viable fish populations. It is possible to accommodate both predators and predation-sensitive species within individual wetlands, by for example constructing pools separated from the main water body, which could function as breeding habitats for amphibians, or by creating gently sloping margins, which organisms could use as a refuge from predators, thus decreasing the predation pressure. Nevertheless, it might be more feasible to accommodate such species in different wetlands, thus promoting a high regional biodiversity. Species interactions between the focal organism groups of this report are summarized in Figure 3. An overview of trophic interactions and the effects of hydrological factors on focal organism groups is shown in Figure 4.

Effect on (B) \ Effect of (A)	Vegetation	Chironomids	Dytiscids	Amphibians	Birds	Fish
Vegetation					P	
Chironomids			P		P	P
Dytiscids	* H			F	P	* P
Amphibians	* H		P		P	* P
Birds	* H, F	F	F	F		C, F

Figure 3. Species interactions between organism groups in this report and their effects on abundance. Fish are included due to their importance as a predator on multiple wetland organisms. Interactions are classified as predation (P), habitat provisioning (H), food source (F), or competition (C) based on the role of organism A (i.e., predation is when organism A predate on organism B, food source when organism B predate on organism A). Colours indicate the effect on abundance: blue squares indicate a positive effect, red a negative effect, and yellow a neutral effect. Grey squares indicate that the effect is unknown. '*' indicates that the same effect occurs on both abundance and species richness.

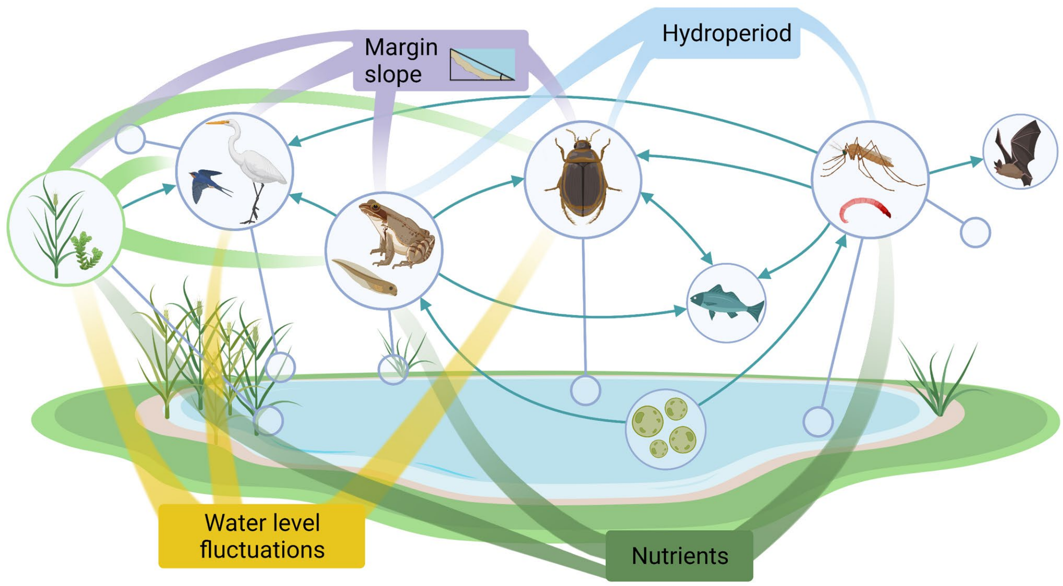
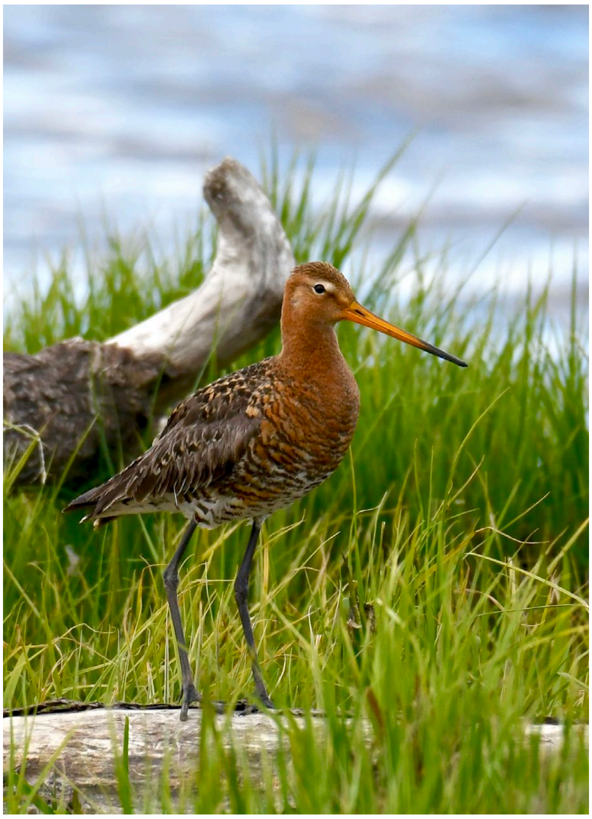


Figure 4. An overview of trophic interactions and effects of hydrological factors on focal organism groups. Focal organism groups are shown in large circles, with small circles indicating examples of their preferred habitat within wetlands. Algae, fish, and bats are included due to their importance as food source or predators. Trophic links are indicated by blue arrows, pointing in the direction of the energy flow. Coloured branches from hydrological factors indicate organisms affected, either abundance or species richness. Coloured branches from vegetation indicates organisms utilizing habitats created by vegetation. [Created with BioRender.com]

In this report, we have focused on the effects of hydrology on biodiversity within individual wetlands, to ensure relevance for wetland construction and restoration projects of different scopes. However, as described in section 2.2, when aiming to attain a high biodiversity and viable populations of wetland-dependent species on a regional or national scale, a landscape perspective on habitat availability and variation is essential. A high diversity of wetland types and characteristics in the landscape allows for various species assemblages and promotes a high regional species richness, in addition to creating opportunities for promoting other wetland services, such as nutrient retention or flood control. Further, multiple wetlands within a region can, for example, enable the use of different management regimes to promote various species, and provide habitats to both predators and predation-sensitive species, such as fish and amphibians, thus enabling conservation of both organism groups. When creating wetlands, the placement and distribution of habitats in the landscape is also important, as it affects dispersal possibilities between habitat patches. Migration between wetlands affects species turnover (variation of species among sites) and, if populations are small, possibly inbreeding rates and population persistence. Amphibian populations, for example, fluctuate naturally, and migration between sites can thus prevent local populations from going extinct during years with small population sizes. Dispersal rates vary between organism groups, and for example birds and dytiscids regularly disperse over large distances, while amphibians generally migrate over shorter distances and at lower rates. Organisms that are poor dispersers are also generally more sensitive to habitat isolation caused by landscape barriers, such as roads, and it is therefore important to consider habitat connectivity when constructing or restoring wetlands to benefit these organisms. Placement may also affect the net result of wetland construction on both local and regional species richness, depending on pre-construction habitat type and biodiversity values. For example, abundances of the western yellow wagtail (*Motacilla flava*, Sw. gulärla), a bird dependent on wet meadows, decreased after wetland construction, likely because its preferred habitat was replaced by open water (Strand & Weisner, 2013). Accordingly, wetland construction should, when possible, be prioritized in areas where current biodiversity values are low.

5.1 Implications for wetland construction, restoration, and management

When constructing or restoring wetlands, it is important to consider what the aim of the project is, as it will affect both design and management decisions. If the primary aim is to increase biodiversity values, it is further necessary to determine which species or organism groups the habitat should promote, preferably with regard to the regional diversity and existing habitats, as described in section 2.2. Generalist species can inhabit different types of wetlands, and most wetlands, provided they are constructed in previously species-poor environments, are therefore likely to increase local biodiversity by providing habitat to such generalists. However, to increase regional diversity and avoid trivialization of the wetland fauna, it may be necessary to provide wetlands of high habitat quality to benefit species with specific requirements, such as many red-listed species. Because such wetlands typically require more planning and optimization than wetlands aimed at more generalist species, the focal species of a project largely determines how resources should be allocated; in projects promoting general biodiversity, more resources can be allocated toward construction rather than planning, and it might even be possible to create more wetlands. An interesting approach, attempting a compromise between creating multiple habitats and optimizing individual wetlands, was used in the LIFE-Goodstream project, aiming to increase water quality and diversity by constructing wetlands along Trönningeån in Halland



The Black-tailed godwit (*Limosa limosa*, Sv. rödspov) is one of the most threatened bird species in Sweden. They require large areas of wet meadows to breed, a habitat that has decreased due to agricultural expansion and intensification (Jörneskog & Molin, 2015). Photo by Maria Nilsson.

county. There, they monitored biodiversity before and after wetland construction and took additional measures to promote biodiversity in sites showing great inherent potential for high species richness (Naturvårdsverket, 2021b). Such measures included, for example, installing nesting boxes for birds and insects, and creating breeding ponds for amphibians. Hence, they were able to promote sensitive species without extensive planning.

Recently, wetland multifunctionality, where wetlands are constructed with the aim of providing multiple ecosystem services, has become the aspiration of many projects. These services can include for example nutrient and water retention, flow regulation, biodiversity, carbon sequestration, and recreation, yet not all functions are necessarily compatible. For example, a high nutrient load can increase the cost efficiency of wetland nutrient retention, but it might simultaneously decrease species richness of vegetation and exclude organisms sensitive to eutrophication, such as amphibians. Similarly, recreation is often an important motivation for wetland construction, but high visitor pressures can have a negative effect on for example breeding birds. In such cases, prioritizing between wetland functions can be facilitated by a well-defined project aim. This applies to other trade-offs as well, such as the common issue of deciding on what is better for conservation - a single large area or several small. No general rule applies to all situations, and for wetland biodiversity, there are potential benefits of both scenarios. Species diversity of some organism groups increase with habitat area, and some threatened wetland species require quite large areas to be at all able to utilize a wetland. However, because species assemblage varies between wetland types, several small wetlands with different characteristics may host a larger variety of species, and multiple small habitats have, for example, been shown to have a similar effect on birds as a single large wetland of corresponding area (Kačergytė, Arlt, et al., 2021). Furthermore, it may be more feasible to create small wetlands, as landowners would not need to give up such large areas of productive land. Considering the varying effects of wetland size, a mix of habitats sizes within the landscape is likely optimal for biodiversity conservation.

As previously mentioned, there are some wetland characteristics that increase biodiversity of multiple organism groups, and it is possible to incorporate these characteristics when creating wetlands. Here, we list some general guidelines to consider when designing wetlands aimed at increasing biodiversity. The list is a compilation of new guidelines, based on this review, and existing guidelines, largely adapted from Feuerbach (2014), in which further descriptions of the recommendations can be found (however, citations to the original work are not included in that report).

- **Location:** when choosing a location for wetland construction, areas which initially have low biodiversity should be prioritized. The distance to other wetland habitats should also be considered, with respect to the dispersal abilities of focal organisms.
- **Surrounding landscape:** depending on focal species, the surrounding landscape can be of varying importance. For example, birds prefer wetlands without surrounding trees (Żmihorski et al., 2016), as birds of prey or egg snatching birds use them as lookout spots, while amphibians, which utilize non-wetland habitats as adults, prefer wetlands in close proximity to suitable forest habitats (Findlay & Houlahan, 1997).
- **Water level:** appropriate water level depends on focal species, but there are some general reference points. Reeds cannot grow at depths over two meters, and cattails are excluded at depths over 70 cm. Wading and dabbling birds prefer water depths between 10 and 60 cm, as it allows them to reach the bottom to feed on plants and invertebrates (Feuerbach, 2014).
- **Water level fluctuations:** variation of water levels can prevent wetlands from overgrowing. Generally, water fluctuations of at least 50 cm will decrease abundance and affect distribution of emergent macrophytes (Feuerbach, 2014), and occasional higher flooding can further decrease the growth of emergent or woody species (Smith et al., 2021). Flooding further benefits wetland birds by increasing food availability (Kačergytė, Arlt, et al., 2021; Żmihorski et al., 2016). Low water levels facilitate germination of many plant species (Raulings et al., 2010; Van Geest et al., 2005), and allowing wetlands to dry out excludes fish and predatory macroinvertebrates, which predate on for example amphibians.
- **Wetland morphology:** gently sloping margins create shallow areas that are important habitats for birds, amphibians, and dytiscids (Brown et al., 2012; Liao et al., 2020; Ma et al., 2010). Islands can benefit birds, as they enable nesting in a habitat protected from terrestrial predators. Islands should be located at least 15 meters from land (Feuerbach, 2014), and it is important that the slopes are gentle, as some aquatic birds otherwise might have trouble getting up on land. A long shoreline creates microhabitats that benefit birds (Hansson et al., 2005), and microtopographic variation increases species richness and complexity of vegetation (Raulings et al., 2010).
- **Tilling, mowing and grazing:** to increase vegetation complexity and prevent wetlands from overgrowing, it is important to enable mowing or grazing. Grazing can further increase biodiversity by creating both variation in vegetation height and microhabitats from for example trampling, which also exposes soil, thus promoting seed germination. To increase microtopographic variation, tilling has been used during wetland construction (Moser et al., 2007).
- **Adapting management to seasonal requirements:** how organisms utilize wetlands often vary between seasons and adapting the management regime to meet the various needs can further promote wetland biodiversity. For example, the effects of water fluctuations on birds depend on seasonality (Ma et al., 2010). During spring and fall migration, varying water levels can increase foraging efficiency, but during the summer, increasing water levels can be detrimental to ground-nesting birds.

5.2 Future research needs

Here, we highlight three areas of interest for future research aiming to understand the relationships between hydrology and biodiversity, and their implications for wetland construction and management.

First, in this report, we have not reviewed how important hydrology is in relation to other wetland characteristics that affect biodiversity. Are there instances where hydrology is more or less important in relation to other characteristics, and how does this vary between wetland types and organism groups? Future research should aim to explore literature regarding such relationships and, if needed, perform complementary field work.

Second, multifunctional wetlands are suggested as nature-based solutions for an array of purposes, including improved water retention and quality, carbon sequestration, biodiversity, and recreation. However, not all wetlands are optimal for all purposes, and there are trade-offs between certain aims, such as biodiversity and recreation. Future research should aim to describe both trade-offs and synergies for wetland multifunctionality, specifically regarding biodiversity.

Finally, in this report, we have suggested a suite of hydrological indicators for measuring aspects of the hydrological regime relevant to biodiversity. These indicators are based on literature describing the relationships between diversity and hydrology but have not yet been tested against data. Indicators could be tested on a small scale, such as in studies of individual wetlands or small multi-wetland landscapes. However, they could potentially also be tested on a larger scale by compiling a dataset that combines biodiversity and hydrological indicators. Such a dataset could be subjected to various types of statistical analysis, modeling, and potentially also more sophisticated machine learning methods, if the dataset is large enough. By exploring and explaining the data with increasing accuracy, these methods could ultimately infer the sensitivity of biodiversity to hydrological factors.

The largest current obstacle when it comes to implementing these methods is the poor data availability regarding biodiversity indicators. Very few large-scale surveys of species exist, and those that do generally only consider one or a few organism groups. Possible workarounds include using commonly surveyed species, such as birds or amphibians, as indicators for general biodiversity. Further, Pärt (2020) investigated the possibilities of using voluntary reports of bird species observations from Artportalen (https://www.artportalen.se/) to analyse the effects of wetland restorations. He highlighted some difficulties of using voluntary reports, including the lack of absence reports (i.e., reports of species not present at a site), a spatial bias towards popular bird watching sites, and a large uncertainty of the number of individuals reported. However, he claims that, for some analyses, it is possible to take these uncertainties into consideration with modifications to the statistical method. Further, Artportalen has since then introduced a form of reporting including absence of species, known as checklist reporting, which facilitates the use of data in scientific studies.

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