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Hydrological drought effects on Diptera families and functional groups in constructed wetlands:
Differences between sampling methods

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Abstract

European summer droughts are becoming more frequent with climate change. Shallow waterbodies, like wetlands are therefore facing an increased risk of temporarily drying out. As flies (Diptera) make up a major part of wetland communities and provide important ecosystem functions, this study investigated how Diptera families are affected by hydrological drought and if the drought response of dipterans depends on their trophic group or water dependency.

To simulate a hydrological summer drought, 7 constructed wetlands in South-West Sweden were drained for 4 weeks during summer 2022. Sea, Land and Air Malaise (SLAM) traps and coloured pan traps were used to sample dipterans both at drained and control sites, before (July), during (August) and after (September) the drought experiment. More than 20,000 specimens were identified to family or lower taxonomic levels and semi-dry weight was determined. Based on this data, drought effects on total dipteran biomass, family composition and diversity, individual families, trophic groups and water dependency groups were analysed.

Total Diptera biomass, as well as most families showed no response to the drought treatment. Chironomidae decreased in abundance through the drainage in the pan trap samples but remained unaffected in the SLAM trap samples. Sciaridae and other soil-moisture dependent taxa increased during the drought in SLAM traps, while they decreased or remained unaffected in pan traps. Terrestrial taxa were not affected by the treatment. Different trophic groups showed no clear response to the drought. Family diversity decreased stronger at the drained wetlands, from July to September, but not immediately during the drought period.

The inconsistencies of drought response between sampling methods might be explained by differing microclimatic conditions correlated to the traps, or by a different range of species caught within them. That most water dependent families were not negatively affected by the drainage suggests that they were successfully inhabiting remaining moist habitats. In conclusion, a temporary hydrological drought does not necessarily affect Diptera communities if moist microhabitats remain.

Popular science summary

Flies, scientifically including midges, mosquitos and craneflies, are often overlooked, but they are one of the most diverse insect groups. By inhabiting a wide range of habitats, they have developed countless different strategies to interact with their environment. Through this, they help to maintain the ecosystems on which humans are dependent. As decomposers they clean up rotting matter, herbivores and carnivores control populations of other organisms, some are pollinators, and many serve as food for fish or birds. In wetland ecosystems, flies can be numerous and many of them depend on water for their development.

By drying out constructed wetlands (shallow ponds) in August 2022, this study investigated how flies respond to drought events, which become more frequent with climate change. For this purpose, about 20,000 flies were sampled in July, August and September, both at drained and undrained wetlands. To obtain information about their life strategies, it was determined to which fly families they belong, and they were categorised into groups based on feeding strategies and water dependency. Then, it was analysed if the total biomass, the number of individuals or the composition of groups changed in response to the drought experiment.

The analysis indicated that the aquatic nonbiting midges tended to decrease during drainage, while moisture-dependent flies tended to increase. Surprisingly though, these results differed strongly depending on which trap was used for catching the insects. Water-independent flies remained unaffected by the drought. Further, the drought effect on fly families was independent from their feeding strategy. Also, no distinct drought effect was found on the total biomass or composition of families.

That many water dependent families were not affected by the drainage suggests that enough moist habitats remained close by. Differences between the trap types might be explained by the fact that they tend to catch different species.

Ethical & societal aspects

Knowledge on how wetland ecosystems are affected by drought can help conservation agencies and landowners to consider climate change scenarios in wetland management decisions. Since the results of this study were inconsistent and strongly depending on the sampling method used, it can be seen as a reminder to always interpret scientific results in a greater context and to be cautious and critical with the interpretation of individual scientific findings.

In order to investigate potential effects of hydrological drought on wetland Diptera, for this study insects were killed with passively and actively collecting traps. To my knowledge, there is no non-lethal method that could have been used to collect and identify Diptera at a similar scale and quality.

Contents

Abbreviations

Glmm	Generalised linear mixed model
M1/M2	SLAM trap 1 or 2 of a sampling location
P_{adj}	Adjusted p-value to avoid type I errors from multiple testing
SLAM trap	Sea, Land and Air Malaise trap
SMHI	Swedish Meteorological and Hydrological Institute

Background

Drought development in Europe

As part of climate change, drought events are increasingly affecting landscapes in Europe (Brás et al., 2021; Senf et al., 2020). While the Mediterranean regions are already experiencing an increase in drought events in all seasons, Scandinavia is expected to see an overall decrease in drought events first (Böhnisch et al., 2021). Assuming moderate to high carbon dioxide emission scenarios, though, spring and summer droughts will start to increase in Scandinavia towards the end of the century (Böhnisch et al., 2021; Spinoni et al., 2018). Depending on the study, there are regional variations in the prediction, but in Sweden the southern and eastern areas seem to face the highest increase of drought events. (Böhnisch et al., 2021; Chen et al., 2021; Spinoni et al., 2018). The summer drought of 2018 showed that droughts can have strong impacts on Swedish landscapes. Exceptional heat and low precipitation in spring and summer of 2018 led to unusually low soil moisture which impaired both agricultural and ecosystem productivity (Peters et al., 2020). Rinne et al. (2020) found that the 2018 drought also led to lowered water levels in Swedish wetlands.

Drought effects on wetland ecosystems

During severe summer droughts, shallow water bodies like wetlands may not only have lower water levels, but can temporarily dry out completely (Moss et al., 2009). The resulting water shortage can affect freshwater ecosystems in several ways (Filazzola et al., 2021; Lake, 2003). Lake (2003) reviewed that the direct lack of water may cause aquatic organisms to dry out or to reach higher densities in the smaller pools of water that remain. Also, smaller volumes of water can heat up more easily, promoting deoxygenation and changes in water chemistry, which can harm aquatic organisms. All these factors can change the composition of the local communities and influence species interactions (Lake, 2003). Lu et al. (2016), for instance, observed that following a drought experiment in a stream, food webs partly collapsed and then reconnected in different ways.

A large part of wetland animals consists of arthropods (Batzer & Wissinger Scott A, 1996). Within wetland ecosystems, arthropods fill important links in the food web between primary producers and larger predators (Batzer et al., 2014). In this way, they contribute substantially to the functioning of wetland ecosystems.

Studies on the effects of drought on arthropods show a mixed picture. Deacon et al. (2019) found that the total insect abundance at South African ponds declined in dry years, but species richness was not affected. While aquatic species are generally thought to be more affected than water-independent taxa, terrestrial arthropods may also be affected by severe drought events (Filazzola et al., 2021). Terrestrial arthropods can however also benefit from the new terrestrial habitats that are created when water bodies dry out (Batzer & Wu, 2020). Studying terrestrial arthropods in forests, Wise and Lensing (2019) found drought effects on several trophic groups and suggested that predators were

affected by bottom-up control through the decline of their prey. Lake (2003) summarised drought effects on community composition, diversity and population density of animals in running waters and reported that insects have several strategies to survive drought events. If they persist in moist microhabitats, they can recolonise freshwater habitats quickly after the drought (Lake, 2003). Many studies which investigated the impact of hydrological extremes on arthropods in freshwater habitats focused on flooding rather than drought (Batzer & Wu, 2020; Plum, 2005), running waters rather than lentic ecosystems (Deacon et al., 2019) and cover either well-studied terrestrial groups like beetles and spiders (Lafage & Pétillon, 2016; Lambeets et al., 2008; Marx et al., 2012; Plum, 2005; Schirmel et al., 2014) or a few prominent aquatic taxa like non-biting midges (Chironomidae) and mosquitoes (Culicidae) (Keiper et al., 2002). The impact of drought on most other Diptera families, has rarely been researched (Batzer & Wu, 2020; Keiper et al., 2002).

Need for studies on drought effects on Diptera

Diptera make up a substantial part of the diversity, abundance and biomass of wetland arthropods (Batzer et al., 2014; Whiles & Goldowitz, 2001). Through their diverse life strategies, Diptera contribute to various ecosystem functions such as decomposition, pollination, and controlling populations of other organisms (Adler & Courtney, 2019; Pfister et al., 2017). Many dipterans also serve as a food source for birds, fish and other small vertebrates (Batzer et al., 2014; Keiper et al., 2002; Plum, 2005). Taxa within Dolichopodidae and Chironomidae are discussed as suitable indicators of water and wetland quality (Batzer et al., 2014; Pollet, 2009), but from over 200 Diptera families worldwide (Bánki et al., 2022) only a few have been studied in relation to drought. Studies on Dolichopodidae found that their community composition is dependent on soil moisture (Gelbič & Olejníček, 2011; Pollet, 2009). A pest species of Sciaridae, which develops in soil, was found to decrease in abundance after a drought treatment (Sun et al., 2019), which might be related to the finding that especially taxa with soil dwelling larvae are affected by drainage (Frouz, 1999). In these two examples, the water dependency of the larval stage seems to be an important factor predicting the susceptibility of dipteran populations to drought. On the other hand, aquatic Culicidae do not seem to decline during drought, probably because of their ability to quickly colonise small water bodies (Kim et al., 2014).

The main reason why Diptera are often omitted from ecological studies is probably that many taxa are difficult to identify and that knowledge on life histories of many dipterans is fragmentary (Frouz, 1999). One way to solve this issue is to do analyses at higher taxonomic ranks than species. This approach has the disadvantage that variability on species level within the investigated taxon cannot be detected, and environmental effects may therefore not always be accurately depicted. For Diptera, however, there is evidence that family level diversity works reasonably well as a proxy for species diversity (Báldi, 2003; Hayford & Gelhaus, 2010; Zou et al., 2020). In some cases, also a broad functional classification of dipterans at family or genus level seems to be possible (Frouz, 1999; Schmera et al., 2017). Functional group classification can be crucial for ecological studies because if appropriate functional groups are selected, the composition of functional groups can provide insight into ecosystem functioning. (Laureto et al., 2015).

From studying whether and which dipteran families and functional groups are affected by summer drought and how long populations take to recover, one could therefore draw conclusions about the effects of drought on wetland ecosystems in general. A significant decline in total Diptera biomass would have implications for species on higher trophic levels. From changes in the abundance of specific families, information for conservation management and incentives for further research could be derived. Drought induced shifts in trophic group composition would indicate a change in food web structures. Finally, potential impacts of drought on groups with a specific water dependency may allow to draw conclusions on the mechanisms behind the effects.

Aims & hypotheses

The main objective of this study is to investigate whether and how a hydrological summer drought affects communities of Diptera in constructed wetlands and if specific families, trophic groups or water dependency groups are particularly susceptible to drought. Therefore, biomass, abundances, community composition and diversity measures of Diptera were determined before, during and after a temporary drainage of wetlands based on family-level identification. Comparing those measurements to respective data from control wetlands the following questions shall be addressed:

1) Is the total biomass of adult Diptera affected by drought?
2) How do the abundances of different dipteran families respond to drought?
3) How do the abundances of different trophic groups within Diptera respond to drought?
4) How do the abundances of dipteran taxa with different water dependency respond to drought?

In case significant effects of drought on Diptera are found in question 1–4, the following additional questions shall be investigated:

5) How well do the populations of drought-affected groups recover after the end of the drought experiment?
6) Are there differences in recovery depending on trophic groups?

Based on these questions, the following hypotheses were developed.

1) As presumably many species in wetland habitats are adapted to wet conditions, a dry-out of wetlands is expected to affect the total biomass of Diptera negatively.
2) Different dipteran families respond differently to hydrological drought due to their varying adaptations and life strategies. Thus, it is assumed that family composition changes as a result of wetland drainage.
3) Abundances of higher trophic levels are likely to be more strongly affected by drought than abundances of lower trophic levels because high trophic levels might be susceptible to desiccation themselves and additionally suffer from a lower availability of host or prey species.
4)
    a) The reduced water availability during drought presumably affects abundances of aquatic taxa more negatively compared to abundances of non-aquatic taxa.
    b) Remaining soil moisture could favour taxa that develop in moist soil.
    c) Taxa which are not directly water-dependent might benefit from new terrestrial habitats during a drought period.
5) In general, populations of drought-affected groups are expected to recover at least partly after a drought, due to migration or perseverance of individuals in wet microhabitats. Though, it might take some time for drought affected groups to recover completely.
6) Drought recovery primarily depends on the migration potential and survival abilities of individual taxa, but additionally populations of higher trophic levels might not recover as easily as populations of lower trophic levels because their host or prey species might need to regain a sufficient population size first if they were drought-affected as well.

Material & methods

Sites & drought experiment

The experiment was conducted during summer 2022 at 16 constructed wetlands, all located in agricultural surroundings in Halland County in southwest Sweden (**Figure 1**). To simulate a summer drought, 7 of the wetlands were drained for about 30 days between 11/07/2022 and 10/08/2022 by setting the water outlets to the lowest possible level. To do this, the outlet pipe (snorkel) was either turned to a horizontal position at the bottom of the wetland or, if a level well was available, the outlet pipe inside the well was removed. Because the water outlets were not always situated at the lowest point of the wetlands, most wetlands could not be entirely drained, which is why small pools of water remained during the experimental drought period (**Figure 2**). Near some of the treatment sites there were also additional wetlands which were not part of the experiment. At the end of the induced drought period, the water outlets were returned to the original state and the wetlands refilled at varying rates after several days to weeks. The other 9 wetlands served as control sites and were not manipulated in any way. For each drained site, at least one control site with similar environmental factors such as livestock grazing, slope and wetland size was included to account for potential influences of those local conditions. All sampling sites are located within 1.5 and 99 km distance from each other. Generally, the area recorded average to slightly elevated temperatures and lower precipitation in summer 2022 compared to the reference period 1991-2020 (**Figure S 1**).

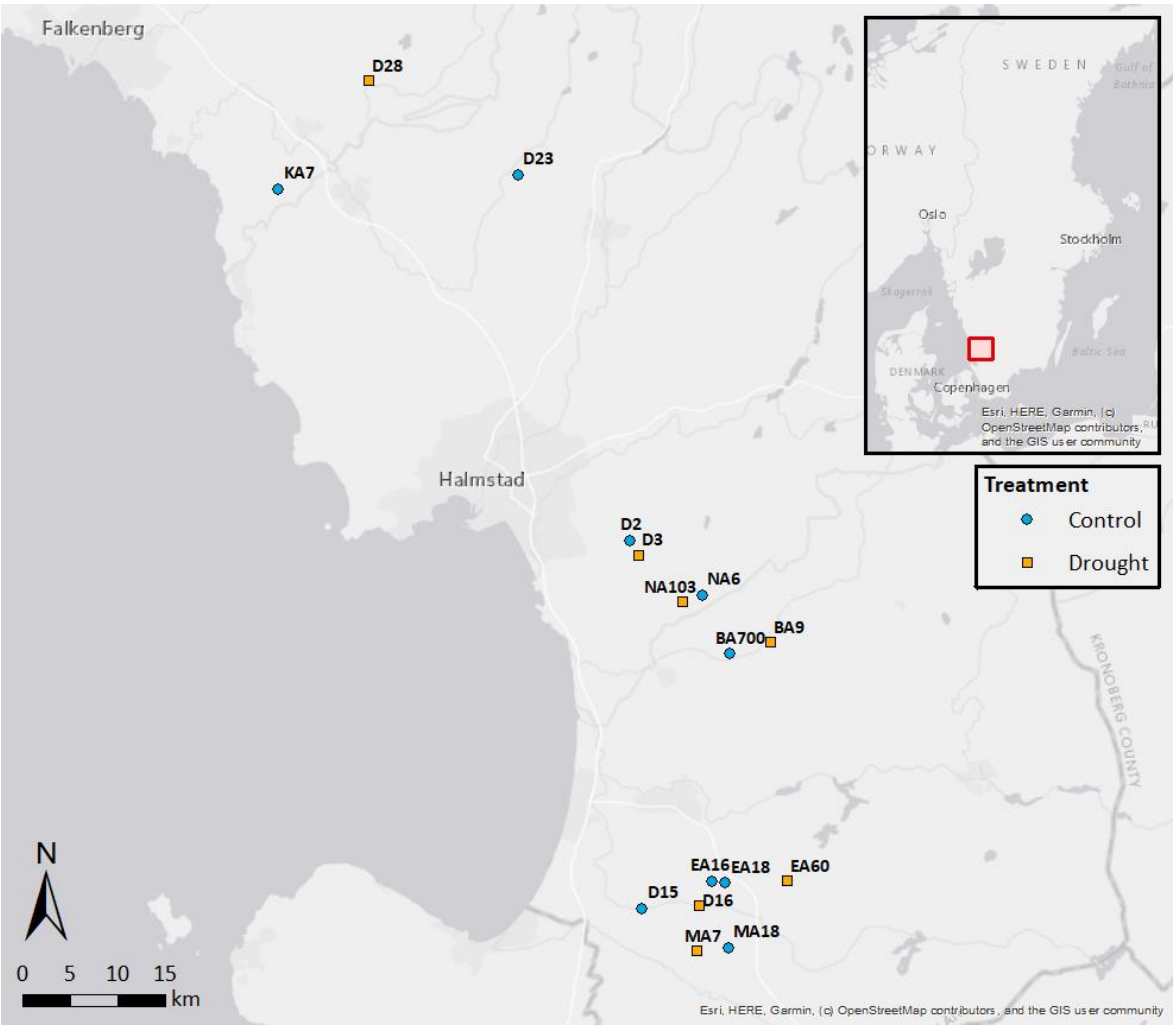

Figure 1 Location of the wetlands within the sampling area in Halland. Insert: Location of the sampling area within Sweden framed in red.

Figure 2 Drone pictures of three of the drained wetlands before and during the drought period, showing different landscapes surrounding the wetlands and different amounts of water remaining after the drainage. Pictures from Hushållningssällskapet Halland.

Sampling

At all sites, arthropods were sampled for three days each in July, right before the drainage (within 01 – 07/07/2022), in August, after 4 weeks of drought (within 06 – 12/08/2022) and in September, 7 weeks after the water outlets were set back to their original state (within 26 – 30/09/2022). To collect a broad range of Diptera, both Malaise traps and coloured pan traps were used. Specifically, two SLAM traps (Sea, Land and Air Malaise traps) were set up with some distance along the waterside of each wetland and additionally, 3 coloured pan traps (yellow, white and blue UV colour) were placed together at one spot on the shoreline between the two SLAM traps. All trap containers were half-filled with water and a drop of detergent and were installed for three consecutive days before being collected. The samples were then drained, and the collected specimens were transferred into tubes with 70% ethanol. During this procedure, the contents of the three coloured pan traps from each wetland were combined into a single pan trap sample per wetland, while the two SLAM trap samples were kept as separate samples. For each of the 16 sites and 3 months this resulted in a total of one Pan trap sample and two Malaise trap samples, abbreviated as “M1” and “M2” in the following.

Sorting & identification

Per site and month, the Diptera of at least one Malaise trap sample (M1) and the combined pan trap sample were sorted. Because of the limited time frame of the project, the second Malaise trap sample (M2) was only sorted for all sites in July as well as for site MA7 in August and site D3 in September. As far as possible, all Diptera of those samples were sorted to family level and counted. To avoid double counting when body parts of specimens had fallen off, only the part with the thorax was counted, as it usually contains most features for identification. For family identification, mainly the key for European Diptera by Oosterbroek (2006) but also the key for British Diptera by Unwin (1981) were used. Following recent studies, Polleniidae were additionally treated as a family separate from Calliphoridae (Cerretti et al., 2019). In cases of doubt, the websites Artfakta från SLU Artdatabanken (2023), Diptera.info (2023) or DrawWing (2023) were used for the visual comparison of features.

If specific genera or species were reliably identified during the sorting process, they were counted as the respective lower taxon to obtain possible additional information on their functional biology in the

data. The family of Sarcophagidae was sorted to the levels of subgenera or species. Males of the Genus *Sarcophaga* were identified by visually comparing their terminalia with pictures from Richet et al. (2011). All other Sarcophagidae were identified using the dichotomous keys of Whitmore et al. (2020) and Pape (1987). Additionally, Peter Hambäck sorted out all Syrphidae with aquatic larvae (within the subfamily Eristalinae) and identified them to genus level. A stereomicroscope with a magnification of 6.7–500x was used for the whole sorting process.

Definition of functional groups

Because species identification is challenging for a wide range of dipterans, in this study, functional characteristics were largely assigned based on family level identifications. The families themselves were also regarded as functional groups because species within a family likely share functional traits due to their genetic similarity even though those shared traits were not specified here. The family level analyses aim to investigate whether certain Diptera families as a whole are affected by drought and whether specific families could even serve as indicators for the disturbance of wetland ecosystems by drought. For the family analyses, the abundances of lower taxa within a family were therefore summed to obtain the abundance of the entire family.

Based on their feeding habits, the identified taxa were categorised into the following trophic groups: “detritivores” (including taxa feeding on fungi and soil organisms), “herbivores” (including algae feeders), “predators” (or generalist carnivores) and “parasitoids” (or specialist carnivores). When the abundances of predators or parasitoids were too low for a statistical analysis, the two groups were merged and analysed as “carnivores”. The trophic grouping of a taxon was based on its larval feeding habits, as it was assumed that, due to its lower mobility, the larval stage would be more affected by the local drought than the imagos. Categorising adult dipterans by their larval feeding habits was also based on the assumption that the majority of specimens caught had developed in the near proximity of the sampling location.

Additionally, all taxa were categorised into functional groups according to their water dependency. First, taxa which have at least one fully aquatic life stage were classified as “aquatic”. Second, taxa which are dependent on moist soil or primarily found in moist habitats during at least one of their life stages were classified as “moisture dependent”. Finally, not directly water or moisture dependent taxa were grouped as “terrestrial”. The family Simuliidae, with larvae developing in running water, was counted as terrestrial in the analyses because they were presumably not directly dependent on the water from the investigated wetlands.

For most taxa, information on both feeding habits and water dependency was taken from Oosterbroek (2006) and Artfakta från SLU Artdatabanken (2023). Specific information on Sarcophagidae was found in Pape (1987) and Richet et al. (2011). If no information on larval feeding habits or water dependency was found, or if those categories were variable within a taxon, it was classified as unknown.

Weighing

For the biomass analysis, the mean biomass of an average specimen per family was estimated by weighing 5 samples of the family and dividing the total weight by the total number of specimens within the 5 samples. The samples were selected by visually selecting a representative range of specimens of different sizes. Within the family of Tabanidae, which was identified to 2 distinct genera, the biomass of both taxa was analysed separately.

The biomass of the samples was determined as semi-dry weight. This procedure was used to reduce the impact of evaporation on the measurements, while the insects should also not dry out completely to avoid damage and to facilitate rewetting for further storage in ethanol. To obtain a workflow for

drying Diptera to semi-dry conditions, test runs with specimens of different sizes were carried out in advance. The aim was to weigh samples as soon as the weight did no longer fluctuate substantially in the range of a tenth of a milligram, while the specimens were also not yet dried out. For large and roundish Diptera, weights were stable after 5 minutes of air drying on a paper towel. Smaller and narrower Dipterans, such as most nematocerans and Acalyptrata, were weighed after 1 minute of drying on a paper towel. Very small and fragile nematocerans were dried for 1 minute on a filter paper instead because very small specimens dry even on weakly absorbent paper and the smoother surface makes them easier to handle. Since a more detailed distinction would have been difficult to implement, the drying times were approximated, and the grouping of families was made by personal assessment (**Table S 1**). The specimens were transferred to the paper towel or filter paper with tweezers and weighed with a precision balance immediately after the respective drying time.

Data analysis

General notes

Since Malaise traps and pan traps can catch different parts of the Diptera community (Devigne & De Biseau, 2014; Ven & De Bruyn, 1991), the data of the two trap types were analysed separately. Also, for each trap type and analysis, the direct effect of the drainage from July to August, as well as the long-term effect from July to September and the potential recovery from August to September were investigated separately. As a result, each statistical analysis was repeated six times using the same methodology but different data sets. In the following, each procedure is only described once by the example of testing the direct effect of the drainage.

As not all samples from the second Malaise trap (M2) were sorted, only one data point per site was included for the tests on the Malaise trap data. If abundance data from M1 and M2 was available, the mean abundance of these was applied to make use of the available data. Calculating means resulted in decimal digits for abundances. But as the multivariate tests used require integer values, the mean abundance values were rounded to the nearest integer.

This procedure did not apply for the pan trap samples, as only one set was collected per site. However, for three pan trap samples no data was available because the trap containers were emptied or disappeared during the sampling period and thus had to be excluded from the analysis. If such a sample from one sampling period was excluded from a test, the corresponding sample from the same location but from the other sampling period was also excluded. Samples that appeared to be disturbed by weather conditions or animals but still contained specimens were included in the analysis because it was unclear to what extent the sampling was impaired and in order to make use of the available data. The statistical analysis was carried out using the software R, version 4.2.2 (R Core Team, 2022).

Biomass analysis

The total biomass of a sample was calculated by extrapolating the estimated weight of one specimen of a taxon to the total number of specimens of that taxon within the sample and then summing up the biomass of all taxa that occurred in the sample. To test whether the drainage of the wetlands had an effect on the total biomass of the collected Diptera compared to the control sites (hypothesis 1), a linear mixed effects model was performed using the *lmer* function from the R package lme4 (Bates et al., 2015). The logarithmic transformation of biomass was used as the response variable and the interaction of month and treatment was used as the explanatory variable. To account for natural variation between the wetlands, site was included as a random effect. Residual plots from the DHARMa package (Hartig, 2022) were used to evaluate the assumptions for the model.

Functional group analysis

Families, trophic groups and water dependency groups were all considered functional groups in this study. Therefore, the statistical analysis of the effect of the drought treatment on each of those categories was largely the same. The effect of the drought treatment on both the composition of the functional groups, as well as single categories within them (hypotheses 2 – 4) was investigated through different generalised linear (mixed) models.

For testing whether changes in the functional group composition occurred as a result of the drought experiment, a multivariate analysis was carried out, using the function *manyglm* from the R package mvabund (Wang et al., 2012) with the composition of functional groups per site as the response variable and the interaction of treatment and month as the explanatory variable. The best fitting error distribution was found to be negative binomial. To check the assumptions for the test, a residuals vs fitted plot was examined and a mean-variance plot for multivariate abundance data was created with the function *meanvar.plot* from mvabund (Wang et al., 2012). If a family was only present in 1/5 or less of the samples of one of the months compared, it was assumed that any influence of the experiment would not be measurable, and the abundance data was excluded from the analysis.

Following the multivariate analysis, univariate analyses were carried out on the same model using the function *anova(model,p.uni = "adjusted")* in order to test the drought effect on individual functional groups. Because the multivariate model could not include wetland location as a random effect, the influence of the drought experiment on single functional groups was additionally tested with generalised linear mixed models, to investigate whether site-specific influences masked potential effects of the experiment in the multivariate analysis. The model was fitted using the function *glmmTMB* from the homonymous package glmmTMB (Brooks et al., 2017), with functional group as the response variable, the interaction of month and treatment as the explanatory variable and site as a random effect. All the abundance data were best described by a negative binomial distribution with quadratic parameterisation, and the test assumptions were checked by analysing residual plots from the DHARMa package. Since the likelihood for a Type I error increases with repeated tests, the p-values were adjusted by multiplying them by the number of functional group categories tested.

Diversity indices

To further evaluate if the potential drought effects on Diptera families affected the diversity of dipterans, both richness and Shannon index were calculated on a family level for each sample. Regarding the Malaise trap data, both indices were calculated based on the rounded mean values of the family abundances. Family richness refers to the number of different families in a sample. The Shannon index (H) was calculated by the following formula, with p_i being the proportion of one taxon within the total abundance of the sample:

$$H = -\sum p_i * ln(p_i)$$

Similarly as in the biomass analysis, the *lmer* function from the lme4 package (Bates et al., 2015) was used to set up a linear mixed effects model for each diversity measure. The respective measure was used as a response variable, while the interaction term of month and treatment served as the explanatory variable and site was considered as a random effect. To test the assumptions of the model, diagnostic plots from the DHARMa package (Hartig, 2022) were used.

Results

Altogether, 66 SLAM trap samples and 45 pan trap samples were sorted, containing a total of 21380 Diptera. 13454 of the specimens were found in the SLAM traps and 7926 in the pan traps. Averaging the abundances of the two SLAM traps M1 and M2, the total number of specimens from the SLAM traps is 9803. In July the SLAM traps caught 7020 individuals, in August 4546 and in September 1882. Here it should be noted that these total abundances cannot be directly compared between July and the other months, since all 32 SLAM trap samples from July were sorted but only 17 each from August and September. The pan traps caught 2322 individuals in July, 5096 in August and 507 in September. In total, the specimens were identified to 53 different families and 36 lower taxa within those families (**Table 1**). Six individuals of nematocerans were so damaged that the family could not be determined. These specimens were only included in the biomass analysis.

Table 1 List of all identified taxa, including abundances in SLAM and pan traps and functional group categorisation. Functional group categories which were unknown for a specific taxon or variable within a taxon are distinguished in the list but grouped as "unknown" in the analyses.

Family	Lower taxon	SLAM abundance	Pan abundance	Trophic group	Water dependency
Agromyzidae	*Cerodontha* sp.	14	6	herbivore	terrestrial
Agromyzidae		74	725	herbivore	terrestrial
Anisopodidae		11	0	detritivore	terrestrial
Anthomyiidae		200	507	variable	terrestrial
Anthomyzidae		4	3	herbivore	moist
Asilidae		2	2	predator	terrestrial
Asteiidae		1	0	unknown	terrestrial
Calliphoridae	*Melanomya nana*	1	1	parasitoid	terrestrial
Calliphoridae		19	361	variable	terrestrial
Carnidae	*Meoneura* sp.	2	436	detritivore	terrestrial
Cecidomyiidae		873	317	variable	terrestrial
Ceratopogonidae		80	14	variable	aquatic
Chaoboridae		54	13	predator	aquatic
Chironomidae		5703	645	herbivore	aquatic
Chloropidae		118	941	variable	variable
Culicidae		8	0	detritivore	aquatic
Dolichopodidae		819	637	predator	moist
Drosophilidae	*Stegana* sp.	1	0	detritivore	terrestrial
Drosophilidae		39	75	detritivore	terrestrial
Empididae	*Dolichocephala* sp.	1	1	predator	aquatic
Empididae		611	79	predator	variable
Ephydridae		36	344	detritivore	variable
Fanniidae		10	2	detritivore	terrestrial
Heleomyzidae		6	0	detritivore	terrestrial
Hybotidae		125	17	predator	unknown
Lauxaniidae		1	0	detritivore	variable
Limoniidae		538	54	detritivore	variable
Lonchopteridae		6	4	detritivore	variable
Micropezidae		6	1	detritivore	variable
Milichiidae		2	1	detritivore	terrestrial

Family	Lower taxon	SLAM abundance	Pan abundance	Trophic group	Water dependency
Muscidae	*Mesembrina meridiana*	8	1	unknown	unknown
Muscidae		168	484	variable	variable
Mycetophilidae		12	2	detritivore	moist
Opomyzidae	*Geomyza* sp.	14	2	herbivore	terrestrial
Opomyzidae	*Opomyza* sp.	0	2	herbivore	terrestrial
Phoridae		61	589	variable	variable
Pipunculidae		1	1	parasitoid	terrestrial
Polleniidae	*Pollenia* sp.	19	33	parasitoid	terrestrial
Psilidae		8	1	herbivore	unknown
Psychodidae		1229	79	detritivore	moist
Ptychopteridae		34	5	detritivore	aquatic
Rhagionidae		3	6	predator	moist
Rhinophoridae		0	17	parasitoid	terrestrial
Sarcophagidae	*Blaesoxipha laticornis*	0	6	parasitoid	terrestrial
Sarcophagidae	*Metopia argyrocephala* gr.	0	1	parasitoid	terrestrial
Sarcophagidae	*Metopia campestris*	0	1	parasitoid	terrestrial
Sarcophagidae	*Ravinia pernix*	0	4	unknown	terrestrial
Sarcophagidae	*Sarcophaga* (*Myorhina*) ♀	0	1	variable	terrestrial
Sarcophagidae	*Sarcophaga* (*Sarcophaga*) ♀	10	37	parasitoid	terrestrial
Sarcophagidae	*Sarcophaga aratrix*	0	4	detritivore	terrestrial
Sarcophagidae	*Sarcophaga carnaria* ♂	0	8	parasitoid	terrestrial
Sarcophagidae	*Sarcophaga incisilobata*	5	20	predator	terrestrial
Sarcophagidae	*Sarcophaga lehmanni* ♂	2	45	parasitoid	terrestrial
Sarcophagidae	*Sarcophaga pumila*	0	2	unknown	terrestrial
Sarcophagidae	*Sarcophaga sinuata*	0	84	variable	moist
Sarcophagidae	*Sarcophaga* sp.	1	0	unknown	terrestrial
Sarcophagidae	*Sarcophaga subvicina* ♂	2	2	parasitoid	terrestrial
Sarcophagidae	*Sarcophaga vagans*	1	0	parasitoid	terrestrial
Sarcophagidae	*Sarcophaga variegata* ♂	5	76	parasitoid	terrestrial
Sarcophagidae	*Senotainia puncticornis*	0	2	parasitoid	terrestrial
Scathophagidae		17	6	variable	variable
Scatopsidae		16	90	detritivore	variable
Sciaridae		1997	312	detritivore	moist
Sciomycidae	*Sepedon* sp.	0	1	parasitoid	aquatic
Sciomycidae		4	1	variable	variable
Sepsidae		85	304	detritivore	variable
Simuliidae		6	1	detritivore	terrestrial
Sphaeroceridae		83	55	detritivore	variable
Stratiomyidae	*Chloromyia formosa*	4	3	detritivore	moist
Syrphidae	*Anasimyia* sp.	4	51	detritivore	aquatic
Syrphidae	*Eristalinus* sp.	0	88	detritivore	aquatic
Syrphidae	*Eristalis* sp.	1	16	detritivore	aquatic
Syrphidae	*Helophilus* sp.	0	29	detritivore	aquatic
Syrphidae	*Sericomyia* sp.	0	2	detritivore	aquatic
Syrphidae	Syrphinae	11	90	variable	variable

Family	Lower taxon	SLAM abundance	Pan abundance	Trophic group	Water dependency
Tabanidae	*Chrysops* sp.	16	6	predator	moist
Tabanidae	*Haematopota* sp.	59	1	predator	moist
Tachinidae	*Ceromya silacea*	1	0	parasitoid	terrestrial
Tachinidae		7	158	parasitoid	terrestrial
Tephritidae		3	0	herbivore	variable
Therevidae		1	1	predator	terrestrial
Tipulidae		184	9	variable	variable
Ulidiidae		1	0	variable	unknown
Unidentified		5	1	variable	variable

Biomass

After calculating average values for the SLAM traps M1 and M2, the summed biomass of Diptera in the Malaise traps was 21.95 g, while the pan traps contained 64.47 g in total. Testing hypothesis 1, on the effect of the drought treatment on total dipteran biomass, no significant effect was found. Neither the short-term trends from July to August, nor the long-term trends from July to September significantly differed between the treatment and control sites in either type of trap (all $p > 0.1$ **Figure 3**).

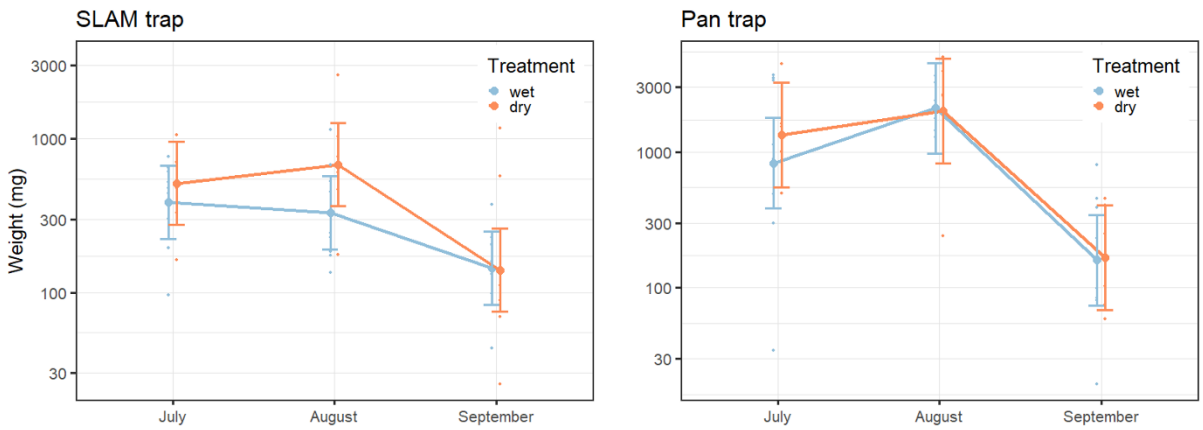

Figure 3 Mean semi-dry weight of Diptera (mg) from SLAM trap samples (left) and pan trap samples (right) per month and treatment. Large points show adjusted means, bars represent 95% CI. Interactions between treatments and paired months had no significant effect ($p > 0.1$).

Family composition & diversity

To assess hypothesis 2, that wetland drainage changes the family composition of Diptera because different families react differently to drought, drought effects on family composition, individual families and family diversity are described. Relating to hypotheses 5 and 6, the result of a recovery test is presented for each significant drought effect on family composition, diversity or individual families between July and August.

Using multivariate analyses per trap type and paired months, no statistically significant effect of the drought treatment was found on the overall family composition of Diptera. Only in the pan trap samples, there was a weak indication that the drainage had a short-term effect on the family composition between July and August (deviance ≈ 58.3, df = 1, residual df = 24, $p \approx 0.076$). Between August and September, the change in family composition in the pan traps was not noticeably different between drained and control sites. Comparing the proportional mean abundances of the most abundant families, the potential short-term effect cannot be attributed to a unidirectional trend in specific families (**Figure 4**, right). Instead, several families showed large variations in their relative

abundances, which cannot be explained by seasonal or local parameters alone. Carnidae were exceptionally dominant at the control sites in July, while Agromyzidae dominated the treatment sites in August. Both families had only very low relative abundances in the other month-treatment combinations. Chironomidae and Dolichopodidae, which both had high relative abundances at the treatment sites in July, seemed to lose their dominance during the drought period in August. In the SLAM trap samples, where no drought effect on family composition was found, change in relative abundances was dominated by Chironomidae and Sciaridae (**Figure 4**, left).

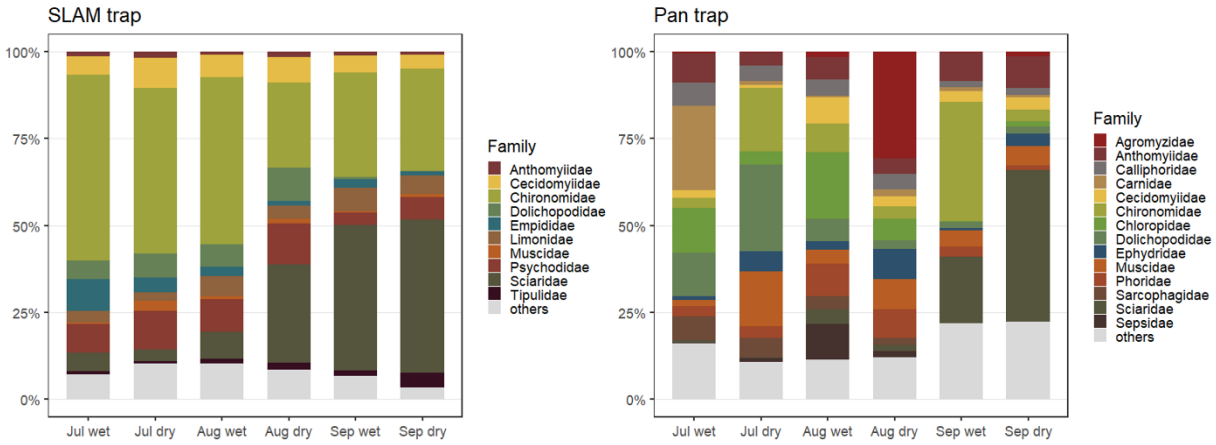

Figure 4 Relative abundances of Diptera families from the SLAM trap (left) and pan trap (right) samples per month and treatment. Families which contributed less than 2% (pan trap) or 1% (SLAM trap) to the total abundance were grouped as "others".

For 29 families enough abundance data in July and August in at least one trap type was available to be included in the analysis of individual families. The univariate generalised linear models showed no drought effect on specific families in the pan trap samples between July and August but a significant treatment-by-month interaction on Chironomidae between July and September (deviance ≈ 12.9, df = 2, $p \approx 0.033$, n = 28). This effect arose because mean chironomid abundances decreased at the drought sites while they increased slightly during that period at the control sites (**Figure 5**, B). However, there was also a high variability between different sites.

In the SLAM trap samples, the drought treatment had a significant short-term effect on the abundances of Sciaridae (deviance ≈ 15.0, $p \approx 0.012$, n = 28) because the mean number increased much stronger at the drained sites than at the control sites between July and August (**Figure 5**, C). After the wetlands filled up again, the abundance of Sciaridae at the treatment sites stayed similarly high, whereas the abundance at the control sites continued to increase slightly, but there was neither a significant treatment-by-month interaction between July and September (long-term effect) nor between August and September (recovery effect). At the end of the experiment, similar numbers of Sciaridae were caught in the SLAM traps of both the control and the treatment sites, while the control sites tended to have slightly more Sciaridae before the drainage. Beyond the drought period, the positive effect of the treatment has therefore only led to an approximation of the sciarid abundances at the treatment sites to the abundances at the control sites.

Using generalised linear mixed models (glmmTMB), which included site as a random effect, the drought effects on single families appeared to be more pronounced. The effect of the treatment-by month interaction on abundances of Chironomidae in the pan traps was strongly significant between July and September (deviance ≈ 168.8, $chi^2 \approx 17.6$, $p_{adj} < 0.001$, n = 28; **Figure 5**, B) but an indication of a drought effect was already found between July and August (deviance ≈ 207.3, $chi^2 \approx 8.5$, $p_{adj} \approx 0.084$, n = 28). While the mean number of Chironomidae at the control sites increased between July and August, the number at the drained sites decreased. No significant effect of the treatment-by-month

interaction was found on chironomid abundances between August and September and in September, chironomid abundances were still lower at the drained wetlands. Within the SLAM trap samples, no influence of the drainage on the family was detected ($p > 0.3$), even though the total number of chironomids in the SLAM traps was about six times as high as in the pan trap samples ($n_{SLAM} = 3871$, $n_{pan} = 645$). Generally, mean chironomid abundances tended to decrease in the SLAM trap samples (**Figure 5**, A).

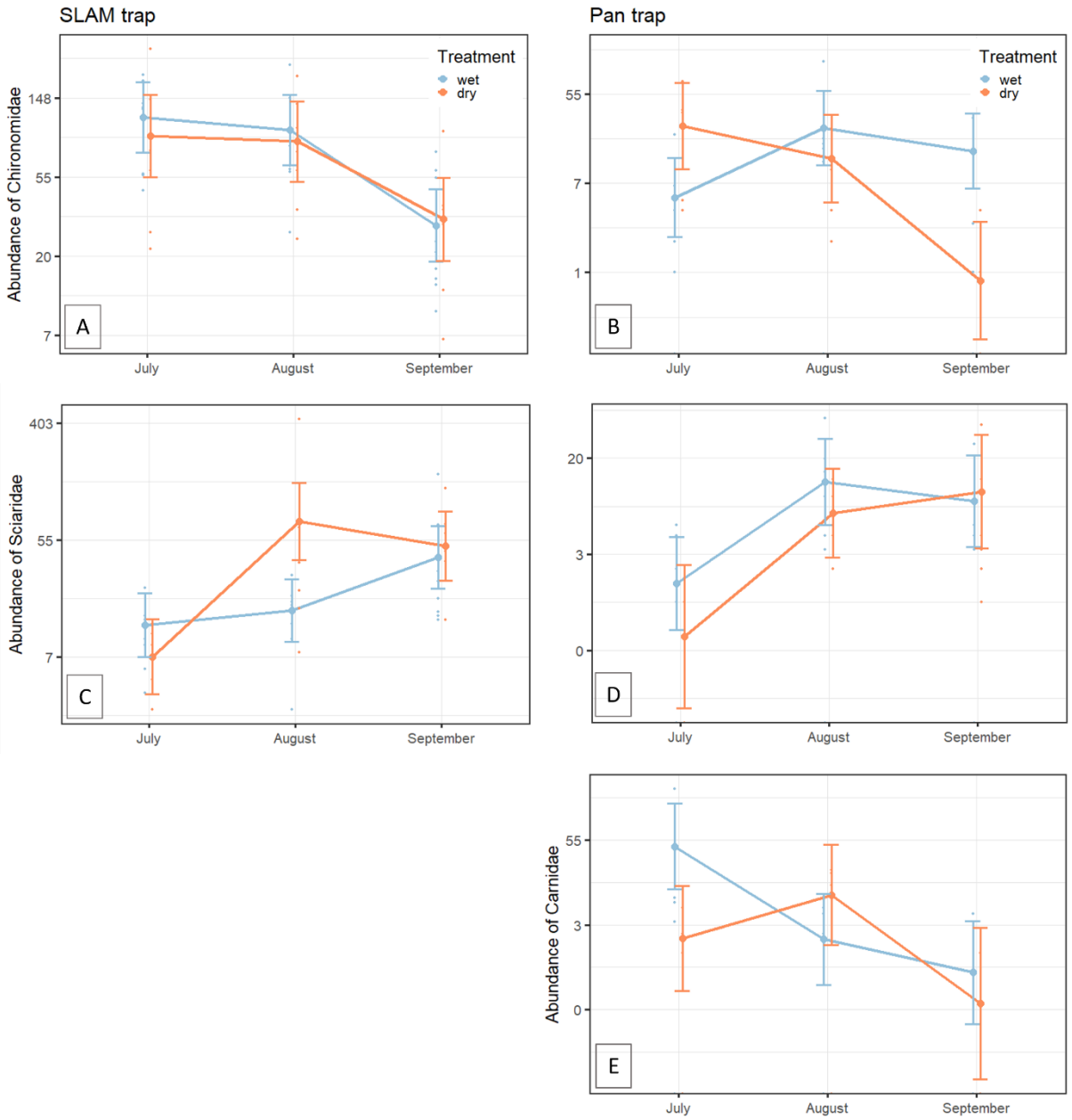

Figure 5 Number of Chironomidae (A, B), Sciaridae (C, D) and Carnidae (E) from SLAM trap samples (left) and pan trap samples (right) per month and treatment. Large points show adjusted means, bars represent 95% CI. Chironomid abundances in pan traps were significantly influenced by the treatment-by-month interaction between July and September (B: glmmTMB, $p_{adj} < 0.001$) and potentially also between July and August (B: glmmTMB, $p_{adj} < 0.1$). Sciarid abundances in SLAM traps were significantly influenced by the treatment-by-month interaction between July and August (C: glmmTMB, $p_{adj} < 0.01$).

The short-term positive drought effect on Sciaridae in the SLAM traps was also more significant in the glmms (deviance ≈ 246.7, $chi^2 \approx 15.2$, $p_{adj} \approx 0.0023$, n = 32; **Figure 5**, C) than in the univariate analysis. Within the pan trap samples, no significant effect of the treatment-by-month interaction on sciarid

abundances was observed (**Figure 5**, D). As the pan traps caught only few Sciaridae in July, it was generally difficult to identify a trend in the pan trap data.

Additionally, the abundances of Carnidae in the pan traps seemed to be positively affected by the treatment between July and August (deviance ≈ 137.5, $chi^2 \approx 8.8$, $p_{adj} \approx 0.072$, n = 28; **Figure 5**, E), but their abundances were generally low, and this result was caused by one large outlier at a control site in July. The abundance of Carnidae in the SLAM trap samples was too low for a statistical analysis. From the interaction plots it is also apparent that the sampling month had a strong influence on the abundance of certain families. In most cases, the highest number of individuals was collected in August and the lowest in September.

Family richness was not immediately influenced by the drought treatment in either type of trap ($p > 0.36$), but there was an indication in the SLAM trap data that, in the long term from July to September, the interaction of treatment and month influenced the family richness of the wetlands ($Chi^2 \approx 3.4$, $p \approx 0.064$, n = 32). At the treatment sites, where the mean richness in July was higher than at the control sites, richness decreased more strongly until September compared to the control sites (**Figure 6**, A). After the treatment, between August and September, the drought treatment even had a significant effect on the change in family richness in the SLAM trap samples ($Chi^2 \approx 6.8$, $p \approx 0.0089$, n = 32). While in July and August the SLAM traps caught more families at treatment sites than at control sites, in September the richness was similarly low regardless of the treatment (**Figure 6**, A). In the pan trap samples, the family richness did not vary much between treatments but more between months, where it was highest in August and lowest in September (**Figure 6**, B).

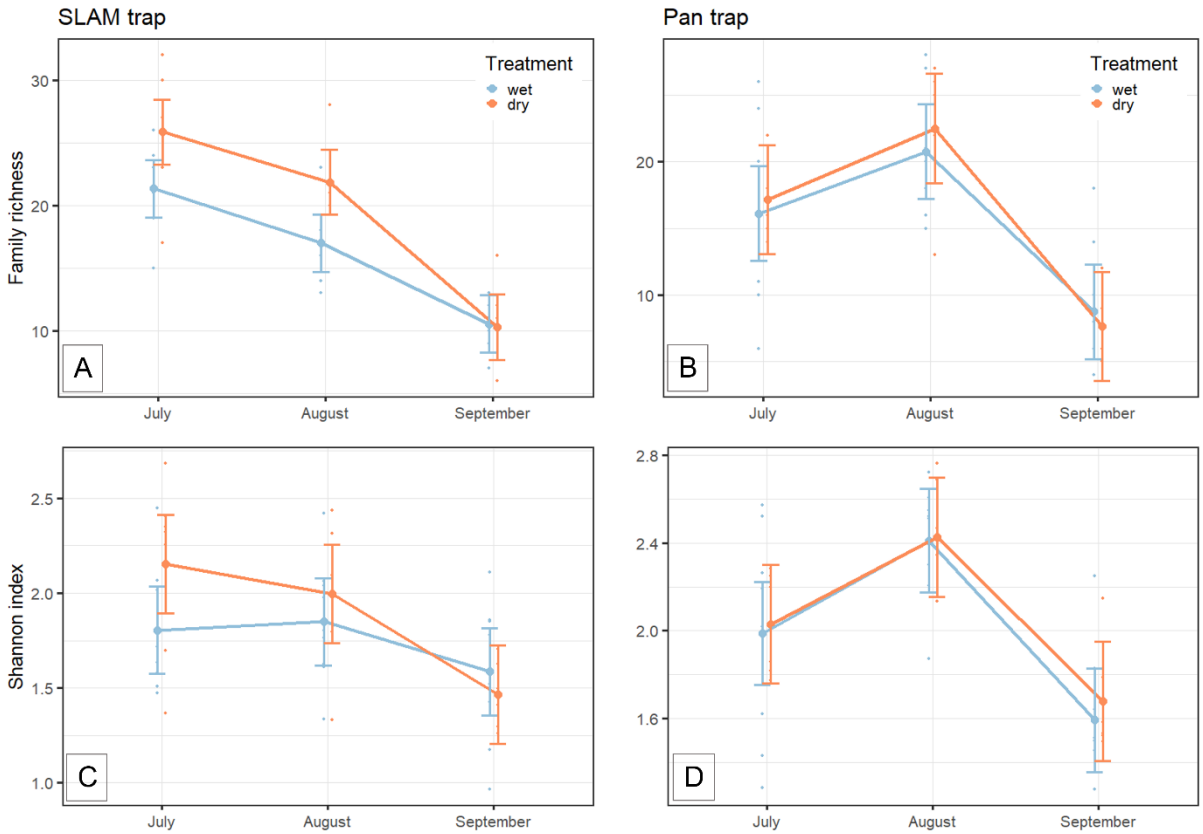

Figure 6 Number of Diptera families (A, B) and Shannon index (C, D) from SLAM trap (left) and pan trap (right) samples per month and treatment. Large points show adjusted means, bars represent 95% CI. In the SLAM traps, the treatment-by-month interaction significantly influenced family diversity between July and September (C: $p < 0.05$), family richness between August and September (A: $p < 0.01$) and potentially also between July and September (A: $p < 0.1$).

The Shannon index in the pan traps also differed mainly between months and not by the drought treatment (**Figure 6**, D). In the SLAM trap samples, the Shannon index generally tended to decrease from July to September (**Figure 6**, C). However, the decrease from July to September was distinctly stronger at the treatment sites than at the control sites, so that the treatment-by-month interaction significantly affected the Shannon index of the SLAM trap samples between July and September ($Chi^2 \approx 5.0$, $p \approx 0.025$, $n = 32$). While the mean Shannon index of the drained sites was distinctly higher than that of the control sites before drainage, it was only slightly higher in August and in September it was even lower than at the untreated sites. None of the observed influences of wetland drainage on family composition, diversity or individual families was however consistent between the samples of both trap types.

Trophic groups

Within the SLAM trap samples, 3405 individuals were categorised as detritivores, 3958 as herbivores, 1155 as predators and 33 as parasitoids. Due to the low number of parasitoids, predators and parasitoids were combined in the analysis as 1188 carnivores. 1274 dipterans from the SLAM traps were classified as unknown because they could not be reliably assigned to a trophic group. The pan traps comprised 1958 detritivores, 1384 herbivores, 783 predators, 389 parasitoids and 3412 individuals of unknown trophic groups. Testing hypothesis 3 that higher trophic levels would be more strongly affected by drought than lower trophic levels, results on the effect of drainage on individual trophic groups as well as the trophic group composition of Diptera are presented here. For tests that showed a significant effect of the treatment between July and August, relating to hypotheses 5 and 6, the recovery of the treatment group between August and September, compared to the development in the control group is also depicted.

Overall, none of the treatment-by-month interactions had a statistically significant influence on the composition of trophic groups in either of the trap types. There was only a weak indication of a long-term effect of the drainage on the composition of trophic groups from the pan traps between July and September (deviance ≈ 16.7, df = 2, residual df = 24, $p \approx 0.094$). Comparing the relative abundances of trophic groups from the pan trap samples by month and treatment, the ratio of detritivores to herbivores seems to be influenced by the treatment-by-month interaction between July and September (**Figure 7**).

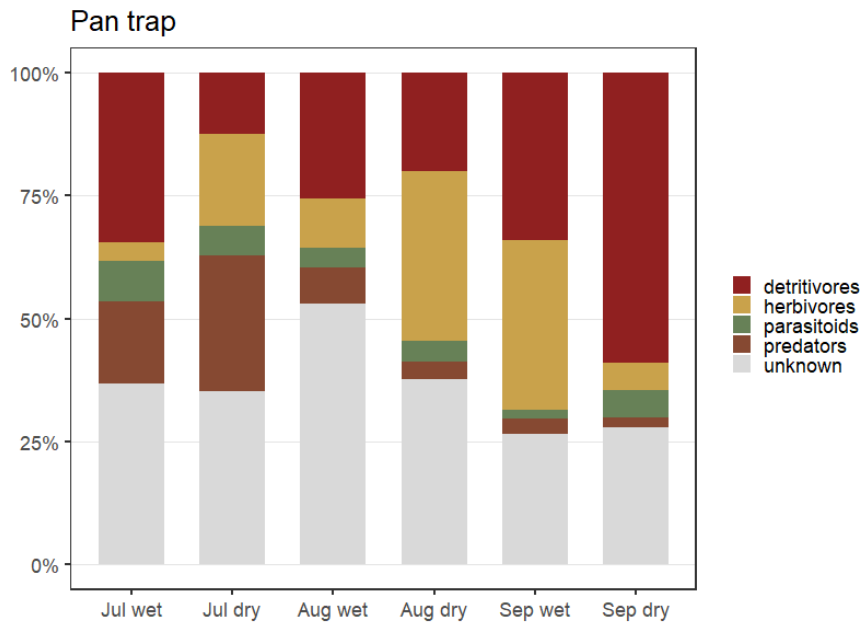

Figure 7 Relative abundances of dipteran trophic groups from the pan trap samples per month and treatment.

Analysing individual trophic groups, the result from the multivariate test derives from a significant negative long-term effect of the drainage on herbivores in pan traps between July and September (univariate manyglm: deviance ≈ 12.0, p_{adj} ≈ 0.023, n = 28; glmmTMB: chi^2 ≈ 15.9, deviance ≈ 177.6, p_{adj} < 0.001; **Figure 8**, B). In July, there were more herbivores at the treatment sites than at the control sites, while in September most herbivores were found at the control sites. But analysing the herbivorous taxa within the pan traps, more than 99% of the abundances were made up by Agromyzidae and Chironomidae (**Figure 8**, C). Agromyzidae though were not relevant for the long-term effect as they were almost exclusively present in August, where most of the abundance can be attributed to 2 samples with mass occurrences at the treatment sites. Therefore, the negative drought effect on herbivores in pan traps can mainly be explained by variations in the abundance of Chironomidae. No drought impact on herbivores was found in the SLAM traps (**Figure 8**, A), but an indication was found that the abundance of detritivores might have been positively influenced by the drought treatment between July and August (glmmTMB: chi^2 ≈ 5.5, deviance ≈ 316.5, p_{adj} ≈ 0.076, n = 32; **Figure 9**, A). When splitting up the mean detritivore abundances per month and treatment to family level, the abundances were dominated by Sciaridae, Psychodidae and Limoniidae (**Figure 9**, C), which made up about 92% of the total detritivore abundance. The increase of detritivores at the drained sites in August can be mainly attributed to Sciaridae and Psychodidae. There was no significant reversal of this trend after the wetlands filled up again, but also no long-term drought effect on the abundances of detritivores in SLAM traps between July and September (**Figure 9**, A) and no significant effect of the interaction on detritivores in the pan trap samples at all (**Figure 9**,B). The category of taxa with unknown trophic group was not significantly influenced by the treatment-by-month interaction in either of the trap types.

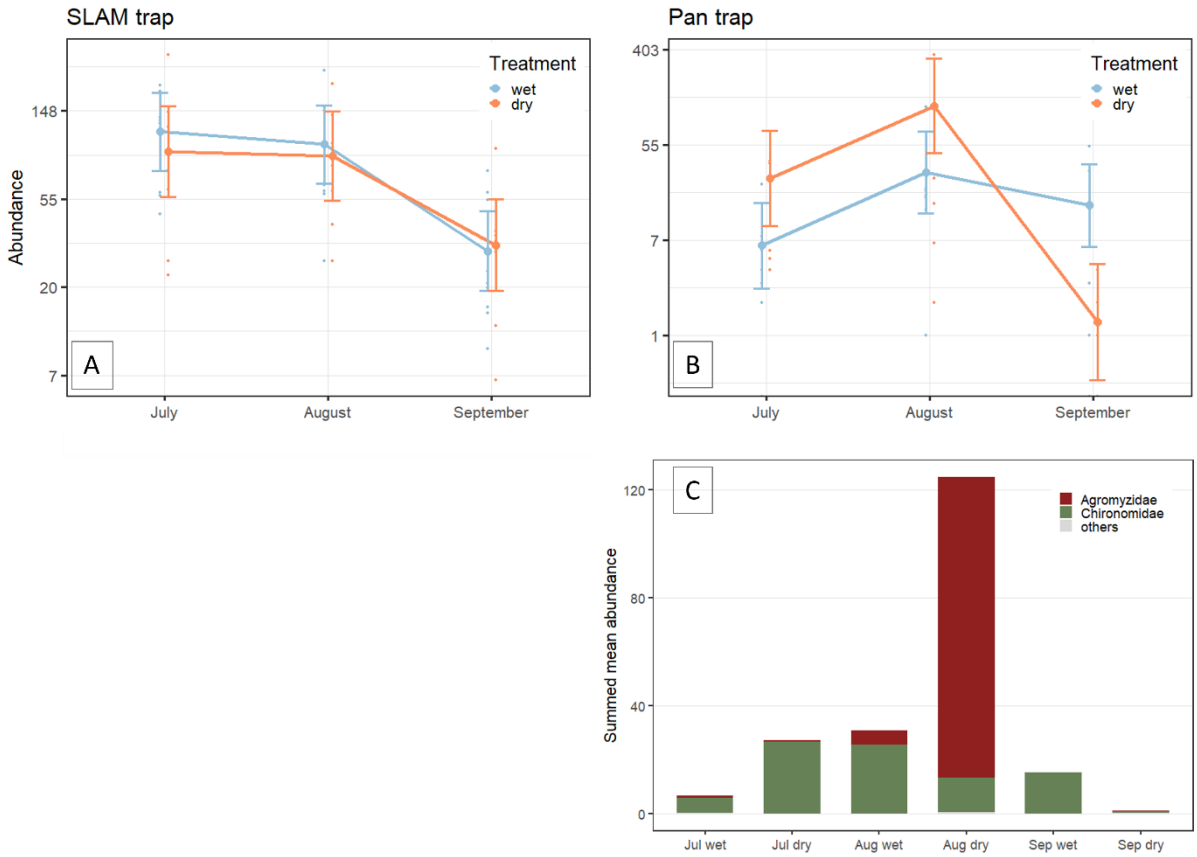

Figure 8 Abundance of herbivores (A, B) and individual herbivorous taxa (C) from SLAM trap (left) and pan trap (right) samples per month and treatment. A, B: Large points show adjusted means, bars represent 95% CI. C: Families which contributed less than 2% to the total abundance were grouped as "others". In the pan traps, the treatment-by-month interaction significantly influenced herbivore abundance between July and September (B: glmmTMB, p < 0.001).

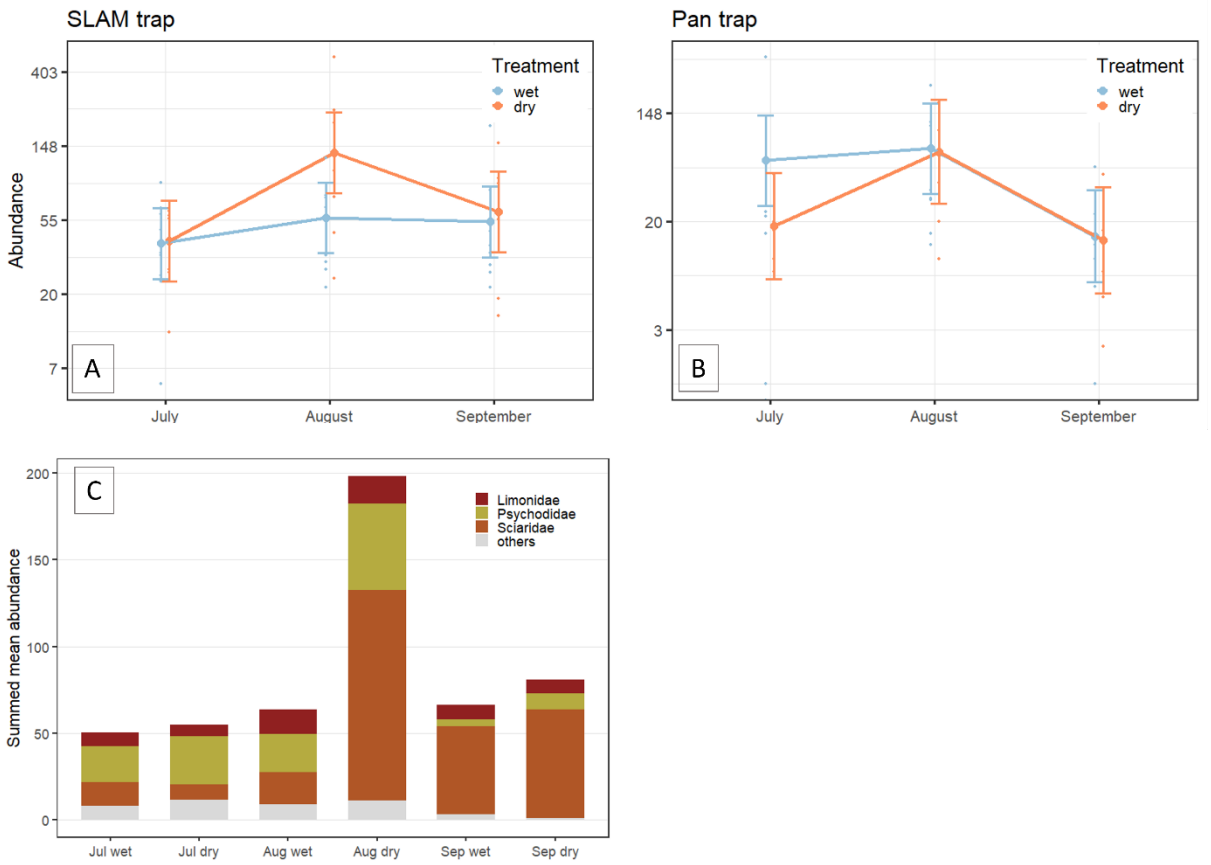

Figure 9 Abundance of detritivores (A, B) and individual detritivorous taxa (C) from SLAM trap (left) and pan trap (right) samples per month and treatment. A, B: Large points show adjusted means, bars represent 95% CI. C: Families which contributed less than 2% to the total abundance were grouped as "others". In the SLAM traps, the treatment-by-month interaction potentially influenced detritivore abundance between July and August (A: glmmTMB, $p < 0.1$).

Water dependency groups

From the SLAM trap samples, 4002 individuals were categorised as aquatic, 3383 as moisture-dependent, 943 as terrestrial and 1498 as unknown regarding their water dependence. In the pan trap samples 865 Diptera were grouped as aquatic, 1133 as moisture-dependent, 2857 as terrestrial and 3071 as unknown. Test results on the drought effect on individual water dependency groups and the composition of water dependency groups were used to assess hypothesis 4, stating that Diptera react differently to drought conditions depending on their water dependency. Referring to hypotheses 5 and 6 about the recovery of different functional groups, the result of a recovery test is presented for each significant drought effect on the water dependency groups between July and August.

The multivariate analyses showed no significant effect of the interactions of treatment and paired months on the composition of water dependency groups, but in the pan traps there was an indication of a changing group composition through the treatment-by month interaction between July and August (deviance ≈ 16.2, df = 1, residual df = 24, $p \approx 0.065$) and also on the long term between July and September (deviance ≈ 12.3, df = 2, residual df = 24, $p \approx 0.085$). Regarding relative abundances, aquatic taxa, moisture dependent taxa and taxa with unknown water dependency group decreased at the treatment sites between July and August, while they increased or remained stable at the control sites (**Figure 10**). In the same period, terrestrial taxa increased in relative abundance at the treatment sites, while they decreased at the control sites. Overall, mainly the moisture dependent and terrestrial

Diptera were affected by the treatment-by-month interaction between July and August. Between July and September, aquatic taxa seemed to be most influenced by the interaction.

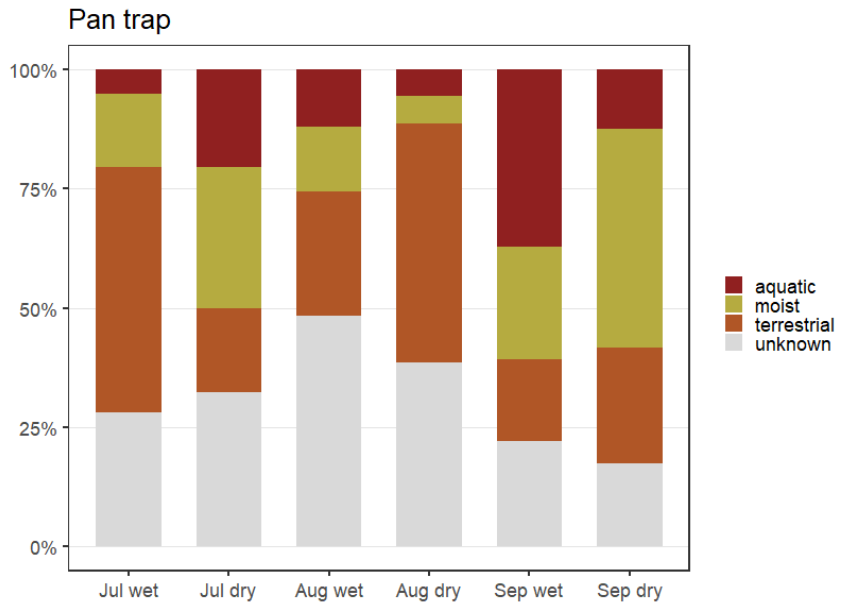

Figure 10 Relative abundances of water dependency groups from the pan trap samples per month and treatment. Moisture dependent Diptera are abbreviated as "moist" in the legend.

Examining single water dependency groups, the drought treatment had a significant negative effect on aquatic dipterans in the pan traps between July and August (glmmTMB: $chi^2 \approx 6.7$, deviance ≈ 226.4, $p_{adj} \approx 0.038$, n = 28) and between July and September (univariate manyglm: deviance ≈ 9.4, $p_{adj} \approx 0.046$, n = 28; glmmTMB: $chi^2 \approx 11.5$, deviance ≈ 194, $p_{adj} \approx 0.0028$; **Figure 11**, B). About 96% of the abundance of aquatic taxa were made up of Eristalinae and Chironomidae. Of these two, the Eristalinae did not experience a decrease in abundance in response to the drought. Thus, as in the analysis of herbivores, Chironomidae seem to be almost exclusively responsible for the observed significant effects of the drainage on aquatic taxa (**Figure 11**, C). Of the less abundant taxa, Chaoboridae, which were only present in August, contributed marginally to the short-term effect by being less abundant at the drained wetlands. In the SLAM trap samples, where Chironomidae showed similar trends in the drained and control wetlands, no drought impact on the total aquatic Diptera was detected. (**Figure 11**, A).

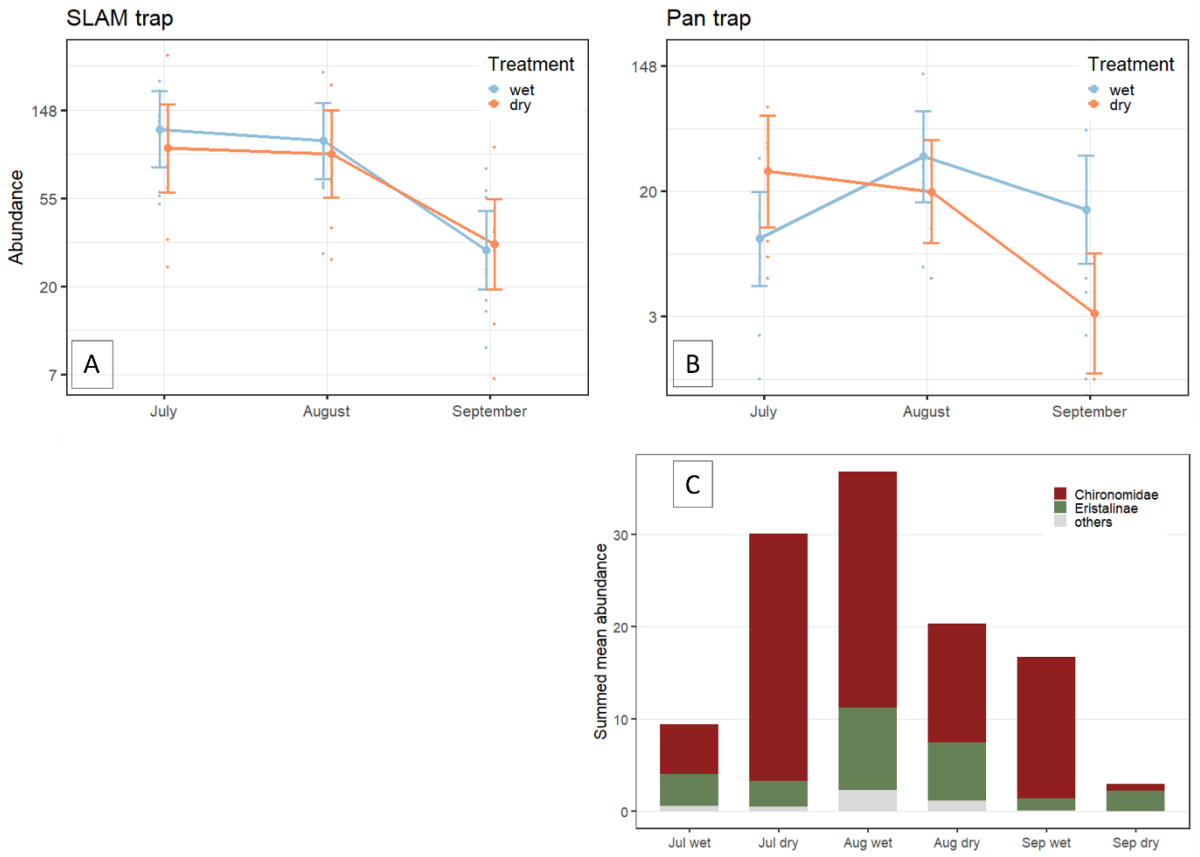

Figure 11 Abundance of aquatic Diptera (A, B) and individual aquatic taxa (C) from SLAM trap (left) and pan trap (right) samples per month and treatment. A, B: Large points show adjusted means, bars represent 95% CI. C: Families which contributed less than 2% to the total abundance were grouped as "others". In the pan traps, the treatment-by-month interaction significantly influenced abundance of aquatic Diptera between July and August (B: glmmTMB, $p < 0.05$) and between July and September (B: glmmTMB, $p < 0.01$).

In the pan traps, the generalised linear mixed models (glmmTMB) also suggested a significant positive short-term effect of the drainage on terrestrial taxa ($chi^2 \approx 7.2$, deviance ≈ 300.4, $p_{adj} \approx 0.029$, n = 28; **Figure 12**, B). When the mean abundances of terrestrial Diptera per month and treatment were split up into different families, it appears that this effect was a consequence from a mass occurrence of Carnidae at the control sites in July and a mass occurrence of Agromyzidae at the treatment sites in August (**Figure 12**, C). Those mass occurrences could be traced back to 1 outlier sample in Carnidae and 2 outlier samples in Agromyzidae. Again, this effect was only found in the pan trap samples but not in the SLAM trap samples (**Figure 12**, A).

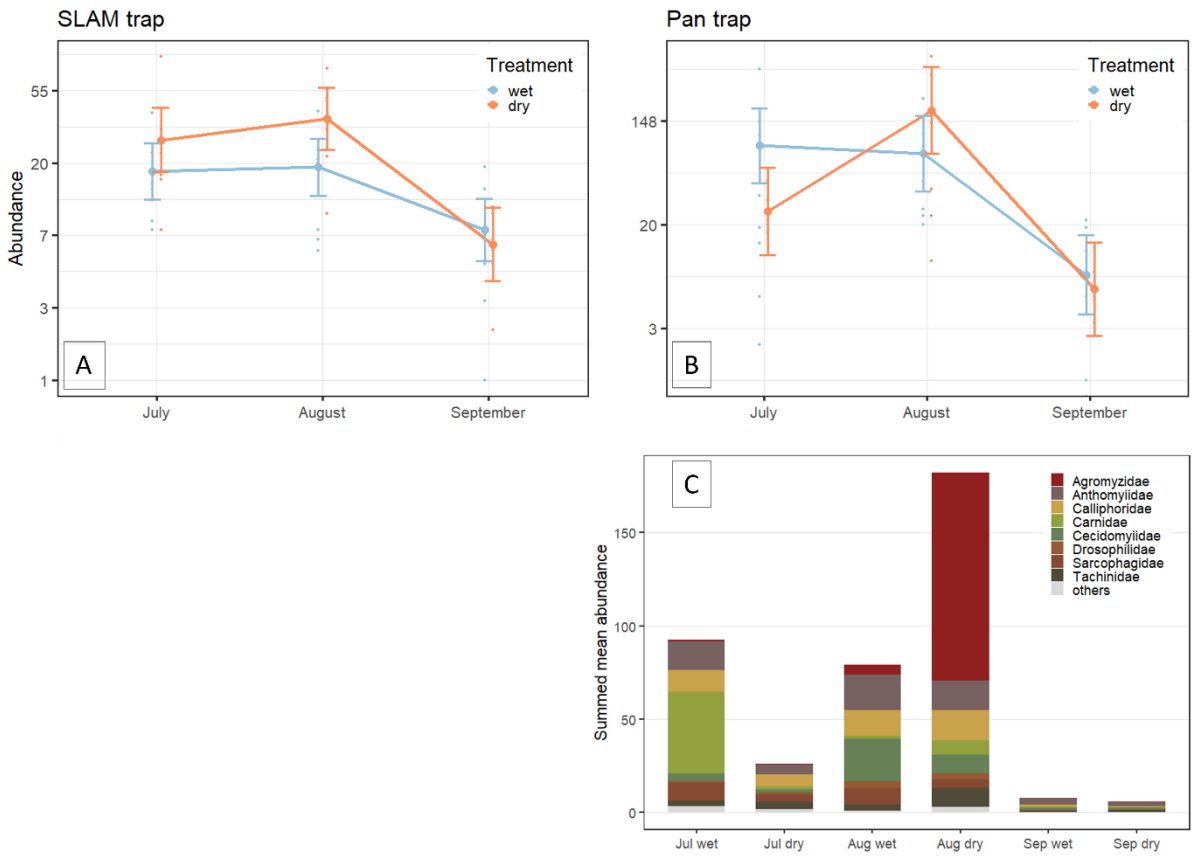

Figure 12 Abundance of terrestrial Diptera (A, B) and individual terrestrial taxa (C) from SLAM trap (left) and pan trap (right) samples per month and treatment. A, B: Large points show adjusted means, bars represent 95% CI. C: Families which contributed less than 2% to the total abundance were grouped as "others". In the pan traps, the treatment-by-month interaction significantly influenced abundance of terrestrial Diptera between July and August (B: glmmTMB, $p < 0.05$).

Furthermore, a weak indication of a negative effect of the treatment-by-month interaction on the moisture dependent taxa was found between July and August in the pan trap samples (glmmTMB: $chi^2 \approx 5.7$, deviance ≈ 243.9, $p_{adj} \approx 0.068$, n = 28; **Figure 13**, B). Looking at the family composition within the moisture dependent taxa from pan traps, Dolichopodidae, Psychodidae and Sciaridae, which made up about 90% of the abundances, all seem to contribute to the potential drought effect (**Figure 13**, D). None of these families were however influenced by the treatment-by-month interactions in the family-level analysis. The wetland-related species *Sarcophaga sinuata*, which made up additional 8% of the abundances showed no detectable response to the drought treatment. In contrast to the negative drought impact on moisture dependent families caught by the pan traps, a positive short-term effect of the drainage on moisture dependent taxa was indicated for the SLAM trap samples by the univariate analysis (deviance ≈ 7.3, $p_{adj} \approx 0.057$, n = 32). Using the generalised linear mixed model (glmmTMB), this positive drought effect on moisture dependent taxa in SLAM traps was statistically significant ($chi^2 \approx 7.2$, deviance ≈ 314.3, $p_{adj} = 0.028$; **Figure 13**, A). Similar to the pan trap catch, about 98% of the abundances were composed of Sciaridae, Psychodidae and Dolichopodidae and all three families clearly increased in abundance at the drained wetlands between July and August but not at the control sites (**Figure 13**, C). In September, moisture dependent dipterans were still more abundant at the treatment wetlands than at the control wetlands, but the difference was not as strong as during the drought period.

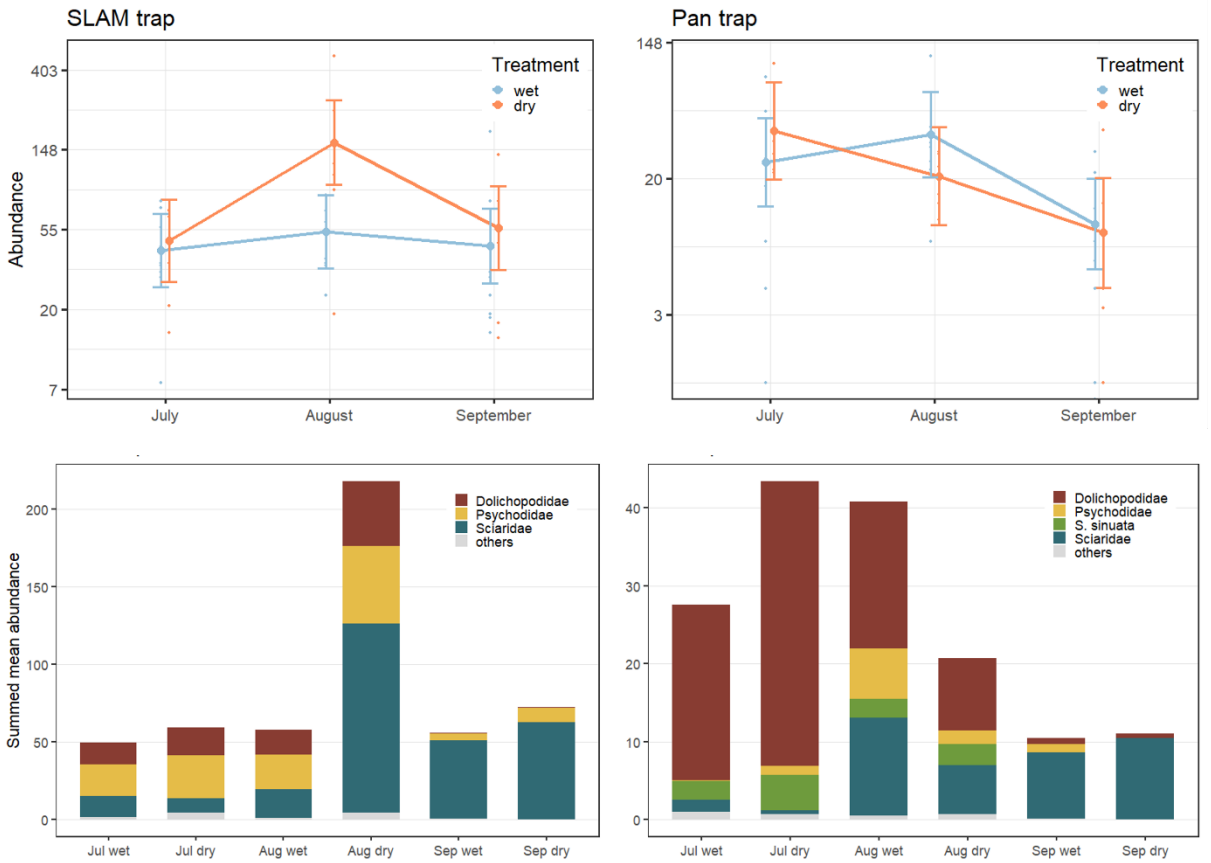

Figure 13 Abundance of moisture dependent Diptera (A, B) and individual moisture dependent taxa (C, D) from SLAM trap (left) and pan trap (right) samples per month and treatment. A, B: Large points show adjusted means, bars represent 95% CI. C, D: Families which contributed less than 2% to the total abundance were grouped as "others". Between July and August, the treatment-by-month interaction significantly influenced abundance of moisture dependent Diptera in the SLAM trap samples (A: glmmTMB, $p < 0.05$) and potentially in the SLAM trap samples (B: glmmTMB, $p < 0.1$).

Discussion

Mixed evidence of drought effects on few dipteran families

Only two out of 29 families, which were individually analysed, showed a significantly different trend in abundance after the drought treatment. While Chironomidae decreased in response to drought in the pan trap samples, Sciaridae increased in the SLAM trap samples at the drained wetlands. Furthermore, a weaker indication for a drought effect on the family Carnidae was detected.

The significant decrease of Chironomidae in the pan traps of the treatment sites, on the other hand, seems to be a plausible consequence of drainage, as most chironomid species are dependent on aquatic habitats (Oosterbroek, 2006). Remaining lower abundances at the treatment sites in September and the non-significant recovery test suggest that the drought affected populations did not recover during the period of several weeks after the wetlands filled up again. Referring to the observation that Chironomidae have good drought-survival strategies (Frouz et al., 2003), this persistent drought effect conflicts with hypothesis 5, that drought affected populations would recover at least partly. It is also surprising that in the SLAM trap samples, the trend in chironomid abundances did not differ between treatment and control sites. The SLAM traps caught much higher numbers of chironomids, suggesting that chironomid communities were at least not generally affected by the experiment. Irrespective of the treatment, abundances in the SLAM trap samples declined between July and September, similar to the pan trap samples from the treatment sites. A decrease of chironomids in September could therefore be a common seasonal trend. If that is the case, it is hard to explain why the abundances in the pan traps of the control sites increased instead.

Trends in the abundance of Sciaridae also differed between the two trap types. While no drought effect was found in the pan trap samples, the numbers in the SLAM traps increased stronger at the drained wetlands, than at the control sites. Sciaridae develop in moist soil and decaying matter (Oosterbroek, 2006) and as the drained wetlands did not dry out completely, it is likely that they benefited from the remaining moist soil and biomass. This observation is consistent with previous studies by Keiper et al. (2002), who found that soil dwelling Tabanidae increased after drainage from flooded to wet soil and by McMahon and Gaugler (1993), who summarised that detritivorous Diptera can be numerous on exposed sediments. Since neither a significant reversal of the drought effect nor a long-term effect of the treatment was found, it can be assumed that only a weak drought effect on sciarid abundances remained until September. Although the treatment led to an increase in abundance, the slight reversal of the trend is equivalent to a partial recovery from the drought effect which which corresponds to hypothesis 5. Why the drainage had no influence on sciarid abundances in the pan trap samples instead, could not be explained, but the pan traps caught only small numbers of sciarids, which may not represent the drought response of the whole family adequately.

As these were the only statistically significant drought effects on individual families, it is not surprising that the multivariate analysis (using manyglm) also found no clear effect of the treatment on family composition. It is however interesting that the only weak evidence of a drought effect on family composition was observed in the pan trap samples between July and August and is therefore not consistent with the two highly significant results from Chironomidae and Sciaridae. Instead, the weaker (nonsignificant) trends in Chironomidae and Carnidae between July and August probably contributed to this result. Comparing relative abundances of the most common families within the pan trap samples, **Figure 4** suggests that family composition was generally variable. Apart from Chironomidae and Carnidae, Agromyzidae and Dolichopodidae also revealed distinct changes in their relative abundance, which could not be explained by sampling month or location alone.

Agromyzidae are not directly related to water (Spencer, 1976), but the strong increase in abundance at only two of the dried wetlands cannot be explained by a gain of terrestrial habitat alone. It is more likely that the two mass occurrences are connected to the presence of suitable host plants at the two sites, as most species are rather host-specific (Spencer, 1976). Due to the short duration of the drainage, the presence of host plants close to the traps was probably not drought-related but coincidental. Dolichopodidae, like Sciaridae, depend on moist soil or organic matter for their development (Oosterbroek, 2006). It was therefore unexpected that relative dolichopodid abundances slightly decreased after the drainage, which presumably increased the area of moist soil. On the other hand, the result agrees with Gelbič and Olejníček (2011), who also observed lower abundances of Dolichopodidae after the partial drainage of a wetland. Further, Pollet (2009) states that the community composition within Dolichopodidae depends on soil moisture, which indicates that different dolichopodid species react differently to hydrological changes and makes it difficult to interpret trends on family level.

The results of the analyses of the drought effect on species diversity were also not consistent between the two trap types. Since the SLAM trap and pan trap catches represented distinctly different parts of the dipteran community, as shown in **Table 1**, this is not surprising though. The mean number of families per site did not change significantly as a result of the drought treatment. The fact that the mean family richness of the treatment sites declined more than that of the control sites after the refilling of the wetlands may be caused by the initial higher richness at the treatment sites in summer which then decreased to a similar level as the control sites in September, where generally few families were found due to rainy weather.

A high Shannon diversity index can result both from high taxon richness and from a uniform distribution of abundances between taxa. The fact that the Shannon index in the SLAM traps was significantly reduced by the drought treatment between July and September but not between August and September implies that the effect was not simply caused by the drought-induced decrease of family richness in September. As no individual family within the SLAM trap samples was significantly affected by the treatment-to-month interaction during this period, it was not possible to find out what caused this change.

Due to these ambiguous results, which were never consistent between the two trap types, it is hard to judge if hypothesis 2 was met. The families that showed possible drought responses were influenced in different ways, which supports hypothesis 2, but in general there were few clearly drought related effects. It is possible that variations in drought response are higher within families than between families, so that some drought effects were not evident at the family level. Another possibility is that the impact of the drainage was not severe enough to lastingly influence dipteran communities because of the remaining water pools, soil moisture and adjacent wetlands. Thus, conflicting with hypothesis 2, no clear influence of the drainage on the dipteran community composition was found.

No drought impact on total dipteran biomass

Contrary to the assumption from hypothesis 1, there was no indication that the total biomass of adult dipterans in the analysed samples was influenced by the drainage of wetlands. This result is in line with the findings from the analysis of family abundances, where only few lightweight taxa revealed relevant drought effects, and some of these showed opposing trends. A previous study by Kajak et al. (1985) though, found the opposite result, that dipteran biomass declined after the drainage of wetlands. Kajak et al. (1985), however, examined natural fens that were dried out in the long term, which is probably not comparable to the short-term experiment on constructed wetlands from this study. After a drought experiment in stream mesocosms, Ledger et al. (2011) also found a general decrease in biomass of aquatic invertebrates. Although, Diptera larvae, belonging to the smaller stream

invertebrates, decreased less strongly than larger aquatic taxa and particularly tiny dipterans like Chironomidae even increased in biomass following the drought experiment. Ledger et al. (2011) did not mention whether the total biomass of aquatic Diptera changed as a result of the treatment, but the counteracting trends show that the biomass of Diptera, even when considering aquatic taxa, is not necessarily affected by drought.

Trophic group analysis biased by few dominant families

All 83 distinguishable taxa were included in the analysis of the trophic groups. But since several taxa could not be clearly assigned to a trophic group, the two potential drought effects on herbivores and detritivores were strongly influenced by only 1-3 abundant taxa, making up over 90% of the abundances.

The significant effect of the treatment-by-month interaction on herbivores between July and September in the pan-trap samples was almost exclusively based on chironomid abundances and is therefore just a replication of the potential drought effect on the family itself and not representative for herbivorous Diptera. This pattern corresponds to the finding that no drought impact on herbivores was found in the SLAM trap samples, as there were no significantly different trends in Chironomidae either. In a review on the ecology of wetland associated Diptera, Keiper et al. (2002) stated that herbivorous Diptera are strongly dependent on the presence of specific host plants. While severe, prolonged drought events may affect wetland plants, it seems unlikely though, that temporary droughts as in this study, affect herbivorous dipterans through a decline of their host plants.

The non-significant increase of detritivores after drainage in the SLAM trap samples mainly resulted from increasing abundances of the two most abundant detritivorous families Psychodidae and Sciaridae. The drainage may have exposed dead organic matter from the wetland which would be favourable for detritivores (Keiper et al., 2002). However, since both Sciaridae and Psychodidae were also classified as moisture dependent, it is questionable if the observed effect can be attributed to their feeding habit alone. Arguing against that is the observation that Limonidae, which are detritivores but include both aquatic and terrestrial species (Oosterbroek, 2006), were not affected by the drought treatment. Since there was no clear reversal of the trend, but also no long-term effect of the drought treatment on detritivores in the SLAM trap samples, it can be assumed that the potential positive drought effect on detritivores persisted to some extent even after the wetlands refilled.

In summary, the trophic group analysis could not reveal convincing evidence of an actual drought effect on dipteran trophic groups. Hypothesis 3, that higher trophic levels would be more affected by drought, was therefore not confirmed, but could also not be thoroughly analysed due to the poor data situation. For a clearer picture, more of the abundant taxa would have to be assigned a trophic group. At the family level, this failed mostly because trophic groups varied within the family and rarely because there was no information about the biology of the family at all. With abundance data on lower taxonomic levels, one could therefore presumably obtain more accurate results. But as species-level identification in many groups is hardly possible or labour-intensive, it could be investigated whether feeding groups for some taxa can also be assigned at subfamily or genus level for example. Difficulties in identification and lack of biological data for certain taxa are probably also the reasons why no comparable studies on drought effects on broad trophic groups within Diptera could be found.

Conflicting results on moisture dependent taxa

Since the analysis of water dependency groups examines the relationship between water availability and water dependency of organisms, the results can explain different mechanisms of how drought affects organisms. Therefore, for the three investigated water dependency groups, specific hypotheses were formulated on how they might be influenced by the drainage of wetlands. While aquatic taxa

were assumed to be impacted by the lack of water (hypothesis 4a), moisture dependent and terrestrial taxa were supposed to profit from an increased availability of moist substrate (4b) and terrestrial habitat (4c), respectively.

The multivariate analysis (using manyglm) showed no significant results for a drought effect on the overall composition of water dependency groups, but indications were found that there was a shift from aquatic and moisture dependent taxa to terrestrial taxa in the pan trap samples between July and August. If the drought was severe enough to affect moisture dependent taxa, this sounds like a plausible result, since according to a review on wetland arthropods by Batzer and Wu (2020), terrestrial taxa can take over after a drought event. These drought effects on aquatic, moisture dependent and terrestrial taxa in the pan trap samples were however not consistent with the results of the SLAM trap samples.

The significant long-term decrease of aquatic Diptera at the drained wetlands, that was found in the pan trap samples, could be solely attributed to trends in the abundant family Chironomidae. Eristalinae, a subfamily of Syrphidae, which were also abundant in pan traps, showed no drought response and although Chaoboridae were much less abundant at the treatment sites than at the control sites in August, this could not be clearly attributed to a drought effect, as they did not occur at all in July. Thus, the drought effect on aquatic Diptera in pan traps only reflects the family trend of Chironomidae which might not be generalisable to other aquatic Diptera, and following this effect, hypothesis 4a could not be clearly confirmed. Since the occurrence of taxa with aquatic lifestages is logically dependent on water availability, it can be assumed that the unaffected taxa were able to colonise adequate aquatic habitats in the vicinity or that the caught specimens hatched from pupae of the previous not drought-affected year. Studying drought effects on river ecosystems, Lake (2003) notes the ability of aquatic taxa to colonise smaller refugia, which may correspond with the observation by Ledger et al. (2011) that aquatic taxa with small body size are less affected by drought.

Looking at the trends of individual families, it became evident that the seemingly drought-related increase in terrestrial taxa only resulted from the combination of mass occurrences of Carnidae at the control sites in July and Agromyzidae at the drained locations in August. None of the other common terrestrial taxa were influenced in their abundance by the drainage. Since no drought effect on terrestrial taxa was found in the SLAM traps either, it can be assumed that terrestrial taxa were generally not affected by the temporary dry-out of the wetlands. They therefore did not benefit noticeably from the new terrestrial habitat, thus opposing hypothesis 4c.

The drought response of moisture dependent taxa was inconsistent between SLAM trap and pan trap samples. The mean abundance of Dolichopodidae, Psychodidae and Sciaridae, which dominated abundances of both trap types, increased in response to wetland drainage in the SLAM traps, but decreased (Dolichopodidae and Psychodidae) or remained unaffected (Sciaridae) in the pan traps. The former result is coherent with hypothesis 4b, that remaining moist substrate, when the shore receded, can favour moisture dependent taxa, but the latter result is contradictory. That Psychodidae and Sciaridae were distinctly more abundant in the SLAM trap samples suggests that these two families at least partially benefited from the drainage. *Sarcophaga sinuata*, a species of Sarcophagidae, which was only caught in pan traps, remained unaffected by the treatment-by-month interaction. To my knowledge though, *S. sinuata* is rather generally related to wet habitats than to the presence of moist substrates like the other taxa. After the wetlands filled up again, the drought effects of all families were largely reversed. In summary, there clearly appear to be drought effects on moisture-dependent taxa, but these are not generalisable and may vary between families and lower taxa. However, as long as there are still moist habitats remaining, it seems likely that a large part of moisture dependent dipterans benefits from temporary droughts in wetlands, which supports hypothesis 4b.

Inconsistencies between sampling methods

The data of the two trap types were analysed separately, because it is well known that study results may be influenced by the sampling method, as different sampling methods catch different parts of the insect community (Devigne & De Biseau, 2014). This effect is also reflected in the Diptera abundances of the different taxa in this study (**Table 1**). It is however surprising that none of the drought effects found in this study was consistent between the two trap types, even within the same family.

A reasonable explanation would be that the two trap types did not only catch different families, but also different species within these families, with different drought responses. This hypothesis could be tested in a follow up study in which, for example, the existing samples of Dolichopodidae could be identified to species level and then analysed in the same way. Using sticky traps for wetland insects, Hoback et al. (1999) found that not only the trap colour but also sun exposure influences insect catches on family level. They caught, among others, more Dolichopodidae on traps in shaded than exposed places. It is therefore conceivable that, particularly under dry conditions, some Diptera sought closer proximity to the tent-shaped SLAM traps than to the sun-exposed pan traps. Since the SLAM traps were partly placed in higher vegetation, this could have additionally created a humid microclimate. Thus, the increase in moisture dependent Diptera in SLAM traps alone could also be interpreted as a retreat of these taxa into moist microhabitats. Also, as the pan traps were just open trays of water, they may have been an attractive freshwater source for Diptera, and the trapped dipterans could have been an easy to access food source for birds. These are only theoretical considerations though, as it is hard to explain how these two factors relate to the presented results. Since the data contained relatively little repetition with 7 treatment and 9 control wetlands and additional dropouts in the pan trap samples, the analysis was also sensitive to unidentified random factors, as in the case of Agromyzidae and Carnidae.

In conclusion, the inconsistent results of this study show that it is reasonable to use several different trap types in insect studies, not only to capture a wider range of the community but also to get a better picture of potential impacts of the sampling method. It also became apparent that in an ecological field study like this one, precise attention must be paid to potential variations in environmental parameters, both in the experimental design and in the interpretation of results.

Implications for wetland ecosystems

Through their various ecological interactions and high abundances, especially in aquatic habitats, Diptera contribute to a variety of ecosystem functions in wetlands (Adler & Courtney, 2019). Major changes in the dipteran community can therefore impact wetland ecosystems. As the total biomass of adult Diptera showed no distinct changes in response to the drought treatment, it can be assumed that the availability of dipterans as food source for insectivorous organisms was not restricted. Larger water dependent insectivores such as amphibians and fish may still have been affected by the drainage themselves. Lacking clear drought-related changes on specific families or trophic groups, it can further be assumed that the local food webs were not seriously disturbed. The low number of drought responses, even in water dependent taxa can probably be explained by the remaining water pools, soil moisture and close by wetlands. It is uncertain how well these experimental conditions simulated a natural summer drought event, but the interesting drought responses in Chironomidae, Sciaridae and Dolichopodidae can be seen as an incentive for further research on these groups regarding drought and wetland drainage. Chironomidae and Dolichopodidae have already been considered as indicator taxa for several water-related issues (Cañedo-Argüelles et al., 2016; Gelbič & Olejníček, 2011; Pollet, 2009). Therefore, it might be interesting to consider the same for Sciaridae or other moisture dependent Diptera.

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Supplementary

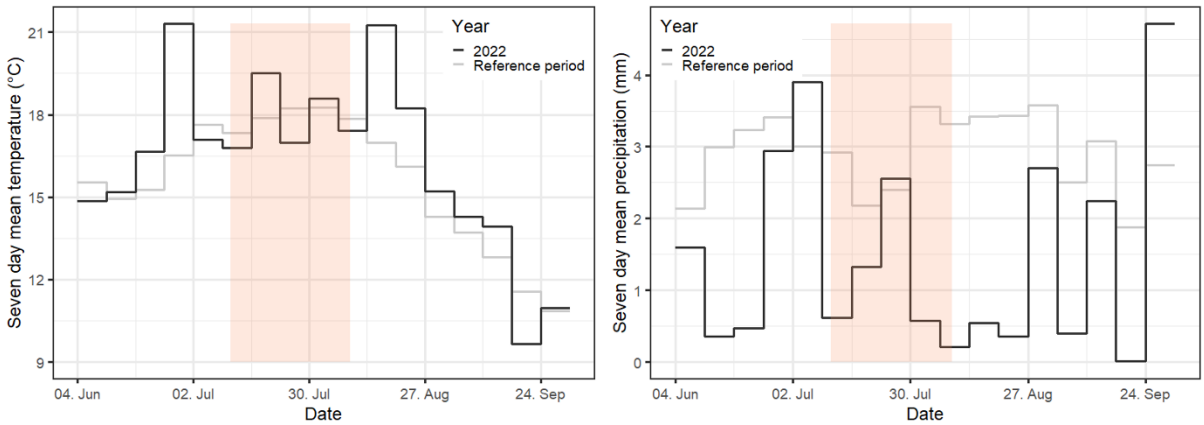

Figure S 1 Seven day mean temperature (left) and precipitation (right) in Halmstad during the sampling period 2022 (black), compared to the reference years 1991-2020 (grey). The period of drainage during 2022 is indicated by red shading. Raw data from SMHI, Sveriges meteorologiska och hydrologiska institut.

Table S 1 Details of the weighing process.

Family	Lower taxon	Drying time (min)	Number of specimens weighed	Mean biomass per specimen (mg)
Agromyzidae		1	386	0.4
Anisopodidae		1	9	4.3
Anthomyiidae		5	79	6.1
Anthomyzidae		1	6	0.5
Asilidae		5	4	66.7
Asteiidae		1	1	0.3
Calliphoridae		5	38	32.1
Carnidae	Meoneura sp.	1	372	0.2
Cecidomyiidae		1	165	0.1
Ceratopogonidae		1	18	0.2
Chaoboridae		1	19	1.6
Chironomidae		1	311	0.6
Chloropidae		1	498	0.4
Culicidae		1	7	3.2
Dolichopodidae		5	75	3.2
Drosophilidae		1	35	0.9
Empididae		1	88	4.2
Ephydridae		1	147	2
Fanniidae		5	7	3.7
Heleomyzidae		5	6	6.9
Hybotidae		1	41	1.6
Lauxaniidae		5	1	11.2
Limoniidae		1	66	3
Lonchopteridae		1	6	1.3
Micropezidae		5	5	7.8
Milichiidae		1	3	0.6
Muscidae		5	48	21.7

Family	Lower taxon	Drying time (min)	Number of specimens weighed	Mean biomass per specimen (mg)
Mycetophilidae		1	6	1.5
Opomyzidae		1	12	2
Phoridae		1	224	0.2
Pipunculidae		1	2	2.2
Polleniidae	Pollenia sp.	5	25	35.8
Psilidae		5	7	9.9
Psychodidae		1	203	0.2
Ptychopteridae		5	27	9.6
Rhagionidae		5	9	14
Rhinophoridae		5	13	5.5
Sarcophagidae		5	11	59.1
Scathophagidae		5	16	13.8
Scatopsidae		1	73	0.1
Sciaridae		1	557	0.3
Sciomycidae		5	5	14.7
Sepsidae		1	204	1.5
Simuliidae		1	7	1.4
Sphaeroceridae		1	36	0.9
Stratiomyidae	Chloromyia formosa	1	5	10.3
Syrphidae		5	31	36.1
Tabanidae	Chrysops sp.	5	12	29.6
Tabanidae	Haematopota sp.	5	34	24.8
Tachinidae		5	39	28.3
Tephritidae		1	3	2.1
Therevidae		5	2	30.8
Tipulidae		5	21	38.1
Ulidiidae		5	1	19.6
Unidentified		1	7	0.0