Arthropods in Constructed Wetlands

Ecosystem Processes and Riparian Biodiversity

David Åhlén

This thesis contains the following chapters:


II. Åhlén D, Peacock M, Urrutia-Cordero P, Hambäck PA. Aquatic productivity subsidies drive shoreline arthropod abundances differently across taxa and trophic levels in constructed wetlands. Manuscript.


Abstract
Constructed wetlands in the agricultural landscape are known to harbor immense arthropod biodiversity, however, riparian arthropod communities have often been neglected compared to aquatic communities when studying environmental responses. These wetlands are highly productive, but vary in form and composition based on its purpose, which influences the communities that inhabit them. Both biotic and abiotic wetland characteristics are known to drive aquatic arthropod community compositions, whereas knowledge is currently lacking as to the influence from characteristic wetland properties on riparian arthropods.

This thesis aimed to shed a light on characteristic wetland drivers on riparian arthropod populations and communities. We explored how chironomid emergence rates and diversities responded to wetland nutrient loads and primary production (Chapter I), and subsequently if trophic cascading relationships could be observed across the aquatic-terrestrial boundary to riparian predator abundances (Chapter II). We also explored how riparian arthropod community compositions responded to wetland hydrologic dynamism, shoreline inclines and vegetation height, and grazing management (Chapter III), and finally how characteristic wetland shoreline properties influenced riparian arthropod diversities and habitat specializations (Chapter IV).

In Chapter I we found that emergence rates and diversities of chironomids increased with aquatic chlorophyll concentrations during parts of the season but decreased during others, and that chironomid taxonomic diversity correlated with the aquatic concentration of methane. These findings support previously suggested trade-offs relationship between emerging chironomids and methane. We expanded on these findings in Chapter II, where we found that both primary- and secondary consumer abundances responded to wetland nutrient loads and chlorophyll concentrations, but that this trophic pathway was more complex than from primary producers, through primary consumers to secondary consumers. In Chapter III we found that some riparian arthropods responded to hydrological dynamism, but that surprisingly many groups were unaffected. We also found that many groups responded to shoreline vegetation height, but that responses were group specific. Similarly, in Chapter IV we found that shoreline properties greatly influenced spider, beetle and predatory Diptera diversities in constructed wetlands, and that their habitat specialized species richness varied greatly between groups.

Altogether, these findings illustrate the complexity of wetland arthropod ecology, and the need for attention to these previously understudied systems. It also highlights the importance of comprehension regarding constructed biodiversity wetlands if the aim is to improve biodiversity across multiple taxa.

Keywords: constructed wetlands, arthropods, community ecology, spiders, insects, hydrology, shoreline properties, primary production, greenhouse gasses, nutrients, grazing management.
ARTHROPODS IN CONSTRUCTED WETLANDS
David Åhlén
Arthropods in Constructed Wetlands
Ecosystem Processes and Riparian Biodiversity

David Åhlén
Furu ike ya
kawazu tobikomu
mizu no oto

- Matsuo Bashō, 1686
English summary

Constructed wetlands in the agricultural landscape have recently been given substantial regional and global emphasis, as they provide natural ecosystem services through nutrient capture and water buffering capacity, and are known to harbour valuable biodiversity. However, not all wetland communities have received equal emphasis, and where one of the most species rich groups have remained woefully understudied, namely terrestrial arthropods. By comparison, aquatic arthropods have received substantial focus, where terrestrial arthropods have mainly been considered a subcommunity to the aquatic community. In this thesis we aimed to study the influence of characteristic wetland properties on terrestrial arthropods to elucidate drivers that governed their populations and community compositions.

The first two chapters of the thesis focused on aquatic wetland productivity and the influence that had on arthropod emergence (Chapter I) and subsequently on riparian predator abundances (Chapter II). We measured aquatic nitrogen and phosphorus loads, together with chlorophyll-a concentrations during spring, summer and fall in constructed wetlands in cultivated landscapes to characterise wetlands based on nutrient status and productivity. This was compared to aquatic emergence rates of chironomid midges (Diptera: Chironomidae), and to abundances of chironomids, sciarids (Diptera: Sciaridae) and riparian predators by the wetlands. We found (I) that emergence rates, taxonomic diversity and feeding group diversity of chironomids from the aquatic part of wetlands increased with
concentrations of chlorophyll-a during certain months, but decreased with chloro-
phyll-a concentrations during others. We also found that wetland phosphorus loads
influenced aquatic methane concentrations which, similar to chironomid abund-
dances and diversities, peaked during summer months. We also found that, chirono-
mid taxonomic diversity correlated positively with methane concentrations, with
a near significant similar relationship between methane concentrations and chiron-
omid emergence rates. This suggested a trade-off relationship between chironomid
communities and methane production in these wetlands. We also found (II) that
greater abundances of chironomids and sciarids by wetlands related to greater
abundances of some spiders, beetles and predatory Diptera. However, wetland nu-
trient loads and chlorophyll-a concentrations also influenced abundances of certain
riparian predators. This suggested that riparian predators utilized multiple wetland
subsidies, and that trophic interactions were more complex than bottom-up rela-
tionships from primary producers, through prey to predators.

The last two chapters of the thesis focused on riparian arthropod population
sizes driven by wetland hydrology dynamics, shoreline vegetation (Chapter III),
and diversity responses from wetland shoreline properties and grazing manage-
ment (Chapter IV). We screened wetland riparian arthropod communities to relate
population sizes to nearly three years’ worth of high resolution hydrology meas-
urements. We studied how riparian populations responded to water table dyna-
mism, inundation frequencies, flood zone sizes, shoreline inclines and shoreline
vegetation height. We also measured the cover of wetland reedbeds, flooded grass-
land areas, and surrounding pastures and meadows to explain how riparian arthро-
pod diversities responded to common wetland properties. We found that (III)
abundances of shoreline Diptera were lower by wetlands with longer durations of
high-water tables whereas abundances of tue bugs (Hemiptera) and caddis flies
(Trichoptera) were lower by wetlands with longer periods of low-water tables.
Wetlands with greater shoreline inundation frequencies also supported less water
scavenger beetles (Hydrophilidae: *Coelostoma*), crane flies (Limoniidae: *Erioptera*) and rove beetles (Staphylinidae: *Stenus*). Surprisingly, total order abundances and community compositions did not always respond similarly to inundation frequencies. This suggested that hydrologic dynamism did not necessarily filter arthropods at higher taxonomic levels, but rather at genus or species level, and as such suggested substantial group specific population responses. We also found that wetland shoreline properties substantially influenced riparian arthropod diversities, and species richness among habitat specializations, and that responses were again group specific. We also found that spider phylogenetic diversity increased, whilst total-, and wetland specialist predatory Diptera species richness decreased with greater shoreline inclines, and that spider trait diversity and wetland specialist beetle species richness increased, but beetle trait diversity decreased with greater flooded grassland areas. This suggested that shoreline properties filtered arthropod community structers differently both across and within taxonomic groups, and that wetlands with varied shoreline properties would best benefit riparian arthropod diversity. Finally, we found that grazing management had little impact on arthropod diversities, but that species richness in generalist and terrestrial specialist Uppland spiders and wetland specialist predatory Diptera in wetlands with larger flooded grassland areas, was lower when grazing livestock were present.

In Conclusion, constructed wetlands in agricultural landscapes posess features essential for arthropod biodiversity, however, requirements of terrestrial arthropod populations are decisively group specific. As such, to provide the most beneficial wetland habitats for arthropod biodiversity, these wetlands should be constructed with varying shorelines, but with primarily gentle slopes and areas that can flood and include some characteristic wetland vegetation, to benefit more riparian ar-
thropods. Alternatively, multiple smaller proximal wetlands with different characteristics in wetlandscapes could fill the same purpose as larger singular wetlands, where metapopulations could easily migrate or disperse between habitats.
Svensk sammanfattning

Anlagda våtmarker i jordbrukslandsbandskapet har på senare år blivit både en global och regional angelägenhet, då de bidrar med naturliga ekosystemtjänster genom näringsretention och att buffra vattenflöden, och då de samtidigt innehar hög biodiversitet. Dock har inte alla våtmarkssamhällen erhållit lika stora kraftansamlingar, där en av de mest artrika grupperna har blivit synnerligen åsidosatt, nämligen landlevande leddjur. Jämförelsevis så har avsevärt mycket mer energi lagts på att studera vattenlevande leddjur, där landlevande leddjur setts som en mindre del av det akvatiska leddjurssamhället. I denna avhandling avsåg vi att studera hur karaktäristiska våtmarksbetingelser påverkar landlevande leddjur för att ta reda på vad som styr deras populations- och samhällssammansättningar.

De första två kapitlen av avhandlingen fokuserade på våtmarkers produktivitet samt hur detta påverkade kläckningstakten hos leddjur (Kapitel I) och vidare abundansen hos strandlevande rovdjur (Kapitel II). Vi mätte vattenkonzentrationer av kväve och fosfor tillsammans med klorofyll-a-koncentrationer under vår, sommar och höst i anlagda våtmarker i kultiverade landskap för att karaktärisera våtmarkerna utifrån näringsstatus och produktivitet. Detta jämfördes sedan med den akvatiska kläckningstakten av fjädermyggor (Diptera: Chironomidae), och abundansen av fjädermyggor och sorgmyggor (Diptera: Sciaridae) vid våtmarkerna. Vi fann att (I) kläckningstakten, den taxonomiska mångfalden och diversiteten hos födgrupper hos fjädermyggor ökade med koncentrationen av klorofyll-a under vissa månader, men minskade med klorofyll-a-koncentrationer under andra. Vi fann också att fosforkoncentrationen påverkade vattenkonzentrationen av metan och, som hos abundansen och mångfalden hos fjädermyggor, var som

De sista två kapitlen av avhandlingen fokuserade på effekten av hydrologiska processer i våtmarker och strandvegetation på populationsstorlekar hos leddjur i strandzonen (Kapitel III), samt mångfaldseffekter förutsatt strandlinjens betingelser och beteshävd (Kapitel IV). Vi granskade leddjurssamhällen i strandzonen av våtmarker för att ta reda på hur populationer svarade mot höguplösta hydrologiska mätserier som samlats in under nästan tre års tid. Vi studerade hur strandlevande populationer påverkades av vattennivådynamiker, översvänningsfrekvenser, storleken på översvämningszonen, strandlinjens höjd samt vegetationshöjden vid strandlinjen. Vi mätte också storleken på våtmarkernas vassbälten, översvämnande gräsmarker, och omkringliggande ängs- och betesmarker för att förklara hur mångfalden hos leddjur i strandzonen påverkades av vanligt förekommande våtmärksbetingelser. Vi fann att (III) förekomsten av tvåvingar i strandlinjen var lägre vid våtmarker med längre perioder av högvatten, medan förekomsten av halvvingar (Hemiptera) och nattsångare (Trichoptera) var lägre vid våtmarker med längre perioder av lågvatten. Våtmarker med högre översvämningsfrekvens hade färre palpbaggar (Hydrophilidae: Coelostoma), småharkrankar (Limoniidae: Erioptera) och kortvingar (Staphylinidae: Stenus). Något överraskande var att totala
abundansen hos ordningar och sammansättningen av samhällena inte alltid svarade likadant gentemot översvämningsfrekvenser. Detta antydde att hydrologiska dynamiker inte nödvändigtvis filtrerade leddjur vid högre taxonomiska nivåer, utan snarare på släktes- eller artnivå, vilket således antydde att det förekom ansenliga gruppsspecifika populationseffekter. Vi fann även att (IV) betingelser hos våtmarkers strandlinjer i hög grad påverkade mångfalden av leddjur, och artrikedomen inom leddjursgrupper av olika habitatspecialister i strandzonen, och att dessa samband återigen var gruppspecifika. Vi fann också att den fylogenetiska diversiteten hos spindlar ökade, medan både den totala- och den våtmarksspecialiserade artrikedomen hos rolevande flugor minskade med högre strandsluttningar, samt att egenskapsdiversiteten hos spindlar och artrikedomen hos våtmarksspecialiserade skalbaggar ökade, medan egenskapsdiversiteten hos skalbaggar minskade med större ytor av översvämnande gräsmarker. Detta antydde att betingelser i strandlinjen filtrerade leddjurssamhällens sammansättning på olika vis både mellan- och inom taxonomiska grupperingar, samt att våtmarker med varierade betingelser längsmed strandlinjen bör gynna mångfalden hos strandlevande leddjur bäst. Slutligen fann vi att beteshävd hade liten påverkan på mångfalden av leddjur, men att artrikedomen hos habitatgeneralister och landlevande specialister hos spindlar, och hos våtmarksspecialiserade rolevande flugor var lägre då betesdjur nyttjade våtmarken.

Sammanfattningsvis innehar anlagda våtmarker i jordbrukslandskapet egenskaper som är nödvändiga för den biologiska mångfalden hos leddjur, dock är behoven inom populationer av strandlevande leddjur klart gruppspecifika. Således bör dessa våtmarker anläggas med en varierande strandlinje, men med huvudsakligen flackare sträder och ytor som kan svämma över och innehålla en våtmarksspecifik flora för att ge de mest gynnsamma förutsättningarna för strandlevande leddjur. Alternativt skulle flera mindre näriggande våtmarker med olika egenskaper i ett
våtmarkslandskap kunna fylla samma syfte som en större våtmark, där metapopulationer lättare kan röra sig mellan habitat.
This thesis is supported by the findings in the four main chapters presented

Chapter I

Chapter II
Åhlén D, Peacock M, Urrutia-Cordero P, Hambäck PA. Aquatic productivity subsidies drive shoreline arthropod abundances differently across taxa and trophic levels in constructed wetlands. Manuscript.

Chapter III

Chapter IV
My participation in the chapters of the thesis

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Participation explanations:

Minor: Contributed in some way, but limited

Significant: Significant contribution to the work

Substantial: Took the lead role and performed the majority of the work
Studies that I collaborated on during the thesis work, not included in this thesis.


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Introduction

What is a wetland?

The first thing people usually think of when pondering wetlands is an ecosystem where a source of water soaks the land surrounding it, and contain large reed beds, fertile vegetation and brimming with life. Some also visualizes it as dark, ominous areas of land, still centred around a water source, but where old crooked trees lean in, with vines hanging off them with insects filling the air and the water being filled with frogs. From an ecologist’s perspective, both are true. Although, we also include fens and bogs covered in sphagnum moss, riverine deltas, vernal pools, ponds, lake and sea shorelines, coral reefs and mangrove forests, and so many other types of habitats. This multitude visualizes an essential problem in wetland ecology. How does one define what a wetland is? A common international definition wetland ecologists refer back to is the one stated in the Ramsar convention (1971), where wetlands are defined as “areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres”. As a general description of a wetland, this definition encompasses most waters where the water depth does not exceed 6 meters, and the shorelines surrounding it. The Ramsar convention (1971) also defines five different types of wetlands, mainly dictated by the hydrological dynamics seen in the habitats. 1) Marine wetlands, being wetlands along sea coastlines, 2) Estuarine wetlands, being delta landscapes, tidal marshes and mangrove forests, 3) La-
custrine wetlands, being wetlands that are associated to lakes, 4) Riverine wetlands, being wetlands formed around rivers and streams, and 5) Palustrine wetlands, being marshlands, swamps and bogs and fens.

In Sweden, another categorization is more commonly used (translated to English): “Wetlands are types of land where water levels lie right below-, at-, or just above the ground surface level during a substantial part of the year, including waters that are covered in vegetation. The limits to how close water levels can be to the ground surface level in wetlands vary. In most cases, the vegetation can be used to separate wetlands from other types of land. At least 50% of the vegetation has to be “hydrophytic”, meaning moisture-loving, for the land to be defined as a wetland. The exceptions are intermittently dried lake-, sea- and streambeds, which are also counted as wetlands, even though they may lack the vegetation“ (Löfroth, 1991). These definitions are better adapted to Swedish environments, and exclude true lakes and seas, and are further categorized into three categories. 1) Bogs and mires, being anoxic peat forming ecosystems such as raised bogs, mixed bogs and fens, 2) Shores, including lake and stream shorelines, and sea shorelines, and 3) Other wetlands, which are not defined as either bogs or shores, for example wet heaths, wet meadows and wet forests.

These all have different characteristics that define them by their natural water source and hydrological dynamics, and by also being influenced by the soil structure and geochemical composition. The one thing they all have in common is that they form around some natural source of water. However, today human realization of the importance of wetlands in the landscape has introduced another type of wetland, Constructed wetlands, being wetlands that are made from dredging, redirecting or damming habitats that collects water to form an artificial wetland.
Wetlands in a changing world

Wetlands today are heralded as one of the most important ecosystems on earth. They host immense biodiversity, mitigate agricultural nutrient runoff and buffer water flows (Meli et al., 2014). Before industrialization, wetlands occurred naturally where hydrological conditions formed them, either by flooding of rivers as seen in estuarine and riverine wetlands, or where water tables in lakes rise and descend as seen in lacustrine wetlands (Ramsar Convention, 1971). Or they may form in other areas where topographical structures traps water and allows for characteristic hydrophytic vegetation to grow as seen in palustrine wetlands. However, before the invention of artificial fertilizers, the only way to increase crop yields was to expand croplands, which is the main reason wetlands in the agricultural and forestry landscapes was drained, and as a result upwards of 87% of natural wetlands have been lost since 1700 (Davidson, 2014). This change has resulted in tremendous biodiversity loss (Gibbs, 2000), recipient water eutrophication from agricultural runoff (Carpenter et al., 1998; Smith, 2003) and altered landscape hydrology (Sterling et al., 2013).

During the last few decades however, actions have been taken to mitigate the negative effects seen through constructing wetlands, which has resulted in beneficial ecosystem services by reducing eutrophication and preventing droughts, and benefiting biodiversity (e.g. Thiere et al., 2009; Meli et al., 2014). Wetland construction mainly takes place in the agricultural landscape where ponds and lakes are established to counterbalance negative effects from large scale agriculture, such as nutrient runoff, aridity due to drainage, and loss of biodiversity as a consequence of habitat fragmentation.
The perfect constructed wetland

Constructing a wetland comes with certain requirements specific to its purpose. Often the landowner who wants to construct the wetland does so either to mitigate nutrient runoff, buffer water flow, benefit biodiversity, or for recreational purposes. Nutrient capture wetlands are generally constructed to capture nitrogen or phosphorus, and for each nutrient wetland structure requirements are set to maximize those benefits (e.g., Vymazal, 2007). These requirements provide limitations on wetland structure, where nitrogen capture wetlands often are shallow with abundant emergent vegetation, whereas wetlands constructed to capture phosphorus need to be deeper with slow flowing water for phosphorus particles to sediment (Reddy et al., 1999; Vymazal, 2007). As a consequence of capturing nutrient runoff, agricultural wetlands are generally categorized as eutrophic based on nutrient loads (IPCC, 2019) with elevated primary production, since nutrient and water limitations for primary producers are alleviated. Water buffering wetlands are often constructed to prevent floods, and are most effective when permeable soils in the shape of floodplains connected to streams and rivers allows for soil saturation (Acreman and Holden, 2013). However, agriculture landowners often restrict the sizes of constructed wetlands to minimize loss of valuable arable land by constructing the wetlands with steep shorelines, and by controlling the high-water table levels through overflow pipes and outlets. As a consequence, constructed wetlands in the agricultural landscape are often small (<1ha) with limited flooding potential. The shape of constructed wetlands in agricultural landscapes would mostly be classified as small lacustrine wetlands (Ramsar Convention, 1971), or as lake or pond shorelines with adjacent wet meadows (Löfroth, 1991).

Wetlands with large shallow flood zones are generally considered to be most beneficial to biodiversity, where aquatic nutrients washes ashore during floods and are utilized by shoreline plants and animals. Most wetlands that are constructed for biodiversity focuses on bird biodiversity, with multiple initiatives both on national
and international levels (e.g. Natura2000). Though, requirements in one group does not necessarily cover the needs of all taxa. For example, a snipe utilizes flood zones to forage whereas a grebe needs open water and a heron regularly hunt along reedy embankments. These are characteristic structures of a wetland, but their composition within a wetland generally dictate the structures of the animal communities that inhabit them. The small size of biodiversity wetlands in the agricultural landscape often limit biodiversity, as larger habitats generally benefit biodiversity by containing a more varied set of microhabitats (Preston, 1962; MacArthur and Wilson, 1967). Nevertheless, by constructing wetlands in the agricultural landscape, local and regional biodiversity generally increases, where communities in newly constructed wetlands soon approach diversities seen in mature agricultural wetlands (Thiere et al., 2009).

Wetlands in the agricultural landscape also naturally change rapidly through succession. Left on its own, highly productive wetlands will quickly overgrow with vegetation such as cattails (Typha sp.) and reeds (mainly Phragmites australis) that root in waterlogged soils as water recedes, and can rapidly expand to cover the entire wetland (Galatowitsch et al., 1999; Zedler and Kercher, 2004). Similarly, willows (Salix sp.) often root along wetland shorelines and can create substantial habitat barriers. Therefore, management regimes often state that wetlands need to be managed to mitigate overgrowth and retain open waters by dredging and shearing aquatic vegetation, and mowing wetland shorelines (e.g. Feuerbach, 2014). Historically, wetlands were commonly used as grazing pastures for livestock, which is also a common way of managing wetlands today by slowing succession from primarily sedge (mainly Carex sp.) and rush (mainly Juncus sp.) to willows and other woody vegetation.

Since wetlands fill many purposes, they are often considered multifunctional ecosystems (Nagabhatla and Metcalfe, 2018). However, considering the size and structural variation in constructed wetland morphologies, it can be argued that a
singular small wetland may be less beneficial for multiple purposes compared to multiple wetlands with varying characteristics, where the intervening distance is short, for both biodiversity and for other functions (Samways et al., 2020; Ferreira et al., 2023; Hambäck et al., 2023).

**Dichotomy of wetland habitats**

The most basic principle of a wetland are the dynamic hydrological conditions, and the interaction of aquatic and terrestrial habitats. In most types of natural wetlands, this dynamic follows temporal cycles ranging from daily tidal fluctuations to seasonal floods. These natural fluctuations create dynamic shoreline habitats with considerable influence from aquatic-terrestrial interactions. Such edge-zones are essential for species that are evolutionarily specialized to inhabit wetland habitats and which often have adaptations that allows them to survive flooding (e.g. Hensel et al., 2016), or to utilize flooding during parts of their life histories (e.g. Vinnersten et al., 2014; Lindström et al., 2021). Both natural and constructed wetlands follow these dynamics, although the temporal variation may be less pronounced and less cyclic in constructed wetlands than in natural wetlands due to water table controls.

The combination of aquatic and terrestrial habitats is unique amongst ecosystems, and allows for considerable variation in community trait compositions among species inhabiting them, and also substantial species turnover across the aquatic-terrestrial boundary, since the full wetland communities include both aquatic-terrestrial and amphibious species. Life histories for species inhabiting aquatic and terrestrial habitats can differ considerably, with some species inhabiting the aquatic habitat for the duration of their lives, whereas others have aquatic life stages during larval development and terrestrial life stages as adults. For example, amphibians in temperate regions often use wetlands and ponds for spawning in the spring where aquatic larvae develop during summer and metamorphs
emerge from the water and prey on invertebrates in the surrounding habitat in late summer and early fall (Stebbins and Cohen, 1997). One of the most abundant and diverse group of animals in wetland ecosystems are arthropods, with both fully aquatic, semi-aquatic and fully terrestrial species. Diving beetles (Coleoptera: Dytiscidae) for example have predominately aquatic life stages with most larvae and adult forms being aquatic predators (Nilsson and Holmen, 1995). Caddis flies (Trichoptera) on the other hand are semi-aquatic, where larvae inhabit aquatic habitats, that emerge from the water after pupation as terrestrial adults. Spiders are also found in abundance along wetland shorelines, with the majority being fully terrestrial, utilizing the abundance of prey that the wetland provides. Many arthropods also utilize the wetland flood zone for larval development. For example, crane fly larvae (Diptera: Tipulidae) often develop in moist soils surrounding wetlands (Oosterbroek, 2006), with a plethora of other taxa having similar life histories. This enigmatic development makes studying their ecology difficult, and is likely one of the reasons why terrestrial arthropods are substantially understudied compared to aquatic arthropods.

Wetlands are often grouped into aquatic habitats, where terrestrial arthropods may be considered a subset of the aquatic community, and as such often understudied compared to the aquatic fauna as is concluded by Batzer and Wu (2020). They also acknowledge that the communities found in wetland systems are not identical to truly aquatic habitats such as lakes or rivers, nor of truly terrestrial systems such as forests or grasslands, and should instead be considered as separate ecosystems, with unique faunas that are specific to wetlands.

**Riparian arthropod requirements**

Truly aquatic arthropod faunas are often linked to the hydrological conditions of the wetlands they inhabit. Some species mainly thrive in habitats with long or
permanent hydroperiods (e.g. midges [Diptera: Chironomidae]) whereas other species may rather require short flooding durations of shoreline structures for hatching and larval development (e.g. mosquitoes [Diptera: Culicidae]). Species may also be influenced by intraspecific competition, and presence of predators in the water (e.g. fish [Zimmer et al., 2002]), or by connectivity to other aquatic habitats for migration between habitats. These species are often tightly linked to aquatic habitats due to their specialization, which may therefore limit their species richness. In comparison, terrestrial species around wetlands may more easily migrate perpendicular to the shoreline of the wetland and utilize the adjacent surrounding terrestrial habitats during floods, and follow the waterline and utilize exposed aquatic resources as waters recede (Rothenbücher and Schaefer, 2006). Since the surrounding terrestrial habitats are often more heterogeneous than the truly aquatic ones, the terrestrial arthropod fauna around wetlands is also often considerably more diverse than the aquatic fauna. However, since the terrestrial arthropod fauna by wetlands is so understudied compared to the aquatic fauna, little is known regarding what drives their populations and communities.

**On riparian arthropod populations**

Niche requirements of arthropods in wetlands vary considerably between species based on their life histories and traits, and as such population sizes of species differ between wetlands as wetlands differ in their composition and dynamics. For example, the mosquito *Aedes sticticus* (Culicidae) can be extremely abundant in habitats with regular spring floods (Lindström et al., 2021), but is often less abundant in wetlands where flood dynamics are more stable. Conversely, midges with fully aquatic larvae are often most abundant in habitats with more permanent waters (Oosterbroek, 2006). Other groups may require properties that are not directly linked with the hydrological aspects of wetlands, but rather secondarily as a consequence of wetland hydrology. For instance, sciarids (Diptera: Sciaridae) may be
abundant in wetlands that maintain high soil moisture, which is required for their larval development (Oosterbroek, 2006), and as such are often abundant in wetlands with broad flood zones. Donacia (Coleoptera: Chrysomelidae) species are rather linked to hydrophytic vegetation, and is mainly found near aquatic habitats with greater abundances of Carex (Ljungberg et al., 2017), whereas dragonfly (Odonata) species have aquatic larvae that require emergent vegetation to climb up during the last larval instar for metamorphosis into adults (Huikkonen et al., 2020) why reeds and cattails may be important. Since wetland habitats may contain hydrological and structural properties that vary between wetlands, populations of arthropods may differ considerably between sites, especially in smaller wetlands with low local habitat heterogeneity.

Relatively many wetland specialist arthropod species also currently appear on national and international red lists (SLU Artdatabanken, 2020; IUCN, 2022), since habitat destruction has resulted in their niche habitats having disappeared. Specialist species, by definition, have narrower niches which means that they are less likely to survive when their main habitat disappear. Particularly in agricultural landscapes where wetlands are rare, the intervening landscape can form buffers that limit metapopulation dynamics, whereby an isolated population may have limited immigration from neighbouring populations (e.g. Preau et al., 2022). Considering that wetlands are essential in maintaining wetland specialist species populations, whilst simultaneously benefitting generalists and terrestrial specialists in depauperate agricultural landscapes, their value to arthropod biodiversity is clear.

On riparian arthropod communities

Larger habitats are often more heterogeneous and fulfil niche requirements of more species, and are therefore often also more species rich (MacArthur and Wilson, 1967). Since agricultural wetlands provides heterogeneity in agricultural landscapes, they will support a greater diversity than the surrounding landscape,
by simply providing this heterogeneity. Similarly, when considering metapopulation dynamics, proximal smaller wetlands may function comparably to a large wetland even if singular wetlands may be homogeneous, by forming a wetlandscape.

When considering community diversities, it is also important to consider how the habitats filter the diversity, and at what level the diversity is studied. Diversity is often studied by means of species richness (Spellerberg and Fedor, 2003), however species richness alone explains only a part of community structure and function. Species may be phylogenetically or functionally clustered, where filtering mechanisms may act on any level of organization. Traits are often taxonomically clustered. For example, Cardoso et al., (2011) showed that spider families are regularly clustered among hunting traits. As such, spider communities may have great species richness but low ecological complexity. Depending on how habitat filtering affects diversities, community functional diversity may still be high if filtering limits certain species, or vice versa where filtering limits certain traits, species richness may still be high. For community functions, these diversity metrics are all important and integral to understanding wetland arthropod communities.

On riparian arthropod food webs

The wetland arthropod community includes both primary consumers and other trophic levels where, for example, wetland beetle communities may contain detritivores (e.g. most Scarabaeidae, some Staphylinidae), herbivores (e.g. Chrysomelidae, Curculionidae, Elateridae), and carnivores (e.g. Dytiscidae, most Carabidae, Hydrophilidae and most Staphylinidae) (SLU Artdatabanken, 2023). Similarly, midge larvae, which are often one of the most abundant arthropod groups found in wetlands, also include multiple feeding guilds (Armitage et al., 1995). Midge larvae have also been observed to be a common prey among wetland predators (Hart and Lovvorn, 2002; Mellbrand and Hambäck, 2010), and may therefore be essential in
wetland arthropod food webs, and may also be an essential part in aquatic-terrestrial energy fluxes. Since terrestrial arthropod predators regularly do not hunt in truly aquatic habitats, the high aquatic productivity may only be accessible to riparian predators through emergence of aquatic insects, or from access to aquatic resources that gets flushed ashore during floods (Hering and Plachter, 1997).

Terrestrial detritivores and herbivores may also benefit from aquatic productivity, as nutrient rich waters deposit detritus along shorelines, or provide necessary nutrients for riparian vegetation. The most common detritivorous arthropods along wetland shorelines are springtails (Collembola) which regularly resides in wetland soil and litter (Batzer and Wu, 2020), and that feed on algal detritus that gets washed ashore or on fungal mycelium. Many riparian predators are specialized in preying on springtails, for example, many species of rove beetles (Staphylinidae: *Stenus*) have mouthparts specially adapted to capture springtails (Kölsch, 2000), and some carabid beetles (Carabidae: *Bembidion*) are also known to feed on springtails in other agro-ecosystems (Bilde et al., 2000).

Spiders are among the most prominent predators along wetland shorelines, with some species having specializations that are beneficial for capturing prey in wetlands. For example, fishing spiders (Pisauridae: *Dolomedes*) that are mainly found in wetland habitats, can skid on the water surface and catch aquatic prey ranging from insects to small fish (e.g. Williams, 1979). However, most spiders along wetland shorelines are generalist predators, but the prey consumed can vary between taxa. Mellbrand and Hambäck (2010) found that spiders primarily utilized resources with aquatic origin along the Baltic Sea shoreline, where insect predators used a greater proportion of prey with terrestrial origin. They also found that diet mixing among chironomids, collembola and terrestrial herbivores differed between wolf spider species. This suggests that aquatic resources are an integral part of riparian predator food-webs, and that prey choice among arthropod predators may differ substantially in what subsidies are utilized.
Wetlands in the agricultural landscape are also known to be a source of beneficial predacious arthropods that disperse into surrounding agricultural lands (Cardona-Rivera et al., 2021), that may be important predators on crop pests. For example, Saqib et al., (2021) found a wide spectrum of insect prey among spider families in managed Brassica crop fields, which suggested that a broad spider community could be very beneficial as a natural source of pest remediation.
Aim of this thesis

As knowledge regarding the terrestrial arthropod community is lacking considerably compared to the aquatic community, we asked four specific questions regarding wetland arthropods which were the basis for the four chapters of the thesis.

Chapter I
Does wetland productivity drive emergence rates of arthropods in wetlands, and can this production be considered a trade-off to greenhouse gas production?

Chapter II
Are there trophic links between wetland productivity, the most abundant arthropod prey originating from wetland habitats and the most abundant predators observed along wetland shorelines?

Chapter III
Does hydrological dynamics, flood zone area, shoreline vegetation and grazing management drive abundances and taxonomic community compositions in curSORial and aerial arthropods in constructed wetlands?

Chapter IV
Does characteristic wetland vegetation, shoreline properties and grazing management affect riparian arthropod species richness, diversities and habitat specializations?
Methods

Selecting sites

Across all chapters we used a set of 68 primarily constructed ponds and wetlands situated in two regions of Sweden, 46 wetlands were situated in Halland in south-western Sweden (56-57°N), and 22 were situated in Uppland in eastern Sweden (59-60°N) (Figure 1). The two regions were selected as the general landscapes were rather different. Halland was dominated by agriculture, where fodder-crops, cereal crops, and vegetable farming were abundant, whereas Uppland hosted a greater proportion of forestry, interspersed with agricultural croplands. Also, since the 1990’s thousands of wetlands had been constructed in Halland, mostly to combat nutrient runoff, but also to benefit biodiversity and for recreational purposes, and as a consequence, Halland hosted a great number of constructed wetlands situated in the agricultural landscape. Constructed wetlands in Uppland were sparser, and were mostly constructed for hunting opportunities, and to promote bird biodiversity. Some Uppland wetlands were also more natural and situated along lake shorelines (e.g. Mälaren and Kärven) and were consequently considerably larger compared to more pond-shaped constructed wetlands (see typical sampled wetlands in Figure 1). In both regions, farmers and landowners regularly used their wetlands as seasonal grazing pastures, where the dominant livestock was cattle, but occasionally also horse, sheep, alpaca and water buffalo, which is a common way to manage wetlands to slow the succession progression.
Figure 1 | Map highlighting the focal regions in this thesis, Halland (left) and Uppland (right) within Sweden, with coloration indicating how many chapters of the thesis singular wetlands were included in, and four aerial photographs of wetlands in Halland to illustrate typical sampled habitats. Photos by: Sofia Hedman.
As the studies were focused on constructed wetlands in the agricultural landscape, we selected wetlands with a maximum of 50% forest coverage in a 50m radius around the aquatic part of the wetland. This criterion omitted wetlands that were fully enclosed in forests, and focused the selection on wetlands that were mainly surrounded by open cultivated and agricultural landscapes, and could be classified as shoreline or wet meadow wetlands (Löfroth, 1991). We categorized wetlands shorelines as steep or gentle from the structure of the embankments and riparian areas, and based on grazing management to include both grazed and non-grazed wetlands. From this categorization, the selected set of wetlands had a range of steep-to-gentle shorelines and included wetlands with and without grazing managements. All wetlands also contained common wetland floras, where shorelines were dominated by sedge and rush, and where banks of reed and cattails were common in the aquatic parts of the wetland.

For each individual study, wetlands were selected from this initial set, to best encompass the variation among predictors used. In Chapter I, 17 constructed wetlands in Uppland were selected, to include wetlands with varying nutrient levels, a set that was expanded on in Chapter II to also include 31 constructed wetlands in Halland. Chapter III included 41 wetlands in Halland, primarily selected on wetland shoreline compositions and hydrology, and Chapter IV included 46 wetlands in Halland, and 22 in Uppland where we focused on shoreline properties and wetland structures.

Collecting arthropods

As the aim of the arthropod collections throughout the studies were to broadly census wetland populations and communities, with particular focus on riparian arthropods. We used four collection methods to best capture the breadth of the full arthropod community. Aerial insects were collected using SLAM (Sea Land and Air Malaise) trapping, whereas cursorial arthropods were collected through pitfall
trapping and suction sampling. To census aquatic insect emergence rates, we used floating emergence traps. As there are considerable variation among group traits, these collection methods were used to sample different taxa. SLAM trapping broadly collect aerial insects, and measured activity density among these taxa. Pitfall trapping similarly measured cursorial activity density, and primarily captured active ground dwelling species. Suction sampling rather measured cursorial arthropod density, as all species residing at the focal collection point got collected, which also included sessile arthropod species.

We positioned SLAM traps as close as possible to the water’s edge, with three 70mm opening pitfall traps placed parallel to the shoreline, spaced approximately 5m apart, centred at the SLAM trap collection point, where both contained water and detergent during 72h of collection. We also performed suction sampling in three 0.15m$^2$ areas, spaced similarly to the pitfall traps along the wetland shoreline, where we used a converted Stihl™ BG85 Leaf blower, to collect spiders, beetles and ants. To capture the emergence rates of chironomid midges from the aquatic part of wetlands, we constructed floating emergence traps (Cadmus et al., 2016) that were placed in duplicate in each wetland for 72h, anchored within 2m of the shoreline and separated by approximately 50m (Figure 2).

All individuals collected were stored in 70% ethanol until identification. The samples were broadly sorted into orders or families initially, where spiders, beetles, and some selected Diptera were later identified to species level for further community and population analyses. Chironomids captured through emergence trapping were also identified to genus level. Identified riparian taxa were categorized based on feeding traits, habitat specialization and applicable body size measurements for later trait-based analyses.
Figure 2 | Illustration of arthropod collection methods explaining how these methods were implemented during collections along wetland shorelines, and which thesis chapters each method was used in.

In total, the arthropods collected during this thesis work tallied above 73,000 individuals across all samplings, with ca 20,000 individuals having been identified to species level, pertaining to nearly 1,000 species. The most abundant taxa among SLAM collected individuals were Diptera, with 72% of all collected individuals, whereas pitfall trapping samples were dominated by spiders (34%) and beetles (29%). Suction sampling was similarly dominated by spiders (63%) and beetles (33%), with emergence trapping almost exclusively captured emerging Diptera (96%) (Figure 3). The most species rich group were beetles with 524 identified
species, with 145 species of spiders, 144 species of predatory Diptera (Dolichopodidae, Empididae and Hybotidae) and 62 species of crane flies (Cylindrotomidae, Limonidae, Pediciidae, Ptychopteridae and Tipulidae).

**Figure 3** | Relative abundance of arthropod orders by each collection method, SLAM trapping, pitfall trapping, suction sampling and emergence trapping.

### Collecting environmental data

#### Nutrients and primary production

Nitrogen (N) and phosphorus (P) concentrations are commonly elevated in agricultural wetlands, and were the two nutrients we focused on as drivers for wetland primary production. Nutrient samples were collected from surface water in both Uppland and Halland and were analysed for N and P concentrations at the
SWEDAC accredited Geochemical Laboratory at the Swedish University for Agricultural Sciences (Uppland samples) and at the Marine Ecology Laboratory at Stockholm University (Halland samples). In-situ aquatic chlorophyll-a concentrations were measured as a proxy for primary production by using a FluoroSense™ probe (in Uppland) or a YSI ProDSS multiprobe™ (in Halland). We were also mindful when drawing conclusions that in-situ chlorophyll measurements are semi-quantitative, as multiple environmental factors may affect the concentration measurements (Kuha et al., 2020).

Wetland hydromorphology

As wetland shoreline edges were commonly difficult to define due to vegetation and varying water levels, we used 1m² resolution digital elevation models (DEM’s, downloaded from SLU geodataportalen- Lantmäteriet on 2023-02-28) to define shoreline slopes as the altitude increase from the water surface altitude to the altitude of where the insect collections took place along the shoreline. In Halland we additionally measured water level fluctuations in the selected wetlands between April 2020 and February 2023 using a pressure sensor transducer (ETM DeltaBlue with barometric pressure sensor), placed at the estimated deepest point of each wetland, that measured the water column every 60 minutes. From these measurements we calculated daily mean water column heights, and converted these to altitude above sea level. These were then used in conjunction with the same 1m² DEM’s to calculate wetland flood zone areas and 10m inundation frequencies around each arthropod collection point (Figure 4A). The measured hydrological dynamics were also used to calculate water level fluctuation amplitudes and maximum durations of high- and low-water table events.
Wetland structure

During arthropod collections, we noted reed bed areas, flooded grassland areas and pastures and meadows surrounding the wetlands, which were transcribed into QGIS (QGIS, 2022) where areas of these features were calculated (Figure 4B). Reed beds were categorized as emergent non-woody vegetation such as common reeds (*Phragmites australis*) or cattails (*Typha sp.*), whereas flooded grassland area was categorized as shoreline areas dominated by sedge and rush. Surrounding pasture and meadow areas were demarked as surrounding grasslands with or without grazing livestock. When performing suction samplings, we also measured maximum vegetation height at all collection points.

**Figure 4** | (A) Demarcation in an example wetland of wetland flood zone and inundation frequency, and (B) areas of reeds, flooded grassland and surrounding pastures and meadows.
Primary findings of the thesis work

Aquatic wetland productivity as a driver in arthropod communities

In Chapter I we found that chironomid emergence rates increased with aquatic chlorophyll-a concentrations during May and June, whereas taxonomic diversity showed a similar pattern during June and July and feeding group diversity increased with chlorophyll-a concentrations only in July. However, taxonomic diversity rather decreased with chlorophyll-a concentrations in May and August, with the same pattern in feeding group diversity in May, June and August. This led us to believe that primary production in wetlands indeed may be a primary driver of wetland biodiversity (Ramey and Richardson, 2017), as chironomids are the most abundant group of insects emerging from wetland habitats, and since chironomids are essential prey to many wetland predators (e.g. Bardwell and Averill, 1997; Almenar et al., 2008).
Figure 5 | Monthly effects of chlorophyll-a concentrations on chironomid emergence rates (A), chironomid taxonomic diversity (B), and chironomid feeding group diversity (C), with linear 95% confidence intervals (CI).

This cascading relationship was less evident in the relation between abundances of chironomids and sciarids and the riparian predator abundances (Chapter II). Nutrient loads and chlorophyll-a concentrations did relate to riparian predator abundances, but this relationship was not clearly conveyed through the abundances of prey that emerge from aquatic or terrestrial wetland habitats, and predator abundance responses differed between taxa.

The abundances of sciarids and chironomids around the wetlands were unrelated to aquatic chlorophyll-a concentrations. However, sciarid abundances increased with phosphorus concentrations, with a similar relationship to chlorophyll-
a concentrations when modelled separately. Since chironomid larvae develop in water whereas sciarid larvae develop in moist shoreline soils (Oosterbroek, 2006), their life history traits could impact the way in which these groups respond to aquatic productivity.

Dwarf spider (Linyphiidae: Erigoninae) abundances increased with sciarid abundances (Figure 6A), whereas water scavenger beetle (Hydrophilidae) abundances increased with chironomid abundances (Figure 6B), and dance fly (Hybotidae) abundances mainly increased with the combined abundances of chironomids and sciarids (Figure 6C). This suggests that there may also be variations in subsidy utilizations among riparian predators by wetlands, similar to what was observed by Mellbrand and Hambäck (2010), where some predatory taxa are more tightly linked to aquatic subsidies, and others to terrestrial subsidies.

Figure 6 | Abundances of (A) dwarf spiders to sciarid abundances, (B) water scavenger beetle to chironomid abundances, and (C) dance fly to cumulative sciarid and chironomid abundances, with linear 95% CI.
Wetlands with greater concentrations of phosphorus supported greater abundances of ground beetles (Carabidae), whereas wetlands with greater nitrogen concentrations contained fewer dwarf spiders but more sheet-web weavers (Linyphiidae: Linyphiinae). However, sheet-web weaver abundances were lower, whereas abundances of long-legged flies (Dolichopodidae) and dance flies were greater, by wetlands with greater chlorophyll-a concentrations.

These findings suggest group specific responses to prey subsidies among riparian predators, but that predator abundances also may be affected by overall system productivity. Since energy transfer across the aquatic-terrestrial boundary is not limited to aquatic insect emergence, but also by the inflow of nutrients and phytoplankton during floods, terrestrial primary consumers, not included in this study may utilize these influxes and transfer the energy to terrestrial predators.

The trade-off of producing copious amounts of insects

In **Chapter I**, we found that the basic primary production aspects in agricultural wetlands that benefit chironomids, were simultaneously linked the production of methane (CH$_4$), which decreased with chlorophyll-a concentrations. Chironomid taxonomic diversity correlated positively with methane concentrations with a near-significant similar relationship between chironomid emergence rates and methane concentrations, suggesting a trade-off between chironomid communities and methane production in agricultural wetlands. This finding is in concordance with previous experimental findings directly linking chironomid larvae consumption of methane oxidizing bacteria in bottom sediments (Jones et al., 2008; Belle et al., 2018), which could increase methane productions.
Disturbances from hydrologic dynamism

In Chapter III we found that wetland hydrology dynamics impacted certain groups of riparian arthropods more than others, and that the responses were not uniform across taxa. Prolonged periods of high-water tables decreased the total abundances of Diptera (Figure 7A), whereas the abundances of true bugs (Hemiptera, Figure 7B) and caddis flies (Trichoptera, Figure 7C) were instead lower by wetlands with prolonged periods of low-water tables. Abundances of water scavenger beetles (Hydrophilidae: Coelostoma, Figure 7D), crane flies (Limoniidae: Erioptera, Figure 7E) and rove beetles (Staphylinidae: Stenus, Figure 7F) were lower by wetlands with greater inundation frequencies. The community composition among Nematocera (Diptera) families was also structured by the wetland’s inundation frequency, whereas the community composition among true bugs was structured by water-table fluctuation amplitudes.
Figure 7 | Abundances of Diptera (A), Hemiptera (B), and Trichoptera (C) to maximum high- (A) and low-water table durations (B and C), with the influence of inundation frequency on Coelostoma (D), Erioptera (E) and Stenus (F) with negative binomial relationships and 95% CI.

These results suggested that riparian arthropod communities were influenced by wetland hydrology dynamics, but that the effects on the populations varied considerably between groups. Floods pose direct disturbances to certain taxa, where for example species with soil-living larvae are unable to escape during high-water table periods, whereas other species may survive by migrating to drier ground or
in temporal refugia (Sienkiewicz and Zmihorski, 2012; Ramey and Richardson, 2017). Some species are similarly sensitive to drought, because their larvae require moist soils for development and where droughts thereby could be detrimental, or where aquatic larval stages that require longer hydroperiods loose habitats during prolonged periods of low-water tables. Additionally, total order abundances and order- or family community compositions did not always respond in the same way to inundation frequencies, suggesting that hydrological filtering mechanisms filtered abundances on genus or even species level.

Wetland shorelines and riparian arthropods

In Chapter III we found that flood zone area had a surprisingly small impact on riparian arthropod abundances and only affected community compositions among wolf spider (Lycosidae) assemblages. The abundances of Piratula showed a quadratic response to flood zone area, with a near significant similar relationship in Pirata, which suggested that these genera were most abundant by wetlands with intermediate flood zone areas. Abundance responses to habitat size can vary between taxa (Hambäck and Englund, 2005), and wetland specialized species may thrive in their specialist habitat, regardless of the size of the habitat. All sampled wetlands were rather small (mean ca 1.5 ha), with some flood zone areas, which could suggest that the size of the flood zone may be inconsequential to most arthropods, as long as there are at least some.

We also found that both riparian populations and communities responded to wetland shoreline slopes. In Chapter III we found that abundances of parasitic wasps (Hymenoptera: Apocrita) were greater by wetlands with steep shorelines that also had greater water table fluctuation amplitudes, but were lower by wetlands with steeper shoreline slopes that had greater inundation frequencies. And in Chapter IV we found that phylogenetic diversity in riparian spiders was greater (Figure 8A), but total species richness and wetland specialized species richness of
predatory Diptera (Dolichopodidae, Empididae and Hybotidae) was lower by wetlands with steeper shoreline inclines (Figure 8B-C). This suggested that shoreline slopes influenced what species resided by wetlands, and that especially wetland specialized predatory Diptera required wetlands with gentle shorelines. Since many constructed wetlands in the agricultural landscape are designed with mostly steep shorelines, this may filter out wetland specialist arthropods from the communities. Simultaneously, steeper shorelines seemed to also benefit certain taxa, which suggested that wetlands with varied shorelines would have best benefitted the arthropod community overall.

**Figure 8** | Shoreline incline influence on spider phylogenetic diversity (A), total species richness in predatory Diptera (B) and wetland specialist species richness in predatory Diptera, with linear 95% CI.
Wetland vegetation

In Chapter IV we found that spider trait diversity increased (Figure 9A), whilst beetle trait diversity decreased (Figure 9B) from flooded grassland area around wetlands. We also found that species richness in wetland specialist beetles was greater by wetlands with greater areas of flooded grassland (Figure 9C), whereas wetland specialist spiders were unaffected by flooded grassland area. This suggested that the relation between trait diversity and wetland specialization worked differently between the two groups. We found that the proportion of predatory beetles was greater by wetlands with larger flooded grassland areas, which likely was driven by the abundance of prey in areas with periodic flooding. As such, the reduced beetle trait diversity by wetlands with large flooded grassland areas was likely a consequence of habitat filtering of non-predatory beetles. The average beetle body size was also greater by wetlands with greater flooded grassland areas, which suggested that flooding regimes of wetlands may have filtered smaller species with less dispersal capabilities.
Figure 9 | Trait diversity in spiders (A) and beetles (B), with species richness in wetland specialist beetles (C) in relation to flooded grassland area, with linear 95% CI.

Wetlands with taller shoreline vegetation supported greater abundances of sheet weavers and rove beetles, but lower abundances of caddis flies, crane flies (Tipulidae: *Tipula*) and dagger flies (Empididae: *Hilara*) and orb weaving spiders (Tetragnathidae) (Chapter III). As sheet weavers and rove beetles are mainly predatory, it is likely that their abundances may be influenced by prey that are abundant in habitats which feed on shoreline vegetation or detritus, or that hatch from soils that are kept moist from greater amounts of shading (e.g. Sciaridae or Collembola). The moist soils may also influence the habitat quality required by the larvae two dipteran groups that showed a negative relationship to vegetation height (Oosterbroek, 2006).
The disturbance of grazing livestock

Finally, we found (Chapters III and IV) that grazing management in constructed agricultural wetlands had relatively small impacts on the riparian arthropod communities, and where populations or communities did respond, it was mostly a negative response. We saw that one genus of dagger flies (Empididae: Rhamphomyia) had greater abundances by wetlands with grazing livestock, whereas abundances of true bugs were lower by grazed wetlands, and species richness of generalist and terrestrial specialist spiders was lower by wetlands with grazing livestock in Uppland wetlands. We also found that species richness in wetland specialist predatory Diptera was greater by wetlands with greater flooded grassland areas where grazing livestock were absent. Grazing management is often considered to benefit the quality of riparian habitats (e.g. Moran et al., 2012; Bucher et al., 2016). However, our findings suggest that this benefit had small overall impacts on arthropod communities, and that sensitive taxa may rather have experienced habitat disturbances from grazing livestock. Since moist soils surrounding wetlands are prone to substantial trampling disturbance from high stocking rates (Cole et al., 2012), these disturbances may influence abundances of both native wetland specialists and opportunistic generalists and terrestrial specialists. As our studies did not focus on stocking rates or trampling damage, and that grazing intensity varied between wetlands, these conclusions were speculative. Grazing may also induce secondary effects, where grazing reduce shoreline vegetation height which in turn could affect the arthropod community as was seen in caddis fly, crane fly, dagger fly, sheet weaver, rove beetle, orb weaver, and sheet weaving spider, and rove beetle abundances. Previous studies have shown that grazing intensity in pastures do influence arthropod diversity and trophic interactions, where grasslands that have been left ungrazed for longer periods hold greater diversities than intensely grazed habitats (Kruess and Tscharntke, 2002). It has also
been suggested that grazing is mainly beneficial to arthropods when habitat heterogeneity increases through intermediate grazing pressure (van Klink et al., 2015). These results suggested complicated group specific relationships between riparian arthropods and grazing livestock, and as such grazing management in wetland habitats needs to be performed with care, and shorter grazing rotation schemes with reduced habitat impacts may lessen the strain on agricultural wetland arthropod communities.
Overall conclusions and future prospects

This thesis work has highlighted multiple aspects of wetland functions and structural properties integral to riparian arthropod community compositions and functions. We have continued to build upon previous entomological and ecological research, and found some new interesting insights. Primarily, and perhaps unsurprisingly, given the enormous variation seen among wetland arthropods, we found that many fundamental wetland characteristics seemed to have substantially different influences on wetland arthropod groups. Simultaneously, many taxa seemed surprisingly resilient to wetland dynamism, where for example wetlands with substantial hydrologic variability had little impact on most arthropod abundances. Grazing also seemed to have moderate influences of both arthropod abundances and diversities, and mostly a negative influence on the taxa that did respond. The seeming resilience of wetland arthropod communities may also be influenced by the fact that wetlands in the agricultural landscape are rare, and that arthropods may congregate there simply because wetlands provide natural heterogeneity in depauperate, human-altered environments. However, our findings suggested that both productivity, hydrology and structure in constructed wetlands had an effect on the arthropods that inhabit them.

The complexity of these ecological systems, with all interacting effects of both abiotic and biotic origin, makes creating a framework of comprehensive community drivers difficult to pinpoint. As a consequence, we narrowed the focus to essential wetland concepts to describe the communities. This focus also omitted ecological concepts that likely further influence wetland arthropod communities.
For example, the results in Chapter II could be expanded on to include prey choice and subsidy utilization in riparian predators using next-generation sequencing of predator gut contents (e.g., Lafage et al., 2020; Hambäck et al., 2021). Wetlands in the agricultural landscape hosts taxa originating from the wetlands themselves and from the surrounding landscape (as we found in Chapter IV), where wetland predators have been suggested to potentially provide natural crop pest remediation to surrounding agriculture (e.g., Cardona-Rivera et al., 2021). By studying predator community compositions and prey preference among these predators, we would gain knowledge of prey utilization and potential benefits of abundant wetland predators to the surrounding landscape.

Results in Chapter III invokes the question of how terrestrial arthropods respond to droughts, with implications from current climate change scenarios. Aquatic arthropods would understandably respond to droughts, but knowledge is lacking on how this may affect terrestrial wetland arthropods (however, see Kirichenko-Babko et al., 2020). Drought in wetlands may severely impact foodwebs as both wetland flora and fauna often are reliant on a stable supply of water, which may both directly and indirectly influence community compositions. Wetland specialists are most likely to be affected, whereas generalists and terrestrial specialists may utilize exposed resources as waters recede and thus benefit from low-water tables initially. However, prolonged periods of drought may influence abundances, with lag-effects into subsequent generations.
References


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