Scale-dependent responses in spider and beetle communities to flooding: The role of dry refuges in wetlands

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Abstract

Flood disturbances act as strong filters on arthropod communities by excluding species that are not adapted to the high water-tables. Sensitive species can survive in these areas by either migrating to more terrestrial habitats or by using dry refuges within the wetland created by topographical heterogeneity. In this study, we examined the role of such refugia and the scale at which these affect arthropod densities, mainly cursorial species, by using previous information on local dryness-wetness of wetlands, as expressed by inundation frequencies at a 2x2 m2 resolution. By focusing on spiders and beetles, these studies indicate that species within Linyphiidae, Staphylinidae and Chrysomelidae were more abundant in the presence of dry refuges at a scale of 10x10 m2, whereas Salticidae preferred wetter areas. Species within Carabidae, Lycosidae and a number of other taxon groups were indifferent to these structures. Moreover, the data seem to suggest that mainly habitat generalists benefit from the refuges. Accordingly, those groups that were impartial to the dry refuges included almost exclusively species that can be categorised as wetland specialists. More generally, the small-scale variability in wetland dryness-wetness creating small-scale refuges may be important to consider for guiding contemporary efforts to restore wetlands as a mean to promote biodiversity.

Introduction

Arthropod species living in wetlands often face more or less regular periods of flooding, during which the habitat is temporally submerged, compromising the life of terrestrial organisms (Batzer and Wu 2020, Plum 2005). Terrestrial species inhabiting these shifting habitats have developed a range of adaptations that allow them to persist despite the regular disturbances (Kolesnikov, et al. 2012, Lafage, et al. 2015, Marx, et al. 2012, Ramey and Richardson 2017, Rothenbücher and Schaefer 2006). Some species simply withstand the floods until the water recedes, which may require special adaptations to avoid drowning. Other species adapt their life cycle to account for regular flooding regimes or retreat to drier grounds, returning when the water is again gone. Among arthropods, previous studies from large flood plains suggest that plant- and leafhoppers (Auchenorrhyncha) often tolerate prolonged submersion and therefore remain in the wetland during floods, whereas most spiders and ground beetles instead tend to move in and out of wetlands in response to fluctuating water levels (Lafage, Sibelle, Secondi, Canard and Petillon 2015, Rothenbücher and Schaefer 2006). However, even among beetles and spiders, some species are well able to survive at least short-term flood events (Kolesnikov, Karamyan and Hoback 2012).

The occurrence of topographical heterogeneities including vegetation that create local dry ground refuges during floods likely influences species survival and recolonization ability. For instance, wetlands often contain a mixture of hummocks and hollows, with the former providing arthropods with safe ground during high-water events. These small-scale heterogeneities have seldom been considered in studies of local arthropod communities and, are in fact rarely quantified even in hydrological studies (but see Diamond, et al. 2021). A study by Datry et al. (2014) demonstrated that heterogeneities in flood disturbance at a larger scale within a flood plain can significantly affect arthropod communities by creating spatial differences in plant successional patterns. However, the two only studies known to us that combined a quantification of small scale heterogeneities in a large wetland and arthropod communities are Åhlén et al. (2023), which quantified inundation frequencies that reflect local wetness-dryness at a 2x2 m^2 resolution and used SLAM (sea, land, air – Malaise) traps for arthropod quantification, and Åhlén et al. (2024). While other studies have incorporated flood dynamics, they generally do so at a coarse scale (but see O'Callaghan, et al. 2013 for an example from the riparian zone of a large river). These studies have documented both positive and negative relations between the inundation frequency and arthropod densities. For instance, Åhlén et al. (2023) found that groups such as leafhoppers were more abundant in frequently flooded areas, whereas dance flies were more prevalent in drier parts of the wetland. This study was however biased by the choice of sampling method. SLAM-traps, like all Malaise traps, primarily capture flying insects and are therefore less suited for quantifying the densities of cursorial species such as spiders and beetles, that are less able to recolonize after disturbances.

In wetlands, spiders and predatory beetles commonly occur at high densities, utilizing the high prey production in these habitats (Ramey and Richardson 2017). Many previous studies have also explored mechanisms underlying community responses of both spiders and predatory beetles, showing the prime importance of the hydrological regime at larger spatial scales (Bonn, et al. 2002, Cartron, et al. 2003, Gerisch, et al. 2006, Jachertz, et al. 2019, Sienkiewicz and Zmihorski 2012, Uetz, et al. 1979). In fact, it has been suggested that the flooding regime is more important than habitat management for both spiders and carabid beetles (Lafage and Petillon 2016). There are also potential differences in responses between spiders and beetles, where these communities are filtered by different environmental factors in wetlands (Åhlén, Jarsjö, et al. 2024). For instance, Lambeets et al. (2008) showed that spider densities decreased strongly with all types of flooding whereas carabid beetles seemingly benefit from intermediate flooding regimes. Their study however used pitfall traps which bias spider catches towards wolf spiders, and carabid beetles, and provide poor density estimates of most other spider groups (Amiar, et al. 2023), and of small staphylinid beetles. Nevertheless, other studies similarly show that carabid beetles are often good indicators of local flooding regimes (Gerisch, Schanowski, Figura, Gerken, Dziock and Henle 2006, Moran, et al. 2012), whereas spider communities seem to be more determined by habitat structure (Bonn, Hagen and Wohlgemuth-Von Reiche 2002, Åhlén, Jarsjö, Jonsell, Klatt, Schneider, Strand and Hambäck 2024), which may directly or indirectly be affected by flooding regimes.

In this study, we first identified sites with varying inundation patterns in a large wetland based on the quantification of small-scale inundation patterns from Åhlén et al. (2023). We then estimated the density and species diversity of beetles and spiders in these sites using suction sampling, which reflect total communities better than pitfall traps, to connect arthropod communities and inundation patterns. We selected sites along two gradients, with wet or dry local (2x2 m^2, centered on the arthropod collection point) conditions and wet or dry conditions at a larger spatial scale (6x6 m^2). To further identify relevant spatial scale of responses, we calculated inundation patterns also at larger distances from the arthropod collection sites. In addition, we measured local habitat characteristic such as vegetation height and soil carbon content that are known to affect arthropod communities in wetlands (Ye, et al. 2024). For an overview of the methods see Figure 1. Our prediction was that arthropod densities in locally very wet sites depend on the presence of dry sites nearby, whereas the opposite pattern would be less important.

Materials and Methods

Study site

The study was performed in a longitudinal fen, the Rastmyran wetland (60°07'35"N 17°53'56"E), which is situated two hours north of Stockholm. The wetland (about 2.5 km long and 0.3 km wide) is situated in a headwater area near a local water divide (Åhlén, et al. 2022) and transected by a stream running south to north (Fig. 2). The wetland is seasonally flooded (wetter in winter-spring and drier in summer-autumn, Åhlén, Jarsjö and Hambäck 2023) and undisturbed from current human activities with no grazing, forestry, water regulation or other activities. The wetland is relatively isolated from adjacent wet habitats and surrounded by a coniferous forest. Within the wetland, there are patches of willow thickets and single bushes, but the vegetation consists mainly of typical wetland plants such as grasses, sedges, horsetails and forbs (e.g., *Lysimachia and Lythrum)* .

Site selection and flooding data

To select sites with variable flooding regimes at small and large spatial scales, we used previously collected data on inundation frequency for the Rastmyran wetland (Åhlén, Jarsjö and Hambäck 2023). In that study, inundation frequency (the proportion of days when each 2x2 m^2 pixel was under water) was estimated across the wetland during the normally unfrozen period from the end of March to the end of October using a combination of water table measurements in the field and extrapolation through a digital elevation model. Water tables were estimated with a HOBO water table logger placed at the in- and outlets of the fen and the digital elevation model was constructed based on data from the Swedish Mapping, Cadastral and Land Registration Authority (for details see Åhlén, Jarsjö and Hambäck 2023). For the purpose of this study, we selected sites that included both homogeneously dry, homogeneously wet and mixed wet/dry conditions. As a measure of inundation heterogeneity during the selection process, we contrasted the inundation frequency in the central pixel (2x2 m^2) and peripheral pixels (within 6x6 m^2) (Fig. 3a). Please note that wet and dry periods are somewhat separated in time, with wetter conditions during spring and drier conditions during summer and autumn.

Dry pixels included those with inundation frequency (IF)$<$0.45, which corresponds to a dry situation during most of summer, whereas wet pixels included those with inundation frequency$>$0.65. The distribution of IF-values across the dry and wet classes was then per definition bimodal in the central pixel (wet=high IF$>$0.65, dry=low IF$<$0.45; Table 1, column 2), but this bimodality did not always translate to peripherical pixels outside the central pixel, which exhibited a more heterogeneous character (Table 1, columns 3-5). Thus, the inundation frequency$<$0.45 in homogeneously dry sites both in the central pixel and for most pixels within 6x6 m^2, and correspondingly $>$0.65 for homogeneously wet sites. In dry-wet sites, the central pixel had an inundation frequency$<$0.45 whereas most peripheral pixels had an inundation frequency$>$0.65, and correspondingly for wet-dry sites. Finally, we included dry-wet/dry and wet-wet/dry sites, meaning that peripheral pixels had variable inundation frequencies with some wet and some dry. Thus, we selected 6 categories with different dry-wet conditions and 10 sites per category (Table 1).

Post selection, to further investigate scale effects, we estimated the mean inundation frequency in successively larger areas (10x10 m^2 … 26x26 m^2, Fig. 3b) surrounding the central pixels (not including the central pixel). We also calculated the proportion of dry pixels within each scale to estimate the occurrence of dry refuges in the vicinity. The inundation frequencies and proportion of dry pixels (IF$<$0.45) were strongly correlated (r$>$0.97) and we therefore dropped the inundation frequency from analysis. Finally, a heterogeneity index was calculated for each site from the proportion of dry to non-dry pixels using the Shannon Diversity Index ($H^{'} = -\sum p_i * ln(p_i)$,$p_i =$ proportion of dry pixels), where low values indicate lower heterogeneity and large values indicate high heterogeneity.

Environmental variables

In each site, we collected data on vegetation height (August) and soil organic content (June). Vegetation was measured within each central pixel by recording the maximum vegetation height at three randomly selected points. Soil samples were collected using a soil core sampler, placed in bags and transported to a laboratory freezer until further processing. The soil organic content was determined using the loss on ignition method. Samples were dried in an oven at 105°C for 24h. After drying, the samples were sieved using a 2mm sieve and weighed on a microscale to obtain the initial weight. The samples were then placed in a high-performance oven at 550°C for 4h. After this, the samples were reweighed, and the loss of ignition was calculated using the formula: [(initial weight-after weight)/initial weight] x100. From this, the soil organic content was derived.

Arthropod data

Arthropods were collected with suction sampling, using a modified leaf blower (Stihl BG85), for 45-60 seconds. In each site, three suction samples, less than 1 m apart, were taken in the central pixel. Before each sampling, a plastic ring (O = 45 cm) was haphazardly placed in the central pixel to delimit the suction area. Arthropods were collected in a cotton bag mounted at the front of the suction device and this bag was emptied into a plastic container. All specimens were transferred to Eppendorf tubes filled with 75% ethanol. In the laboratory, we sorted and counted spiders and beetles. All specimens were sorted to family, and partly identified to genus or species (spiders – all families, beetles – only Staphylinidae and Carabidae) by ourselves or experts. In some cases, mainly juvenile spiders, specimens could not be identified to lower taxonomic levels. Those individuals were included in total density estimates but only in species counts if no individuals of that genus were identified to a lower taxonomic level. We thereafter rarefied species number for each site using the alpha-command in BAT (Cardoso, et al. 2015).

For further community analyses, we scored traits; main habitat preference (beetles and spiders), feeding guild (beetles) and hunting guild (spiders). Habitat preference was obtained from artfakta.se, based on expert assessment, using the approach of Ahlen et al. (2024). In short, species are scored as wetland specialists if indicated habitat preferences mainly include wetland habitat types, as terrestrial specialist is preferences mainly include terrestrial habitat types, and as habitat generalist when the preference include both wetland and terrestrial habitat types. Beetle feeding guilds (carnivore, herbivore, other feeders) were based on artfakta.se and spider hunting guilds (ambush hunter, ground hunter, orb web weaver, sheet web weaver and space web weaver) were based on Cardoso et al. (2011). For lists of traits and species classifications, see Appendix 1.

Statistical analyses

We first compared total density and rarefied species diversity, separately for beetles and spiders, between the six predefined flooding categories (wet-wet, wet-dry, wet-wet/dry, dry-dry, dry-wet, dry-wet/dry) using a GLM with negative binomial error distribution for density and with an ANOVA for species diversity. We then modelled total density and diversity in the same way as a function of the local inundation frequency (within the 2x2 m^2 pixel) and the proportion of dry pixels at the different scales (6x6 m^2 … 26x26 m^2) as explanatory variables. For models at each scale, we thereafter calculated pseudo-R^2 (density) and R^2(diversity) and related these to the scale. The spatial scale with the highest R^2 was thereafter selected for further analyses. In the third step, we again modelled total density and rarefied species diversity as a function of the proportion of dry pixels at the optimal scale but in these models, we also included the inundation heterogeneity (at the optimal spatial scale) and environmental factors (vegetation height and soil carbon content) as explanatory variables. These models were simplified by excluding non-significant variables. Finally, we used manyglm from the mvabund (Wang, et al. 2012) to examine community responses (at a family level) as a function of environmental variables and the optimal flooding scale. These analyses were performed separately for beetles and spiders, and we excluded families with few (<20) specimens. Finally, we repeated the analyses using habitat preferences and species traits respectively as response variables. All analyses were performed in R 4.2.2 (R Core Team 2023).

Results

A combined total of 3542 arthropod individuals were collected in June and August, with an approximately equal number of spiders (1703) and beetles (1839). The spider assemblage included 18 families and 114 species, with Linyphiidae, Lycosidae and Salticidae being the most abundant families. The beetle assemblage included 22 families and 136 species, with Staphylinidae, Chrysomelidae and Carabidae being the most abundant families.

When comparing spider and beetle responses based on the design characteristics, we found that only total beetle density varied between categories ($X_{5,59}$=18.8, $P<0.005$), which occurred because sites classified as dry-dry had a higher beetle density (Fig. 4). Spider density did not vary between the different flooding categories ($P>0.1$), and neither did rarefied species richness ($P>0.2$) of beetles and spiders. When comparing explanatory power of the proportion of dry pixels between spatial scales, we found that the variance explained (R^2) for both spider and beetle densities was highest when the proportion of dry pixels was estimated at the scale of 10x10 m^2 (Fig. 5a). At this scale, both spider (LR=5.9, df = 56, $p<0.02$) and beetle (LR = 11.8, df = 56, $p<0.0006$) densities increased with the proportion of surrounding dry pixels (Fig. 5b), and there was no effect of the local (2x2 m^2) wetness-dryness, as expressed by the local inundation frequency. Rarefied species richness was not significant at any scale for either spiders or beetles, and was therefore not further analysed. When we included environmental variables and the heterogeneity index, we found that none of these variables explained variation in either the density or species richness of either spiders or beetles and these variables are not further discussed.

The multivariate analyses through manyGLM similarly showed that the proportion of dry pixels affected the community structure of both spiders (Wald=4.6, $p<0.007$) and beetles (Wald=5.2, $p<0.001$). These differences occurred because the densities of Staphylinidae (Wald=3.6, $p<0.005$) and Chrysomelidae (Wald=2.9, $p<0.03$) increased, with a similar non-significant trend Linyphiidae (Wald=2.5, $p<0.08$), whereas Salticidae (Wald=2.7, $p<0.04$) decreased with the proportion of dry pixels at the respective optimal spatial scale (Fig. 6, adjusted p-values). Other included groups (Lycosidae, Thomisidae, Tetragnathidae, Carabidae, Curculionidae and Coccinellidae) did not vary with the proportion of dry pixels. To further examine families with significant responses, we repeated the manyGLM at a genus level for Linyphiidae, Salticidae and Staphylinidae for genera with at least 20 specimens. For Linyphiidae, we could include five genera (*Bathyphantes, Oedothorax, Porrhomma, Savignia, Silometopus*) and for these only *Savignia* (Wald=2.7, $p<0.03$) increased with the proportion of dry pixels. For Salticidae, we could only include two genera (*Attulus* and*Marpissa*) and only *Attulus* (Wald=2.6, $p<0.03$) decreased with the proportion of dry pixels. For Staphylinidae, we found somewhat similar responses for all five included genera (*Amischa* ,*Erichsonius* , *Paederus* , *Rybaxis* , *Stenus*), but only *Amischa* (Wald=2.8, $p<0.04$) and *Rybaxis* (Wald=3.3, $p<0.01$) significantly increased with the proportion of dry pixels. The other genera had $0.05<p<0.1$.

When comparing habitat preferences, we found a relationship between the proportion of dry pixels and the density of beetles (Wald=4.6, $p<0.002$) but not of spiders (Wald=2.1, $p>0.2$). The relationship for beetles was caused by a positive relationship between density and the proportion of dry pixels for habitat generalists (Wald=4.4, $p<0.002$). When comparing traits, we found positive relationships between density and the proportion of dry pixels for both beetles (Wald=4.6, $p<0.001$) and spiders (Wald=4.4, $p<0.02$). For beetles, all three trophic groups (carnivores, herbivores and other consumers) responded similarly ($\text{Wald}_{\text{carnivores}}=3.2$, $p<0.007$; $\text{Wald}_{\text{herbivores}}=2.7$, $p<0.009$; $\text{Wald}_{\text{other}}=3.9$, $p<0.002$). For spiders, only sheet web weaver densities (Wald=3.3, $p<0.008$) showed a relationship to the proportion of dry pixels, matching the result for Linyphiidae that includes the sheet web weavers.

Discussion

Seasonal flooding and associated changes in the wetness-dryness conditions of wetlands is a major disturbance for species inhabiting wetlands, requiring them either to survive during periods of high water or to disperse and recolonize once the water subsides. The ability to survive these conditions may depend on the availability of dry refuges nearby. This study found differences among arthropod groups in their relationship to dry refuges. For instance, genera within Staphylinidae and Linyphiidae were more abundant in sites with a higher proportion of refuges, whereas groups such as Carabidae and Lycosidae appeared less sensitive. Interestingly, one group, Salticidae, showed the opposite response, being more abundant in sites that experienced longer inundation periods. We also observed that the spatial scale of refuges played an important role. The highest predictive power was found when the proportion of dry refuges was estimated for a 10x10 m^2 area surrounding the sampling site. In contrast, the proportion of dry refuges immediately surrounding the sampling sites (i.e., within 2x2 m^2) was less significant.

To interpret these results, it is important to first consider the composition of these dry refuges. Most wetlands are heterogeneous, consisting of a mixture of wet and dry areas (Diamond, Epstein, Cohen, McLaughlin, Hsueh, Keim and Duberstein 2021). This particular wetland is a relatively flat fen, primarily covered by grasses and sedges, but it also features microtopographic variation. Notably, solid and relatively high hummocks (height: 30-50 cm, diameter: 20-30 cm), composed mainly of*Carex* species, dominate parts of the area. These hummocky areas represent some of the key dry refuges, although other dry refuges include areas with higher but more evenly elevated ground. In this study, the pixel size used to estimate local wetland wetness-dryness (expressed in terms of inundation frequencies) was 2x2 m^2. As a result, each pixel may contain multiple hummocks as well as intervening hollows, which tend to remain flooded for longer time periods. Please note that the digital elevation model (DEM) and inundation frequency estimates should be interpreted relative and not as absolute measures. While differences between sites are likely accurate, the absolute levels may be influenced by both measurement errors and annual variations. For the purpose of this study, the wet sites are consistently wetter than dry sites whereas the absolute wetness-dryness estimates or inundation frequencies may be somewhat biased.

The observed differences between arthropod groups in their relationship to the presence of dry refuges may be linked to both species traits and habitat preferences. Currently, we know relatively little about the specific traits for these species groups connected to the ability to survive flooding. One possibility is that differences in the ability to move through vegetation or climb onto the hummocks may play a role. It is therefore notable that groups favoured by a higher proportion of dry pixels (e.g., Linyphiidae and Staphylinidae) include species that commonly climb vegetation as well as species that are comparatively small. Interestingly, while climbing abilities might influence distribution patters in some groups, the height of vegetation in flooded areas did not appear to affect spider and beetle densities.

In contrast, arthropod groups such as Carabidae and Lycosidae, which showed no clear relationship with the presence of dry refuges, consist mostly of larger, cursorial species. It is possible that these groups are less able to climb the hummocks, instead using their higher mobility to evade flooding and recolonise (Bates, et al. 2006, Lafage, Sibelle, Secondi, Canard and Petillon 2015). As a result, species within Carabidae and Lycosidae that cannot survive flooding are likely filtered out of the community. Meanwhile, flood sensitive species within Linyphiidae and Staphylinidae may persist by moving to the hummocks or other dry refuges. Consequently, we would expect that the Linyphiidae and Staphylinidae contain a higher proportion of species that do not necessarily have wetlands as their main and only habitat. Our data also showed that Carabidae (93%) and Lycosidae (86%) had a much higher proportion of wetland specialists than Linyphiidae (54%) and Staphylinidae (47%). Furthermore, half of the genera classified as habitat generalists responded positively to dry refuges (*Amischa*,*Rybaxis* and *Savignia but not Bathyphantes, Erichsonius* and *Oedothorax*), whereas none of the genera among wetland specialists showed a positive response to dry refuges despite the much higher number of species. Notice that these genera are primarily represented by a single species each in the data set (Appendix 1).

Comparing our results to previous studies in wetlands or riparian habitats poses certain challenges. For instance, studies in floodplains by Jachertz et al. (2019) suggest that carabids can serve as reliable indicator species across different substrates (see also Gerisch, Schanowski, Figura, Gerken, Dziock and Henle 2006), whereas carabids in our study did not vary with any variable. However, in that study, the key indicator species among carabids belonged to*Bembidion*, a common group of riparian species that is entirely absent in our fen. Additionally, the seasonal flooding patterns in floodplains differ markedly from those in fens, potentially leading to distinct effects on arthropod community. A similar discrepancy was also evident when comparing our findings to our previous studies (Åhlén, Hedman, Jarsjö, Klatt, Schneider, Strand, Tack, Åhlén and Hambäck 2024). In that study, similar to the present research, we found that Staphylinidae had lower densities in wetlands with more frequent inundation events, but in contrast, the responses of Linyphiidae differed between the two studies. These differences may be attributed to the contrasting wetland structures and possibly to differences in flooding patterns. The study by Åhlén et al. (2024) examined 41 constructed wetlands, where the riparian zones were relatively limited, and terrestrial habitats were often located within 10 m of the sampling site. These constructed wetlands differ significantly from the current study's setting – a much larger fen where true terrestrial habitats are often more than 100 m away from sampling sites. Moreover, habitat size in the previous study was highly variable, a factor shown to influence the proportion of wetland specialists (Åhlén, Jarsjö, Jonsell, Klatt, Schneider, Strand and Hambäck 2024).

Only one arthropod group, jumping spiders (Salticidae), showed a response opposite to that of the other groups by being more abundant in the wetter parts of the wetland. This response was primarily observed in one genus (*Attulus*, mainly *A. caricis*). The fact that very few arthropod taxa responded positively to flooding contrasts with the patterns observed in arthropods captured using Malaise traps (Åhlén, Jarsjö and Hambäck 2023). These traps mainly capture flying species, and the groups responding positively to flooding included tree- and leafhoppers (Auchennorhyncha, see also Rothenbücher and Schaefer 2006), aphids and psyllids (Sternorhyncha), gall midges (Cecidomyiidae) and grass flies (Chloropidae). A common characteristic among these groups is that they are primarily plant feeders (with the exception of some Chloropidae). Their positive response to flooding may be related to differences in plant quality or quantity between wetter and drier sites (but see Sipura, et al. 2002 for a different view on plant quality in wetlands). Alternatively, these species may benefit from the observed lower densities of several predator groups in the wetter parts of the wetland (see also Verschut and Hambäck 2018).

To conclude, our study identified several arthropod groups that appear to benefit from the presence of nearby dry refuges, with habitat generalists particularly showing a positive response to these refuge structures. Interestingly, the observed neighbourhood effects were relatively small, covering only about 10 m^2. This finding is crucial for future research on arthropod community structures in wetlands, as it narrows the spatial scale over which such structures need to be estimated, at least when studying beetles and spiders. A surprising result was that heterogeneity itself did not appear to influence arthropod distributions, suggesting that movements within the immediate neighborhood is common. Compared to drier habitats, such as meadows, there is quite limited information on the habitat variables that shape arthropod communities in wetlands. Whereas our study highlights the importance of dry refuges during flooding periods, the availability and role of such structures vary across wetland types. Future research should focus not only on species traits that may explain responses to flooding but also on wetland characteristics and the spatial and temporal variability of hydrological processes driving floods. For instance, the small-scale variability in wetland wetness-dryness reflecting absence or presence of wetland refuges may not necessarily be well represented in hydrological process models, nor be detectable in openly available observation datasets including remote sensing products, and may therefore need increased attention. This can be particularly important for guiding contemporary efforts to restore wetlands as a mean to promote biodiversity, and mitigate potential adverse effect on biodiversity of climate change and human activities.

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Table 1 . Hydrological characteristics of selected categories (mean±S.D., N=10). Inundation frequency (IF) was calculated as the mean proportion of days where the pixel was inundated either for the central pixel or in the peripheral pixels (excluding the central pixel). Dry proportion is the proportion in the peripheral pixels with IF<0.45, and the heterogeneity index is calculated with the Shannon Diversity Index for the peripheral pixels.

Category	IF central (2x2 m^2)	IF peripheral (6x6 m^2)	Proportion of dry pixels (6x6 m^2)	Heterogeneity index (6
Dry-Dry	27.2±7.1	24.6±3.9	0.98±0.05	0.08±0.16
Dry-Wet	28.7±6.9	65.3±12.3	0.22±0.22	0.75±0.23
Dry-Wet/Dry	26.9±8.9	58.8±6.0	0.30±0.12	0.95±0.14
Wet-Wet	82.8±3.6	85.1±3.8	0±0	0±0
Wet-Dry	80.0±2.8	45.3±8.0	0.56±0.20	0.81±0.31
Wet-Wet/Dry	78.1±3.2	51.2±8.4	0.42±13	0.94±0.15

Figure legends

Figure 1. Overview of the study from field collections to statistical analyses

Figure 2. The study site Rastmyran wetland, a fen in central Uppland, Sweden. The right-hand figure shows the pattern of inundation frequencies across the wetland, quantified during the snow free period from the end of March to early October (maps made with GADM [Global Administrative Areas, accessed 22 November 2024, available at http://gadm.org] and Natural Earth, waterways from the Humanitarian OpenStreetMap Team [accessed 29 November 2024, available at http://data.humdata.org/dataset/example]).

Figure 3. Sites were selected based on inundation frequencies from Åhlén et al. (2023) to (a) include combinations of wet and dry pixels (pixel-size = 2x2 m^2), and thereafter (b) categorised based on the proportion of dry pixels at multiple scales around the central pixel.

Figure 4. ***Species richness and total density of spiders and beetles (mean±S.E.) for the selected combinations of inundation frequencies in the central pixel and in surrounding pixels (6x6 m^2) (see Fig. 3a).***

Figure 5. Explained variance (pseudo-R^2) *of density in relation to proportion of dry pixels at different scales for spiders and beetles, and the total density of spiders and beetles at the optimal scale.*

Figure 6. The total density of dominant spider and beetle families, in relation to the proportion of dry pixels.

Figure 1.

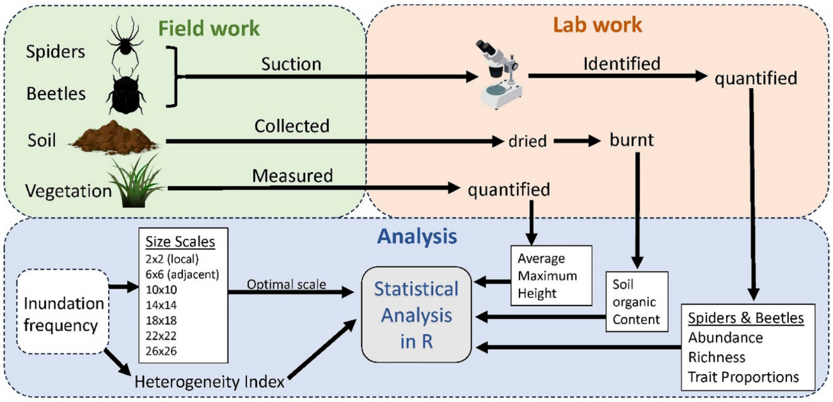


Figure 2

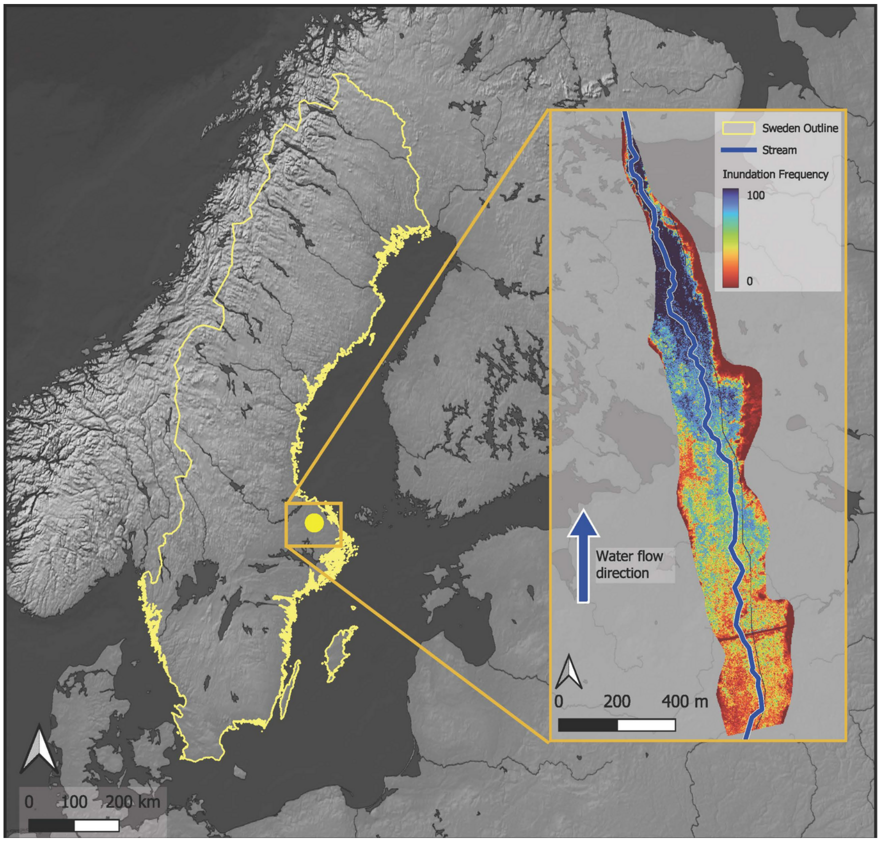


Figure 3

Hosted file

`image3.emf` available at https://authorea.com/users/882558/articles/1261176-scale-dependent-responses-in-spider-and-beetle-communities-to-flooding-the-role-of-dry-refuges-in-

`wetlands`

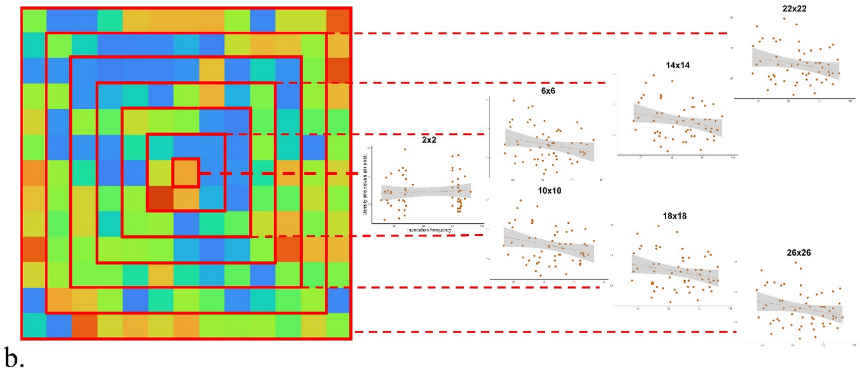


Figure 4

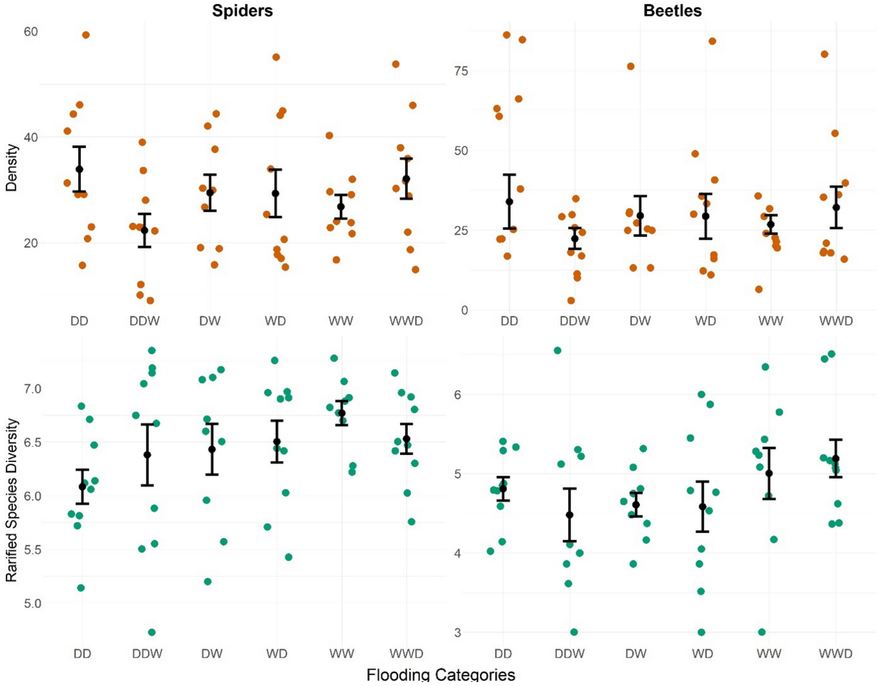


Figure 5

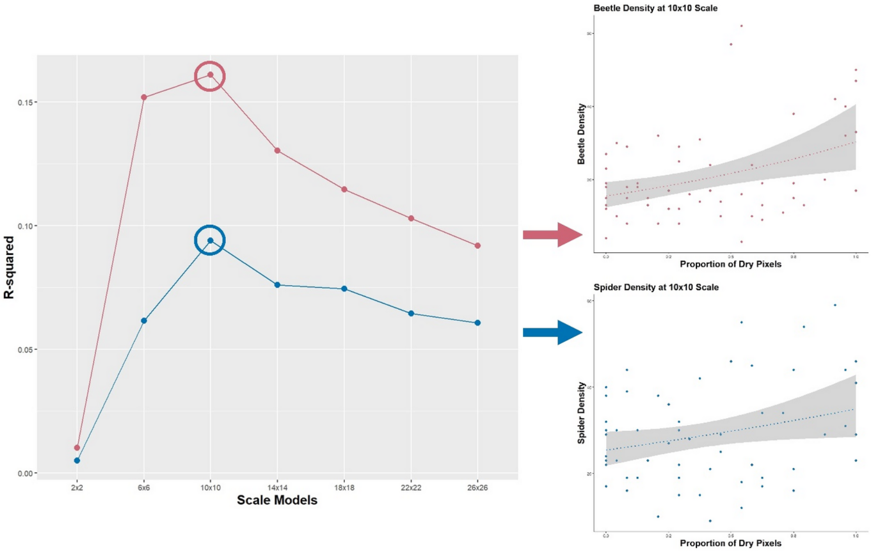
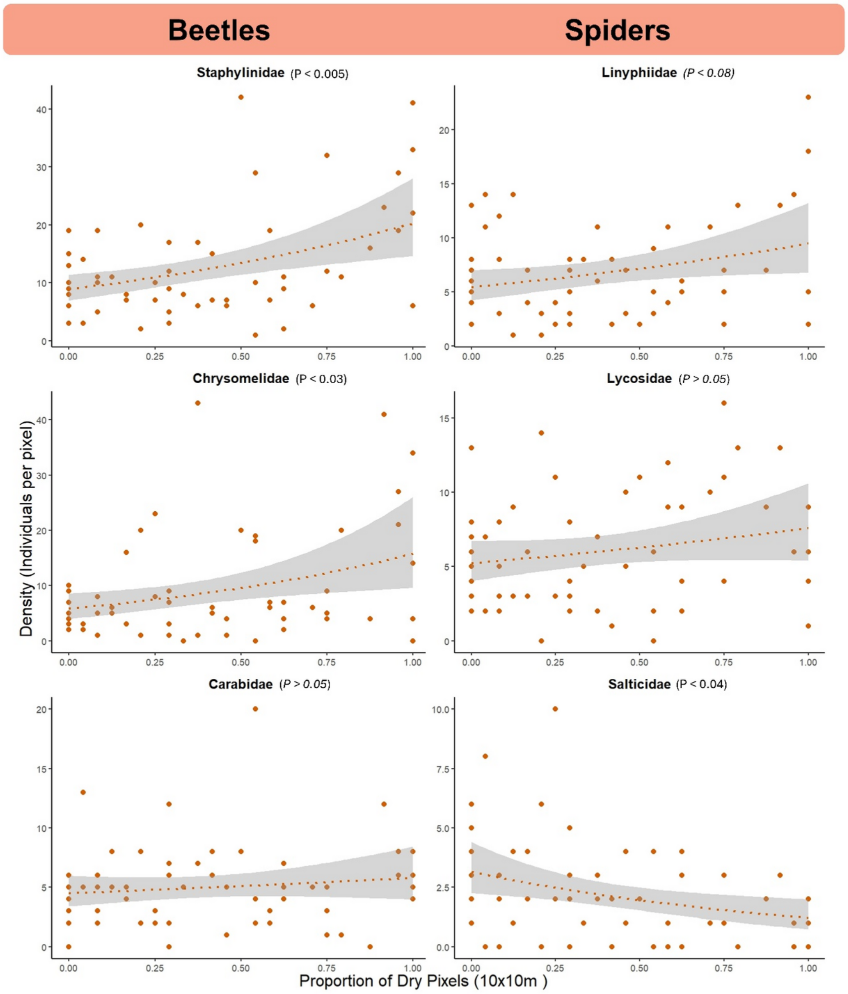

R-squared
0.15
0.10
0.05
0.00
2x2
6x6
10x10
14x14
18x18
22x22
26x26
Scale Models
Beetle Density at 10x10 Scale
Beetle Density
Proportion of Dry Pixels
Spider Density at 10x10 Scale
Spider Density
Proportion of Dry Pixels

Figure 6


Beetles
Spiders
Staphylinidae (P < 0.005)
0
10
20
30
40
Linyphiidae (P < 0.08)
0
5
10
15
20
Chrysomelidae (P < 0.03)
0
10
20
30
40
Lycosidae (P > 0.05)
0
5
10
15
Carabidae (P > 0.05)
0
5
10
15
20
Salticidae (P < 0.04)
0.0
2.5
5.0
7.5
10.0
0.00
0.25
0.50
0.75
1.00
Density (Individuals per pixel)
Proportion of Dry Pixels (10x10m)