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RESEARCH PAPER

Hydrological dynamics, wetland morphology and vegetation structure determine riparian arthropod communities in constructed wetlands

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ABSTRACT

Wetland hydrological dynamics often dictate the composition of biological communities found in or near wetlands, either directly or through changes in vegetation composition. However, much remains unknown, particularly regarding how riparian arthropods respond to such dynamics. In this study, we used high-resolution hydrological data, along with presence of grazing livestock and shoreline vegetation height from 41 constructed wetlands in south-western Sweden to explore flood zone areas, flood frequencies, vegetation and grazing as drivers of the resident arthropod communities. The collected material consisted of 26,817 arthropods, where the dominant groups were Diptera (13,258 specimens), spiders (6,207) and Coleoptera (2,858), which were collected using SLAM (Sea Land and Air Malaise) trapping, along with pitfall trapping and vacuum sampling of riparian arthropods. We found group-specific responses to inundation frequencies, where wetlands with higher frequencies had lower abundances of some beetles and tipulids, and where wetlands with longer low-water table periods contained less trichopterans and heteropterans. In contrast, the size of flood zone areas only affected some wolf spider groups, that were more abundant in wetlands with intermediately sized flood zones. Shoreline vegetation height affected multiple groups, spiders, beetles and dipterans, but in different directions, whereas presence of grazing livestock had limited impact on abundances and community compositions. Given the variable responses to wetland hydrological and structural drivers, it seems that wetland arthropod communities would benefit from a high local wetland habitat variability, or wetlandscapes where individual wetlands have differing hydrological dynamics, morphology and vegetation.

Introduction

The loss of natural wetlands during the agricultural industrialization, and subsequent efforts to re-establish them with constructed wetlands, has likely shifted the role of wetlands in the hydrological system and in the landscape as a whole. Whereas natural wetlands appeared where geohydrologic aspects of the landscape formed them, constructed wetlands in the agricultural landscape are implemented as a response to specific needs, e.g., nutrient retention, soil erosion mitigation, biodiversity conservation, flood control or recreation (Davidson, van Dam, Finlayson & McInnes, 2019; Hambäck, Dawson, Geranmayeh, Jarsjö, Kacergyte et al., 2023; Swartz & Miller, 2021), and constructions may or may not depend on hydrogeomorphological conditions. Because the requirements for specific functions determine the position and morphology of the constructed wetland, these wetlands often lack resemblance to naturally occurring wetlands. Constructed wetlands typically have relatively steep shorelines, more or less large areas of open water, more stable water tables and proportionally smaller flood zones, which may affect the flood dynamics of the wetland. The intentional creation of wetlands in the agricultural landscape, irrespective of purpose, obviously alters the natural habitat characteristics, which are crucial for a diverse range of animal species, but current knowledge is insufficient to predict what wetland characteristics determine the abundance of which animal groups. Increasing the knowledge about

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these characteristics may therefore broaden our understanding about the ecological roles of constructed wetlands in these human-engineered landscapes.

Hydrological processes are obviously key to many ecological processes in wetlands, but it is likely that animal species vary in their response to the same hydrological aspect. For instance, floods and droughts will likely affect aquatic, semi-aquatic and terrestrial species differently. Responses of some groups are well known, such as the fact that most amphibians require temporarily inundated and fish-free habitats during spawning and pre-metamorphosis (Porej & Hetherington, 2005) whereas wading birds benefit from the high prey abundance and the soft texture of water-logged soils (Smart, Gill, Sutherland & Watkinson, 2006; Żmihorski, Pärt, Gustafson & Berg, 2016). Responses of other groups, such as arthropods, are less well studied in wetlands, particularly in the temporally flooded areas, despite their high species richness (Batzer, 2013). In contrast to arthropods developing in the water, we largely lack knowledge about key environmental factors promoting high abundance and species richness of arthropods in the wet riparian zones (Batzer & Wu, 2020). As a consequence, we also have limited capacity to predict the role of constructed wetlands for riparian arthropods, and how these wetlands can be constructed to better support arthropod diversity. Improving the design of constructed wetlands is important not the least because wetlands contain many threatened arthropod species (Artdatabanken, 2022), many of which likely declined during centuries of wetland drainage.

In order to understand species responses in the flood zone, we also need to quantify the hydrological processes affecting flood dynamics simultaneously with quantifications on the occurrence and abundance of focal arthropod groups. Flooding obviously depends on precipitation events, but also on the size of the catchment for the focal wetland and on wetland morphology (Acreman & Holden, 2013; Bullock & Acreman, 2003; Åhlén, Thorslund, Hambäck, Destouni & Jarsjö, 2022). Many studies speculate about the connection between hydrological dynamics and the richness and abundance of arthropods (Batzer, 2013; Bonn, Hagen & Wohlgemuth-Von Reiche, 2002; Datry, Corti, Belletti & Piegay, 2014; Lambeets, Vandegehuchte, Maelfait & Bonte, 2008; Ramey & Richardson, 2017), but few studies have attempted to connect quantitative descriptions of flood dynamics and descriptions of arthropod communities. A conclusion from such studies, however, is that the hydrological dynamics may be more important than for instance grazing on arthropod groups such as carabid beetles and spiders (e.g., Lafage & Pétillon, 2016; Moran, Gormally & Skeffington, 2012). In order to better understand how different taxa respond to flooding, Åhlén et al. (2023) quantified spatial variation in flooding frequency at a high resolution (2×2 m^2) within one large wetland and simultaneously trapped flying insects. They found large differences among arthropod groups where some groups had higher abundance in frequently flooded areas whereas other groups had higher abundance in drier areas or did not vary with the flood frequency. Their study, however, focused mainly on flying insects, which should be less affected by small-scale variation.

This work aimed to connect hydrological dynamics and local environmental factors in constructed wetlands to the abundance and community composition of riparian arthropods, including both flying insects and mainly cursorial arthropods such as spiders and beetles. Because we had no prior information about flooding during site selection, we used shoreline slope as a proxy with the assumption that more shallow slopes are more frequently flooded. We then collected high-resolution hydrological data to delineate flood zone size, estimate inundation frequency, and calculate average consecutive days with hydrological high- and low-water table of constructed wetlands in south-western Sweden. We used these hydrological variables, along with shoreline slope, vegetation height and presence-absence of grazing livestock to examine how wetland characteristics drive arthropod abundance and community composition in the riparian zone of the constructed wetland. As dynamic hydrological conditions may benefit resilient riparian arthropods, whilst being detrimental to sensitive species, our objective was to examine which arthropod taxa could benefit, and which could be disadvantaged by wetland flooding dynamics. In conjunction with wetland hydrology, we also wanted to explore if shoreline vegetation and grazing livestock impacted arthropod community compositions in these dynamic habitats.

Materials and methods

Site selection

We initially selected constructed lentic freshwater wetlands situated in the county of Halland between 56.5°N and 57°N on the Swedish west coast (Fig. 1). The county is hemi-boreal and dominated by cereal and livestock agriculture, with less forestry industries which otherwise is common at higher latitudes. Some thousands of wetlands have been constructed in the last three decades, mainly to mitigate nutrient runoff to the nearby Kattegat strait, increase biodiversity, promote birds and ornithology, and to buffer water flows (Fleischer, Gustafson, Joelsson, Pansar & Stibe, 1994; Strand & Weisner, 2013). All selected wetlands were constructed, with a central pond and more or less large riparian wet areas, and varied in size from 0.07 ha to 10.96 ha, with most having maximum water table controls with pipe outlets that prevent flooding. We selected wetlands based on (i) shoreline slope, to obtain a gradient of wetlands with shallow and steep shorelines, and (ii) presence of grazing livestock, to include both grazed and ungrazed sites along the shoreline slope gradient. Sites with >50 % forest cover within a 50 m radius around the shoreline were omitted to specifically focus on wetlands in proximity to agriculture. Most wetlands contained characteristic hydrophytic plants with shorelines typically being dominated by sedges (Cyperaceae) and rushes (Juncaceae). We obtained an initial set of 50 wetlands varying in hydrological conditions, morphology and management, situated in the agricultural landscape, and all containing typical wetland flora. Wetlands varied in the occurrence of grazing animals, that included cattle, horses and, in one site, sheep. Their numbers varied over time, and because we lack information on stocking density, occurrence of grazing animals is treated as presence/absence.

Arthropod collection

To sample the full arthropod community, we used three sampling methods, which differ in target species based on mode of locomotion and area covered. Aerial species were sampled using SLAM (Sea, Land and Air Malaise) traps, whereas cursorial species were sampled using pitfall traps and vacuum sampling. Collections were performed three times during the spring and summer of 2020 to capture seasonal variation; late May (period 1), late June to early July (period 2) and late August to early September (period 3). SLAM traps, one per site, with the collection bottle containing water and detergent, were placed close to the water edge (<2 m distance) during three consecutive nights for each sampling period. Pitfall traps were only used during period 1 using three 70 mm pitfall traps, containing water and detergent, per site along a 10 m gradient parallel to the shore and within 5 m of the SLAM trap. Vacuum sampling was performed during periods 2 and 3 with a converted Stihl™ BG85 Leaf blower. We sampled arthropods within three spots, delineated with a 45 cm diameter hoop, close to the water's edge along a 10 m gradient parallel to the shoreline. Individuals were manually collected from the vacuum sample, using an insect pooter, after evacuating the contents into a container. All samples were stored in 70 % ethanol until sorting specimens to order, with specific taxon groups being sorted to lower taxonomic levels. We focused on arthropod orders that were sufficiently abundant in the samples, defined as having a total of >100 individuals, and being present in >70 % of the sites (see Appendix A: Table 1). During period 3, we also estimated the average maximum vegetation height at the three vacuum sampling points.

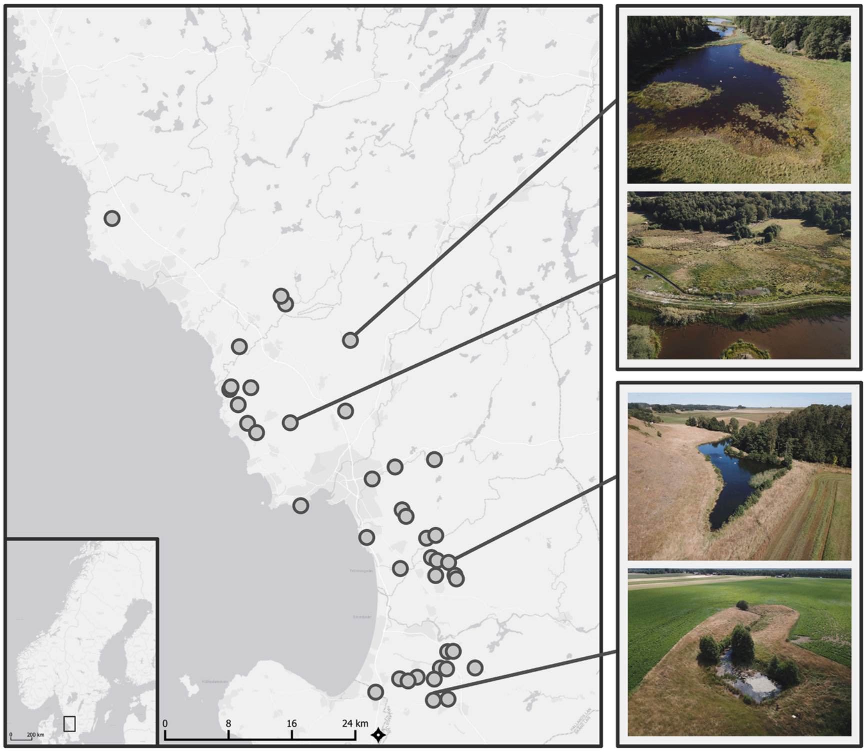

Fig. 1. Overview of the study area including 41 wetlands on the Swedish west coast, and pictures of representative wetlands with shallow shorelines and larger flood zones (top right), or with steeper shorelines and small flood zones (bottom right). Photos: Sofia Hedman.

Hydrology

From April 2020 to February 2023, we measured water table fluctuations in the wetlands by deploying a pressure sensor transducer measuring water levels (ETM DeltaBlue with barometric pressure sensor) at each wetland's estimated deepest point. The sensor measured the differential pressure between water and air to quantify the water column depth every 60 min and the data logger transmitted values wirelessly to a server, from which we calculated daily mean water tables. We restricted the analysis to wetlands where we retrieved at least one year of consecutive data, which excluded 9 wetlands from further analysis (see Appendix A: Table 2). From collected water table data, we calculated a range of hydrological variables relating to inundation frequencies, amplitude and temporal extent of extreme conditions (drought or floods).

We first converted daily mean water levels to meters above sea level and combined these values with a digital elevation model (DEM, downloaded from SLU geodataportalen-Lantmäteriet on 2023–02–28) in order to estimate flood zone areas during different times of the year (QGIS, ver. 3.26.3). The downloaded DEM used remote sensing data from autumn 2019, prior to our field campaign, and we used the water tables from 2020 to calibrate field estimates and the DEM at a 1 m^2 resolution. Some wetlands were excluded because calculated flood zone areas seemed unrealistic, where the model indicated either that the permanent water was partly dry or flooding in strange areas. These errors are likely due to problems in synchronizing field measurements and remote sensing data, due to extreme water tables underlying the DEM. Based on the data, we calculated the daily inundation frequency in a circle (10 m diameter) centred on the SLAM trap. The procedure was to first calculate proportion of time that each pixel in the circle was inundated and then averaged these frequencies across all pixels per circle. In addition, we quantified high- and low-water conditions as the maximum number of consecutive days that water tables were above halfway between the average water table and the altitude of the SLAM trap being high-water table duration, and maximum number of days water tables were below the lower 5 %-percentile as low-water table duration. Finally, we calculated the water-table fluctuation amplitude as the mean water-table level subtracted from the 95 %-percentile water level.

To compare calculated flood zone areas with estimates based on vegetation structures, we calculated the areas of flooded grasslands and reeds next to the constructed wetlands using QGIS. Flooded grasslands were defined as habitats dominated by sedges (*Carex* spp.) and rushes (*Juncus* spp.) whereas reeds include habitats dominated by high and emergent vegetation such as bulrushes (*Typha* spp.) and reeds (*Phragmites australis*).

Statistical analyses

Cumulated arthropod abundances across specific collection methods and the three collection periods per site were used to determine effects from environmental conditions on the arthropod abundance. Total abundances of each species group (Araneae, Coleoptera, Diptera, Hemiptera, Lepidoptera, Megaloptera, Trichoptera, parasitic wasps and Formicidae) were analysed separately using glm models from the MASS package (Venables & Ripley, 2002). Depending on residual plots, distribution family was selected for best model fit. Environmental predictors in the full model included inundation frequency, calculated flood zone area [ln-transformed], shoreline slope [ln-transformed], maximum number of consecutive days with extreme (high- and low-) water tables, grazing (presence/absence), the grazing-by-flood zone interaction and the shoreline slope-by-inundation frequency interaction. The grazing-by-flood zone interaction was included because trampling animals may damage the soft soil and indirectly affect arthropods living in the soil. The slope-by-inundation frequency interaction was included because the consequence of the latter may depend on the steepness of the shoreline. As a consequence of multiple collinear relationships of high-water table durations and of calculated flood zone area to other predictors, these factors were only included in models where the collinearity would be of minimal impact. We reduced the full model using the dredge function from the MuMIn package (Bartoń, 2022), where selected models had ΔAICc<2 (Akaike Information Criterion, with correction for small sample sizes) from the best suited model (see final model selection in Appendix A: Table 3).

Multivariate community responses for taxonomic groups (Araneae, Coleoptera, Brachycera, Nematocera and Hemiptera taxa, Fig. 2B, and Appendix A: Table 1) were estimated using manyglm models from the mvabund package (Wang, Naumann, Eddelbuettel, Wilshire & Warton, 2022) with negative binomial distributions and the same set of predictors as in the univariate glm models. We analysed these models both at a family level and at the genus level within family. The responses were estimated with consideration to high-dimensional data, and with corrections for correlations of variables using ridge regularization (Warton, 2008), and residuals were inspected graphically but never showed signs of heterogeneity. All statistical modelling was performed in R version 4.2.1 (R Core Team, 2022).

Results

In total, we collected 26,817 arthropod specimens, from groups that contained >100 specimens and were present in >70 % of the sites. These included Diptera (13,258 specimens), spiders (6207), Coleoptera (2858), parasitic wasps (1387), Formicidae (1011), Hemiptera (906), Trichoptera (582), Megaloptera (419) and Lepidoptera (189) (Fig. 2A, and Appendix A: Table 1).

The inundation frequency close to the arthropod sampling points varied between 0.5 % and 68.0 %. The maximum duration of high-water tables was 261 days, and the maximum duration of low-water table was 53 days, where the calculated water-table fluctuation amplitudes varied between 0.03 m and 0.75 m. The shoreline height varied between 0.01 m and 2.88 m, and the average vegetation height varied between 0.09 m and 1.23 m (see Appendix A: Table 4). Wetland morphology, vegetation and hydrological variables were related in multiple ways. Wetlands that supported a higher vegetation had shorter high-water table durations, smaller estimated flood zones and smaller flooded grassland areas (Fig. 3). Wetlands with steeper shoreline slopes also had a higher vegetation, whilst having shorter high-water table durations, smaller flood zone areas, smaller flooded grassland areas and lower inundation frequencies, whereas wetlands with greater water-table fluctuation amplitudes also had longer high-water table durations, and larger flood zone- and flooded grassland areas (Fig. 3). Wetlands that had longer durations of high-water tables also had larger flood zone and flooded grassland areas and more frequent inundations, whilst wetlands with larger flood zone areas also were more frequently inundated and had larger flooded grassland areas (Fig. 3).

Arthropod abundance and community composition

Araneae: the total spider abundance did not vary with any measured environmental variable, but the manyglm suggested that the spider community varied with vegetation height (Wald value (Wv) = 4.05, $P <$ 0.01). The effect on the community arose because the abundance of Tetragnathidae (dominated by *Pachygnatha clerckii*) was lower in wetlands with higher vegetation (Table 2, Fig. 5B). At the genus level for Linyphiidae, we additionally found that *Hypomma* and *Tenuiphantes* increased in abundance with vegetation height (Fig. 4F and G) and there was a close to significant trend in the opposite direction for *Erigone* (Table 2). For Lycosidae, the relation to the flood zone area seemed non-linear for some genera and we therefore included area^2 in the analysis. The model suggested that the abundances of *Piratula* was highest at wetlands with intermediate flood zone areas, with a similar near-significant trend for *Pirata* (Table 2).

Coleoptera: the total beetle abundance was unaffected by all environmental variables, but the beetle community composition varied with the inundation frequency (Wv=3.89, $P < 0.05$). The univariate analyses suggested that Staphylinidae abundance was lower in wetlands with more frequent inundations (Table 2, Fig. 4E). At the genus level, we found effects for Staphylinidae and Hydrophilidae but not for Carabidae, Chrysomelidae or Curculionidae. *Stenus* and *Coelostoma* decreased with higher inundation frequencies (Fig. 4F and G), whereas *Cercyon* and *Tachyporus* increased with vegetation height (Table 2, Fig. 5H and I).

Diptera: the total Diptera abundance was lower in wetlands with longer periods of high-water tables (Table 1, Fig. 4A), and the manyglm suggested that the community composition of both Brachycera (flies, Wv=3.70, $P < 0.05$) and Nematocera (midges, gnats and crane flies, Wv=5.05, $P < 0.01$) varied with the vegetation height. The univariate analyses suggested that one group of predatory flies (Empididae) as well as the nematoceran family Tipulidae were less abundant in wetlands with higher vegetation (Table 2, Fig. 5C and D). The Nematocera community composition additionally varied with inundation frequency (Wv=3.75, $P < 0.05$). At the genus level, we found that *Tipula* and *Hilara* decreased with vegetation height (Fig. 5E and J), whereas *Erioptera* decreased with an increasing inundation frequency (Fig. 4H) and *Rhamphomyia* was more abundant at grazed sites (Table 2).

Hemiptera: the total abundance of Hemiptera (true bugs) was lower in wetlands with longer periods of low water tables (Table 1, Fig. 4B), and higher in wetlands that did not have grazing livestock (Table 1). Similarly, the community composition of true bugs varied with the low

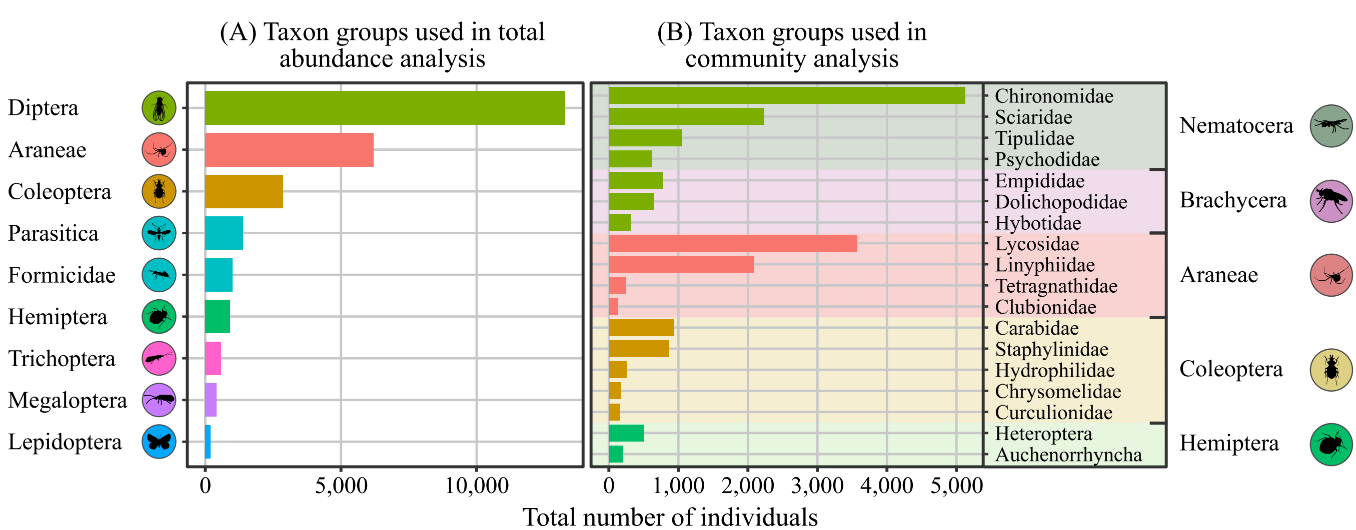

Fig. 2. Total number of individuals for (A) major groups and (B) subgroupings used in analyses.

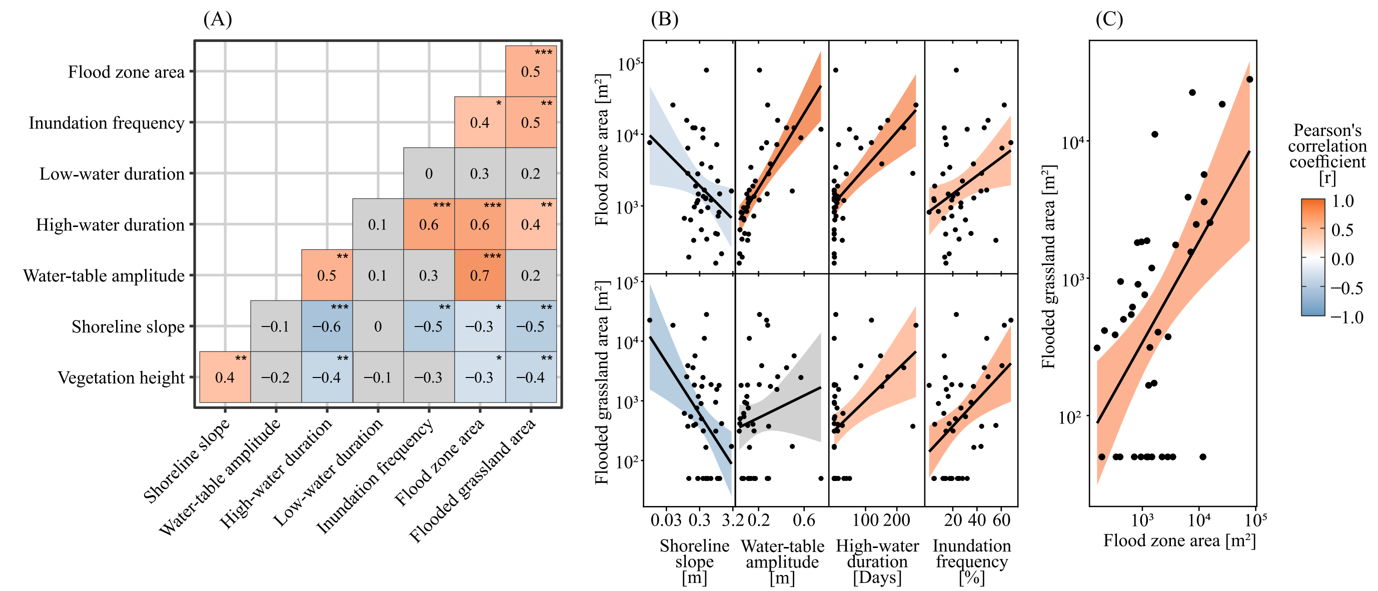

Fig. 3. Correlations of habitat characteristics with Pearson's correlation coefficients and significance levels, $P < 0.05$ *, $P < 0.01$ ** and $P < 0.001$ *** (A), and collinearity relationships of calculated flood zone areas and observed flooded grassland areas to wetland morphologies and hydrology (B) and the relationship between calculated flood zone area and measured flooded grassland areas (C) with 95 % confidence intervals (CI).

water table duration (Wv=2.99, $P < 0.05$) and presence of grazing livestock (Wv=3.11, $P < 0.01$), but also with the water table fluctuation amplitude (Wv=3.22, $P < 0.05$). The univariate analyses suggested that this effect occurred because the Heteroptera abundances were greater in wetlands without grazing livestock and lower in wetlands with longer duration of low water-tables (Table 2). However, wetland water-table fluctuation amplitude had no effect on either Auchenorrhyncha or Heteroptera.

Hymenoptera: the total abundance of ants (Formicidae) was higher in wetlands with steeper shoreline slopes (Table 1), and was also higher in wetlands that had more frequent inundations (Table 1, Fig. 4D). Parasitic wasp abundance, however, was greater in wetlands with steeper shorelines that had greater water-table fluctuation amplitudes, but was lower in wetlands with steeper shorelines that had higher inundation frequencies (Table 1).

Other taxa: Trichoptera abundances were lower in wetlands with longer periods of low-water table durations and in wetlands with higher vegetation (Table 1, Fig. 4C and Fig. 5A). Total Lepidoptera and Megaloptera abundances were unaffected by all global predictors.

Discussion

Understanding the environmental factors affecting the abundance and community composition of wetland arthropods necessitates closer collaborations between hydrological and ecological research. In this paper, we quantified a range of hydrological properties in constructed wetlands and found that different predictive variables affected different arthropod orders. Inundation frequency affected communities of Coleoptera (mainly Staphylinidae), Nematocera and ants (Formicidae), length of drought periods and water-table amplitudes affected Hemiptera (and particularly Heteroptera), length of flood periods affected total Diptera abundance whereas shoreline slope affected Hymenoptera (mainly ants) abundance. In addition, vegetation height around the wetland seem to be a key factor for several groups whereas the presence of grazing animals seems less important.

As expected, wetland morphology and hydrological dynamics were tightly linked, where shallow shorelines and greater water-table fluctuation amplitudes and inundation frequencies resulted in greater flood zone areas. However, when comparing calculated flood zone area and the observed flooded grassland area, the two measurements correlated substantially but not completely. Differences were seen in wetlands where vegetation measures indicated no flooded grasslands but where the hydrological data suggested the presence of such areas. As the calculated flood zone area is tightly linked to the water-table amplitude in conjunction with the shoreline slope, it is possible that wetlands that have substantial water-table fluctuations during shorter periods do not take on characteristic hydrophytic flora, but rather house vegetation similar to drier grasslands. This discrepancy was especially evident in two wetlands that have large fluctuations due to impacts of nearby ditches. In these wetlands, water levels increased dramatically at high water levels in the ditches and drained rapidly after the flood. The flood zones are therefore dry most of the time and may not promote wetland vegetation dominated by sedges or rushes. Note however that the definition of flooded grasslands might not be indicative of the actual area being flooded, but rather where the soil and hydrological conditions allow for hydrophytic plants to thrive.

The connection between hydrological properties and arthropod species abundances is likely complex, and connected to life histories of different species groups and their dependence on wet soils for larval development. Flooding per se is likely negative for many terrestrial arthropods by drowning larvae and adults, but species differ in their sensitivity by being able to reach drier grounds or by surviving in temporal refuges (Adis & Junk, 2002; Ramey et al., 2017; Rothenbücher & Schaefer, 2006; Sienkiewicz & Zmihorski, 2012). The inundation frequency, which is the proportion of days when the ground is flooded, generally had a negative impact on affected groups. For instance, abundances of *Coelostoma* (fam. Hydrophilidae), *Stenus* (fam. Staphylinidae) and *Erioptera* (fam. Limoniidae) were lower in more frequently inundated wetlands. A previous study, Åhlén et al. (2023), similarly found that inundation frequencies correlated with several groups of insects, including groups where abundances decreased and those where abundances increased with the inundation frequency. Our study found fewer groups responding to the inundation frequency. One explanation could be that the natural wetland considered in Åhlén et al. (2023) included environments across the full range of inundation frequencies, from very low (near 0 %) to very high (almost 100 %), whereas the constructed wetlands considered in this study exhibited less inundation with a maximum frequency of 68 % (mean 26 %). Moreover, the wetland in Åhlén et al. (2023) was much larger and was flooded over many hectares whereas the constructed wetlands in our study had much

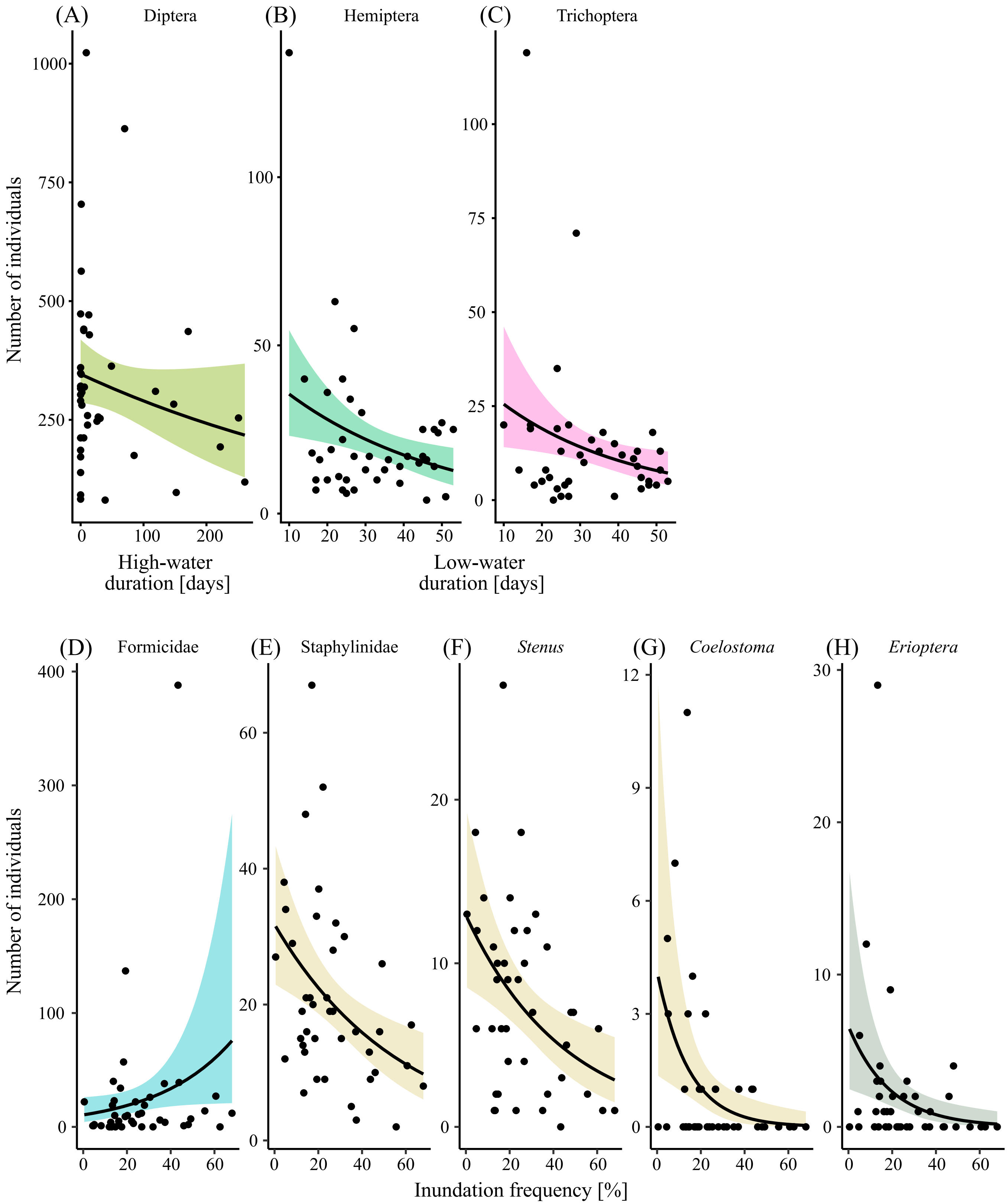

Fig. 4. Responses in (A) Diptera, (B) Hemiptera, (C) Trichoptera, (D) ants (Formicidae), (E) Staphylinidae, (F) *Stenus*, (G) *Coelostoma* and (H) *Erioptera* to high-water table duration (A), low-water table duration (B-C) and shoreline inundation frequency (D-H) with a generalized linear slope assuming negative binomial distributions and with 95 % CI.

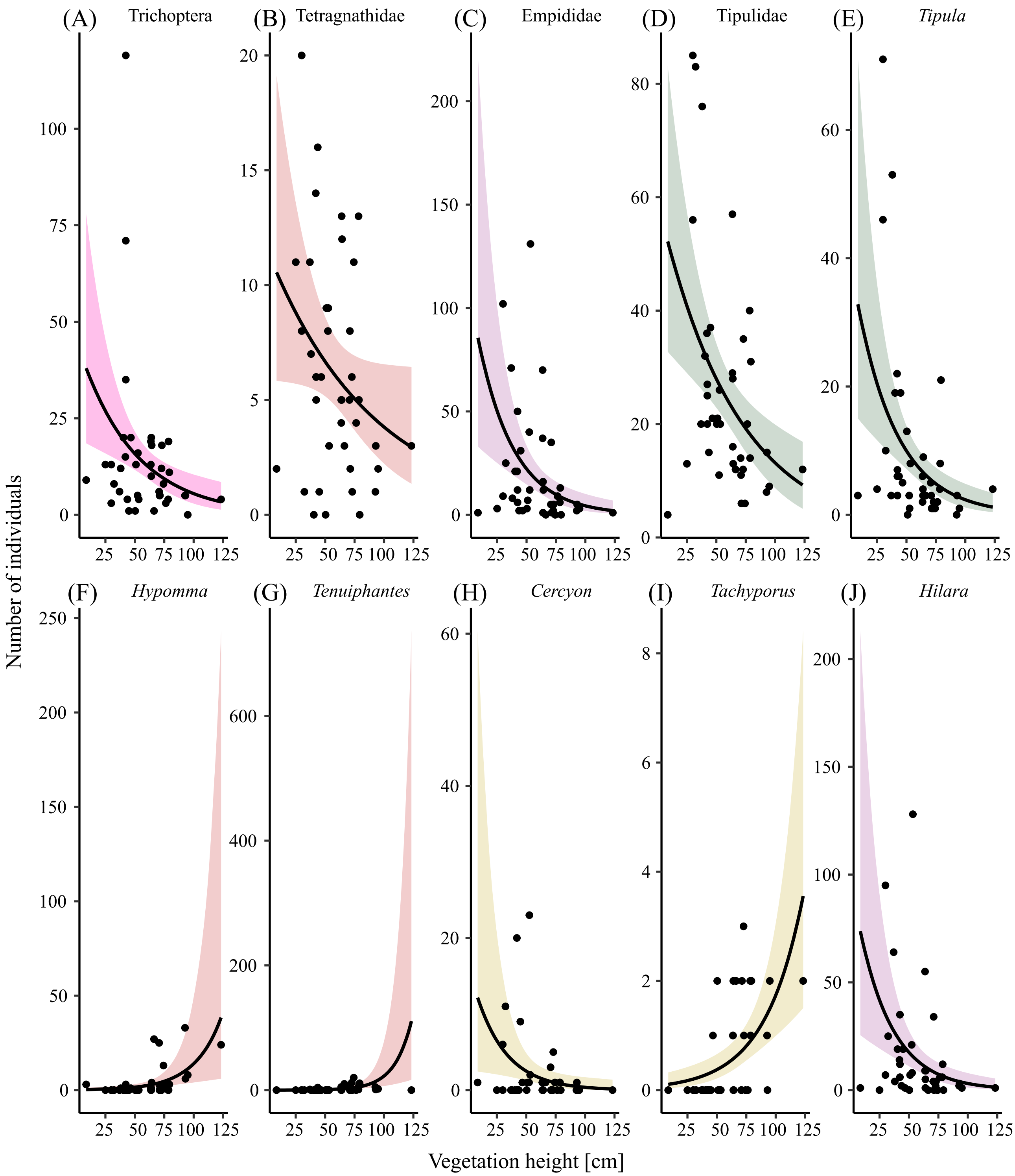

Fig. 5. Responses in abundance of (A) Trichoptera, (B) Tetragnathidae, (C) Empididae, (D) Tipulidae, (E) *Tipula*, (F) *Hypomma*, (G) *Tenuiphantes*, (H) *Cercyon*, (I) *Tachyporus* and (J) *Hilara* to average vegetation height at collection point with a generalized linear slope assuming negative binomial distributions and with 95 % CI.

smaller flood zones. Conversely, we found that ants were more abundant in wetlands with greater inundation frequencies, which suggests that riparian ant colonies may be resilient to inundation. This finding is corroborated by findings by Lafage et al. (2015) that saw rapid recolonization by ants following flooding events. In either case, arthropod groups do not necessarily respond similarly to inundation. Some groups require moist soils for larval development (e.g. Sciaridae), but frequent flooding events might cause negative responses due to drowning (Plum, 2005), whilst low frequencies might not provide the level of moisture required for larval development. An interesting aspect is that inundation frequency sometimes structured community compositions but at the same time was inconsequential in driving total order abundances. This finding suggests that environmental filtering from inundation frequencies may have limited impact in higher taxonomic organizations but rather drives habitability on genera or even species level due to differences in their respective ecologies.

The analyses indicated a resilience in wetland arthropods to extreme high water table durations. Although we found lower abundance of

Table 1
Responses in abundance by different taxa to driving predictors with P-values and GLM estimates (SE).

Abundance response	Grazing	Vegetation height	Shoreline slope	High-water duration	Low-water duration	Inundation frequency	Water-table amplitude x Shoreline slope	Inundation frequency x Shoreline slope
Diptera				P<0.05 -0.003 (0.001)				
Hemiptera	P<0.05 -0.48 (0.20)				P<0.01 -0.02 (0.008)			
Parasitic wasps							P<0.01 5.78 (1.82)	P<0.01 -0.04 (0.01)
Formicidae			P<0.001 1.72 (0.56)			P<0.01 0.04 (0.01)		
Trichoptera		P<0.05 -0.02 (0.006)			P<0.05 -0.03 (0.01)			

Table 2
Univariate responses to driving predictors from manyglm models with univariate GLM estimates (SE). Multivariate responses are reported in the Results section on the groups modelled, where all univariate responses have a corresponding multivariate effect on that group. Note that *Pirata* and *Piratula* responses include both flood zone area [bracketed] and the quadratic response.

Univariate community response	Grazing	Vegetation height	Flood zone Area^2	Low-water duration	Inundation frequency
Araneae					
Linyphiidae					
Erigone		P=0.06 -0.03 (0.009)			
Hypomma		P<0.05 0.04 (0.02)			
Tenuiphantes		P<0.01 0.07 (0.02)			
Lycosidae					
Pirata			P=0.07 [7.11 (2.52)] -0.94 (0.37)		
Piratula			P<0.05 [11.71 (4.24)] -1.96 (0.66)		
Tetragnathidae		P<0.05 -0.02 (0.006)			
Coleoptera					
Hydrophilidae					
Cercyon		P<0.05 -0.04 (0.02)			
Coelostoma					P<0.05 -0.07 (0.02)
Staphylinidae					P<0.05 -0.02 (0.005)
Stenus					P<0.05 -0.02 (0.007)
Tachyporus		P<0.01 0.03 (0.008)			
Brachycera					
Empididae		P<0.01 -0.03 (0.009)			
Hilara		P<0.05 -0.03 (0.01)			
Rhamphomyia	P<0.05 2.09 (0.55)				
Nematocera					
Tipulidae		P<0.001 -0.02 (0.004)			
Erioptera					P<0.05 -0.05 (0.02)
Tipula		P<0.01 -0.03 (0.008)			
Hemiptera					
Heteroptera	P<0.01 -0.87 (0.28)			P<0.05 -0.04 (0.01)	

Diptera in wetlands with longer durations of high-water tables, other groups did not vary with the length of flood periods. Thus, most arthropods inhabiting these wetlands seem well able to tolerate some extreme disturbance events. This finding contrasts with earlier studies that showed strong effects from long flood events. For instance, Sienkiewicz and Żmihorski (2012) found that the abundance of some carabid beetles increased after strong flood events but also that the overall species richness decreased. However, this and other studies emphasizing the negative effects of flooding originate from large river valleys where flooding may be more extensive and imply higher water flows than what is observed in our constructed wetlands (Bonn et al., 2002; Lambeets et al., 2008; Uetz, Vanderlaan, Summers, Gibson & Getz, 1979). Furthermore, Antvogel and Bonn (2001) found great variation in carabid community compositions between microhabitats within a small stretch of an alluvial river forest, which indicates that there can be substantial within-habitat turnover of arthropod community compositions. This conclusion could suggest that even though general characteristics vary substantially between wetlands, within-wetland variation could still be larger (see also Datry et al., 2014; Åhlén et al., 2023).

The variable that most commonly structured arthropod communities was vegetation height, which may be an indirect effect of flooding (see Fig. 3A), but may also be affected by various management activities such as grazing or hay making. The responses to vegetation height showed variations between groups but both beetle, spider and dipteran communities were structured by vegetation height. In some cases, effects are likely traced to the need of developing larvae in open soil (*Tipula* [Tipulidae] and *Hilara* [Empididae]), but this pattern was not consistent among groups having such larval development. In other cases, effects may rather be that web-building spiders (*Hypomma* and *Tenuiphantes* [Linyphiidae]) need vegetation structures for web constructions, matching earlier studies (Lyons, Ashton, Powell & Oxbrough, 2018). Interestingly, there were also two cursorial spider groups (*Erigone* [Linyphiidae] and *Pachygnatha* [Tetragnathidae]) that seemingly were negatively affected by high vegetation. These predatory species may of course also depend on the prey community and where response depend more on prey availability than on vegetation structure.

Wetlands with prolonged periods with low-water tables pose different challenges but also opportunities for species. In this study, we found negative relations between the length of low water tables and the abundances of both bugs (dominated by Heteroptera) and caddisflies (Trichoptera). Caddisfly larvae are aquatic and may be disadvantaged in wetlands that have long periods of low-water tables from desiccation or loss of habitat. The collected heteropterans were mainly terrestrial (dominated by the genus *Orius*). As a stressor, low-water tables may imply a reduction in the abundance of taxa that require stable access to water.

The size of the flood zone had surprisingly small impacts on arthropod abundances, with only a non-linear relationship to wolf spiders (*Pirata* [near sign.] and *Piratula*) where abundances were greatest in wetlands with intermediately sized flood zones. Larger habitats typically equate to greater abundances and species richness by providing greater and more heterogeneous habitats (Preston, 1962; Williams, 1964). However, the relationship between habitat size and abundance is often complicated and varies between taxa (Hambäck & Englund, 2005), whereas the predictions on a positive relationship between habitat size and species richness mainly apply to total richness and not richness density (Strandmark, Aggemyr, Cousins & Hambäck, 2020), as measured here. Moreover, most arthropods inhabiting wetlands are likely specialized wetland species, and may require certain wetland characteristics, which are provided regardless of flood zone size. As all sampled wetlands provided at least some flood zone, the variation among wetlands may not have been great enough to show the impact of having no flood zone at all, which could indicate that having flood zones, regardless of size, provides good habitat for arthropods to thrive. Midges (e.g. Chironomidae) and gnats (e.g. Sciaridae) are among the most common insects found in constructed wetlands, and are common prey to several shoreline arthropod predators (Hambäck, Cirtwill, Grudzinska-Sterno, Hoffmann, Langbak et al., 2022). Responses in midge and gnat abundance could therefore potentially affect abundance of predators (cf. Dreyer, Hoekman & Gratton, 2012), and this connection should be further studied as a driving variable for arthropod communities in constructed wetlands.

Conclusions

Our results showed that hydrological dynamics drive abundances of some arthropod groups in constructed wetlands. The study also found that many groups are unaffected by certain hydrological dynamics, including wetland arthropods that are well adapted to withstand disturbances from flooding, and low-water events. Many groups also respond to vegetation structure along wetland shorelines, but where the height of the vegetation affects groups differently. It is evident from the present results that arthropod community structure is driven by group-specific requirements, and that varying wetlandscapes would benefit arthropods in general the most. However, truly natural wetlands are rare in agriculture-dominated landscapes, which makes comparisons between natural and constructed wetlands difficult. As such, further studies are needed to compare community responses between truly natural and artificial fluctuations.

Data accessibility statement

The data supporting the findings in this study are openly available on Dryad [https://doi.org/10.5061/dryad.2280 gb62c].

CRediT authorship contribution statement

David Åhlén: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sofia Hedman:** Writing – review & editing, Methodology, Investigation. **Jerker Jarsjö:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Björn K. Klatt:** Writing – review & editing, Methodology, Investigation. **Lea D. Schneider:** Writing – review & editing, Methodology, Investigation. **John Strand:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Ayco Tack:** Writing – review & editing, Supervision. **Imenne Åhlén:** Writing – review & editing, Resources, Methodology, Formal analysis. **Peter A. Hambäck:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.09.010.

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