# **RESEARCH ARTICLE**



# Arthropod diversity in constructed wetlands is affected strongly by shoreline properties but only weakly by grazing

Revised: 5 August 2024

David Åhlén<sup>1,2</sup> | Jerker Jarsjö<sup>2,3</sup> | Mats Jonsell<sup>4</sup> | Björn K. Klatt<sup>5,6</sup> | Lea D. Schneider<sup>6</sup> | John Strand<sup>6</sup> | Peter A. Hambäck<sup>1,2</sup>

<sup>1</sup>Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden

<sup>2</sup>Department for Environmental Science, The Bolin Centre for Climate Research. Stockholm University, Stockholm, Sweden

<sup>3</sup>Department of Physical Geography, Stockholm University, Stockholm, Sweden

<sup>4</sup>Department of Ecology, Swedish University of Agricultural Sciences, Stockholm, Sweden

<sup>5</sup>Department of Biology, Lund University, Lund, Sweden

<sup>6</sup>The Rural Economy and Agricultural Society, Eldsberga, Sweden

#### Correspondence

David Åhlén, Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm SE-106 91. Sweden. Email: david\_aahlen@hotmail.com

#### Present address

Björn K. Klatt, School of Business, Innovation and Sustainability, Biology & Environmental Sciences, Halmstad University, Halmstad, Sweden

**Funding information** Naturvårdsverket; Svenska Forskningsrådet Formas

### Abstract

Aim: Aquatic-terrestrial transition zones contain features essential for many species that often benefit wetland biodiversity. Shallow flood-zone areas and reed beds are indicative of natural wetland habitats; however, how such features affect the native arthropod biodiversity in constructed wetlands is scarcely investigated. We asked how these shoreline features, as well as wetland shoreline properties and grazing management, influence riparian arthropod diversities and habitat specializations.

Location: Constructed wetlands, Sweden.

Taxa: Araneae, Coleoptera, Diptera.

Methods: Taxonomic-, phylogenetic- and trait diversities, along with habitat specialist species richness, were measured in riparian spiders, beetles and selected Diptera in 68 constructed wetlands in two regions of Sweden. We ran structural equation models to estimate direct and indirect effects from shoreline slope, flooded grassland, reed areas and grazing management on group diversities, and used multivariate models to determine drivers on habitat specialist species richness.

Results: Flooded grassland and reed area, along with shoreline slope influenced arthropod diversities, and responses differed between arthropod groups and diversity metrics. Spider trait diversity was greater in wetlands with larger flooded grassland areas, whilst beetle trait diversity was reduced. Spider phylogenetic diversity was greater in wetlands containing larger reed areas and in wetlands with steeper shorelines. However, species richness in predatory flies was greater in wetlands with more gentle shorelines. Grazing management had limited effects on arthropod diversities; however, species richness in wetland specialist and generalist predatory dipterans was greater in the absence of grazers in wetlands with greater flooded grassland areas.

Main Conclusions: As requirements vary considerably among arthropods, care must be taken when constructing and managing wetlands to benefit arthropod biodiversity. The present results suggest wetlands with a varied shoreline, albeit with greater proportions of flood areas, or multiple adjacent wetlands with varying shores in a wet landscape and a mild grazing regiment, would accommodate a more diverse arthropod fauna.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). Journal of Biogeography published by John Wiley & Sons Ltd.

#### KEYWORDS

agriculture, Arthropods, biodiversity, constructed wetlands, grazing management, shoreline properties, Sweden

# 1 | INTRODUCTION

Ponds and wetlands in agricultural landscapes are often biodiversity hotspots, where many arthropod species benefit from the high plant productivity and the mixture of breeding habitats (Denny, 1994; Kingsford et al., 2016). However, agricultural landscapes are often depauperate of wetlands because wet habitats were drained to gain croplands and to increase agricultural productivity (Davidson, 2014; Zedler & Kercher, 2005). The historical draining of wetlands has likely reduced arthropod populations and a high number of wetland species are currently on national and international red lists (IUCN, 2022; SLU Artdatabanken, 2020). In recent years, landscapes are again rewetted, with an increasing number of constructed or restored wetlands, particularly in open landscapes (Graversgaard et al., 2021), to reduce downstream eutrophication, mitigate flooding or promote bird diversity (Hambäck et al., 2023; Meli et al., 2014; Swartz & Miller, 2021). Irrespective of their purpose, constructed wetlands and ponds can be beneficial for a range of species. For instance, Strand and Weisner (2013) found that amphibian colonization was equally common in wetlands independent of the original management purpose. Nevertheless, constructed wetlands are often made like ponds with flooded grasslands around, and do not resemble the natural wetlands that were once drained. For these constructed wetlands, we lack much information on the habitat structures and their importance for biodiversity (Batzer & Wu, 2020).

The transition zone between the open water and the terrestrial surroundings provides temporarily flooded vegetated habitats that are often rich in spiders and various insect groups (Batzer & Wu, 2020). Besides benefitting arthropod groups that specialize in wetlands, generalists and terrestrial specialists may benefit from the high primary production and prey abundance in flooded areas (Ramey & Richardson, 2017). Previous studies suggest that arthropod species respond differently to habitat attributes, and key attributes often include aspects such as flooding regime, grazing or shoreline structures (Åhlén et al., 2023; Lafage & Petillon, 2016; Ramey & Richardson, 2017). This pattern is particularly apparent for beetle species, where both carabids and staphylinids are often affected by the flood regime (Bonn et al., 2002; Sienkiewicz & Zmihorski, 2012), as well as by the presence of grazing livestock (Cajaiba et al., 2018; Waite et al., 2022). Similarly, many crane fly species require periodically flooded soil during juvenile development (Stubbs, 2021) whereas certain beetle species feed on hydrophytic vegetation (Rheinheimer & Hassler, 2010). However, we lack substantial information on how wetland habitat structures support arthropod communities with different levels of specialization to wetlands, a knowledge that is imperative to understanding the effects of rewetting the landscape on arthropod diversity (Batzer & Wu, 2020).

Species richness alone does not describe the structure of a community, and additional important measures include phylogenetic and trait diversity. These measures complement species richness by accounting for species similarities and differences in the community and thereby describe the ecological complexity of a community. For example, a species-rich spider community may contain a narrow trait diversity and lack ecological complexity because all spiders are carnivorous and related spider species are of similar size. On the other hand, spider species differ in hunting strategies (e.g. active hunters, sheet web weavers, etc.), where trait diversity is perhaps driven more by ecological factors than taxonomic or phylogenetic diversity. Beetle communities similarly contain multiple feeding guilds and habitat specialists, but may also show a great degree of species clustering, for example, Chrysomelidae and Curculionidae are herbivorous and most Carabidae and Staphylinidae are predatory (e.g. Stasiov et al., 2021). Thereby, only the combination of measures can sufficiently describe an arthropod community by combining information on diversity and complexity (Baulechner et al., 2019; Din et al., 2019).

The different diversity measures depend on the spatial scale but often correlate (Petchey & Gaston, 2002), where deviations may indicate underlying filtering mechanisms (Ndiribe et al., 2013). For instance, if communities are mainly filtered by habitat characteristics or if disturbances are strong drivers of community membership, we expect species with similar traits and similar fundamental niches to cluster, which would tend to reduce trait diversity within habitats but increase trait diversity between habitats (Ndiribe et al., 2013). On the other hand, interspecific competition should result in negative associations between species with similar traits and overdispersion of trait diversity relative to taxonomic diversity. Environmental variables may also affect diversity measures differently, which again provide indications of underlying ecological processes (e.g. Baulechner et al., 2019; Nanni et al., 2021). For instance, the independent effects of environmental variables on trait or phylogenetic diversity, whilst accounting for taxonomic species richness, may indicate an environmental filtering mechanism due to trait similarities or dissimilarities.

We examined how shoreline habitats and grazing management in constructed wetlands determine the taxonomic, phylogenetic and trait diversity of key wetland arthropod communities. The constructed wetlands in our study constitute ponds of open water with surrounding flooded areas. We focused on spiders, beetles and some dipteran families in the riparian zone because they are diverse in constructed wetlands and relatively easy to identify. To disentangle the roles of environmental variables on measures of diversity, and to identify underlying filtering mechanisms, we used structural equation models (SEMs). We hypothesized that gentle shoreline slope increases riparian zone size and thereby increases several diversity measures and that the species richness of wetland specialists is higher in constructed wetlands with gentle shorelines and expansive flood zones. Finally, we hypothesized that reed bed area, amount of beneficial surrounding habitats and grazing livestock similarly increase biodiversity. These hypotheses were tested for wetlands of different sizes, landscape positions and environmental characteristics situated in two regions within Sweden.

# 2 | MATERIALS AND METHODS

#### 2.1 | Wetland selection

We sampled arthropods in 68 wetlands in two regions of Sweden, Halland on the Swedish west coast (56.5-57°N, 46 sites) and Uppland in eastern Sweden (59-60°N, 22 sites), during the summer of 2020 (Figure 1). Both regions are hemi-boreal, but Halland is dominated by agriculture whereas Uppland is largely dominated by forestry interspersed with agriculture. To mitigate nutrient runoff and algal blooms in the nearby Kattegat strait, thousands of wetlands have been constructed in Halland since 1990. Constructed wetlands in Uppland are scarcer and are mostly constructed to increase hunting opportunities. When selecting wetlands, we visited wetlands in predominately agricultural landscapes and selected those with <50% forest cover in a 50m perimeter to omit wetlands enclosed by forest. We categorized wetlands based on shoreline slope to include gentle to steep shoreline conditions. Furthermore, as farmers often utilize wetlands in the agricultural landscape for livestock grazing, we included both grazed and ungrazed wetlands but did not account

for stocking densities or animal species. To account for wetland size effects, we chose wetlands of varying sizes (0.05–11.95 ha). We also limited the analysis to lentic, freshwater wetlands with partially open water surfaces. This site selection yielded replicates of wet mead-ows or marshes that included a part with open water, with varying shoreline morphology, size, management and wetland structure, situated in open habitats and mostly surrounded by agricultural lands.

# 2.2 | Arthropod collection

To capture the breadth of arthropod species across the season, we sampled each wetland in (1) late May to early June, (2) late June to early July and (3) August to early September. To sample Diptera and other flying insects, we used SLAM (Sea, Land and Air Malaise) traps placed within 2m of the water's edge. One SLAM trap was placed per site during three consecutive nights per sampling period. To sample spiders and beetles, we used pitfall trapping and suction sampling. We placed three pitfall traps (diameter 70mm) containing water and detergent perpendicular to the shoreline, spaced 5 m apart and within 10m from the SLAM trap. Traps were anchored with tent pegs to prevent hydrological pressure from lifting them from the soil. Pitfall trapping was used during periods 1 and 3 in Uppland and during period 1 in Halland. Suction sampling was performed by vacuuming all ground and vegetation within a 45 cm diameter hoop at three sampling points, similar to the placement of pitfall traps, using a converted leaf blower. Suction sampling was done in Uppland during periods 1 and 3, and in Halland during periods 2 and 3.

We focussed on six species-rich taxa that occur commonly in wetlands; spiders (Araneae), beetles (Coleoptera), dance flies (Hybotidae),



**FIGURE 1** Example pictures of typical wetlands, along with (a) 46 locations in Halland-, and (b) 22 locations in Uppland region in Sweden. Photographs by David Åhlén (top) and Sofia Hedman (bottom).

WILEY<sup>\_</sup> Journal of Biogeography

dagger flies (Empididae), long-legged flies (Dolichopodidae) and crane flies and their allies (Tipulidomorpha [Tipulidae, Limoniidae, Pediciidae, Cylindrotomidae, Ptychopteridae]). Spiders are all predatory with either active hunting (e.g. Lycosidae, Erigoninae and Clubionidae) or web building (e.g. Linyphiinae, Theridiidae and Araneidae) (Pedro Cardoso et al., 2011). Beetles include predators (e.g. Carabidae and Staphylinidae), whose larvae mainly develop in or on the soil (Stasiov et al., 2021), as well as those with herbivorous (e.g. Chrysomelidae), omnivorous (e.g. Coccinellidae) or detritivorous larvae. Dance flies, dagger flies and long-legged flies are mainly predatory (hereafter predatory Diptera), and most species develop as larvae in wet soil or detritus (Chvála, 1983). Crane flies similarly develop mainly in moist soils and feed on detritus (Stubbs, 2021). Diversity estimates are based mainly on adults as larvae are more difficult to identify. However, juvenile spiders, identified as genus, were included as one species within that genus when no adults were collected for that site.

### 2.3 | Habitat structure and management

We calculated areas of flooded grassland, reeds, pastures and meadows in a 500m radius surrounding the collection point using QGIS 3.26.3 (QGIS, 2022), as landscape factors in the analysis. Flooded grasslands, defined as habitats dominated by sedges and rushes (Cyperaceae and Juncaceae), are indicative of riparian flood zones essential for many arthropod wetland species. Reed beds were defined as areas with tall, emergent, non-woody vegetation with reeds and bulrushes dominating. Pastures and meadows (grazed or nongrazed) were defined as terrestrial grasslands with or without evidence of grazing animals (cattle, sheep, horses or other livestock). As a proxy for shoreline slope, we calculated the elevational difference between the SLAM trap position and the water level using  $1 \times 1 \text{ m}^2$ aerial digital elevation models (Markhöjdmodell grid 1+, downloaded on 2023-02-28 from SLU geodataportalen © Lantmäteriet) per wetland.

### 2.4 | Diversity estimates and statistical analyses

We used four diversity measures in the statistical analyses; total species richness, rarefied species richness, rarefied phylogenetic diversity and rarefied trait diversity. Total species richness was quantified as the number of species per site, and the rarefication of diversity was based on the number of individuals using the alpha function in the BAT package (Cardoso et al., 2015). To estimate phylogenetic diversity, we first constructed a phylogeny for each taxon group separately using phyloT v2 (https://phylot.biobyte.de/), which generates phylogenetic trees based on the NCBI taxonomy. Phylogenies were constructed at the genus level, with zero branch lengths for species, and edited to make trees symmetric with total branch length equal for all genera (see Appendix S1). Traits used for calculating the trait diversity included body sizes and dispersal mode

which could influence community dynamics (e.g. De Bie et al., 2012), as well as trophic group and prey capture strategy as feeding traits (see Appendix S2). Dispersal mode (ballooning or not, following Bell et al., 2005) and prey capture strategy (following Pedro Cardoso et al., 2011) were only available for spiders. Trait distances between species were calculated using funct.dist (with gower distances) in package mFD (Magneville et al., 2022) and clustered using hclust before calculating rarefied trait diversity in BAT.

Species were categorized as wetland specialists, habitat generalists and terrestrial specialists using the classification of Swedish species (www.artfakta.se), which reports main and secondary habitat preferences based on expert opinions. For each species, we scored wetland affinity as high when the main habitat was some wetland type (shoreline, wet meadow/bog and aquatic), terrestrial affinity as high when the main habitat was some terrestrial type; and lower affinities if only a secondary habitat was indicated in corresponding categories. The species was scored as wetland specialist if primary or secondary habitats were dominated by wetland types and as a terrestrial specialist if dominated by terrestrial habitat types. If affinities included both habitat types equally then the species was categorized as a habitat generalist. If habitat information was lacking, we used landscape-type preferences to determine specialization (see Appendix S2).

To estimate the direct and indirect effects of environmental variables on the diversity estimates, we used piecewise SEMs and the command psem from the package piecewiseSEM (Lefcheck, 2016). Based on the original hypothesis, we selected wetland habitat variables that were governed by wetland morphology (shoreline slope, flooded grassland- and reedbed area) and surrounding terrestrial grassland area, that could be of relevance to describe arthropod community metrics. We ran linear models using the presence/absence of grazers (mainly cattle and sheep), region (Uppland and Halland), shoreline height difference (hereafter slope), flooded grassland and reedbed areas and terrestrial grassland area as fixed factors. Wetland habitat variables were log-transformed to obtain linearity. Residual plots were inspected to confirm underlying assumptions of normally distributed residuals and homoscedasticity. The maximum models were optimized by removing variables based on relevance and AIC scores. The regional diversity differences should be treated with caution as they may originate from true regional differences as well as from non-contemporaneous sampling. For this reason, we ran the final models for each region separately, finding both concordance and differences between regions (see Appendix S3). Following the trait diversity results in the SEMs, we ran linear models on community-weighted means of traits from the driving predictors of trait diversity to understand trait-specific responses. Finally, to examine the effects on species richness in wetland specialists, generalists and terrestrial specialists, we ran multivariate manyglm models from the mvabund package (Wang et al., 2022). Spider, beetle and predatory dipteran communities were analysed separately, where cumulative univariate responses from each group provided multivariate community responses and univariate group responses. All analyses were run in R 4.2.1 (R Core Team, 2022).

# 3 | RESULTS

# 3.1 | Arthropod abundances and wetland characteristics

In total, we sampled 19,132 individuals and 870 species. Beetles and spiders were the two most abundant and species-rich groups with 7107 individuals from 521 species, and 6862 individuals from 145 species, respectively. The predatory Diptera consisted of 3192 individuals from 142 species, whereas crane flies consisted of 1971 individuals from 62 species. The area of flooded grassland decreased with the steepness of the slope (p < 0.001), and differed between regions (p < 0.01). Uppland wetlands had larger flooded grassland areas (Figure 2).

# 3.2 | Spiders

The spider SEM included all credible links (p = 0.08, Fisher's  $C_{df=26} = 36.9$ , Figure 2a) (model structure in Appendix S4). Total

spider species richness was greater in Uppland than in Halland (p < 0.001) with an interactive effect of region and reed area on spider species richness (p < 0.04). This interaction arose because the spider richness increased with the reed area only in Uppland. Rarefied species richness was not directly related to any environmental variable but was only positively related to total species richness (p < 0.001). In contrast, phylogenetic diversity was directly and positively related to both shoreline slope (p < 0.002) and reed area (p < 0.002), in addition to being correlated with rarefied species richness (p < 0.001). Finally, trait diversity was correlated with phylogenetic diversity (p < 0.001), rarefied species richness (p < 0.001), and was higher in wetlands with a larger flooded grassland area (p < 0.03).

Journal of

The multivariate analysis suggested that the spider community was affected by reed area (p < 0.03, Deviance=8.7), region (p < 0.001, Dev.=26.4) and by the interaction between grazing and region (p < 0.001, Dev.=20.0). The following univariate analyses showed that the richness of wetland specialist spiders increased with reed area (p < 0.02, Dev.=7.6, Figure 3a), whereas other groups





2327

WILEY



FIGURE 3 Spider species richness across specializations as a response to reed area (a-c) with linear relationship and 95% confidence intervals (CI), and from grazing management in Halland and Uppland (d-i).

did not vary with reed area (Figure 3b,c). Richness was also greater in Uppland than in Halland for both wetland (p < 0.003, Dev. = 17.6) and terrestrial (p < 0.01, Dev. = 7.9) specialists, but not for generalist species. Finally, spider species richness in Uppland was greater in ungrazed than in grazed wetlands for both generalist (p < 0.04, Dev. = 5.2, Figure 3h) and terrestrial specialist (p < 0.002, Dev. = 12.3, Figure 3i) species.

When examining the effects on community-weighted trait means, we found that patterns for spiders were mainly explained by dispersal and hunting strategy. First, the proportion of spiders using ballooning was lower in Uppland compared with Halland ( $F_{1,65}$ =36.1, p <0.001), and lower in wetlands with greater reed areas ( $F_{1,65}$ =4.7, p <0.05). Second, the proportion of web-building spiders was higher in wetlands with a steeper shoreline slope ( $F_{1,65}$ =4.1, p <0.05).

# 3.3 | Beetles

The beetle diversity SEM also included all credible links (p=0.36, Fisher's  $C_{df=26}$ =28.0, Figure 2b; model structure in Appendix S4). Total beetle species richness was greater in Uppland than in Halland (p<0.001), and all other diversity measures were related (Figure 2b). The only measure directly related to an environmental variable was trait diversity which decreased with the flooded grassland area (p<0.02).

In the multivariate analysis, the beetle community was affected by reed area (p < 0.001, Dev. = 17.5), flooded grassland area (p < 0.005, Dev. = 15.4), but also varied between regions (p < 0.001, Dev. = 74.2). The univariate analyses indicated that these patterns arose because the number of wetland specialized species increased with both reed area (p < 0.007, Dev. = 9.3, Figure 4a) and flooded grassland area (p < 0.02, Dev. = 9.2, Figure 4d). At the same time, the number of terrestrial species showed an opposite response, decreased with reed area (p < 0.03, Dev. = 6.1, Figure 4c) and with a similar tendency in relation to flooded grassland area (p = 0.08, Dev. = 4.2, Figure 4f). In contrast, generalist species richness did not vary with either variable (Figure 4b,e). Finally, Uppland had a higher richness than Halland of both wetland specialized species (p < 0.001,

Dev.=30.4), generalist species (p<0.001, Dev.=35.2) and terrestrial specialist species (p<0.006, Dev.=8.6).

When examining effects on community-weighted trait means, we found that the proportion of predatory beetle species increased from 60% in wetlands with no flooded grasslands to 80% in wetlands with the highest area of flooded grasslands ( $F_{1,66}$ =4.4, p <0.05). This pattern was even stronger when removing wetlands completely lacking flooded grasslands ( $F_{1,55}$ =5.6, p <0.05). In addition, the average beetle body size similarly increased with the area of flooded grasslands ( $F_{1,66}$ =8.1, p <0.01) and was lower in Uppland compared with Halland ( $F_{1,66}$ =4.9, p <0.05).

# 3.4 | Predatory Diptera

The predatory Diptera SEM included all credible links (p=0.82, Fisher's  $C_{df=28}$ =21.1, Figure 2c) (model structure in Appendix S4). Total species richness was lower in wetlands with a steeper shoreline slope (p<0.05), whereas other diversity metrics had no direct relationship with environmental variables (Figure 2c). However, rarefied species richness directly increased with total species richness (p<0.05) which also increased with phylogenetic diversity (p<0.001). Rarefied species richness was positively related to trait diversity (p<0.001, Figure 2c).

The multivariate analyses suggested that the predatory dipteran community was driven by shoreline slope (p < 0.02, Dev.=9.3), and by the interaction between flooded grassland area and grazing (p < 0.006, Dev.=10.5). Univariate analyses showed that these effects arose because the species richness of wetland specialist flies decreased with shoreline slope (p < 0.008, Dev.=6.8, Figure 5a) and increased with flooded grassland area but only when not grazed (p < 0.04, Dev.=4.9, Figure 5g). Similarly, generalist species richness increased with flooded grassland areas when not grazed, and decreased when grazed (p < 0.04, Dev.=5.2, Figure 5e,h), whereas the richness of terrestrial specialist species did not vary with any environmental variable (Figure 5c,f,i). There were no effects from environmental variables on community-weighted trait means.



FIGURE 4 Beetle species richness across specializations as a response to reed area (a-c) and flooded grassland area (d-f) with linear relationship and 95% CI.



FIGURE 5 Predatory dipteran species richness across specializations as a response to height difference of mean water surface levels and shoreline height at collection point (a–c), and flooded grassland area in Halland and Uppland (d–i) with linear relationships and 95% CI.

# 3.5 | Crane flies

The crane fly SEM included all credible links (p=0.65, Fisher's  $C_{df=24}$ =20.85, Figure 2d) (model structures in Appendix S4). Total species richness was unaffected by all environmental variables, but total species richness was positively related to rarefied species richness (p<0.001), which was positively related to phylogenetic diversity (p<0.001), as well as trait diversity (p<0.001). The trait diversity was greater in Halland than in Uppland (p<0.05; the mean body size of crane flies was smaller in Uppland compared with Halland;  $F_{1.66}$ =7.5, p<0.01).

# 4 | DISCUSSION

The present study shows that shoreline habitat structure of constructed wetlands affects arthropod diversity and community composition, but differently depending on arthropod group and diversity measure. The diversity is predicted by either the slope of the shoreline, the amount of flooded grassland or the reed bed area. For instance, wetlands with larger flooded grassland areas had higher trait diversity of spiders, but lower trait diversity of beetles, whereas reed areas increased the phylogenetic spider diversity. Finally, wetlands with steeper shorelines had higher spider phylogenetic diversity, but also a lower species richness of predatory flies. Grazing only affected spider species richness and only in Uppland, where it was higher in wetlands with shoreline grazing. There were additional regional differences with greater total species richness in spiders and beetles in Uppland compared to Halland, whilst trait diversity of crane flies was greater in Halland compared to Uppland. Finally, for all groups, there were strong relationships between diversity measures; total species richness, rarefied species richness, phylogenetic diversity and trait diversity.

# 4.1 | Shoreline morphology driving diversities in riparian arthropods

We expected flooded grassland areas, characterized by gently sloped shorelines, to be the main driver of diversity and wetland specializations. This expectation was confirmed for the species richness of wetland specialist beetles and wetland specialist flies in ungrazed habitats. However, the pattern showed large variation between WILEY<sup>\_</sup> Journal of Biogeograph

arthropod groups and was notably different when comparing spiders and beetles. In particular, larger flooded grassland areas around wetlands increased the trait diversity of spiders but at the same time decreased the trait diversity of beetles. This pattern, combined with the fact that the species richness of wetland specialist beetles was positively related to the flooded grassland area but not to spiders, suggests that trait diversity and wetland specialization are differently related in the two groups. Although wetland specialist species should benefit from typical wetland characteristics, expansive flood zones may require specialized feeding traits that affect the niche breadth of spiders and beetles differently (see also Lambeets et al., 2008; Moran et al., 2012).

When examining trait means, we found that the proportion of predatory beetles was greater in wetlands with larger flooded grassland areas, presumably because greater flood zones support a high abundance of prey that these beetles feed upon. It thus seems that the trait diversity of beetles is reduced in wet habitats because nonpredatory feeding types are more strongly filtered from the beetle community. The predatory beetle community in wetlands and riparian areas is often dominated by rove beetles (Staphylinidae) and ground beetles (Carabidae), in which many common species have a diet of springtails (Collembola), mites, arthropod larvae and other detritivorous invertebrates on or in the wet soil (Baulechner et al., 2022; Betz & Kölsch, 2004; Chen & Wise, 1999; Oberholzer & Frank, 2003; Yamazaki, 2006). In addition, ground beetles and rove beetles often have comparatively narrow habitat preferences, which makes them suitable as indicator species (Bohac, 1999; Gerisch et al., 2006) but also filter species strongly along dry-wet gradients. Finally, the average body size of beetles was greater in wetlands with larger areas of flooded grassland, suggesting that differences in community structure between wetlands with different flooded grassland areas could additionally be due to frequent flooding causing smaller species with less dispersal capacity to be excluded.

In contrast, variability in spider traits could not explain their increased trait diversity in wetlands with larger flooded grassland areas. The mechanics behind the discrepancies in trait diversity responses between spiders and beetles from flooded grassland areas are therefore still unclear, but match observations from other studies (e.g. Bonn et al., 2002), where the ground beetle assemblage varied with the flooding regime but where spider communities varied with habitat structure. These group differences may be due either to inherent differences in habitat selection between spiders and beetles or because differences in hunting mode and the capacity to use aquatic resources filter spider and beetle communities differently. Feeding habits among spiders typically vary less than among beetles and most spider species commonly use aquatic resources such as midges (Chironomidae) compared with beetle species that more seldom utilize aquatic resources (Mellbrand & Hambäck, 2010). Feeding habits could thus be a weaker filter on the wetland spider community, and structural properties of the environment may instead be more important. Increased niche breadth would then rather be due to changes in the physical composition of the habitat creating novel possibilities for net construction (cf. Cattin et al., 2003).

This conclusion is supported by the finding that the phylogenetic diversity and proportion of wetland species increased with reed area and that both phylogenetic diversity and the proportion of web spider species (increasing phylogenetic diversity) were higher at wetlands with steeper shorelines. On the other hand, previous studies show that many spiders are sensitive to flooding and that frequently flooded areas typically contain habitat generalists and particularly cursorial species among wolf spider species (Bonn et al., 2002). Hence, web spiders may be more sensitive to flooding and steeper slopes thereby providing refuges during high water events. On the other hand, previous studies have almost exclusively used pitfall trapping that biases community descriptions towards wolf spider species (Amiar et al., 2023) whereas our data are based both on pitfall trapping and vacuum sampling that better describes the full spider community. In either case, our study indicates complementary effects of different types of wetland morphology, suggesting that a varied shoreline may provide the greatest spider community niche breadth in wetlands.

# 4.2 | Influence of grazing management

Prior to the study, we expected grazing to be an important determinant of arthropod diversity, in interaction with shoreline slope, by increasing the quality of riparian habitats (e.g. Bucher et al., 2016; Moran et al., 2012). However, our data suggest that grazing has small effects on the species richness of riparian arthropods and, if anything, decreases the richness of generalist and terrestrial specialist spiders. Moreover, both wetland specialist and generalist predatory dipteran species richness increased with flooded grassland areas only when grazers were not present. These effects might be an effect of disturbance, where high abundance of grazing animals causes excessive trampling disturbance in flood zone areas (Cole, Brocklehurst, McCracken, et al., 2012). One interesting example was one wetland in Halland with rotating grazing regimes where cattle graze only a week per month. Even though this is a single case, this wetland had a high species richness, with many species being exclusive to that location and many endangered and specialized beetle species. In either case, it seems that many grazed wetlands may have too high stocking rates, disturbing arthropod species that are not directly associated with grazing livestock, leading to suggestions to fence the area closest to water as a conservation measure (Cole, Brocklehurst, McCracken, et al., 2012). However, such effects may differ among taxa, where high grazing intensities negatively affected pollinating insects by reducing floral abundances (Cole et al., 2015) and positively affected the functional diversity of ground beetles (Cole, Brocklehurst, Elston, et al., 2012). Additionally, faeces produced by livestock may influence arthropod community compositions, as it provides niches required for certain species (Nanni et al., 2021; Waite et al., 2022). These findings, similar to ours, indicate complicated relationships between grazing and arthropod diversity, presumably dependent on the grazing intensity but also due to the multifaceted impacts of grazing animals in riparian habitats

where they both reduce vegetation heights and increase damage from trampling. Grazing effects also vary depending on vegetation type (Torma et al., 2023), but the present information anyway suggests that a variable grazing regime with only partial access to the immediate shore may be most beneficial for arthropod communities.

# 4.3 | Regional differences in diversities

The higher total species richness of spiders and beetles in Uppland compared to Halland could suggest regional variation in wetland structures that affect species richness. Wetlands in Uppland are constructed to benefit birds, as hunting opportunities, which result in different shoreline structures compared with wetlands in Halland that are mainly constructed to catch nutrients. However, since the direct regional effects mainly affect non-rarefied species richness in spiders and beetles, the observed regional differences in species richness may be a consequence from differences in sampling effort. On the other hand, when running SEMs separately for the region, we found similar estimates as for the models including all data, which validates the conclusion that observed effects were independent of region. Additionally, total species richness in predatory dipterans and crane flies, where regional sampling efforts were more similar, was not different between regions.

### 4.4 | Considerations in trait diversities

In our functional trait analysis, we used a limited number of traits per species, due to a lack of relevant traits for arthropods for allowing multitrait analyses. On the other hand, as the meta-analysis by Jeliazkov and Chase (2024) showed, different traits may respond differently to the same environmental factors which obscures the relationship to trait diversity. In their analysis, it was apparent that single-trait analyses typically outperformed multitrait analyses. Nevertheless, additional traits, particularly those reflecting abilities to sustain flooding, could have improved model predictions. Unfortunately, there is quite limited knowledge of traits affecting species survival in flooded habitats beyond the facts that species differ in submersion tolerance and that high dispersal capacity allows fast recolonization after floods recede (Kolesnikov et al., 2012; Lambeets et al., 2008; Rothenbucher & Schaefer, 2006).

# 4.5 | Conclusions

Our study indicates that shoreline properties matter for arthropod diversity when constructing wetlands in agricultural and cultivated landscapes. The species richness of wetland specialist beetles and flies correlated positively with flooded grassland areas and gentle slopes, and particularly in ungrazed wetlands. However, responses varied greatly between spiders, beetles and dipterans. A general recommendation would therefore be to make shoreline slopes

variable around constructed wetlands but with a dominance of seasonally flooded shores and with some reedy areas. Alternatively, multiple proximal wetlands with varying structures would provide a heterogeneous wetlandscape that benefits a broader set of species. In this context, it is important to remember that the extent of flooded grasslands not only depends on the steepness of the shore but also on the variability in water tables, which depends on both the catchment area and outlet solutions, factors not included in this analysis. It is also notable that grazing animals may or may not have positive effects on arthropod diversity in flood zones depending on their density and therefore also on the amount of trampling damage disturbing the nearshore habitats. Due to the large variability in types of grazing animals and their density, it is evident that our study was too heterogeneous for more firm conclusions. In either case, it seems that both the design of the constructed wetland and subsequent management will determine the effect on the arthropod community and diversity in the riparian zone around the wetland.

### ACKNOWLEDGEMENTS

We thank Victor Ericsson for the initial sorting of samples, and further colleagues who assisted in species identification: Magnus Persson (Dolichopodidae), Raul Vicente (spiders), Sven Hellqvist (Empididae and Hybotidae), Joel Hallqvist and Petter Andersson (beetles) and Michael Andersson (Tipulidomorpha). No permits were required to perform the data collection for this manuscript. However, we thank the landowners for allowing us to perform collections on their lands. This paper is a contribution from project 2018-843 (to PAH) from the Swedish Research Council Formas and project 802-0091-19 (to JS, JJ and PAH) from the Swedish Environmental Protection Agency.

#### CONFLICT OF INTEREST STATEMENT

The authors of this study have no conflicting interests to report.

#### DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are openly available on Dryad at https://doi.org/10.5061/dryad.f7m0cfz42. [Temporary link for review: https://datadryad.org/stash/share/VR7W7qg5n9 XGX-HGg87VLqpkGbWTf4EdS04NsqVV6nc].

# ORCID

David Åhlén https://orcid.org/0000-0002-1903-6842 Peter A. Hambäck https://orcid.org/0000-0001-6362-6199

#### REFERENCES

- Åhlén, I., Jarsjö, J., & Hambäck, P. A. (2023). Connecting wetland flooding patterns to insect abundance using high-resolution inundation frequency data. Wetlands, 43(6), 74. https://doi.org/10.1007/ s13157-023-01716-0
- Amiar, D., Leandro, C., Courtial, C., & Petillon, J. (2023). A comparison of two widely used methods for estimating taxonomic and functional diversities of epigeal arthropods in some temperate grasslands. *Entomologia Experimentalis et Applicata*, 171, 867–877. https://doi. org/10.1111/eea.13371

ILEY<sup>\_</sup> Journal of Biogeography

- Batzer, D. P., & Wu, H. (2020). Ecology of terrestrial arthropods in freshwater wetlands. Annual Review of Entomology, 65(1), 101–119. https://doi.org/10.1146/annurev-ento-011019-024902
- Baulechner, D., Diekötter, T., Wolters, V., & Jauker, F. (2019). Converting arable land into flowering fields changes functional and phylogenetic community structure in ground beetles. *Biological Conservation*, 231, 51–58. https://doi.org/10.1016/j.biocon.2019.01.005
- Baulechner, D., Jauker, F., & Wolters, V. (2022). Carabid adaptation to a collembolan diet: Hunting efficiency and nutritional value. *Ecological Entomology*, 47(2), 242–248. https://doi.org/10.1111/ een.13106
- Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005). Ballooning dispersal using silk: World fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, 95(2), 69–114. https://doi.org/10. 1079/ber2004350
- Betz, O., & Kölsch, G. (2004). The role of adhesion in prey capture and predator defence in arthropods. Arthropod Structure & Development, 33(1), 3–30. https://doi.org/10.1016/j.asd.2003.10.002
- Bohac, J. (1999). Staphylinid beetles as bioindicators. Agriculture Ecosystems & Environment, 74(1-3), 357-372. https://doi.org/10. 1016/s0167-8809(99)00043-2
- Bonn, A., Hagen, K., & Wohlgemuth-Von Reiche, D. (2002). The significance of flood regimes for carabid beetle and spider communities in riparian habitats—A comparison of three major rivers in Germany. *River Research and Applications*, 18(1), 43–64. https://doi.org/10. 1002/rra.632
- Bucher, R., Andres, C., Wedel, M. F., Entling, M. H., & Nickel, H. (2016).
  Biodiversity in low-intensity pastures, straw meadows, and fallows of a fen area—A multitrophic comparison. *Agriculture, Ecosystems and Environment, 219*, 190–196. https://doi.org/10.1016/j.agee. 2015.12.019
- Cajaiba, R., Périco, E., da Silva, W., Vieira, T., Dalzochio, M., Bastos, R., Cabral, J. A., & Santos, M. (2018). How informative is the response of ground Beetles' (Coleoptera: Carabidae) assemblages to anthropogenic land use changes? Insights for ecological status assessments from a case study in the Neotropics. Science of the Total Environment, 636, 1219–1227.
- Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global patterns of guild composition and functional diversity of spiders. *PLoS* One, 6(6), e21710. https://doi.org/10.1371/journal.pone.0021710
- Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT–biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, 6(2), 232–236. https://doi.org/10. 1111/2041-210x.12310
- Cattin, M. F., Blandenier, G., Banasek-Richter, C., & Bersier, L. F. (2003). The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. *Biological Conservation*, 113(2), 179–188. https://doi.org/10.1016/s0006-3207(02)00297-5
- Chen, B. R., & Wise, D. H. (1999). Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology*, *80*(3), 761–772. https://doi.org/10.1890/0012-9658(1999)080[0761: Bulopa]2.0.Co;2
- Chvála, M. (1983). The Empididae (Diptera) of Fennoscandia and Denmark. Part II, General part, the families Hybotidae, Atelestidae and Microphoridae. Brill.
- Cole, L. J., Brocklehurst, S., Elston, D. A., & McCracken, D. I. (2012). Riparian field margins: Can they enhance the functional structure of ground beetle (Coleoptera: Carabidae) assemblages in intensively managed grassland landscapes? *Journal of Applied Ecology*, 49(6), 1384–1395. https://doi.org/10.1111/j.1365-2664.2012.02200.x
- Cole, L. J., Brocklehurst, S., McCracken, D. I., Harrison, W., & Robertson, D. (2012). Riparian field margins: Their potential to enhance biodiversity in intensively managed grasslands. *Insect Conservation and Diversity*, 5(1), 86–94. https://doi.org/10.1111/j.1752-4598.2011. 00147.x

- Cole, L. J., Brocklehurst, S., Robertson, D., Harrison, W., & McCracken, D. I. (2015). Riparian buffer strips: Their role in the conservation of insect pollinators in intensive grassland systems. Agriculture Ecosystems & Environment, 211, 207–220. https://doi.org/10.1016/j. agee.2015.06.012
- Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, 65(10), 934–941. https://doi.org/10.1071/Mf14173
- De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W., & Declerck, S. (2012). Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters*, 15, 740-747. https://doi.org/10.1111/j.1461-0248.2012.01794.x
- Denny, P. (1994). Biodiversity and wetlands. Wetlands Ecology and Management, 3, 55-61.
- Din, A., Abd Halim, W., Ahmad, S., & Yaakop, S. (2019). Dung beetles (Coleoptera: Scarabaeidae) composition to three different ecosystem functions: A study case in Malaysia. *Tropical Life Sciences Research*, 30, 69–82. https://doi.org/10.21315/tlsr2019.30.3.5
- Gerisch, M., Schanowski, A., Figura, W., Gerken, B., Dziock, F., & Henle, K. (2006). Carabid beetles (Coleoptera, carabidae) as indicators of hydrological site conditions in floodplain grasslands. *International Review of Hydrobiology*, 91(4), 326–340. https://doi.org/10.1002/ iroh.200610888
- Graversgaard, M., Jacobsen, B. H., Hoffmann, C. C., Dalgaard, T., Odgaard, M. V., Kjaergaard, C., Powell, N., Strand, J. A., Feuerbach, P., & Tonderski, K. (2021). Policies for wetlands implementation in Denmark and Sweden—Historical lessons and emerging issues. *Land Use Policy*, 101, 105206. https://doi.org/10.1016/j.landusepol. 2020.105206
- Hambäck, P. A., Dawson, L., Geranmayeh, P., Jarsjö, J., Kacergyte, I., Peacock, M., Collentine, D., Destouni, G., Futter, M., Hugelius, G., Hedman, S., Jonsson, S., Klatt, B. K., Lindström, A., Nilsson, J. E., Pärt, T., Schneider, L. D., Strand, J. A., Urrutia-Cordero, P., ... Blicharska, M. (2023). Tradeoffs and synergies in wetland multifunctionality: A scaling issue. *Science of the Total Environment*, 862, 160746. https://doi.org/10.1016/j.scitotenv.2022.160746
- IUCN. (2022). The IUCN Red List of Threatened Species. Version 2022-2. https://www.iucnredlist.org
- Jeliazkov, A., & Chase, J. M. (2024). When do traits tell more than species about a metacommunity? A synthesis across ecosystems and scales. American Naturalist, 203(1), E1-E18. https://doi.org/10. 1086/727471
- Kingsford, R. T., Basset, A., & Jackson, L. (2016). Wetlands: conservation's poor cousins. Aquatic Conservation: Marine and Freshwater Ecosystems, 26(5), 892–916. https://doi.org/10.1002/aqc.2709
- Kolesnikov, F. N., Karamyan, A. N., & Hoback, W. W. (2012). Survival of ground beetles (Coleoptera: Carabidae) submerged during floods: Field and laboratory studies. *European Journal of Entomology*, 109(1), 71–76. https://doi.org/10.14411/eje.2012.009
- Lafage, D., & Petillon, J. (2016). Relative importance of management and natural flooding on spider, carabid and plant assemblages in extensively used grasslands along the Loire. *Basic and Applied Ecology*, 17(6), 535–545. https://doi.org/10.1016/j.baae.2016.04.002
- Lambeets, K., Vandegehuchte, M. L., Maelfait, J. P., & Bonte, D. (2008). Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology*, 77(6), 1162–1174. https://doi.org/ 10.1111/j.1365-2656.2008.01443.x
- Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. https://doi.org/10.1111/2041-210x.12512
- Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D., & Villéger, S. (2022). mFD:

An R package to compute and illustrate the multiple facets of functional diversity. *Ecography*, 2022(1): e05904. https://doi.org/10. 1111/ecog.05904

- Meli, P., Benayas, J. M. R., Balvanera, P., & Ramos, M. M. (2014). Restoration enhances wetland biodiversity and ecosystem service supply, but results are context-dependent: A meta-analysis. *PLoS One*, 9(4), e93507. https://doi.org/10.1371/journal.pone.0093507
- Mellbrand, K., & Hambäck, P. A. (2010). Coastal niches for terrestrial predators: A stable isotope study. *Canadian Journal of Zoology*, 88(11), 1077-1085.
- Moran, J., Gormally, M., & Skeffington, M. S. (2012). Turlough ground beetle communities: The influence of hydrology and grazing in a complex ecological matrix. *Journal of Insect Conservation*, 16(1), 51-69. https://doi.org/10.1007/s10841-011-9393-8
- Nanni, A., Krug, P., Cicchino, A., & Quintana, R. (2021). Effects of intensive human management on the taxonomic and functional diversity of ground beetles in a planted forest landscape. *Biodiversity and Conservation*, 30, 3717–3735.
- Ndiribe, C., Salamin, N., & Guisan, A. (2013). Understanding the concepts of community phylogenetics. *Evolutionary Ecology Research*, 15(8), 853–868.
- Oberholzer, F., & Frank, T. (2003). Predation by the carabid beetles *Pterostichus melanarius* and *Poecilus cupreus* on slugs and slug eggs. In. *Biocontrol Science and Technology*, 13, 99–110.
- Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3), 402– 411. https://doi.org/10.1046/j.1461-0248.2002.00339.x
- QGIS. (2022). QGIS geographic information system. Open Source Geospatial Foundation Project http://qgis.org
- R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Ramey, T. L., & Richardson, J. S. (2017). Terrestrial invertebrates in the riparian zone: Mechanisms underlying their unique diversity. *Bioscience*, 67(9), 808–819. https://doi.org/10.1093/biosci/bix078
- Rheinheimer, J., & Hassler, M. (2010). Die Rüsselkäfer Baden-Württembergs. Verlag regionalkultur, Karlsruhe.
- Rothenbucher, J., & Schaefer, M. (2006). Submersion tolerance in floodplain arthropod communities. *Basic and Applied Ecology*, 7(5), 398– 408. https://doi.org/10.1016/j.baae.2006.05.005
- Sienkiewicz, P., & Zmihorski, M. (2012). The effect of disturbance caused by rivers flooding on ground beetles (Coleoptera: Carabidae). European Journal of Entomology, 109(4), 535–541. https://doi.org/ 10.14411/eje.2012.067
- SLU Artdatabanken. (2020). Rödlistade arter i Sverige 2020. SLU.
- Stasiov, S., Litavsky, J., Majzlan, O., Svitok, M., & Fedor, P. (2021). Influence of selected environmental parameters on rove beetle (Coleoptera: Staphylinidae) communities in central European floodplain forests. Wetlands, 41(8), 115. https://doi.org/10.1007/s13157-021-01496-5
- Strand, J. A., & Weisner, S. E. B. (2013). Effects of wetland construction on nitrogen transport and species richness in the agricultural landscape-experiences from Sweden. *Ecological Engineering*, 56, 14-25. https://doi.org/10.1016/j.ecoleng.2012.12.087
- Stubbs, A. (2021). British craneflies: British entomological and natural history society.
- Swartz, T. M., & Miller, J. R. (2021). The American Pond Belt: An untold story of conservation challenges and opportunities. *Frontiers in Ecology and the Environment*, 19(9), 501–509. https://doi.org/10.1002/fee.2381

Torma, A., Revesz, K., Galle-Szpisjak, N., Seat, J., Szel, G., Kutasi, C., Malenovsky, I., Batary, P., Gallé, R., & Galle, R. (2023). Differences in arthropod communities between grazed areas and grazing exclosures depend on arthropod groups and vegetation types. *Agriculture Ecosystems & Environment*, 341, 108222. https://doi.org/ 10.1016/j.agee.2022.108222

ournal of Biogeography

- Waite, E., Houseman, G., Jensen, W., Reichenborn, M., & Jameson, M. (2022). Ground beetle (Coleoptera: Carabidae) responses to cattle grazing, grassland restoration, and habitat across a precipitation gradient. *Insects*, 13(8), 696.
- Wang, Y., Naumann, U., Eddelbuettel, D., Wilshire, J., & Warton, D. (2022). Mvabund: Statistical methods for Analysing multivariate abundance data. R package version 4.2.1 https://CRAN.R-project. org/package=mvabund
- Yamazaki, K. (2006). Feeding of a shore-inhabiting ground beetle, Scarites aterrimus (Coleoptera: Carabidae). Coleopterists Bulletin, 60(1), 75-79. https://doi.org/10.1649/869.1
- Zedler, J. B., & Kercher, S. (2005). Wetland resources: Status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources, 30, 39–74. https://doi.org/10.1146/annurev.energy. 30.050504.144248

#### BIOSKETCH

We are a group of researchers collaborating on wetland ecosystem services, wetland hydrology and riparian arthropod community ecology (https://biowetland.se/). We are interested in constructed wetland ecosystem functioning, and how management processes and morphology affect the terrestrial arthropod community, and also the hydrological dynamics in these systems.

**Author contributions:** Study conceived by DÅ., PAH. and JS., designed by DÅ. and PAH, data collected by DÅ., PAH and LS., analysed by DÅ. and PAH., and written and reviewed by all authors. All authors have approved and are accountable for the manuscript.

# SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Åhlén, D., Jarsjö, J., Jonsell, M., Klatt, B. K., Schneider, L. D., Strand, J., & Hambäck, P. A. (2024). Arthropod diversity in constructed wetlands is affected strongly by shoreline properties but only weakly by grazing. *Journal of Biogeography*, *51*, 2323–2333. <u>https://doi.</u> org/10.1111/jbi.14997

2333